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HABITAT SELECTION BY ELF OWLS AND WESTERN SCREECH-OWLS  
IN THE SONORAN DESERT

by

Paul Christopher Hardy

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A Thesis Submitted to the Faculty of the  
SCHOOL OF RENEWABLE NATURAL RESOURCES  
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In the Graduate College  
THE UNIVERSITY OF ARIZONA

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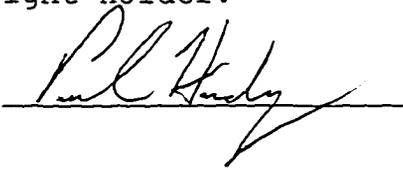
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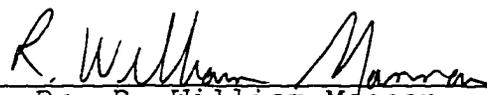
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## DEDICATION

I dedicate this thesis to my parents, Richard and Becky, to my grandmother, Esther Ewing, to my brother, Mark, and to my partner, Rhonda Wayson. Your love and support have encouraged me to pursue what is important to me. Thank you for believing in me in both the hard times and the good times. I love you all.

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**ABSTRACT**

Little is known about habitat selection by elf owls (Micrathene whitneyi) and western screech-owls (Otus kennicottii). From 1994 to 1996 in the Sonoran Desert, I used point counts and nest searches to examine habitat selection by both species at multiple spatial scales. The abundance of both species had a positive association with percent cover of washes and mesquite (Prosopis spp.) at the scale of the study area. At both the scale of the study area and the nesting area, elf owls selected areas with high densities of mature saguaros (Carnegiea gigantea) and saguaro cavities. Elf owls nested only in woodpecker cavities in saguaros, whereas western screech-owls nested in both saguaro cavities and in natural cavities in mesquite. Western screech-owls nested nearly exclusively in gilded flicker (Colaptes chrysoides) cavities when they nested in saguaros. Patterns of nest cavity selection by elf owls suggest they may choose cavities that provide thermoregulatory advantages. I give management recommendations based on my findings.

CHAPTER 1: NEST SITE SELECTION BY ELF OWLS AND WESTERN  
SCREECH-OWLS IN THE SONORAN DESERT

INTRODUCTION

The elf owl (Micrathene whitneyi) is a migrant that breeds in the southwestern U.S. and northern Mexico and the western screech-owl (Otus kennicottii) is a year-round resident throughout much of western North America and Mexico. Both species are small, nocturnal, secondary cavity-nesters (SCNs) and are sympatric throughout most of the elf owl's breeding range (Phillips et al. 1964, AOU 1983, Johnsgard 1988). Along with the federally endangered cactus ferruginous pygmy-owl (Glaucidium brasilianum cactorum), elf owls and western screech-owls are the principal nocturnal members of the unique community of SCNs in the Sonoran Desert (Bent 1938, Phillips et al. 1964).

These owls cannot excavate their own nest cavities and must rely on old woodpecker holes or natural cavities. A lack of available cavities may limit nesting populations of SCNs (von Haartman 1957, Hamerstrom et al. 1973, van Balen et al. 1982, Brush 1983, Village 1983, Brawn and Balda 1989). Consequently, studies of habitat selection by SCNs have focussed on nest site selection (e.g., van Balen et al. 1982, McCallum and Gehlbach 1988, Belthoff and Ritchison 1990, Negro and Hiraldo 1993, Pogue and Schnell 1994).

These studies have shown a variety of features of the nest cavity, nest tree, and surrounding vegetation to be important selection criteria.

Features of the nest cavity shown to be important in nest site selection include the orientation, dimensions, and height of the cavity. Cavity orientation can ameliorate microclimate effects (e.g., Conner 1975, Stauffer and Best 1982, Raphael 1985) and cavity openings of a certain diameter may impede entry by competitors and/or predators (van Balen et al. 1982, Rendell and Robertson 1989). Peterson and Gauthier (1985) and Belthoff and Ritchison (1990) found that inner cavity dimensions were important in selection, and increasing the volume of nest boxes in experimental studies resulted in larger clutch sizes for some species (e.g., Karlsson and Nilsson 1977). Selection of cavities located relatively high above the ground may decrease predation (Nilsson 1984).

The species, vigor, height, and diameter of the nest tree have been shown to be important in nest site selection (Mannan et al. 1980, Raphael and White 1984, Gutzwiller and Anderson 1987). Selection of trees of a certain species or vigor by SCNs often reflects woodpecker use (Ligon 1968, Goad and Mannan 1987). The height of the nest tree may affect predation rates (Martin 1988). The dbh of the nest tree largely constrains the dimensions of the cavities

within it and is often correlated with the number of cavities within a tree (van Balen et al. 1982).

Features of the surrounding vegetation shown to be important in nest site selection include the densities of trees and cavities (e.g., Swallow et al. 1988, Martin and Roper 1988). Probability of predation may decrease with increasing abundance of potential nest sites (trees and cavities), possibly because predators must search more empty sites to find an occupied site (Martin 1988). Alternatively, extra nest cavities in the vicinity of the nest may provide renesting sites in the case of nest failure (Rendell and Robertson 1994) or nest usurpation (van Balen et al. 1982), and may enable facultative polygamy (Petit 1991, Rendell and Robertson 1994). At broader scales, topographic features such as the slope and aspect of the land have been shown to influence site selection (e.g., Forsman et al. 1977).

Despite the finding that features of the cavity, tree, and surrounding vegetation and topography have variously been shown to be important in nest site selection by SCNs, and are likely not mutually-exclusive criteria, few studies have simultaneously examined the influence of all 3. Assessing each dimension of nesting habitat might provide insight into which combination of features best predicts selection and/or about which dimension is most important.

During 1995 and 1996, I studied nest site selection by the elf owls and western screech-owls on Barry M. Goldwater Air Force Range (BMGR) in southwestern Arizona using a multi-scaled approach. At the scale of the study area, I determined if general vegetation types, physiographic types, and/or topographic features were used out of proportion to their availability by nesting elf owls and western screech-owls. At the scale of the nesting area, I assessed which combination of features of the cavity, tree, and surrounding vegetation best predicted nest site selection. Finally, at the scale of the nest tree, I examined whether owls selectively chose cavities from those available within the nest tree.

#### **Species Studied**

Elf owl.--The elf owl has been relatively well-studied for a nocturnal species. It and the flammulated owl (Otus flammeolus) are the only 2 neotropical migratory owls in North America (Ligon 1968, McCallum 1994a). The elf owl is predominantly insectivorous and occurs in a wide range of xeric to riparian plant communities in the southwestern U.S., nesting throughout most of southern Arizona and southwestern New Mexico (Millsap 1988). The species exhibits wide environmental tolerances in central and southcentral Arizona, where it occupies nearly all plant communities with arborescent vegetation up to 2,000 m in

elevation (Ligon 1968, Johnson et al. 1979, Monson and Phillips 1981, Millsap 1988).

In the Sonoran Desert, elf owls nest in cavities excavated by gila woodpeckers (Melanerpes uropygialis) and gilded flickers (Colaptes chrysoides [Goad and Mannan 1987, Millsap 1988]). Most cavities are in saguaro (Carnegiea gigantea) and cardon (Pachycereus pringlei) cacti (Goad and Mannan 1987, Millsap 1988). Species that may compete with elf owls for nest cavities include the western screech-owl, ferruginous pygmy-owl (Glaucidium brasilianum), American kestrel (Falco sparverius), gila woodpecker, gilded flicker, ladder-backed woodpecker (Picoides scalaris), brown-crested flycatcher (Myiarchus tyrannulus), ash-throated flycatcher (M. cinerascens), purple martin (Progne subis), European starling (Sturnus vulgaris), Lucy's warbler (Vermivora luciae), house finch (Carpodacus mexicanus), and house sparrow (Passer domesticus). In the Sonoran Desert, elf owls have not been documented to nest in cavities other than those excavated by woodpeckers (Bent 1938, Ligon 1968, Goad and Mannan 1987, Millsap 1988).

Millsap (1988) hypothesized that vegetation features other than the availability of saguaros and saguaro cavities play a minor role in elf owl nest site selection. This assertion was supported by Goad and Mannan (1987), who found that mature saguaros were used out of proportion to their

availability and that densities of mature saguaros and saguaro cavities were significantly higher around nests than around random points. Other vegetation characteristics played a minor role in nest site selection (Goad and Mannan 1987). Goad (1985) believed that the high density of saguaros around nests was due to a clumped distribution of saguaros (spatial pattern was not tested quantitatively).

Based on thermoregulatory experiments, Ligon (1968) hypothesized that in the Sonoran Desert, elf owls would select cavities that provided a favorable microclimate. However, Goad and Mannan (1987) found that the height and diameter of nest cavities did not significantly differ from available cavities, and that the orientation of nest cavities was random. Goad and Mannan (1987) concluded that apparently any cavity in a saguaro was a suitable nest.

Male elf owls migrate from their winter range in southern and central Mexico to arrive on the breeding grounds by mid to late March in Arizona (Ligon 1968, Millsap 1988). Ligon (1968) found that desert breeding areas were occupied 2-3 weeks earlier than breeding areas in riparian forests at higher elevations. Male elf owls appear to arrive on breeding grounds, locate cavities, and set up territories prior to the arrival of females (Ligon 1968, Millsap 1988). Pair formation begins as soon as females arrive and is completed even at higher elevations by mid

April (Ligon 1968, Millsap 1988). Male elf owls sing from potential nest cavities, attracting their mates to the cavities (Ligon 1968). Clutches are completed by early May and average 3 eggs (Ligon 1968, Millsap 1988). The nestling period begins by early June, and fledging occurs by early July (Ligon 1968, Goad and Mannan 1987). Both adult and juvenile elf owls have completely migrated from the breeding grounds by late September (Millsap 1988).

Few good estimates of breeding densities exist outside of the Madrean evergreen woodlands (Johnson et al. 1981), but I calculated estimates of 0.05 nests/ha, 0.20 nests/ha, and 0.24 nests/ha (Walker 1974, Goad and Mannan 1987, Bibles 1992, respectively) from studies conducted in the Arizona Upland subdivision of the Sonoran Desert.

The elf owl is considered to be common in the Sonoran Desert (Monson and Phillips 1981) and is not listed as threatened or endangered under the Endangered Species Act of 1973 (ESA), as amended. The species is classified as endangered by the California Department of Fish and Game (LeFranc and Millsap 1984) due to its precarious status on the western periphery of its range in southeastern California. The elf owl is protected by the Migratory Bird Treaty Act (C.F.R. 50:10,21).

Western screech-owl.--Although there is some literature on the western screech-owl (hereafter, screech-owl) in the

southwestern United States (reviewed by Johnson et al. 1979), little of this work has been done in the Arizona Upland subdivision of the Sonoran Desert. The majority of information has been obtained from southeastern Arizona or along the Gila, Salt, and Verde rivers (Johnson et al. 1981) and is largely qualitative. Here, breeding pairs in mesquite bosques and cottonwood (Populus spp.)-mesquite riparian woodlands have been reported to be as close as 50 m apart (Johnson et al. 1981). Two studies from the Sonoran Desert (Miller and Miller 1951, Johnson et al. 1981) estimated pairs to be 180-360 m apart and 275 m apart, respectively. Like elf owls, screech-owls are obligate cavity nesters. Potential competitors for nest cavities are the same as listed above for elf owls. Anecdotal reports indicate that screech-owls nest only in saguaros in the Sonoran Desert (Bent 1938, Johnsgard 1988). Bendire (1892) and Miller and Miller (1951) observed that bajadas and xeroriparian areas had higher densities of nesting screech-owls than the surrounding uplands.

Screech-owls eat a wide variety of prey items, ranging from invertebrates, principally insects, to all classes of vertebrates, primarily rodents and songbirds (Craighead and Craighead 1956, Brown et al. 1986). In the closely-related eastern screech-owl (Otus asio), proportionately more invertebrates are consumed during the nestling period

(Ritchison and Cavanagh 1992).

Little is known about the breeding chronology of screech-owls in the Sonoran Desert, but records exist from near Tucson of an incubating female on 26 March (Bendire 1892) and "half-grown" nestlings on 21 May (Bent 1938). On BMGR, the incubation period begins around 1 April and lasts about 30 days (unpubl. data). Three to 4 eggs are laid (Bent 1938). The nestling period lasts about 28 days, and owlets fledge by late May (unpubl. data). Thus, screech-owls nest approximately 1 month earlier than elf owls on BMGR.

Screech-owls are considered to be common in the Sonoran Desert (Phillips et al. 1964) and are not listed as threatened or endangered under the ESA. Although a year-round resident, the species is protected by the Migratory Bird Treaty Act. Screech-owls were on the National Audubon Society's Blue List (Tate 1981) without published evidence of decline. For eastern screech-owls, Gehlbach (1994) noted that population cycles and local movements may be confused with declines.

#### **Study Area**

BMGR is located in the Sonoran Desert of southwestern Arizona and is the nation's second largest aerial gunnery training range. It occupies approximately 10,900 km<sup>2</sup> of

unpopulated land in Maricopa, Pima, and Yuma counties, and represents one of the largest and best preserved regions of native desert remaining in the U.S. BMGR's pristine state can be attributed to limited public access, and to the fact that <5% of the total land area is impacted by training activities.

The landscape of BMGR is dominated by low, isolated mountain ranges separated by broad basins and is comprised of 2 major vegetation types: the Arizona Upland and the Lower Colorado River Valley subdivisions of the Sonoran Desert. The Arizona Upland subdivision includes the paloverde (Cercidium spp.)-mixed-cacti scrub series and paloverde-catclaw (Acacia greggii) xeroriparian associations. Various cacti, such as jumping cholla (Opuntia spp.), and saguaro are prominent members of this subdivision. The Lower Colorado River Valley subdivision includes the creosote (Larrea tridentata)-white bursage (Ambrosia dumosa) series, and in runnels and washes, the Mixed-scrub series. The Mixed-scrub series is xeroriparian in nature and includes many species common to the Arizona Upland subdivision, including blue paloverde (C. floridum), ironwood (Olneya tesota), mesquite, and catclaw acacia (Turner and Brown 1994).

Temperatures for the Arizona Upland and Lower Colorado

River Valley regions average 29-30° C in the summer and 11-12° C in the winter; mean annual precipitation is 20-30 cm (Sellers et al. 1985).

My 2 study sites were in the northeastern area of BMGR south of Interstate 8 and east of Highway 85. The Saucedo Mountains study site ranges from 366-686 m in elevation and is primarily ecotonal between the Lower Colorado River Valley and Arizona Upland subdivisions. The Sand Tank Mountains study site ranges from 547-853 m in elevation and consists primarily of Arizona Upland vegetation (Hardy and Morrison 1996).

## **METHODS**

### **Nest Searches**

I searched for nests in association with conducting point count surveys for owls in 1995 and 1996 (see Chapter 2). I conducted surveys along 6 point transects (3 in each study site) and each transect consisted of 10 survey stations (60 stations total). Stations were spaced at 0.8-km intervals (0.5 mi) in systematically-random fashion. I used compass triangulation data from surveys to identify areas of concentrated singing activity and focussed nest searches in these areas. I conducted nest searches during the nestling period (mid April through late May for screech-owls; late May through early July for elf owls). Nestling elf owls are very vocal and may be heard 50-100 m away, facilitating location of nests (Goad 1985, pers. obs.). Nestling screech-owls are less vocal and can be heard 25-50 m away (pers. obs.).

Before I considered a cavity to be a nest, nestlings had to be heard within the cavity and an adult owl had to be observed within the cavity. I stipulated that an adult owl had to be seen because vocalizations of nestling gila woodpeckers are similar to those of nestling elf owls and are occasionally heard at night (pers. obs.).

To allow estimation of nest density using distance sampling theory (Buckland et al. 1993), I measured the

distance (m) from each nest located to the nearest survey station.

Elf owl nests as an index of reproductive success.--A measure of habitat quality should be based on some measure of reproductive success (Van Horne 1983, Kellner et al. 1992, McCallum 1994b). A nest is often considered "successful" if it produces  $\geq 1$  fledgling (e.g., Vickery et al. 1992). Because I verified fledging at few elf owl nests, I did not assess reproductive success by this definition. However, I observed  $\geq 2$  fledglings at all 9 elf owl nests at which I attempted to confirm fledging and Ligon (1968) observed that 100% of elf owl nestlings fledged ( $n = 29$  nests). Thus, I am confident that elf owl nests found during the nestling phase are a good surrogate of reproductive success. Fledging rates of nestling screech-owls are much lower than that of elf owls (Gehlbach 1994). Thus, the screech-owl nests found during the nestling period are unlikely to represent an acceptable index of reproductive success.

### **Vegetation Sampling**

Definition of scale.--In detailing vegetation sampling and statistical analyses below, I attempt to describe scale in an unambiguous manner. My definition of scale includes both the domain to which statistical inferences apply and the experimental units of interest (Kuehl 1994). For

example, "nest site selection" is an ambiguous description of scale because it refers only to the experimental units (nest sites) and says nothing about the domain of inference. "Nest site selection within the territory," which is equivalent to "nest site selection at the scale of the territory," is a less ambiguous description of scale because it includes both the domain within which inferences can be made (the territory) and the experimental units about which inferences can be made (nest sites).

Nest site selection within the study area.--I sampled vegetation and physiographic characteristics along 8, 200-m point-intercept transects (Bonham 1989:108) radiating out from each survey station. I used these data to estimate the abundance (percent cover) of vegetation types and physiographic types within the study area. I determined the direction of the first transect by randomly spinning a compass, and directed subsequent transects 45 degrees from the previous. I paced-off transects and spaced intercept-points at 5-m intervals (40 per transect).

I recorded the general vegetation type (xeroriparian, creosote, or mixed-cacti) and physiographic type (wash, flat, bajada, or upland) at each intercept-point. The xeroriparian type included any drainage with bank full width >1.0 m (Cole 1994) and its associated frequent flood plain area (Ohmart and Anderson 1982); these areas were dominated

by tall (>2 m), dense vegetation. The creosote vegetation type was dominated by creosotebush and bursage. The mixed-cacti vegetation type was dominated by yellow paloverde (Cercidium microphyllum), saguaros, and various species of small shrubs and cacti.

I defined physiographic types following Barbour et al. (1987): "wash," same as xeroriparian above; "flat," any non-wash area with slope  $\leq 1\%$ ; "bajada," any non-wash area with slope  $> 1\%$  and  $\leq 5\%$ ; and "upland," any non-wash area with slope  $> 5\%$ . I calculated percent cover of vegetation types and physiographic types by dividing the number of intercepts in each respective cover type by the total number of intercept-points.

To help determine if the vegetation types and physiographic types at nests differed from their abundance in the study area, I also recorded the general vegetation type and physiographic type at each nest.

Nest site selection within the nesting area.--At each nest, I measured features of the vegetation surrounding the nest saguaro, features of the nest saguaro, and features of the nest cavity (Table 1). To sample vegetation surrounding nest saguaros, I centered a 25-m-radius plot (0.2 ha) on each nest. I used this plot size instead of the commonly-used 11.4-m-radius plot (0.04 ha [Noon 1981]) because it approximates the size of elf owl territories

indicated by Ligon (1968). Furthermore, Ligon (1968) described elf owl territories as being centered on the nest. No data are available for screech-owl territory size, but pairs have been described as being as close as 50 m apart in the desert southwest (Johnson et al. 1981). Thus, I elected to use the same plot size for both species. Because I did not measure territory or home range size for either species, I refer to selection at the scale of the nesting area rather than at the scale of the territory or home range.

