

Importance of environmental and spatial gradients on patterns and consequences of resource selection

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Abstract. Strategies to conserve rare species require identifying resources that function as important habitat elements and that promote high demographic performance. Assessing the relative importance of resources, however, can be confounded by natural variation in resource availability and by the hierarchical spatial structure in which resources are organized. Because availability and relative importance of resources often vary across environmental and spatial gradients, we used gradients together with resource selection functions and variance decomposition to assess the relative importance of resources to nest site selection and reproductive performance of Ferruginous Pygmy-Owls (*Glaucidium brasilianum*). We measured habitat characteristics of 106 nests and paired available sites at five spatial scales across a 220-km gradient of precipitation and vegetation in northwest Mexico, in a region adjacent to the southwestern United States where pygmy-owls have declined to near extinction. Resources explained 76–85% of variation in nest site selection and 21–31% of variation in reproductive performance across all spatial scales combined. Although we found evidence of resource selection at each scale, the magnitude of selection and influence of resources on reproductive performance were greatest where availability of selected resources were low and where temperature extremes and predation risk likely increased the relative importance of these resources. At larger scales, geographic changes in resource use corresponded with changes in availability, whereas at smaller scales, resource use varied little despite changes in availability, suggesting higher specificity and importance of resources at smaller scales. At the smallest scale, owls selected nest cavities with smaller entrances, larger volume, greater height, and orientations that produced cooler microclimates in the hottest regions of the study area; these choices promoted higher reproductive performance. Cavity resources explained more variation in selection and reproductive performance than resources at larger scales, highlighting their importance as conservation targets. High correlation of resource characteristics among spatial scales, however, indicated that selection of resources at small scales depended on characteristics of resources at larger scales. Assessing how resource selection changes in response to underlying variation in resource availability can help prioritize resources most important for conservation and management.

Key words: *environmental gradients; Ferruginous Pygmy-Owl; Glaucidium brasilianum; habitat quality; habitat selection; resource selection function; spatial scale; variance decomposition.*

INTRODUCTION

Identifying resources that influence habitat selection and demography of animal populations is fundamental to conservation and management, yet can be challenging in natural settings. When both availability and use of a resource is high, this resource might not be classified as “selected” and its importance to animals could be underestimated (Johnson 1980, Manly et al. 2002). In contrast, when availability of a resource is low, due to inherent rarity or the actions of other organisms (Kluyver and Tinbergen 1953, Werner et al. 1983, Sherry and Holmes 1988), animals may use other

resources that are less preferred but are more readily available. In these circumstances, resources may be classified as “selected,” but their importance to the animal could be overestimated. Some of these challenges in assessing resource selection and importance can be reduced by studying populations across broad environmental gradients along which biotic and abiotic conditions vary. Because some ecological processes are influential at only certain points along environmental gradients (Buehler and Keith 1982), gradients provide opportunities to evaluate how changes in resource availability and importance affect resource selection. Further, assessing resource selection along gradients (e.g., Karr and Freemark 1983, Garshelis 2000, Fortin et al. 2008) can help to identify important resource thresholds and to distinguish resources that are important locally vs. those that are important universally.

Although gradients provide novel opportunities for assessing variation in resource selection, animals often

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FIG. 1. Ferruginous Pygmy-Owl (*Glaucidium brasilianum*) and typical nest site. The nest was located in the giant saguaro cactus (*Carnegiea gigantea*) in the foreground (left-hand photo) and was within the Arizona Upland subdivision of the Sonoran Desert in northern Sonora, Mexico. Trees and shrubs around the nest saguaro include mesquite (*Prosopis velutina*) and triangle-leaf bursage (*Ambrosia deltoidea*). Photo credits: A. D. Flesch (left); S. L. Jacobs (right).

perceive resources at multiple spatial scales simultaneously (Hildén 1965), which complicates evaluating the sets of interrelated choices made by animals. Moreover, because resources are organized hierarchically and resource characteristics are often correlated across spatial scales (Wiens 1989), selection at one scale might reflect resources being selected at other scales (Kristan 2006). Unless a high proportion of variation in resource selection is explained uniquely at one or more scales, identifying the scale at which particular resources are most important may be impossible (Cushman and McGarigal 2002). Because selection should be strongest for resources at scales that are most important to reproduction and survival, understanding interrelationships among resource availability, selection, spatial scale, and demography can help identify resources that are critical to conservation of rare species.

Demographic consequences of resource selection should be a fundamental consideration of management strategies because they reflect the ultimate importance of a resource to a species (Hobbs and Hanley 1990, Rosenzweig 1991, Garshelis 2000). Although resources exhibiting strong selection are often associated with higher demographic performance (Nilsson 1984, Sonerud 1985, Brown and Shine 2004, Doak et al. 2006), some studies show no such relationship (Holway 1991, Mayhew 1997, Solarz and Newman 2001). These findings may not provide evidence that resources selected by a species are unimportant or that these choices are not adaptive, but instead could indicate constraints on the expression of ideal choices in natural settings or that the processes that have shaped resource selection behaviors over the long term may not be evident in short-term studies. Regardless, understanding relationships between

resource selection and demography can help identify resources important for developing effective conservation strategies (Clark and Shutler 1999).

To understand variation in the patterns and consequences of resource selection and to translate these findings into effective conservation and management strategies, we assessed nest site selection and reproductive performance of Ferruginous Pygmy-Owls (*Glaucidium brasilianum*; Fig. 1) at multiple spatial scales across a broad environmental gradient in northwestern Mexico. The approach we describe is novel because we assessed how variation in resource availability across broad environmental and spatial gradients affected patterns of resource selection, and then evaluated how resources with spatially varying effects on selection influenced demography. These findings are relevant to managers because pygmy-owls have declined to endangered levels in the southwestern United States due to habitat loss (Johnson et al. 2003) yet are still common locally in adjacent northwestern Mexico in areas where woodlands occur in association with giant columnar saguaro cacti (*Carnegiea gigantea*) that provide nest cavities (Fig. 1; Flesch and Steidl 2006). Our objectives were to evaluate the relative importance of resources to nest site selection and reproductive performance of pygmy-owls across environmental and spatial gradients and to evaluate the ecological and evolutionary implications of these patterns for management.

METHODS

We studied resource selection along a 220-km longitudinal gradient in northern Sonora, Mexico (Fig. 2), along which elevation varied three-fold (340–1150 m), annual rainfall varied more than twofold (20–50

