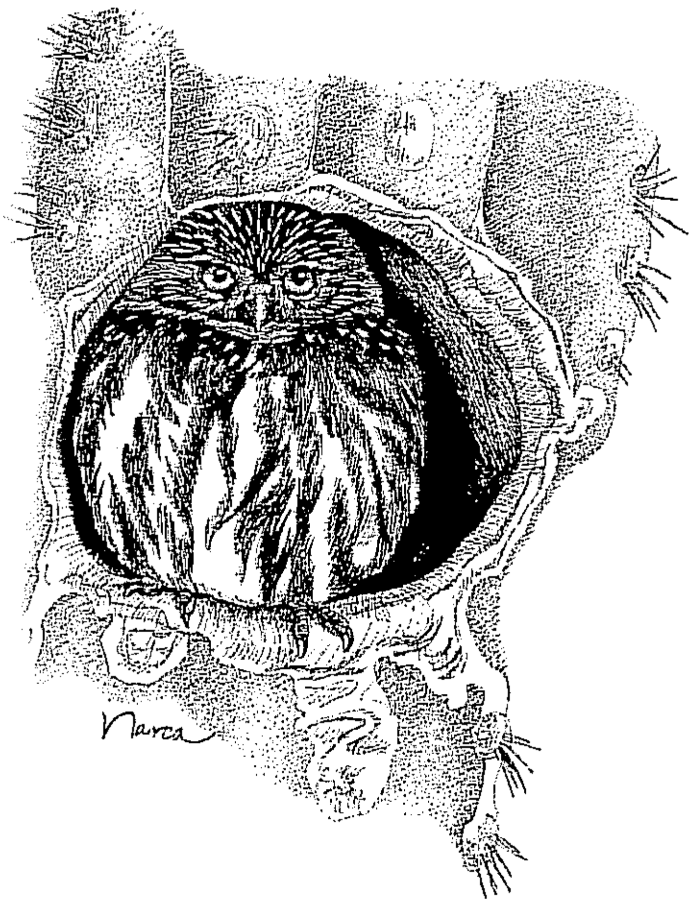
DISTRIBUTION, ABUNDANCE, AND HABITAT OF CACTUS FERRUGINOUS PYGMY-OWLS IN SONORA, MEXICO

by

AARON D. FLESCH



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DISTRIBUTION, ABUNDANCE, AND HABITAT OF CACTUS FERRUGINOUS PYGMY-OWLS IN SONORA, MEXICO

by

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STATEMENT BY AUTHOR

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ABSTRACT

Recovery of the federally endangered cactus ferruginous pygmy-owl (*Glaucidium brasilianum cactorum*) in Arizona may be facilitated by emigrants from neighboring Sonora, Mexico. In northern Sonora, however, pygmy-owls were thought to be rare or absent within 200 km of Arizona. In 2000 and 2001, I quantified abundance, distribution, and habitat characteristics of pygmy-owls across Sonora. I detected 524 pygmy-owls at 2,812 stations along 392 transects (1,113 km). Relative abundance (no. males/stations ± SE) was high in both northern (0.38 ± 0.04) and southern (0.67 ± 0.07) Sonora and low in central (0.13 ± 0.03) Sonora. Density (no. males/100 ha ± SE) was highest in Sinaloan Deciduous Forest (2.00 ± 0.82) and moderate in Semidesert Grassland (0.99 ± 0.45) and Sinaloan Thornscrub (0.85 ± 0.37). Density of owls in the 4 vegetation subdivisions of the Sonoran Desert combined was 0.67 ± 0.32 and ranged from 1.47 ± 0.61 in Arizona Uplands to 0.08 ± 0.04 in Central Gulf Coast desertscrub. Density on upper bajadas was 2.5 to 17 times greater than on lower bajadas in Semidesert Grassland, Sinaloan Thornscrub, and on the Plains of Sonora, and was 4.5 times lower in Arizona Uplands. Relative abundance was higher on the Coastal Plain (0.18 ± 0.02) than in interior valleys and foothills of the Sierra Madre Occidental (<0.01 ± <0.01). Over 72% of pygmy-owls I located were aggregated along only 18.9% of transects and abundance was moderately clumped across the state. In the north, abundance corresponded closely with geographic trends in the environmental factors important in habitat selection; in the south, however,

there was little correspondence at higher elevation where Colima pygmy-owls (*Glaucidium palmarum*) often replaced ferruginous in tall tropical forests.

Although associations between pygmy-owls and specific environmental factors varied somewhat geographically, owls typically occupied areas with moderate vegetation volume, taller upland canopy height, riparian areas dominated by mesquite (*Prosopis* sp.) and chino (*Havardia mexicana*), and upland areas dominated by mesquite, ironwood (*Olneya tesota*), tropical deciduous forest species, and large columnar cacti. Large columnar cacti had a strong influence on occupancy and abundance of pygmy-owls especially where large cacti were less common. Factors related to riparian vegetation and the size and density of drainages had a strong influence on occupancy and abundance of pygmy-owls in arid northern Sonora but not in the relatively mesic south. Occupancy and abundance were lower in areas altered by agriculture, and were higher in areas with low to moderate levels of woodcutting in Sinaloan Thornscrub, which reduced vegetation volume improving conditions for owls. Although occupancy was often lower where grazing intensity was high, the influence of grazing intensity varied with elevation and topography. Pygmy-owls were detected regularly in both riparian and upland vegetation areas, however almost all owls were detected in uplands when volume of vegetation between 3 and 6 m above ground exceeded 20%. Existence of a well-distributed population of pygmy-owls in northern Sonora enhances recovery potential in neighboring portions of Arizona. Management strategies designed to augment or develop habitat characteristics that promote occupancy by pygmy-owls is an important step toward recovery of pygmy-owls in Arizona.

INTRODUCTION

Distributions of organisms are determined, in part, by environmental tolerances. Climate, soils, and topography interact to determine the distribution of plant communities and to define regional gradients in vegetation (Merriam 1894, Shreve 1951, Whittaker and Niering 1965, Whittaker 1967). Although many studies have documented associations between birds and environmental features along vegetation gradients (e.g., Bond 1957, Smith 1977, Kendeigh and Fawver 1981), most have been restricted to small areas, ignoring variation in patterns of habitat use across large geographic areas (but see Collins 1983, Knopf et al. 1990, Grzybowski et al. 1994, Parody and Parker 2002). Although the template for habitat selection is likely consistent throughout a species' range, variation in the relative importance of environmental features likely varies across these gradients.

Environmental gradients occur at multiple spatial scales. In lowlands east of the Gulf of California in northwestern Mexico, annual precipitation increases more than 5 times from northwest to southeast, and frequency and intensity of frost declines from north to south (Shreve 1951, Hastings and Humphrey 1969, Brown 1982). These climatic gradients produce profound changes in vegetation, which transitions from desert in the north into thornscrub and tropical deciduous forest in the south (Gentry 1942, Shreve 1951, Wiseman 1980, Brown 1982). Changes in topography and soils between valley bottoms and the mountains they drain produce smaller scale vegetation gradients within landscapes (Yang and Lowe 1956, Phillips and MacMahon 1978, Bowers and Lowe 1986). These changes in topography and their associated vegetation gradients influence the structure of bird communities (Vander Wall and MacMahon 1984, Naranjo and Raitt 1993).

In addition to physical factors, species distributions are influenced by biotic factors such as predation or competition. In general, biotic interactions tend be more important in limiting distributions at lower latitudes and physical factors tend to be more important at higher latitudes (Darwin 1859, Dobzhansky 1950, MacArthur 1972). For example, climatic extremes may limit a species' distribution at high latitudes and increased abundance or diversity of predators and competitors may limit distribution at low latitudes (Pianka 1970, Gross and Price 2000).

Within the geographic distribution of a species, abundance has been predicted to be highest near the center and decrease toward the edges of the range (Grinnell 1922, Hengeveld and Haeck 1982, Rapoport 1982, Brown 1984), although evidence for this pattern for birds has been mixed (Emlen et al. 1986, Robbins et al. 1986, Scott et al. 1986). This prediction assumes that characteristics that define habitat tend to occur more frequently near the geographical center of the range (Brown 1984, 1995). For species that have declined at the northern edge of their range such as cactus ferruginous pygmy-owls (*Glaucidium brasilianum cactorum*), this pattern suggests reduced prospects for recovery.

Cactus ferruginous pygmy-owls are the northernmost subspecies of ferruginous pygmy-owls in western North America, and are distributed from southern Arizona south to Nayarit, Mexico (van Rossem 1937, Phillips 1966). Although once described as locally common in lowland central and southern Arizona (Bendire 1888, Fisher 1893, Breninger 1898, Gilman 1909), pygmy-owls have been extirpated throughout much of their former range in Arizona. In 1997, the U.S. Fish and Wildlife Service (USFWS) listed the Arizona population as endangered (USFWS 1997).

Recovery of cactus ferruginous pygmy-owls (hereafter pygmy-owls) in Arizona could be fostered by immigration of owls from occupied areas in northern Sonora, Mexico. Although historical records exist throughout Sonora, pygmy-owls were thought to be absent, rare, or uncommon in northern Sonora and nesting records were only from the extreme south (USFWS 1997, Russell and Monson 1998). Since 1925, there have been only 5 known records of pygmy-owls in Sonora north of 30° N latitude (van Rossem 1945, Rosenberg 1981, Hunter 1988, Duncan 2000).

In Arizona, pygmy-owls occupied areas with cottonwood (*Populus fremontii*) and mesquite (*Prosopis* sp.) woodlands along valley bottoms (Bendire 1888, Fisher 1893, Breninger 1898, Gilman 1909, Aiken 1937) or xeroriparian vegetation and adjacent desertscrub (Brandt 1951, Hensley 1954, Phillips et al. 1964, Monson and Phillips 1981). Although the importance of mesic riparian systems for pygmy-owls in Arizona has been debated, all areas occupied by pygmy-owls recently are in xeroriparian areas dominated by microphyllous species and adjacent desertscrub or semidesert grassland (USFWS 1997, Cartron et al. 2000). In Sonora, pygmy-owls occupy desertscrub, thornscrub, and tropical deciduous forest (Russell and Monson 1998), primarily in vegetation associations with giant cacti (van Rossem 1945). Further south, pygmy-owls occupy deciduous and evergreen woodlands, thickets, thornscrub, and savannah, especially semi-open areas in arid lowlands with scattered patches of dense vegetation (Schaldach 1963, Monroe 1968, Ridgely 1976, Hilty and Brown 1986, Johnsgard 1988, Stiles and Skutch 1989, Binford 1989, Howell and Webb 1995, Ridgely and Greenfield 2001).

Current interest in pygmy-owls in Mexico focuses on their significance for recovery efforts in Arizona, although populations in Sonora may be threatened by habitat loss, fragmentation, and degradation due to vegetation clearing and livestock grazing (USFWS 1997). Currently, over half of Sonora's fuel-wood comes from northern areas where mesquite and ironwood woodlands have declined (Búrquez and Martínez-Yrízar 1997, Suzán et al. 1997). Agricultural development has converted over 1 million ha of riparian forest and thornscrub on the deltas of the Ríos Yaqui and Mayo, approximately 150,000 ha of mesquite woodland and desertscrub on the Río Sonora delta, and altered virtually all accessible mesic riparian areas in lowland Sonora (Felger and Lowe 1976, Búrquez and Martínez-Yrízar 1997, pers. obs). Further, an estimated 1.2 million ha have been cleared or altered to establish buffelgrass (*Pennisetum ciliare*) pastures in the past half century (Cox et al. 1988, Búrquez et al. 1996).

Consequently, information on distribution, abundance, and habitat of pygmy-owls in Sonora will facilitate conservation and recovery strategies in Arizona. Further, as secondary, obligate cavity-nesters, pygmy-owls require large trees or columnar cacti, but the relative importance of other habitat features is unknown. My objectives were to quantify patterns of distribution and abundance of pygmy-owls and identify environmental features related to their presence and abundance in Sonora.

STUDY AREA

Sonora is the most northwestern state in mainland Mexico (26°-32° N, 109°-115° W), sharing much of its northern border with Arizona (Fig. 1). Two main physiographic regions characterize the landscape, basin and range on the Coastal Plain to the west, and interior foothills, mountains, and valleys of the Sierra Madre Occidental to the east. Although the elevational range varies from 0 to 2620 m, much of Sonora lies in lowlands below 1000 m. Several major rivers drain interior regions including the Ríos Asunción (Magdalena), Sonora, Yaqui, and Mayo, and other smaller rivers drain portions of the Coastal Plain including, Sonoyta, San Ignacio, Bacoachi, and Matapé.

Sonora encompasses a range of biomes that include most major Mexican vegetation communities (Leopold 1950, Rzedowski 1978). Across Sonora, quantity of summer rainfall, intensity and duration of frost, and geomorphic gradients contribute to a transition in vegetation from open deserts to coniferous and tropical forest (Shreve 1951,

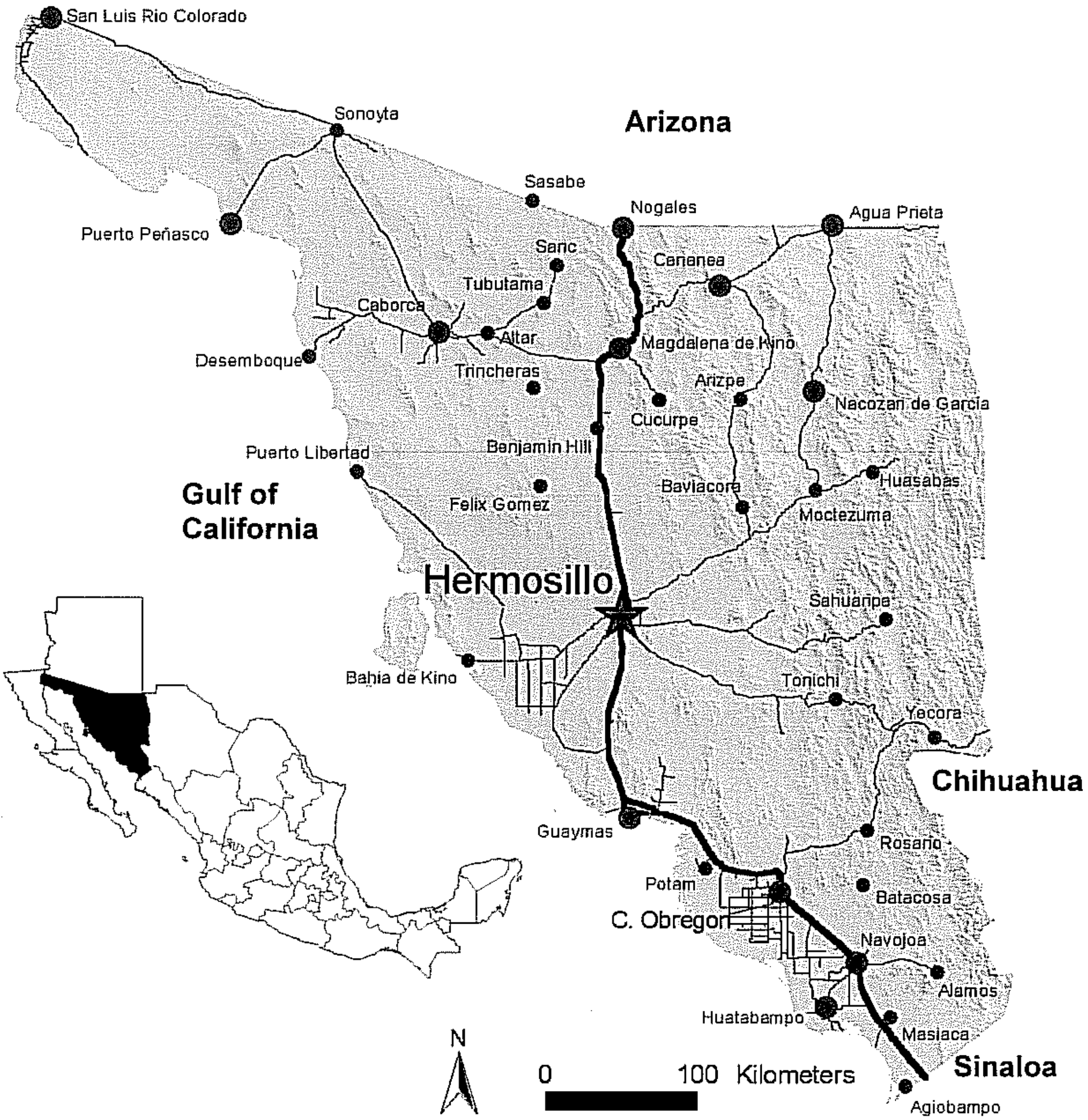

Figure 1. Map of State of Sonora illustrating major cities, roads, and topography. Inset map denotes the position and size of Sonora in reference to other Mexican states and to Arizona.

Wiseman 1980, Brown 1982, Búrquez et al. 1992). Local topography also contributes to vegetation transitions, especially in arid northern regions. In desert uplands, coarser soils with higher water availability support greater plant diversity on upper bajadas (coalesced alluvial fans or piedmonts) (Yang and Lowe 1956, Phillips and MacMahon 1978, Bowers and Lowe 1986). Along drainages, deep sandy soils on floodplains or relatively shallow, moist soils at the edges of mountains support the greatest vegetation structure (Shreve 1951).

Western Sonora includes the entire Plains of Sonora subdivision and portions of 3 of 5 other Sonoran Desert subdivisions: Lower Colorado River Valley, Arizona Upland, and Central Gulf Coast (Brown and Lowe 1980). Lower Colorado River Valley desertscrub in northwestern Sonora is the driest subdivision, characterized by open uplands of shrubs and subshrubs with trees restricted mainly to drainages (Shreve 1951, Turner and Brown 1982). The Central Gulf Coast subdivision occupies a 40-km band along the Gulf of California in west-central Sonora where sarcocaulescent ("fleshy stemmed") and succulent vegetation are dominant. Arizona Upland desertscrub occupies a 50-to 100-km band in northern Sonora characterized by low woodland or scrubland of leguminous trees and large columnar cacti such as saguaros (*Carnegiea gigantea*). The Plains of Sonora is the most mesic and southern subdivision, which includes extensive areas of savannah and thornscrub, and is dominated by woody trees and shrubs rather than cacti. Semidesert and Sonora Savannah Grasslands replace desertscrub at higher elevations east and north of Arizona Uplands and at scattered locations on the Plains of Sonora (Brown 1982).

Although these grasslands are floristically similar to the Sonoran Desert, columnar cacti are rare above 1050 m due to freezing temperatures; mesquite (*Prosopis velutina*) is the dominant tree.

Subtropical vegetation with Sinaloan affinities and montane vegetation with Madrean affinities replace desertscrub and grassland to the south and east. In eastern Sonora, Madrean Evergreen Woodland dominated by oaks (*Quercus* sp.) and pines (*Pinus* sp.) occur at elevations generally above 1,200 m (Marshall 1957, Brown 1982). Sinaloan Thornscrub occupies a large area on the Coastal Plain and foothills below 950 m in southern and central Sonora. Dense, drought deciduous, often thorny trees or shrubs dominate, and along with succulents, form a closed canopy from 2 to 8 m tall (Gentry 1942, Brown 1982). Shrubs of the north transition to trees further south and ultimately form Sinaloan Deciduous Forest mainly on slopes in southeast Sonora between 300 and 1050 m (Gentry 1942, 1982). Although floristically similar to thornscrub, Sinaloan Deciduous Forest is distinguished by greater height, larger leaf area, and an increased proportion of mesomorphic and tropical species (Gentry 1982, Martin et al. 1998, van Devender et al. 2000). Sinaloan Riparian Evergreen Forest is restricted to mesic watercourses within forest and thornscrub, principally in canyons (Minckley and Brown 1982). In these tropical environments, soil moisture is available year-round and sustains broadleaf evergreen species (e.g., *Ficus* sp.).

METHODS

Field Methods

Site selection: I sampled all of Sonora, except areas above 1,200 m, the Gran Desierto de Altar (west of the Río Sonoyta), and the Chihuahuan Desert, where pygmy-owls have never been observed (van Rossem 1945, USFWS 1997, Russell and Monson 1998). I stratified the state by both major vegetation community and by topographic formation. Vegetation strata included the 4 subdivisions of the Sonoran Desert and the 3 other major vegetation communities found below 1,200 m, Semidesert/Sonoran Savannah Grassland, Sinaloan Thornscrub, and Sinaloan Deciduous Forest. I then stratified each vegetation community into 4 topographic formations: valley bottoms, lower bajadas, upper bajadas, and mountain canyons. Valley bottoms included lowest elevation drainage in a landscape, lower bajadas included lowlands below or within the lower half of outwash plains, upper bajadas included the upper half of outwash plains, and mountains were steeper upland areas often forming canyons.

To select sampling points, I generated random UTM coordinates and used Instituto Nacional de Estadistica Geografia e Informatica (INEGI) 1:250,000 and 1:50,000 topographic maps and Brown and Lowe's (1980) Biotic Communities map to classify the vegetation communities at points. I then selected a sample of random points proportional to aerial coverage of each community except in the border region (Arizona Uplands and Semidesert Grassland) where I sampled with slightly higher intensity. When plant community boundaries on maps did not conform to vegetation in the field, I reclassified points to the appropriate vegetation community (Gentry 1942, Shreve 1951, Brown 1982, Turner et al. 1995, Martin et al. 1998, Búrquez et al. 1999, Robichaux and Yetman 2000). I then selected 1 transect along the closest accessible (within 1 km of a road) drainage (>2 m wide) within each topographic formation that occurred within 20 km of random points. In addition to establishing transects at random points, I surveyed some areas incidentally and consider these surveys separately.

Owl surveys: I used recorded, conspecific territorial calls to elicit responses from pygmy-owls. I used similar survey timing, distances between consecutive stations, and duration of calling and listening intervals used recently in Arizona and Texas (Lesh and Corman 1995, Mays 1996, USFWS 2000). At each station, I alternated listening and calling sequences every 30 to 45 sec and included listening periods during the first and last 30 sec. For the first 25 transects surveyed, I remained at stations for 6 to 10 min to estimate times to first detection. For the 33 pygmy-owls detected, average time to response was 3.0 ± 0.3 min and never greater than 6 min. Therefore, I spent 8 min at stations during the remainder of surveys. I surveyed between mid-January and late-May, predominantly during early morning (1 hr before and 3 hrs after sunrise) and occasionally (2% of surveys) during evening (2 hrs before and 1 hr after sundown). Because pygmy-owls likely establish breeding territories earlier in warmer, lower elevation areas, I surveyed these areas first to account for potential temporal variation in response rates. I did not survey during steady rain or when wind speed consistently exceeded 20 kph.

Along each transect, I established a series of 3 to 12 stations in drainage channels spaced 350 to 400 m apart. When I detected an owl, I established the next station 550 to 600 m from the previous one to reduce the probability of detecting the same bird more than once. For each owl, I estimated distance to initial point of detection, compass direction, sex (based on vocalization), vegetation zone (upland, riparian, or undetermined), station closest to initial point of detection, and whether an owl was located outside of the targeted topographic formation. I used distance and direction of responses to differentiate among multiple owls that did not respond simultaneously to estimate the number of owls along each transect.

Environmental measurements: I characterized vegetation, geographic, physiographic, and land-use features at survey stations and along transects. I classified physiographic locations of each transect as Coastal Plain, foothills or interior valleys of the Sierra Madre Occidental, or a transition area that included the first valley and associated mountains or foothills adjacent to the Coastal Plain. I counted the number of drainages within 1 km of transects and calculated drainage density as number per 100 m. I used a GPS receiver and INEGI 1:50,000 scale topographic maps to determined the UTM coordinates and elevation of the first and last survey station along each transect and I calculated transect slope as total elevation change per m of transect.

At each station, I calculated an index of topographic complexity equal to the sum of the absolute value of elevation change 400 m perpendicular to drainages. I used a rangefinder and compass to record the directional orientation and width of drainage corridors at stations. I recorded presence of surface water and ranked intensity (high, medium, low, or none) of land use in 5 categories: grazing, agriculture, wood-cutting, buffelgrass planting, and low-density housing and averaged measurements among stations along transects. I based these rankings on the degree of vegetation disturbance and influence of land-use on vegetation (Table 1).

At each station, I used a rangefinder to record the distance to and species of the nearest large columnar cactus and tree (live or dead) with cavity potential (>3 m tall and >20 cm dbh for cacti, >6 m tall and >30 cm dbh for trees) within 400 m, in 4, 90° quarters denoted by drainages and a perpendicular line across them. Because drainage channels were typically not vegetated, I measured distances from the edge of channels, which facilitated comparisons among transects along drainages of varying width. From these measurements I determined presence or absence, relative abundance (% stations where substrates present for transects or % quarters present for stations), and density (no./ha) of potential cavity harboring substrates (Table 1).

I described physical structure and species composition of riparian and upland vegetation at survey stations out to 400 m from drainage channels. At each station, I ranked the degree of contrast between riparian and upland vegetation as low, medium, or high. I used a rangefinder to measure the width of riparian vegetation associations on both sides of drainages. I ranked dominance of up to 3 vegetation formations (woodland,

Table 1: Names, definitions, and units for environmental variables used to quantify habitat of ferruginous pygmy-owls in Sonora, Mexico 2000-01.

Group *Subgroup* Variable	Description (units)
Physiography	
Phyisographic province	Coastal Plain, Sierra Madre Occidental, or transition
Elevation	mean elevation between start and end stations (m)
Latitude	UTM north Zone 12 (m)
Longitude	UTM east Zone 12 (m)
Slope	change in elevation divided by transect length (m/m)
Topographic complexity	elevation change w/in 400 m perpendicular to drainage (m)
Orientation	mean compass direction of transect (degrees)
Water presence or abundance	presence/absence or percent stations where water present (%)
Drainage width	width of drainage corridor based on flow indicators (m)
Drainage density	no. of mapped drainages within 1 km per 100 m (no./100 m)
Land Use	
Grazing intensity	rank, based on vegetation disturbance [a]
Agriculture intensity	rank, based on vegetation disturbance [a]
Buffelgrass intensity	rank, based on vegetation disturbance [a]
Wood-cutting intensity	rank, from selective wood-cutting through clear-cutting [a]
Low density housing intensity	generally ranch buildings or small villages [a]
Vegetation	
Riparian formation types	
Gallery woodland dominance	large gallery woodland trees generally >10 m tall (%)
Woodland dominance	closed canopy or patchy woodland generally <10 m tall (%)
Riparian scrub dominance	riparian shrubs along drainage (%) (see Appendix A)
Desertscrub dominance	open canopy woodland or scrubland of scattered trees, shrubs, subshrubs, and/or cacti (%)
Thornscrub dominance	dense closed canopy of shrubs or trees between 2 to 6 m tall (%)
Forest dominance	tall extensive associations of trees >8 m tall (%)

Table 1: Continued

Group *Subgroup* Variable	Description (units)
Savannah dominance	open scattered trees with matrix of grass or subshrubs (%)
Agriculture dominance	associations of agricultural plants in cleared areas <1m tall (%)
Riparian structure	
Width of vegetation association	total width of riparian vegetation on both sides of drainage (m)
Structural contrast	degree of contrast between upland and riparian vegetation (none-0; low-1; mod.-2; high-3)
Mean canopy height	mean canopy height of riparian vegetation (m)
Vegetation volume	volume in 5 height classes (%) [b]
Total riparian veg. volume	sum of vegetation volume in all strata (%)
Riparian composition	
Species dominance	relative dominance for plant species (%) (Appendix A)
Species group dominance	relative dominance for species groups (%) (Appendix A)
Upland formation types [c]	
Woodland dominance	closed canopy woodland generally <10 m tall (%)
Desertscrub dominance	open canopy woodland or scrubland of scattered trees, shrubs, subshrubs, and/or cacti (%)
Thornscrub dominance	dense closed canopy associations generally <6 m tall (%)
Forest dominance	tall extensive associations of tropical tree species >8 m tall (%)
Savannah dominance	open scattered trees with matrix of grass or subshrubs (%)
Agriculture dominance	associations of agricultural plants in cleared areas <1m tall (%)
Upland structure [c]	
Mean canopy height	mean canopy height of upland vegetation (m)
Vegetation volume	volume in 5 height classes (%) [b]
Total upland veg. volume	sum of vegetation volume in all strata (%)
Upland composition [c]	
Species dominance	relative dominance for plant species (%) (Appendix A)
Species group dominance	relative dominance for species groups (%) (Appendix A)
Cavity harboring substrates	relative dominance for species groups (%) (Appendix A)

Table 1: Continued

Group *Subgroup* Variable	Description (units)
Large cacti presence	presence or absence of large columnar cacti with cavity potential (>3 m tall and 20 cm dbh) within 400 m
Large cacti abundance	transects: no. of stations with large cacti within 400 m divided by total stations, stations: no. of quarters with large cacti within 400 m divided by 4 quarters (%)
Large cacti density	relative no. of large cacti per unit area (based on nearest neighbor distance measures) (no./ha)
Large trees presence	presence or absence of large trees or snags with cavity potential (>6 m tall and 30 cm dbh) within 400 m
Large tree abundance	transects: no. of stations with large trees within 400 m divided by total stations; stations: no. of quarters with large trees within 400 m divided by 4 quarters (%)
Large trees density	relative no. of large cacti per unit area (based on nearest neighbor distance measures) (no./ha)
Height of large trees	mean height of large trees and snags considered (m)

[a] Land use intensity ranks, none-0; low-1; mod.-2; high-3.

[b] Vegetation height classes, 0-1, 1-3, 3-6, 6-12, ≥12 m.

[c] Upland measurements averaged for both sides of transect except where riparian vegetation >400 m wide.

desertscrub, thornscrub, riparian scrub, gallery woodland, savannah, grassland, agriculture, and wetland) by percent cover at each station in both upland and riparian areas. I ranked up to 3 canopy species in order of dominance (most common ranked by height), except in Sinaloan plant communities where I ranked up to 5 species (Appendix A). Similarly, I ranked up to 2 understory species in order of dominance. I visually estimated average canopy height (to the nearest m) in both upland and riparian areas excluding columnar cacti unless they were dominant. I estimated vegetation volume to the nearest 10% when values were between 20 and 80% and to the nearest 5% otherwise in 5 height strata: 0-1 m, 1-3 m, 3-6 m, 6-12 m, and >12 m above ground. I calculated an index of total vegetation volume by summing volumes across height strata. I measured upland vegetation on both sides of riparian corridors but averaged all measurements.

Data Analyses

Abundance estimation: I estimated density of males (no./100 ha) based on radial distances to initial detection points using program Distance 4.0 (Thomas et al. 2001). To account for variation in detectability across vegetation communities (Oelke 1981, Verner 1985), I only considered owl detections within 400 m. I used Akaike's Information Criterion (AIC) as a guide to model selection. When AIC were similar among models I selected those with higher precision. I estimated density and relative abundance (no. males/station) within each topographic formation nested within vegetation communities. Estimates within vegetation communities were weighted by the aerial coverage of each topographic formation that I estimated from 10-km-radius plots centered on random points from INEGI 1:250,000 topographic maps. Plots that contained >1 vegetation community were weighted by coverage of each community. Owls detected outside of target topographic formations (e.g., canyon transect with owl detected on adjacent upper bajada) were excluded from analyses. Because too few owls occurred along individual transects for transect-based estimates of density, I used relative abundance estimates for most analyses and density estimates to compare abundance among vegetation and topographic strata.

Detectability and seasonality: To determine if 8 min surveys were adequate to detect potentially responsive pygmy-owls, I calculated the cumulative frequency of time-until-detection for each successive min for all owls by sex. To determine if time-until-detection varied across the survey period (Jan. through June), I used log-linear regression for Poisson counts adjusted for overdispersion (SAS Institute 2000, Ramsey and Schafer 2002), after accounting for the potential influences of elevation, latitude, longitude, year, sex, and distance to initial point of detection. To determine if relative abundance varied across the survey period, I used log-linear regression for Poisson counts after accounting for differences in habitat characteristics.

Habitat characteristics: I assessed environmental factors associated with presence of pygmy-owls at 2 scales, transects and individual stations within transects. I assessed factors associated with relative abundance of pygmy-owls along transects occupied by ≥1 male pygmy-owl. To identify factors associated with presence of pygmy-owls along transects, I used multiple logistic regression (mLR). To identify factors associated with presence of owls at stations, I used mLR with Generalized Estimator Equations (GEE) with the "exchange" fixed correlation matrix to adjust for within-transect correlations (Kleinbaum and Klein 1994, SAS Institute 2000). To identify factors associated with relative abundance of pygmy-owls along occupied transects, I used multiple linear regression. To identify factors related to detection of males versus females or detections of owls in upland versus riparian vegetation, I used mLR with GEE adjustments. When comparing stations with males to those with females, I only considered stations where females were detected before April 1st, because their detectability declined precipitously later in the breeding season (unpubl. data). For each individual detected, I only considered the station closest to the initial point of detection and excluded others (n = 177) from analyses.

To guide model selection, I used stepwise variable selection ($P < 0.25$ to enter, $P < 0.10$ to stay), Cp statistics, and lack-of-fit or drop-in-deviance tests (Hosmer and Lemeshow 1989, Ramsey and Schafer 2002). Before building models, I screened explanatory variables to reduce redundancy and retained the most biologically meaningful variable from correlated pairs ($r > 0.7$). When the number of potential explanatory variables was high, I first fit several smaller models with groups of related variables (physiographic features, vegetation formations, land-use, vegetation structure and composition) to eliminate those with little explanatory power ($P < 0.25$) (Ramsey and Schafer 2002:348). To determine how habitat selection varied across topography within landscapes, I fit second-order interactions between important environmental factors and topographic formations I though to be biologically meaningful. I weighted transects by the number of stations surveyed to adjust for unequal survey effort. I assessed environmental factors related to occupancy and relative abundance within vegetation communities and then pooled vegetation communities to assess patterns across the state.