I surveyed vegetation around each saguaro along 8, 25-m point-intercept transects. I spaced intercept-points at 5-m intervals (5 per transect). At each intercept-point, I collected information in 4 vertical height classes: 0 m (ground level); >0 m to 1.0 m (understory); >1.0 m to 2.5 m (mid-canopy); and >2.5 m (overstory). I identified shrubs, trees, and most cacti to species. For each plant species and substrate, I determined the number of "hits" in each height class with the aid of a graduated extendable pole (both live and dead vegetation were tallied). I divided this number by the total number of intercept-points (40 points per nest) to estimate percent cover by height class, as well as percent cover of perennial vegetation (all woody species combined).

Within each 25-m-radius plot, I recorded the number of trees and cacti >2.5 m tall with average stem diameter >15

cm (generating estimates of density); 2.5 m is a considered a minimum height for roosting by these species (Goad and Mannan 1987). I also recorded the number of cavities within these structures. Following Goad and Mannan (1987), I categorized saguaro cacti as: (1) <3 m tall with no branches; (2)  $\geq 3$  m tall with no branches or branches <6 cm in length; (3) >4 m tall with branches 6 cm to 1 m in length; (4) >5 m tall with 1-2 branches >1 m in length; (5) >5 m tall with 3 or more branches >1 m in length; or (6) >2 m tall with a broken top. These categories were mutually-exclusive and included all saguaros. The number of saguaros per plot did not include the nest saguaro itself.

I analyzed saguaros in more detail for the following reasons: (1) due to their importance to the owls of interest (Ligon 1968, Goad and Mannan 1987, Millsap 1988); (2) >96% of all cavities occurred in saguaros (unpubl. data); (3) saguaros of various structure classes are used differentially by elf owls (Goad and Mannan 1987); and (4) the point-intercept method tends to under-sample saguaros due to lack of canopy cover (e.g., Bibby et al. 1992).

Centered on each nest saguaro, I also measured distance to the nearest wash, percent slope (with a clinometer), and aspect of the terrain (degrees from true north).

Features of the nest saguaro itself that I measured were: structure category (described above); height (ground

to highest point); diameter at breast height (dbh); and number of cavities per woodpecker species (excluding the nest cavity). I measured height with a graduated telescoping pole and dbh with a forester's dbh tape.

Features of the nest cavity that I measured were: height (ground to bottom lip); compass orientation of opening; location (branch or stem); and diameter. I used cardboard disks attached to an extendable pole to determine if nest cavities were excavated by gila woodpeckers or gilded flickers (Goad and Mannan 1987). Kerpez and Smith (1990a) showed that gila woodpecker cavities were reliably differentiated from gilded flicker cavities based on the vertical and horizontal diameters of their entrances. I did not measure inner-dimensions of cavities due to the dangers of climbing saguaros and because dimensions differ based on the excavating species (McAuliffe and Hendricks 1988, Kerpez and Smith 1990a).

For each nest saguaro, I located a nearest potentially-available, but unused saguaro (McCallum and Gehlbach 1988) (hereafter, "potential" is equivalent to "potentially-available"). This saguaro had to be >50 m from the nest saguaro (to avoid plot overlap), had to be in the same vegetation type and physiographic type as the nest, and had to have at least 1 potential cavity. To be considered potentially-available to elf owls, a cavity had to be

unoccupied, or occupied by a brown-crested flycatcher, purple martin, or Lucy's warbler. Brown-crested flycatchers and purple martins are the only 2 SCNs arriving later on the breeding grounds than elf owls (Phillips et al. 1964, pers. obs.) and Lucy's warblers are the only local SCNs smaller than elf owls. In addition, the cavity had to be  $\geq 3.4$  m high, the lowest recorded height for an elf owl nest in a saguaro (Goad and Mannan 1987). To be considered potentially-available to screech-owls, a cavity had to be  $\geq 3.2$  m high and not occupied by a woodpecker species; 3.2 m is the lowest height I recorded for a screech-owl nest in a saguaro. When necessary, I examined cavities with a mirror attached to an extendable pole to determine if they were occupied and if they went down into the saguaro. When I located a potential nest saguaro, I measured the same features as described above for the surrounding vegetation, nest saguaro, and nest cavity.

Establishing comparison plots at the nearest potential nest saguaro constituted a paired study design. I used a paired design to help control the many sources of variability associated with physical separation of sampling sites, leading to more powerful comparisons (Kuehl 1994:256). As noted by McCallum and Gehlbach (1988), because statistical significance is influenced by what the researcher deems as "available" to the animal, there is no

perfectly objective way to test for nest site selection. For example, had I considered cavities of any height and from any vegetation type to be available, my results may have been statistically significant, but biologically unmeaningful. By restricting availability data to cavities and vegetation that owls might reasonably be expected to use, I decreased the probability of obtaining significant results, but increased the realism of the tests (McCallum and Gehlbach 1988). By using only the nearest, potentially-available sites as controls, I increased the likelihood that unused sites represented those selected against rather than those unoccupied because they were not assessed by owls (i.e., were unavailable). Further merits of paired designs are discussed by Ratti and Garton (1994).

Nest cavity selection within the nest saguaro.--To enable inferences about the selection of nest cavities from within the nest saguaro, I measured the height, orientation, location, and diameter (as described above) of all potential nest cavities in the nest saguaro itself.

## **ANALYSES**

### **Density of Nests**

I used program Distance, V2.2 (Laake et al. 1996) to calculate the density of nests for the overall study area and for each study site separately. Program Distance is based on distance sampling theory and density is estimated using a detectability function (Buckland et al. 1993). Sample data are the set of distances to the objects of interest. The program uses Akaike's Information Criteria (Akaike 1973) to select the most parsimonious of several competing models. Potential models are the uniform, half-normal, negative exponential, and hazard rate (with associated series expansions [Buckland et al. 1993]). As recommended by Buckland et al. (1993), I calculated densities separately for each year in order to avoid pseudoreplication (Hurlbert 1984).

### **Spatial Distribution of Nests**

I tested if the spatial distribution of nests within a 400-m radius of each survey station was random, clumped, or uniform. It was within this radius that I found most or all nests (see Results). To determine if the pattern was random, I used a log-likelihood ( $G$ ) goodness-of-fit test of the Poisson distribution (Zar 1996:573). If the distribution of nests was significantly non-random, I used a  $G$  goodness-of-fit test of the negative binomial distribution

(Ludwig and Reynolds 1988). The negative binomial is characteristic of clumped (aggregated) populations (Ludwig and Reynolds 1988). If the distribution of nests did not significantly differ from the negative binomial, I used Green's index (Ludwig and Reynolds 1988) to measure the degree of clumpiness; Green's index varies between 0 (for random) and 1 (for maximum clumping). The count data for these tests were the number of nests found within a 400-m radius of each survey station.

#### **Nest Site Selection Within the Study Area**

I used  $G$  goodness-of-fit tests to determine if the number of nests in each vegetation and physiographic type differed from that expected based on the abundance of these cover types in the study area. If a significant difference was indicated by the  $G$ -test, I used Bailey's simultaneous confidence intervals (Cherry 1996) to determine which vegetation and physiographic types were used out of proportion to their abundance.

#### **Nest Site Selection Within the Nesting Area**

I examined nest site selection by analyzing variables from 3 observational units: the vegetation surrounding nest saguaros, the nest saguaro, and the nest cavity. I used multiple, case-control logistic regression (ccLR [Hosmer and Lemeshow 1989]) to determine which combination of explanatory variables best distinguished between used and

potential nest sites. Each nest site represented a case, and each paired, potential nest site, a control. To avoid pseudoreplication (Hurlbert 1984), I included only nest saguaros that constituted independent uses in the analyses (i.e., saguaros used in both 1995 and 1996 were counted as 1 nest).

Case-control logistic regression is analogous to randomized block analysis of variance, but does not rely on the assumptions of normal theory (Hosmer and Lemeshow 1989). Case-control logistic regression accommodates both categorical and continuous explanatory variables, preventing the necessity of conducting separate tests for each class of variables and controlling the comparison-wise error rate. In cCLR, the data vector of habitat measurements is equal to the value of the case minus the control,  $x_k = x_{1k} - x_{0k}$ , and the probability that a nest site will be used, given the vector, is calculated as:

$$P(1|x_k) = \frac{e^{g(x_k)}}{1 + e^{g(x_k)}},$$

where  $e$  equals the base of natural logarithms;  $g(x_k)$  (known as the logit) is equal to  $\beta_1 X_1 + \beta_2 X_2 + \dots + \beta_i X_i$ ;  $\beta_i$  equals the regression coefficient for the explanatory variables; and  $X_i$  equals the explanatory variable (Hosmer and Lemeshow 1989). As  $X_i$  increases by 1 unit, the odds that a nest will be used change by a multiplicative factor of  $e^{\beta_i}$  after controlling

for all other variables in the model.

Because collinearities among explanatory variables can bias estimates of standard error in cCLR (Hosmer and Lemeshow (1989:126-133), I tested all explanatory variables for multicollinearity (Pearson  $r$ ) prior to building cCLR models. I retained 1 variable from each highly intercorrelated pair ( $r \geq 0.7$ ) judged to be most biologically significant and easiest to measure.

Following Hosmer and Lemeshow (1989:84), I further reduced the data set by conducting univariate analyses. For continuous variables, I used paired  $t$ -tests. For categorical variables, I conducted  $G$ -tests for homogeneity (Zar 1996:489). In the case of cavity orientation, I used Raleigh's test (Zar 1996:615) to determine if nest cavity and potential cavity orientation was non-random. Mean vector length ( $\bar{r}$ ) is a measure of the concentration of nest orientations around the mean nest orientation and can vary from 0 to 1. Zero indicates nest orientations so dispersed that there is no mean orientation, and 1 indicates that all nests are oriented in the same direction (Zar 1996:616). If nest cavity orientation was significantly non-random, I used the  $G$ -test for homogeneity to determine if orientations differed between used and potential cavities. I categorized orientations (degrees from true north) as:  $337.6 - 22.5 =$  north;  $22.6 - 67.5 =$  northeast;  $67.6 - 112.5 =$  east;  $112.6 -$

157.5 = southeast; 157.6 - 202.5 = south; 202.6 - 247.5 = southwest; and 292.6 - 337.5 = northwest. Variables whose univariate test had a  $P$ -value  $< 0.10$  were retained as candidates for the cCLR model (Hosmer and Lemeshow 1989:84).

I submitted the screened data set to stepwise selection procedures (Hosmer and Lemeshow 1989:106-118). To account for possible differences between study sites, a site variable and all site by habitat variable interaction terms were also considered for entry into the model. The score statistic was used to determine variable entry and the likelihood ratio statistic to determine variable removal. Following Hosmer and Lemeshow (1989:108), I used a  $P$ -value of 0.25 to determine which variables were entered into the model, and a  $P$ -value of 0.10 to determine which variables were removed. The most statistically important variable at any step is the one that produces the greatest change in the log-likelihood relative to a model not containing the variable (Hosmer and Lemeshow 1989:106).

After building a preliminary model using stepwise selection, I tested the assumption of a linear relationship between the response variable and the continuous explanatory variables (Hosmer and Lemeshow 1989:88). All continuous variables were linear in the logit, precluding transformations.

I assessed the final fit of the cCLR model with a

lack-of-fit-test (Sall and Lehman 1996:279). I verified the importance of each variable in the model by examining the significance of the Wald statistic and by calculating drop-in-deviance tests (Hosmer and Lemeshow 1989:137-138).

Interspecific nest site selection.--Many factors may lead to interspecific differences in nest site selection between the elf owls and screech-owls. The large difference in body size may cause the species to choose cavities of different sizes. Screech-owls pose a predatory threat to elf owls (Gehlbach 1994), potentially causing a negative association between the species. Finally, because screech-owls are year-round residents, they may have a competitive advantage (exploitation) over elf owls.

I examined how nest sites differed between the 2 species using multiple logistic regression (LR) analyses. I screened the data set, built models, and evaluated models as described above for cCLR, with the exception that t-tests were not paired.

Spatial distribution of mature saguaros.--To examine Goad's (1985) hypothesis that patterns of nest site selection by elf owls might be due to a clumped distribution of large saguaros (at the scale of the nesting area), I determined the distribution of large (>5 m tall), cavity-bearing saguaros as described above. The count data for these analyses were the number of mature saguaros found

within the 25-m-radius nest plots and potential nest plots.

#### **Nest Cavity Selection Within the Nest Saguaro**

To examine nest cavity selection within saguaros, I compared features of nest cavities with those of potential cavities within nest saguaros. Rather than average all potential cavity heights and orientations across nest saguaros (pseudoreplication [Hurlbert 1984]), I calculated the mean height and orientation of potential cavities for each nest saguaro and paired these means with nest cavity heights and orientations. I screened the data set as above using paired  $t$ -tests,  $G$ -tests, and Rayleigh's tests. I then built a cCLR model (as above) to determine which combination of variables best distinguished between used and potential nest cavities.

## RESULTS

### Nest Searches

I located 68 independent elf owl nests, 38 of which were in the Sand Tank site. All elf owl nests were located in saguaros. Twenty-three of 37 nest saguaros used by elf owls in 1995 (62.2%; excluding 5 that fell between years) were reoccupied in 1996. With 2 exceptions, when nest saguaros were reused, elf owls renested in the previous year's cavity unless it was occupied by a gila woodpecker. Gila woodpeckers nested in cavities that elf owls had nested in the previous year on 7 occasions. I recorded 1 probable case of polygyny by elf owls in which I observed the same male repeatedly feed 2 females that occupied cavities approximately 50 m apart. All other nests were apparently occupied by monogamous pairs. Other SCNs often concurrently nested in the same saguaro as elf owls (1 other species on 30 occasions; 2 other species on 3 occasions): gila woodpecker ( $n = 27$ ), brown-crested flycatcher ( $n = 5$ ), ash-throated flycatcher ( $n = 3$ ), and gilded flicker ( $n = 1$ ).

I found 12 screech-owl nests, 7 of which were in the Saucedo site. Ten nests were in saguaro cavities and 2 were in mesquite cavities. All 12 nests were located in 1996 (I searched for nests too late in 1995). One screech-owl nest saguaro was concurrently occupied by a nesting gilded flicker.

### Density of Nests

For the overall study area, the density of elf owl nests was 0.032 nests/ha in both 1995 (SE = 0.001, 91 df, 95% C.I. 0.022 - 0.046) and 1996 (SE = 0.0008, 102 df, 95% C.I. 0.023 - 0.046). The uniform model with cosine adjustment (Laake et al. 1996) was the most parsimonious for both years of data.

The Sand Tank site had a higher density of elf owl nests than the Saucedá site for both years ( $P$ 's < 0.05). In 1995, elf owl nest density in the Sand Tank site was 0.049 nests/ha (SE = 0.002, 48 df, 95% C.I. 0.030 - 0.081), whereas elf owl nest density in the Saucedá site was 0.018 nests/ha (SE = 0.0009, 43 df, 95% C.I. 0.012 - 0.029). In 1996, nest density in the Sand Tank site was 0.046 nests/ha (SE = 0.0015, 52 df, 95% C.I. 0.032 - 0.065), whereas nest density in the Saucedá site was 0.016 nests/ha (SE = 0.0006, 29 df, 95% C.I. 0.010 - 0.022). The uniform model with cosine adjustment was again the most parsimonious for all site by year combinations.

Screech-owl nest density for the overall area in 1996 was 0.033 nest/ha (uniform model with cosine adjustment). Due to small sample size, however, precision was low (SE = 0.030, 12 df, 95% C.I. -0.032 - 0.098). Thus, I did not attempt to calculate screech-owl nest density for each study site separately.

### **Spatial Distribution of Nests and Mature Saguaros**

The spatial distribution of elf owl nests within 400 m of each survey station was random for the overall area ( $X^2 = 2.30$ , 2 df,  $P = 0.32$ ) and for each study site separately (Sauceda Site:  $X^2 = 0.69$ , 2 df,  $P = 0.71$ ; Sand Tank Site:  $X^2 = 3.90$ , 2 df,  $P = 0.14$ ).

The distribution of mature saguaros within nest plots was non-random for the overall area ( $X^2 = 10.06$ , 2 df,  $P < 0.05$ ) and for each study site separately (Sauceda Site:  $X^2 = 9.72$ , 1 df,  $P < 0.005$ ; Sand Tank Site:  $X^2 = 11.97$ , 2 df,  $P < 0.005$ ). The distribution of mature saguaros within nest plots did not significantly differ from the negative binomial for the overall area ( $X^2 = 0.43$ , 1 df,  $P = 0.53$ ) or for either study site (Sauceda Site:  $X^2 = 1.43$ , 2 df,  $P = 0.50$ ; Sand Tank Site:  $X^2 = 0.56$ , 1 df,  $P = 0.44$ ), suggesting a clumped pattern. The degree of clumpiness was low (Green's Index: overall = 0.07; Sauceda Site = 0.11; Sand Tank Site = 0.04).

The spatial distribution of mature saguaros within potential nest plots was also non-random for the overall area ( $X^2 = 9.56$ , 2 df,  $P < 0.05$ ) and for each study site separately (Sauceda Site:  $X^2 = 8.42$ , 1 df,  $P < 0.005$ ; Sand Tank Site:  $X^2 = 11.27$ , 2 df,  $P < 0.005$ ). The distribution of mature saguaros did not significantly differ from the

negative binomial for the overall area ( $X^2 = 0.46$ , 1 df,  $P = 0.51$ ) or for either study site (Sauceda Site:  $X^2 = 1.38$ , 2 df, 0.52; Sand Tank Site:  $X^2 = 0.58$ , 1 df,  $P = 0.43$ ), again suggesting a clumped pattern. The degree of clumpiness was again low (Green's Index: overall = 0.11; Sauceda Site = 0.17; Sand Tank Site = 0.09).

#### **Nest Site Selection Within the Study Area**

Sixty-six of 68 elf owl nests were located in the mixed-cacti vegetation type and 51 of 68 nests (75%) were located in the bajada physiographic type. Vegetation types ( $G = 51.2$ , 2 df,  $P < 0.0001$ ) and physiographic types ( $G = 72.9$ , 3 df,  $P < 0.0001$ ) were used significantly out of proportion to their abundance. Elf owls used the mixed-cacti vegetation type significantly more than expected and others significantly less than expected (Figure 1). Elf owls used the bajada physiographic type significantly more than expected and washes and flats significantly less than expected (Figure 1).

Ten screech-owl nests (83.3%) were located in the mixed-cacti vegetation type and 2 were in the xeroriparian vegetation type. Seven screech-owl nests were in the bajada physiographic type, 3 were in the upland type, and 2 were in the wash type. The sample of screech-owl nests did not meet minimum cell size requirements for  $G$ -tests (all expected

values  $>0$ , at least 80% of observed values  $>5$  [Agresti 1990]), so I did not perform the test.

**Nest Site Selection Within the Nesting Area: Elf Owl**

Features of vegetation surrounding nests.--After eliminating highly-intercorrelated variables, 6 features of the surrounding vegetation significantly differed between used and potential nest sites (Table 2). Mature ironwoods, the 2 tallest structure classes of saguaros, and saguaro cavities were found in significantly higher densities at used sites than at potential sites (Table 2). The cover of understory ocotillo (Fouquieria splendens) was significantly greater at used sites than at potential sites, whereas cover of overstory mesquite was significantly less at used sites (Table 2).