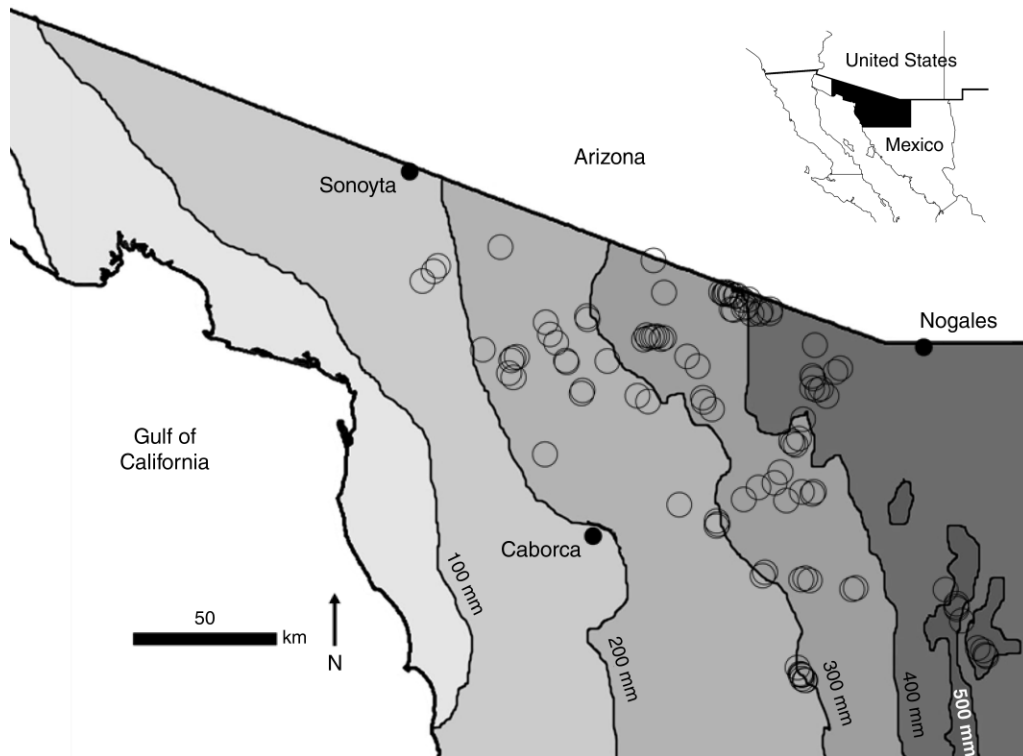


FIG. 2. Rainfall gradient and distribution of Ferruginous Pygmy-Owl nests ($n = 106$; open circles) and major towns (solid circles) across the study area in northern Sonora, Mexico, 2001–2003. Each progressively darker band indicates a 100-mm increase in annual rainfall.

cm), and mean maximum temperature in summer ranged from 36°C to 39°C; this wide range of climate and physiography drive striking variation in vegetation (Shreve 1951, Brown 1982). Vegetation transitioned from desert scrub in the south and west to a mosaic of woodland and savannah at higher elevations in the north and east. In the lowest, most arid regions, Lower Colorado River Valley desert scrub was dominated by shrubs such as creosote (*Larrea tridentata*) and bursage (*Ambrosia* sp.), with trees restricted mainly to riparian areas. At moderate elevations, Arizona Upland desert scrub was dominated by woodlands and scrub of short leguminous trees such as paloverde (*Parkinsonia* sp.), ironwood (*Olneya tesota*), and mesquite (*Prosopis velutina*). At higher elevations, semidesert grasslands were dominated by open woodlands and savannah of mesquite, acacia (*Acacia* sp.), and bunchgrasses. Riparian vegetation varied less across the gradient, and was dominated by woodlands of mesquite and acacia with Mexican ebony (*Havardia mexicana*) restricted to more mesic areas in the east and south. Saguaro cacti occurred across the entire gradient, primarily in uplands.

Sampling design

To obtain a representative sample of nests along the gradient, we selected random points throughout much

of northern Sonora at elevations <1200 m. We surveyed transects clustered around 121 random points and at 48 additional points that we located nonrandomly in areas where few pygmy-owls were detected during surveys. At each random point, we established a transect 1–5 km in length along the closest drainage ≥ 2 m wide in each of four topographic formations (valley bottoms, lower bajadas, upper bajadas, and canyons) that occurred within 20 km of the point; at each nonrandom point, we placed one transect along a drainage. Between 2001 and 2003, we broadcast recorded territorial calls along transects to elicit responses from pygmy-owls (Flesch and Steidl 2007), searched for nests along a random subset ($n = 68$ of 112) of occupied transects, and examined nest contents with a small pole-mounted video camera.

To assess factors that explained nest site selection by pygmy owls, we compared each nest to a paired site that we selected at random and centered on a potential nest substrate (saguaro or tree) with a suitable cavity (≥ 4.0 cm in diameter and ≥ 10 cm deep) within estimated home ranges (Design III of Manly et al. 2002). Because home ranges (95% fixed kernel) of nesting males in the study area are ≤ 59 ha ($n = 19$; A. D. Flesch, unpublished data), which equals a circular area with a 433 m radius, we selected paired sites to be within 400 m of each nest. We considered all cavities available to pygmy-owls because

they initiate nesting earlier than most species or can appropriate cavities occupied by most other species. We measured environmental features centered on nest and available sites at nest cavity, nest substrate, and at three nest area scales. We selected nest area scales based on patterns of spatial use by nesting pygmy-owls: 15-m (0.07 ha) and 30-m (0.28 ha) plots included areas within which males typically roost, and 90-m (2.54 ha) plots were similar in size to 50% fixed-kernel use areas during the nesting season ($\bar{x} \pm SE = 2.8 \pm 0.6$ ha, $n = 19$; A. D. Flesch, unpublished data).

To measure reproductive performance, we inspected nest cavities two to five times per nesting attempt to monitor nest survival and to count eggs and nestlings. To time our final visit to nests to coincide with the period immediately before fledging, we estimated the age of nestlings using a daily photographic key of nestling development (G. Proudfoot, unpublished data). We considered nests to have failed if they were empty before young could have reached 26 days old, which is the youngest age we have observed successful fledging; most young fledge 28 days after hatching (Proudfoot and Johnson 2000). We defined productivity as the number of nestlings that survived to within one week of fledging, which was correlated closely with the number of young that actually fledged based on a subset of nests that we monitored every few days ($r = 0.90$, $P < 0.001$, $n = 25$). Nests not visited at times appropriate for estimating productivity ($n = 28$) were excluded from analyses.

Environmental features

At nest area scales, we measured distances from each nest and available site to the nearest drainage channel ≥ 2 m wide and nearest upland or riparian vegetation edge that we defined based on structural and floristic contrast. At each nest area scale, we estimated visually percent cover of each vegetation formation (woodland, desert scrub, savannah, and thornscrub), volume of vegetation in five height strata (0–1 m, 1–3 m, 3–6 m, 6–12 m, and >12 m above ground) that we summed to estimate total vegetation volume, and the relative proportion that each plant species contributed to total volume. We estimated cover and volume to the nearest 10% when values were 20–80% or to the nearest 5% otherwise. At the 15-m and 30-m scales, we identified all woody and succulent plants that were ≥ 2 m tall, used a measuring pole to estimate height, and calculated density and mean and maximum height of each species and all woody species combined. At the 90-m scale, we estimated visually the height of woody species to the nearest 0.5 m and calculated mean and maximum height. To reduce potential observer bias in visual estimates, two observers estimated features independently at each plot, and then averaged estimates.

At the substrate scale, we identified nest and random substrates to species and measured height with a clinometer and diameter at breast height (dbh) with a

measuring tape. We counted the number of suitable cavities and saguaro branches >0.5 m long, and classified the vegetation formation and location (upland or riparian) immediately around substrates.

At the cavity scale, we measured entrance area, height, and orientation, classified location as branch or trunk, and generated an index of cavity volume for each cavity within each nest substrate. To estimate entrance area, we placed a ruler mounted on a pole at the widest horizontal and vertical dimensions of the cavities, read measurements to the nearest 0.5 cm with binoculars, and then averaged dimensions and assumed circular geometry. When excavating saguaro cavities, woodpeckers often sever different numbers of skeletal support ribs that then grow around the hollow internal chamber and produce external stem swelling (McAuliffe and Hendricks 1988). Therefore, as an index of cavity volume, we classified the amount of swelling below entrances as: 0, no swelling; 1, small bulge in $<180^\circ$ of stem; 2, moderate bulge in $>180^\circ$ of stem; and 3, large bulge around entire stem.

Data analyses

To compare resources used vs. those available and to compare successful vs. failed nests, we used likelihood ratio (G) or Fisher's exact tests for categorical variables and paired or two-sample t tests for continuous variables. To determine whether cavity orientation was random, we used Raleigh's test and mean vector length (r_a) to quantify dispersion, which ranges from 0 (maximum) to 1 (minimum). If orientation was nonrandom, we used likelihood ratio tests to assess differences in orientation between nest and available cavities classified into eight categories (north, northeast, east, southeast, south, southwest, west, and northwest) and differences in orientation between successful and failed nests in four categories (north, east, south, west) because data were sparser.