<u>Distribution of abundance</u>: To describe spatial variation in abundance, I compared a frequency distribution of the number of males per transect with random (Poisson) or clumped (negative binomial) patterns (Ludwig and Reynolds 1988). I used the standardized Morisita index of dispersion to assess degree of aggregation (-1 = maximum uniformity, 1 = maximum aggregation) and weighted abundance estimates by survey effort for each transect (Krebs 1989). When assessing conformity to a Poisson distribution, I assumed each transect had an equal probability of harboring owls. I examined two hypotheses regarding owl abundance: (1) that it was greatest at the center of the geographic range then declined gradually and symmetrically toward the edges, and (2) that abundances tended to be more similar at nearby localities than distant ones (Hengeveld and Haeck 1982, Rapoport 1982, Brown 1984). I plotted relative abundance versus latitude to illustrate patterns of abundance across the northern portion of the owl's range, then compared the distribution to a normal distribution. To evaluate spatial autocorrelation in abundance, I compared variation estimated from transects within

landscapes to that estimated from an equal number of transects selected at random in the same topographic formations throughout Sonora. Each cluster of transects at a random point was considered a sample of a landscape.

I used simple and multiple linear regression to quantify patterns of relative abundance across latitude, longitude, and elevation. To determine if relative abundance patterns corresponded with geographic trends in abundance of environmental factors that comprised habitat, I used multiple linear regression to determine environmental factors that explained relative abundance of pygmy-owls along transects within regions of interest. I then regressed the first Principal Component of important environmental factors with latitude, longitude, and elevation and compared these patterns to those for relative abundance of pygmy-owls.

Dispersion: To evaluate dispersion of landscapes occupied by pygmy-owls, I calculated the nearest unique distance between occupied points in neighboring landscapes using GIS (ESRI 1996). I compared nearest known neighbor distances within and among geographic regions (north, central, and south) and across latitude and longitude. I weighted distances by density of effort (no. landscapes sampled/unit area) within each region which resulted in an 11.6% increase in distances in northern Sonora and an 11.8% decrease in central Sonora relative to southern Sonora.

Floristics: I grouped plant species with similar growth form and physiognomy for analyses (Appendix A). For example, I combined all species of paloverde (*Parkinsonia* sp.) into one group, and combined the columnar cacti etcho (*Pachycereus pecten-arboriginum*) and sahuira (*Stenocerus montanus*) into another group. I distinguished broadleaf (*Populus*, *Salix*, *Fraxinus*) from microphyllous (*Havardia mexicana* and *Albizia sinaloënis*) gallery woodland species and tropical deciduous (*Lysiloma*, *Ceiba*, and *Tabebuia*) from tropical evergreen (*Ficus*, *Cinnamomum*, and *Drypetes*) forest species. To calculate percent dominance of species, species groups, and vegetation formations (e.g. woodland, desertscrub, etc.), I used ranked scores as integral factors in determining relative dominance of each species and formation at stations. All means are reported ±1 standard error.

RESULTS

Effort and Detections

I surveyed 2,812 stations along 392 transects (1,113 km) during 342 hrs of survey effort. Transect length averaged 2,719 ± 39.9 m, with 7.2 ± 0.09 stations per transect spaced an average of 440 ± 3.2 m apart. Effort was greatest in Sinaloan Thornscrub ($n = 140$ transects) and lowest in Lower Colorado River Valley desertscrub ($n = 20$) (Table 2). Effort was relatively even across topographic formations except where access was limited (canyons) or formations were uncommon (canyons in Plains of Sonora or lower bajadas in Sinaloan Deciduous Forest).

Table 2: Effort, numbers, and abundance of ferruginous pygmy-owls in vegetation and topographic strata in Sonora, Mexico 2000-01.

Vegetation community	Cover[a]	Effort		No. detected		Frequency of Occurrence	Relative Abundance[b]		Density[c]	
Topographic formation	%	transect	length	males	female	%	$\bar{x}$	SE	$\bar{x}$	SE
Arizona Upland	14	69	272.9	116	19	68	0.20	0.04	1.47	0.61
valley bottom	5	13	43.1	36	4	77	0.35	0.08	1.27	0.36
lower bajada	38	20	64.3	50	9	90	0.31	0.05	3.19	1.16
upper bajada	47	27	79.4	26	6	48	0.12	0.03	0.71	0.27
canyon	10	9	31.7	4	0	44	0.05	0.02	0.34	0.24
Lower Colorado River Valley	9	20	49.5	6	4	35	0.04	0.02	0.24	0.13
valley bottom	9	6	14.8	2	1	40	0.04	0.03	0.09	0.05
lower bajada	72	11	26.6	4	3	36	0.05	0.02	0.35	0.18
upper bajada	14	2	5.0	0	0	0	0.00	0.00	0.00	0.00
canyon	5	1	3.2	0	0	0	0.00	0.00	0.00	0.00
Central Gulf Coast	9	21	54.5	9	3	14	0.02	0.01	0.08	0.04
valley bottom	3	2	7.6	8	2	100	0.47	0.13	2.38	1.07
lower bajada	64	4	8.8	0	0	0	0.00	0.00	0.00	0.00
upper bajada	13	8	18.1	1	1	13	0.02	0.02	0.04	0.03
canyon	20	7	20.1	0	0	0	0.00	0.00	0.00	0.00
Plains of Sonora	21	65	179.1	66	14	45	0.08	0.03	0.56	0.31
valley bottom	7	17	49.9	29	2	50	0.23	0.06	1.06	0.34
lower bajada	57	19	53.2	7	2	26	0.03	0.02	0.07	0.03
upper bajada	33	23	61.2	21	9	48	0.14	0.04	1.22	0.69
canyon	3	6	14.8	9	1	33	0.15	0.15	1.45	1.53

Table 2: Continued

Vegetation community Topographic formation	Cover[a]	Effort		No. detected		Frequency of Occurrence	Relative Abundance[b]		Density[c]	
	%	transect	length	males	female	%	$\bar{x}$	SE	$\bar{x}$	SE
Semidesert Grassland	9	56	152.4	70	5	50	0.19	0.07	0.99	0.45
valley bottom	7	16	49.1	21	0	44	0.22	0.08	0.81	0.36
lower bajada	24	15	40.4	13	4	53	0.15	0.04	0.50	0.26
upper bajada	52	16	41.6	23	1	56	0.22	0.07	1.23	0.48
canyon	17	9	21.4	13	0	55	0.17	0.09	1.02	0.69
Sinaloan Thornscrub	33	140	348.9	110	12	36	0.12	0.04	0.85	0.37
valley bottom	7	41	108.0	43	3	18	0.18	0.05	0.88	0.28
lower bajada	33	39	98.1	27	3	37	0.12	0.03	0.54	0.20
upper bajada	32	28	64.4	26	3	46	0.14	0.05	1.55	0.68
canyon	28	32	78.4	14	3	23	0.07	0.03	0.40	0.23
Sinaloan Deciduous Forest	5	21	51.4	48	15	86	0.40	0.14	2.00	0.82
valley bottom	4	3	9.2	9	33	100	0.40	0.01	2.89	1.16
lower bajada	4	1	3.0	4	1	100	0.57	0.57	3.61	2.08
upper bajada	25	7	19.4	16	9	86	0.40	0.12	1.53	0.56
canyon	67	10	24.1	23	2	75	0.39	0.16	2.01	0.82
All transects combined[d]	100	392	1,112.9	429	72	48	0.13	0.04	0.82	0.37

[a] Estimates for vegetation communities based on relative coverage within study area. Estimates for topographic formations based on relative coverage within vegetation communities.

[b] No. males within 400 m/ no. stations. Estimates for vegetation communities weighted by coverage of topographic formations.

[c] No. males within 400 m/100 ha. Estimates for vegetation communities weighted by coverage of topographic formations.

[d] Statewide estimates weighted by coverage of vegetation communities.

I detected 438 males, 74 females, and 12 pygmy-owls of unknown sex along transects and an additional 112 pygmy-owls incidentally. Mean time to detection was 2.6 ± 0.1 min ($n = 520$) with 97.5% of owls detected in ≤7 min. On average, females took only 0.2 ± 0.26 min longer to respond than males ($t_{509} = 0.86$, $P = 0.38$). Although owls detected in late January (3.3 ± 0.4 min) took 1.4 ± 0.4 min longer to respond than those in late March (1.9 ± 0.2 min, $t_{506} = 3.43$, $P = 0.006$), time to detection did not vary across the survey period ($\chi^2_{511} = 0.64$, $P = 0.42$) after adjusting for the influence of elevation, latitude, longitude, year, sex, and distance to initial point of detection. Additionally, relative abundance did not vary systematically across the survey period ($\chi^2_{365} = 0.01$, $P = 0.93$) after adjusting for important environmental factors.

Distribution and Abundance

Pygmy-owls were common in northern and southern Sonora and generally uncommon in central Sonora (Fig. 2). Within 150 km of Arizona pygmy-owls were rare to locally common between Saric and Sonoyta, rare west of Mexico Route 2, and absent west of Sonoyta and north of Magdalena (Fig. 3). Owls occurred at elevations between 10 and 1,100 m but only above 1,000 m in northern Sonora (Sasabe and east of Magdalena) and only below 30 m in extreme southwestern Sonora or along large drainages (Ríos Yaqui and San Ignacio).

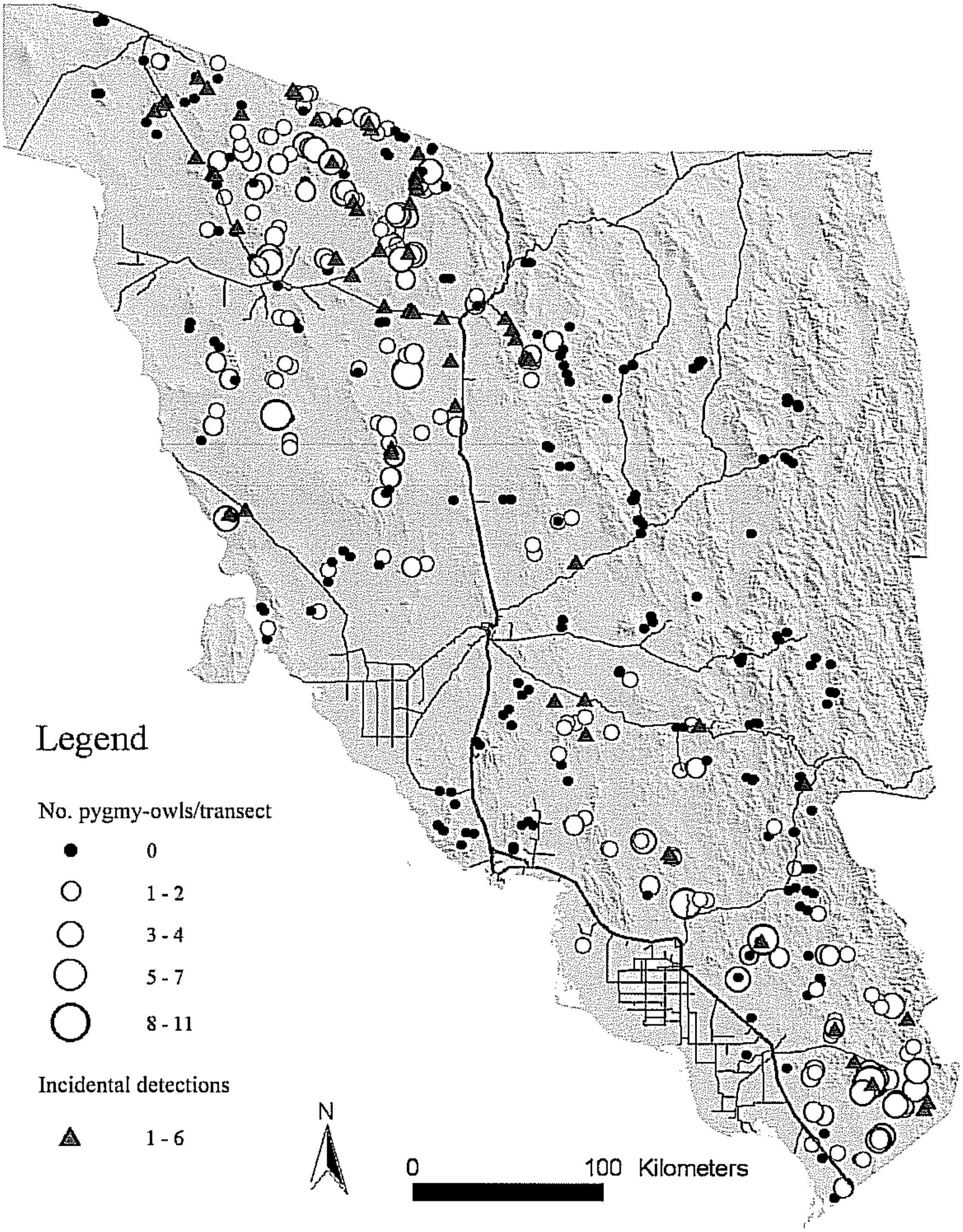

Figure 2. Distribution and abundance (no. detected/transect) of ferruginous pygmy-owls in Sonora, Mexico 2000-01. Number of pygmy-owls detected on transects indicated by size of circles.

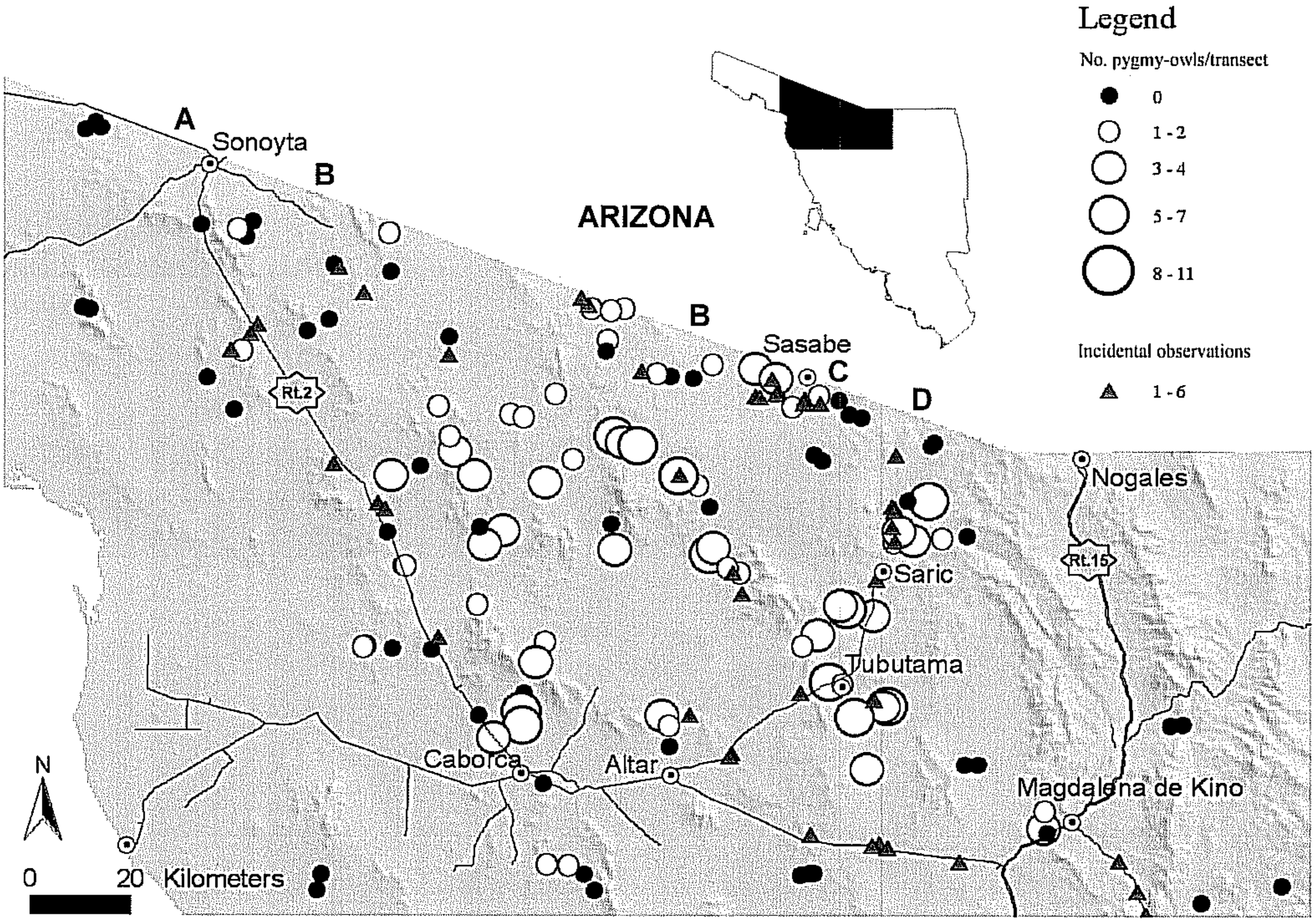

Figure 3. Distribution and abundance (no. detected/transect) of ferruginous pygmy-owls in northern Sonora, Mexico 2000-01. Notation indicates (A) Organ Pipe Cactus National Monument, (B) Tohono O'odham Reservation, (C) Buenos Aires National Wildlife Refuge, (D) and Coronado National Forest.

Of the 145 landscapes sampled statewide, 95 (65.5%) harbored ≥1 pygmy-owl. Pygmy-owls occurred along 48% of transects at a density of 0.82 ± 0.37 males/100 ha statewide (Table 2). Relative abundance ranged from 0 to 1.25 males/station and averaged 0.13 ± 0.04 statewide. Density (males/100 ha) was high in Sinaloan Deciduous Forest (2.00 ± 0.82) and Arizona Upland desertscrub (1.47 ± 0.61), moderate in Semidesert Grassland (0.99 ± 0.45), Sinaloan Thornscrub (0.85 ± 0.37), and Plains of Sonora desertscrub (0.56 ± 0.31), and low in Lower Colorado River Valley (0.26 ± 0.13) and Central Gulf Coast (0.08 ± 0.04) desertscrub (Table 2). Density in the Sonoran Desert was slightly lower than statewide estimates (0.67 ± 0.32).

Relative abundance was higher on the Coastal Plain (0.18 ± 0.01 males/station, $n = 297$) and adjacent foothills and valleys (0.14 ± 0.04, $n = 41$) than in interior foothills and valleys of the Sierra Madre Occidental (0.003 ± 0.033, $n = 50$) ($F_{2, 285} = 12.26$, $P < 0.0001$). On the Coastal Plain, owls occurred along 52.4% of transects compared to only 2.0% of transects ($n = 1$ of 50) in the interior (Fig. 2).

Habitat Characteristics

Because pygmy-owls occupied a variety of vegetation communities with different structures and compositions, I assessed environmental factors associated with pygmy-owls both within vegetation communities and across the state. I assessed characteristics associated with occupancy at the scale of both transects and stations, and also assessed characteristics associated with relative abundance along only those transects occupied by ≥1 male pygmy-owl.

Sonoran Desert: Odds of ≥1 pygmy-owl occupying a transect increased with abundance of large trees and cacti with cavity potential, and with dominance of chino trees (*Havardia mexicana*) in riparian areas (Table 3). Chino was dominant along only 17.9% of transects ($n = 30$ of 168), and owls occurred along 88.9% ($n = 16$ of 18) of transects where chino dominance exceeded 12%. Occupancy by pygmy-owls along transects increased with dominance of riparian woodlands, larger riparian vegetation areas, and taller upland canopy height, although the influence of these factors varied with longitude (Table 3). In the western and central portions of the Sonoran Desert, occupancy increased more with width of riparian areas than in the east ($\chi^2_{154} = 5.76$, $P = 0.016$, for interaction) (Fig. 4*a*). Similarly, the influence of riparian woodlands and upland canopy height on occupancy was greatest in the western portion of the Sonoran Desert ($\chi^2_{154} = 7.13$, $P = 0.0076$, for woodland x longitude interaction; $\chi^2_{154} = 11.60$, $P = 0.0007$, for canopy height x longitude interaction) (Fig. 4*b* and *c*).

Patterns of owl occupancy varied among vegetation subdivisions of the Sonoran Desert. In Arizona Upland and Plains of Sonora desertscrub, the odds of occupancy by pygmy-owls along transects increased with abundance of large cacti and with drainage width (Table 3). On the Plains of Sonora, large cacti were present at 61.7 ± 6.6% of stations

Table 3: Variables that explained variation in occupancy of ferruginous pygmy-owls along survey transects in Sonora, Mexico 2000-01. *P*-values and odds ratios from multiple logistic regression within vegetation communities.

Vegetation community *Subdivision* Variable	Occupied		Unoccupied			
	$\bar{x}$	SE	$\bar{x}$	SE	*P*	Odds [a]
Sonoran Desert [b]						
Riparian woodland dominance x longitude (%, 10 km)	2355.8	161.7	1284.3	150.5	0.0076	1.39
Riparian vegetation width x longitude (m, 10 km)	4628.7	647.8	3160.8	603.0	0.0016	1.01
Upland canopy height x longitude (m, 10 km)	110.2	33.7	96.6	39.9	0.0007	1.02
Large cacti abundance (%)	84.0	3.1	57.4	4.6	0.0007	1.03
Large trees abundance (%)	57.0	4.3	25.3	3.4	0.0003	1.03
Riparian chino dominance (%)	7.5	1.9	1.1	0.4	0.0006	1.02
Arizona Upland desertscrub [c]						
Drainage width (m)	15.4	2.1	8.2	1.3	0.0023	1.32
Large cacti abundance (%)	97.4	1.1	83.1	6.7	0.0029	1.09
Riparian woodland dominance (%)	61.9	4.9	30.7	6.4	0.013	1.03
Plains of Sonora desertscrub [d]						
Drainage width (m)	24.5	4.5	11.3	2.1	0.018	1.05
Large cacti abundance (%)	61.6	6.6	16.7	5.0	<0.0001	1.04
Lower Colorado River Valley and Central Gulf Coast desertscrub [e]						
Riparian woodland dominance (%)	48.4	3.6	13.7	6.7	0.0024	1.08
Semidesert Grassland [f]						
Large cacti abundance (%)	89.7	3.5	33.5	7.3	0.0020	1.02

Table 3: continued

Vegetation community *Subdivision* Variable	Occupied		Unoccupied			
	$\overline{x}$	SE	$\overline{x}$	SE	P	Odds [a]
Large trees abundance (%)	42.5	6.8	74.5	6.7	0.027	0.98
Upland canopy height (m)	2.5	0.1	2.3	0.1	0.043	620.20
Sinaloan Thornscrub [g]						
Coastal Plain [h]	54.7	4.3	45.3	4.3	0.0003	12.18
Sierra Madre Occidental [h]	2.5	1.4	97.5	1.4	0.0005	0.01
Riparian vegetation width x woodland dominance (m, %)	7018.6	1417.8	6807.2	1027.8	0.023	0.17
Large cacti abundance (%)	86.5	3.8	55.9	4.7	<0.0001	1.06
Riparian canopy height (m)	5.2	0.3	4.0	0.1	0.0015	2.24
Riparian tropical deciduous forest species (%)	19.6	3.3	14.1	2.3	0.011	1.06
Riparian mesquite dominance (%)	25.1	2.7	24.6	1.8	0.0022	1.09

[a] A 1-unit increase in the explanatory variable results in a change in the odds of owl occupancy.

[b] $\chi^2 = 104.3$, df = 10, $n = 168$, $P < 0.0001$, $R^2 = 0.45$.

[c] $\chi^2 = 34.6$, df = 3, $n = 64$, $P < 0.0001$, $R^2 = 0.41$.

[d] $\chi^2 = 31.6$, df = 2, $n = 62$, $P < 0.0001$, $R^2 = 0.37$.

[e] $\chi^2 = 15.1$, df = 1, $n = 41$, $P = 0.0001$, $R^2 = 0.37$.

[f] $\chi^2 = 56.0$, df = 3 , $n = 55$, $P < 0.0001$, $R^2 = 0.76$.

[g] $\chi^2 = 89.4$, df = 9, $n = 132$, $P < 0.0001$, $R^2 = 0.56$.

[h] Values equal percent transects occupied or unoccupied in each physiographic province.

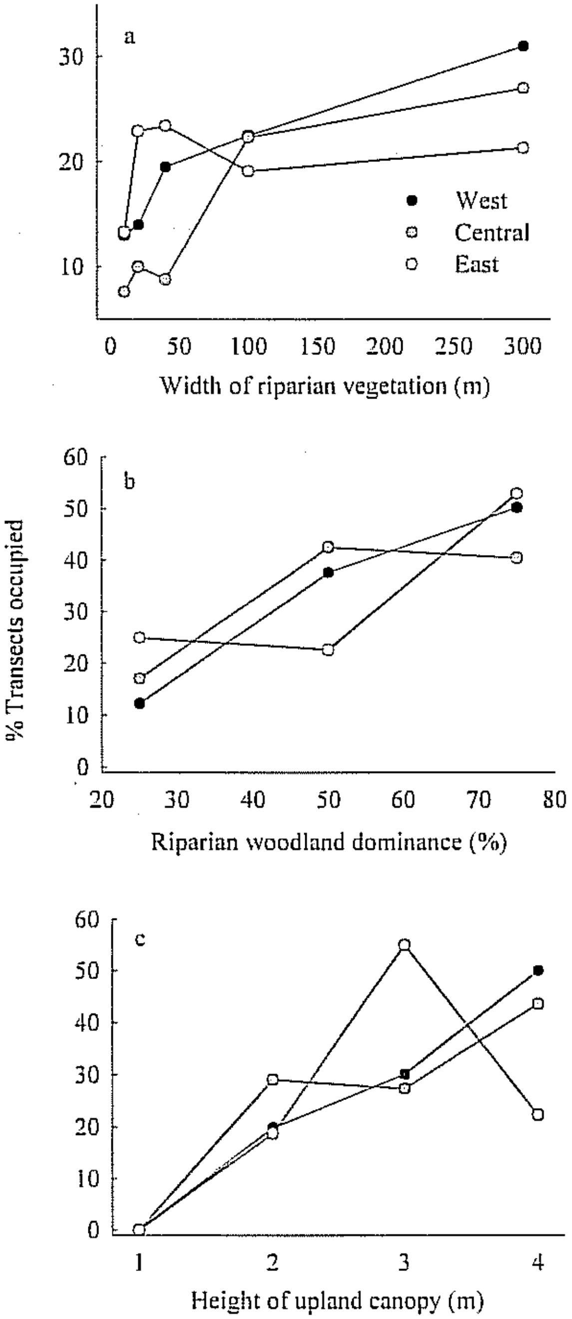

Figure 4. Influence of (a) width of riparian vegetation (m), (b) riparian woodland dominance (m), and (c) mean height of upland canopy (m) across longitude on occupancy by ferruginous pygmy-owls along survey transects in the Sonoran Desert, Sonora, Mexico 2000-01.

along occupied transects versus only 16.7 ± 5.0% of stations along unoccupied transects, a 3.7-fold difference. In Arizona Uplands, however, this disparity was much lower (Table 3). Occupancy increased with dominance of riparian woodlands in Arizona Uplands ($\chi^2_{58} = 6.12$, $P = 0.013$) but not on the Plains of Sonora ($\chi^2_{61} = 0.17$, $P = 0.68$) (Table 3). In Lower Colorado River Valley and Central Gulf Coast desertscrub, dominance of riparian woodlands was the only factor that differentiated occupied from unoccupied transects (Table 3) ($\chi^2_{25} = 9.22$, $P = 0.0024$), with occupied transects having 3.5 times greater riparian woodland dominance than unoccupied transects.

Occupancy of individual stations within transects increased with abundance of large cacti and trees, with cacti especially influential (Table 4). Pygmy-owls occupied only 1.9% (n = 7 of 396) of stations where large cacti were absent versus 9.6% (n = 68 of 711) where large trees were absent. At 57% of occupied stations where cacti were absent, large chinos were present. Associations between occupancy by owls and abundance of large cacti varied among topographic formations ($\chi^2_{1108} = 8.69$, $P = 0.034$, for interaction). In lower elevation topographic formations (lower bajadas and valley bottoms), occupancy increased with cacti abundance, however in upper elevation topographic formations (canyons and upper bajadas), where cacti were 38% more abundant ($t_{1125} = 6.53$, $P <$ 0.0001, linear contrast), owl occupancy was highest at moderate levels of cacti abundance (Fig. 5).

Table 4: Variables that explained variation in occupancy of ferruginous pygmy-owls at survey stations, Sonora, Mexico 2000-01. *P*-values and odds ratios from multiple logistic regression with GEE adjustments within vegetation communities.

Vegetation community *Subdivision* Variable	Occupied		Unoccupied			
	$\bar{x}$	SE	$\bar{x}$	SE	P	Odds[a]
Sonoran Desert[b]						
Drainage width (m)	20.7	1.5	13.2	0.7	0.045	1.01
Large cacti abundance (%)	78.0	2.2	50.7	1.5	<0.0001	1.02
Large trees abundance (%)	40.1	2.8	18.3	1.0	0.0070	1.01
Riparian - woodland dominance (%)	61.6	2.6	35.0	1.3	0.014	1.01
- mesquite dominance (%)	39.8	1.9	21.2	0.8	<0.0001	1.02
- chino dominance (%)	9.2	1.5	3.0	0.4	0.013	1.02
Upland - desertscrub dominance (%)	76.1	2.5	69.1	1.3	0.060	1.01
- canopy height (m)	2.8	0.10	2.3	0.03	<0.0001	1.79
- ironwood dominance (%)	16.1	1.4	13.4	0.6	0.0022	1.02
- mesquite dominance (%)	24.4	1.6	14.0	0.7	0.0014	1.02
- paloverde dominance (%)	27.0	1.4	25.2	0.7	0.044	1.01
Arizona Upland desertscrub[c]						
Large cacti abundance (%)	87.1	8.2	77.7	1.7	0.0048	1.02
Riparian vegetation width x woodland dominance (m, %)	71.6	8.3	21.7	2.4	0.10	1.01
Riparian - mesquite dominance (%)	44.6	2.3	25.5	1.5	0.018	1.02
Upland - canopy height (m)	2.9	0.06	2.5	0.04	0.017	1.84
- mesquite dominance (m)	29.2	1.8	14.7	1.3	0.0093	1.02
- ironwood dominance (m)	11.1	1.4	9.3	0.8	0.020	1.03

Table 4: continued.

Vegetation community *Subdivision* Variable	Occupied		Unoccupied			
	$\overline{x}$	SE	$\overline{x}$	SE	P	Odds [a]
Plains of Sonora desertscrub [d]						
Drainage width (m)	29.2	3.6	14.4	1.0	0.038	1.02
Large cacti presence [e]	38.1	2.3	61.9	2.3	<0.0001	49.40
Large trees presence [e]	25.5	2.1	74.5	2.1	0.030	2.72
Riparian - chino dominance (%)	19.8	3.5	3.4	0.6	0.045	1.04
Upland - ironwood and paloverde dominance (%)	55.0	3.7	49.2	1.5	0.0024	1.02
Lower Colorado River Valley and Central Gulf Coast desertscrub [f]						
Drainage width (m)	18.4	4.3	14.9	2.1	0.044	1.16
Upland canopy height (m)	2.6	0.20	1.8	0.04	0.058	10.50
Semidesert Grassland [g]						
Topographic complexity (m)	39.8	3.6	54.0	3.4	0.0004	0.98
Large cacti abundance (%)	81.5	2.8	32.1	2.3	<0.0001	1.03
Upland - canopy height (m)	2.6	0.06	2.4	0.05	0.049	1.77
- desertscrub dominance (%)	46.4	4.8	29.2	4.1	0.050	1.01
- saguaro dominance (%)	5.2	0.8	0.7	0.2	0.0072	1.06
Sinaloan Thornscrub [h]						
Agriculture intensity (none-0; low-1; med.-2; high-3)	0.3	0.10	0.6	0.04	0.0017	0.57
Wood-cutting intensity (none-0; low-1; med.-2; high-3)	1.0	0.11	0.8	0.04	0.0095	0.65
Large cacti abundance (%)	78.7	3.0	41.3	1.5	0.0006	1.02
Large trees abundance (%)	58.4	3.3	45.3	1.4	0.0021	1.01

Table 4: continued.

Vegetation community *Subdivision* Variable	Occupied		Unoccupied			
	$\overline{x}$	SE	$\overline{x}$	SE	P	Odds [a]
Riparian - canopy height (%)	5.9	0.3	4.3	0.1	0.013	1.21
- woodland dominance (%)	60.7	3.0	47.9	1.4	0.041	1.01
Upland - thornscrub dominance (%)	6.2	3.2	74.0	1.3	0.017	0.99
- tropical deciduous forest species (%)	45.3	3.2	40.1	1.2	0.023	0.99
Sinaloan Deciduous Forest [i]						
Topographic complexity (m)	122.3	12.0	211.5	16.8	0.055	0.99
Large cacti density (%)	16.9	7.5	7.1	1.2	<0.0001	1.05
Large trees density (%)	23.7	6.6	48.3	9.7	0.0002	0.98
Upland - canopy height (m)	5.8	0.3	7.2	0.3	0.019	0.73
Riparian - vegetation volume 1-3 m (%)	28.9	1.7	29.0	1.8	0.013	0.95

[a] A 1-unit increase in the explanatory variable results in a change in the odds of owl occupancy.

[b] $\chi^2 = 385.6$, df = 12, $n = 1126$, $P < 0.0001$.

[c] $\chi^2 = 352.9$, df = 9, $n = 422$, $P < 0.0001$.

[d] $\chi^2 = 191.8$, df = 6, $n = 429$, $P < 0.0001$.