Features of nest saguaros.--Elf owl nest saguaros ranged in height from 5.0 m to 11.9 m with a mean of 8.6 m (SE = 0.20,  $\underline{n}$  = 68) and ranged in dbh from 37 cm to 62 cm with a mean of 48.8 cm (SE = 0.72,  $\underline{n}$  = 68). Nest saguaros were significantly taller than potential nest saguaros (Table 2). The number of potential cavities within nest saguaros ranged from 0 to 25, with a mean of 7.2 (SE = 0.56,  $\underline{n}$  = 68), and nest saguaros had significantly more potential cavities than did potential nest saguaros (Table 2). Thirty-four of 68 (50%) nests were in saguaros  $>5$  m tall with  $>2$  branches and this structure category was used more

frequently than expected on the basis of potential-availability (Figure 2).

Features of nest cavities.--Fifty-nine of 68 elf owl nests (86.8%) were located in gila woodpecker cavities; these cavities were used more often than expected based on the availability of potential cavities (Figure 3). Nest cavities ranged from 3.0 m to 9.2 m in height with a mean of 6.1 (SE = 0.16,  $n = 68$ ) and were significantly higher than potential cavities (Table 2). Nest cavity orientation was non-random, with a mean of 358° ( $r = 0.31$ ,  $P < 0.02$ ,  $n = 68$ ). Nest cavity orientation differed from that expected based on potential cavity orientation ( $G = 12.67$ , 7 df,  $P = 0.080$ ) and north-facing cavities were used more frequently than expected (Figure 4). The proportion of nest cavities located in branches and stems did not significantly differ from that expected based on the location of potential cavities (Figure 5).

cCLR model.--The final cCLR model for nest site selection within the nesting area fit well ( $X^2 = 17.31$ , 66 df,  $P = 1.00$ ) and contained variables for number of potential cavities within the nest saguaro and density of mature saguaros (>5 m tall with 1-2 branches [Table 3]). After controlling for the density of mature saguaros, each additional potential cavity in a saguaro increased the

estimated odds it was used for nesting by a factor of 4.4. Controlling for the number of potential cavities, each additional mature saguaro in the plot increased the odds a site was used for nesting by a factor of 2.2.

**Nest Site Selection Within the Nesting Area: Screech-Owl**

Features of vegetation surrounding nests.--Contrary to the patterns observed for elf owls, mature ironwoods and the 2 tallest structure classes of saguaros were found in significantly lower densities at screech-owl nest sites than at potential sites (Table 4). The cover of overstory perennial vegetation was also significantly lower around screech-owl nests. Because I located only 2 screech-owl nests in trees, I did not statistically analyze these data (see Table 5). No saguaros were found within 200 m of either tree nest.

Features of nest saguaros.--Screech-owl nest saguaros ranged in height from 4.7 m to 10.9 m with a mean of 8.1 m (SE = 0.64,  $\underline{n}$  = 10) and ranged in dbh from 45 cm to 59 cm with a mean of 52.9 cm (SE = 1.29,  $\underline{n}$  = 10). Nest saguaros had a significantly greater dbh than potential nest saguaros (Table 4). The number of potential cavities within nest saguaros ranged from 2 to 15 with a mean of 5.1 (SE = 1.26,  $\underline{n}$  = 10) and did not differ from the number of potential cavities within potential nest saguaros (Table 4). However, the number of gilded flicker cavities was greater within

nest saguaros than within potential nest saguaros ( $t = 3.06$ , 9 df,  $P = 0.009$ ). Screech-owl nests were evenly-distributed across saguaro structure classes (Figure 2).

Features of nest cavities.--Nine of the 10 screech-owl nests located in saguaros were in cavities excavated by gilded flickers and these cavities were used out of proportion to their potential-availability (Figure 3). The 1 screech-owl nest not in an obvious gilded flicker cavity was intermediate in size between a gila woodpecker and gilded flicker cavity (vertical diameter = 6.2 cm; horizontal diameter 7.1 cm). Nest cavity height ranged from 3.2 m to 8.6 m with a mean of 6.2 (SE = 0.55,  $n = 10$ ) and did not significantly differ from potential cavity height (Table 4). The orientation of nest cavities did not significantly differ from random ( $\chi = 0.09$ ,  $P > 0.50$ ,  $n = 10$ ) and the location of nest cavities did not differ from that expected based on location of potential cavities (Figure 5).

CCLR model.--The final cCLR model fit acceptably well ( $\chi^2 = 4.32$ , 9 df,  $P = 0.23$ ) and contained 3 variables for cavity diameter, saguaro dbh, and the density of mature ironwood trees (Table 3). After accounting for other variables in the model, the odds of a screech-owl nesting in a gilded flicker cavity were estimated to be 46.9 times the

odds of it nesting in a gila woodpecker cavity. A 1-cm increase in saguaro dbh increased the odds it was used for nesting by a factor of 1.8, and a 1-tree increase in the density of mature ironwoods decreased the odds a site was used by a factor of 0.3.

#### **Interspecific Nest Site Selection**

The LR model that best-distinguished between elf owl and screech-owl nest sites fit well ( $X^2 = 32.34$ , 34 df,  $P = 0.49$ ) and contained variables for cavity diameter and density of mature saguaros (Table 6). Controlling for the density of mature saguaros, the odds of an elf owl nesting in a gila woodpecker cavity were estimated to be 79.6 times the odds of a screech-owl doing so. Controlling for cavity diameter, the estimated odds of a nest site being that of an elf owl increased by a factor of 2.2 for each additional mature saguaro in the territory plot.

#### **Nest Cavity Selection Within the Nest Saguaro**

Elf owl.--As was found at the scale of the nesting area, elf owls selected cavities that were significantly higher than potential cavities ( $t = 1.71$ , 64 df,  $P = 0.087$ ) and that were oriented to the north significantly more often than expected based on potential cavity orientation ( $G = 13.59$ , 7 df,  $P = 0.059$ ). However, unlike at the scale of the nesting area, gila woodpecker cavities were selected in

proportion to their potential-availability ( $G = 7.88$ , 1 df,  $P = 0.005$ ) and nest cavities were located in the main stem more frequently than expected based on location of potential cavities ( $X^2 = 6.49$ , 1 df,  $P = 0.011$ ).

The cCLR model fit well ( $X^2 = 57.93$ , 67 df,  $P = 0.75$ ) and contained variables for cavity height, cavity location, and cavity orientation (Table 7). Controlling for other variables in the model, a 1-m increase in a cavity's height increased the estimated odds it would be used for nesting by a factor of 2.2 (Table 7). The odds of an elf owl selecting a cavity in the main stem were estimated to be 2.8 times the odds of it selecting a branch cavity and the odds of an elf owl selecting a north-facing cavity were estimated to be 1.8 times the odds of it selecting a cavity of a different orientation.

Screech-owl.--Cavity selection within nest saguaros was similar to cavity selection within the nesting area for screech-owls. Screech-owl nests were again located in gilded flicker cavities more frequently than expected based on potential-availability (Fisher's Exact Test,  $P = 0.012$ ,  $n = 10$ ). The location of screech-owl nests did not differ from that expected based on potential cavity location (Fisher's Exact Test,  $P = 0.98$ ,  $n = 10$ ) and nest cavity height did not significantly differ from potential cavity

height ( $\underline{t} = 0.69$ , 9 df,  $\underline{p} = 0.51$ ).

The cCLR model for cavity selection within nest saguaros fit well ( $X^2 = 11.41$ , 9 df,  $\underline{p} = 0.25$ ) and contained a variable for cavity diameter. The odds of a screech-owl selecting a gilded flicker cavity within the nest saguaro were estimated to be 13.56 times the odds of it selecting a gila woodpecker cavity (Table 7).

## DISCUSSION

### Nest Site Selection

Because SCNs do not excavate their own nest cavities, their breeding distributions are potentially limited by a lack of suitable cavities (e.g., von Haartman 1957, Van Balen et al. 1982). Some SCNs, such as barn owls and house wrens (Troglodytes aedon), are general in their choice of cavities, nesting in both bird-excavated cavities and a wide-variety of natural cavities (Gehlbach 1994). Others, like purple martins and flammulated owls, appear to nest almost exclusively in cavities excavated by birds (e.g., Stutchbury 1991, McCallum 1994a). Pitts (1991) termed the former species wide tolerance SCNs, and the latter species, narrow tolerance SCNs. This is an important distinction, as the breeding distributions of narrow tolerance SCNs are delimited by the distributions of excavating species, whereas the distributions of wide tolerance species are delimited only by the presence of substrate capable of housing cavities. Past work has shown the screech-owl to be a wide tolerance SCN and the elf owl to be a narrow tolerance SCN (Bendire 1898, Bent 1938, Ligon 1968, Millsap 1988). Elf owls have only been documented to nest in woodpecker-excavated cavities (Ligon 1968, Millsap 1988, this study).

In addition to nesting only in woodpecker cavities, elf

owls have the narrowest known thermoneutrality zone of any North American owl (Ligon 1969), and thermoregulatory constraints may influence nest cavity selection in extreme environments such as the Sonoran Desert. Ligon (1968) concluded that summer temperatures in the Sonoran Desert are above the upper thermoneutrality limit of elf owls. Soule (1964) found that internal temperatures of saguaro cavities were 3° to 7° C cooler than ambient temperatures during the elf owl's breeding season; this temperature change would be the difference between the elf owl being within or outside of its thermoneutrality zone. Consequently, Ligon (1968) predicted that elf owls would nest only in saguaros in the Sonoran Desert. My study and others (Ligon 1968, Goad and Mannan 1987, Millsap 1988, Bibles 1992) support this prediction.

Nest site selection within the study area.--Patterns of nest site selection by elf owls within the study area reflected that elf owls nested only in saguaros on BMGR. The finding that most elf owl nests were located in the mixed-cacti vegetation type and in the bajada and upland physiographic types is expected given that these cover types had relatively higher densities of saguaros (unpubl. data). Steenbergh and Lowe (1983) found that all age classes of saguaros occurred in their highest densities on rocky

bajadas and uplands. Rocky substrate is conducive to the establishment of young saguaros and stability of mature saguaros (Steenbergh and Lowe 1983).

Although elf owl nests were rarely located in washes, my observations suggest that washes are nonetheless important to elf owls during the breeding season. Whereas female elf owls diurnally-roosted in nest cavities during the incubation and nestling periods, male elf owls usually ( $n = 23$ ) diurnally-roosted in washes (unpubl. data). In addition, I (Chapter 2) found that increasing abundance of elf owl nests was associated increasing cover of washes. Korol and Hutto (1984) found that a significantly greater proportion of saguaros located in washes had cavities than saguaros located in other physiographic areas. However, their wash transects included saguaros within 20 m of the wash edge. Had I used their definition, 41.2% of nests would have been in washes (no elf owl nests were located >75 m from a wash).

In addition to their ability to nest in cavities not excavated by woodpeckers, experimental work has shown screech-owls to be much more efficient thermoregulators than elf owls (Ligon 1969). Consequently, the breeding distribution of screech-owls in the Sonoran Desert is not likely limited to areas with saguaros. Indeed, I observed screech-owls nesting in both woodpecker-excavated cavities

in saguaros and in natural cavities in mesquites. Finding that screech-owls nested in mesquites is significant because other than in mesic riparian areas (Bendire 1898), screech-owls have not been documented to nest in tree cavities in the Sonoran Desert. I update the data of Bent (1938) and Johnsgard (1988) who wrote that screech-owls nest only in saguaros in the Sonoran Desert. Screech-owls were observed nesting in all vegetation and physiographic types except for the creosote vegetation type and the flats physiographic type. These were the only 2 cover types with a marked absence of both trees and saguaros.

Selection within nesting areas and nest saguaros: elf owl.--At the scale of the study area, elf owls appear to be limited to nest in woodpecker-excavated cavities in saguaros and the cover types that contain such cavities. At the scale of the nesting area and nest saguaro, random choice of nest sites would suggest that any woodpecker-excavated cavity in a saguaro is suitable for nesting, whereas non-random choice of nest sites would suggest that certain features are preferred (e.g., McCallum and Gehlbach 1988). As noted by McCallum (1994), inference about preferences can be strengthened with information on the degree of habitat saturation. If the habitat is not saturated, occupied sites are likely to be the most highly preferred of those available. Only 25% of the potential nest cavities within

elf owl nest plots and 20% of potential cavities on unused plots were occupied by nesting SCNs (unpubl. data), suggesting that habitat was not saturated. The many differences between elf owl nest sites and unused sites both within the nesting area and within the nest saguaro suggest that woodpeckers excavate sufficient numbers of cavities to enable owls to occupy preferred sites.

Although Goad and Mannan (1987) and Millsap (1988) suggested that vegetation surrounding nests plays a minor role in nest site selection by elf owls, my results suggest that features of the surrounding vegetation, nest saguaro, and nest cavity are all important in nest site selection on BMGR. The variables that best distinguished between nest sites and potential nest sites were the density of mature saguaros surrounding the nest saguaro and the number of potential nest cavities in the nest saguaro. Other studies have shown the number of cavities and/or structures suitable for cavities surrounding nests to be important criteria for nest site selection by SCNs (e.g., Swallow et al. 1986, Martin and Roper 1988). The large number of potential cavities in the nest saguaro itself is a unique facet of the nest saguaro environment. Potential nest cavities in the vicinity of the nest provide SCNs with renesting sites in the case of nest failure (Rendell and Robertson 1994) or nest usurpation (Lindell 1996), and may be used as roost

sites (Gehlbach 1994).

Having alternate cavities should be particularly important in a dynamic and potentially-competitive nesting environment such as experienced by SCNs in saguaros. The patterns of reoccupancy that I observed illustrate the importance of alternate cavities: in 7 of the 8 cases when gila woodpeckers occupied elf owl nests from the previous year, elf owls nested in other cavities within the same saguaro; in 5 of the 6 cases when nest saguaros died between 1995 and 1996, elf owls nested in cavities <15 m of the previous year's nest saguaro.

Although total cover of perennial vegetation did not differ between elf owl nest sites and unused sites, the density of mature ironwood trees and cover of ocotillo were greater around nests than around unused sites. Goad and Mannan (1987) also concluded that total cover of perennial vegetation was unimportant in nest site selection, but did not consider floristics. Behavioral observations suggest that the importance of ironwood and ocotillo may be related to prey delivery behavior of male elf owls. I found that 85% of the time ( $n = 62$ ), owls stopped at a perch <15 m from the cavity prior to delivering a prey item rather than directly approaching the cavity (unpubl. data). This behavior involved perching on a tree or saguaro branch within view of the cavity entrance, looking around several

times, exchanging call notes with the female, then delivering the item. Ironwoods and ocotillos were the most frequently used perches (unpubl. data). If elf owls select sites that enable this common behavior, the density of ironwood and cover of ocotillo should be greater in front of nest cavities than behind them. Therefore, I recalculated ironwood density and cover of ocotillo in the front and back of each nest cavity separately and compared these values within used sites ( $t$ -test). Density of ironwood and cover of ocotillo were both significantly greater in front of used nest cavities ( $P < 0.05$ ), supporting my post hoc hypothesis.

Although some patterns of nest cavity selection by elf owls were consistent between scales (nest cavities higher than potential nest cavities and oriented to the north more frequently than expected), some patterns differed. Whereas elf owls selected gila woodpecker cavities out of proportion to their availability within the nesting area, they selected gila woodpecker cavities in proportion to their availability within the nest saguaro. These contrasting results are explained by the fact that elf owls nested in saguaros that contained a high ratio of gila woodpecker cavities to gilded flicker cavities (approximately 10:1), whereas the ratio of gila woodpecker cavities to gilded flicker cavities in potential nest saguaros was much less (approximately 2:1). Forty-four of 68 nests contained only gila woodpecker

cavities. Thus, a random selection of cavities within nest saguaros would reveal significant selection within the nesting area.

McAuliffe and Hendricks (1988) showed that saguaros containing gilded flicker cavities had a much higher mortality rate than saguaros containing only gila woodpecker cavities. Because saguaros with only gila woodpecker cavities live longer than those with gilded flicker cavities, they accumulate more cavities over time. Thus, 2 potential advantages of selecting saguaros with all or mostly gila woodpecker cavities are that these saguaros are more likely to provide nest sites in the future (important to a species that shows site fidelity) and these saguaros provide more alternate cavities (discussed above). Furthermore, McAuliffe and Hendricks (1988) suggested that agonistic behavior between gila woodpeckers and gilded flickers may manifest itself in a negative association of nests of the 2 species in the same saguaro. I tested for this kind of displacement by calculating the number of saguaros in each of the following 4 categories: 1) those with only gila woodpecker cavities; 2) those with only gilded flicker cavities; 3) those containing cavities excavated by both species; and 4) those lacking nest cavities altogether. I then compared the observed numbers of saguaros contained in each category to the null

expectation, given a random distribution of the observed number of nest cavities of each species among saguaros. Saguaros with only gila woodpecker cavities and only gilded flicker cavities occurred more frequently than expected and saguaros with cavities of both species occurred less frequently than expected based on a random distribution of nest cavities among saguaros ( $P < 0.05$ ), suggesting nest cavity displacement. This negative association may explain the high ratio of gila woodpecker to gilded flicker cavities in elf owl nest saguaros and the low ratio of gila woodpecker to gilded flicker cavities in screech-owl nest saguaros.

Many of my findings suggest that elf owls selected cavities that provided thermoregulatory advantages. Soule (1964) found that north-facing cavities had a cooler microclimate than south-facing cavities, and that cavity temperature was lower for cavities higher in the saguaro. In addition, cavities in the thicker main stem (Steenbergh and Lowe 1977) would be expected to be better insulated than branch cavities. I did not measure microclimate within cavities.

Although non-random nest orientation has been reported for primary cavity nesting species (Conner 1975, Inouye 1976, Korol and Hutto 1984), it has rarely been reported for SCNs (McEllin 1979, Raphael 1985), and has not been reported

in owls. Because SCNs do not excavate their nest cavities, non-random orientation merely reflects excavator preferences if cavities are selected in proportion to their abundance. Therefore, it is more meaningful to compare the orientation of cavities used by SCNs to the orientations of cavities excavated by primary cavity nesters. When this has been done, only American kestrels have been observed to nest in cavities with orientations different than available cavities (Raphael 1985). Despite my significant findings at both the scale of the nesting area and the nest saguaro, elf owl nest orientations were quite dispersed (see Figure 4) and results should be interpreted with caution.

Unlike my study, Goad and Mannan (1987) found that elf owl nest cavities did not differ from those available with respect to location, diameter, and height, and orientation. This finding occurred despite the fact that a low percentage of available cavities were occupied by SCNs (perhaps enabling elf owls to be selective). Goad and Mannan (1987) concluded that apparently any cavity within a saguaro represented a potential nest. As to the differences in nest cavity selection between BMGR and Saguaro National Monument, the latter site averages 200 m to 500 m higher in elevation, has mean temperatures 2° to 4° C cooler (Sellers et al. 1985), and has different prevailing winds and precipitation

patterns than BMGR (Bob Davidson, National Weather Service, pers. commun.). Thermoregulatory constraints may not be as much of a factor in the more moderate summer climate of Saguaro National Monument, perhaps enabling elf owls to choose a wider variety of cavities. Geographic variation in nest cavity selection within a species is common (e.g., Gutzwiller and Anderson 1987, Keith 1989). For example, 2 studies (Inouye et al. 1981, Korol and Hutto 1984) from Organ Pipe Cactus National Monument (<50 km south of my study area) reported that gila woodpecker nest cavities were non-randomly oriented, whereas a study near Tucson (Kerpez and Smith 1990a) reported that the species' nest cavities were randomly oriented. Like my study area, Organ Pipe Cactus National Monument experiences higher temperatures and different weather patterns than the Tucson area (Sellers et al. 1985).