To determine factors that explained nest site selection, we used case-controlled logistic regression (ccLR) for 1:1 pairs at the nest substrate and nest area scales (Proc LOGISTIC in SAS) and 1: m pairs at the nest cavity scale, with m equaling the number of available cavities within nest substrates (Proc PHREG in SAS; SAS Institute 2002). We considered only saguaros when assessing selection at the substrate scale because other substrates were rarely used. To determine factors that explained variation in nest spacing, which we measured as the distance between neighboring nests along the same transect, we used least-squares regression on environmental features averaged at the 90-m scale. To determine factors that explained nest success, we used logistic-exposure models to model the probability of nest survival (Shaffer 2004) and least-squares regression to model productivity. To compare the relative amount of variation in nest survival and productivity explained by factors at different spatial scales, we assessed each

response at each spatial scale separately then compared adjusted r^2 among models.

When modeling resource selection and reproductive performance, if pairs of explanatory variables were correlated ($r > 0.7$) we retained the variable that had the greatest explanatory power. In all logistic regression models, we adjusted for potential overdispersion by including a scaling parameter estimated as the Pearson chi-square statistic divided by degrees of freedom. Because the number of explanatory variables was high at nest area scales, we fit several smaller models consisting of groups of related variables, biologically meaningful interactions, quadratic terms, and year of measurement, and then used stepwise selection ($P < 0.25$ to enter, $P < 0.10$ to stay) to eliminate variables with little explanatory power. We then combined results of these smaller models to generate final models for inference (Ramsey and Schafer 2002).

To describe how resource use and availability changed across the gradient, we assessed variation in characteristics of resources that explained selection and reproductive performance across latitude and longitude and among nests in desert scrub and semidesert grasslands; we used least-squares regression for resources measured as continuous variables and logistic regression for resources measured as categorical variables. To describe how resource selection changed across the gradient, we developed a metric that we named "magnitude of selection" to quantify the degree of resource selection at each site. To calculate this metric, we first used ccLR to create resource selection functions (RSF; Manly et al. 2002), and then evaluated RSF from each spatial scale with the values of used and available resources measured at each site. Once evaluated, each RSF predicted the proportional probability of use for used and available resources at each site and spatial scale. To compute the magnitude of selection, we calculated the difference between these probabilities at each site and spatial scale and used this quantity as a response variable to assess geographic variation in selection with least-squares regression. Predictions from RSF are approximately proportional to probability of use (Manly et al. 2002, Lele and Keim 2006) and are appropriate in our study because probability of use was small relative to availability, and no used or available sites were misclassified (Keating and Cherry 2004). To simplify interpretation and to facilitate comparisons across scales, we scaled probabilities from each RSF so that availability was standardized to zero for a site with average values of resources; we log-transformed these values to reduce the effects of values with high leverage.

We used two approaches to assess the relative importance of resources among spatial scales. First, we assessed the amount of variation in nest site selection, nest survival, and productivity explained by resources at each scale and all scales combined by computing the ratio of variation (deviance or sum-of-squares) ex-

plained by selected resources to variation explained by the overall model. Second, we used variance decomposition to determine the proportion of variance of resources measured at each scale that was (shared) or was not (pure) attributable to resources at other scales (Whittaker 1984). For these analyses, we pooled data across vegetation communities and considered each nest area scale individually.

RESULTS

We located 106 nests between 360 m and 1085 m elevation; 104 were in saguaros and 2 were in large Mexican ebony trees. Most nests were in Arizona Upland desert scrub (52%) and semidesert grasslands (46%), with two (2%) in Lower Colorado River Valley desert scrub. Productivity averaged 2.8 ± 0.2 young/attempt (range = 0–5, $n = 78$), clutch size averaged 4.0 ± 0.1 eggs/clutch (range = 2–5, $n = 68$), and apparent nest success was 86% ($n = 94$).

Nest site selection

Most nests were in savannah (41%), desert scrub (35%), or woodland (23%), with woodland selected twice as frequently as available, desert scrub selected 33% less frequently than available, and savannah selected approximately in proportion to its availability ($G_{3,206}^2 = 10.00$, $P = 0.019$). Although only 20% of nests were in riparian vegetation, nests averaged >35% closer than available substrates to drainage channels and vegetation edges; nests in desert scrub were nearly twice as close to these features as nests in grasslands (Table 1).

At nest area scales, resources that affected selection varied with scale (Table 2). At the 90-m scale, owls selected nest areas that had greater vegetation volume than available; at the 30-m scale, owls selected nest areas with greater cover of woodlands and volume of saguaros than available; at the 15-m scale, owls selected nest areas with greater abundance of cavities and taller maximum tree heights than available. Resources at the 30-m and 15-m scales affected selection more in desert scrub than in grassland (Table 2).

In desert scrub, where plant species composition was more variable, several additional resources affected selection. At both the 90-m and 30-m scales in desert scrub, odds of selection decreased as volume of paloverde increased, and paloverde often replaced mesquite around nest and available substrates ($r \leq -0.59$, $P < 0.001$). At the 30-m scale in desert scrub, selection increased with density of trees regardless of species, whereas at the 15-m scale selection increased with density of mesquite trees (Table 1).

At the nest substrate scale, saguaros selected for nesting were taller, contained more cavities, and had more arms than those available (Table 3). Odds of a saguaro being selected increased by a factor of 1.4 with each 1-m increase in height and by 1.3 with each additional cavity (Table 4).

TABLE 1. Resources measured around Ferruginous Pygmy-Owl nests ($n = 106$) and paired random plots at nest area scales in Sonoran desert scrub and semidesert grasslands in northern Sonora, Mexico, 2001–2003.