[e] Values equal percent stations occupied or unoccupied when categorical variable present.

[f] $\chi^2 = 28.9$, df = 3, $n = 140$, $P < 0.0001$.

[g] $\chi^2 = 222.5$, df = 6, $n = 359$, $P < 0.0001$.

[h] $\chi^2 = 385.6$, df = 9, $n = 834$, $P < 0.0001$.

[i] $\chi^2 = 123.9$, df = 6, $n = 115$, $P < 0.0001$.

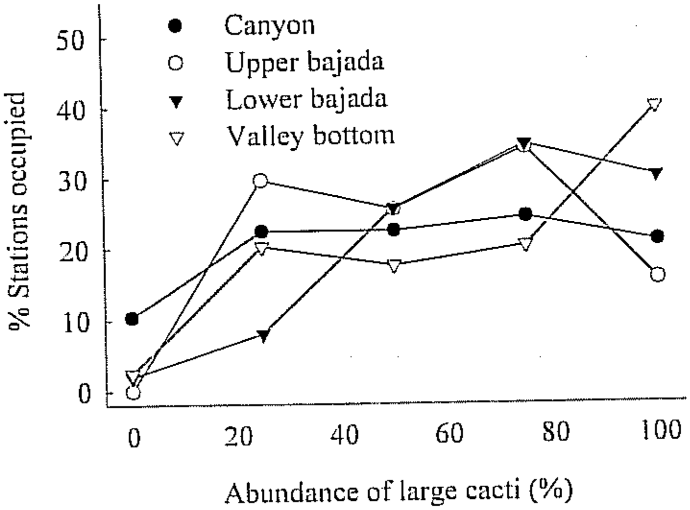

Figure 5. Influence of large cacti abundance (% quarters present) across topography on occupancy by ferruginous pygmy-owls at survey stations in the Sonoran Desert, Sonora, Mexico 2000-01.

Occupancy at stations increased with height of upland vegetation throughout the Sonoran Desert but was most influential in more xeric subdivisions (Fig. 6). In Lower Colorado River Valley and Central Gulf Coast desertscrub, for example, each additional m of upland vegetation height increased the odds of owl occupancy 4.8 times more than in Arizona Uplands (Table 4). In the more mesic Plains of Sonora subdivision, however, occupancy varied little with height of upland vegetation ($\chi^2_{61} = 0.68$, $P = 0.41$). Although pygmy-owls have been considered riparian obligates in Arizona, height of riparian canopy failed to explain occupancy ($\chi^2 \leq 2.32$, $P \geq 0.13$) after upland vegetation height and other more influential factors were considered.

Occupancy at stations increased with dominance of riparian woodlands throughout the Sonoran Desert (Table 4). In Arizona Uplands, however, the influence of riparian woodland dominance on occupancy depended somewhat on the width of riparian areas ($\chi^2_{1108} = 2.69$, $P = 0.10$, for interaction). Occupancy increased with width of riparian areas only in areas where woodland dominance exceeded 35% (Fig. 7).

Occupancy at stations was associated with dominance of upland desertscrub although the relationship varied among topographic formations ($\chi^2_{1108} = 14.94$, $P = 0.0019$, for interaction). Compared to upper elevation topographic formations, occupancy increased with dominance of desertscrub in lower elevation topographic formations where riparian areas averaged 240% larger ($t_{1122} = 13.78$, $P < 0.0001$, linear contrast) and where woodlands were 69% more dominant ($t_{1113} = 8.13$, $P < 0.0001$, linear contrast).

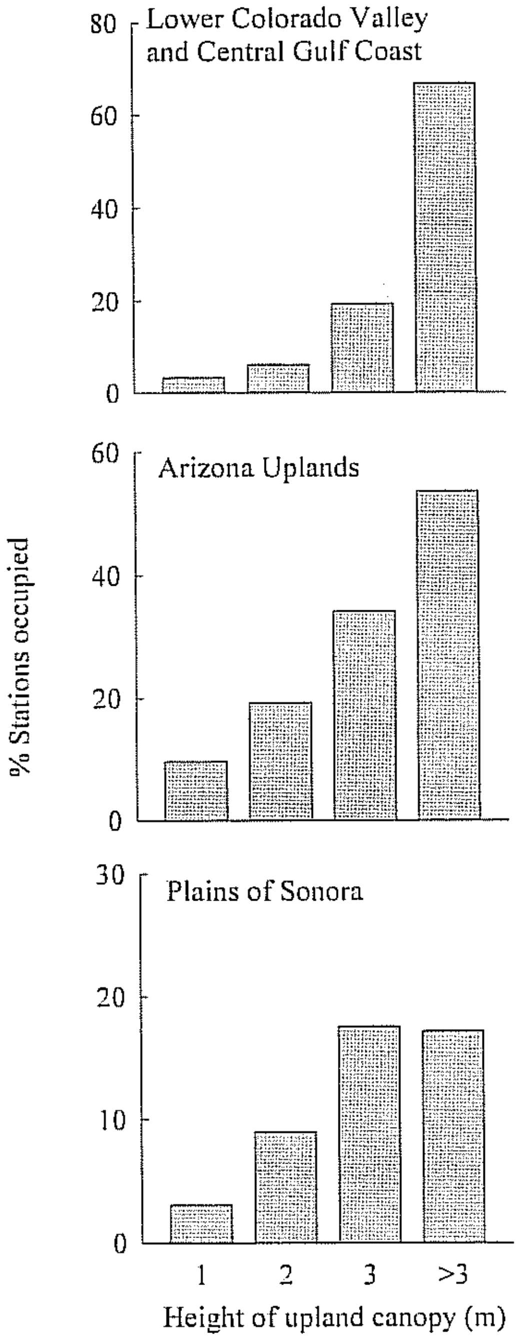

Figure 6. Influence of mean height of upland canopy (m) on occupancy by ferruginous pygmy-owls at survey stations across subdivisions of the Sonoran Desert, Sonora, Mexico 2000-01.

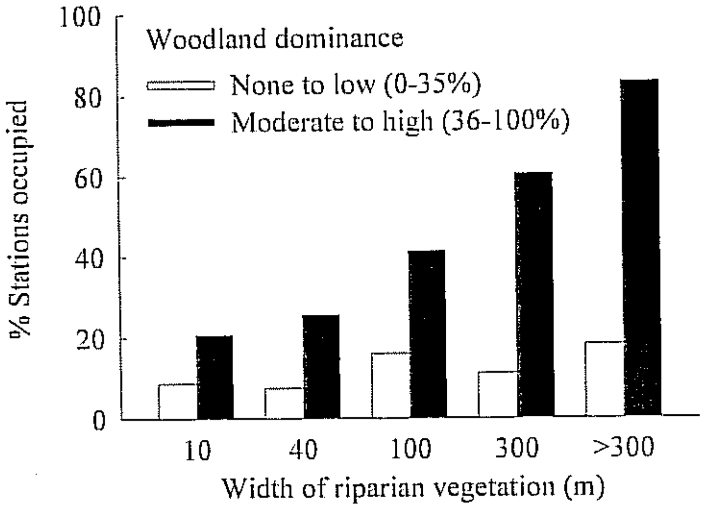

Figure 7. Influence of width of riparian vegetation (m) at high and low dominance of riparian woodland formations (%) on occupancy by ferruginous pygmy-owls at survey stations in the Arizona Uplands subdivision of the Sonoran Desert, Sonora, Mexico 2000-01.

In contrast, occupancy declined with dominance of desertscrub in upper elevation topographic formations ($Z_{1108} \leq 3.45$, $P \geq 0.0006$, for desertscrub x formation interactions).

Occupancy at stations increased with dominance of mesquite and chino in riparian areas; associations with mesquite were stronger in Arizona Uplands and those with chino were stronger on the Plains of Sonora (Table 4). Occupancy increased steadily with dominance of mesquite and ironwood (*Olneya tesota*) in uplands and slightly with paloverde (*Parkinsonia* sp.) (Fig. 8*a*, *c*, and *d*). In Arizona Uplands, occupancy increased with dominance of mesquite in uplands in all topographic formations ($\chi^2_{406} = 1.51$, $P = 0.68$, for interaction) where mesquite was approximately 2 times more dominant at occupied than at unoccupied stations ($t_{421} = 4.51$, $P < 0.0001$, *t*-test) (Table 4). Associations between occupancy and dominance of paloverde in uplands varied somewhat among topographic formations ($\chi^2_{1108} = 6.51$, $P = 0.089$, for interaction); on upper bajadas occupancy declined with increasing paloverde dominance ($Z_{1108} = 2.61$, $P = 0.0090$, interaction).

Along transects occupied by pygmy-owls in the Sonoran Desert, 6 environmental factors explained variation in relative abundance of pygmy-owls ($F_{6, 67} = 8.86$, $P < 0.0001$) (Table 5). Relative abundance increased with drainage density, upland canopy height, and abundance of large cacti with cavity potential, and decreased with slope (Fig 9). Relative abundance also increased with dominance of ironwood in uplands but declined

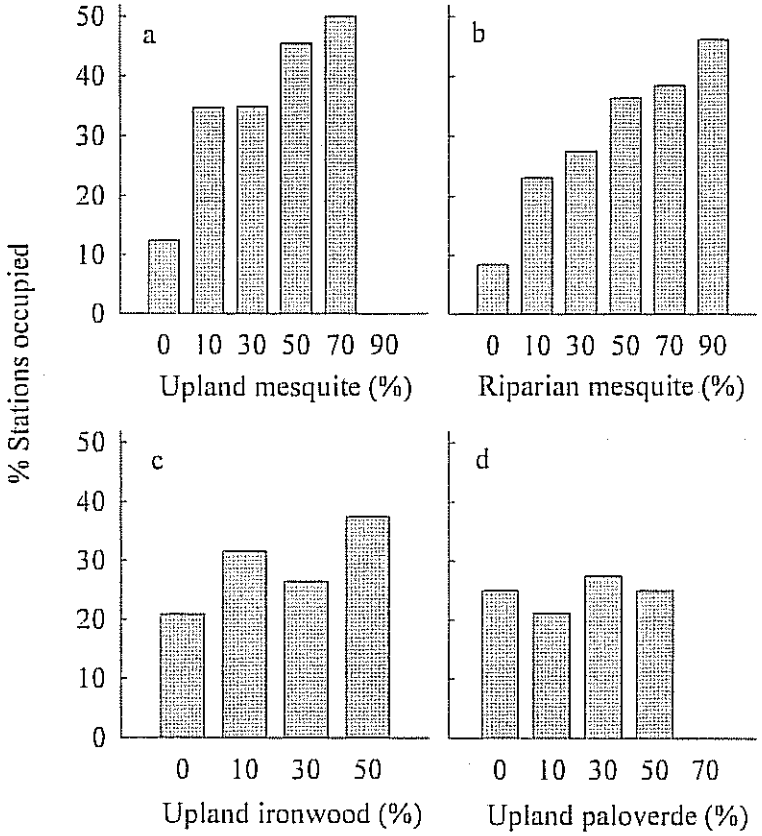

Figure 8. Influence of mesquite dominance (%) in (a) upland and (b) riparian areas and dominance of (c) ironwood and (d) paloverde in uplands on occupancy by ferruginous pygmy-owls at survey stations in the Sonoran Desert, Sonora, Mexico 2000-01.

Table 5: Variables that explained variation in relative abundance of ferruginous pygmy-owls along occupied survey transects in Sonora, Mexico 2000-01. *P*-values and parameter estimates from multiple linear regression within vegetation communities.

Vegetation community *Subdivision* Variable	$\hat{\beta}$	SE	*t*	*P*
Sonoran Desert [a]				
Slope (m/m)	-6.24	2.16	2.88	0.0054
Drainage density (no./100 m)	0.032	0.011	2.85	0.0058
Large cacti abundance (%)	0.17	0.079	2.12	0.037
Upland - canopy height (m)	0.11	0.032	3.30	0.0015
- ironwood dominance (%)	0.55	0.16	3.30	0.0012
Riparian - ironwood dominance (%)	-0.41	0.13	3.07	0.0031
Arizona Upland desertscrub [b]				
Drainage width (m)	0.063	0.022	2.86	0.0075
Drainage density x longitude (no./100 m, km)	0.0013	0.00059	2.13	0.042
Riparian - mesquite dominance (%)	0.39	0.14	2.70	0.011
Upland - ironwood dominance (%)	0.93	0.30	3.13	0.0038
Plains of Sonora desertscrub [c]				
Topographic complexity (m)	0.0022	0.0010	2.15	0.043
Slope (m/m)	-8.06	2.80	2.88	0.0090
Large cacti abundance (%)	0.22	0.090	2.49	0.021
Riparian - chino dominance (%)	0.55	0.15	3.75	0.0012
Semidesert Grassland [d]				
Drainage abundance (m/m)	0.041	0.014	2.87	0.0089
Riparian - woodland dominance (%)	0.67	0.16	4.27	0.0003
- vegetation volume 1-3 m (%)	-0.014	0.0042	3.43	0.0024
Upland - saguaro cacti (%)	0.017	0.0079	2.20	0.039
Sinaloan Thornscrub [e]				
Riparian - woodland dominance (%)	0.28	0.11	2.57	0.014
- palo joso dominance (%)	0.94	0.29	3.25	0.0024
- tropical evergreen forest species (%)	0.45	0.17	2.58	0.014
Upland - forest dominance (%)	0.83	0.29	2.77	0.0087
- vegetation volume 1-3 m (%)	-0.0058	0.0026	2.22	0.032

Table 5: Continued

Vegetation community *Subdivision* Variable	$\hat{\beta}$	SE	t	P
Sinaloan Deciduous Forest [f]				
Slope (m/m)	-3.19	1.50	2.12	0.054
Riparian - tropical deciduous forest species (%)	0.60	0.29	2.09	0.057

[a] $F_{6,\,67} = 8.86$, $P < 0.0001$, $n = 74$, $R^2 = 0.44$.

[b] $F_{6,\,31} = 7.73$, $P < 0.0001$, $n = 38$, $R^2 = 0.60$.

[c] $F_{4,\,21} = 9.07$, $P = 0.0002$, $n = 26$, $R^2 = 0.76$.

[d] $F_{4,\,22} = 9.14$, $P = 0.0002$, $n = 27$, $R^2 = 0.62$.

[e] $F_{5,\,39} = 8.80$, $P < 0.0001$, $n = 45$, $R^2 = 0.54$.

[f] $F_{2,\,13} = 3.79$, $P = 0.051$, $n = 16$, $R^2 = 0.37$.

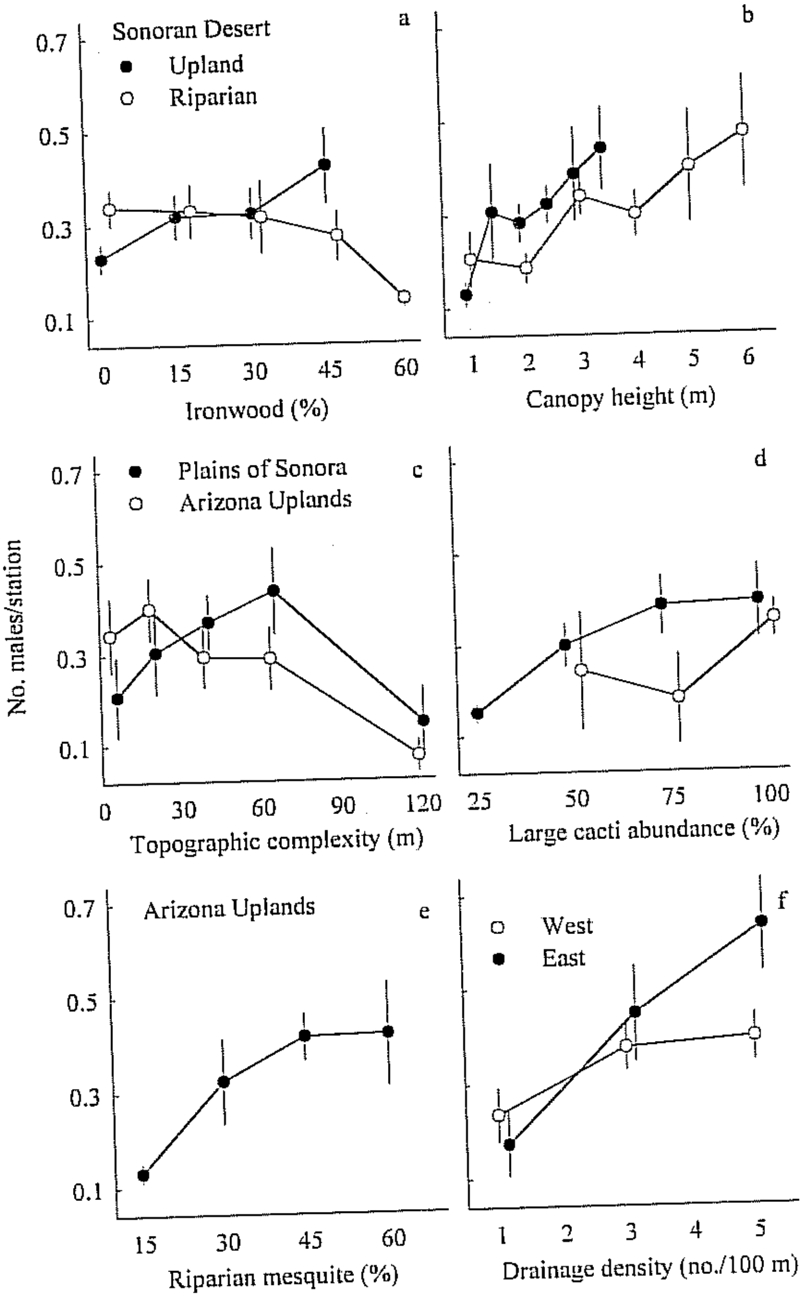

Figure 9. Influence of (a) ironwood dominance (%) and (b) height of canopy vegetation (m) in upland and riparian areas in the Sonoran Desert, (c) topographic complexity (m), and (d) large cacti abundance (%) in Arizona Upland and Plains of Sonora desertscrub, and (e) riparian mesquite dominance (%) and (f) drainage density (no./100 m) in Arizona Upland desertscrub on relative abundance (no. males/station ± SE) of ferruginous pygmy-owls along occupied survey transects in Sonora, Mexico 2000-01.

with dominance of ironwood in riparian areas (Fig. 9*a*). Owl abundance increased with abundance of large cacti on the Plains of Sonora, but not in Arizona Uplands ($t_{37} = 1.04$, $P = 0.30$) where cacti abundance was 58% higher ($t_{64} = 6.49$, $P < 0.0001$, linear contrast) than on the Plains of Sonora (Fig. 9*d*). The influence of drainage density on owl abundance varied with longitude in Arizona Uplands ($t_{32} = 2.13$, $P = 0.042$, for interaction), but not on the Plains of Sonora ($t_{25} = 0.29$, $P = 0.77$). Owl abundance increased with increasing drainage density in the east and less so in the west (Fig. 9*f*). Owl abundance declined with increasing slope on the Plains of Sonora and peaked at moderate levels of topographic complexity.

<u>Semidesert Grasslands</u>: Transects occupied by pygmy-owls in semidesert grasslands had taller upland canopy height and more large cacti with cavity potential than unoccupied transects (Table 3). Pygmy-owls occupied over 80% of transects when cacti abundance exceeded 75% but did not occur where cacti were absent (Fig. 10*a*). Occupancy declined beyond moderate abundance of large trees (Fig. 10*b*).

Occupied stations had greater dominance of desertscrub and saguaro cacti in uplands, greater abundance of large cacti, and taller upland canopy height than unoccupied stations (Table 4). Occupancy increased with dominance of upland desertscrub up to moderate levels and with height of upland canopy until 4 m (Fig. 11*a* and *b*). Occupancy was highest at moderate levels of topographic complexity and owls were not detected at stations with >150 m elevation change within 400 m. In canyons, where topographic

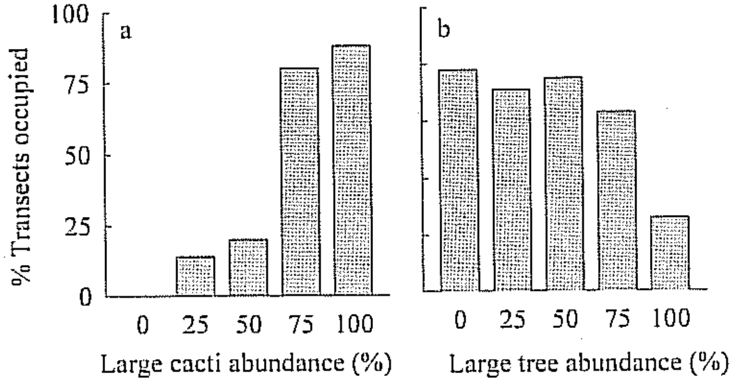

Figure 10. Influence of (a) large cacti and (b) large trees abundance (% stations present) on occupancy by ferruginous pygmy-owls along survey transects in Semidesert Grasslands, Sonora, Mexico 2000-01.

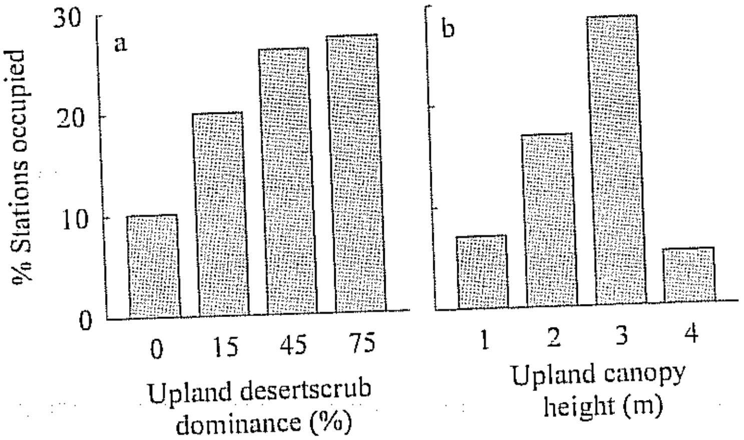

Figure 11. Influence of (a) dominance of upland desertscrub (%) and (b) mean height of upland canopy (m) on occupancy by ferruginous pygmy-owls at survey stations in Semidesert Grasslands, Sonora, Mexico 2000-01.

complexity was approximately 3 times higher than in other formations (85 ± 8.6 m, $t_{63} = 5.86$, $P < 0.0001$, linear contrast), stations occupied by owls had 63% lower topographic complexity than unoccupied stations ($t_{63} = 2.81$, $P = 0.0069$). Because topographic complexity at occupied stations increased with elevation ($t_{63} = 3.84$, $P = 0.0003$; linear regression), complexity was approximately 2 times higher above 900 m (58.6 ± 8.1 m, $t_{63} = 3.13$, $P = 0.0038$) than below 900 m (30.0 ± 4.1 m).

The influence of grazing intensity on occupancy varied among topographic formations ($\chi^2_{3\,46} = 7.29$, $P = 0.063$, for interaction). On upper bajadas, occupancy rates declined sharply as grazing intensity increased (Fig. 12), with intensity averaging 25% less at occupied versus unoccupied stations ($t_{95} = 2.27$, $P = 0.015$). Although grazing intensity was highest in the lower elevation portions of landscapes ($t_{63} = 2.54$, $P = 0.014$, linear regression), occupancy by pygmy-owls was highest where grazing intensity was highest along valley bottoms (Fig. 12).

Along occupied transects, 4 environmental factors explained variation in relative abundance of pygmy-owls ($F_{4,\,22} = 9.14$, $P = 0.0002$) (Table 5). Abundance increased with drainage density and dominance of upland saguaros and riparian woodlands (Fig. 13*a*, *b*, and *c*). Relative abundance was greatest at moderate volumes of riparian vegetation between 1 and 3 m above ground and declined thereafter (Fig. 13*d*).

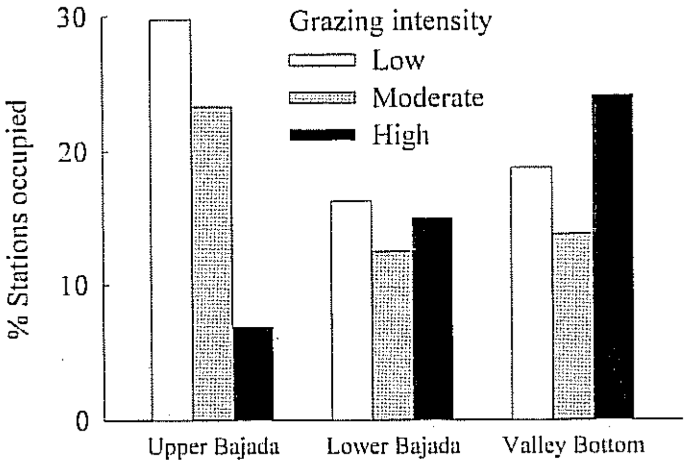

Figure 12. Influence of grazing intensity across topography on occupancy by ferruginous pygmy-owls at survey stations in Semidesert Grasslands, Sonora, Mexico 2000-01.

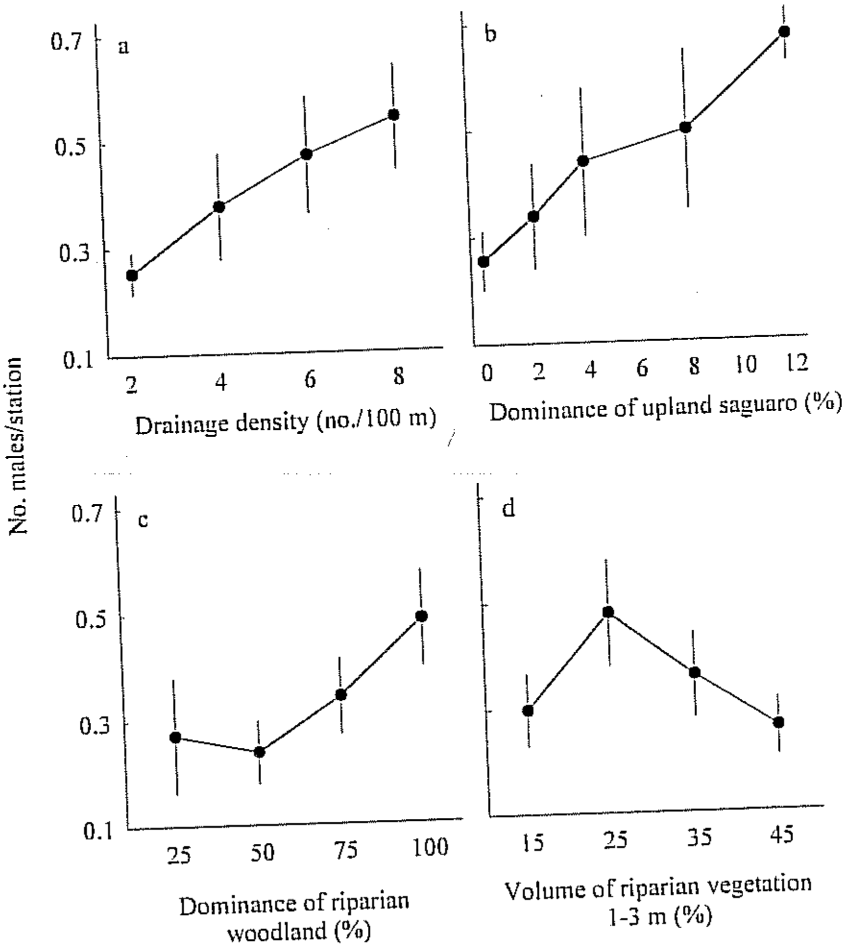

Figure 13. Influence of (a) drainage density (no./100 m), (b) upland saguaro cacti dominance (%), (c) riparian woodland dominance (%), and (d) riparian vegetation volume 1-3 m above ground (%) on relative abundance (no. males/station ± SE) of ferruginous pygmy-owls in Semidesert Grasslands, Sonora, Mexico 2000-01.

Sinaloan Thornscrub: Transects occupied by pygmy-owls had higher abundance of large cacti and different structure and composition of riparian vegetation compared to unoccupied transects (Table 3). Occupancy increased with height of riparian vegetation; 78.6% ($n = 11$ of 14) of transects were occupied where canopy height exceeded 6 m compared to only 21.5% ($n = 14$ of 65) where canopy height was ≤ 4 m (Fig. 14*a*). In contrast to patterns in the Sonoran Desert (Tables 3 and 4), upland canopy height had no effect on occupancy after accounting for other factors ($\chi^2_{117} = 0.46$, $P = 0.80$). Canopy height in riparian and in upland vegetation areas, however, were correlated ($r = 0.24$, $P < 0.0067$). Occupancy was highest where dominance of mesquite and tropical deciduous forest species in riparian areas exceeded 50% (Fig 14*c* and *d*). The association between occupancy and dominance of riparian woodlands varied with size of riparian areas ($\chi^2_{122} = 5.19$, $P = 0.023$, for interaction). As in Arizona Uplands (Fig. 7), occupancy was highest when dominance of woodlands exceeded 35%, however, in Sinaloan Thornscrub, occupancy was highest when riparian areas were narrow (Fig. 15).

Occupancy at stations increased with abundance of both large cacti and large trees, with cacti especially influential (Table 4). Owls occupied only 1.2% ($n = 4$ of 337) of stations where large cacti were absent versus 6.2% ($n = 17$ of 276) where large trees were absent. At 75% of occupied stations where large cacti were absent, large chinos or cottonwoods (*Populus mexicana*) were present. Etcho cacti occurred at 90.1% ($n = 91$ of 101) and saguaros at 10.9% ($n = 11$ of 101) of occupied stations.

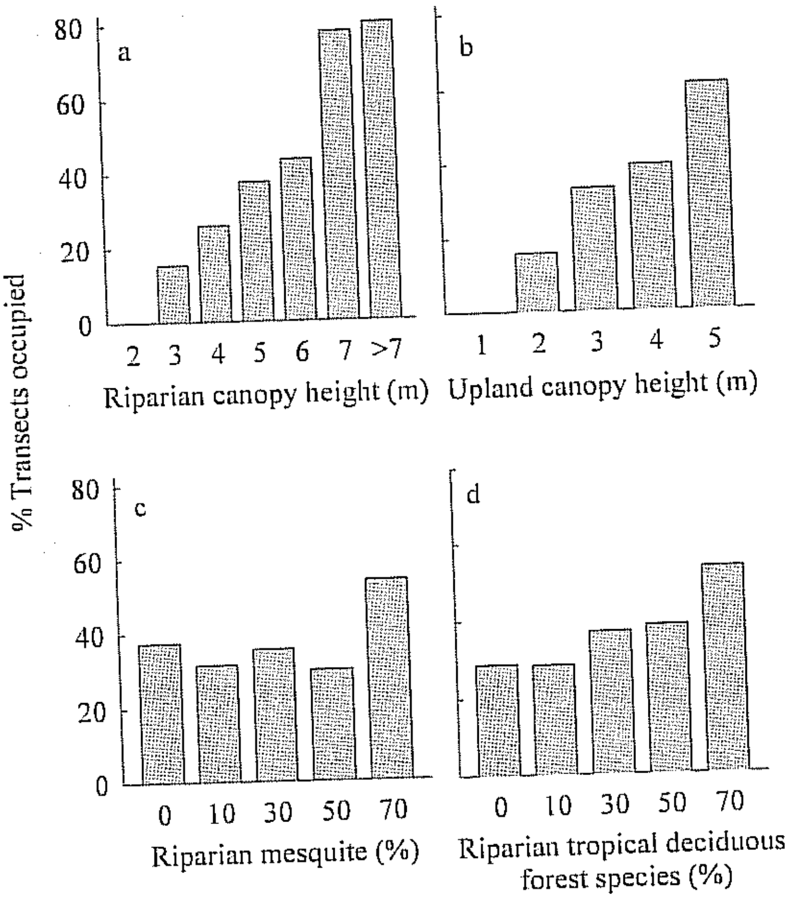

Figure 14. Influence of mean canopy height (m) in (a) upland and (b) riparian vegetation areas and dominance (%) of (c) mesquite and (d) tropical deciduous forest species in riparian areas on occupancy by ferruginous pygmy-owls along survey transects in Sinaloan Thornscrub, Sonora, Mexico 2000-01.

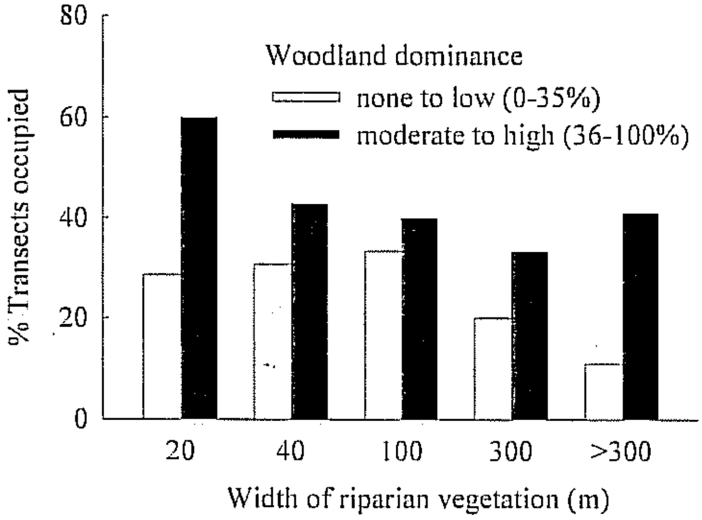

Figure 15. Influence of width of riparian vegetation (m) at high and low dominance (%) of riparian woodland on occupancy by ferruginous pygmy-owls at survey stations in Sinaloan Thornscrub, Sonora, Mexico 2000-01.