Selection within nesting areas and nest saquaros:  
screech-owl.--Features of the surrounding vegetation, nest saquaro, and nest cavity also seemed important in nest site selection by screech-owls. In fact, the cCLR model included variables from all 3 dimensions of nesting habitat: cover of understory perennial vegetation, nest saquaro dbh, and nest cavity diameter.

Screech-owls nested in areas characterized by lower cover of understory perennial vegetation than potential

sites. Closely related eastern screech-owls and flammulated owls seem to prefer nest sites with open subcanopy space with sparse shrub cover (McCallum and Gehlbach 1988, Robbins et al. 1989, Belthoff and Ritchison 1990, Gehlbach 1994) and McCallum and Gehlbach (1988) suggested that the flight behavior of these species was related to their preference for open vegetation around the nest. The flight behavior of eastern screech-owls and flammulated owls differs from that I observed for elf owls, as both species tend to fly low (1-2 m above ground) into the nest area and then rise abruptly to the cavity (McCallum and Gehlbach 1988). Similarly, upon leaving the nest, these owls dive steeply, then level off and fly 1-2 m above ground. I observed similar flight behavior by screech-owls on BMGR.

Unlike elf owls, screech-owls nested almost exclusively in gilded flicker cavities. Although the larger body size of screech-owls does not absolutely limit them from entering gila woodpecker cavities (Gehlbach 1994, pers. obs.), the much smaller interior of gila woodpecker cavities (Kerpez and Smith 1990a) may constrain the large brood sizes characteristic of the species (Johnsgard 1988). The fact that screech-owls selected saguaros of large dbh for nesting indicates that cavity volume may also be a consideration. In Oregon and Washington, screech-owls only used cavities in trees with a minimum dbh of 30.5 cm (Thomas et al. 1979).

Belthoff and Ritchison (1988) found that eastern screech-owls chose cavities of greater volume than unused cavities. I did not measure volume of cavities.

The total number of cavities (regardless of excavating species) and density of mature saguaros surrounding screech-owl nests was significantly less than at unused sites. However, I examined gilded flicker cavities separately and found there were significantly more gilded flicker cavities surrounding nest saguaros and than surrounding potential nest saguaros. Thus, having alternate gilded flicker cavities may be important in nest site selection by screech-owls.

#### **Nest Reoccupancy**

My finding that elf owls often reoccupied nest cavities from the previous year is consistent with the work of Goad (1985), who found that 69.6% of nests were reused from the previous year. Comparably, Stutchbury (1991) observed that purple martins reoccupied 44.4% of the previous year's nest cavities in saguaros. Fidelity to nest sites is widespread among birds, but is particularly common in migratory species that are territorial (e.g., Darley et al. 1971, Newton and Marquiss 1982, Reynolds and Linkhart 1987). Individuals able to reoccupy the previous year's site often experience higher reproductive success than those that do not (e.g., Reynolds and Linkhart 1987). Reoccupancy of nest sites by

SCNs has rarely been examined, but reuse of the previous year's nest cavity by SCNs is not expected due to parasite loading (e.g., Nilsson 1986) and increased predatory threat (Sonerud 1985, 1989). Nonetheless, elf owls (and possibly other SCNs) seem to commonly reoccupy saguaro cavities in the Sonoran Desert. Because I did not band elf owls, I could not verify their individual identities.

Finding gila woodpeckers frequently nesting in elf owl nest cavities from the previous year is unexpected as well. It is puzzling that gila woodpeckers would chose a recently used nest, given the potential for parasite loading, and because primary cavity nesters usually excavate a new nest each year (Short 1979). Gila woodpeckers have also been observed nesting in purple martin cavities from the previous year (Stutchbury 1991).

#### **Density and Spatial Distribution of Nests**

My study is the first to quantify elf owl nest density. My estimates of density are consistent with the estimate I derived from Walker (1974), but much lower than those I derived from Goad and Mannan (1987) and Bibles (1992). Goad and Mannan (1987) and Bibles (1992) conducted their studies in Saguaro National Monument, and differences in nest density may be due to the higher densities of mature saguaros at that site (Steenbergh and Lowe 1983, Goad and Mannan 1987, Bibles 1992). The finding that uniform

detectability functions were always included in models to estimate nest density illustrates the territorial spacing of elf owls. Density of elf owl nests on BMGR is very similar to that reported for the ecologically similar flammulated owl (Otus flammeolus) in Colorado (0.021 nests/ha [Reynolds and Linkhart 1987]) and New Mexico (0.029 nests/ha [McCallum et al. 1995]).

The nests of many SCNs exhibit a clumped distribution (e.g., Stutchbury 1991, Rendell and Robertson 1994). This pattern is often reflective of colonial breeding (Stutchbury 1991) and may enable facultative polygamy (Rendell and Robertson 1994). I found that elf owl nests were randomly distributed, and observed probable polygyny on only 1 occasion, suggesting that polygamy by elf owls is uncommon on BMGR.

The low density and non-clumped distribution of elf owl nests is suggestive of strong intraspecific territoriality. On only 1 occasion did I find elf owl nests <100 m apart. Goad and Mannan (1987) found a similar pattern of nest spacing and thought that territorial behavior (rather than numbers of nest cavities) limited the number of nesting elf owls on Saguaro National Monument. In contrast to the wide spacing among elf owl nests, 6 of 12 screech-owl nests were <50 m from elf owl nests (minimum = 20 m). Similarly, Gehlbach (1987) often observed elf owls and eastern

screech-owls nesting <50 m apart in Texas. Thus, interspecific territoriality between elf owls and screech-owls may not be as strong as intraspecific territoriality or may not exist.

Spatial distribution of mature saguaros.--Mature, multi-branched saguaros were spatially-clumped at the scale of the nesting area, supporting Goad's (1985) contention that some patterns of nest site selection by elf owls may be due to a clumped distribution of saguaros. As in my study, Goad (1985) found that densities of mature saguaros were higher around nest saguaros (20-m-radius plot) than around random points. Because elf owls often nest in mature saguaros, this result may reflect the clumpiness of mature saguaros.

Although I found that the distribution mature saguaros was clumped and the distribution of nests was random, I emphasize that the spatial scale at which I examined the distribution of mature saguaros (25-m-radius plot) differed from the scale at which I determined the distribution of nests (400-m-radius plot). It may be that the "clumps" of saguaros found within the 25-m-radius plots are randomly distributed at a larger scale and that elf owls are selecting these "clumps." I cannot test this possibility with my data.

#### RECOMMENDATIONS FOR MANAGEMENT AND FUTURE RESEARCH

My results demonstrate the importance of large, structurally-complex saguaros to elf owls. Such saguaros are most often found in bajadas and uplands within the mixed-cacti vegetation type and such cover types should be prioritized for elf owl management on BMGR. Within the mixed-cacti vegetation type, mature saguaros that contain multiple gila woodpecker cavities should be preserved. To do so, I recommend that the U.S. Air Force avoid bombing and ground maneuvers in areas with mature saguaros and continue its no-grazing policy on BMGR. Over-grazing (>10 head/100 ha/year) reduces the number and quality of sites suitable for saguaro germination, and by the removal of protective low-level plant cover and mechanical breakdown of detritus, increases vulnerability of young plants to destruction by freezing and other natural environmental hazards (Steenbergh and Lowe 1969, 1976, 1977; Steenbergh and Warren 1977). Protecting areas with stands of mature saguaros is likely to benefit other SCNs on BMGR as well.

Although my findings suggest that elf owls select cavities that provide a favorable microclimate, I did not measure the microclimate of nest cavities and recommend that future studies of nest site selection do so. Ideally, future studies should attempt to relate microclimate (and other habitat variables) to habitat quality. Measuring

habitat quality would entail a demographic study of banded individuals. Although elf owl nests found during the nestling phase seem to be a indicative of habitat quality (see also Chapter 2), this needs to be confirmed as I did not follow the history of nests. Because elf owl nests are easily located and adults owls seem to be faithful to nest sites, the species is well-suited to demographic study. Of note is that an Air Force biologist and I had considerable success capturing elf owls from cavities using a butterfly net. Banding individuals and monitoring nests over time can also be used to confirm the strong nest site fidelity for elf owls suggested by our observations and those of Goad and Mannan (1987), and can be used to examine temporal patterns of nest cavity use by screech-owls as well.

Although the small sample of nests limits the strength of inferences about nest site selection by screech-owls, it appears that stands of saguaros sufficiently large to house gilded flicker cavities and xeroriparian washes containing mature trees should received special management consideration.

Future nest searches for screech-owls (during the nestling period) should take place from mid April thru late May in the Sonoran Desert and should be done in both upland areas with saguaros and washes void of saguaros. I also recommend that future studies take into account the

microclimate and inner dimensions of cavities. Future research can be used to examine some of the patterns of nest site selection suggested here. For example, do screech-owls use only gilded flicker cavities?; is the preference of open vegetation surrounding the nest related to flight behavior and/or prey availability?; are large saguaros preferred because they enable woodpeckers to excavate larger cavities?

**CHAPTER 2: ABUNDANCE AND HABITAT ASSOCIATIONS OF ELF OWLS  
AND WESTERN SCREECH-OWLS IN THE SONORAN DESERT**

**INTRODUCTION**

The migratory elf owl (Micrathene whitneyi) and resident western screech-owl (Otus kennicottii) are common breeding birds throughout most of their range in the U.S. In the Sonoran Desert, both species are associated with structurally diverse uplands containing saguaros (Carnegiea gigantea), mesquite (Prosopis velutina) woodlands, and cottonwood (Populus spp.)-willow (Salix spp.) riparian areas (Bent 1938, Johnson et al. 1979, Millsap 1988).

In the Sonoran Desert, breeding populations of elf owls and western screech-owls continue to be threatened by rapid urbanization and by degradation of riparian woodlands (Krueper 1993), and face possible competition from European starlings (Sturnus vulgaris) for nest cavities (Kerpez and Smith 1990b). Unfortunately, outside of nest site selection by elf owls (Ligon 1968, Goad and Mannan 1987), little quantitative information exists on either species' population parameters or habitat associations. If wildlife managers are to determine the long-term status of populations of elf owls and western screech-owls and examine relationships between owl abundance and habitat alterations and/or competition from European starlings, baseline

information on these species' abundance and habitat associations must be collected.

From 1994 thru 1996, I used point counts with the aid of broadcast recordings (Johnson et al. 1981, Fuller and Mosher 1987) to sample elf owls and western screech-owls (hereafter, screech-owls) in the Sonoran Desert. I used survey data to estimate the relative abundance of owls, to establish a baseline for monitoring abundance over time, and to examine owl-habitat relationships.

#### **Study Area**

Barry M. Goldwater Air Force Range (BMGR) is located in southwestern Arizona and is the nation's second largest aerial gunnery training range. It occupies approximately 10,900 km<sup>2</sup> of unpopulated land in Maricopa, Pima, and Yuma counties, and represents one of the largest and best preserved regions of native desert remaining in the United States. BMGR's pristine condition can be attributed to limited public access and the fact that <5% of the total land area is impacted by training activities. The landscape of BMGR is dominated by low, isolated mountain ranges separated by broad basins and is comprised of two major vegetation types: the Arizona Upland and the Lower Colorado River Valley subdivisions of the Sonoran Desert. The Arizona Upland subdivision includes the paloverde (Cercidium

spp.)-mixed-cacti scrub series and paloverde-catclaw (Acacia greggii) xeroriparian associations. Various cacti, such as jumping cholla (Opuntia spp.) and saguaro, are prominent members of this subdivision. The Lower Colorado River Valley subdivision includes the creosote (Larrea tridentata)-white bursage (Ambrosia dumosa) series, and in runnels and washes, the Mixed-scrub series. The Mixed-scrub series is xeroriparian in nature and includes many species common to the Arizona Upland subdivision, including blue paloverde (C. floridum), ironwood (Olneya tesota), mesquite, and catclaw acacia (Turner and Brown 1994).

Temperatures for the Arizona Upland and Lower Colorado River Valley regions average 29°-30° C in the summer and 11°-12° C in the winter; mean annual precipitation is 20-30 cm (Sellers et al. 1985).

My 2 study sites were in the northeastern area of BMGR south of Interstate 8 and east of Highway 85. The sites are >80 km from the nearest urban center (Phoenix) and European starlings are absent. The Saucedo Mountains study site ranges from 366-686 m in elevation and is primarily ecotonal between the Lower Colorado River Valley and Arizona Upland subdivisions. The Sand Tank Mountains study site ranges from 547-853 m in elevation and consists primarily of Arizona Upland vegetation (Hardy and Morrison 1996).

## METHODS

### Point Count Surveys

To determine abundance of elf owls and screech-owls, I conducted broadcast surveys along point transects. I also surveyed for the federally-endangered cactus ferruginous pygmy-owl (Glaucidium brasilianum cactorum), which I did not detect. I broadcasted male territorial songs (Cornell Laboratory of Ornithology 1995) using a modified Realistic® powerhorn set at moderate volume, and a cassette player.

In each study site, I established 3 transects consisting of 10 stations each (60 stations total). I located transects along roads to decrease travel time between stations and permit more stations to be surveyed in a night (Fuller and Mosher 1987). Roads were generally 1-vehicle-width or less and followed the terrain, thus minimally impacting local vegetation. I randomly located the first station, then systematically-spaced others at 0.8-km (0.5 mi) intervals. If a road curved and 2 stations were closer than 0.8 km apart, I extended road distance until stations were straight-line 0.8-km distant. Given the small territory sizes of the owls of interest (Ligon 1968, Johnsgard 1988), this spacing made it highly probable that detections were independent.

I surveyed transects 4 times per year (1994-1996) between mid March and late May. This interval includes most

of the breeding seasons of elf owls and screech-owls (Bent 1938, Ligon 1968, Goad and Mannan 1987, Johnsgard 1988). To ensure that the migratory elf owl had arrived on the breeding grounds, I monitored its calling activity several nights each year before initiating surveys.

I started all surveys within 30 min after sunset and completed them within 4 hours. Elf owls and screech-owls are believed to be most responsive and closer to their daytime roosts and/or nests during this interval (Ligon 1968, Johnson et al. 1981, Goad 1985). I alternated the direction transects were surveyed (e.g., 1 to 10 or 10 to 1) to help avoid a temporal bias.

I played species' songs in random order in an attempt to reduce the influence of broadcasts on species' response rates (e.g., reduction in response due to habituation [Johnson et al. 1981, Smith et al. 1987, Morrell et al. 1991]). At each station, there was an initial 30-sec rest-period (Reynolds et al. 1980) to allow birds to settle down from any disturbance caused by my arrival. This was followed by a 2-min count-period during which all detections were noted. I used these data to determine if owls were vocalizing spontaneously or in response to broadcasts. I then played the first species' song for 30 sec during which the megaphone was rotated 360 degrees. This was followed by a 2-min count-period, with all detections noted. I repeated

this routine until I had broadcasted recordings of all 3 species. I spent approximately 10 min at each station.

I noted detections of all vocalizing elf owls and screech-owls, as well as detections of other owls (e.g., great-horned and barn [Tyto alba] owls) and nocturnal birds (e.g., common poorwill [Phalaenoptilus nuttallii] and lesser nighthawk [Chordeiles acutipennis]). Such species represent potential predators and competitors to elf owls and screech-owls. When I heard an owl, I recorded its species and sex.

After completing the 10-min survey period, my field assistant and I used compasses to take triangulation bearings on all singing owls. We used 2-way radios to keep track of track of owl movements and assure that we triangulated on the same owl. I used compass triangulation data to generate a map of locations of singing owls and used this map to estimate the number of territories within each species' aural envelope (defined below). I considered a group of locations to be a territory if  $\geq 3$  locations (from the same year) were within a 50-m-radius circle. This radius corresponds to a conservative estimate of territory size for elf owls and screech-owls (Ligon 1968, Johnson et al. 1981, Goad and Mannan 1987). I estimated territory density in order to determine if it was related to reproductive success (see below).

I did not conduct surveys during inclement weather (heavy rains; winds >30 kph). Such weather would likely have a negative impact the responsiveness of owls, my ability to detect owls, and/or my ability to access survey areas (Fuller and Mosher 1987).

### **Vegetation Sampling**

Bird abundance from point counts is best related to features of the vegetation and substrate if these features are measured within a species' aural envelope (the distance within which vocalizations can be heard [e.g., Wolf et al. 1995]). In light of this, I estimated the aural envelope of elf owls and screech-owls and sampled vegetation within this distance. To measure the aural envelope, an assistant and I would locate a singing owl and approach as close as possible without disturbing it. While one observer remained near the owl, another would pace away and determine the maximum distance at which the owl could still be heard. Hand-held radios enabled us to account for owl movements and changes in singing activity. I conducted these tests ( $n = 30$ ) in relatively flat ( $0\% \geq \text{slope} < 5\%$ ) areas during weather conditions allowable by the survey protocol. I estimated the aural envelope to be 232 m for elf owls (95% C.I. = 206.1 - 257.9) and 151 m for screech-owls (90% C.I. = 129.2 - 172.9).

I sampled vegetation and substrate within each species'

aural envelope on 8 point-intercept transects (Bonham 1989:108) radiating out from each survey station. I randomly determined the direction of the first transect and directed subsequent transects 45 degrees from the previous. I paced-off transects, spacing intercept-points at 5-m intervals (46 points/transect for elf owls; 30 points/transect for screech-owls).

Because the strength of models to predict bird-habitat relationships often vary greatly based on the scale at which habitat variables are measured (e.g., Wiens 1985), I sampled both macrohabitat (cover of vegetation types and physiographic types) and microhabitat (cover of plant species and substrate) variables. Doing so allowed me to determine which measurement scale explained relatively more variability in owl abundance. I sampled microhabitat variables by collecting information in 4 vertical height classes at each intercept-point: 0 m (ground level); >0 m to 1.0 m (understory); >1.0 m to 2.5 m (mid-canopy); and >2.5 m (overstory). I identified shrubs, trees, and cacti to species. For each plant species and substrate, I determined the number of "hits" in each height class with the aid of a graduated, extendable pole (both live and dead vegetation were tallied). I divided this number by the total number of point-intercept points (368 points/station for elf owls; 240 points/station for screech-owls) to estimate percent cover

of each plant species and substrate by height class, as well as percent cover of perennial vegetation (all woody species combined).

I also recorded the general vegetation type (xeroriparian, creosote, or mixed-cacti) and physiographic type (wash, flat, bajada, or upland) at each intercept-point. The xeroriparian vegetation type included any drainage with bank full width  $>1$  m (Cole 1994) and its associated frequent flood plain area (Ohmart and Anderson 1982); these areas were dominated by tall ( $>2$  m), dense vegetation. The creosote vegetation type was dominated by creosotebush and bursage. The mixed-cacti vegetation type was dominated by yellow paloverde (Cercidium microphyllum), saguaros, and various species of small shrubs and cacti.