Scale and resource	Desert scrub ($n = 58$)					Grassland ($n = 48$)				
	Nest		Available		P	Nest		Available		P
	\bar{x}	SE	\bar{x}	SE		\bar{x}	SE	\bar{x}	SE	
Scaleless										
Distance to drainage channel (m)	58.0	8.8	105.5	15.1	0.0063	107.0	14.1	146.8	18.3	0.0030
Distance to vegetation edge (m)	35.3	5.7	85.8	11.6	0.0003	75.0	10.1	98.4	12.6	0.047
15 m radius										
Cavity abundance (no./15 m)	1.5	0.3	0.4	0.1	0.0019	0.7	0.2	0.2	0.1	0.0071
Plant (≥ 2 m) density (no./ha.)	693.0	51.4	506.1	38.9	0.0013	537.2	47.3	436.6	45.3	0.038
Saguaro density (no./ha)	62.4	7.1	64.6	7.7	0.80	34.3	6.1	27.6	3.8	0.22
Saguaro volume (%)	6.2	1.0	4.8	0.8	0.17	4.9	1.1	2.9	0.8	0.022
Paloverde density (no./ha)	51.7	12.1	75.8	13.6	0.17	6.7	4.4	15.6	7.3	0.068
Creosote density (no./ha)	103.9	24.1	63.4	15.0	0.13	24.4	19.1	11.2	6.7	0.37
Ironwood density (no./ha)	54.1	11.0	56.1	11.1	0.86	0.0	...	0.0
Mesquite density (no./ha)	193.8	22.8	80.1	12.8	0.0001	285.5	30.6	241.8	34.1	0.15
Mean vegetation (≥ 2 m) height (m)	3.1	0.1	3.1	0.1	0.90	3.0	0.1	3.0	0.1	0.24
Maximum vegetation height (m)	6.0	0.3	5.2	0.2	0.016	5.3	0.2	4.7	0.1	0.012
Vegetation volume 0–1 m above ground (%)	22.4	1.1	18.2	1.2	0.0011	22.5	1.1	20.4	1.2	0.30
Vegetation volume 1–3 m above ground (%)	19.7	1.2	14.1	1.0	0.0001	21.5	1.6	19.5	1.5	0.20
Vegetation volume 3–6 m above ground (%)	10.2	0.9	6.6	0.7	0.0009	9.3	0.8	7.2	0.6	0.021
Vegetation volume 6–12 m above ground (%)	3.4	0.5	1.6	0.4	0.0070	2.0	0.4	1.0	0.3	0.0054
Woodland cover (%)	26.6	3.5	10.9	2.3	0.0001	26.8	3.2	20.8	2.9	0.092
Desert scrub cover (%)	56.7	4.9	74.3	4.6	0.0084	4.6	2.7	5.7	2.9	0.22
Savannah cover (%)	12.3	3.2	10.6	3.5	0.98	62.8	3.9	69.3	4.0	0.31
30 m radius										
Cavity abundance (no./30 m)	2.6	0.5	1.5	1.2	0.0093	1.3	0.4	0.3	0.1	0.0063
Plant (≥ 2 m) density (no./ha.)	569.3	38.7	435.9	31.7	0.0019	433.1	37.2	367.8	32.9	0.036
Saguaro density (no./ha)	42.8	5.1	43.0	6.1	0.89	15.6	3.3	12.3	2.5	0.15
Saguaro volume (%)	4.7	0.7	3.8	0.6	0.32	3.2	0.7	1.6	0.5	0.0009
Paloverde density (no./ha)	40.9	7.6	63.2	9.6	0.033	8.9	4.1	11.0	4.5	0.32
Paloverde volume (%)	10.9	1.8	22.2	2.8	0.0001	2.2	1.0	3.8	1.5	0.072
Creosote density (no./ha)	88.2	18.7	60.3	11.6	0.13	4.7	3.2	4.7	3.6	0.95
Ironwood density (no./ha)	45.0	8.5	45.8	8.1	0.10	0.0	...	0.1	0.1	...
Mesquite density (no./ha)	169.1	20.2	72.3	10.3	0.0001	237.7	23.4	209.0	22.9	0.13
Mean vegetation (≥ 2 m) height (m)	3.2	0.1	3.1	0.1	0.87	3.1	0.1	3.0	0.1	0.059
Maximum vegetation height (m)	7.0	0.3	5.9	0.2	0.0026	6.1	0.2	5.4	0.1	0.0016
Vegetation volume 0–1 m above ground (%)	22.8	1.0	19.7	1.0	0.0035	23.6	1.0	21.1	1.1	0.17
Vegetation volume 1–3 m above ground (%)	20.6	1.1	16.0	1.1	0.0005	23.2	1.4	18.8	1.3	0.0019
Vegetation volume 3–6 m above ground (%)	11.4	0.9	7.8	0.5	0.0001	10.1	0.7	7.6	0.6	0.0047
Vegetation volume 6–12 m above ground (%)	4.2	0.6	2.1	0.3	0.0043	2.6	0.4	1.5	0.3	0.0008
Woodland cover (%)	30.3	3.0	13.6	2.4	0.0001	30.7	3.0	20.3	2.5	0.0007
Desert scrub cover (%)	52.4	4.3	69.8	4.5	0.0032	2.4	1.5	3.3	2.0	0.28
Savannah cover (%)	12.1	2.9	10.3	3.3	0.96	59.3	3.6	71.1	3.4	0.021
90 m radius										
Mean vegetation (≥ 2 m) height (m)	4.3	0.2	3.4	0.1	0.0003	3.7	0.1	3.4	0.1	0.0003
Maximum vegetation height (m)	8.8	0.4	7.4	0.3	0.0047	6.9	0.1	6.3	0.1	0.0005
Saguaro volume (%)	4.3	0.8	3.8	0.6	0.51	2.2	0.5	1.7	0.5	0.30
Paloverde volume (%)	13.8	1.6	22.6	2.4	0.0002	3.3	1.0	4.7	1.4	0.16
Creosote volume (%)	6.0	1.2	9.1	1.9	0.11	1.1	0.5	1.6	0.7	0.50
Ironwood volume (%)	17.3	2.3	17.4	2.2	0.97	0.0	...	0.0
Mesquite volume (%)	39.6	3.0	26.3	2.9	0.0001	68.3	3.0	65.7	3.9	0.40
Vegetation volume 0–1 m above ground (%)	24.7	1.0	20.8	0.8	0.0002	24.4	1.0	22.6	1.0	0.24
Vegetation volume 1–3 m above ground (%)	23.9	1.1	17.2	0.9	0.0001	24.8	1.3	20.4	1.1	0.0001
Vegetation volume 3–6 m above ground (%)	14.2	0.9	9.1	0.6	0.0001	12.1	0.7	8.8	0.5	0.0001
Vegetation volume 6–12 m above ground (%)	5.9	0.5	4.1	0.3	0.0005	4.4	0.3	2.6	0.4	0.0001
Woodland cover (%)	34.7	2.5	18.7	1.9	0.0001	33.5	2.6	24.4	2.3	0.0001
Desert scrub cover (%)	48.1	3.4	66.6	3.4	0.0001	1.5	0.9	4.2	2.0	0.036
Savannah cover (%)	9.1	2.1	9.1	2.7	0.62	57.1	3.2	64.5	3.1	0.075

Note: P values are from paired t tests.

At the nest cavity scale, nest cavities differed from available cavities by entrance area, volume, orientation, and height (Table 4). Owls selected cavities within a much narrower range of entrance areas than available (Fig. 3A), and selection was strongest for cavities with

small- to moderate-sized entrances and lower outside this range ($\chi^2_{432} = 8.59$, $P = 0.0034$, for test of the quadratic term; Fig. 3B). Overall, nest entrances averaged 9.2 ± 2.3 cm² smaller than available cavities and entrance area of nest cavities declined as abun-

TABLE 2. Resources that explained nest site selection by Ferruginous Pygmy-Owls at three nest area scales in semidesert grassland ($n = 48$) and Sonoran desert scrub ($n = 58$) in northern Sonora, Mexico, 2001–2003.

Vegetation community, scale, and resource	Estimate	SE	χ^2	P	Odds ratio†
Grassland					
15 m radius					
Cavity density (no./15 m)	0.73	0.42	3.00	0.083	2.1
Maximum vegetation height (m)	0.76	0.33	5.15	0.023	2.1
Saguaro volume (%)	0.13	0.074	2.87	0.090	1.1
30 m radius					
Woodland cover (%)	0.08	0.025	10.4	0.0013	1.1
Saguaro volume (%)	0.44	0.14	10.4	0.0013	1.6
90 m radius					
Vegetation volume 3–6 m above ground (%)	0.46	0.14	11.4	0.0007	1.6
Vegetation volume 6–12 m above ground (%)	0.86	0.25	12.0	0.0005	2.4
Desert scrub					
15 m radius					
Cavity density (no./15 m)	1.23	0.35	12.0	0.0005	3.4
Maximum vegetation height (m)	2.75	0.76	13.0	0.0003	15.6
Height of neighboring saguaros (m)	2.37	0.62	14.4	0.0001	10.7
Mesquite density (no./ha)	0.02	0.0047	15.1	0.0001	1.02
Vegetation volume 0–1 m above ground (%)	0.23	0.064	13.1	0.0003	1.3
30 m radius					
Height of neighboring saguaros (m)	1.18	0.41	8.26	0.0040	3.3
Woodland cover (%)	0.04	0.018	5.58	0.018	1.04
Tree density (no./ha)	0.0032	0.0015	4.63	0.031	1.01
Saguaro volume (%)	0.17	0.086	4.16	0.041	1.2
Paloverde volume (%)	-0.09	0.030	8.93	0.0028	0.91
90 m radius					
Total vegetation volume (%)	0.08	0.024	9.99	0.047	1.1
Paloverde volume (%)	-0.08	0.042	3.93	0.0016	0.92

Note: P values and odds ratios are from case-controlled logistic regression for 1:1 pairs.
 † Effect of a 1-unit increase in the resource on the odds of selection.

TABLE 3. Resources measured at Ferruginous Pygmy-Owl nest ($n = 81$) and available cavities within nest substrates ($n = 359$) and at nest and available saguaros ($n = 104$) in northern Sonora, Mexico, 2001–2003.