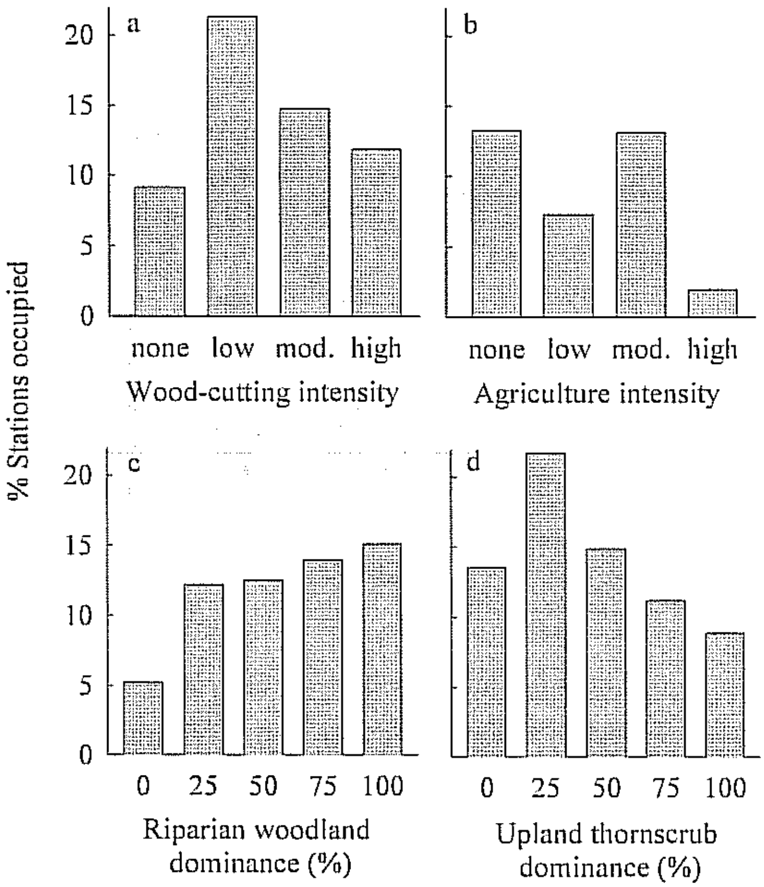

Figure 16. Influence of (a) wood-cutting and (b) agriculture intensity, and (c) dominance of riparian woodland (%), and (d) upland thornscrub on occupancy by ferruginous pygmy-owls at survey stations in Sinaloan Thornscrub, Sonora, Mexico 2000-01.

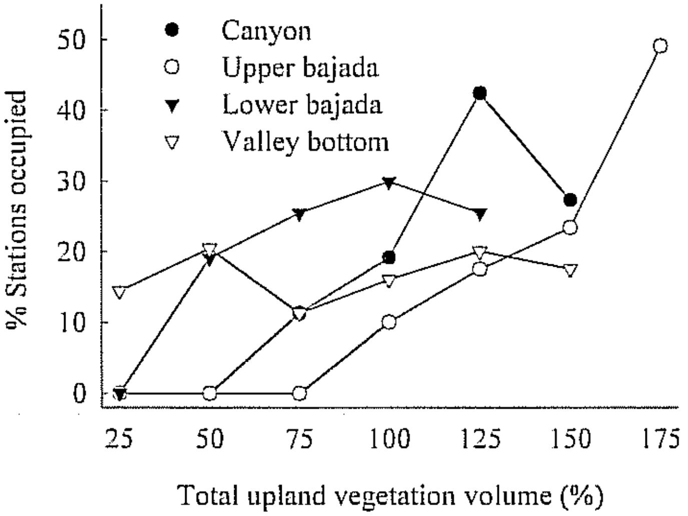

Figure 17. Influence of total upland vegetation volume (%) across topography on occupancy by ferruginous pygmy-owls at survey stations in Sinaloan Thornscrub, Sonora, Mexico 2000-01.

Relative abundance increased with dominance of riparian woodland and upland forest and with dominance of tropical evergreen species in riparian areas (Table 5, Fig. 18). Relative abundance was highest where the volume of upland vegetation between 1 and 3 m above ground was between 30 and 40% (Fig. 18*d*). In contrast to other vegetation communities, there was only a weak association between abundance of pygmy-owls and abundance of large cacti ($t_{43} = 1.65$, $P = 0.11$).

Sinaloan Deciduous Forest: Pygmy-owls occupied 85.7% of transects ($n = 18$ of 21) in this vegetation community, preventing meaningful comparisons between occupied and unoccupied transects. At stations within transects, however, occupancy by pygmy-owls increased with density of large cacti and declined with density of large trees (Table 4, Fig. 19*c* and *d*). Occupancy was highest at moderate volume of riparian vegetation between 1 and 3 m above ground (Fig. 19*e*). Occupancy was greatest when topographic complexity was <100 m and I never found pygmy-owls where complexity was >400 m (Fig. 19*a*). Relative abundance of ferruginous pygmy-owls tended to be highest in areas with low to moderate slope and increased with dominance of tropical deciduous forest species in riparian areas (Table 5).

In contrast to patterns in vegetation communities in northern Sonora, occupancy declined with increasing upland canopy height; I never found pygmy-owls in forests >11 m tall that were often on slopes (Fig. 19*b*). In canyons, ferruginous pygmy-owls were often replaced by Colima pygmy-owls (*Glaucidium palmarum*) in tall tropical forest on steep

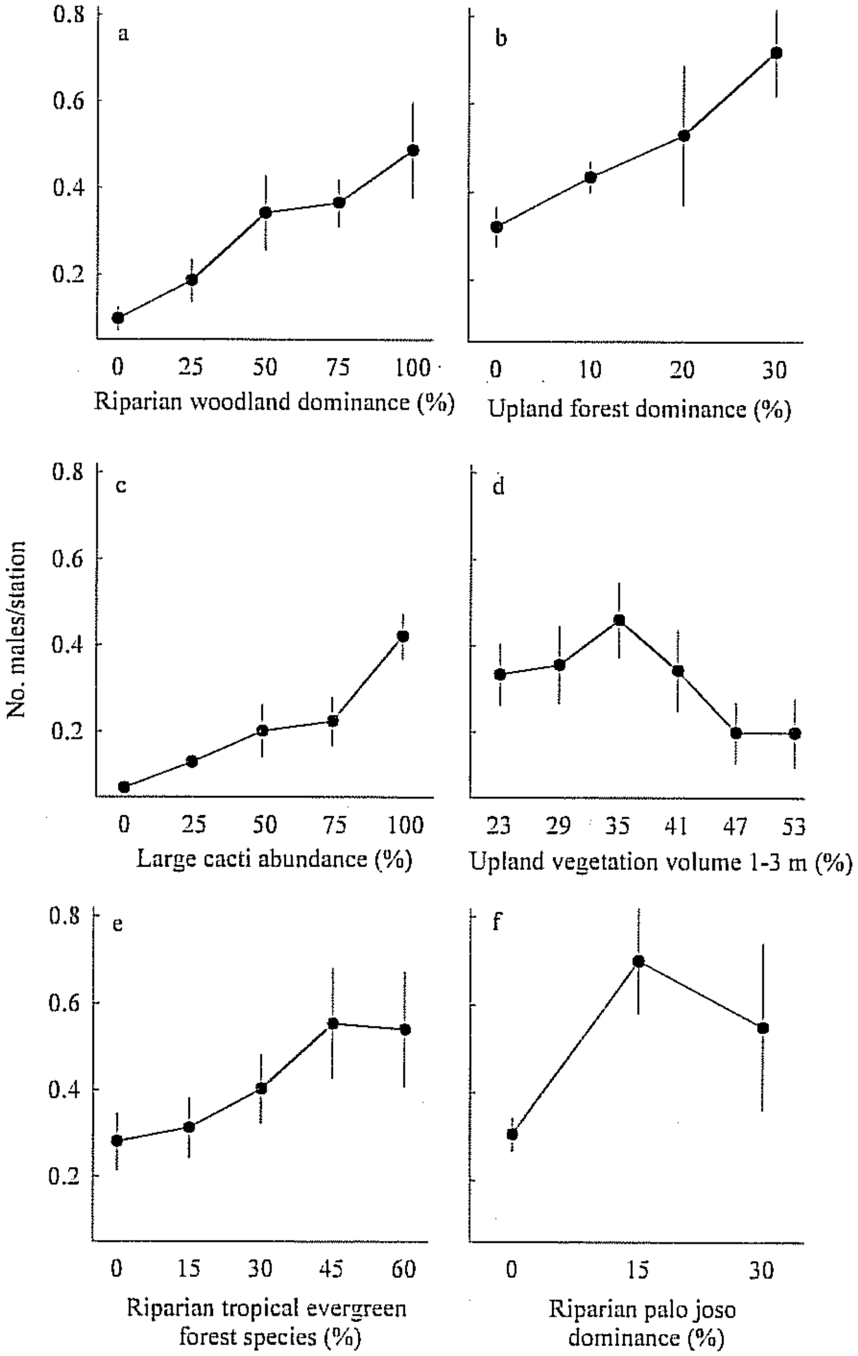

Figure 18. Influence of (a) riparian woodland and (b) upland forest dominance (%), (c) large cacti abundance (% stations present), (d) upland vegetation volume 1-3 m above ground (%), and (e) tropical evergreen species and (f) palo joso dominance (%) in riparian areas on relative abundance (no. males/station ± SE) of ferruginous pygmy-owls along occupied survey transects in Sinaloan Thornscrub, Sonora, Mexico 2000-01.

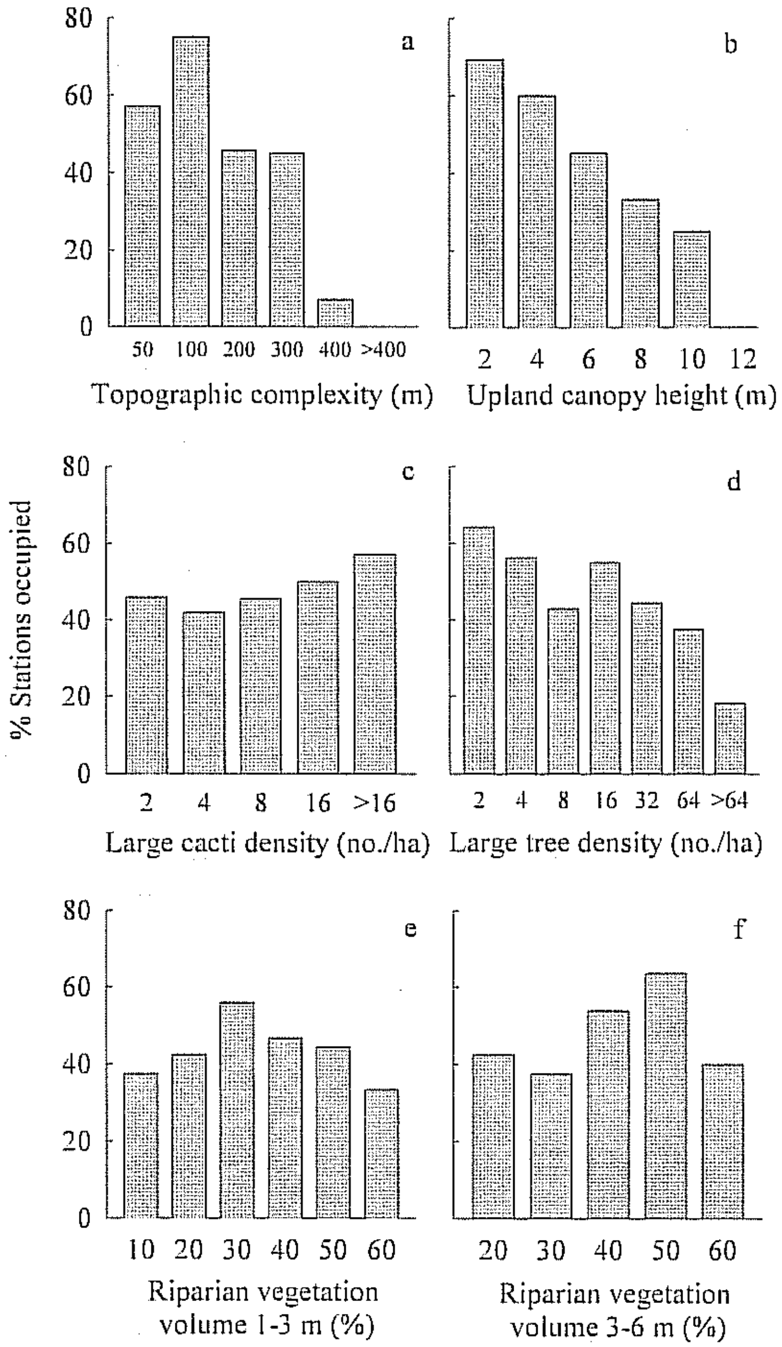

Figure 19. Influence of (a) topographic complexity (m), (b) mean height of upland canopy (m), (c) large cacti and (d) large tree density (no./ha), and (e) riparian vegetation volume 1-3 m and (f) 3-6 m above ground (%) on occupancy by ferruginous pygmy-owls at survey stations in Sinaloan Deciduous Forest, Sonora, Mexico 2000-01.

slopes. At stations where only ferruginous pygmy-owls were detected ($n = 18$), upland canopy height averaged 2.7 ± 0.6 m shorter than those with only Colima pygmy-owls (10.0 ± 0.4 m, $n = 16$, $t_{32} = 4.32$, $P < 0.0001$). Further, at stations where only ferruginous pygmy-owls were detected, topographic complexity averaged 143.3 ± 29.1m lower than those with only Colima pygmy-owls (350.0 ± 21.2 m, $t_{32} = 4.90$, $P < 0.0001$).

Statewide Patterns: *Physiography* - Along transects, occupancy varied with slope, although the association depended on latitude ($\chi^2_{353} = 8.65$, $P = 0.033$, for interaction) and was most evident in upper elevation topographic formations where slope averaged 1.4 ± 0.2 times greater than in lower elevation formations ($t_{374} = 8.07$, $P < 0.0001$, linear contrast) (Tables 6 and 7). Along transects in northern and central Sonora, occupancy declined as slope increased, and I found no owls along transects with high slope in the north (Fig. 20). In the south, however, occupancy was highest along transects with moderate to high slope (Fig. 20). At stations within transects, occupancy declined with topographic complexity especially in canyons, where complexity averaged 3.2 times greater than in other formations (Tables 8 and 9).

Relative abundance of pygmy-owls increased with drainage density, although the relationship varied somewhat with latitude ($t_{153} = 1.77$, $P = 0.078$, interaction) (Table 10). In northern Sonora, relative abundance more than doubled from areas with low (1/100 m) to high (≥7/100 m) drainage density, whereas in the south, no such pattern was evident (Fig. 21*a*). Occupancy at stations increased with drainage width on upper bajadas, but

Table 6: Variables that explained variation in occupancy of ferruginous pygmy-owls along survey transects in Sonora, Mexico 2000-01. *P*-values and odds ratios from multiple logistic regression [a].

	Occupied		Unoccupied			
Variable	$\bar{x}$	SE	$\bar{x}$	SE	*P*	Odds [b]
Coastal Plain [c]	52.4	2.6	47.6	2.6	0.0001	5.81
Sierra Madre Occidental [c]	2.0	0.7	98.0	0.7	0.0004	0.002
Slope x latitude (m/m, km)	47.2	3.6	60.1	4.4	0.0033	0.05
Large cacti abundance (%)	87.2	1.9	54.4	3.0	<0.0001	1.04
Grazing intensity (none-0; low-1; med.-2; high-3)	1.79	0.06	1.83	0.05	0.018	0.21
Riparian vegetation width x woodland dominance (m, %)	60.4	5.9	47.6	5.4	0.011	0.98
Riparian - mesquite dominance (%)	33.1	1.8	23.5	1.4	0.0004	1.04
- chino dominance (%)	7.3	1.0	5.9	0.8	0.013	1.04
Upland - mesquite, ironwood, paloverde, and catclaw dominance (%)	48.5	2.4	42.4	2.2	0.014	1.02

[a] $\chi^2 = 196.1$, df = 13, $n = 374$, $P < 0.0001$, $R^2 = 0.40$.

[b] A 1-unit increase in the explanatory variable results in a change in the odds of owl occupancy.

[c] Values equal percent transects occupied and unoccupied in each physiographic province.

Table 7: Variables that explained variation in occupancy of ferruginous pygmy-owls along survey transects within topographic formations, Sonora, Mexico 2000-01. *P*-values and odds ratios are from multiple logistic regression within topographic formations.

	Occupied		Unoccupied			
Topographic formation Variable	$\overline{x}$	SE	$\overline{x}$	SE	*P*	Odds [a]
Valley Bottoms [b]						
Large cacti abundance (%)	83.0	4.0	36.7	5.7	0.0003	1.04
Grazing intensity x elevation (rank 0-3, 100 m)	8.5	0.9	10.3	0.9	0.0038	0.50
Upland desertscrub x latitude (%, 10 km)	160.6	19.9	75.7	16.3	0.017	0.68
Riparian canopy height (m)	4.9	0.3	4.1	0.2	0.016	1.80
Upland tropical deciduous forest species dominance (%)	16.0	4.0	17.1	4.0	0.014	0.95
Lower Bajadas [c]						
Riparian vegetation width x latitude (10 m, 10 km)	2398.2	597.3	2286.7	342.0	0.013	0.99
Riparian vegetation width x woodland dominance (m, %)	40.6	8.0	45.9	9.2	0.057	0.95
Large cacti abundance (%)	83.4	3.7	47.4	6.0	<0.0001	1.04
Grazing intensity (none-0; low-1; med.-2; high-3)	1.8	0.1	2.0	0.1	0.049	0.39
Riparian - canopy height (m)	4.0	0.2	3.5	0.1	0.019	1.90
- mesquite dominance (%)	40.3	3.5	28.7	2.6	0.0081	1.05
Upper Bajadas [d]						
Slope x latitude (m/m, km)	46.8	3.4	71.6	7.4	0.024	0.47
Large cacti abundance (%)	86.7	3.8	61.0	6.0	0.0006	1.03
Riparian - mesquite dominance (%)	31.7	3.2	18.2	2.7	0.0067	1.04
- chino dominance (%)	8.4	2.0	2.6	0.9	0.027	1.07

Table 7: Continued

Topographic formation Variable	Occupied		Unoccupied			
	$\overline{x}$	SE	$\overline{x}$	SE	P	Odds[a]
Canyons[e]						
Slope x latitude (m/m, km)	100.0	15.6	105.8	15.3	0.0015	0.56
Large cacti abundance (%)	96.5	1.9	75.3	5.1	0.0010	1.10
Riparian - woodland dominance (%)	46.4	6.1	33.4	4.5	0.0048	1.04
- vegetation volume 1-3 m (%)	36.0	2.1	30.5	2.0	0.013	1.10

[a] A 1-unit increase in the explanatory variable results in a change in the odds of owl occupancy.

[b] $\chi^2 = 74.4$, df = 7, $n = 97$, $P < 0.0001$, $R^2 = 0.57$.

[c] $\chi^2 = 60.4$, df = 9, $n = 104$, $P < 0.0001$, $R^2 = 0.45$.

[d] $\chi^2 = 49.6$, df = 6, $n = 103$, $P < 0.0001$, $R^2 = 0.37$.

[e] $\chi^2 = 47.2$, df = 6, $n = 72$, $P < 0.0001$, $R^2 = 0.50$.

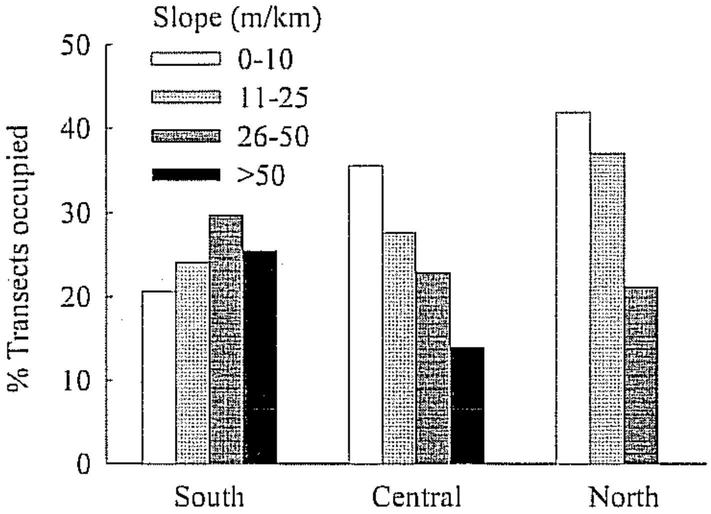

Figure 20. Influence of transect slope (m/km) across latitude on occupancy by ferruginous pygmy-owls along survey transects in Sonora, Mexico 2000-01.

Table 8: Variables that explained variation in occupancy of ferruginous pygmy-owls at survey stations, Sonora, Mexico 2000-01. *P*-values and odds ratios from multiple logistic regression with GEE adjustments [a].

Variable	Occupied		Unoccupied			
	$\bar{x}$	SE	$\bar{x}$	SE	*P*	Odds [b]
Topographic complexity (m)	51.5	3.7	61.3	1.7	0.0003	0.99
Large cacti presence [c]	24.5	0.9	75.5	0.9	<0.0001	21.5
Large trees presence [c]	21.2	0.8	78.8	0.8	<0.0001	2.5
Riparian - woodland dominance (%)	57.9	1.8	42.6	0.9	0.0075	1.9
- vegetation volume 6-12 m (%)	9.5	0.5	6.5	0.1	0.0012	1.03
- mesquite dominance (%)	34.2	1.4	25.9	0.6	0.0015	2.7
- tropical deciduous forest sp. dominance (%)	9.0	1.0	7.5	0.4	0.033	2.3
- palo joso dominance (%)	1.8	0.5	0.5	0.1	0.014	12.1
Upland - forest dominance (%)	8.8	1.1	2.5	0.3	0.019	4.1
- canopy height (m)	3.3	0.08	2.6	0.03	0.0002	1.3
- vegetation volume 6-12 m (%)	5.1	0.3	3.3	0.1	0.025	0.96
- saguaro dominance (%)	4.1	0.4	1.2	0.1	<0.0001	25.8
- hecho dominance (%)	1.2	0.2	0.3	0.1	0.0038	148.1
- tropical evergreen forest species dominance (%)	0.5	0.1	0.3	0.1	0.025	68.7
- mesquite dominance (%)	23.4	1.3	19.4	0.6	0.0003	3.4
- paloverde dominance (%)	16.4	0.9	15.4	0.4	0.0028	3.9
- ironwood dominance (%)	8.1	0.8	7.3	0.3	0.0002	7.0

[a] $\chi^2 = 1554.9$, df = 18, $n = 2432$, $P < 0.0001$.

[b] A 1-unit increase in the explanatory variable results in a change in the odds of owl occupancy.

[c] Values equal percent stations occupied or unoccupied when categorical variable present.

Table 9: Variables that explained variation in occupancy of ferruginous pygmy-owls at survey stations within topographic formations, Sonora, Mexico 2000-01. *P*-values and odds ratios are from multiple logistic regression with GEE adjustments within topographic formations.

Topographic formation Variable	Occupied $\bar{x}$	Occupied SE	Unoccupied $\bar{x}$	Unoccupied SE	*P*	Odds[a]
Valley Bottoms[b]						
Riparian vegetation width x woodland dominance (m, %)	141.9	11.8	100.9	5.8	0.0087	1.01
Large cacti presence[c]	19.4	1.6	35.6	1.9	<0.0001	24.0
Large trees presence[c]	16.7	1.5	61.1	2.0	0.0088	2.51
Riparian - agriculture dominance (%)	1.7	0.8	9.5	0.9	0.052	0.12
- palo joso dominance (%)	4.6	1.3	1.4	0.4	0.013	29.4
- tropical evergreen forest species dominance (%)	7.7	1.9	3.3	0.6	0.042	8.9
Upland - canopy height (m)	3.0	0.09	2.5	0.05	0.0042	1.7
- total vegetation volume (%)	69.6	2.5	74.8	1.4	0.027	0.98
- desertscrub dominance (%)	51.0	3.9	27.6	1.7	0.015	2.5
- tropical deciduous forest species dominance	15.3	2.5	16.9	1.3	0.035	0.17
Lower Bajadas[d]						
Riparian vegetation width x woodland dominance (m, %)	45.5	6.6	43.0	3.2	0.0027	0.99
Large cacti abundance (%)	83.7	2.7	40.9	1.8	<0.0001	22.0
Riparian - mesquite dominance (%)	41.9	3.0	30.4	1.1	0.0027	3.6
- scrub dominance (%)	11.6	2.3	7.5	0.8	0.018	8.1
Upland - canopy height (m)	2.9	0.1	2.4	0.04	0.021	1.7
- desertscrub dominance (%)	56.5	4.5	41.4	1.8	0.010	3.1
Upper Bajadas[e]						
Drainage width x latitude (m, 10 km)	4.4	0.4	2.8	0.2	0.087	0.90
Large cacti presence[c]	17.6	1.5	52.1	2.0	<0.0001	73.7

Table 9: continued.

Topographic formation Variable	Occupied		Unoccupied			
	$\bar{x}$	SE	$\bar{x}$	SE	P	Odds [a]
Large trees presence [c]	11.9	1.3	21.9	1.6	0.0007	2.46
Riparian - vegetation volume 6-12 m (%)	9.0	0.8	5.1	0.2	0.032	1.06
- mesquite dominance (%)	30.9	2.4	22.7	1.1	0.039	1.01
Upland - vegetation volume 1-3 m (%)	32.0	1.3	25.7	0.6	0.026	1.02
- vegetation volume 3-6 m (%)	19.8	1.3	11.3	0.4	0.023	1.03
- large columnar cacti dominance (%)	4.9	0.9	2.0	0.3	0.021	1.07
- mesquite, ironwood, paloverde, catclaw	51.1	3.5	52.7	1.5	0.0018	1.02
Canyons [f]						
Topographic complexity (m)	147.6	10.4	157.5	4.8	0.0008	0.99
Riparian vegetation width x woodland dominance (m, %)	31.3	5.6	16.7	1.2	0.0057	1.03
Large cacti abundance (%)	87.8	3.2	63.9	1.9	0.0051	6.6
Riparian - scrub dominance (%)	6.6	2.1	12.8	1.1	0.029	0.18
Upland - canopy height (m)	4.6	0.3	3.1	0.1	0.0032	1.7
- forest dominance (%)	27.9	5.0	6.8	1.1	0.015	9.6
- vegetation volume 6-12 m (%)	7.5	1.2	4.4	0.3	0.011	0.98
- hecho dominance (%)	2.0	0.7	0.3	0.09	0.011	3 x 10^4
- mesquite dominance (%)	27.2	3.9	26.8	1.3	0.0084	9.8

[a] A 1-unit increase in the explanatory variable results in a change in the odds of owl occupancy.

[b] $\chi^2 = 412.9$, df = 13, $n = 619$, $P < 0.0001$.

[c] Values equal percent stations occupied or unoccupied when categorical variable present.

[d] $\chi^2 = 371.0$, df = 9, $n = 674$, $P < 0.0001$.

[e] $\chi^2 = 400.9$, df = 11, $n = 639$, $P < 0.0001$.

[f] $\chi^2 = 256.0$, df = 12, $n = 491$, $P < 0.0001$.

Table 10: Variables that explained variation in relative abundance of ferruginous pygmy-owls along occupied survey transects in Sonora, Mexico 2000-01. *P*-values and parameter estimates from multiple linear regression [a].

Variable	$\hat{\beta}$	SE	*t*	*P*
Drainage density (no./100 m)	0.016	0.009	1.87	0.063
Large cacti abundance (%)	0.24	0.07	3.54	0.0005
Riparian - vegetation width (m)	0.001	0.0001	4.72	<0.0001
- woodland dominance (%)	0.019	0.06	3.18	0.0018
- agriculture dominance (%)	-0.80	0.31	2.60	0.010
Upland - canopy height (m)	0.045	0.012	3.68	0.0003

[a] $F_{6, 155} = 11.4$, $P < 0.0001$, $n = 162$, $R^2 = 0.31$.

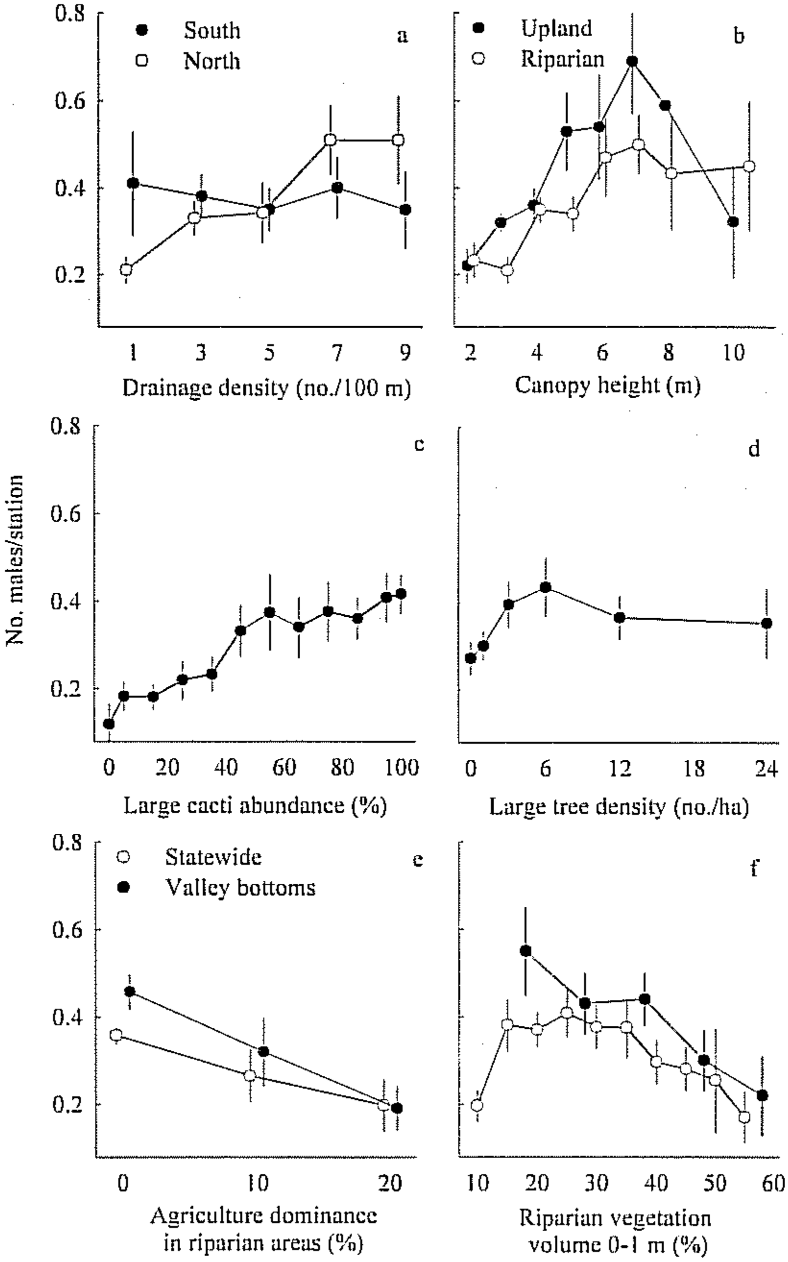

Figure 21. Influence of (a) drainage density (no./100 m) across latitude, (b) mean height of canopy in upland and riparian vegetation areas (m), (c) large cacti abundance (% stations present), and (d) large tree density (no./ha) throughout Sonora, and (e) agriculture dominance (%) and (f) riparian vegetation volume 0-1 m above ground (%)in statewide and in valley bottoms on relative abundance (no. males/station ± SE) of ferruginous pygmy-owls along occupied survey transects in Sonora, Mexico 2000-01.

not on lower bajadas (Table 11, Fig. 22*a*). At stations on upper bajadas, the influence of drainage width also varied somewhat with latitude ($\chi^2_{628} = 2.92$, $P = 0.087$, for interaction). Occupancy increased approximately 3-fold from small to large drainages in northern Sonora, whereas in both central and southern Sonora, occupancy was highest along drainages of moderate width (Fig. 22*b*).

Vegetation - Occupancy increased with dominance of riparian woodlands in all topographic formations and with dominance of upland forests in canyons, where forests were mainly found (Table 6, 7, and 9). Dominance of riparian woodlands often had a greater influence on occupancy when riparian areas were wide (Tables 6 and 9). Along transects on lower bajadas, the influence of width of riparian areas on occupancy varied with latitude ($\chi^2_{90} = 6.11$, $P = 0.013$, for interaction) (Table 7). Occupancy increased with width of riparian areas in northern Sonora but decreased with width of riparian areas in southern Sonora. Occupancy also increased with dominance of mesquite, gallery woodland microphyllous species, tropical deciduous and evergreen forest species, and saguaro and etcho cacti (Table 6 and 8).

The relationship between occupancy by pygmy-owls and total volume of upland and riparian vegetation varied among topographic formations ($\chi^2_{2404} \geq 11.23$, $P \leq 0.011$, interactions), but were often similar within in each formation. Along valley bottoms, occupancy at stations decreased with increasing vegetation volume especially in uplands

Table 11: Variables that explained variation in relative abundance of ferruginous pygmy-owls along occupied survey transects within topographic formations in Sonora, Mexico 2000-01. *P*-values and parameter estimates from multiple linear regression.