I defined physiographic types following Barbour et al. (1987): "wash," same as xeroriparian above; "flat," any non-wash area with slope  $\leq 1\%$ ; "bajada," any non-wash area with slope  $>1\%$  and  $\leq 5\%$ ; and "upland," any non-wash area with slope  $>5\%$ . I estimated percent cover of vegetation and physiographic types as described above for plant species and substrate.

On 4 vegetation transects (the first randomly selected and others separated by 90 degrees) I established 25-m-radius plots at the 150-m point. I recorded the number of saguaros within these plots and categorized them

following Goad and Mannan (1987): (1) <3 m tall with no branches; (2)  $\geq 3$  m tall with branches <6 cm length or no branches; (3) >4 m tall with branches 6 cm to 1 m in length; (4) >5 m tall with 1-2 branches >1 m in length; (5) >5 m tall with 3 or more branches >1 m in length; or (6) >2 m tall with a broken-top. These categories were mutually-exclusive and included all saguaros. I analyzed saguaros in more detail for the following reasons: (1) their importance to the owls of interest (Ligon 1968, Goad and Mannan 1987, Johnsgard 1988, Millsap 1988); (2) >96% of all cavities occurred in saguaros (unpubl. data); (3) saguaros of various structure classes are used differentially by elf owls (Goad and Mannan 1987); and (4) the point-intercept method tends to under-sample saguaros due to their lack of canopy cover (e.g., Bibby et al. 1992).

Abundance versus availability of vegetation.--The "availability" of habitat components, referring to their accessibility and procurability (Johnson 1980), differs from the "abundance" of habitat components, which refers only to their absolute quantity (Johnson 1980, Morrison et al. 1992:139). In theory, one should be able to measure the amounts and kinds of habitat components available to animals; however, in practice, it may be impossible to assess availability from an animal's point of view (Morrison et al. 1992:139). I measured the abundance of vegetation

and substrate, rather than the true availability; henceforth, this is reflected in my terminology.

### **Estimation of Reproductive Success**

Population density or abundance is often used to assess habitat quality because a greater number of individuals within an area is thought to reflect larger amounts of the necessary resources to sustain a species (Van Horne 1983). However, many studies have shown density or abundance to be a misleading indicator of habitat quality (e.g., Van Horne 1983, Johnson and Temple 1986, Vickery et al. 1992) and advocate that studies of animal abundance should also consider reproductive success (or an index thereof).

Reproductive success is most often determined by finding and determining the outcome of nests. The process is time consuming, requires skill, and is expensive. I wanted to examine reproductive success, but could not follow the history of each nest due to time constraints. Instead, I conducted intensive nest searches within each species' aural envelope and determined if nest density per station was related to territory density per station. I conducted these searches in 1995 and 1996 during the nestling period of each species (late May thru early July for elf owls; late April thru late May for screech-owls). I did not assess reproductive success for screech-owls due to difficulties in locating their nests (see Chapter 1).

A nest is often considered successful if it produces  $\geq 1$  fledgling (e.g., Vickery et al. 1992). However, I considered an elf owl nest found during the nestling period to be indicative of reproductive success because I observed  $\geq 2$  fledglings at all 9 elf owl nests at which I attempted to confirm fledging and because Ligon (1968) observed that 100% ( $n = 29$  nests) of elf owl nestlings fledged (i.e., nests located during the nestling period have a very high probability of producing  $\geq 1$  fledgling). Elf owl nests are easily located during the nestling period due to the loud vocalizations of nestlings, which may be heard 50 to 100 m away (Goad 1985, pers. obs.), and I am confident that I found all nests within the species' aural envelope. Estimates of nest density from program DISTANCE (Laake et al. 1993) were consistent with this belief (see Chapter 1).

### **Analyses**

Vegetation of study area.--I sampled 71 vegetation and substrate features at each survey station. I used  $t$ -tests (2-tailed) to determine if each of these features differed between study sites. I did not analyze variables for which the frequency of occurrence was small ( $\leq 5$  cases per variable). I tested each variable for normality and equality of variance by examining skewness, kurtosis, and probability plots (Zar 1996:128). When both samples appeared to be normal, but exhibited unequal variances, I

used Welch's approximate  $t$ -test (Zar 1996:129). When samples appeared non-normal, log, square root, and arcsine transformations successfully normalized them (Zar 1996:277-284).

Point count surveys.--For elf owls and screech-owls, and for their potential predators and competitors, I calculated indices of abundance (no. birds detected visit<sup>-1</sup> station<sup>-1</sup>) for each year of survey data and for the pooled data set (1994-1996). For each species, I determined if indices of abundance differed among years or between study sites using multivariate, repeated-measures ANOVA (rmANOVA [Norusis 1990:111-137]). I included study site (2) as the among-subjects factor and year (3) as the within-subjects factor. I considered survey stations ( $n = 60$ ) to be the sampling units. I tested the assumptions of multivariate normality using skewness, kurtosis, and normal probability plots, and tested for homogeneity of variance-covariance matrices with Box's  $M$  test (Morrison 1976:341). The assumptions of rmANOVA were met for both owl species, precluding variable transformations. If the main effects of rmANOVA were significant in the absence of significant interactions, I used Tukey's test (Zar 1996:265) to determine where differences existed.

I also used rmANOVA to test for interspecific

differences in small owl abundance. I included study site as the among-subjects factor and year and species as within-subjects factors. I tested the assumptions of rmANOVA as above; all assumptions were met.

Multiple regression models.--I used multiple regression analysis (MR [Zar 1996:Chapter 19]) to determine which combination of vegetation and substrate variables best predicted owl species' abundance. I used pooled indices of abundance as response variables as they allowed me to determine which stations owls used consistently over time. I built models for macrohabitat (vegetation types and physiographic types) and microhabitat (cover of plants and substrate) explanatory variables.

I used stepwise selection procedures (Belsley 1980:217) to build 3 separate MR models for each species: a vegetation type model, a physiographic type model, and a microhabitat model. Prior to building the microhabitat models, I reduced the data set by eliminating all variables for which the frequency of occurrence was small ( $\leq 5$  cases per variable) and then tested all variables for multicollinearity (Pearson  $r$ ). I retained 1 member of each highly intercorrelated pair ( $r \geq 0.7$ ) judged to be more biologically significant and easiest to measure (Norusis 1990:97). To control for potential differences between study sites, an indicator variable for study site and all

2-way interaction terms involving study site were also considered for entry into all models (Belsley et al. 1980). I used a P-value of 0.25 to determine which variables entered into the model, and a P-value of 0.10 to determine which variables were removed (Belsley et al. 1980).

For all MR models, I evaluated the assumptions of linearity and homogeneity of variances by examining scatterplots of standardized residuals, and the assumption of normality of residuals by examining a histogram of studentized residuals (Belsley et al. 1980). When necessary, I used log, square root, and arcsine transformations (Norusis 1990:88) to meet these assumptions.

Potential predators and competitors.--Abundances of potential predators and competitors are better thought of as covariates with owl abundance than as explanatory variables. In light of this, I used Pearson correlation coefficients in lieu of MR to measure associations between species' abundances. I conducted correlation analyses for yearly and pooled indices of abundance.

Physiographic interspersions.--Several authors have suggested that abundance of elf owls and screech-owls is greatest in areas with an interspersions of cover types (Bendire 1892, Bent 1938, Millsap 1988), so I examined this relationship. To do so, I categorized stations based on which physiographic types were represented within each

species' aural envelope. Categories ranged from one type present to all four types present (14 possible categories). I used G-tests for homogeneity (Zar 1996:470) to determine if the physiographic types present at stations of high owl abundance (30 stations of highest pooled abundance) differed from those at stations of low owl abundance (30 stations of lowest pooled abundance).

Relationship between density and reproductive success.--

For 1995 and 1996 separately, I placed each station into a density category based on the number of elf owl territories within the aural envelope. The number of territories per station ranged from 0 to 3, for a total of 3 density categories (stations with 0 territories not included). I calculated an index of reproductive success per station by dividing the number of nests per station ("successes") by the number of territories (attempts). I then used the Kruskal-Wallis test (Zar 1996:197-202) to determine if reproductive success differed among density categories.

I used program SPSS/PC+, V5.0.1 (1992) to perform all statistical analyses and considered  $\alpha = 0.10$  to be significant. I used  $\alpha = 0.10$  instead of  $\alpha = 0.05$  to improve the power of statistical tests (Zar 1996). Following Milton (1992:375), I defined the strength of  $R^2$  values (coefficients of determination) from MR and correlation

analyses as follows:  $\underline{R}^2 < 0.25 =$  "weak";  $0.25 < \underline{R}^2 < 0.75 =$   
"moderate"; and  $\underline{R}^2 > 0.75 =$  "strong."

## RESULTS

### Vegetation of Study Area

Thirty of 71 features of the vegetation and substrate that I measured significantly differed between study sites (summarized in Table 8). The Sand Tank site had significantly greater cover of perennial vegetation, saguaros, the mixed-cacti vegetation type, and uplands, whereas the Saucedo site had significantly greater cover flats and of the xeroriparian and creosote vegetation types.

### Owl Surveys

Intraspecific abundance.--Whereas elf owl abundance did not significantly differ among years ( $F_{2,57} = 0.536$ ,  $P = 0.588$ ), screech-owl abundance significantly declined each year of the study ( $F_{2,57} = 15.301$ ,  $P < 0.0001$  [Table 9]). Neither elf owl ( $F_{2,57} = 0.057$ ,  $P = 0.945$ ) nor screech-owl ( $F_{2,57} = 0.743$ ,  $P = 0.480$ ) abundance showed significant study site by year interactions (Figure 6).

Interspecific abundance.--The site x species x year interaction was not significant ( $F_{2,57} = 0.216$ ,  $P = 0.806$ ). The species effect depended upon year (species x year interaction:  $F_{2,57} = 10.004$ ,  $P < 0.0001$ ), as elf owls were significantly more abundant than screech-owls in 1995 and 1996, but not in 1994 (Table 9).

Potential predators and competitors.--In addition to

elf owls and screech-owls, nocturnal species detected during surveys were great-horned owls, barn owls, common poorwills, and lesser nighthawks (Table 9). All 4 species were detected in each study site. I incidentally detected long-eared owls (Asio otus) in the Saucedo site. In both 1994 and 1995, I observed this species communally-roosting (10-15 individuals) from mid to late March in large, xeroriparian washes.

For the pooled data set (1994-1996), elf owl abundance had a significant positive correlation with screech-owl abundance (Table 10); the strength of this association varied considerably among years, but was always positive. Elf owl abundance had significant positive correlations with common poorwill abundance every year of the study, whereas screech-owl abundance had negative correlations with common poorwill abundance every year (Table 10).

#### **Multiple Regression Models**

Vegetation types.--The vegetation type MR model for elf owls was moderately strong ( $R^2_{adj} = 0.354$ ,  $SE = 0.150$ ). Controlling for other variables in the model, cover of the xeroriparian and mixed-cacti vegetation types each explained a significant amount of variation in elf owl abundance (Table 11). The vegetation type model for screech-owls was weak ( $R^2_{adj} = 0.158$ ,  $SE = 0.106$ ); however, xeroriparian cover

explained a significant amount of variation in screech-owl abundance (Table 11).

Physiographic types.--The physiographic type MR model to predict elf owl abundance was moderately strong ( $R^2_{adj} = 0.332$ , SE = 0.133), whereas the model to predict screech-owl abundance was weak ( $R^2_{adj} = 0.155$ , SE = 0.120). After accounting for other variables in the models, cover of washes, bajadas, and uplands each explained a significant amount of variation in elf owl abundance (Table 11), whereas cover of washes and uplands each explained significant variation in screech-owl abundance (Table 11).

Microhabitat variables.--The microhabitat MR model to predict elf owl abundance was moderately strong ( $R^2_{adj} = 0.671$ , SE = 0.244). Controlling for other variables in the model, cover of understory and overstory perennial vegetation, cover of overstory mesquite, and density of mature saguaros each explained a significant amount of variation in elf owl abundance (Table 11).

The microhabitat MR model to predict screech owl abundance was also moderately strong ( $R^2 = 0.525$ , SE = 0.231). In light of other variables in the model, cover of understory perennial vegetation and cover of overstory mesquite each explained a significant amount of variation in screech-owl abundance (Table 11).

### **Physiographic Interspersion**

A combination of bajadas, uplands, and washes was present at stations of high elf owl abundance significantly more frequently than at stations of low abundance (Figure 7). For screech-owls, used stations had a combination of flats, uplands, and washes, or bajadas, uplands, and washes more frequently than did unused stations (Figure 7). Stations where only 1 or 2 physiographic types were present were rarely used by either elf owls or screech-owls.

### **Relation between density and reproductive success**

The percentage of successful nests per station did not differ based on territory density in 1995 ( $X^2 = 0.01$ , 2 df,  $P = 0.997$ ) or in 1996 ( $X^2 = 0.11$ , 2 df,  $P = 0.944$ ). Overall (1995 and 1996 combined), I found nests on 68 of the 75 (90.7%) territories that I identified.

Van Horne (1983) suggested that from a management perspective, it is preferable to define habitat quality as a product of density and reproductive success. Because elf owl reproductive success (by my definition) was near 100% regardless of territory density, an increasing number of nests (or territories) per station is probably indicative of increasing habitat quality. Thus, it is meaningful to determine the association between the indices of elf owl abundance from surveys and the number of nests per station;

if indices of abundance from surveys are highly predictive of the number of nests, then surveys may be a reasonable means of assessing habitat quality. Because I included all vocalizing owls (including females, non-territorial males, etc.) in calculating the indices of abundance, abundance may not be as closely related to reproductive success as was the number of territories.

I determined how predictive the indices of elf owl abundance were of the number of elf owl nests per station using linear regression. I tested the linearity of the model using a runs test (Zar 1996:435). Regression models were strong for both 1995 and 1996 ( $R^2 = 0.75$ ,  $R^2 = 0.77$ , respectively [Figure 8]).

## DISCUSSION

### Owl Abundance

This study is the first to quantitatively assess the abundance of elf owls and screech-owls over time. Whereas elf owl abundance was stable among years, screech-owl abundance declined markedly. These disparate patterns may be due to differences in seasonal movements and/or diet between the species. Whereas elf owls are migratory and prey almost exclusively on invertebrates (Bent 1938, Ligon 1968), screech-owls are year-round residents, with the majority of their diet (by mass) consisting of vertebrates (Craighead and Craighead 1956, Brown et al. 1986, Johnsgard 1988). Local populations of resident great-horned owls (Table 9), red-tailed hawks (Buteo jamaicensis), and Harris' hawks (Parabuteo unicinctus) also declined during the study (Hardy et al. 1996).

Population cycles are characteristic of many raptor species reliant upon vertebrate prey (e.g., Craighead and Craighead 1956, Marks et al. 1994), including eastern screech-owls (Gehlbach 1994). Such cycles are often related to abundance of prey. My study was conducted during a prolonged drought in the Sonoran Desert (National Climatic Data Center 1994-1996); however, precipitation was above average in the elf owl's winter range (Bob Davidson, National Weather Service, pers. commun.). As drought often

causes population declines in desert mammals and reptiles (e.g., Polis 1991, Vitt 1991), my data may reflect a declining phase in cyclic screech-owl abundance. I emphasize, however, that my study was only conducted over a 3-year period. Continued monitoring that is coupled with studies of prey populations and weather data is the only way to properly address the above issues.

Indices of elf owl abundance from my study are very similar to those reported by Millsap (1988) for the Arizona Upland subdivision of the Sonoran Desert (mean no. individuals/survey station = 0.70), but considerably less than Millsap (1988) reported for sycamore (Platanus spp.) and cottonwood-willow mesic riparian associations. Other than Millsap's (1988) estimates, studies of elf owl abundance are anecdotal in nature and/or poorly standardized (e.g., Bendire 1892, Bent 1938, Johnson et al. 1979, Johnson et al. 1981). Breeding densities of 0.05 pairs/ha, 0.24 nests/ha, and 0.20 nests/ha can be derived from the literature (Walker 1974, Goad and Mannan 1987, Bibles 1992, respectively). The nest densities from my nest searches (approximately 0.03 nests/ha) are consistent only with the first figure. Goad and Mannan (1987) and Bibles (1992) conducted their studies on Saguaro National Monument where higher nest densities may reflect the higher densities of mature saguaros at that site relative to BMGR (Steenbergh

and Lowe 1983, Goad and Mannan 1987).

The majority of information on screech-owl abundance has been obtained from southeastern Arizona or along the Gila, Salt, and Verde rivers (Johnson et al. 1981). Here, pairs in mesquite bosques and cottonwood-mesquite riparian woodlands have been reported as close as 50 m apart. Anecdotal studies from the Arizona Upland subdivision of the Sonoran Desert reported territorial pairs to be 180-360 m apart, 300 m apart, and 275 m apart (Miller and Miller 1951, Phillips et al. 1964, Johnson et al. 1981, respectively). Assuming symmetric circles around territories, these figures suggest densities ranging from 0.01 pairs/ha to 0.035 pairs/ha. Using the aural envelope to estimate density from my study, screech-owl density ranged from 0.04 pairs/ha in 1994 to 0.005 pairs/ha in 1996. Future surveys of elf owls and screech-owls should strive for standardization, quantify observer effort, and estimate the aural envelope if meaningful comparisons among studies and years are to be made.

The abundance of both elf owls and screech-owls was consistently greater in the Sand Tank study site. In addition, I found more nests of each species in the Sand Tank site (see Chapter 1). The Saucedo and Sand Tank sites differed in general vegetation type, with more of the mixed-cacti vegetation type and less of the creosote vegetation

type in the Sand Tank site. The differences in the cover of many plant species and substrate were generally consistent with this difference in vegetation types. For example, the higher densities of saguaros and saguaro cavities, and greater cover of triangle-leaf bursage, paloverde, ocotillo, and rocky ground in the Sand Tank site would be expected in an area with more cover of mixed-cacti vegetation. The basic differences in cover types between mountain ranges (and associated higher density of potential nest sites) may explain the higher breeding abundances of elf owls and screech-owls in the Sand Tank site.

#### **Habitat Associations**

Vegetation types and physiographic types.--Increasing abundance of elf owls was associated with increasing cover of both the xeroriparian and mixed-cacti vegetation types, whereas increasing abundance of screech-owls was only associated with increasing cover of the xeroriparian type. This finding may be due to the fact that screech-owls were often detected from washes far removed (>1.5 km) from the mixed-cacti vegetation type, whereas elf owls were only detected from areas with a combination of mixed-cacti and washes. Indeed, elf owls seem to nest only in woodpecker cavities in saguaros on BMGR and, consequently, were only found nesting in the mixed-cacti vegetation type. In contrast, screech-owls seem to nest in any substrate large

enough to house a nest cavity, including saguaros and trees (2 screech-owl nests located in trees >400 m from the nearest saguaro). The lower  $R^2$  values for screech-owls for both the vegetation type and physiographic type MR models are likely reflective of this species' more general nesting requirements.

The fact that I did not detect elf owls in areas devoid of saguaros suggests that they do not use microphyllous trees for nesting on BMGR. To my knowledge, other than in mesic riparian areas, elf owls have only been documented to nest in saguaros in the Sonoran Desert, possibly due to thermoregulatory constraints (Ligon 1968, Goad and Mannan 1987, Millsap 1988).