Scale and resource	Nest		Available		P
	\bar{x}	SE	\bar{x}	SE	
Cavity					
Entrance area (cm ²)	25.2	1.1	34.5	2.5	0.0001
Height (m)	5.7	0.2	5.3	0.2	0.030
Cavity in arm (%)	58.0	5.5	59.1	5.5	0.90
Stem bulge					
Small (%)	40.7	5.5	37.6	5.4	0.061
Moderate (%)	38.2	5.4	19.8	4.4	0.0007
Large (%)	11.1	3.5	1.7	1.4	0.0003
Orientation					
West (%)	9.9	3.3	18.7	4.3	0.071
Northwest (%)	14.8	4.0	11.4	3.5	0.45
Northeast (%)	4.9	2.4	10.9	3.5	0.15
East (%)	8.6	3.1	8.1	3.0	0.82
Southeast (%)	9.9	3.3	9.8	3.3	1.00
South (%)	19.8	4.4	13.7	3.8	0.17
Southwest (%)	19.8	4.4	16.2	4.1	0.42
Substrate					
No. arms	4.6	0.3	2.7	0.3	0.0001
No. cavities	4.4	0.4	2.3	0.2	0.0001
Height (m)	7.7	0.2	6.8	0.2	0.0002
Diameter at breast height (cm)	52.2	0.7	48.9	0.7	0.0001
Upland location (%)	80.2	3.9	87.7	3.2	0.19

Note: P values are from paired t tests for continuous factors and Fisher's exact tests for categorical factors.

dance of saguaros within nest areas increased ($t_{104} \geq 2.05$, $P \leq 0.043$).

Owls selected nest cavities with more external stem swelling than available. Odds of a cavity with a

TABLE 4. Resources that explained nest site selection of Ferruginous Pygmy-Owls at the nest cavity and nest substrate scales in northern Sonora, Mexico, 2001–2003.

Scale and resource	Estimate	SE	χ^2	P	Odds ratio†
Cavity					
Entrance area (cm ²)	-0.07	0.02	8.96	0.0028	0.94
Height (m)	0.34	0.16	4.89	0.028	1.4
Stem bulge					
Small (%)‡	3.9	1.07	12.12	0.0003	47.8
Moderate (%)‡	4.5	1.08	17.12	<0.0001	87.7
Large (%)‡	6.5	1.29	25.13	<0.0001	642.6
West orientation§	-1.4	0.62	5.15	0.023	0.24
Year	-3.2	1.40	4.89	0.027	0.04
Substrate					
No. arms	0.20	0.08	5.08	0.024	1.2
No. cavities	0.24	0.09	6.75	0.0094	1.3
Height (m)	0.30	0.16	3.65	0.056	1.4

Note: P values and odds ratios are from case-controlled logistic regression for 1: m pairs at the cavity scale comparing 81 nest cavities to 359 available cavities within nest substrates and for 1:1 pairs comparing 104 nest saguaros to 104 paired available saguaros.

† Effect of a 1-unit increase in the resource on the odds of selection.

‡ Reference level equals no stem bulge.

§ Reference level equals north-facing orientation.

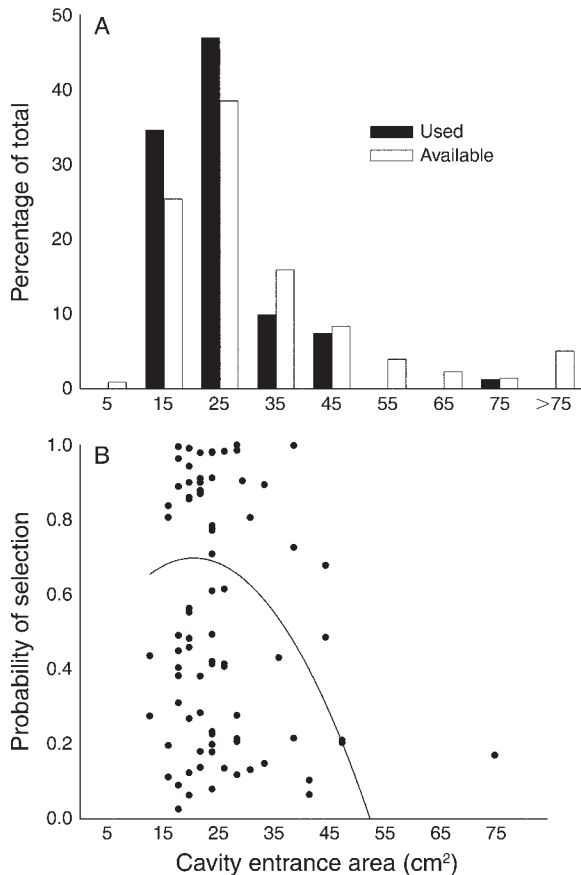


FIG. 3. (A) Size distribution of entrance areas for nest cavities used by ($n = 81$) and available to ($n = 359$) Ferruginous Pygmy-Owls within nest substrates, and (B) relationship between probability of selection and area of nest cavity entrances in northern Sonora, Mexico, 2001–2003. Probability of selection is based on case-controlled logistic regression for 1: m pairs; the extreme observation near 75 cm² had little influence on the overall relationship.

moderate-sized stem bulge being selected were 88 times that for cavities with no bulge after accounting for other factors (Table 4). Only 21% of available cavities had moderate or high levels of stem swelling, yet 49% of nests were within these types of cavities.

Orientation of both nest ($\bar{x} = 224^\circ$, $r_a = 0.21$, $P = 0.033$, $n = 81$) and available cavities ($\bar{x} = 253^\circ$, $r_a = 0.17$, $P < 0.001$, $n = 359$) were nonrandom (Fig. 4). Owls were 76% less likely to select west-facing cavities compared to north-facing cavities (Table 4), with most nests orientated south or southwest (40%) or north or northwest (27%), which was proportional to availability ($G_{7, 426}^2 = 8.91$, $P = 0.26$). Probability of use of west-facing cavities, however, declined markedly along a 220-km gradient from east to west and along a 125-km gradient from south to north ($\chi_{79}^2 \geq 4.57$, $P \leq 0.033$), despite no systematic variation in availability ($\chi_{357}^2 \leq 1.71$, $P \geq 0.19$) (Fig. 5). Similarly, probability of use of north-facing cavities increased somewhat from east to west

along the same geographic gradient ($\chi_{79}^2 = 3.06$, $P = 0.080$) despite no variation in availability ($\chi_{357}^2 = 0.46$, $P = 0.50$). Overall, 72% of west-facing nests ($n = 18$ of 25) were in the cooler eastern portion of the study area, whereas 67% of north-facing nests ($n = 12$ of 18) were in the hotter western portion.

Nest spacing

Spacing between neighboring nests ($n = 39$ pairs) averaged 1064 ± 73 m (range = 308–2126 m) and decreased across the study area by 44 ± 17 m/10 km from west to east ($t_{36} = 2.63$, $P = 0.013$) and 31 ± 15 m/10 km from north to south ($t_{36} = 2.07$, $P = 0.046$); density of saguaros did not affect spacing ($t_{36} \leq 1.11$, $P \geq 0.28$). Spacing between nests increased as volume of creosote around nests increased ($t_{37} = 3.48$, $P = 0.001$) and decreased as total vegetation volume around nests increased ($t_{37} = 2.64$, $P = 0.012$).