Topographic formation Variable	$\hat{\beta}$	SE	*t*	*P*
Valley Bottoms [a]				
Large cacti abundance (%)	0.40	0.12	3.48	0.0012
Riparian - vegetation width (m)	0.00057	0.00019	2.99	0.0046
- agriculture dominance (%)	-1.55	0.46	3.35	0.0017
- vegetation volume 0-1 m (%)	-0.0062	0.0029	2.10	0.042
Lower Bajadas [b]				
Large cacti abundance (%)	0.35	0.087	3.96	0.0004
Riparian woodland dominance (%)	0.19	0.077	2.52	0.016
Upland - vegetation volume 6-12 m (%)	0.018	0.0080	2.00	0.054
- tropical deciduous forest species (%)	0.32	0.15	2.18	0.036
- mesquite, ironwood, paloverde, and catclaw dominance (%)	0.34	0.12	2.58	0.014
Upper Bajadas [c]				
Grazing intensity (none-0; low-1; med.-2; high-3)	-0.077	0.032	2.31	0.026
Riparian - vegetation width (m)	0.0018	0.00042	4.22	0.0001
Upland - vegetation volume 3-6 m (%)	0.0096	0.0023	4.15	0.0002
Canyons [d]				
Variance topographic complexity	-0.00002	0.000001	2.15	0.043
Large trees abundance (%)	0.44	0.13	3.33	0.0031
Riparian - tropical deciduous forest species (%)	0.93	0.24	3.74	0.0011
- mesquite dominance (%)	0.94	0.33	2.77	0.011
Upland - thornscrub or shrub species (%)	-0.77	0.28	2.72	0.013

[a] $F_{4,42} = 7.69$, $P < 0.0001$, $n = 47$, $R^2 = 0.42$.

[b] $F_{5,35} = 8.25$, $P < 0.0001$, $n = 41$, $R^2 = 0.57$.

[c] $F_{3,42} = 12.51$, $P < 0.0001$, $n = 46$, $R^2 = 0.47$.

[d] $F_{5,22} = 5.20$, $P = 0.0027$, $n = 28$, $R^2 = 0.54$.

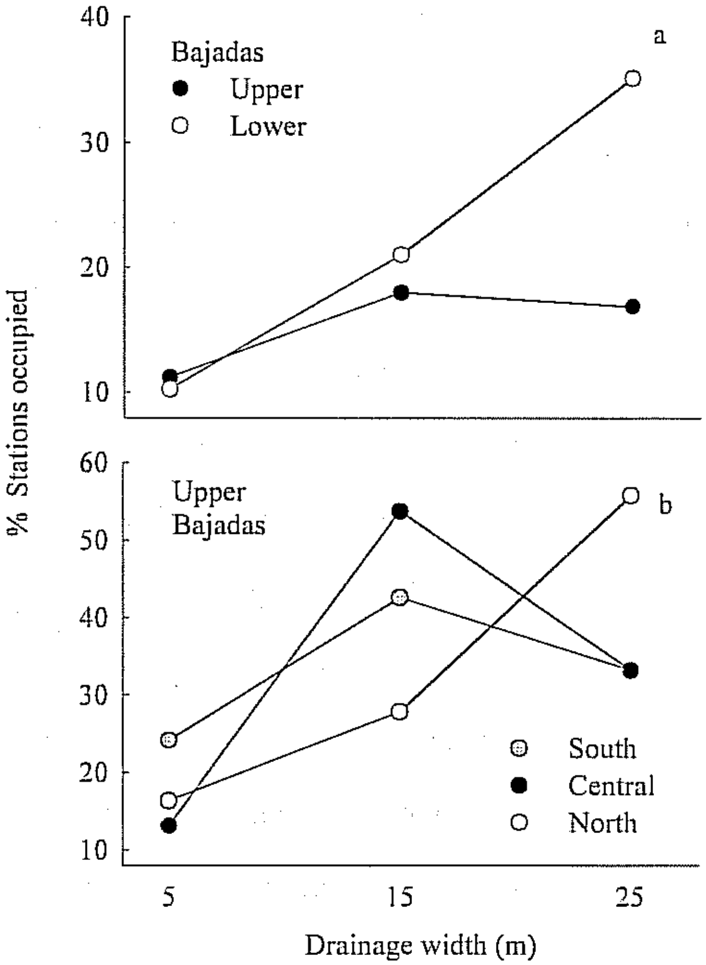

Figure 22. Influence of drainage width (m) on (a) upper and lower bajadas and (b) across latitude on upper bajadas on occupancy by ferruginous pygmy-owls at survey stations in Sonora, Mexico 2000-01.

(Fig. 23). In contrast, on upper bajadas, occupancy increased consistently as vegetation volume increased (Fig. 23).

Of the 6 environmental factors associated with relative abundance of pygmy-owls throughout Sonora, width of riparian areas and height of the upland canopy explained more than 52% of total variation (Table 10). Owl abundance increased markedly with width of riparian areas until 100 m and slightly thereafter. Owl abundance also increased with height of upland canopy to about 7 m, above which it declined sharply (Fig. 21*b*). Because upland vegetation was tallest on steep, southern slopes ($t_{372} = 10.42$, $P < 0.0001$) where ferruginous pygmy-owls were generally not found, the influence of upland canopy height varied somewhat with latitude ($t_{153} = 1.65$, $P = 0.10$, for interaction). Relative abundance tended to decline as volume of riparian vegetation between 0 and 1 m above ground increased, and was highest at moderate to low vegetation volume (Fig. 21*f*).

Cavity substrates - Although occupancy increased with density of large cacti until about 1 per ha (Fig. 24*b*), presence of at least 1 large cactus was more important than abundance or density of cacti in distinguishing occupied from unoccupied stations (Table 8, Fig. 24*a*). Relative abundance of pygmy-owls also increased with both abundance ($t_{155} = 3.54$, $P = 0.0005$) and density ($t_{155} = 2.16$, $P = 0.0033$) of large cacti, with abundance explaining approximately 2.6 times more variation in owl abundance than density.

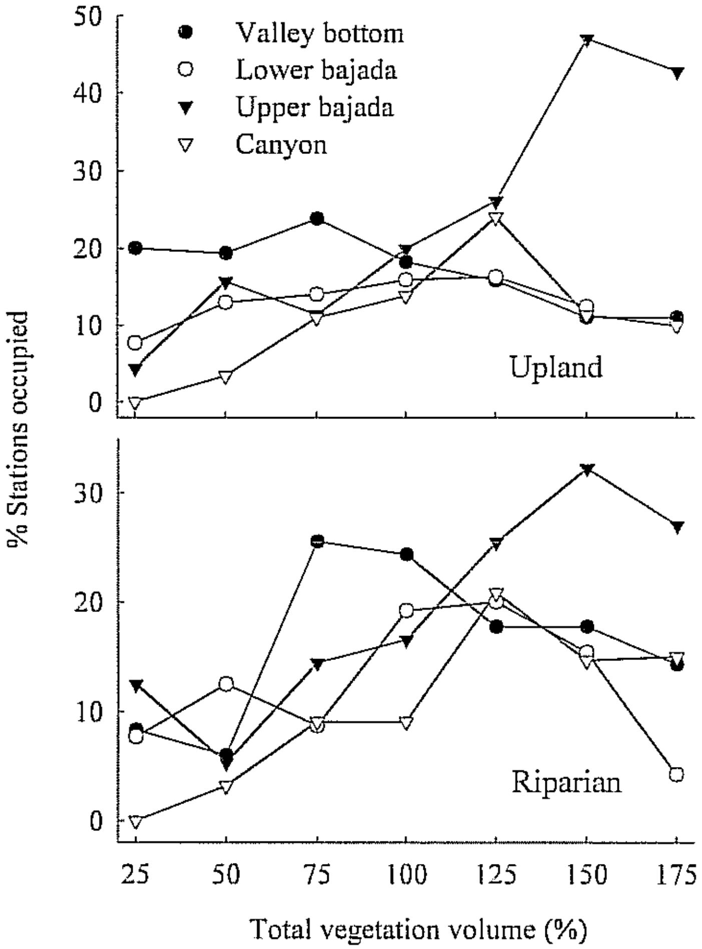

Figure 23. Influence of total upland and riparian vegetation volume (%) across topography on occupancy by ferruginous pygmy-owls at survey stations in Sonora, Mexico 2000-01.

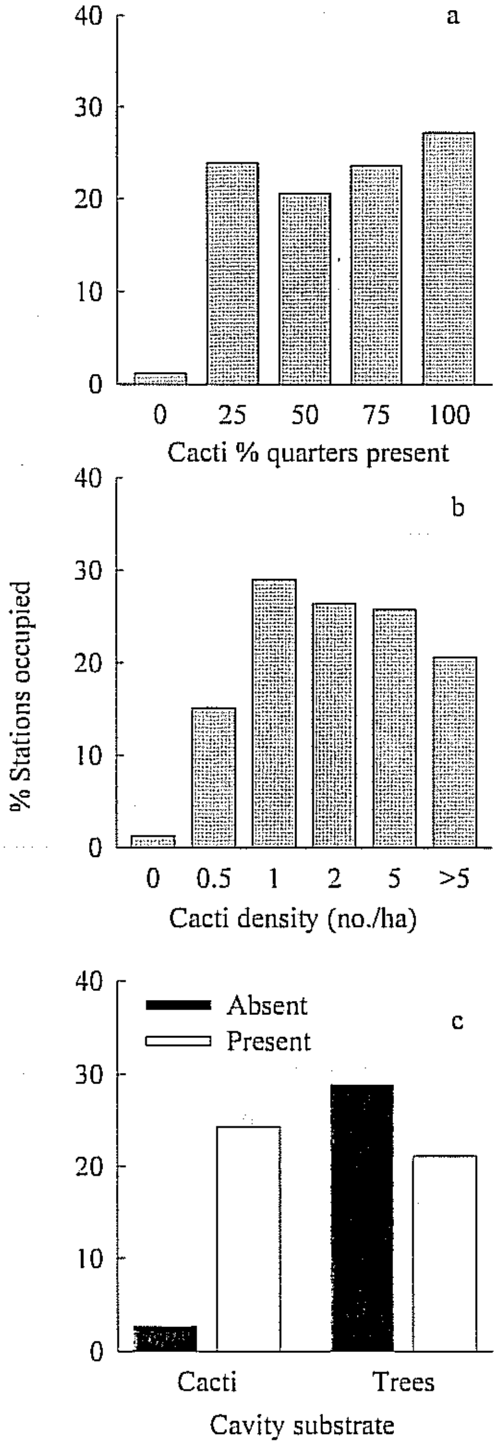

Figure 24. Influence of (a) presence and relative abundance (% quarters present) and (b) density (no./ha) of large cacti, and (c) presence of large cacti and trees on occupancy by ferruginous pygmy-owls at stations Sonora, Mexico 2000-01.

In addition to large cacti, owl occupancy at stations was also associated with presence of large trees, although trees had much less influence than cacti (Table 8). Owls occurred at only 2.7% ($n = 11$ of 402) of stations where large cacti were absent versus 28.9% where large trees were absent (Fig. 24*c*). After accounting for cacti abundance and other influential factors (Table 10), relative abundance of pygmy-owls did not vary with tree density ($t_{154} = 0.12$, $P = 0.90$, regression) (Fig. 21*d*). Relative abundance of pygmy-owls was near zero when large cacti ($t_{166} = 1.15$, $P = 0.25$) but not large trees ($t_{166} \geq 6.37$, $P < 0.0001$, for tests of intercepts = 0) were absent.

Along transects, occupancy by pygmy-owls increased with relative abundance of large cacti in all topographic formations (Tables 7). At stations, however, the influence of abundance of large cacti on occupancy varied somewhat among topographic formations ($\chi^2_{2408} = 6.38$, $P = 0.095$, for interaction). Cacti influenced owl occupancy less at stations on upper bajadas ($Z_{2408} = 1.99$, $P = 0.047$) where cacti were 44% more abundant than in lower elevation topographic formations ($t_{2477} = 11.13$, $P < 0.0001$, linear contrast). Similarly, relative abundance of owls along occupied transects increased with abundance of large cacti only on lower bajadas and valley bottoms (Table 11). Along these transects, cacti were 14.8 ± 6.7% less abundant than in upper elevation topographic formations ($t_{163} = 1.92$, $P = 0.057$, linear contrast) where 76% of occupied transects had maximum (100%) cacti abundance.

Associations between occupancy by pygmy-owls and potential cavity substrates varied depending on the species of substrate considered. Along transects, occupancy was associated most strongly with abundance of saguaros ($\chi^2_{347} = 49.01$, $P < 0.0001$), however, the influence of etcho abundance increased to the south ($\chi^2_{347} = 12.96$, $P = 0.0003$, for etcho x latitude interaction) after considering other influential factors (Table 6). There was no association between occupancy by pygmy-owls and abundance of organ pipe cacti (*Stenocerus thurberi*) or cardón (*Pachycereus pringlei*) ($\chi^2_{347} \leq 0.84$, $P \geq 0.36$). Relationships between relative abundance of pygmy-owls and abundance of these 4 large cacti species were identical to those for owl occupancy along transects. When considering species groups of potential cavity trees (Appendix A), occupancy by pygmy-owls at stations increased more with abundance of gallery woodland microphyllous species ($\chi^2_{2404} = 7.69$, $P = 0.0056$) than with other groups of trees such as tropical evergreen or deciduous forest species.

Land use - Grazing was ubiquitous throughout Sonora and present along 98.4% of transects ($n = 361$ of 367) and 95.2% of stations ($n = 2362$ of 2481) with low to moderate intensity (1.5 ± 0.1). Occupancy by pygmy-owls along transects decreased as grazing intensity increased after adjusting for other factors (Table 6). On lower bajadas, occupancy declined approximately 37.7% from low to high grazing intensity. Along valley bottoms, the influence of grazing intensity on occupancy varied with elevation ($\chi^2_{81} = 8.36$, $P = 0.0038$, for interaction); above 700 m elevation, occupancy decreased with grazing intensity and at elevations below 350 m, occupancy increased with grazing intensity (Fig. 25*a*). Abundance of pygmy-owls decreased as grazing intensity increased on upper bajadas where intensity was higher (2.0 ± 0.1, $t_{163} = 2.61$, $P = 0.010$, linear contrast) than in other formations (1.6 ± 0.1) (Table 11). Abundance of owls, however, was highest at moderate grazing intensity (Fig. 25*b*).

Abundance of pygmy-owls declined as dominance of agriculture in riparian areas increased, especially along valley bottoms where agriculture was much more common than in other formations ($t_{163} = 3.40$, $P = 0.0009$, linear contrast) (Tables 10 and 11, Fig. 21*e*). Agricultural disturbance in riparian areas of valley bottoms was 5.6 times lower at occupied than at unoccupied stations. Agriculture was present at only 7.0% ($n = 28$ of 402) of occupied stations at moderate intensity (2.1 ± 0.1) overall. At stations, owl occupancy was not associated with intensity of wood-cutting ($\chi^2_{2476} = 0.36$, $P = 0.55$), which was present at 35.6% ($n = 143$ of 402) of occupied stations at low to moderate intensity (1.6 ± 0.1). High intensity clear-cutting occurred at only 13.3% of occupied stations and only in the extreme south. Although human-made structures such as houses occurred at 10.7% of occupied stations, there was no association between occupancy and these structures ($\chi^2_{2476} = 0.81$, $P = 0.37$) after considering other factors.

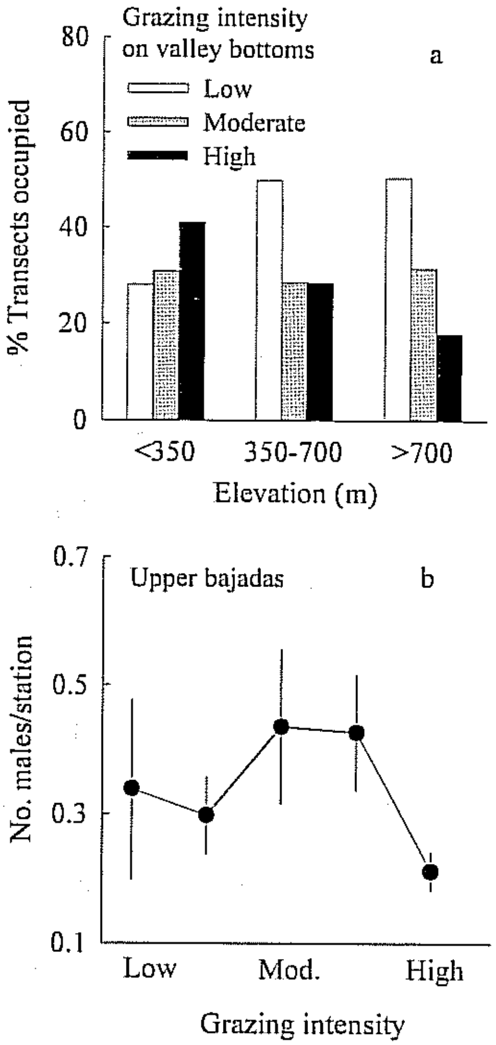

Figure 25. Influence of grazing intensity on (a) valley bottoms across elevation on occupancy, and (b) upper bajadas on relative abundance (no. males/station ± SE) of ferruginous pygmy-owls along survey transects in Sonora, Mexico 2000-01

Sex Differences

Stations where only females were detected ($n = 24$) differed from those where only males were detected ($n = 379$) by having greater dominance and density of large cacti, higher abundance of large trees, and somewhat lower upland canopy height (Table 12). Stations where only females were detected had approximately 350% greater density ($t_{401} = 2.27$, $P = 0.024$, t-test) and 42% greater dominance of large cacti ($t_{401} = 1.85$, $P = 0.065$, t-test), as well as 37% greater abundance of large trees ($t_{401} = 2.08$, $P = 0.038$, t-test) (Fig. 26).

Detections in Upland versus Riparian Areas

The proportion of pygmy-owls detected in upland versus riparian vegetation areas varied among vegetation communities. At stations ($n = 321$) where initial detection locations could be determined (80.1% of total detections), 44.2% were in uplands, 53.3% in riparian areas, and 2.5% included ≥ 1 detections in both upland and riparian areas. Detections were almost evenly distributed between upland and riparian areas in the Sonoran Desert (upland = 48.9%, riparian = 51.1%, $n = 137$) and Sinaloan Thornscrub (upland = 46.3%, riparian = 53.7%, $n = 80$). In Semidesert Grassland, however, most detections were in riparian areas (upland = 40.8%, riparian = 59.2%, $n = 49$) and in Sinaloan Deciduous Forest, most detections were in upland areas (upland = 80.9%, riparian = 19.1%, $n = 47$).

Table 12: Variables that explained variation in occupancy of male ($n = 379$) and female ($n = 24$) ferruginous pygmy-owls at survey stations in Sonora, Mexico 2000-01. P-values and odds from multiple logistic regression with GEE adjustments [a].

	Female		Male			
Variable	$\bar{x}$	SE	$\bar{x}$	SE	P	Odds [b]
Large cacti density (no./ha)	26.3	13.7	7.7	1.9	0.087	0.99
Large tree abundance (%)	65.6	8.1	48.0	2.1	0.0074	0.98
Large cacti dominance (%)	10.3	2.9	6.0	0.6	0.075	0.96
Upland canopy height (m)	3.0	0.3	3.3	0.1	0.038	1.39

[a] $\chi^2 = 163.0$, df = 4, $P < 0.0001$.

[b] Odds >1 equal higher likelihood of occupancy by a male.

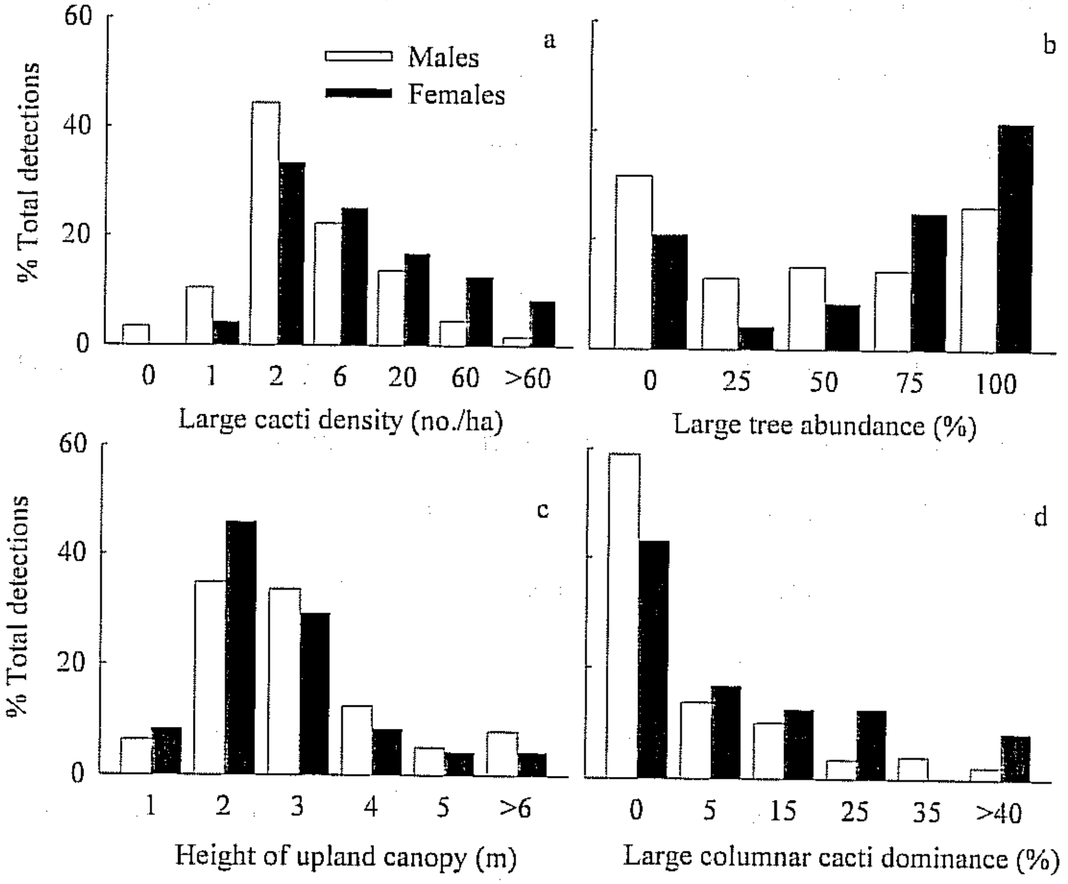

Figure 26: Influence of (a) large cacti density (no./ha), (b) large tree abundance (% quarters present), (c) mean height of upland canopy (m), and (d) dominance of large columnar cacti (%) on detection of male versus female ferruginous pygmy-owls in Sonora, Mexico 2000-01.

Odds of detecting a pygmy-owl in riparian areas increased with increasing size of riparian zones, canopy height, and dominance of woodlands (Table 13). Odds of detecting a pygmy-owl in upland areas increased as volume of upland vegetation between 0 and 1 m, and 3 and 6 m above ground increased. More pygmy-owls were detected in upland areas when width of riparian vegetation zones were ≤100 m or volume of upland vegetation between 3 and 6 m above ground was >20%. Overall, only 2.8% ($n = 4$ of 142) of detections in riparian areas occurred when volume of upland vegetation between 3 and 6 m exceeded 40%. In Sinaloan Thornscrub, occupancy in uplands increased with large cacti density ($\chi^2_{71} = 3.56$, $P = 0.059$), which was 7 times higher than at stations where owls were detected in riparian areas ($t_{78} = 2.53$, $P = 0.013$). Gallery woodland deciduous species were uncommon (4.7 ± 1.4% dominance) at stations where owls were detected in riparian areas. With the exception of the lower Río Yaqui, when dominance of gallery woodland deciduous species was ≥33% owls were detected in either uplands ($n = 7$ of 12) or in woodlands on terraces ($n = 5$ of 12) rather than in deciduous woodlands along drainages.

Geographic Trends in Abundance and Environment

Statewide and Regional Patterns: The relationship between relative abundance and longitude varied with elevation ($t_{369} = 3.61$, $p = 0.0003$) and latitude ($t_{369} = 4.27$, $P < 0.0001$, for interactions). Relative abundance was high in northern and southern Sonora and low in central Sonora ($t_{373} = 6.47$, $P < 0.0001$, quadratic term) (Fig. 27). In northern

Table 13: Variables that explained variation in initial detection locations of ferruginous pygmy-owls in riparian (n = 142) or upland (n = 164) vegetation areas at survey stations in Sonora, Mexico 2000-01. P-values and odds from multiple logistic regression with GEE adjustments [a].

	Riparian		Upland			
Variable	$\bar{x}$	SE	$\bar{x}$	SE	P	Odds [b]
Riparian - vegetation width (m)	204.2	19.8	79.9	7.0	0.0005	1.01
- woodland dominance (%)	63.1	2.6	47.6	3.0	0.0055	1.01
Upland - vegetation volume 0-1 m (%)	26.0	1.1	28.2	0.9	0.056	0.91
- vegetation volume 3-6 m (%)	12.3	0.7	19.7	1.1	0.0004	0.96
Grazing intensity (low-1; med.-2; high-3)	1.7	0.1	1.8	0.1	0.066	0.72

[a] $\chi^2 = 341.2$, df = 5, $P < 0.0001$.

[b] Odds >1 equal higher likelihood of initial detection in riparian vegetation.

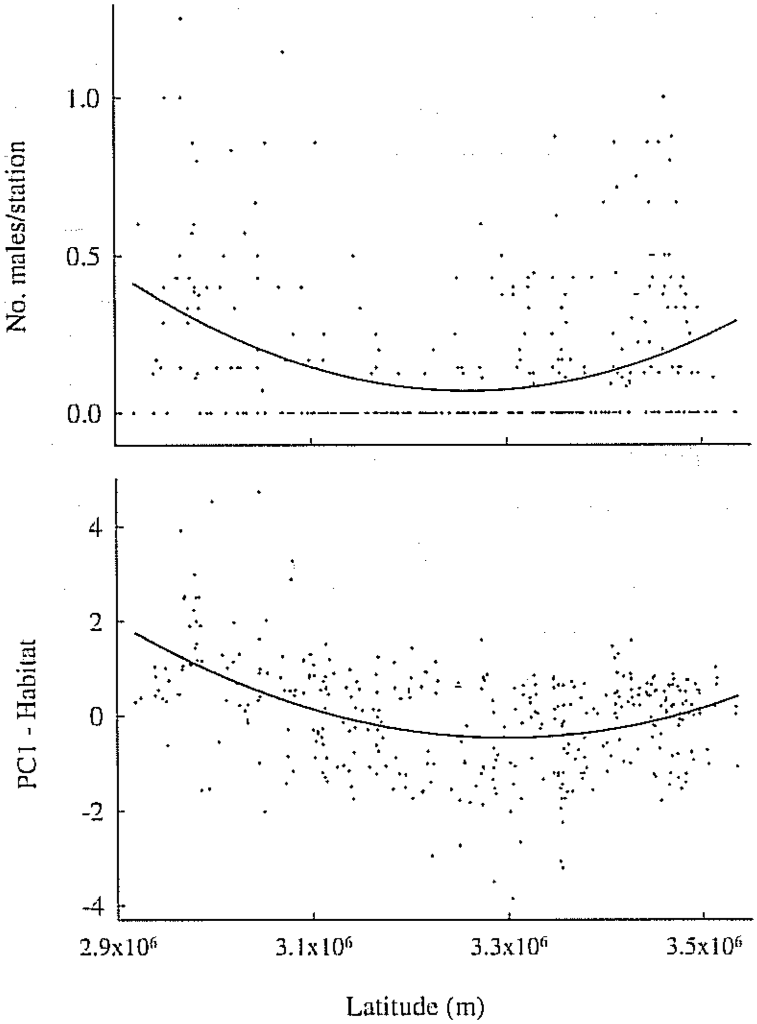

Figure 27. Relative abundance (no. males/station) of ferruginous pygmy-owls and the first Principal Component of environmental factors that comprised habitat varied with latitude (m) across Sonora, Mexico 2000-01. Latitude noted in UTM northing Zone 12 coordinates.

Sonora within 150 km of Arizona, relative abundance was highest between 600 and 800 m elevation ($t_{144} = 4.16$, $P < 0.0001$, quadratic term) and near the latitudinal and longitudinal centers of distribution ($t_{144} \geq 3.11$, $P \leq 0.0023$, quadratic terms) (Fig. 28). In southern Sonora within 150 km of Sinaloa, relative abundance was highest near 400 m elevation ($t_{65} = 1.96$, $P = 0.055$, quadratic term), decreased with longitude ($t_{66} = 2.96$, $P = 0.0043$), and did not vary across latitude ($t_{66} = 1.27$, $P = 0.209$) (Fig. 28).

Patterns in abundance of pygmy-owls often corresponded with patterns in abundance of environmental factors that comprised owl habitat. Throughout Sonora, the relationship between owl abundance and latitude closely matched patterns along the first principal component generated from environmental factors that explained variation in owl abundance (34.7% of variation in riparian woodland dominance, width of riparian area, abundance of large cacti, and upland canopy height). Both relationships exhibited nearly identical amplitude, wavelength, and skew (Fig. 27). Similarly, in northern Sonora, the relationship between owl abundance and latitude, longitude, and elevation matched patterns along the first principal component generated from environmental factors that explained variation in owl abundance (28.6% of variation in drainage density, riparian woodland dominance, abundance of large cacti, upland ironwood dominance, and upland canopy height) (Fig. 28). In southern Sonora, however, patterns of relative abundance across elevation and latitude did not correspond with the first principal component generated from environmental factors that explained variation in owl abundance (56.8%

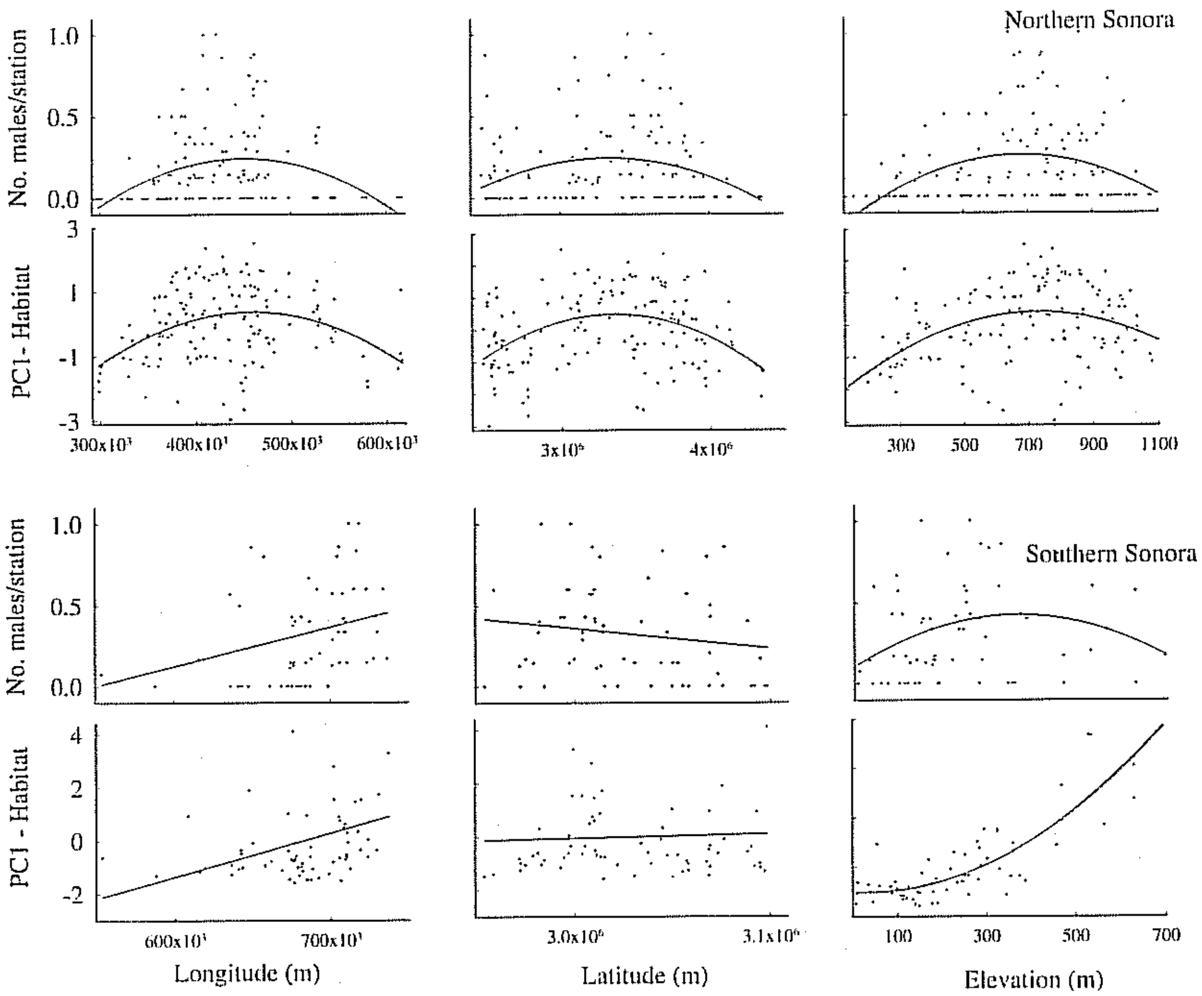

Figure 28. Relative abundance (no. males/station) of ferruginous pygmy-owls and the first Principal Component of environmental factors that comprised habitat varied with longitude (m), latitude (m), and elevation (m) in northern and southern Sonora, Mexico 2000-01. Latitude and longitude noted in UTM northing and easting Zone 12 coordinates.

of variation in slope, riparian woodland dominance, riparian and upland canopy height, and volume of upland vegetation between 6 and 12 m above ground) (Fig. 28).