Microhabitat.--Microhabitat MR models included similar variables for each species. Results suggest that cover of understory perennial vegetation and cover of overstory mesquite are important to elf owls and screech-owls in the region. Given this finding, it is not surprising that the abundance of both species was also associated with increasing xeroriparian cover. Availability of singing perches and roost sites, favorable thermal cover, protection from predators, and increased prey availability may be factors which influence these species to inhabit areas with high cover of perennial vegetation and mesquite (Vander Wall

and MacMahon 1984). Increased availability of nest sites may also be a factor for the screech-owl (Johnson et al. 1981, Chapter 1).

Although screech-owls are known to be closely associated with mesquite in the desert regions of Arizona (Phillips et al. 1964, Johnson et al. 1981), this association is not well-established for elf owls. Although elf owl abundance was positively associated with cover of overstory mesquite at the spatial scale of this investigation (scale determined by the aural envelope), elf owl nest sites were characterized by significantly lower cover of mesquite than paired, random sites (Chapter 1). This illustrates how the conclusions drawn about habitat selection are dependent upon the spatial scale of the investigation (e.g., Wiens 1985). The finding that nest sites have lower than expected cover of mesquite may be because mature saguaros outcompete mesquite for water, resulting in mesquite mortality in the immediate area (within 25 m) of the nest (Steenbergh and Lowe 1977, 1983). Mesquite may be important to elf owls and screech-owls at the broader scale of this study because of abundance of arthropods associated with this tree species. Mesquite bosques in the southwestern deserts produce an abundance of arthropods, and are used heavily by insectivorous breeding birds (Ohmart and Anderson 1982, Rosenberg et al. 1991). On

a per-tree basis, mesquite provides one of the richest pollen and nectar sources in the Sonoran Desert (Ohmart and Anderson 1982). Simpson et al. (1977) reported that mesquite produces more pollen per floral unit than any other insect-pollinated desert tree in North America. In addition, mesquites often contained natural cavities sufficiently large to provide nest sites for screech-owls (see Chapter 1; unpubl. data).

The density of the most structurally-complex category of saguaros (>5 m tall with >2 branches) was important in predicting elf owl abundance. In studies of nest site selection, Goad and Mannan (1987) and I (Chapter 1) used the same classification system for saguaros and found that elf owls nested in saguaros >5 m tall with >2 branches more frequently than expected. In addition, both studies found that the density of mature saguaros was greater around nest sites than around random points. Thus, even at the broader scale at which this study was conducted, the density of mature saguaros seems to be important. The close association between elf owl abundance and the number of nests per station highlights the importance of the density of mature saguaros.

The similarities in habitat associations between elf owls and screech-owls are highlighted by the significant positive correlation between these species' abundances.

This association is not necessarily expected since these owls are potential competitors and elf owls may be preyed upon by the larger screech-owls (Johnsgard 1988, Gehlbach 1994). However, these similarities help facilitate management because protecting and enhancing elf owl habitat will likely benefit screech-owls as well.

### **Reproductive Success**

Regardless of year, I found that the number of elf owl nests from the nestling period did not differ based on territory density. Similarly, Goad (1985) found that 19 of 20 elf owl territories (determined by spot-mapping) produced nestlings. Thus, if the reproductive success of elf owls (defined here as the percentage of territories producing  $\geq 1$  nestling) changes with increasing territory density, territory densities did not reach high enough levels to produce an effect in my study or Goad's (1985) study.

My findings suggest that an increasing number of elf owl nests per unit area is indicative of habitat quality. Thus, because abundance estimates from my surveys were highly predictive of the number of nests per station, surveys may be a reasonable means of indexing of habitat quality for elf owls in some areas of the Sonoran Desert. The fact that vocalizing females and non-singing males were also used in calculating the indices of elf owl abundance could explain why the association between abundance and

number of nests was not even closer. I recalculated the indices of elf owl abundance using only detections of singing males and found that the amount of variation in the number of nests explained by the indices of abundance increased considerably ( $R^2 > 0.85$ ). Thus if managers are to use indices of elf owl abundance to assess habitat quality, they should consider using only the number of singing males in calculating the index.

Table 1. Features of the surrounding vegetation and substrate, saguaros, and cavities measured at nest sites of elf owls and western screech-owls, Barry M. Goldwater Air Force Range, Arizona, 1995-1996.

Observational Unit	Feature Measured
Surrounding vegetation and substrate <sup>a</sup>	--% cover <sup>b</sup> of plant species
	--% cover of substrate <sup>c</sup>
	--% cover of perennial vegetation <sup>d</sup>
	--Density of mature tree species <sup>e</sup>
	--Density of saguaros <sup>f</sup>
	--Distance (m) from nest to nearest wash
	--% slope (at nest)
	--Slope aspect (at nest; degrees from true north)
Nest Saguaros	--Structure category <sup>f</sup>
	--Number of potentially-available <sup>g</sup> cavities (per woodpecker sp.)
	--Saguaro height (m; ground to highest point)
	--Diameter at breast height (cm;

Table 1 continued.

Observational Unit	Feature Measured
Nest Cavities	<p>measured at 1.5 m above ground)</p> <p>--Height (m; ground to lower lip)</p> <p>--Diameter<sup>b</sup> (whether excavated by gila woodpecker or gilded flicker)</p> <p>--Orientation of opening (degrees from true north)</p> <p>--Location (branch or main stem)</p>

<sup>a</sup>Vegetation features measured within 25-m-radius plot centered on nest; plot size based on previously-recorded territory sizes of elf and western screech-owls.

<sup>b</sup>% cover calculated by height class: 1)  $\leq 5$  cm = ground level; 2)  $>5$  cm - 1 m = understory; 3)  $>1$  m - 2.5 m = mid-canopy; 4)  $>2.5$  m = overstory.

<sup>c</sup>Substrate categorized by particle diameter: 1)  $\leq 1$  mm = soils; 2)  $>1$  mm - 15 cm = gravel; 3)  $>15$  cm - 1 m = cobble; 4)  $>1$  m = rock.

<sup>d</sup>% cover of all woody species combined.

<sup>e</sup>Number of trees  $>2.5$  m tall with stem diameter  $>15$ cm within 25-m-radius of nest.

Table 1 continued.

<sup>f</sup>Saguaros categorized as: 1) <3 m tall, 0 branches; 2)  $\geq 3$  m tall, 0 branches or  $\geq 1$  branch <6 cm long; 3) >4 m tall,  $\geq 1$  branch 6 cm - 1 m long; 4) >5 m tall, 1-2 branches >1 m long; 5) >5 m tall,  $\geq 2$  branches >1 m long; 6) >2 m tall with broken-top.

<sup>g</sup>To be considered potentially-available to elf owls, cavities had to be  $\geq 3.4$  m high and unoccupied, or occupied by purple martin, brown-crested flycatcher, or Lucy's warbler; for western screech-owls, cavities had to be  $\geq 3.2$  m high and not occupied by a woodpecker species.

<sup>h</sup>Vertical and horizontal diameters of cavities used to determine excavating woodpecker species (Kerpez and Smith 1990a); gila woodpecker: mean vertical diameter = 4.7 cm, mean horizontal diameter = 5.1 cm; gilded flicker: mean vertical diameter = 6.3 cm, mean horizontal diameter = 7.9 cm.

Table 2. Features of surrounding vegetation, saguaros, and cavities at elf owl nest sites ( $n = 68$ ) and at unused but potential nest sites, Barry M. Goldwater Air Force Range, Arizona, 1995-1996.

Category Variable	<u>Used</u>		<u>Potential</u>		<u>P<sup>a</sup></u>
	<u>X</u>	SE	<u>X</u>	SE	
Surrounding Vegetation <sup>b</sup>					
Cavity Density <sup>c</sup>	28.42	1.04	11.45	0.69	<0.001
Class 5 <sup>d</sup> Saguaro					
Density	0.82	0.15	0.34	0.11	0.006
Class 4 <sup>d</sup> Saguaro					
Density	0.99	0.19	0.37	0.21	0.013
Ironwood Density	3.87	0.62	2.24	0.36	0.004
% Cover Overstory <sup>e</sup>					
Mesquite	0.11	0.07	0.44	0.17	0.075
% Cover Understory <sup>f</sup>					
Ocotillo	0.30	0.04	0.07	0.05	0.045
% Cover Understory					
Wolfberry	1.43	0.25	0.86	0.23	0.056
% Cover Understory					
Perennial Vegetation	37.37	1.89	35.22	1.82	0.414
% Cover Mid-Canopy <sup>g</sup>					

Table 2 continued.

Category Variable	<u>Used</u>		<u>Potential</u>		<u>P</u> <sup>a</sup>
	<u>X</u>	SE	<u>X</u>	SE	
Surrounding Vegetation					
Perennial Vegetation	11.44	0.92	12.43	1.09	0.471
% Cover Overstory					
Perennial Vegetation	2.91	0.41	3.38	0.47	0.447
Saguaro					
Total Cavities	7.21	0.56	2.22	0.18	<0.001
Saguaro Height (m)	8.57	0.20	7.80	0.21	0.018
Saguaro DBH (cm)	48.76	0.72	48.32	0.65	0.649
Cavity					
Cavity Height (m)	6.14	0.16	5.63	0.19	0.041

<sup>a</sup>Significance of paired t-test.

<sup>b</sup>Features of surrounding vegetation measured within 25-m-radius plot centered on nest saguaro.

<sup>c</sup>Density refers to number of structures (e.g., cavities, trees) within 25-m-radius plot.

<sup>d</sup>Class 5 saguaros = >5 m tall with at least 3 branches >1 m

Table 2 continued.

long; class 4 saguaros = >5 m tall with 1-2 branches >1 m long.

<sup>c</sup>Overstory = >2.5 m tall.

<sup>f</sup>Understory = >0 m - 1 m tall.

<sup>g</sup>Mid-canopy = >1 m - 2.5 m tall.

Table 3. Case-control logistic regression models for nest site selection by elf owls and western screech-owls, Barry M. Goldwater Air Force Range, Arizona, 1995-1996. Categories for response: 1 = used nest site; 0 = unused but potential nest site.

Species	Variable	$\beta$	SE	Wald $X^2$	$P$	Odds Ratio
Elf Owl	Density of Mature Saguaros <sup>a</sup>	0.793	0.395	4.023	0.041	2.210
	Total Cavities <sup>b</sup>	1.486	0.554	7.210	0.007	4.421
Western						
Screech-Owl	Cavity Diameter <sup>c</sup>	3.849	1.807	4.025	0.043	46.923
	Saguaro DBH <sup>d</sup>	0.604	0.302	3.849	0.049	1.829
	Density of Mature Ironwood <sup>e</sup>	-1.252	0.703	3.171	0.075	0.286

<sup>a</sup>Number of saguaros >5 m tall with 1-2 branches (>1 m long) within 25-m-radius of nest saguaro.

<sup>b</sup>Total number of potentially-available cavities in nest saguaro. To be considered potentially-available to elf owls, cavities had to be  $\geq 3.4$  m high and unoccupied, or occupied by purple martin, brown-crested flycatcher, or Lucy's warbler.

Table 3 continued.

<sup>c</sup>Whether nest cavity excavated by gilded flicker ( $x = 1$ ) or gila woodpecker ( $x = 0$ ).

<sup>d</sup>Diameter of nest saguaro (cm) measured 1.5 m above ground.

<sup>e</sup>Number of ironwood trees  $>2.5$  m tall with stem diameter  $>15$  cm within 25-m-radius of nest saguaro.

Table 4. Features of surrounding vegetation, saguaros, and cavities at western screech-owl nest sites ( $n = 10$ ) and at unused but potential nest sites, Barry M. Goldwater Air Force Range, Arizona, 1995-1996.

Category Variable	<u>Used</u>		<u>Potential</u>		<u>P<sup>a</sup></u>
	<u>X</u>	SE	<u>X</u>	SE	
Surrounding Vegetation <sup>b</sup>					
Class 5 <sup>c</sup> Saguaro					
Density	0.25	0.14	0.75	0.23	0.082
Class 4 <sup>c</sup> Saguaro					
Density	0.63	0.21	1.25	0.26	0.081
Ironwood Density <sup>d</sup>	0.75	0.54	3.00	0.69	0.019
% Cover Understory <sup>e</sup>					
Perennial Vegetation	31.21	6.33	38.75	7.27	0.444
% Cover Mid-Canopy <sup>f</sup>					
Perennial Vegetation	9.80	2.77	12.65	3.44	0.527
% Cover Overstory <sup>g</sup>					
Perennial Vegetation	1.41	0.76	4.21	1.30	0.079
Saguaro					
Total Cavities	5.11	1.26	3.71	1.46	0.474
Saguaro Height (m)	8.14	0.64	7.95	0.66	0.840

Table 4 continued.

Category Variable	<u>Used</u>		<u>Potential</u>		<u>p</u> <sup>a</sup>
	<u>X</u>	SE	<u>X</u>	SE	
Saguaro DBH (cm)	52.63	1.41	46.38	2.12	0.024
Cavity					
Cavity Height (m)	6.15	0.55	5.79	0.41	0.609

<sup>a</sup>Significance of paired t-test.

<sup>b</sup>Features of surrounding vegetation measured within 25-m-radius plot centered on nest saguaro.

<sup>c</sup>Class 5 saguaros = >5 m tall with at least 3 branches >1 m long; class 4 saguaros = >5 m tall with 1-2 branches >1 m long.

<sup>d</sup>Density refers to number of structures (e.g., cavities, trees) within 25-m-radius plot.

<sup>e</sup>Understory = >0 m - 1 m tall.

<sup>f</sup>Mid-canopy = >1 m - 2.5 m tall.

<sup>g</sup>Overstory = >2.5 m tall.

Table 5. Features of western screech-owl nests located in mesquite trees, Barry M. Goldwater Air Force Range, Arizona 1996. Both nests located in large, xeroriparian washes.

Nest	Tree Height(m)	Tree DBH(cm)	Cavity Height(m)	Cavity Diameter <sup>a</sup> (cm)	Cavity Depth(cm)	Cavity Orientation	Perennial Cover <sup>b</sup>
1	6.5	38.0	2.1	18.2 vert. 14.1 horz.	49.0	208°	59.3%
2	7.8	43.3	2.8	19.8 vert. 17.5 horz.	46.3	229°	64.3%

<sup>a</sup>Vert. = vertical diameter of nest cavity; horz. = horizontal diameter of nest cavity.

<sup>b</sup>Percent cover of perennial vegetation measured within 25-m-radius of nest tree.

Table 6. Logistic regression model to predict whether nests sites were those of elf owls ( $y = 1$ ) or western screech-owls ( $y = 0$ ), Barry M. Goldwater Air Force Range, Arizona, 1995-1996.

Variable*	$\beta$	SE	Wald $X^2$	$P$	Odds Ratio
Density Mature					
Saguaros	0.789	0.392	4.021	0.045	2.201
Cavity Diameter	4.377	1.798	5.024	0.025	79.599
Constant	-3.214	1.320	5.002	0.029	

\*Density mature saguaros = number of saguaros >5 m tall with 1-2 branches >1 m long within 25-m-radius of nest saguaro; cavity diameter = whether nest cavity excavated by gila woodpecker ( $x = 1$ ) or gilded flicker ( $x = 0$ ).

Table 7. Case-control logistic regression models for nest cavity selection within the nest saguaro by elf owls and western screech-owls, Barry M. Goldwater Air Force Range, Arizona, 1995-1996. Categories for response: 1 = used nest cavity; 0 = unused but potential<sup>a</sup> nest cavity.

Species	Variable <sup>b</sup>	$\beta$	SE	Wald $X^2$	P	Odds Ratio
Elf Owl	Cavity Location	1.047	0.531	3.892	0.049	2.848
	Cavity Height	0.781	0.371	4.325	0.038	2.184
	Cavity Orientation	0.614	0.302	3.854	0.047	1.847
Western						
Screech-Owl	Cavity Diameter	2.607	1.303	4.942	0.048	13.562

<sup>a</sup>To be considered potentially-available to elf owls, cavities had to be  $\geq 3.4$  m high and unoccupied, or occupied by purple martin, brown-crested flycatcher, or Lucy's warbler; for western screech-owls, cavities had to be  $\geq 3.2$  m high and not occupied by a woodpecker species.

Table 7 continued.

<sup>b</sup>Cavity location = whether cavity located in main stem ( $x = 1$ ) or branch ( $x = 0$ ) of saguaro; cavity height = distance (m) from ground to bottom lip of cavity; cavity orientation = whether cavity oriented to the north ( $x = 1$ ; north =  $337.5^\circ - 22.5^\circ$ ) or not ( $x = 0$ ).

Table 8. Percent cover of vegetation and substrate in the Saucedo and Sand Tank study sites, Barry M. Goldwater Air Force Range, Arizona.

Variable	<u>Saucedo Site</u>		<u>Sand Tank Site</u>		P <sup>a</sup>
	<u>X</u>	SD	<u>X</u>	SD	
Soils <sup>b</sup>	17.6	12.0	6.4	3.8	<0.001
Rocky ground <sup>c</sup>	46.9	11.7	66.1	8.5	<0.001
Organic Litter <sup>d</sup>	13.8	4.8	13.1	5.4	0.598
Woody Debris <sup>e</sup>	2.4	1.5	3.5	1.3	0.004
Herbaceous spp.	26.0	13.7	15.8	10.8	0.002
Triangle-leaf					
Bursage	2.1	2.5	16.5	4.5	<0.001
Creosotebush	10.2	3.0	9.2	3.6	0.247
Ocotillo	0.1	0.4	0.4	0.4	0.005
Whitethorn Acacia	0.5	0.5	0.1	0.2	<0.001
Other shrub spp.	3.2	3.5	3.1	3.7	0.915
Catclaw Acacia	2.8	4.0	1.5	1.4	0.102
Desert Willow	1.1	2.5	0.0	0.0	<0.001
Ironwood	1.8	3.1	3.8	2.6	0.009
Mesquite	3.4	4.9	1.3	3.4	0.059
Paloverde spp.	3.4	3.6	7.2	3.8	<0.001
Other tree spp.	0.9	1.1	0.9	1.2	0.989

Table 8 continued.

Variable	<u>Sauceda Site</u>		<u>Sand Tank Site</u>		<u>P</u> <sup>a</sup>
	<u>X</u>	SD	<u>X</u>	SD	
Saguaro class <sup>f</sup> 1	0.23	0.28	0.44	0.37	<0.001
Saguaro class 2	0.09	0.12	0.21	0.15	<0.001
Saguaro class 3	0.06	0.07	0.19	0.18	<0.001
Saguaro class 4	0.04	0.06	0.15	0.10	<0.001
Saguaro class 5	0.02	0.04	0.08	0.07	<0.001
Saguaro class 6	0.01	0.02	0.02	0.02	0.885
Other cacti spp.	0.12	0.17	0.14	0.15	0.631
Saguaro Cavities <sup>g</sup>	2.5	5.1	4.9	4.9	0.068
Perennial Veg. <sup>h</sup>	30.8	16.4	45.2	19.2	0.003
Xeroriparian VT <sup>i</sup>	27.0	22.8	16.5	12.4	0.032
Mixed-cacti VT	37.1	27.5	77.6	18.6	<0.001
Creosote VT	35.9	40.7	5.9	6.1	<0.001
Flat PT <sup>i</sup>	21.1	27.4	9.8	10.7	0.042
Bajada PT	34.1	24.2	38.7	32.5	0.537
Upland PT	17.8	15.6	35.0	33.9	0.016

<sup>a</sup>Significance of t-test (2-sided); Welch's approximate t used in cases of unequal variances.