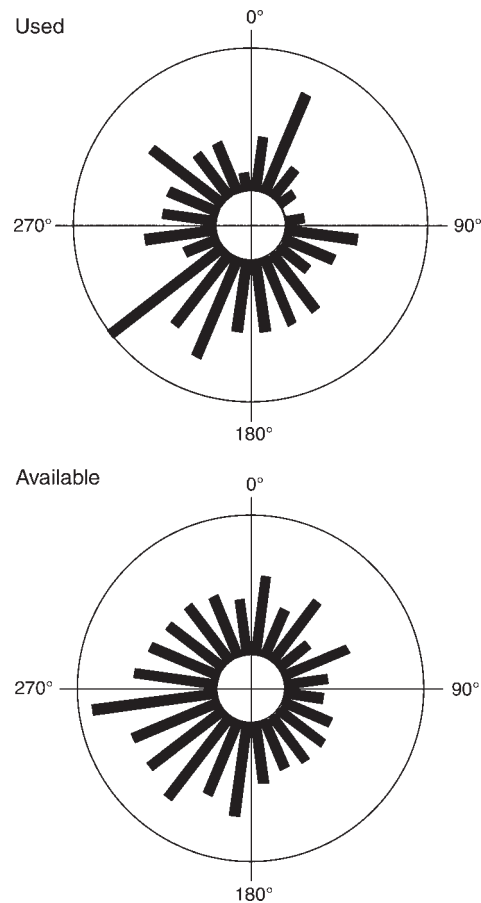


FIG. 4. Circular distribution of cavity entrance orientations for nest ($n = 81$) and available ($n = 359$) cavities that were located within nest substrates used by Ferruginous Pygmy-Owls in northern Sonora, Mexico, 2001–2003. The numbers represent the cardinal directions: 0°, north; 90°, east; 180°, south; and 270°, west. Owls tended to avoid west-facing cavities and use north-facing cavities.

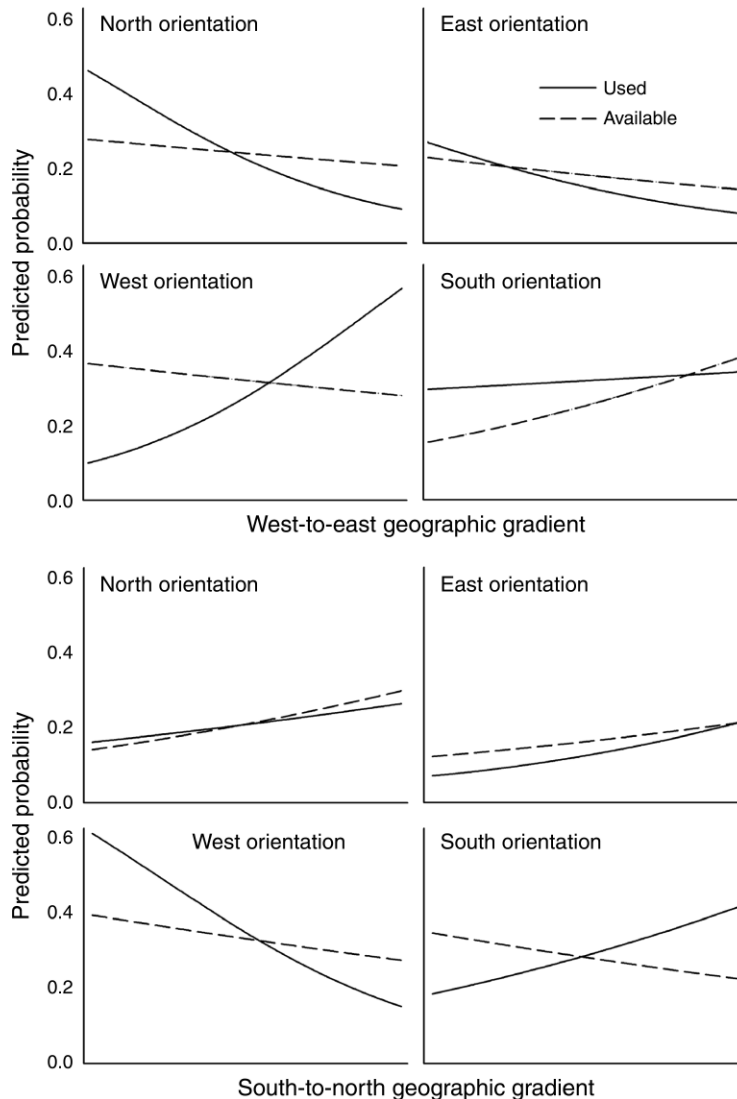


FIG. 5. Predicted probability of use and availability of cavities with different entrance orientations across a 220-km longitudinal gradient (east–west) and 125-km latitudinal gradient (south–north) in northern Sonora, Mexico, 2001–2003. Probability of use of hotter west-facing cavities declined markedly from east to west and from south to north despite little variation in availability, whereas probability of use of cooler north-facing cavities increased somewhat from east to west despite little variation in availability.

Reproductive performance

At nest area scales in desert scrub, nest survival increased as woodland cover increased at the 90-m scale and as maximum tree height increased at the 30-m and 15-m scales (Table 5). In grasslands, however, nest survival at the 90-m scale declined as volume of creosote increased and at the 30-m scale declined as density of paloverde increased.

At the substrate scale, each 1-m increase in substrate height increased the odds of nest survival by a factor of 1.7 (Table 5) with successful nests (7.8 ± 0.2 m) averaging 18% taller than failed nests ($t_{92} = 2.34$, $P = 0.022$). At the cavity scale, nests that survived differed from those that failed by height, entrance area, and

orientation (Table 5). For each 1-m increase in cavity height, odds of survival increased by a factor of 2.3 with successful nests (5.8 ± 0.1 m) averaging 32% taller than failed nests ($t_{92} = 3.66$, $P < 0.001$). Nest survival was greatest for nest cavities with small- to moderate-sized entrances and lower outside this range (Fig. 6). Nests that survived were 67% less likely to face west than other directions compared to failed nests; 24% of nests in west-facing cavities failed ($n = 8$ of 33) compared to only 13% in south-facing ($n = 4$ of 32), 9% in east-facing ($n = 1$ of 11), and 0% in north-facing ($n = 18$) cavities. Nest survival also increased somewhat as the amount of external stem swelling increased ($\chi^2_{15} = 3.14$, $P = 0.076$) and clutch sizes increased by 0.6 ± 0.3 eggs/clutch across the entire range of stem swelling ($t_{63} = 1.84$, $P = 0.070$).

TABLE 5. Resources that explained nest survival of Ferruginous Pygmy-Owls at the nest cavity, nest substrate, and nest area scales in northern Sonora, Mexico, 2001–2003.

Scale and resource	Estimate	SE	χ^2	<i>P</i>	Odds ratio†
Cavity					
Entrance area (cm ²)	0.17	0.072	5.68	0.017	1.19
Entrance area × entrance area (cm ²)	-0.0021	0.0008	6.19	0.013	1.00
Height (m)	0.84	0.290	8.36	0.0038	2.32
West orientation‡	-1.1	0.52	4.41	0.036	0.33
Substrate					
Height (m)	0.55	0.208	6.95	0.0084	1.73
Area in grassland					
30 m, paloverde density (no./ha)	-0.015	0.0073	4.31	0.038	0.99
90 m, creosote volume (%)	-0.098	0.0439	5.02	0.025	0.91
Area in desert scrub					
15 m, maximum vegetation height (m)	1.27	0.451	7.96	0.0048	3.56
15 m, vegetation volume 3–6 m above ground (%)	-0.15	0.046	10.13	0.0015	0.86
30 m, maximum vegetation height (m)	5.09	1.601	10.12	0.0015	162.39
30 m, vegetation volume 3–6 m above ground (%)	-0.15	0.043	12.22	0.0005	0.86
90 m, woodland cover (%)	0.052	0.0236	4.78	0.029	1.05
90 m, vegetation volume 3–6 m above ground (%)	-0.12	0.068	3.27	0.070	0.89

Note: *P* values and odds ratios are from logistic-exposure models, and analyses at the nest cavity and nest substrate scales include nests in both vegetation communities.

† Effect of a 1-unit increase in the resource on the odds of daily nest survival.

‡ Compared to all other orientations.