Patterns within Vegetation Communities: Trends in abundance of pygmy-owls across latitude, longitude, and elevation varied among vegetation communities. In Arizona Uplands, relative abundance decreased with longitude and increased with latitude and elevation (Table 14, Figs. 29-31). In contrast, in Semidesert Grassland, abundance decreased with elevation and increased with longitude (Table 14, Figs. 29 and 30). Longitude had approximately twice the influence on relative abundance in Arizona Uplands and Semidesert Grassland after adjusting for the effects of latitude (Table 14). On the Plains of Sonora, relative abundance increased with latitude and elevation. In Lower Colorado River Valley desertscrub, pygmy-owls occurred near the periphery of the Arizona Upland subdivision but not below 250-m elevation. In Sinaloan Thornscrub and Deciduous Forest, relative abundance decreased with elevation and latitude (Table 14) (Figs. 29 and 31). In Sinaloan Thornscrub, owls occupied only 6.3% ($n = 2$ of 32) of transects above 550 m and only 13.6% ($n = 8$ of 59) of transects in the northern half Sinaloan Thornscrub.

Patterns of relative abundance within vegetation communities often corresponded with abundance of important environmental factors. In Semidesert Grassland ($t_{53} \geq 2.13$, $P \leq 0.038$) and Sinaloan Thornscrub ($t_{131} \geq 5.07$, $P \leq 0.001$), for example, relative abundance of pygmy-owls and large cacti decreased along the same geographic gradients (Table 14).

Table 14: Geographic trends in relative abundance of ferruginous pygmy-owls in vegetation communities in Sonora, Mexico 2000-01. Parameter estimates from multiple (latitude and longitude) or simple (elevation) linear regression.

		South to north			West to east			Elevation		
Vegetation community	*n*	$\hat{\beta}^{a}$	SE	*P*	$\hat{\beta}^{a}$	SE	*P*	$\hat{\beta}^{b}$	SE	*P*
Arizona Upland	69	0.011	0.006	0.087	0.020	0.007	0.007	0.052	0.017	0.004
Lower Colorado River Valley	20	-0.005	0.003	0.131	0.002	0.002	0.678	0.005	0.012	0.715
Central Gulf Coast	21	-0.004	0.009	0.663	-0.013	-0.013	0.381	0.008	0.029	0.779
Plains of Sonora	65	0.007	0.004	0.080	0.006	0.006	0.409	0.027	0.011	0.016
Semidesert Grassland	56	-0.015	0.009	0.110	-0.026	-0.026	0.007	-0.107	0.030	<0.001
Sinaloan Thornscrub	140	-0.008	0.002	<0.001	0.001	0.001	0.700	-0.035	0.008	<0.001
Sinaloan Deciduous Forest	21	-0.050	0.026	0.071	-0.004	-0.004	0.933	-0.093	0.051	0.085
All communities	392	-0.001	0.001	0.288	0.000	0.002	0.972	0.002	0.004	0.608

[a] Average change in relative abundance across 10-km intervals.

[b] Average change in relative abundance across 100-m intervals.

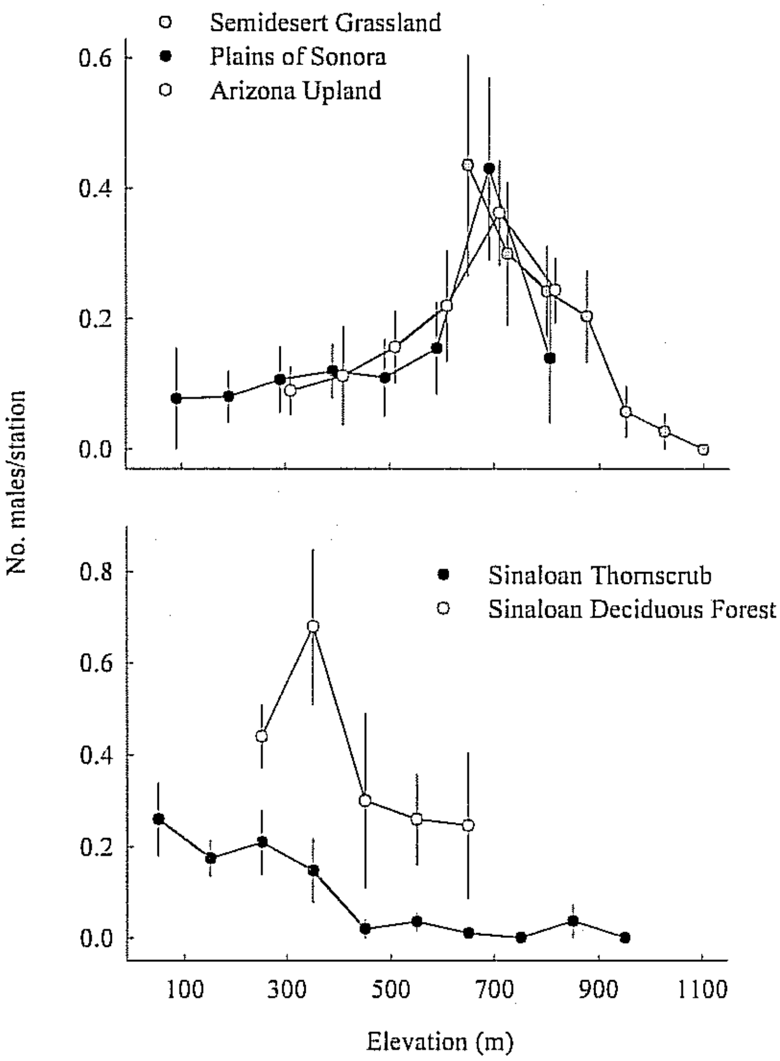

Figure 29. Influence of elevation (m) across vegetation communities on relative abundance (no. males/station ± SE) of ferruginous pygmy-owls along survey transects Sonora, Mexico 2000-01

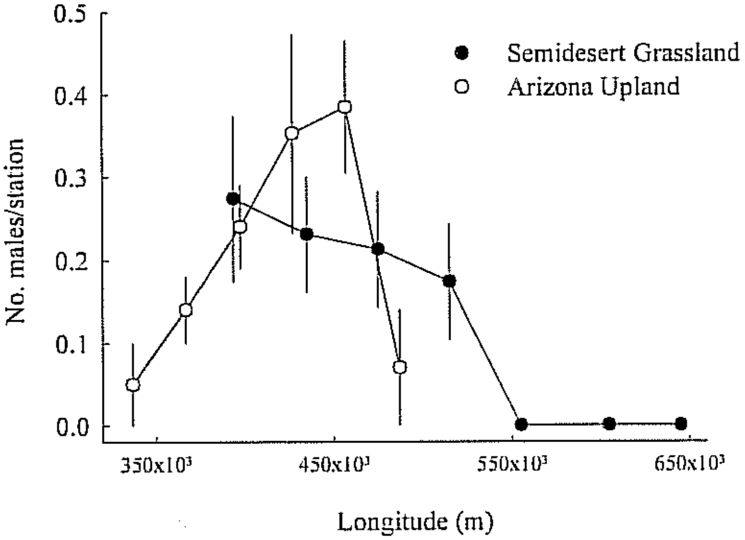

Figure 30. Influence of longitude (m) in Arizona Upland desertscrub and Semidesert Grasslands on relative abundance (no. males/station ± SE) of ferruginous pygmy-owls along survey transects Sonora, Mexico 2000-01. Longitude noted in UTM easting Zone 12 coordinates.

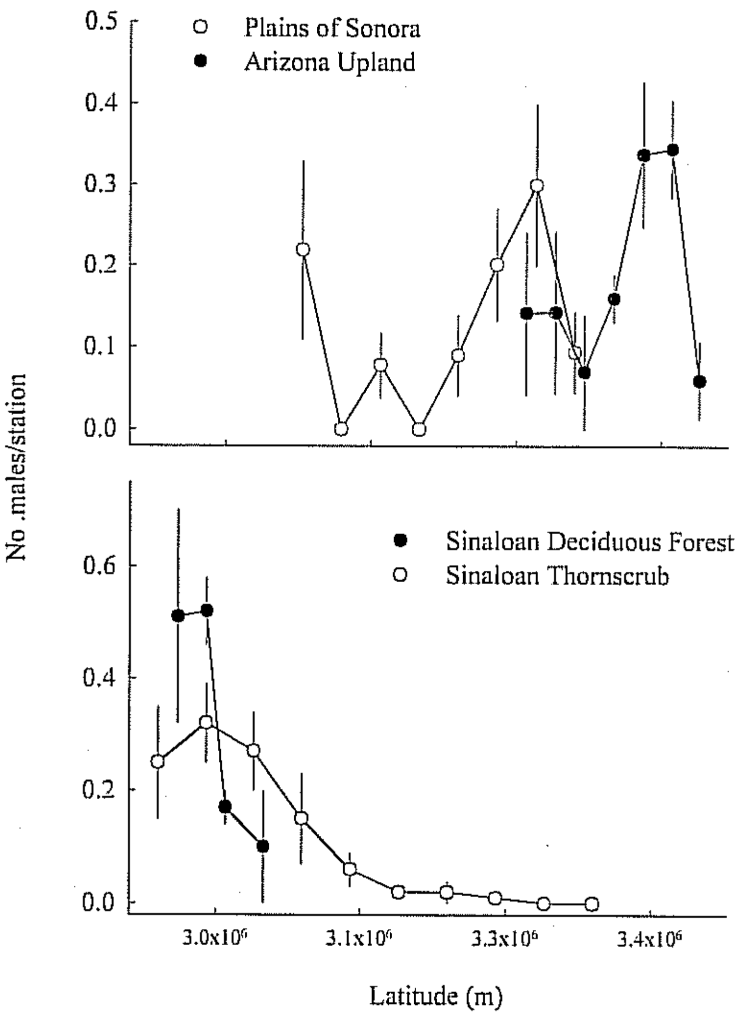

Figure 31. Influence of latitude (m) in Arizona Upland and Plains of Sonora desertscrub, Sinaloan Thornscrub and Sinaloan Deciduous Forest on relative abundance (no. males/station ± SE) of ferruginous pygmy-owls along survey transects in Sonora, Mexico 2000-01. Latitude noted in UTM northing Zone 12 coordinates.

In Arizona Uplands, relative abundance was highest at elevations where riparian mesquite and upland ironwood dominance where greatest ($t_{63} \geq 2.52$, $P \leq 0.014$, regression). In Lower Colorado River Valley desertscrub, owls were only found in locations where dominance of riparian woodland was high ($t_{19} \geq 2.22$, $P \leq 0.040$, regression).

Patterns across Topographic Formations: Density of owls varied across topographic formations within each vegetation community (Table 2). In Sinaloan Thornscrub, density on upper bajadas was approximately 3 times greater than on lower bajadas and almost 2 times greater than along valley bottoms (Table 2). In Plains of Sonora desertscrub and Semidesert Grassland, density on upper bajadas was 17 and 2.5 times greater than on lower bajadas, respectively. In Arizona Upland desertscrub, however, density on lower bajadas was 4.5 times greater than on upper bajadas and 2.5 times greater than along valley bottoms. Densities along valley bottoms were typically similar to vegetation community-wide estimates. Densities in canyons were low except in Sinaloan Deciduous Forest where canyon land cover was high (67%) and in Plains of Sonora desertscrub where canyons were rare (3%) (Table 2) and topographic complexity was low. Density and relative abundance estimates among topographic formations generally corresponded, although, density was often higher on bajadas and lower along valley bottoms than suggested by relative abundance estimates (Table 2).

Patterns of pygmy-owl abundance within topographic formations often corresponded with patterns of important environmental factors. Abundance of large cacti, for example, was 33 to 67% higher ($t \geq 3.01$, df ≥ 355, $P \leq 0.0028$) on upper than lower bajadas in the 3 vegetation communities where pygmy-owl density was highest on upper bajadas (Table 2). In Arizona Uplands where owl density was much higher on lower bajadas, however, abundance of large cacti was nearly equal on upper and lower bajadas ($t_{420} = 0.69$, $P = 0.49$). Additionally, stations on lower bajadas in Arizona Uplands had 13% taller upland canopy height ($t_{420} = 2.43$, $P = 0.015$), 28% greater upland mesquite dominance ($t_{420} = 2.20$, $P = 0.029$), and 30% greater riparian woodland dominance ($t_{420} = 2.47$, $P = 0.014$, linear contrasts) than those on upper bajadas.

Distribution of Abundance

Across Sonora, owl abundance matched the negative binomial distribution closely (Fig. 32) and abundance was moderately clumped (standardized Morisita index of dispersion = 0.50, $s^2/\bar{x}$ ratio = 3.89). Four or more pygmy-owls occurred along only 18.9% of transects but 72.1% of owls were aggregated along these transects. In contrast, 0 or 1 owl occurred on 69.7% of transects. Relative abundance was spatially autocorrelated, as variation in relative abundance within landscapes was 4.3 times lower than that among landscapes ($t_{252} = 9.79$, $P < 0.0001$, t-test). Relative abundance was high in northern and southern Sonora and low in central Sonora (Fig. 27). Large-scale abundance patterns across latitude in the northern portion of pygmy-owls' range followed a bimodal

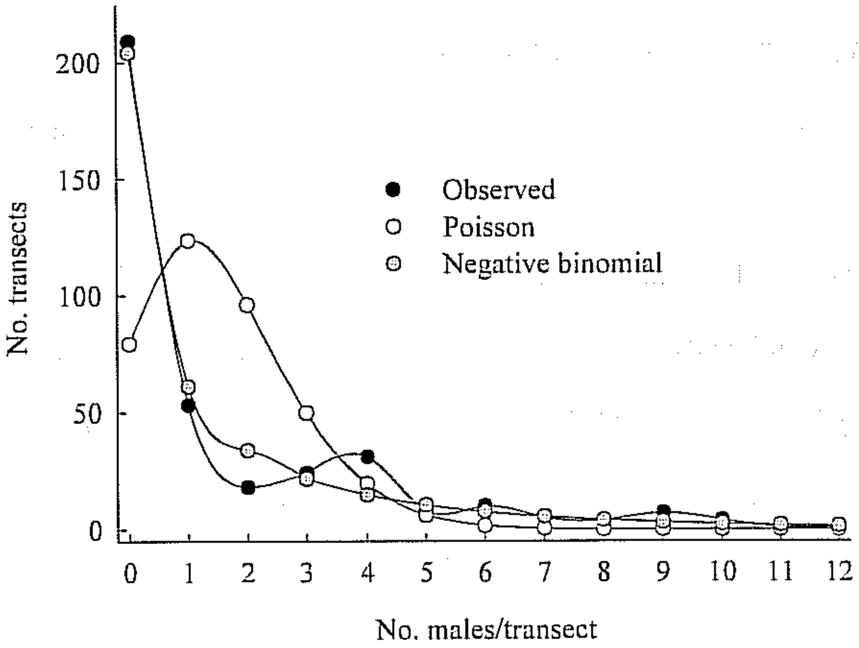

Figure 32. Observed and expected frequencies of the number of male ferruginous pygmy-owls detected along 376 transects in Sonora, Mexico 2000-01. Expected frequencies based on Poisson and negative binomial distributions typical of random and aggregated dispersion respectively. Number of males per transect weighted by the number of stations/transect.

distribution; a broad plateau of high abundance occurred in the south followed by a narrow trough of low abundance in central Sonora and a spike in the north.

Dispersion

Dispersion patterns of occupied landscapes varied throughout Sonora. In northern Sonora, distances between occupied landscapes were lower in the center of the region and increased to the east and west ($t_{45} = 2.49$, $P = 0.016$, quadratic term). Nearest-known occupied landscapes ranged from 7 to 31 km apart (16 ± 2.6 km) in north-central Sonora, 13 to 39 km (23.9 ± 3.8 km) in northeastern Sonora, and 6 to 75 km (21.2 ± 2.9 km) in northwestern Sonora. Nearest-known-neighbor distances were lower in northern and southern Sonora and slightly higher in central Sonora ($t_{92} = 2.06$, $p = 0.042$, quadratic term). Dispersion of occupied landscapes in central Sonora ranged from 9 to 51 km and averaged 22.9 ± 2.3 km.

Floristic Description of Pygmy-owl Habitat

<u>Statewide Patterns</u>: Composition of riparian vegetation at occupied stations varied among vegetation communities. Mesquite was dominant in all communities except Sinaloan Deciduous Forest (Table 15). Chino occurred in all vegetation communities, although

Table 15: Percent dominance of overstory plant species or species groups in riparian vegetation at stations occupied by ferruginous pygmy-owls in 4 vegetation communities of Sonora, Mexico.

	Sonoran Desert		Semidesert Grassland		Sinaloan Thornscrub		Sinaloan Deciduous Forest	
Species or group [a]	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
Ironwood	10.8	1.4	0.3	0.3	0.7	0.5		
Catclaw acacia	10.2	1.2	15.3	2.3	2.4	0.8		
Mesquite	39.4	1.9	56.5	2.9	25.5	2.6	5.2	2.1
Paloverde	14.5	1.3	5.0	1.3	2.0	0.7	0.6	0.6
Chino	9.1	1.5	4.6	1.4	10.8	1.8	4.6	1.7
Gallery woodland deciduous sp.	1.4	0.7	4.9	2.2	6.3	1.9	1.5	0.9
Riparian scrub sp.	3.4	0.9	3.4	1.4	0.2	0.2	1.3	1.0
Mauto	0.5	0.3			8.5	1.8	5.9	1.6
Torote or copal	0.9	0.4			0.8	0.5	2.0	0.8
Boat-thorn acacia	0.3	0.2			4.5	1.2	5.9	1.7
Guasima	0.2	0.2			7.4	1.4	9.6	2.9
Bebelama and tempisque	0.2	0.1					2.3	0.9
Tepeguaje					0.7	0.5	4.5	1.5
Palo joso					6.9	1.7	1.0	1.0
Kapok					0.9	0.5	4.4	1.4
Amapa					0.4	0.2	4.6	1.5
Fig					0.9	0.3	13.3	2.5
Mexican bald-cypress					4.2	1.8	10.3	3.3
Uvalama					1.3	0.9	3.0	1.4
Other species	9.1		10.0		15.6		20.0	
Stations occupied	183		64		100		52	

[a] See Appendix A for species groups and Latin names.

chino dominance was approximately 2 times greater in the Sonoran Desert and Sinaloan Thornscrub where it comprised 10.0 ± 1.5% of overstory vegetation ($t_{395} = 2.68$, $P = 0.0077$, linear contrast). Gallery woodland deciduous species occurred in all communities, although dominance was roughly 3 times greater in Semidesert Grassland and Sinaloan Thornscrub where they comprised 5.5 ± 1.5% of overstory vegetation at occupied stations ($t_{395} = 2.69$, $P = 0.0075$). Plant species richness was lowest in Semidesert Grassland and highest in Thornscrub, where plants of both Sonoran and Sinaloan affinities occurred. In Sinaloan Deciduous Forest, tropical evergreen species comprised 44.0 ± 2.5% of riparian vegetation and were 2.5 times more common than in Thornscrub ($t_{395} = 8.61$, $P < 0.0001$, linear contrast). In comparison, tropical deciduous forest species were only 55% more common in Sinaloan Deciduous Forest ($t_{395} = 3.30$, $P = 0.001$, linear contrast).

Across Sonora, composition of vegetation in upland areas was more variable than that in riparian areas at occupied stations (Table 16). In desertscrub and grasslands of northern Sonora, microphyllous species dominated upland vegetation (79.5 ± 2.0%) (Table 16). Sinaloan Thornscrub and Deciduous Forest included numerous broadleaf species (7.2 ± 0.6%) however, such as torote (*Bursera* sp.), kapok (*Ceiba acuminata*), and amapa (*Tabebuia* sp.). Succulents occurred in all regions (8.2 ± 0.7%) but were approximately 2 times more common in the Sonoran Desert than in other vegetation communities ($t_{393} = 4.52$, $P < 0.0001$, linear contrast). In northern regions, understory species were characterized by subshrubs [(e.g. bursage (*Ambrosia* sp.) and brittlebush (*Encelia* sp.)]

Table 16: Percent dominance of overstory plant species or species groups in upland vegetation associations at stations occupied by ferruginous pygmy-owls in 4 vegetation communities of Sonora, Mexico.

	Sonoran Desert		Semidesert Grassland		Sinaloan Thornscrub		Sinaloan Deciduous Forest	
Species or group [a]	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
Mesquite	24.2	1.6	52.0	2.8	14.3	2.1	3.6	1.4
Paloverde	27.0	1.4	13.9	2.8	6.8	1.2	0.6	0.6
Ironwood	16.0	1.3	0.9	0.5	2.6	1.0		
Ocotillo	3.0	0.5	2.6	0.7	0.2	0.2		
Saguaro	6.5	0.8	6.3	1.1	0.3	0.1		
Catclaw acacia	1.1	0.3	8.3	1.8				
Creosote	9.1	1.3	5.2	1.6				
Cardón	1.6	0.6						
Organ pipe	1.3	0.4			0.4	0.2	1.8	0.2
Agricultural sp.	0.7	0.4			3.2	1.3	0.6	0.6
Torote and copal	0.8	0.3			5.8	1.1	14.1	1.7
Boat-thorn acacia	0.2	0.1			19.4	2.2	16.6	2.7
Jatropha cordata	0.3	0.2			3.9	0.9	1.3	0.7
Mauto					9.9	1.4	36.6	2.1
Etcho					2.3	0.7	4.9	1.1
Tepeguaje					2.3	0.9	0.9	0.6
Kapok					2.6	0.6	2.5	0.5
Amapa					0.7	0.3	2.9	0.7
Brasil							1.8	0.9
other species	8.0		10.8		25.3		11.8	
Stations occupied	182		64		98		54	

[a] See Appendix A for species groups and Latin names.

and grass mixed with woody shrubs [e.g. wolfberry (*Lycium* sp.), hackberry (*Celtis* sp.)] and succulents [cholla or prickly pear (*Opuntia* sp.)]. In southern regions, understory species were composed of more large woody shrubs [papache or papachillo (*Randia* sp.)] and short trees [brasil (*Haematoxylon brasiletto*) and mamoa (*Erythroxylum mexicanum*)] (Table 17).

Sonoran Desert: Riparian overstory vegetation was typically dominated by mesquite and included lesser quantities of paloverde and ironwood (Table 15). These species were also dominant in uplands but included proportionally more paloverde and ironwood than in riparian areas. Other common riparian dominants included catclaw acacia (*Acacia greggii* and *A. occidentalis*) and chino. Gallery woodland deciduous species accounted for only 1.4% of riparian dominants and occurred at only 2.7% ($n = 5$ of 183) of occupied stations. Wolfberry, riparian scrub species (*Hymenoclea* sp. and *Baccharis* sp.), canyon ragweed (*Ambrosia ambrosioides*), and desert hackberry (*Celtis pallida*) comprised approximately 56% of the understory in riparian areas, whereas triangle-leaf or white bursage (*Ambrosia deltoidea* or *A. dumosa*), creosote (*Larrea tridentata*), cholla or prickly pear, white brittlebush (*Encelia farinosa*), and wolfberry comprised approximately 65% of the understory in uplands (Tables 17 and 18).

Composition of riparian vegetation varied across topography and vegetation subdivisions. Mesquite was approximately 27% more abundant in Arizona Uplands ($t_{177} = 2.06$, $P = 0.041$, linear contrast) where dominance was 40% greater on valley bottoms and lower

Table 17: Percent dominance of understory plant species or species groups in riparian vegetation at stations occupied by ferruginous pygmy-owls in 4 vegetation communities of Sonora, Mexico.

	Sonoran Desert		Semidesert Grassland		Sinaloan Thornscrub		Sinaloan Deciduous Forest	
Species or group [a]	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
White and triangle-leaf bursage	2.8	1.2						
Burroweed	0.2	0.2	3.8	2.1				
Mesquite	2.4	0.9	5.5	2.4	1.3	1.0		
Wolfberry	20.0	2.6	14.2	3.3	7.1	2.0		
Desert hackberry	9.7	2.0	9.3	3.2	6.7	2.3		
White brittlebush	3.1	1.2	1.6	1.6	1.0	1.0		
Riparian scrub sp.	16.0	2.1	23.0	2.0	8.8	1.4	3.3	1.9
Forbs	3.9	1.3	8.2	2.7	3.0	1.1	3.3	1.9
Catclaw acacia	4.5	1.2	7.7	2.5	2.4	1.2	1.3	0.9
Canyon ragweed	10.6	2.0	1.1	1.1	5.4	1.7	4.0	2.1
Grasses	5.4	1.5	12.0	3.3	6.4	1.9	7.3	2.6
Vallesia glabra	0.9	0.7			5.7	1.9		
Papache					13.5	2.8	14.0	3.7
Papachillo					5.4	1.8	1.3	1.3
Boat-thorn acacia					3.4	1.3	4.0	2.5
Croton sp. and *Acalypha* sp.					3.7	1.3	3.3	1.7
Ambrosia cordifolia					1.7	1.0	2.0	1.4
Garabullo					0.4	0.2	4.6	1.5
Berraco					0.4	0.4	4.0	2.4
Batayaqui					0.3	0.3	6.0	2.2
Mamoa							2.7	1.6
Piocha							2.7	1.8
other species	20.5		13.6		23.4		39.5	
Stations occupied	154		61		99		50	

[a] See Appendix A for species groups and Latin names.

Table 18: Percent dominance of understory plant species or species groups in upland vegetation at stations occupied by ferruginous pygmy-owls in 4 vegetation communities of Sonora, Mexico.

	Sonoran Desert		Semidesert Grassland		Sinaloan Thornscrub		Sinaloan Deciduous Forest	
Species or group [a]	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
White and triangle-leaf bursage	20.3	2.4	9.3	2.4				
Burroweed and snakeweed	0.3	0.2	15.1	2.9				
Creosote	14.7	2.1	13.0	2.8	0.7	0.7		
Mesquite	2.0	0.7	4.5	1.4	3.7	1.5		
Catclaw acacia	1.9	0.7	8.8	3.1	0.6	0.3		
Acacia (other sp.)	3.4	1.1	5.1	2.1	0.6	0.4		
Wolfberry	8.5	1.7	2.8	1.2	1.1	0.5		
Desert hackberry	2.1	0.7	1.4	1.0	0.6	0.6		
White brittlebush	9.9	2.1	4.2	2.0	0.7	0.5		
Caesalpinia sp.	2.7	0.9			2.6	0.9	0.9	0.9
Prickly pear and cholla	11.0	1.9	5.9	1.8	3.4	1.4	0.6	0.4
Forbs	1.4	0.6	4.8	1.8	4.5	1.4	2.1	1.3
Grasses	7.0	1.6	19.7	4.3	5.4	1.7	4.6	2.3
Jatropha	3.2	1.1	0.3	0.3	5.8	1.8	1.6	0.8
Papachillo					6.7	1.6	2.2	1.0
Papache					1.5	0.9	4.3	1.4
Boat-thorn acacia					12.5	2.5	12.0	3.3
Brasil					0.6	0.4	9.0	3.0
Croton sp. and *Acalypha* sp.					18.7	2.9	26.0	3.9
Sycamore-leaf jatropha					1.5	0.9	2.8	1.6
Ambrosia cordifolia					1.8	0.8	3.6	1.3
Mamoa							5.9	2.6
other species	11.6		5.1		27.0		24.0	
Stations occupied	153		59		89		54	

[a] See Appendix A for species groups and Latin names.

Valley desertscrub were dominated mainly by creosote (57.6 ± 6.8%) with lesser quantities of mesquite (10.2 ± 6.2%), ironwood (8.5 ± 4.3%), and paloverde (7.0 ± 3.8%). Uplands at only 2 occupied stations were dominated entirely by creosote, where owls were likely restricted to open bands (38 to 60 m wide) of mesquite-ironwood woodland in riparian areas. Succulents dominated 45.8 ± 8.7% of uplands in Central Gulf Coast desertscrub and included extensive cardón forests (30.0 ± 7.4%). In addition to cacti, paloverde (16.6 ± 3.8%), mesquite (11.7 ± 4.7%), and ocotillo (5.8 ± 2.2%) were also dominant.

Semidesert Grasslands: Approximately 56% of riparian vegetation at occupied stations was dominated by mesquite with an additional 15% catclaw acacia (Table 17). Chino and paloverde dominated only 4 to 5% of overstory vegetation with approximately 60% of understory composed of riparian scrub species, grasses, wolfberry, and desert hackberry (Table 16 and 18). Gallery woodland deciduous species dominated only 4.9% of riparian vegetation, especially velvet ash (*Fraxinus velutina*) and willow (*Salix* sp.), which were present at 9.4% ($n = 6$ of 64) of stations mainly along valley bottoms (14.3 ± 6.1%). Mesquite and catclaw acacia were distributed evenly among topographic formations ($F_{3, 60} \leq 1.33$, $P \geq 0.28$) whereas chino was much more common on upper bajadas (11.5 ± 3.6%, $t_{60} = 3.53$, P = 0.0008, linear contrast) than in other topographic formations (1.5 ± 0.9%).

Plant species richness was low in uplands and composition was similar to riparian areas (Tables 15 and 16). Mesquite was dominant (52.0 ± 2.8%), and increased approximately 21.3 ± 2.4% from canyons to valley bottoms ($t_{62} = 2.87$, $P = 0.0056$, regression). Other common overstory species included catclaw acacia (8.3 ± 1.8%) and paloverde (13.9 ± 2.8%). Grasses, burroweed (*Isocoma tenuisecta*), snakeweed (*Gutierrezia* sp.) creosote, and bursage comprised 57% of understory dominants. Saguaros were found within 400 m of all occupied stations, were dominant at 40.6% ($n = 26$ of 64), and ranked fourth in overall dominance (6.3 ± 1.1%).

Sinaloan Thornscrub: In addition to mesquite, riparian areas at occupied stations included a wide variety of species. Palo joso (*Albizia sinalöensis*), chino, and gallery woodland deciduous species were more common in Thornscrub than in other communities (Table 15). Palo joso and gallery woodland deciduous species were most common in valley bottoms where dominance was 4.4 and 2.7 times greater than on upper bajadas (joso, 16.9 ± 4.0%; gallery woodland deciduous species, 14.4 ± 4.6%). In valley bottoms, galley woodland deciduous species included cottonwood (8.7 ± 3.2%), willow (3.2 ± 1.8%), and gamúchil (*Pithecellobium dulce*, 2.0 ± 0.6%) and occurred principally along the Río Yaqui below Presa Obregón. Mesquite dominance was highest in lower elevation topographic formations (31.8 ± 4.6%) and decreased in higher elevation topographic formations ($t_{96} = 2.84$, $P = 0.0055$, regression). Tropical deciduous and evergreen forest species were most dominant in canyons (deciduous, 35.2 ± 7.1%, evergreen, 19.1 ± 5.5%) and upper bajadas (deciduous, 24.5 ± 6.9%; evergreen, 24.2 ± 5.2%) and included amapa, kapok, mauto, tepeguaje (*Lysiloma watsonii*) figs (*Ficus* sp.), and guasima (*Guazuma ulmifolia*). Understory species often included papache or papachillo, *Vallesia glabra*, grasses, and species common in desertscrub (Table 18).

In uplands, tropical species generally replaced those in desertscrub especially in upper elevation topographic formations. Ironwood and paloverde were uncommon and replaced by boat-thorn acacia (*Acacia cochliacantha*), mauto, and torote (generally *B. fagroidies* or *B. laxiflora*) (Table 16). Boat-thorn acacia and mesquite dominated 45.1 ± 4.1% of overstory vegetation and were 2.3 times less common in upper elevation topographic formations ($t_{94} = 5.04$, $P < 0.0001$, linear contrast). In contrast, tropical deciduous forest species were 35% more common in upper elevation topographic formations (53.8 ± 7.3%, $t_{94} = 4.80$, $P < 0.0001$, linear contrast). Tropical evergreen forest species were rare (1.4 ± 0.5%). Etchos were dominant at only 14.3% ($n = 14$ of 98) of stations and relatively evenly distributed among topographic formations ($F_{3,\,94} = 0.84$, $P = 0.49$, range = 1.5 to 4.0%).

Sinaloan Deciduous Forest: Tropical evergreen species dominated riparian vegetation especially in valley bottoms (73.8 ± 8.0%) where sabino (*Taxodium distichum* var. *mexicanum*, 47.6 ± 9.2%) and figs (23.8 ± 9.4%) were most common. Although species typical of tropical deciduous forests were rare along valley bottoms (2.4 ± 0.9%), they dominated about a third of riparian vegetation (31.9 ± 9.8%) in higher elevation topographic formations. Unlike northern vegetation communities, mesquite dominance was low in riparian areas (Table 15). Broadleaf species attained maximum dominance in canyons (29.6 ± 4.8%) and included amapa, bebelama (*Sideroxylon persimile*), tempisque (*S. tepicence*), torote (generally *B. gradifolia* and *B. pennicilata*), kapok, and tampiceran (*Platymiscium trifoliolatum*). Oaks (*Quercus* sp.) were rare and dominated only 3.3 ± 1.2% of riparian vegetation. Common understory species included papache (*Randia echinocarpa*), grasses, batayaqui (*Montanoa* sp.), garabullo (*Pisonia capitata*), and berraco (*Stemmadenia tomentosa*) (Table 18).

Mauto was approximately 2 times more dominant than other species in uplands (Table 16) and evenly distributed among topographic formations ($F_{3, 50} = 1.63$, $P = 0.20$, range = 33.5 to 49.3%). Boat-thorn acacia was common on valley bottoms and bajadas (26.2 ± 5.0%) but rare in canyons (3.3 ± 1.4%) where more mesomorphic species dominated. Torote (23.8 ± 2.6%) and amapa (5.6 ± 1.6%) were approximately 4 times more common in canyons than other topographic formations ($t_{49} \geq 2.21$, $P \leq 0.039$, linear contrasts). Buffelgrass was dominant at 11.1% of stations ($n = 6$ of 54) and occurred at low to moderate dominance (21.9 ± 5.6%). In these landscapes owls occurred in a mosaic of tropical forest, thornscrub (or early successional forest), and artificial savannah. Croton, (*Croton* sp.), boat-thorn acacia, brasil, mamoa, and papache dominated 59.4 ± 2.3% of understory species.