<sup>h</sup>Non-organic matter  $\leq 1$  mm in diameter.

Table 8 continued.

<sup>c</sup>Non-organic matter >1 mm in diameter.

<sup>d</sup>Organic matter  $\leq$ 2 cm in diameter.

<sup>e</sup>Organic matter >2 cm in diameter

<sup>f</sup>Saguaro cacti categorized as: 1) <3 m tall with no branches; 2)  $\geq$ 3 m tall with branches <6 cm length or no branches; 3) >4 m tall with branches 6 cm to 1 m in length; 4) >5 m tall with 1-2 branches >1 m in length; 5) >5 m tall with 3 or more branches >1 m in length; or 6) >2 m tall with a broken-top.

<sup>g</sup>Number of woodpecker-excavated cavities/ha.

<sup>h</sup>Combined cover of all perennial plant species.

<sup>i</sup>VT = vegetation type: xeroriparian = any drainage with bank full width >1 m (Cole 1994) and its associated frequent flood plain area (Ohmart and Anderson 1982); mixed-cacti = dominated by yellow paloverde, saguaros, and various species of small shrubs and cacti; creosote = dominated by creosotebush and bursage.

<sup>j</sup>PT = physiographic type: wash = same as xeroriparian above; flat = any non-wash area with slope  $\leq$ 1%; bajada = any non-wash area with slope >1% and  $\leq$ 5%; upland = any non-wash area with slope >5%.

Table 9. Abundance (no. individuals detected visit<sup>-1</sup> survey station<sup>-1</sup>) of elf owls and western screech-owls and of their potential predators and competitors, Barry M. Goldwater Air Force Range, Arizona, 1994-1996.

Species	1994		1995*		1996*	
	$\bar{X}$	SE	$\bar{X}$	SE	$\bar{X}$	SE
Elf Owl	0.653A <sup>a</sup>	0.064	0.633A	0.062	0.712A	0.079
Western Screech-owl	0.633A	0.070	0.392B	0.055	0.206C	0.039
Great-horned owl	0.190A	0.031	0.133A	0.024	0.047B	0.017
Barn owl	0.047A	0.016	0.046A	0.022	0.029A	0.012
Common Poorwill	0.481A	0.061	0.444A	0.057	0.492A	0.060
Lesser nighthawk	--- <sup>b</sup>	---	0.043A	0.024	0.034A	0.021

\* = Years in which the abundances of elf owls and western screech-owls significantly differed ( $\alpha = 0.10$ ).

<sup>a</sup>For each species, means with different letters significantly differ (Tukey's Test,  $\alpha = 0.10$ ).

<sup>b</sup>No abundance data for lesser nighthawk in 1994.

Table 10. Correlations (Pearson  $r$ ) between the abundance<sup>a</sup> of elf owls and western screech-owls and the abundance of potential predators and competitors, Barry M. Goldwater Air Force Range, Arizona, 1994-1996.

Species <sup>b</sup>	Correlated With <sup>c</sup>	1994	1995	1996	1994-1996
ELOW	WESO	0.55**	0.33*	0.13	0.47**
	GHOW	0.24	0.12	0.05	0.05
	BAOW	-0.14	0.01	-0.15	0.09
	COPO	0.24*	0.23*	0.34*	0.33*
	LENI	---	-0.09	-0.11	-0.10
WESO	ELOW	0.55**	0.33*	0.13	0.47**
	GHOW	0.12	-0.03	-0.14	0.03
	BAOW	-0.01	-0.16	-0.18	-0.08
	COPO	-0.11	-0.09	-0.21*	-0.12
	LENI	---	-0.02	0.06	0.01

\* =  $p < 0.01$ ; \*\* =  $p < 0.001$ .

<sup>a</sup>Abundance = number of individuals detected  $\cdot$  visit<sup>-1</sup>  $\cdot$  survey station<sup>-1</sup> ( $n = 60$  survey stations).

<sup>b</sup>Species: ELOW = elf owl; WESO = western screech-owl.

<sup>c</sup>GHOW = great-horned owl; BAOW = barn owl; COPO = common poorwill; LENI = lesser nighthawk (no data for lesser nighthawk in 1994).

Table 11. Multiple linear regression models relating abundance of elf owls and western screech-owls (no. individuals detected  $\cdot$ visit $^{-1}$   $\cdot$ survey station $^{-1}$ ) to percent cover of vegetation and substrate, Barry M. Goldwater Air Force Range, Arizona, 1994-1996.

Model				
Species				
Variable	<u><math>\beta</math></u>	<u>SE</u>	<u>T</u>	<u>P</u>
Vegetation Type <sup>a</sup>				
Elf Owl				
Xeroriparian	0.0125	0.0025	4.947	<0.0001
Mixed-cacti	0.0043	0.0019	2.230	0.0298
Study site <sup>b</sup>	0.1243	0.1249	0.996	0.3237
Constant	-0.0464	0.0206	-2.176	0.0303
Western Screech-owl				
Xeroriparian	0.0064	0.0022	2.877	0.0057
Mixed-cacti	0.0042	0.0043	0.996	0.3238
Study site	-0.0010	0.0017	-0.583	0.5623
Constant	0.0517	0.2286	0.228	0.8205
Physiographic Type <sup>c</sup>				
Elf Owl				
Wash	0.0128	0.0026	4.824	<0.0001

Table 11 continued.

Model				
Species				
Variable	<u><math>\beta</math></u>	<u>SE</u>	<u>T</u>	<u>P</u>
Bajada	0.0036	0.0009	2.012	0.0421
Upland	0.0028	0.0009	2.446	0.0133
Study site	0.2801	0.0992	2.824	0.0066
Constant	-0.2337	0.4527	-0.503	0.6170
Western Screech-owl				
Wash	0.0083	0.0030	2.779	0.0074
Bajada	0.0129	0.0063	2.032	0.0469
Upland	0.0014	0.0013	1.762	0.1223
Study site	-0.0502	0.1401	0.342	0.7339
Constant	-0.0533	0.1823	0.291	0.7721
Microhabitat <sup>d</sup>				
Elf Owl				
PERVEG2	0.0129	0.0049	2.650	0.0105
PERVEG4	0.0193	0.0076	2.551	0.0138
DENSG5	0.0809	0.0318	2.545	0.0136
ME4	0.0086	0.0029	2.967	0.0044
Constant	0.0419	0.0235	-1.780	0.1200

Table 11 continued.

Model				
Species				
Variable	<u><math>\beta</math></u>	<u>SE</u>	<u>T</u>	<u>P</u>
Western Screech-owl				
PERVEG2	0.0436	0.0187	2.331	0.0234
ME4	0.0134	0.0018	7.494	<0.0001
Study site	0.2669	0.0670	3.984	0.0002
Constant	-0.0198	0.0115	-1.720	0.0910

<sup>a</sup>Percent cover of vegetation types: xeroriparian type = any drainage with bank full width >1 m (Cole 1994) and associated frequent flood plain (Ohmart and Anderson 1982); mixed-cacti type = areas dominated by yellow paloverde (Cercidium microphyllum), saguaros, and various species of small shrubs and cacti.

<sup>b</sup>Binary indicator variable for study site: 1 = Sand Tank site; 2 = Saucedá site.

<sup>c</sup>Percent cover of physiographic types: wash = any drainage with bank full width >1 m (Cole 1994) and associated frequent flood plain (Ohmart and Anderson 1982); bajada = any non-wash area with slope >1% and  $\leq$ 5%; upland = any non-

Table 11 continued.

wash area with slope >5%.

<sup>d</sup>Microhabitat variables: PERVEG2 = % cover of understory ( $\leq 1$  m tall) perennial vegetation; PERVEG4 = % cover of overstory (>2.5 m tall) perennial vegetation; ME4 = % cover of overstory mesquite; DENSG5 = density of saguaros >5 m tall with at least 3 branches >1 m long (# per 25-m-radius plot).

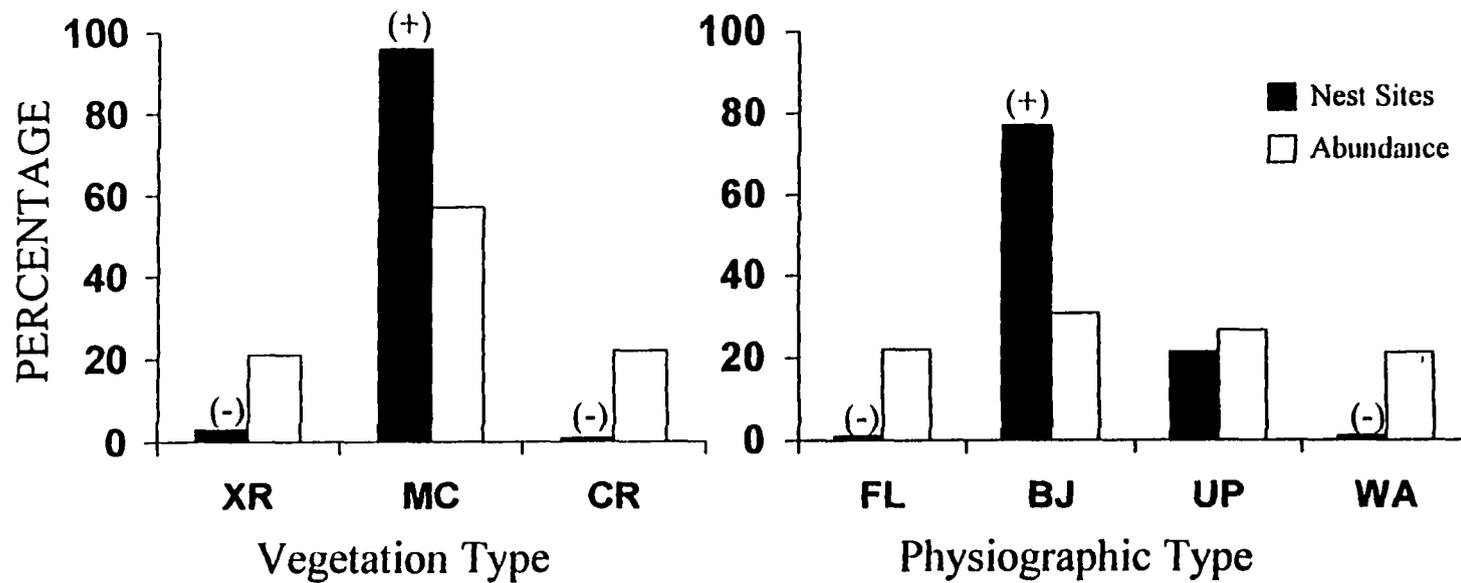


Figure 1. The abundance (% cover) of vegetation types and physiographic types in the study area and percentage of elf owl nests ( $n = 68$ ) found in each cover type, Barry M. Goldwater Air Force Range, Arizona, 1995-1996. Vegetation types: XR = xeroriparian, CR = creosote, MC = mixed-cacti. Physiographic types: FL = flat (slope  $\leq 1\%$ ); BJ = bajada ( $1\% > \text{slope} \leq 5\%$ ); UP = upland (slope  $> 5\%$ ), WA = wash (drainages with bank full width  $> 1$  m and associated frequent flood plain [Ohmart and Anderson 1982]). A (+) or (-) indicates cover types used more or less than expected based on their abundance in the study area (Bailey's simultaneous confidence intervals [Cherry 1996])

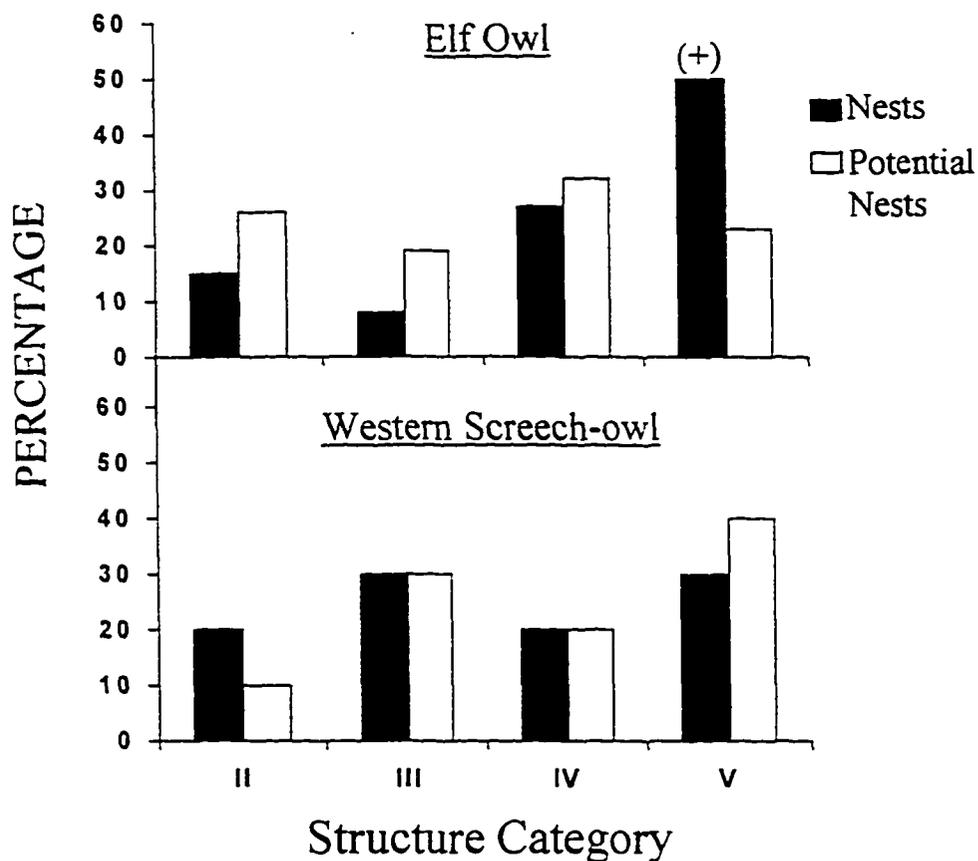


Figure 2. Structure categories of nest saguaros and unused but potential nest saguaros for elf owls ( $n = 68$ ) and western screech-owls ( $n = 10$ ), Barry M. Goldwater Air Force Range, Arizona, 1995-1996. Structure categories: II) >3 m tall with no branches or branches <6 cm in length; III) >4 m tall with branches 6 cm - 1 m in length; IV) >5 m tall with 1-2 branches >1 m in length; V) >5 m tall with >2 branches >1 m in length.  $G$ -test for homogeneity: elf owl ( $G = 11.95$ , 4 df,  $P = 0.017$ ); western screech-owl (no test performed due to insufficient sample size). A (+) indicates structure category used significantly ( $P < 0.10$ ) more than expected based on potential nest saguaro categories (Bailey's simultaneous confidence intervals [Cherry 1996]).

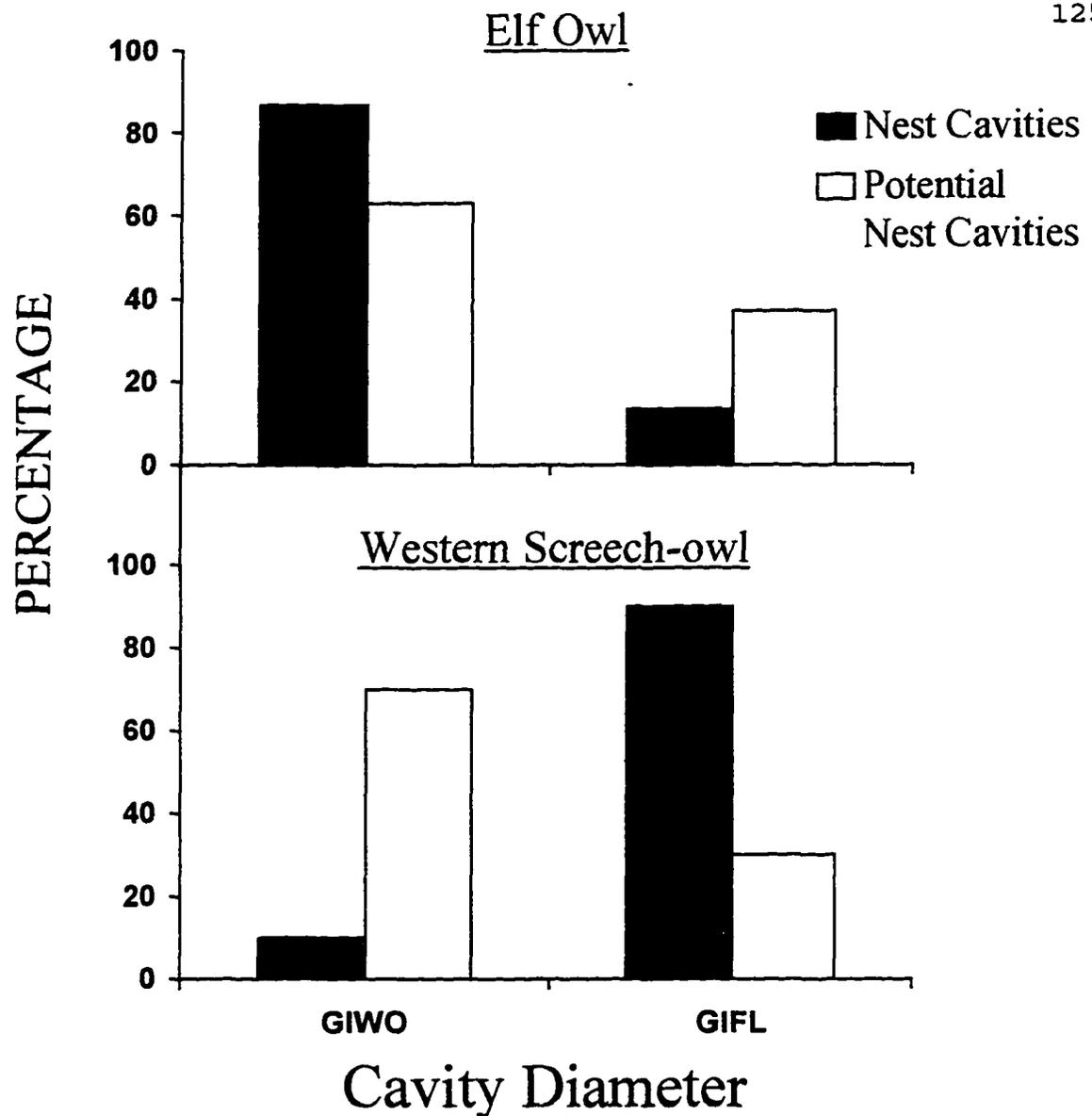
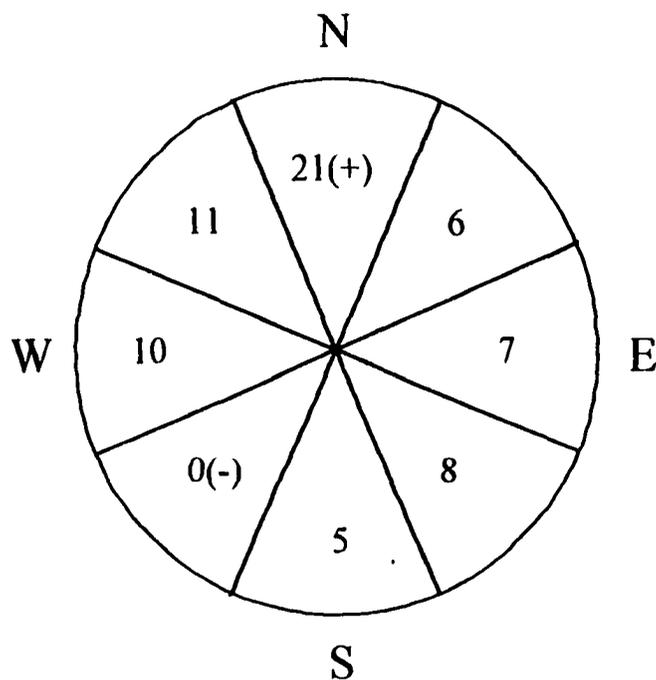


Figure 3. Diameter of nest cavities and unused but potential nest cavities for elf owls ( $G = 17.89$ ,  $n = 68$ , 1 df,  $P = 0.002$ ) and western screech-owls (Fisher's Exact Test,  $n = 10$ ,  $P = 0.015$ ), Barry M. Goldwater Air Force Range, Arizona, 1995-1996. Cavities categorized as having been excavated by gila woodpeckers (GIWO) or gilded flickers (GIFL).