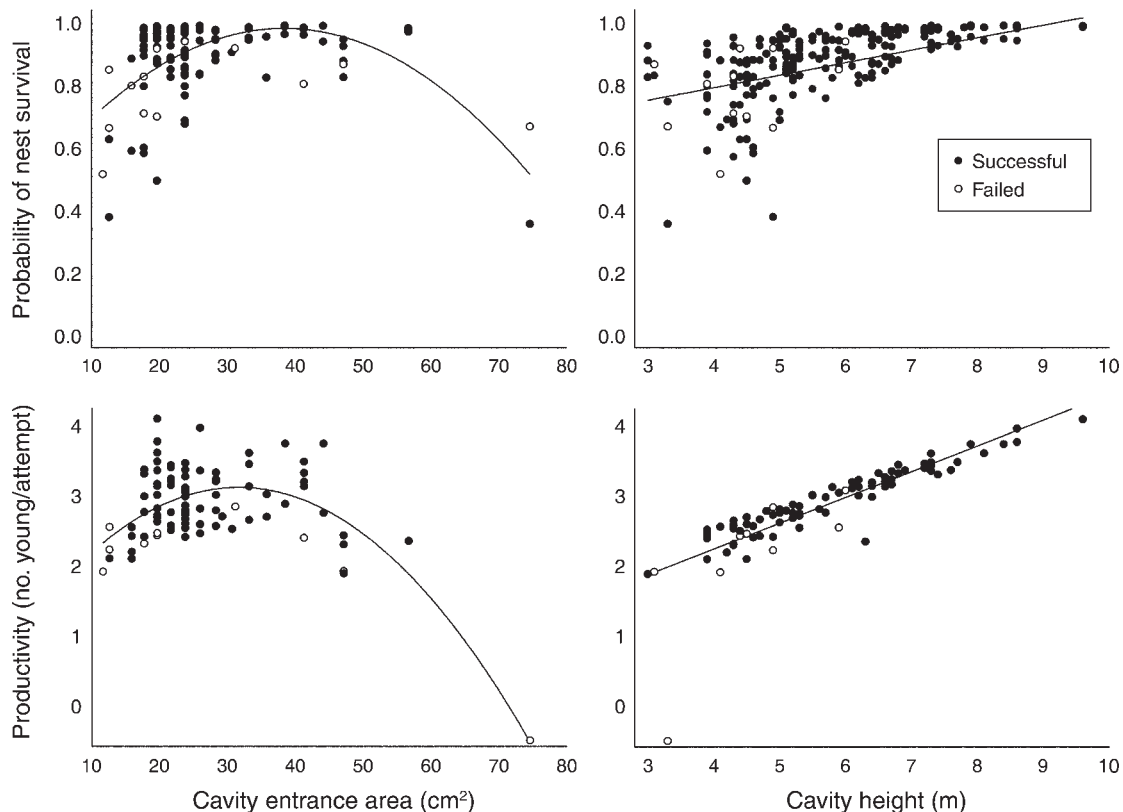


FIG. 6. Influence of nest cavity entrance area and nest cavity height on probability of nest survival ($n = 94$) and productivity ($n = 76$) of Ferruginous Pygmy-Owls in northern Sonora, Mexico, 2001–2003. Nest survival was predicted from a logistic-exposure model adjusted for the effects of cavity entrance area, cavity height, and cavity orientation. Productivity was predicted from a least-squares regression model adjusted for the effects of cavity entrance area and cavity height. Observations near 75 cm² had little influence on the overall relationships.

TABLE 6. Resources that explained productivity (no. young/attempt) of Ferruginous Pygmy-Owls at nest area scales in semidesert grassland ($n = 37$) and Sonoran desert scrub ($n = 39$) in northern Sonora, Mexico, 2001–2003.

Vegetation community, scale, and resource	Estimate	SE	t	P
Grassland				
15 m, mesquite density (no./ha)	0.0026	0.0012	2.18	0.037
30 m, vegetation volume 1–3 m \times vegetation volume 1–3 m (%)	0.0047	0.0027	1.76	0.087
90 m, vegetation volume from 3–6 m (%)	0.094	0.053	1.78	0.083
Desert scrub				
15 m, mean vegetation height (m)	1.25	0.62	2.01	0.052
30 m, mean vegetation height (m)	1.27	0.60	2.12	0.041
30 m, total vegetation volume \times total vegetation volume (%)	–0.0013	0.0005	2.84	0.0074
90 m, vegetation volume 3–6 m \times vegetation volume 3–6 m (%)	–0.0096	0.0044	2.17	0.037
90 m, desert scrub cover (%)	–0.018	0.010	1.74	0.093

Note: P values and parameter estimates are from multiple linear regression.

Variation in productivity at the 90-m and 30-m scales varied with vegetation volume in both vegetation communities; in desert scrub, productivity was higher at moderate vegetation volume whereas in grassland it was higher at high vegetation volume (Table 6). At both the 30-m and 15-m scales in desert scrub, productivity increased with mean vegetation height, whereas at the 15-m scale in grassland, productivity increased with density of mesquite (Table 6). At substrate and cavity scales, productivity increased by 0.3 ± 0.1 young/attempt with each 1-m increase in nest height ($t_{74} \geq 2.54$, $P \leq 0.013$). At the cavity scale, productivity was highest in nest cavities with small- to moderate-sized entrances and lower outside this range ($t_{72} = 2.05$, $P = 0.044$, test for quadratic term; Fig. 6).

In desert scrub, resources at larger nest area scales explained more variation in productivity (at 90 m $r^2 = 0.13$, at 30 m $r^2 = 0.27$) than in nest survival ($r^2 = 0.01$ and 0.15), whereas at the 15-m scale resources explained similar variation in productivity ($r^2 = 0.07$) and in nest survival ($r^2 = 0.07$). At the substrate scale, resources explained similar variation in nest survival ($r^2 = 0.06$) and productivity ($r^2 = 0.07$), whereas at the cavity scale resources explained somewhat more variation in nest survival ($r^2 = 0.20$) than in productivity ($r^2 = 0.14$).

Geographic variation in resource availability and use

Availability of resources selected by owls at nest area scales varied geographically. Volume of total vegetation at the 90-m scale, woodland cover and tree density at the 30-m scale, and maximum tree height and mesquite density at the 15-m scale all increased in availability across geographic dimensions of the study area ($t_{104} \geq 1.94$, $P \leq 0.055$; Fig. 7). Use of these resources by owls tracked availability across the same geographic gradients at the same spatial scales ($t_{104} \geq 2.44$, $P \leq 0.016$; Fig. 7). Although resource use and availability varied somewhat between vegetation communities, geographic patterns of resource use tracked availability similarly in both communities (Fig. 7).

Availability of resources selected by owls at nest substrate and nest cavity scales also varied geographically and in more complex ways than at nest area scales,

yet resource use was more consistent across space than at larger spatial scales (Fig. 7). At the nest cavity scale, heights of available cavities increased from east to west ($t_{357} = 2.24$, $P = 0.026$), yet heights of used cavities did not vary ($t_{79} = 1.39$, $P = 0.17$). Entrance areas of available cavities decreased by 1.2 ± 0.3 cm²/10 km from north to south ($t_{357} = 3.82$, $P < 0.001$), yet entrances of used cavities decreased by half this rate (0.6 ± 0.2 cm²/10 km, $t_{79} = 2.98$, $P = 0.004$). At the nest substrate scale, both available and used substrates were taller at middle latitudes ($t_{103} = 2.00$, $P \leq 0.047$, quadratic terms; Fig. 7) where abundance of saguaros was greatest ($t_{103} = 2.27$, $P \leq 0.024$). Similarly, entrance areas of available cavities were smaller and cavity heights greater ($t_{356} = 2.24$, $P \leq 0.026$) at middle latitudes, with similar patterns for used cavities ($t_{78} = 1.83$, $P \leq 0.071$).