DISCUSSION

Distribution and Abundance

Although pygmy-owls were thought to be absent or rare in northern Sonora, they range from rare to locally common along a portion of the border with Arizona (Fig. 3). In northern Sonora, pygmy-owls were most common between 600 and 800 m elevation and near the ecotone between Arizona Upland desertscrub and Semidesert Grasslands. In southern Sonora, pygmy-owls were common in tropical forest and thornscrub between 10 and 500 m elevation. Although all previous nesting records were from the extreme south (Russell and Monson 1998), I located 35 nests within 10 km of Arizona.

Pygmy-owls were distributed widely on the Coastal Plain of Sonora and absent in interior valleys and foothills, except those adjacent to the Coastal Plain (Appendix B). Although habitat is less abundant in the interior, I observed areas with mesquite woodlands and large columnar cacti that were similar to areas occupied by owls on the Coastal Plain. Throughout their range, ferruginous pygmy-owls occupy lowlands more commonly than foothills and mountainous regions (Schaldach 1963, Schauensee 1970, Johnsgard 1988, Binford 1989, Howell and Robbins 1995, Howell and Webb 1995, König et al. 1999) and in Sonora they were most common on bajadas and valley bottoms where topographic complexity was low. Colima pygmy-owls replaced ferruginous at higher elevations, especially on canyons slopes with tall tropical forest, which is consistent with observations from further south (Schaldach 1963, Howell and Robbins 1995). When both species were detected simultaneously, ferruginous pygmy-owls always called from areas near canyon bottoms or adjacent flats and Colima pygmy-owls called from steeper slopes.

I found pygmy-owls in northern Sonora between early January and late May with little variation in abundance. Therefore, pygmy-owls seem to be permanent residents in northern Sonora as in other portions of their range (Schaldach 1963, Monroe 1968, Stiles and Skutch 1989, Binford 1989, Howell and Webb 1995, Proudfoot 1996, Abbate et al. 1999, 2000).

Habitat Characteristics

Across Sonora, pygmy-owls occupied areas with a broad range of environmental conditions from open desertscrub with scattered short-trees to closed-canopy tropical forest. All areas occupied by owls supported large columnar cacti or large trees with cavity potential and either scrub, woodland or forest vegetation with woody trees ≥2 m tall. In the Sonoran Desert, pygmy-owls occupied upland desertscrub or savannah with woody trees and saguaros, riparian woodland, or well-developed desertscrub along drainages. In Semidesert Grasslands, pygmy-owls occupied mesquite woodland or dense savannah associated with one or more drainages and upland savannah or scrub with scattered trees or shrubs and saguaros. In Sinaloan Thornscrub, owls occupied gallery woodlands, riparian woodlands and adjacent thornscrub, tall well-developed thornscrub, or a mosaic of artificial openings and native vegetation. In Sinaloan Deciduous Forest, owls occupied both closed and open-canopied upland forest often on low to moderate slopes, gallery woodland along drainages, forest edges, or a mosaic of artificial savannah and native forest.

The relative importance of specific environmental features varied geographically. In general, in areas where important habitat features such as cavity substrates or vegetation structure were rare, these factors had a stronger influence on occupancy and abundance compared to areas where they were common. Such variation illustrates the importance of local information in understanding wildlife – habitat relationships and the potential problems of applying information collected in only a small portion of a species' range to other areas.

Vegetation Structure: Pygmy-owls were often associated with areas of open vegetation structure with low to moderate densities of large trees and moderate vegetation volume. Owl abundance was generally highest in areas with low to moderate volume of riparian understory (0-1 m) vegetation (Fig. 21*f*). Although vegetation structure at occupied areas was open with moderate volume, most occupied areas had high horizontal heterogeneity, characterized by scattered patches of dense vegetation, similar to descriptions from other portions of the range (Monroe 1968, Hilty and Brown 1986, Stiles and Skutch 1989, Howell and Webb 1995, Cartron 2000, Ridgely and Greenfield 2001). In naturally open grasslands, abundance of pygmy-owls was highest when the volume of riparian midstory vegetation was moderate (Fig. 13*d*). As upland vegetation became increasingly dense in thornscrub and tropical forests, pygmy-owls were most common when the volume of upland midstory vegetation and density of large trees were moderate (Figs. 18*d* and 19*d*).

Pygmy-owls were most abundant in woodland and forests with moderate vegetation volume a scattered opening and least abundant in dense thornscrub. In thornscrub, owls were usually absent from thickets in the north and increased in abundance to the south where vegetation was taller and the midstory more open. Selection of areas with open vegetation structure is likely related to foraging and flight behaviors. Pygmy-owls typically use a "sit-and-wait" hunting strategy that may be most effective when visibility is high. Open areas that afford higher visibility have been associated with greater capture success for owls (Longland and Price 1991). Further, abundance and diversity of owl prey may be greatest in areas with high horizontal heterogeneity and a variety of microhabitats (Rosenzweig and Winakur 1969, Price 1978, Germano and Hungerford 1981, Jones 1988). Open areas in woodland and savannah interspersed with scattered, dense patches of vegetation, likely provide escape cover while facilitating typical short flights below the canopy.

Relative importance of upland and riparian vegetation - Throughout Mexico, pygmy-owls are not restricted to riparian vegetation (Binford 1989, Howell and Webb 1995, Cartron et al. 2000). In Arizona, however, most historical accounts describe pygmy-owls in broadleaf riparian vegetation along major valley bottoms (Bendire 1888, Fisher 1893, Breninger 1898, Gilman 1909, Swarth 1914). In Sonora, a combination of features of both upland and riparian areas seemed essential for occupancy.

Along drainages in northern Sonora, habitat was often less common in uplands compared to riparian areas that generally provided well-developed vegetation structure. In uplands, however, vegetation structure suitable for owls was less common and therefore had a greater influence on occupancy or abundance of pygmy-owls especially in more xeric vegetation communities (Fig. 6). When saguaros were absent from riparian areas, owls were also absent unless adjacent uplands supported a combination of saguaros and woody trees. Therefore, factors such as height of upland vegetation influenced occupancy and abundance more than riparian structure (Tables 3 and 4).

Riparian vegetation influenced occupancy and abundance of pygmy-owls most in areas where uplands lacked essential habitat features, such as in thornscrub where dense vegetation in uplands often precluded occupancy and owls were restricted to riparian woodland. As upland vegetation approached forest-like structure to the south and in the upper elevation portions of landscapes, owls primarily occupied upland areas. In arid portions of the Sonoran Desert, owls extended their distribution in xeroriparian vegetation along large drainages even where upland structure was unsuitable. If saguaros were present in or immediately adjacent to large xeroriparian areas or areas with numerous narrow bands xeroriparian vegetation in close proximity, they were often occupied by pygmy-owls regardless of upland structure.

In addition to a combination of both upland and riparian vegetation, the ecotone between these areas seemed especially important to pygmy-owls. In Arizona Uplands, density of pygmy-owls was approximately 2 times greater on lower bajadas than valley bottoms but relative abundance was nearly equal (Table 2). Because pygmy-owls were often detected near the ecotone between upland and riparian vegetation areas, detection distances were shorter on lower bajadas where riparian areas were approximately 3 times narrower. Nest-site selection in northern Sonora indicated that distance to the nearest vegetation edge explained patterns of pygmy-owl nest placement, and nests were often closer to edges than available substrates (Flesch and Steidl 2002). Edges may provide better visibility or access to multiple resources and often support higher abundance of prey such as songbirds (Johnston 1970, Gates and Gysel 1978, Szaro and Jakle 1985). Many other raptor species are also associated with vegetation edges (e.g. Morrman and Chapman 1996) including Eurasian pygmy-owls (*G. passerinum*) (Strom and Sonerud 2001).

Vegetation Composition: *Riparian areas* - Pygmy-owls were associated with mesquite woodlands throughout much of northern Sonora and in the lower elevation portions of landscapes in parts of southern Sonora. In the upper elevation portion of landscapes in the Sonoran Desert, pygmy-owls were only common along larger drainages dominated by mesquite or chino. Pygmy-owls were uncommon or absent along smaller drainages that often supported more paloverde and ironwood and less mesquite.

Although historical descriptions of areas occupied by pygmy-owls in Arizona imply the importance of broadleaf deciduous trees, microphyllous species were more important to occupancy in Sonora. With few exceptions, pygmy-owls did not occupy galleries of cottonwoods and willows, and those that did often called from upland areas or mesquite-dominated terraces that supported only microphyllous species. Comparing the relative value of broadleaf versus microphyllous riparian vegetation to pygmy-owls is complicated, however, because virtually all broadleaf communities have been altered by agriculture or other anthropogenic disturbances. In comparison to mesic riparian vegetation, xeroriparian areas appear to support similar abundance and diversity of reptiles (Jones 1981, Jones 1988), the principal food of pygmy-owls during summer in Arizona (Abbate et al. 1999, Flesch 1999).

Upland areas - Occupancy by pygmy-owls increased steadily with dominance of mesquite and ironwood in uplands but not with paloverde. Owls may select areas dominated by ironwood and mesquite, in part, because their denser shade mitigates maximum temperature extremes (Suzán et al. 1996) and richness of plant species and other life-forms is high under ironwood (Búrquez and Quintana 1994, Tewksbury and Petrovich 1994). The dense branching structure of paloverde (especially *P. microphylla*) also has fewer open horizontal limbs that afford favorable perches (pers. obs.). Additionally, mesquite or ironwood is often associated with higher abundance or diversity of prey species such as lizards, small mammals, or birds (Germano and Hungerford 1981, Tewksbury and Petrovich 1994, Lloyd et al. 1998).

Cavity Substrates: *Large cacti* - Large columnar cacti are a critical component of pygmy-owl habitat. Without the nest cavities they provide, vast areas of desertscrub, grassland, and thornscrub would not be occupied by pygmy-owls. Although large cacti were important throughout Sonora, their relative importance varied with their abundance. In the lower elevation topographic formations where well-developed vegetation structure was generally more common, columnar cacti were often less abundant and therefore more influential. In central Sonora, where saguaros were rare, pygmy-owl distribution closely corresponded with the distribution of saguaros (Table 3).

In large part, pygmy-owl distribution in northern Sonora reflected the distribution of saguaros. Saguaros are limited by duration and intensity of freezing events at high elevations and high latitudes (Shreve 1911, Niering et al. 1963, Nobel 1980) and are most common on well-drained rocky soils in the upper elevation portions of landscapes and on south and east-facing aspects (Steenbergh and Lowe 1977, Pierson and Turner 1998). In contrast, fine alluvial substrates in the lower elevation portions of landscapes are less favorable for saguaros and thermal inversions (Shreve 1912, Turnage and Hinckley 1938) can confine them to slightly higher elevations (Steenbergh and Lowe 1977, Parker 1988, Turner et al. 1995). In regions where saguaros were uncommon, owl abundance was greatest on upper bajadas or areas adjacent to rock outcrops or low hills with higher topographic complexity. Where saguaros were common, owl abundance was highest in the lower elevation portions of landscapes where vegetation structure was often better developed.

Presence of a single adult saguaro was often as influential to pygmy-owl occupancy as presence of multiple individuals. Because cavity excavation is concentrated on only a few individuals in areas where large cacti are rare, the number of cavities per cactus may be inversely related to cacti density (Flesch and Steidl unpubl. data). Therefore areas with varying cacti densities may have a similar number of potential nest-sites.

Not all species of large columnar cacti are important for pygmy-owls. Organ pipe cacti rarely attained sufficient girth to support cavities large enough for pygmy-owls. Similarly, in the northern portion of their range, etchos were often too narrow to support large cavities but became increasingly important to the south where they attained greater girth. Although cardón were restricted to coastal areas, these cacti supported wide trucks and arms suitable for woodpecker excavation like saguaros.

Trees versus cacti - In northern Sonora pygmy-owls seemed to be obligated to areas with large cacti, although when large trees with cavities were also present, the dependence on cacti was less apparent. Where large cacti were absent, owls did not occupy extensive mesquite woodlands even when tree heights exceeded 10 m. Maximum daily temperatures in saguaro cavities are moderated by their high water content (Soule 1964) and may offer better microclimates relative to cavities in trees. Saguaros may be more difficult to climb for mammalian or reptilian predators. Additionally, the size threshold at which trees support cavities of suitable size is quite large; I only observed cavities used by pygmy-owls in chino and palo joso >15 m tall. Of 102 independent nests found in northern Sonora, only 2 were in tree cavities (chinos) and they occurred in areas where cacti were absent and mean canopy height exceeded 10 m (Flesch and Steidl, unpubl. data).

Geographic Trends in Habitat: Environmental factors that explained occupancy and abundance of pygmy-owls varied across Sonora (Tables 3, 4, and 5) and corresponded to gradients of aridity. Across Sonora, precipitation increases from west to east and north to south (Shreve 1951, Hastings and Humphrey 1969, Brown 1982) and gradients of habitat structure varied mainly with latitude across the state and with longitude in the north (Tables 3, 6, and 7). Pygmy-owls did not occupy steep slopes with sparse vegetation in the north, and occupancy increased toward the south as tropical vegetation replaced desertscrub (Fig. 20). Drainage density and the amount of riparian woodland were important in determining occupancy and abundance of pygmy-owls in arid northern regions but not in more mesic southern Sonora (Figs. 13 and 21*a*). In Arizona Uplands, where rainfall increases more than 2 times from west to east (Turner and Brown 1982), width of riparian vegetation, woodland dominance, and height of upland vegetation had the greatest influence on occupancy in the arid west (Fig. 4). In Semidesert Grassland and eastern Arizona Uplands, owl abundance increased sharply with drainage density

(Figs 9*f* and 13*a*). In the xeric western portion of Arizona Uplands, drainage density was slightly less influential and owl abundance was likely limited by of suite of other factors.

Latitudinal and longitudinal patterns in habitat use were complicated by smaller-scale topographic variation within landscapes. For example, larger drainages were especially influential to occupancy by pygmy-owls on upper but not lower bajadas where more limited moisture and shallower soil depth limit vegetation structure (Fig. 22*a*). Furthermore, on upper bajadas drainage size was most influential in the arid north (Fig. 22*b*).

Land Use and Threats: *Agriculture*- Agriculture influenced the distribution of pygmy-owls mainly along mesic valley bottoms. Although owls rarely occurred where agriculture intensity was high, areas with low to moderate intensity were occasionally occupied, especially when the altered land area was small and patches of native vegetation were retained. Away from major river deltas where native vegetation was uncommon, small farms along wet drainages occasionally retained some habitat elements important to owls. When agriculture was limited to areas along the main channel, owls occupied adjacent terraces and uplands. Although damming and water diversion have eliminated vast areas of habitat along major rivers, pygmy-owl distribution extends well beyond mesic valley bottoms and is likely not seriously threatened by agriculture in Sonora.

Woodcutting- Along large valley bottoms in northern Sonora, past destruction of mesquite woodlands (Stevens 1885, Neff 1947, Shreve 1951) adjacent to uplands with large cacti has likely reduced the quantity of pygmy-owl habitat. Although many of these once vast woodlands have not recovered, those along secondary and tertiary drainages have remained or recovered, and today form centers of pygmy-owl abundance in the north.

Woodcutting for fuel is widespread in Sonora and often done sustainably except near large charcoal operations and cities. Typical fuelwood cutting is often rotated among numerous trees over many years, removes only a few major branches per tree, selects for taller trees, opens midstory vegetation, which may improve conditions for pygmy-owls.

Extensive clearcutting associated with converting native vegetation into open buffelgrass pastures constitutes a serious threat to pygmy-owls. With the establishment of buffelgrass comes an increase in fire frequency in a plant community with no adaptation to fire (Búrquez et al. 1996). Fire often kills or critically weakens saguaros (Steenbergh and Lowe 1977, McLaughlin and Bowers 1982, Wilson et al. 1996) and may be especially detrimental where saguaros are already uncommon. Pygmy-owls, however, regularly occupied areas in or adjacent to buffelgrass clearings that formed a mosaic of artificial savannah and native vegetation.

Grazing - Livestock grazing may have both positive and negative effects on suitability of habitat for pygmy-owls. Livestock grazing seems to negatively influence regeneration of saguaros (Niering et al. 1963, Niering and Whittaker 1965, Steenbergh and Lowe 1977, Abouhaider 1989, 1992) and I found that density of large columnar cacti tended to be lower in areas with higher grazing intensity ($t_{374} = 1.80$, $P = 0.072$, regression). In lower elevation topographic formations where large cacti were less common, grazing seemed to have had its greatest influence on owl occupancy (Table 7). Grazing, however, also creates openings and reduces ground cover, which can enhance habitat suitability for pygmy-owls in areas with high vegetation volume. For example, along low elevation valley bottoms where large cacti were common, occupancy increased with grazing intensity, but at high elevations where cacti were uncommon, occupancy decreased (Fig. 24*a*).

Although livestock grazing may increase habitat suitability for pygmy-owls in the short-term, long-term effects on prey and cacti regeneration merit consideration. Pygmy-owls are prey generalists (Proudfoot and Beasom 1997) and during the breeding season in Arizona they consume lizards primarily, with birds, small mammals, and insects comprising smaller portions of the diet (Abbate et al. 1999, Flesch 1999). Although effects vary among vegetation communities, species, and intensity, grazing appears to negatively influence abundance and diversity of prey taxa (Fleischner 1994) such as lizards (Jones 1981) and small mammals (Medin and Clary 1989, Hayward et al. 1997). Because grazing often favors species that forage in the open (Reynolds 1950, Jones and

Longland 1999), that are often more susceptible to owl predation (Longland and Price 1991), limited grazing may increase prey availability.

Compared to Arizona, grazing intensity in northern Sonora is high, and has reduced vegetation cover, increased summer temperatures, and contributed to more rapid soil desiccation following rain (Balling 1988, Bryant et al. 1990, Balling et al. 1998), none of which are conducive to saguaro regeneration (Alcorn and Kurtz 1959, McDonough 1964, Turner et al. 1966, Nobel 1980). Saguaro populations are maintained by episodic regeneration surges during ideal conditions (Pierson and Turner 1998), and factors that suppress long-term saguaro regeneration could have catastrophic effects on pygmy-owl populations.

Sex Differences

Habitat selection can vary between sexes (Mills 1976, Morton et al. 1987) and may involve an emphasis for selection of nest-sites in females and calling perches for males (Sedgwick and Knopf 1992). Throughout Sonora, female pygmy-owls occupied sites with greater density and dominance of potential nest substrates and shorter upland vegetation compared to males. During the breeding season in Arizona, males selected calling perches in the tallest trees available, which may promote advertisement to females and aid in territorial maintenance (Flesch 2003).

Distribution of Abundance

Pygmy-owls were distributed in relatively few areas of high abundance, with abundance more similar at nearby sites than at distant sites. Although abundance is predicted to be greatest near the center of a species' geographic range and to decline gradually toward the edges (Hengeveld and Haeck 1982, Rapoport 1982, Brown 1984), abundance patterns of pygmy-owls did not conform to this prediction. Instead, I observed a bimodal pattern with peaks in northern and southern Sonora separated by central Sonora, where columnar cacti and suitable vegetation structure were rare. Such an exception is anticipated when one or more important environmental factors exhibit spatial variation (Brown 1984, 1995). Although unimodal patterns of abundance are often expected, the spatial arrangement of important environmental factors, dispersal potential, and biotic interactions can potentially produce a myriad of patterns.

Correspondence between Geographic Patterns of Owl and Habitat Abundance

A species' distribution is limited by both physical and biotic factors. Physical factors such as climate both directly and indirectly through its effects on resources are often more influential in limiting distribution at high latitudes, whereas at low latitudes biotic factors such as competition seem to be more important (Darwin 1859, MacArthur 1972). Additionally, when distribution is limited by climate, it is often the extreme, not mean, environmental conditions that are limiting (Taylor 1934). In northern Sonora, abundance patterns of pygmy-owls corresponded with geographic trends in abundance of the environmental factors that comprised owl habitat (Fig. 28). In the south, however, the degree of correspondence was lower, especially at higher elevations (Fig. 28). Pygmy-owls may be limited by vegetation structure in northwestern Sonora, which is limited by moisture and by the effects of extreme freezing events on saguaros (Niering et al. 1963, Steenbergh and Lowe 1976, 1977) at higher elevations. Although my study area did not extend to the southern range boundary, in subtropical environments of southeastern Sonora, pygmy-owls may be limited by biotic factors such as competition rather than physical factors (Pianka 1970, Gross and Price 2000). At higher elevation and lower longitude, Colima pygmy-owls replaced ferruginous on steeper slopes and in upper elevation tropical forest.

Dispersion

Connectivity facilitates movement and genetic interchange among populations and reduces threats associated with small populations (Soulé 1987). Juvenile pygmy-owls disperse between 2 and 35 km from their natal sites (Abbate et al. 2000, Proudfoot and Johnson 2000, USFWS 2002), therefore landscape connectivity may be important to long-term persistence. In northern Sonora, landscapes occupied by pygmy-owls were least dispersed near the center of their distribution, and this area (upper Plomo, Sasabe, and Altar Valleys) may facilitate connectivity with adjacent areas in Arizona and prove instrumental to recovery.

Management Recommendations

Sonora: Actions that maintain or enhance habitat and connections among patches of habitat are consistent with pygmy-owl conservation. Because pygmy-owls are aggregated into relatively few areas of high abundance, conserving these areas would provide a foundation for a broad-scale conservation program. Importantly, several areas that seem to provide habitat are unoccupied; these areas are often >50 km from occupied areas. Near the limits of their range, therefore, occupancy may not represent the potential of an area to support pygmy-owls. Consequently, identification of areas for conservation and recovery of pygmy-owls should be based on a combination of the environmental features present, proximity to a potential source population, and current occupancy.

In the Sonoran Desert and Semidesert Grasslands, a combination of environmental features conducive to management were associated with occupancy of pygmy-owls. Areas that support microphyllous or microphyllous and broadleaf woodlands with adjacent arborescent desertscrub or savannah with ≥1 adult saguaro are especially important to pygmy-owls. Additionally, well-developed desertscrub with a combination of tall ironwood and mesquite trees and saguaros within 250 m of xeroriparian woodlands, areas where high drainage density produces multiple bands of arborescent desertscrub in close proximity, and mesquite savannah with ≥1 adult saguaro within 250 m of a patch of woodland are also important to pygmy-owls.

In Sonora, pygmy-owls are threatened in specific locations where large areas of native vegetation are being eradicated for buffelgrass pastures or agriculture. In these areas, retaining patches of undisturbed native vegetation, scattered large trees and cacti within clearings, and riparian woodlands may maintain habitat for pygmy-owls. Where fires in buffelgrass pastures threaten remaining large trees and cacti, removing fine fuels around these important habitat elements before the fire season may minimize damage and adverse effects on pygmy-owl habitat. The last remnants of once vast cottonwood forests are critically endangered along the lower Ríos Yaqui and Mayo; immediate restoration of in-stream water flow and periodic seasonal floods below the dams may facilitate their recovery (Hill et al. 1991, Poff et al. 1997, Stromberg 2001).

Elimination or inadequate regeneration of large columnar cacti is perhaps the greatest threat to pygmy-owls in northern and central Sonora. Where large cacti are rare or threatened, erecting nest boxes (Proudfoot 1996) or translocating saguaros may provide nest cavities as a means of temporarily maintaining this critical habitat element while management actions to reestablish columnar cacti are enacted. Site-specific criteria for locating supplemental nest structures should match characteristics of nest-sites used by pygmy-owls in northern Sonora (Flesch and Steidl 2002).

Because characteristics that influenced habitat selection by pygmy-owls varied geographically, management recommendations should be based primarily on data collected at a local scale. This approach eliminates potential problems when information collected in a portion of a species range is applied to broader areas.

Arizona: Significant populations of pygmy-owls in adjacent Sonora may facilitate recovery of pygmy-owls in Arizona. The relative contribution of these populations to recovery in Arizona depends on their size, connectivity with adjacent areas in Arizona, and suitability of habitat in Arizona. Areas along the border that provide either breeding habitat or large contiguous tracts of vegetation with similar structure to breeding habitat will be most easily permeated by emigrants. Excluding areas south of Tohono O'odham Nation, 3 areas with populations of pygmy-owls in close proximity to Arizona may provide a source of immigrants to Arizona. The most important area is near Sasabe, Sonora, which contains the largest known population of owls within dispersal distance of Arizona with few topographic or habitat-related barriers to dispersal (Fig. 3). In 2001 and 2002, we located 32 nests that produced 77 young within 10 km of Sasabe (Flesch and Steidl unpubl. data). The upper Río Altar Valley north of Saríc also contains a fairly large population, but it is farther from Arizona and areas of high elevation (>1,200 m) with little breeding habitat may limit connectivity (Fig. 3). Lastly, the area near Sonoyta is also important, however pygmy-owl populations here are smaller, more dispersed, and intensive woodcutting and agriculture along the Río Sonoyta may reduce connectivity.

In areas adjacent to large populations where vegetation structure provides suitable structure but cavities are rare, artificial cavities may increase pygmy-owl density. Near Sasabe, for example, vegetation structure and composition are similar to that of occupied areas south of the border, but both saguaros and pygmy-owls become increasingly rare north of the border. In these areas, installing nest boxes or translocating saguaros is the step we consider most viable for augmenting pygmy-owl populations in Arizona.

Restoring or improving degraded habitat may also enhance connectivity between distant habitat patches, including those in Arizona. Such efforts may be particularly valuable where large areas of mesquite woodland and savannah occur without saguaros. For example, installing nest boxes or translocating saguaros north of Sasabe, Arizona may promote occupancy in this area and dispersal of pygmy-owls into suitable but unoccupied habitat near Tucson.

North-central Sonora harbors a large well-distributed population of pygmy-owls that contrasts sharply with the widely dispersed, smaller populations in Arizona. In some areas, this contrast seems to be a result of limited cavities for nesting north of the border which have been shown limiting for other raptors (e.g. Hamerstrom et al. 1970). High abundance in northern Sonora offers more auspicious recovery prospects in neighboring portions of Arizona than was anticipated.

LITERATURE CITED

Abbate, D. J., W. S. Richardson, R. Wilcox, M. Terrio, and S. Belhumeur. 1999. Cactus ferruginous pygmy-owl investigations in Pima and Pinal counties, Arizona: 1997-1998. Region V Wildlife Program. Arizona Game and Fish Department, Tucson, Arizona.

Abbate, D. J., W. S. Richardson, R. L. Wilcox, and S. Lantz. 2000. Cactus ferruginous pygmy-owl investigations in Pima and Pinal Counties, Arizona: 1999. Region V Wildlife Program. Arizona Game and Fish Department, Tucson, Arizona.

Abouhaider, F. 1989. Influence of livestock grazing on saguaro seedling establishment. M.S. Thesis, Arizona State University, Tempe, Arizona.

Abouhaider, F. 1992. Influence of livestock grazing on saguaro seedling establishment. Pages 57-61 *in* C. P. Stone and E. S. Bellantoni, editors. Proceedings of the Symposium on Research in Saguaro National Monument. Tucson, Arizona.

Aiken, C. E. 1937. Birds of the Southwest. Colorado College Publication General Series 212. Colorado Springs, Colorado.

Alcorn, S. M. and E. D. Kurtz, Jr. 1959. Some factors affecting the germination of seed of the saguaro cactus (*Carnegiea gigantea*). American Journal of Botany 46:526-529.

Balling, R. C. Jr. 1988. The climate impact of a Sonoran Desert vegetation discontinuity. Climate Change 13:99-109.

Balling, R. C. Jr., J. M. Klopatek, M. L. Hilderbrantd, C. K. Moritz, and C. L. Watts 1988. Impacts of land degradation on historical temperature records from the Sonoran Desert. Climate Change 40:669-681.

Bendire, C. E. 1888. Notes on the habits, nests, and eggs of the genus *Glaucidium* Boie. Auk 5:366-372.

Bent, A. C. 1938. Life histories of North American birds of prey, part 2. U.S. National Museum Bulletin 170.

Bond, R. R. 1957. Ecological distribution of breeding birds in the upland forest of southern Wisconsin. Ecological Monographs 27:351-384.

Bowers, M. A. and C. H. Lowe. 1986. Plant-form gradients on desert bajadas. Oikos 46:284-291.

Brandt, H. 1951. Arizona and its bird life. The Bird Research Foundation, Cleveland, OH.

Breninger, G. F. 1898. The ferruginous pygmy-owl. Osprey 2:128.

Brown, D. E. (ed.). 1982. Biotic communities of the American Southwest: United States and Mexico. Desert Plants 4:1-342.

Brown, D. E. and C. H. Lowe. 1980. Biotic communities of the southwest. U.S. Department of Agriculture Forest Service GTR-RM-78. Rocky Mountain Range and Experiment Station, Fort Collins, Colorado.

Brown, J. H. 1984. On the relationship between abundance and distribution of species. The American Naturalist 124:255-279.

Brown, J. H. 1995. Macroecology. University of Chicago Press, Chicago, Illinois.

Bryant, N. A., L. F. Johnson, A. J. Brazel, R. C. Balling, C. F. Hutchison, and L. R. Beck. 1990. Measuring the effects of overgrazing in the Sonoran Desert. Climate Change 17:243-264.

Búrquez A. A., A. Martínez-Yrízar, and P. S. Martin. 1992. From the high sierra to the coast: changes in vegetation along Highway 16, Maycoba-Hermosillo. Pages 239-252 *in* C. F Clark, J. Roldán-Quintana, and R. H. Schmidt, editors. Geology and mineral resources of the northern Sierra Madre Occidental, Mexico. El Paso Geological Society, El Paso, Texas.

Búrquez A. A. and M. Angeles-Quintana. 1994. Islands of diversity: ironwood ecology and the richness of perennials in a Sonoran Desert biological reserve. Pages 9-27 *in* G. P. Nabhan and J. Carr, editors. Ironwood: an ecological and cultural keystone of the Sonoran Desert. Conservation International Occasional Papers No. 1, Washington, D.C.

Búrquez A. A., A. Martínez-Yrízar, M. Miller, K. Rojas, M. Angeles-Quintana, and D. Yetman. 1996. Mexican grasslands and the changing aridlands of Mexico: an overview and a case study in northwestern Mexico. Pages 21-32 *in* B. Tellman et al., editors. The future of arid grasslands: identifying issues, seeking solutions. Proceedings RMRS-P-3. U.S. Department of Agriculture Forest Service, Rocky Mountain Research Station, Fort Collins, Colorado.

Búrquez A. A. and A. Martínez-Yrízar. 1997. Conservation and landscape transformations in Sonora, Mexico. Journal of the Southwest 39:371-398.

Búrquez A., A. Martínez-Yrízar, R. S. Felger, and D. Yetman. 1999. Vegetation and habitat diversity at the southern edge of the Sonoran Desert. Pages 36-67 *in* R. H. Robichaux, editor. Ecology of Sonoran Desert plants and plant communities. University of Arizona Press, Tucson, Arizona.

Cartron, J. L. and D. M. Finch, editors. 2000. Ecology and conservation of the cactus ferruginous pygmy-owl in Arizona. General Technical Report RMRS-GTR-43. U.S. Department of Agriculture Forest Service, Rocky Mountain Research Station, Ogden, Utah.

Cartron, J-L. E., S. H. Stoleson, S. M. Russell, G. A. Proudfoot, and W. S. Richardson. 2000. The ferruginous pygmy-owl in the tropics and at the northern end of its range: Habitat relations and requirements. Pages 47-55 *in* J-L. E. Cartron and D. M. Finch, editors. Ecology and conservation of the cactus ferruginous pygmy-owl in Arizona. General Technical Report RMRS-GTR-43. U.S. Department of Agriculture Forest Service, Rocky Mountain Research Station, Ogden, Utah.

Collins, S. L. 1983. Geographic variation in habitat structure of the black-throated green warbler (*Dendroica virens*). Auk 100:382-389.

Cox, J. R., M. H. Martin, F. A. Ibarra, J. H. Fourie, N. F. G. Rethman, and D. G. Wilcox. 1988. The influence of climate and soils on four African grasses. Journal of Range Management 41:127-139.

Darwin, C. 1859. On the origin of the species by means of natural selection. John Murray, London, U.K.

Dobzhansky, T. 1950. Evolution in the tropics. American Scientist 38:209-211.

Duncan, R. B. 2000. Working ferruginous pygmy-owl distributional database for Sonora, Mexico. R. B. Duncan Associates, Tucson, Arizona.

Emlen, J. T., M. J. De Jong, M. J. Moermond, T. C. Rusterholz, and R. P. White. 1986. Density trends and range boundary constraints of forest birds along a latitudinal gradients. Auk 103:791-803.

ESRI. 1996. ArcView Version 3.2. Environmental Systems Research Institute, Redlands, California.

Felger, R. S and C. H. Lowe. 1976. The island and coastal vegetation and flora of the northern part of the Gulf of California. Contributions to the Science Natural History Museum Los Angeles 285:1-59.

Fisher, A. K. 1893. The hawks and owls of the U.S. in relation to agriculture. U.S. Department of Agriculture Division of Ornithology and Mammalogy Bulletin 3:1-210.

Fleischner, T. L. 1994. Ecological costs of livestock grazing in western North America. Conservation Biology 8:629-644.

Flesch, A. D. 1999. Cactus ferruginous pygmy-owl surveys and nest monitoring on and around the Buenos Aires National Wildlife Refuge, Altar Valley, Arizona. U.S. Fish and Wildlife Service Cooperative Agreement no.1448-00002-99-G943. Buenos Aires National Wildlife Refuge, Sasabe, Arizona.

Flesch, A. D. and R. J. Steidl. 2002. Nest-site selection by cactus ferruginous pygmy-owls in northern Sonora Mexico. Final report to Sonoran Joint Venture, Migratory Bird Office, U.S. Fish and Wildlife Service. USFWS Cooperative Agreement # 1448-20181-01-J862.