## Nest Cavities



## Potential Cavities

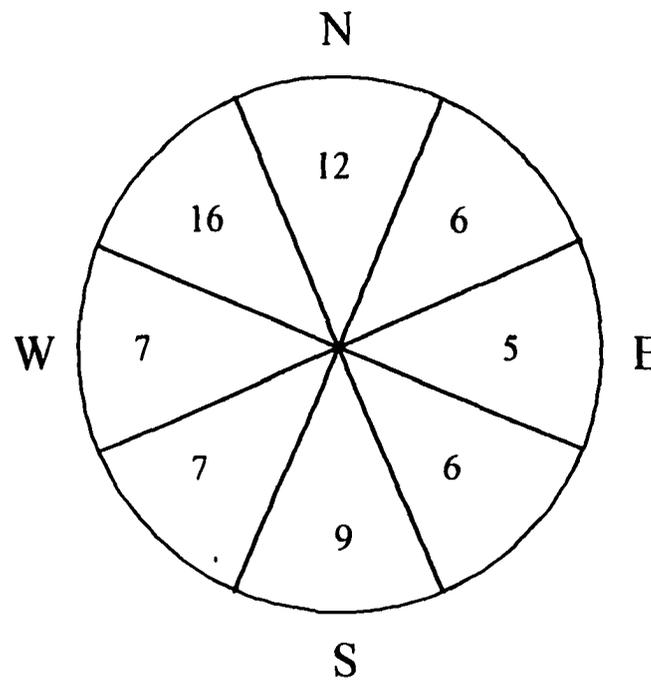


Figure 4. Orientations of elf owl nest cavities ( $n = 68$ ) and those of unused but potential nest cavities in the vicinity of the nest, Barry M. Goldwater Air Force Range, Arizona, 1995-1996. A (+) or (-) indicates orientation categories used significantly ( $P < 0.10$ ) more or less than expected based on availability (Bailey's simultaneous confidence intervals [Cherry 1996]).

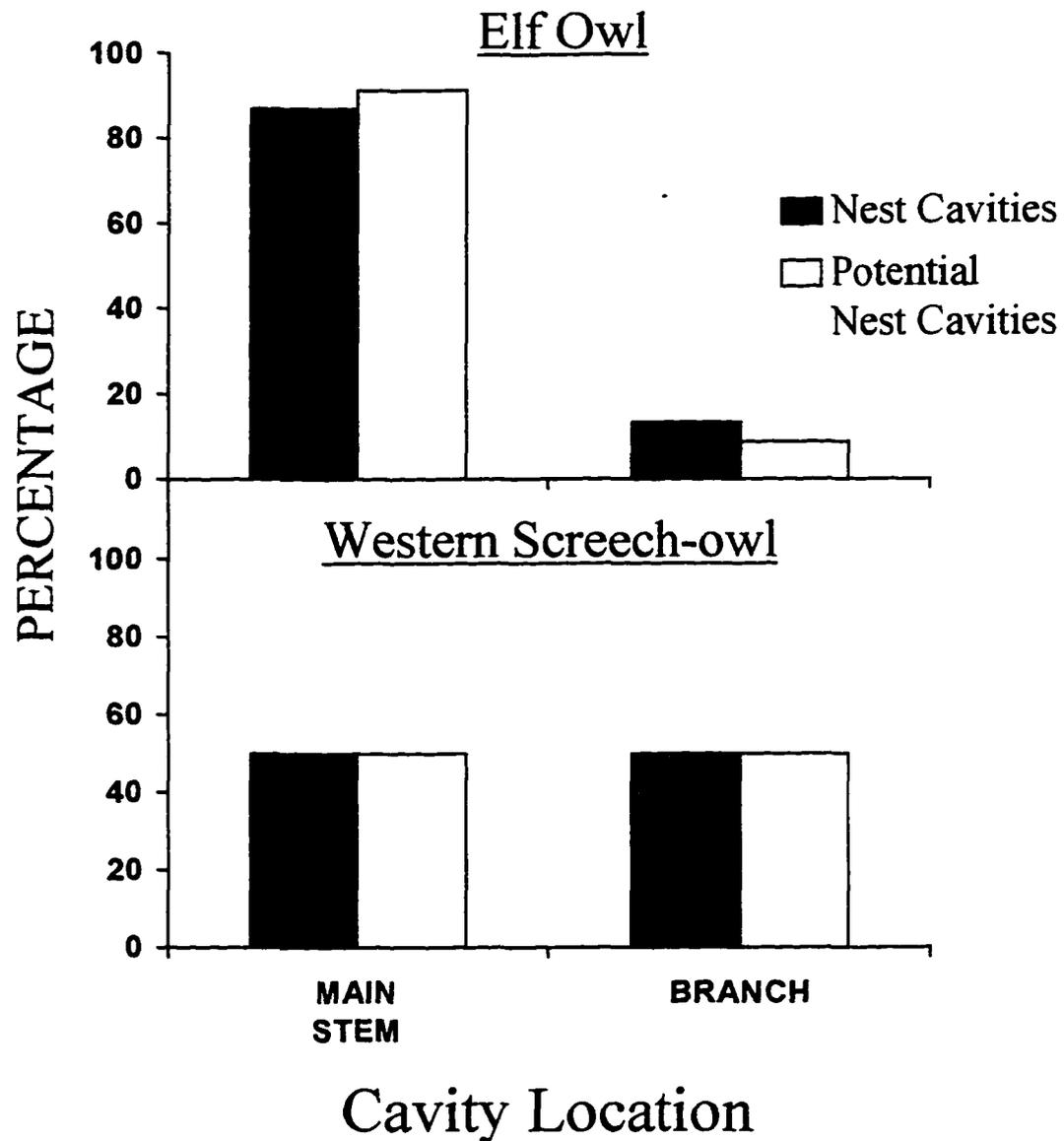


Figure 5. Location of nest cavities and unused but potential nest cavities for elf owls ( $G = 1.14$ ,  $n = 68$ , 1 df,  $P = 0.29$ ) and western screech-owls ( $n = 10$ ), Barry M. Goldwater Air Force Range, Arizona, 1995-1996. Cavities categorized as being in the main stem or in a branch of the saguaro.

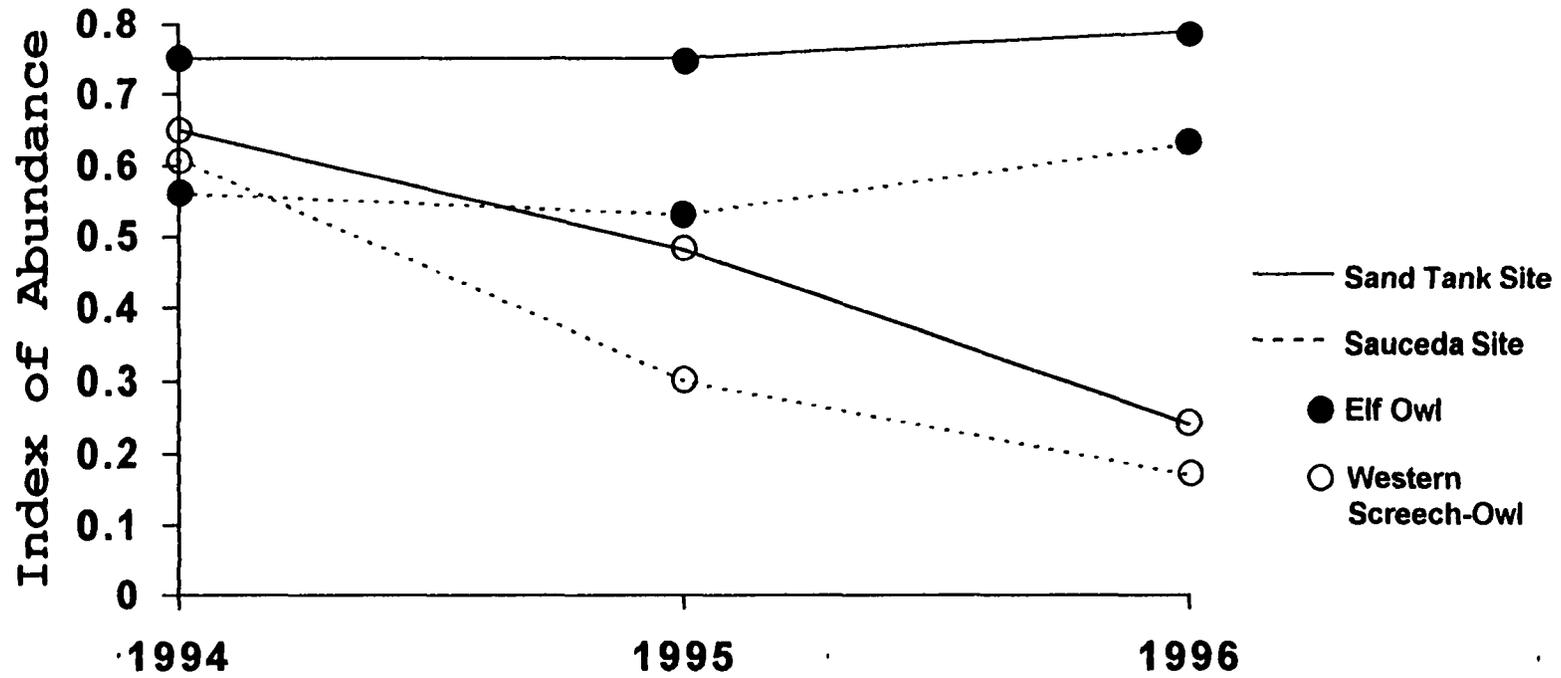


Figure 6. Indices of abundance (no. owls detected  $\cdot$  visit<sup>-1</sup>  $\cdot$  survey station<sup>-1</sup>) for elf owls and western screech-owls in the Sauceda and Sand Tank study sites, Barry M. Goldwater Air Force Range, Arizona, 1994-1996.

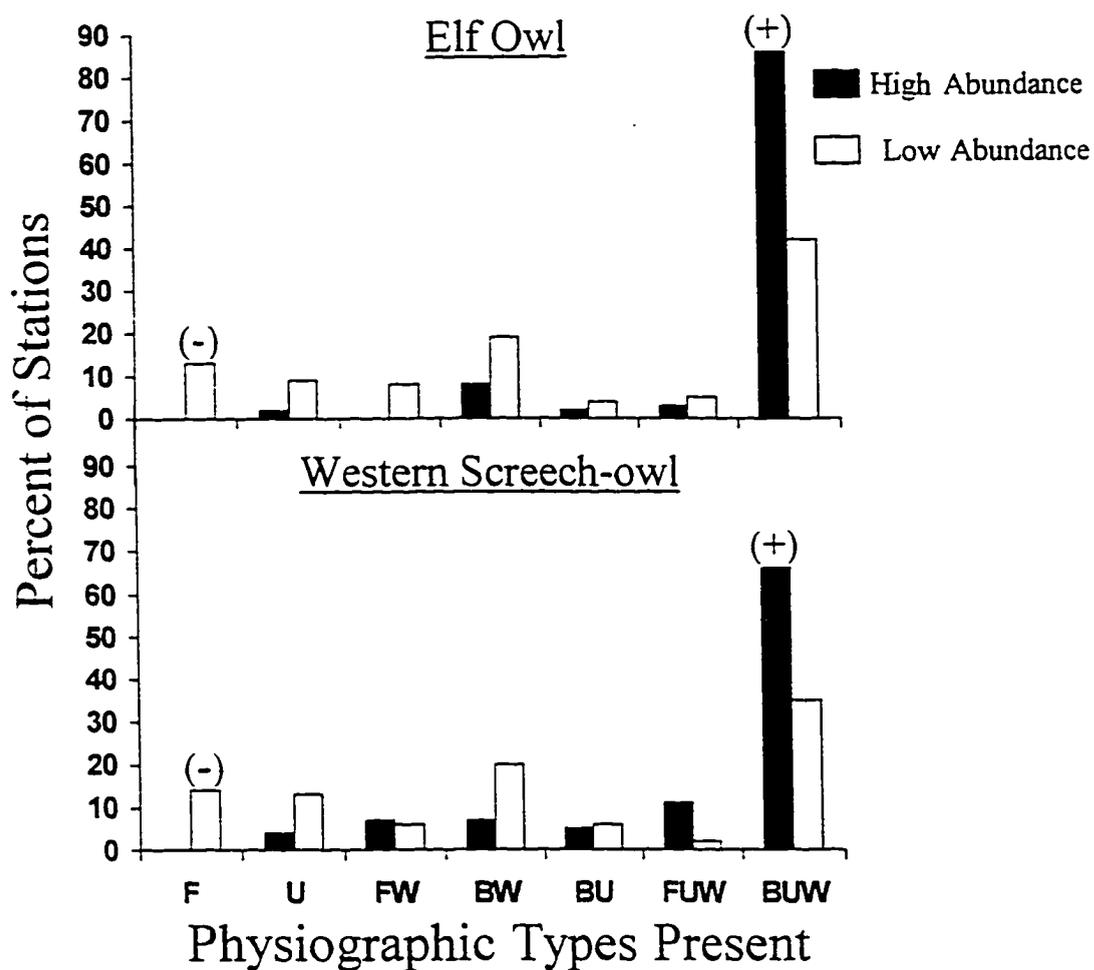


Figure 7. Physiographic types present at survey stations ( $n = 68$ ) of high versus low abundance of elf owls and western screech-owls, Barry M. Goldwater Air Force Range, 1994-1996. F = only flats (slope  $\leq 1\%$ ) present within 200-m radius of survey station; U = only uplands (slope  $> 5\%$ ) present; FW = both washes (drainage with bank full width  $> 5$  m) and flats present; BW = both bajadas ( $1\% < \text{slope} < 5\%$ ) and washes present; BU = both bajadas and uplands present; FUW = flats, uplands, and washes all present; BUW = bajadas, uplands, and washes all present. A (-) indicates category used less frequently than expected, a (+) indicates category used more frequently than expected (Bailey's simultaneous confidence intervals [Cherry 1996]).

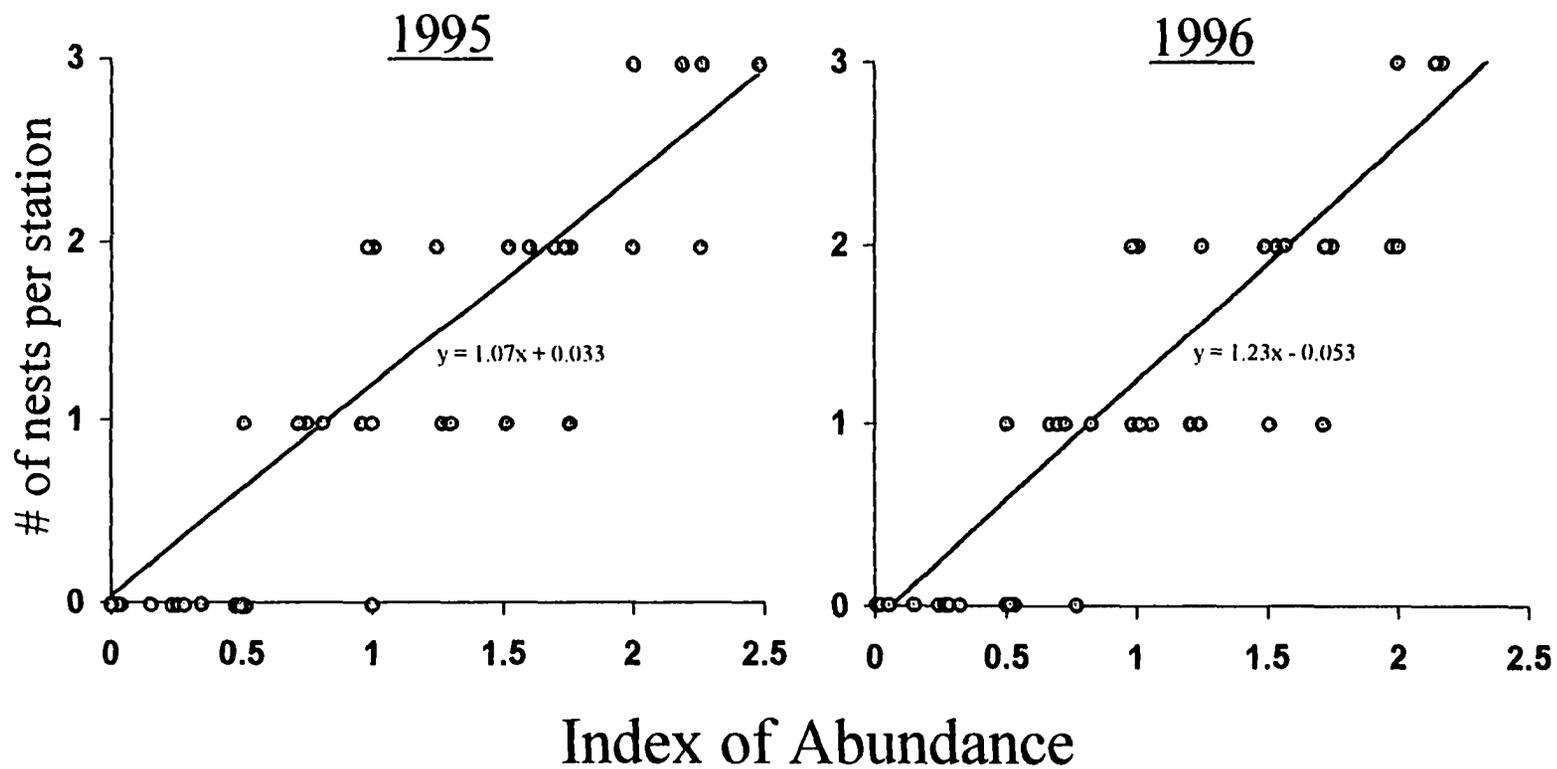


Figure 8. Linear relationship between elf owl abundance (no. individuals detected  $\cdot$  visit $^{-1}$   $\cdot$  survey station $^{-1}$ ) and number of elf owl nests per survey station, Barry M. Goldwater Air Force Range, 1995-1996.

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