Flesch, A. D. 2003. Perch-site selection and spatial use by cactus ferruginous pygmy-owls in south-central Arizona. Journal of Raptor Research 37:151-157.

Gates, J. E. and L. W. Gysel. 1978. Avian nest dispersion and fledging success in forest-field ecotones. Ecology 59:871-883.

Gentry, H. S. 1942. Río Mayo plants: A study of the flora and vegetation of the Valley of the Río Mayo in Sonora. Carnegie Institute of Washington, Publication 527.

Gentry, H. S. 1982. Sinaloan deciduous forest. Desert Plants 4:73-77

Germano, D. J. and C. R. Hungerford. 1981. Reptile population changes with manipulation of Sonoran desertscrub. Great Basin Naturalist 41:129-138.

Gilman, M. F. 1909. Some owls along the Gila River of Arizona. Condor 11:145-150.

Grinnell, J. 1922. The role of the "accidental." Auk 39:373-380.

Gross, S. J. and T. D. Price. 2000. Determinants of the northern and southern range limits for a warbler. Journal of Biogeography 27:869-878.

Grzybowski, J. A., D. J. Tazik, and G. D. Schnell. 1994. Regional analysis of black-capped vireo breeding habitats. Condor 96:512-544.

Hastings, J. R. and R. R. Humphrey. 1969. Climatological data and statistics for Sonora and northern Sinaloa. University of Arizona Institute of Atmospheric Physics. Technical Report on Meteorology and Climatology of Arid Regions 19:1-96.

Hayward, B., E. J. Heske, and C. W. Painter. 1997. Effects of livestock grazing on small mammals at a desert cienega. Journal of Wildlife Management 61:123-129.

Hengeveld, R. and J. Haeck. 1982. The distribution of abundance. I. Measurements. Journal of Biogeography 9:303-316.

Hensley, M. M. 1954. Ecological relations of the breeding bird population of the desert biome in Arizona. Ecological Monographs 24:185-207.

Hill, M. T., Platts, W. S. & Beschta, R. L. 1991. Ecological and geomorphological concepts for instream and our-of-channel flow requirements. Rivers 2:198-210.

Hilty, S. H. and W. L. Brown. 1986. A guide to the birds of Colombia. Princeton University Press, Princeton, New Jersey.

Hosmer, D. W., Jr. and S. Lemeshow. 1989. Applied logistic regression. Wiley and Sons, New York.

Howell, S. N. G. and M. Robbins. 1995. Species limits of the least pygmy-owl (*Glaucidium minutissimum*) complex. Wilson Bulletin 107:7-25.

Howell, S. N. G. and S. Webb. 1995. A guide to the birds of Mexico and northern Central America. Oxford University Press, Oxford, U. K.

Hunter, W. C. 1988. Status of the cactus ferruginous pygmy-owl (*Glaucidium brasilianum cactorum*) in the United States and northern Mexico. U.S. Fish and Wildlife Service, Phoenix, Arizona.

Johnsgard, P. A. 1988. North American owls: Biology and natural history. Smithsonian Institution Press, Washington D.C.

Johnston, D. W. 1970. High density of birds breeding in a modified deciduous forest. Wilson Bulletin 62:79-82.

Jones, A. L. and W. S. Longland. 1999. Effects of cattle grazing on salt desert rodent communities. American Midland Naturalist 141:1-11.

Jones, K. B. 1981. Effects of grazing on lizard abundance and diversity in western Arizona. The Southwest Naturalist. 26:107-115.

Jones, K. B. 1988. Distribution and habitat associations of herpetofauna in Arizona: comparisons by habitat type. Pages 109-128 *in* R. C. Szaro, K. E. Stevenson, and D. R. Patton, editors. Management of amphibians, reptiles, and small mammals in North America). General Technical Report GTR-RM-166; U.S. Department of Agriculture Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colorado.

Kendeigh, S. C. and B. J. Fawver. 1981. Breeding bird population of the Great Smoky Mountains, Tennessee and North Carolina. Wilson Bulletin 93:218-242.

Kleinbaum, D. G. and M. Klein. 2002. Logistic regression: a self-learning text. Springer-Verlag, New York.

Knopf, F. L., J. A. Sedgwick, and D. B. Inkley. 1990. Regional correspondence among shrubsteppe bird habitats. Condor 92:45-53.

König, C., F. Weick, and J-H Becking. 1999. Owls: a guide to the owls of the world. Yale University Press, New Haven, Connecticut.

Krebs, C. J. 1989. Ecological methodology. Harper and Row, New York.

Leopold, A. S. 1950. Vegetation zones of Mexico. Ecology 31:507-518.

Lesh, T. D. and T. E Corman. 1995. Cactus ferruginous pygmy owl surveys in Arizona: 1993-1995. Nongame and Endangered Wildlife Program Technical Report 76. Arizona Game and Fish Department, Phoenix, Arizona.

Longland, W. S. and M. V. Price. 1991. Direct observation of owls and heteromyid rodents: can predation risk explain microhabitat use? Ecology 72:2261-2273.

Lloyd, J., R. W. Mannan, S. DeStephano, and C. Kirkpatrick. 1998. The effects of mesquite invasion on a southeastern Arizona bird community. Wilson Bulletin 110:403-408.

Ludwig, J. A. and J. F. Reynolds. 1988. Statistical ecology: a primer on methods and computing. Wiley and Sons, New York.

MacArthur, R. H. 1972. Geographical ecology: patterns in the distribution of species. Harper and Row, New York.

Marshall, J. T. Jr. 1957. Birds of pine-oak woodland. Pacific Coast Avifauna 32:1-125.

Martin, P. S., D. Yetman, M. Fishbein, P. Jenkins, T. R. van Devender, and R. Wilson, editors. 1998. Gentry's Río Mayo plants: the tropical deciduous forest and environs of northwest Mexico. University of Arizona Press, Tucson, Arizona.

Mays, J. L. 1996. Population size and distribution of cactus ferruginous pygmy-owls in Brooks and Kenedy Counties, Texas. M.S. Thesis, Texas A & M University-Kingsville, Texas.

McDonough, W. T. 1964. Germination responses of *Carnegiea gigantea* and *Lemaireocereus thurberi*. Ecology 45:155-159.

Minckley, W. L. and D. E. Brown. 1982. Sinaloan riparian evergreen forest and woodland. Desert Plants 4:575-577.

McLaughlin, S. P. and J. E. Bowers. 1982. Effects of wildfire on a Sonoran Desert plant community. Ecology 61:246-248.

Medin, D. E. and W. P. Clary. 1989. Small mammal populations in a grazed and ungrazed riparian habitat in Nevada. Research paper INT-413. U.S. Forest Service, Intermountain Research Station, Ogden, Utah.

Merriam, C. H. 1894. Laws of temperature control of the geographic distribution of terrestrial animals and plants. National Geographic Magazine 6:229-238.

Meyer de Schauensee, R. 1970. A guide to the birds of South America. Livingston Publishing Co., Winnewood, Pennsylvania.

Mills, G. S. 1976. American kestrel sex ratios and habitat separation. Auk 93:740-748.

Monroe, B. L., Jr. 1968. A distributional survey of the birds of Honduras. Ornithology Monographs 7:1-458.

Monson, G. and A. R. Phillips. 1981. Annotated checklist of the birds of Arizona. University of Arizona Press, Tucson, Arizona.

Morrman, C. E. and B. R. Chapman. 1996. Nest-site selection of red-shouldered and red-tailed hawks in a managed forest. Wilson Bulletin 108:357-368.

Morton, E. S., J. F. Lynch, K. Young, and P. Mehlhop. 1990. Do male Hooded Warblers exclude females from nonbreeding territories in tropical forest? Auk 104:133-135.

Naranjo, L. G. and R. J. Raitt. 1993. Breeding bird distribution in Chihuahuan desert habitats. Southwestern Naturalist 38:43-51.

Neff, J. A. 1947. Notes on some birds of Sonora. Condor 49:32-34.

Niering, W. A., R. H. Whittaker, and C. H. Lowe. 1963. The saguaro: a population in relation to environment. Science 142:15-24.

Niering, W. A. and R. H. Whittaker. 1965. The saguaro problem and grazing southwest national monuments. National Parks Magazine 39:4-9

Nobel, P. S. 1980. Morphology, nurse plants, and minimum apical temperatures for young *Carnegiea gigantea*. Botanical Gazette 141:188-191.

Oelke, H. 1981. Limitations of estimating bird populations because of vegetation structure and composition. Pages 316-321 *in* C. J. Ralph and J. M. Scott, editors. Estimating numbers of terrestrial birds. Studies in Avian Biology 6.

Parker, K. C. 1988. Environmental relationships and vegetation associates of columnar cacti in the northern Sonoran Desert. Vegetatio 78:125-140.

Parody, J. M. and T. H. Parker. 2002. Biogeographic variation in nest placement: a case study with conservation implications. Diversity and Distributions 8:11-20.

Phillips, A. R., J. T. Marshall, Jr., and G. Monson. 1964. The birds of Arizona. University of Arizona Press, Tucson, Arizona.

Phillips, A. R. 1966. Further systematic notes on Mexican birds. Bulletin of the British Ornithological Club 86:86-94.

Phillips, D. L. and J. A. MacMahon. 1978. Gradient analysis on a Sonoran Desert bajada. Southwestern Naturalist 23:669-680.

Pianka, E. R. 1970. Comparative autecology of the lizard *Cnemidophorus tigris* in different parts of its geographical range. Ecology 51:703-720.

Pierson, E. A. and R. M. Turner. 1998. An 85-year study of saguaro (*Carnegiea gigantea*) demography. Ecology 79:2676-2693.

Poff, N. L., Allan, J. D., Bain, M. B., Karr, J. R., Prestegaard, K. L., Richter, B. D. and Stromberg, J. C. 1997. The natural flow regime: a paradigm for river conservation and restoration. BioScience 47:769-784.

Price, M. V. 1978. The role of microhabitat in structuring desert rodent communities. Ecology 59:910-921.

Proudfoot, G.A. 1996. Natural history of the cactus ferruginous pygmy-owl. M.S. Thesis, Texas A & M University, Kingsville, Texas.

Proudfoot, G. A., and S. L. Beasom. 1997. Food habits of nesting ferruginous pygmy-owls in southern Texas. Wilson Bulletin 109:741-748.

Proudfoot, G. A. and R. R. Johnson. 2000. Ferruginous pygmy-owl (*Glaucidium brasilianum*). No. 498 *in* A. Poole and F. Gill, editors. The birds of North America. The birds of North America Inc., Philadelphia, Pennsylvania.

Ramsey, F. L. and D. W. Schafer. 2002. The statistical sleuth: a course in methods of data analysis. Wadsworth, Pacific Grove, California.

Rapoport, E. H. 1982. Areography: geographical strategies of species. Pergamon, Oxford, U.K.

Reynolds, H. G. 1950. Relation of Merriam's kangaroo rats to range vegetation in southern Arizona. Ecology 31:456-463

Ridgely, R. S. 1976. A guide to the birds of Panama. Princeton University Press, Princeton, New Jersey.

Ridgely, R. S. and P. J. Greenfield. 2001. Birds of Ecuador volume I: status, distribution, and taxonomy. Comstock Publishing Associates, Ithaca, New York.

Robichaux, R. H. and D. Yetman, editors. 2000. The tropical deciduous forest of Alamos: Biodiversity of a threatened ecosystem in Mexico. University of Arizona Press, Tucson, Arizona.

Robbins, C. S., D. Bystrak, and P. H. Geissler. 1986. The breeding bird survey: Its first fifteen years, 1965-1979. U.S. Fish and Wildlife Resource Publication 157:1-196.

Rosenberg, K. V., J. P. Hubbard, and G. H. Rosenberg. 1981. The changing seasons: southwest region. American Birds 35:211-215.

Rosenzweig, M. L. and J. Winakur. 1969. Population ecology and desert rodents communities: habitats and environmental complexity. Ecology 50:558-572.

Russell, S. M. and G. Monson. 1998. The birds of Sonora. University of Arizona Press, Tucson, Arizona.

Rzedowski, J. 1978. La vegetacion de Mexico. Limusa-Wiley, Mexico D. F.

SAS Institute. 2000. SAS/STAT user's guide. Version 8. SAS Institute, Cary, N.C.

Schaldach, W. J., Jr. 1963. The avifauna of Colima and adjacent Jalisco, Mexico. Monographs of the Western Foundation of Vertebrate Zoology 1:1-100.

Scott, J. M., S. Mountainspring, F. L. Ramsey, C. B. Kepler. 1986. Forest bird communities of the Hawaiian Islands: their dynamics, ecology, and conservation. Studies in Avian Biology 9:1-431.

Sedgwick, J. A. and F. Knopf. 1992. Describing willow flycatcher habitats: scale perspectives and gender differences. Condor 94:720-733.

Shreve, F. 1911. The influence if low temperatures on the distribution of the giant cactus. Plant World 14:136-146.

Shreve, F. 1912. Cold air drainage. Plant World 15:110-115.

Shreve, F. 1951. Vegetation of the Sonoran Desert. Carnegie Institute of Washington Publication no. 591. Washington D.C.

Smith, K. G. 1977. Distribution of summer birds along a forest moisture gradient in an Ozark watershed. Ecology 58:810-819.

Soulé, M. E., editor. 1987. Viable populations for conservation. Cambridge University Press, Cambridge U. K.

Soule, O. H. 1964. The saguaro tree-hole microenvironment in southern Arizona. II. Summer. M. S. Thesis, University of Arizona, Tucson, Arizona.

Steenbergh, W. F. and C. H. Lowe. 1976. Ecology of the saguaro: I. the role of freezing weather on a warm-desert plant population. Pages 49-92 *in* Research in Parks National Park Service Symposium Series No. 1. U.S. Government Printing Office, Washington D.C.

Steenbergh, W. F. and C. H. Lowe. 1977. Ecology of the saguaro: II. reproduction, germination, establishment, growth, and survival of the young plant. National Park Service Scientific Monograph Series No. 8. U.S. Government Printing Office, Washington D.C.

Steenbergh, W. F. and C. H. Lowe. 1983. Ecology of the saguaro: III. growth and demography. National Park Service Scientific Monograph Series No. 17. U.S. Government Printing Office, Washington D.C.

Stephens, F. 1885. Notes on an ornithological trip to Arizona and Sonora. Auk 2:225-231.

Stiles, F. G. and A. F. Skutch. 1989. A guide to the birds of Costa Rica. Comstock Publishing Associates, Ithaca, New York.

Strom, H. and G. A. Sonerud. 2001. Home range and habitat selection in the pygmy owl (*Glaucidium passerinum*). Ornis Fennica 78:145-158.

Suzán, H., G. P. Nabhan, and D. T. Patten. 1996. The importance of *Olneya tesota* as a nurse plant in the Sonoran Desert. Journal of Vegetation Science 7:635-644.

Suzán, H., D. T. Patten, and G. P. Nabhan. 1997. Exploitation and conservation of ironwood (*Olneya tesota*) in the Sonoran Desert. Ecological Applications 7:948-957.

Suzán, H., G. Malda, D. T. Patten, and G. P. Nabhan. 1999. Effects of exploitation and park boundaries on legume trees in the Sonoran Desert. Conservation Biology 13:1497-1501.

Swarth, H. S. 1914. A distributional list of the birds of Arizona. Pacific Coast Avifauna 10:1-133.

Szaro, R. C. and M. D. Jakle. 1985. Avian use of desertscrub riparian habitat islands and its adjacent scrub habitat. Condor 87:511-519.

Taylor, W. P. 1934. Significance of extreme and intermittent conditions in distribution of species and management of natural resources, with a restatement of Leiberg's law of the minimum. Ecology 15:374-379.

Tewksbury, J. J. and C. A. Petrovich. 1994. The influences of ironwood as a habitat modifier species: case study on the Sonoran Desert coast of the Sea of Cortez. Pages 29-54 *in* G. P. Nabhan and J. Carr, editors. Ironwood: an ecological and cultural keystone of the Sonoran Desert. Conservation International Occasional Papers No. 1, Washington, D.C.

Thomas, L., Laake, J.L., Strindberg, S., Marques, F.F.C., Borchers, D.L., Buckland, S.T., Anderson, D.R., Burnham, K.P., Hedley, S.L., and Pollard, J.H. 2001. Distance 4.0. Beta 4. Research Unit for Wildlife Population Assessment, University of St. Andrews, UK. http://www.ruwpa.st-and.ac.uk/distance/.

Turnage, W. V. and A. L. Hinckley. 1938. Freezing weather in relation to plant distribution in the Sonoran Desert. Ecological Monographs 8:529-550.

Turner, R. M., S. M. Alcorn, G. Olin, and J. A. Booth. 1966. The influence of shade, soil, and water on saguaro seedling establishment. Botanical Gazette 127:95-102.

Turner, R. M. and D. E. Brown. 1982. Sonoran desertscrub. Desert Plants 4:181-221.

Turner, R. M., J. E. Bowers, and T. L. Burgess. 1995. Sonoran Desert plants: an ecological atlas. The University of Arizona Press, Tucson, Arizona.

United States Fish and Wildlife Service. 1997. Endangered and threatened wildlife and plants: determination of endangered species status for the cactus ferruginous pygmy-owl in Arizona; Final Rule, March 10, 1997. Federal Register 62:10730-10747.

United States Fish and Wildlife Service. 2000. Cactus ferruginous pygmy-owl survey protocol. Arizona Ecological Services Field Office, Phoenix, Arizona.

United States Fish and Wildlife Service. 2002. Endangered and Threatened Wildlife and Plants; Designation of Critical Habitat for the Arizona Distinct Population Segment of the Cactus Ferruginous Pygmy-owl *(Glaucidium brasilianum cactorum*); Proposed Rule, November 27, 2002. Federal Register 67:71032-71064.

United States Fish and Wildlife Service. 2003. Cactus ferruginous pygmy-owl *(Glaucidium brasilianum cactorum*) draft recovery plan. Albuquerque, New Mexico.

Van Rossem, A. J. 1937. The ferruginous pigmy owl of northwestern Mexico and Arizona. Proceedings of the Biological Society of Washington 50:27-28.

Van Rossem, A. J. 1945. A distributional survey of the birds of Sonora, Mexico. Occasional Papers Museum of Zoology, Louisiana State University 21:1-379.

Van Devender, T. R., A. C. Sanders, R. K. Wilson, and S. A. Meyer. 2000. Vegetation, flora, and seasons of the Río Cuchujaqui, a tropical deciduous forest near Alamos, Sonora. Pages 36-101 *in* R. H. Robichaux and D. Yetman, editors. The tropical deciduous forest of Alamos: Biodiversity of a threatened ecosystem in Mexico. University of Arizona Press, Tucson, Arizona.

Vander Wall, S. B. and J. A. MacMahon. 1984. Avian distribution patterns along a Sonoran Desert bajada. Journal of Arid Environments 7:59-74.

Verner J. 1985. Assessment of counting techniques. Current Ornithology 2:247-302.

Whittaker, R. H. 1967. Gradient analysis of vegetation. Biological Review 42:207-264.

Whittaker, R. H. and W. A. Niering. 1965. Vegetation of the Santa Catalina Mountains, Arizona: a gradient analysis of the south slope. Ecology 46:429-452.

Wilson, R.C., Narog, M.G., Corcoran, B.M., and Koonce, A.L. 1996. Postfire saguaro injury in Arizona's Sonoran Desert. Pages 247-252 *in* P.F. Ffolliott et al., editors. Effects of fire on Madrean Province Ecosystems-a symposium proceedings. General Technical Report RM-GTR 289, U.S. Department of Agriculture Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colorado.

Wiseman, F. M. 1980. The edge of the tropics: the transition from tropical to subtropical ecosystems in Sonora. Mexico. Geoscience and Man 21:141-156.

Yang, T. W. and C. H. Lowe. 1956. Correlation of major vegetation climaxes with soil characteristics in the Sonoran Desert. Science 123:542

Zar, J. H. 1996. Biostatistical analysis. Prentice Hall, Upper Saddle River, New Jersey.

Appendix A: Scientific, common, and family names of dominant canopy and understory plant species and structure groups found in riparian and upland vegetation plots Sonora, Mexico 2000-01.

Scientific name (species or group)	Common name	Family	Structure Group [a]
Abutilon sp.	indian mallow	Malvaceae	
Acacia angustissima	whiteball acacia	Fabaceae	TS
Acacia cochliacantha	boat-thorn acacia	Fabaceae	TS or TDF
Acacia constricta	white-thorn acacia	Fabaceae	TS
Acacia coulteri		Fabaceae	TDF
Acacia farnesiana	sweet acacia	Fabaceae	
Acacia greggii & occidentalis	catclaw acacia	Fabaceae	
Acacia pennatula	feather acacia	Fabaceae	TDF
Acacia pringlei	guamuchilillo	Fabaceae	TS
Acacia willardiana	palo blanco	Fabaceae	
Agave sp.	agave	Agavaceae	SUC
Agonandra racemosa	mata chamaco	Opiliaceae	TEF
Albizia sinalöensis	palo joso	Fabaceae	GWM
Aloysia sp.	bee brush	Verbenaceae	RS
Alvaradoa amorphoides	palo torcido	Simaroubaceae	TDF
Ambrosia ambrosioides	canyon ragweed	Asteraceae	RS
Ambrosia cordifolia	chicurilla	Asteraceae	SS
Ambrosia deltoidia	triangle-leaf bursage	Asteraceae	SS
Ambrosia dumosa	white bursage	Asteraceae	SS
Amorpha fruticosa	false indigo bush	Fabaceae	
Anisacanthus thurberi	desert honeysuckle	Acanthaceae	
Aphananthe monoica	guasimilla	Ulmaceae	TEF
Ardisia revoluta	aguapepe	Myrsinaceae	TEF
Atamisquea emarginata	palo zorillo	Capparaceae	
Atriplex canescens	four-wing saltbush	Chenopodiaceae	
Atriplex polycarpa	desert saltbrush	Chenopodiaceae	
Atriplex sp.	saltbrush	Chenopodiaceae	
Baccharis glutinosa	seepwillow	Asteraceae	RS
Baccharis sarothroides	desert broom	Asteraceae	RS
Bebbia juncea	bebbia	Asteraceae	RS
Berberis haematocarpa	algarita	Berberidaceae	
Bouvardia sp.	chuparosa	Rubiaceae	
Brickellia sp.	brickell bush	Asteraceae	SS
Brongniartia alamosana	palo piojo	Fabaceae	TDF
Bursera (other species)	torote	Burseraceae	TDF
Bursera hindsiana & microphylla	copal	Burseraceae	

Bursera simaruba & arborea	torote colorado, palo mulato	Burseraceae	TEF
Caesalpinia caladenia	palo piojo blanco	Fabaceae	TS
Caesalpinia palmeri	piojo	Fabaceae	TS
Caesalpinia platyloba	palo colorado	Fabaceae	TDF
Caesalpinia pulcherrima	bird-of-paradise	Fabaceae	TS
Caesalpinia pumila	bird-of-paradise	Fabaceae	TS
Caesalpinia sp.	bird-of-paradise	Fabaceae	TS
Calliandra sp.	fairy duster	Fabaceae	
Cannibus sativa/indica	marajuana	Cannabanaceae	
Carnegiea gigantea	saguaro	Cactaceae	SUCC
Casimiroa edulis	zapote	Rutaceae	TEF
Cedrela odorata	cedro	Meliaceae	TEF
Ceiba acuminata	kapok, pochote	Bombaceae	TDF
Celtis iguanea	cumbro, garabato	Ulmaceae	
Celtis pallida	desert hackberry	Ulmaceae	
Celtis reticulata	netleaf hackberry	Ulmaceae	
Chilopsis linearis	desert willow	Bignoniaceae	
Chloroleucon mangense	palo pinto	Fabaceae	TDF
Cinnamomum hartmanii	haya	Lauraceae	TEF
Cochlospermum vitifolium	palo barril	Cochlospermaceae	TDF
Colubrina triflora	palo cachorra	Rhamnaceae	
Colubrina viridis	palo colorado	Rhamnaceae	
Condalia sp.	crucillo	Rhamnaceae	
Condalia warnockii	crucillo	Rhamnaceae	
Conzattia multiflora	palo joso de la sierra	Fabaceae	TDF
Cordia parvifolia	vara prieta	Boraginaceae	
Cordia sonorea	palo de asta	Boraginaceae	TDF
Coursetia glandulosa	coursetia, samota	Fabaceae	TS
Croton sp.	croton	Euphorbiaceae	
Cryptostegia grandiflora	bejuco	Asclepiadaceae	
Diospyros sonorae	persimmon, guayparin	Ebenaceae	TEF
Dodonaea viscosa	hopbush	Sapindaceae	TS
Drypetes gentryi	cortopico	Euphorbiaceae	TEF
Encelia farinosa	white brittlebush	Asteraceae	SS
Encelia frutescens	green brittlebush	Asteraceae	SS
Erythrina flabelliformis	coral bean, chilicote	Fabaceae	TDF
Erythroxylum mexicanum	mamoa	Erythroxylaceae	
Esenbeckia hartmanii	palo amarillo	Rutaceae	TS
Eucalypyus sp.	eucalyptus	Myrtaceae	
Euphorbia sp.	euphorbia	Euphorbiaceae	
Eysenhardtia polystachya	kidneywood	Fabaceae	TS
Ficus sp.	fig	Moraceae	TEF
Forchammeria watsoni	jito	Capparaceae	

Forestiera sp.	desert olive	Oleaceae	
Fouquieria macdougalii & diguetii	tree ocotillo	Fouquieriaceae	TS
Fouquieria splendens	ocotillo	Fouquieriaceae	
Frankenia sp.	saladito	Frankeniaceae	SS
Fraxinus gooddingii	goodding ash	Oleaceae	
Fraxinus velutina	ash, fresno	Oleaceae	GWD
Guaiacum coulteri	guayacan	Zygophyllaceae	
Guazuma ulmifolia	guasima, picklenut	Sterculiaceae	TEF
Gutierrezia sorathrea	snakeweed	Asteraceae	SS
Haematoxylon brasiletto	palo de brasil	Fabaceae	TS
Havardia mexicanum	chino	Fabaceae	GWM
Havardia sonorae	palo gato, Sonoran ebany	Fabaceae	TS
Hintonia latiflora	copalquin	Rubiaceae	TDF
Hymenoclea monogyra	burrobush	Asteraceae	RS
Hyptis sp.	lavender	Labiatae	RS
Ipomoea arborescens	tree morning glory, palo santo	Convolvulaceae	TDF
Isocoma acradenia	alkali goldenbush	Asteraceae	SS
Isocoma tenuisecta	burroweed	Asteraceae	SS
Jacquinia pungens	San Juanito	Theophrastaceae	TS
J. cardiophylla, cinerea, & cuneata	limberbush, jatropha	Euphorbiaceae	
Jatropha cordata	torota blanca	Euphorbiaceae	TS
Jatropha malacophylla	sycamore-leaf jatropha	Euphorbiaceae	
Juglans sp.	walnut	Juglandaceae	GWD
Juniperus sp.	juniper	Cupressaceae	
Karwinskia humboldtiana	cacachila	Rhamnaceae	TS
Koeberilinia spinosa	all-thorn	Koeberliniaceae	
Krameria sp.	rhatany	Krameriaceae	SS
Larrea tridentata	creosote	Zygophyllaceae	
Lophocerus shottii	senita	Cactaceae	SUC
Lycium sp. & *Phalothamnus* sp.	lycium, wolfberry	Solanaceae, Phytolaccaceae	
Lysiloma microphyllum	mauto	Fabaceae	TDF
Lysiloma watsoni	tepeguaje	Fabaceae	TDF
Maclura tinctoria	mora	Moraceae	TEF
Malpighia emarginata & Bunchosia	granadilla	Malpighiaceae	
Melochia tomentosa	malva rosa	Sterculiaceae	
Mimosa sp.	mimosa	Fabaceae	TS
Montanoa sp.	batayaqui	Asteraceae	
Nicotiana glauca	tree tobacco	Solanaceae	
Olneya tesota	ironwood, palo fiero	Fabaceae	
Opuntia sp.	prickly pear or cholla	Cactaceae	SUC
Otatea acuminata	otate, Mayo bamboo	Poaceae	
Pachycereus pecten-arboriginum	hecho	Cactaceae	SUCC

Pachycereus pringlei	cardon	Cactaceae	SUCC
Parkinsonia sp.	paloverde	Fabaceae	
Parthenium tomentosum		Asteraceae	
Pennisetum ciliare	bufflegrass	Gramineae	GRAS
Pilosocereus alensis	pitahaya barbona	Cactaceae	SUC
Piscidia mollis	palo blanco	Fabaceae	
Pisonia capitata	garabullo	Nyctaginaceae	
Pithecellobium confine	ejoton	Fabaceae	
Pithecellobium dulce	guamuchil	Fabaceae	TDF or GWD
Plantanus sp.	sycamore	Plantanaceae	GWD
Platymiscium trifoliolatum	tampiceran	Fabaceae	TEF
Pluchea sericea	arrowweed	Asteraceae	RS
Populus mexicana & fremontii	cottonwood	Salicaceae	GWD
Prosopis sp.	mesquite	Fabaceae	
Prunus zinggii	cherry, jeco guasiqui	Rosaceae	TEF
Pseudobombax palmeri	cuajilote	Bombaceae	TDF
Psidium guajava	guava, guayaba	Myrtaceae	TEF
Psidium sartorianum	arrallan	Myrtaceae	TEF
Psorothamnus spinosus	smoke tree	Fabaceae	
Quercus sp.	oak	Fagaceae	
Randia echinocarpa	papache	Rubiaceae	
Randia laevigata	sapuchi	Rubiaceae	
Randia obocarpa	papachillo	Rubiaceae	
Randia thurberi	papachillo	Rubiaceae	
Ricinus communis	castor bean	Euphorbiaceae	
Ruellia sp.	rama parda	Acanthaceae	
Salix sp.	willow, sauce	Salicaceae	GWD
Sambucus mexicana	elderberry	Caprifoliaceae	GWD
Sapindus saponaria saponaria	western soapberry	Sapindaceae	TEF
Sebastiana bilocularis	Mexican jumping bean	Euphorbiaceae	
Sebastiana pavoniana & cornuta	yerba de la flecha	Euphorbiaceae	
Senecio sp.	senecio	Asteraceae	
Senna atomaria	palo zorillo	Fabaceae	TDF
Sideroxylon occidentale	bebelama	Sapotaceae	
Sideroxylon persimile	bebelama	Sapotaceae	TEF
Sideroxylon tepicence	tempisque	Sapotaceae	TEF
Simmondsia chinensis	jojoba	Simmondsiaceae	
Solanum erianthum	lengua de buey	Solanaceae	
Solanum hindsianum	tomatillo espinoso	Solanaceae	
Stegnosperma watsonii	amole	Stegnospermataceae	
Stemmadenia tomentosa	berraco, huevos del toro	Apocynaceae	TDF
Stenocerus montanus	sahuira	Cactaceae	SUCC
Stenocerus thurberi	organ pipe, pitahaya	Cactaceae	SUCC

Tabebuia impetiginosa & chrysantha	amapa	Bignoniaceae	TDF
Tacoma stans	yellow bells	Bignoniaceae	
Tamarisk sp.	tamarisk	Tamaricaceae	
Taxodium distichum mexicanum	sabino, Mexican bald-cypress	Cupressaceae	TEF
Trichilia hirta & americana	piocha	Meliaceae	
Trixis californica	trixis	Asteraceae	SS
Trophis racemosa	granadilla	Myrsinaceae	
Vallesia glabra	cacarahue	Apocynaceae	
Vitex mollis	uvalama	Verbenaceae	TEF
Willardia mexicana	venus tree	Fabaceae	TDF
Wimmeria mexicana	algodoncillo	Clethraceae	TDF
Yucca sp.	Yucca	Liliaceae	
Zanthium sp.	cocklebur	Asteraceae	
Zanthoxylum fagara	lime pricklyash	Rutaceae	
Zizuphys amole	amole dulce	Rhamnaceae	
Zizuphys obtusifolia	graythorn, espina gris	Rhamnaceae	
	forbs	various families	
	grass	Gramineae	GRAS
	agricultural plants	various families	
	wetland plants	various families	

[a] Structure groups include (GRAS) - grasses, (GWD) - gallery woodland deciduous, (GWM) - gallery woodland microphyllous, (RS) - riparian scrub, (SS) - subshrubs, (SUC) - succulents, (SUCC) - large columnar succulents, (TDF) - tropical deciduous forest, (TEF) - tropical evergreen forest, (TS) - thornscrub or canopy shrub.

Appendix B. Distributional notes.

Although ferruginous pygmy-owls have been reported in interior Sonora (Russell and Monson 1998), surveys in these areas rarely recorded owls. East of Moctezuma, columnar cacti were absent and the nearest occupied sites over 100 km away. Although pygmy-owls were not found in the middle Río Sonora Valley near Arizpe, I suspect that they may occur. This area is near the northeastern edge of saguaro distribution (Steenbergh and Lowe 1977, Turner et al. 1995) and within 50 km of occupied areas to the west (Fig. 2). I suspect sightings on the plateau northeast of Alamos, were a species other that *G. brasilianum*. In this region, I did not find ferruginous pygmy-owls much above the broad valley bottom at El Taymuco, but found Colima pygmy-owls on forested slopes, and expect northern pygmy-owls (*Glaucidium gnoma*) in Madrean evergreen woodland on the plateau. Although ferruginous pygmy-owls have nested in oaks in southeast Sonora, this area (Güirocoba) is immediately adjacent to the Coastal Plain, supports a mosaic of tropical forest and oak woodland, and is similar to other nearby areas (Choquincahui) where they occurred near the ecotone of oak woodland.