Magnitude of selection differed between vegetation communities. At all nest area scales combined, selection averaged 2.4 times greater in desert scrub than in grassland (Fig. 8). Selection decreased in grassland from large to small area scales, with the opposite pattern expressed in desert scrub where selection at the 15-m scale was especially strong (Fig. 8). In desert scrub, selection at the cavity scale was much higher than at the substrate scale.

Magnitude of selection tended to be greatest at scales where relationships between resources and reproductive performance were strongest. At nest area scales, for example, resources explained twice as much variation in productivity in desert scrub ($r^2 = 0.47$) than in grassland ($r^2 = 0.23$). At the nest cavity scale, resources explained more variation in productivity and nest survival ($r^2 = 0.14$ and 0.20 , respectively) than at the substrate scale ($r^2 = 0.07$ and 0.06).

At nest area scales, geographic variation in resource selection (Fig. 9) corresponded with geographic variation in resource use (Fig. 7), yet there was more variation at spatial scales and in vegetation communities where magnitude of selection was greatest (Fig. 8). In desert scrub, selection increased from north to south at the 30-m scale and from north to south and west to east at the 15-m scale ($t_{56} \geq 1.93$, $P \leq 0.059$), but did not

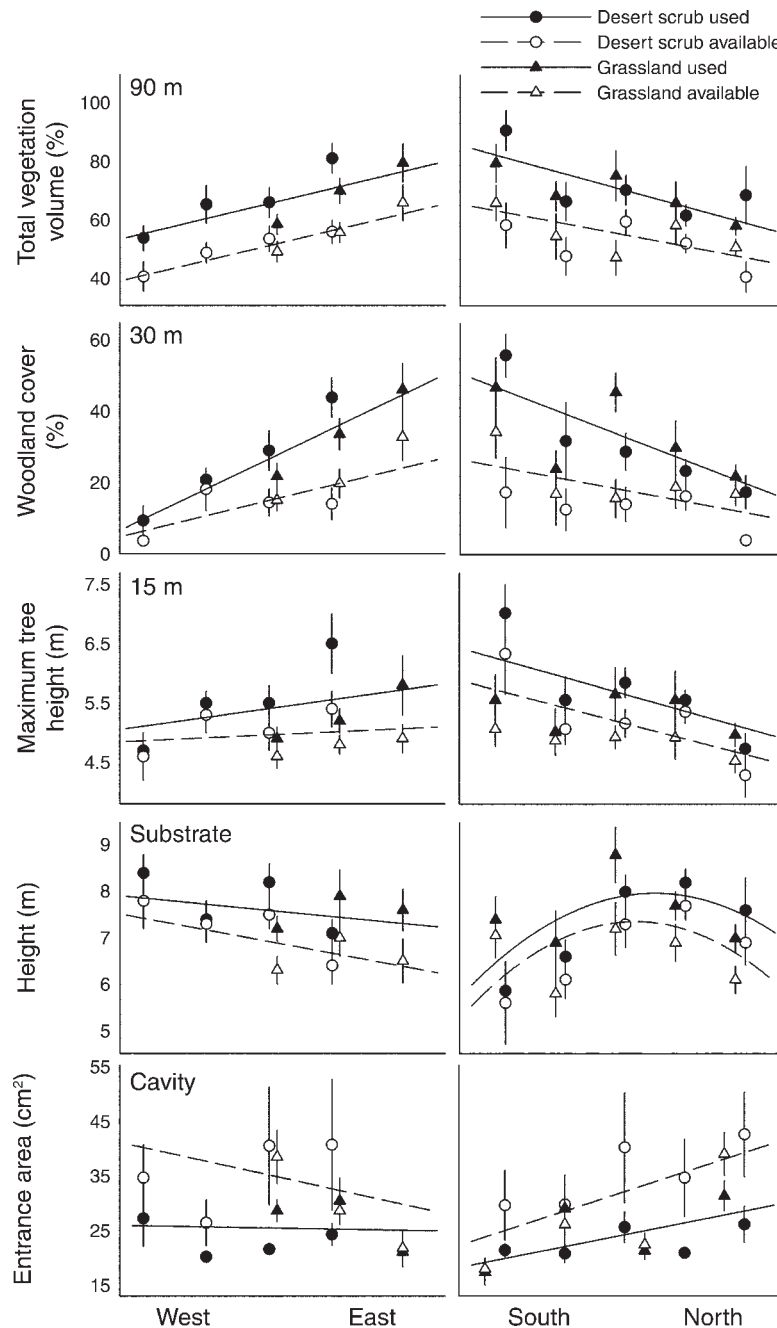


FIG. 7. Geographic variation in use and availability of resources that explained nest site selection of Ferruginous Pygmy-Owls at five spatial scales and in two vegetation communities in northern Sonora, Mexico, 2001–2003. Geographic axes indicate a 220-km longitudinal gradient (east–west) and 125-km latitudinal gradient (south–north). Use and availability are represented by single lines predicted from least-squares regression for both vegetation communities combined. Points and error bars indicate means \pm SE for points grouped by proximity within each vegetation community. We summed volume across five height strata (0–1 m, 1–3 m, 3–6 m, 6–12 m, and >12 m) above ground to estimate total vegetation volume.

vary geographically at the 90-m scale ($t_{56} \leq 1.18$, $P \geq 0.24$) (Fig. 9). In grassland, selection increased slightly from west to east at the 90-m scale and from north to south at the 30-m scale ($t_{46} \geq 1.74$, $P \leq 0.090$), but did not vary at the 15-m scale ($t_{46} \leq 1.30$, $P \geq 0.20$). In contrast, at the substrate scale, resource use tracked

availability and the degree of selection did not vary geographically ($t_{102} \leq 1.11$, $P \geq 0.27$). At the cavity scale, selection was greatest at middle latitudes in desert scrub ($t_{37} = 2.22$, $P = 0.034$) where availability of optimal cavity resources was greatest (Fig. 9). At the western edge of the study area, selection at nest area

scales was indistinguishable from zero ($t_{104} \leq 1.27$, $P \geq 0.21$, test of intercepts = 0).

Cross-scale correlations

At all spatial scales combined, resources explained 76–85% of variation in nest site selection (Table 7). Both total and pure variation in selection that was explained by resources at the cavity scale was much greater than at the substrate scale and somewhat greater than at area scales. Although variation explained solely by cavity resources was high, 38–44% of variation was shared among scales, indicating that selection of resources at large scales was not independent of resources at small scales.

At all spatial scales combined, resources explained 27–31% of variation in nest survival and 21–25% of variation in productivity (Table 7). Total variation in nest survival was explained principally by resources at the cavity scale and less by resources at substrate and area scales; although patterns were similar for productivity, resources at area scales explained proportionally more variation. Pure variation in nest survival was also explained largely by resources at the cavity scale; although patterns were similar for productivity, resources at area scales explained more variation proportionally (Table 7). Pure components of variation were much greater for nest survival and productivity than that shared among scales, and most shared variation was between resources at cavity and substrate scales. Shared components of variation were too low relative to pure components to attribute resources at larger scales to associations between reproductive performance and cavity resources.

DISCUSSION

Patterns of nest site selection by birds have been explained by biotic factors, such as predation (Martin and Roper 1988, Martin 1998) and proximity to food (Lenington 1980, Sedgwick and Knopf 1992), and by abiotic factors, such as microclimates (Calder 1973, With and Webb 1993). Although these factors can simultaneously influence nest site selection, their relative importance may vary across space with changes in the availability, quality, and necessity of resources. In northwest Mexico, Ferruginous Pygmy-Owls occupy environments where daily temperatures often exceed 40°C, requiring resources and behaviors to mitigate exposure. Across the region we studied, water availability increases and temperature decreases from west to east and varies abruptly between upland and adjacent riparian areas (Shreve 1951). These changes and the vegetation gradients they produce created heterogeneous distributions of resources that were important to nesting pygmy-owls. Because many other cavity-nesting species inhabit this region, the strong patterns of nest site selection we observed likely reflected a combination of behavioral differentiation among species driven by interspecific interactions and high heterogeneity in

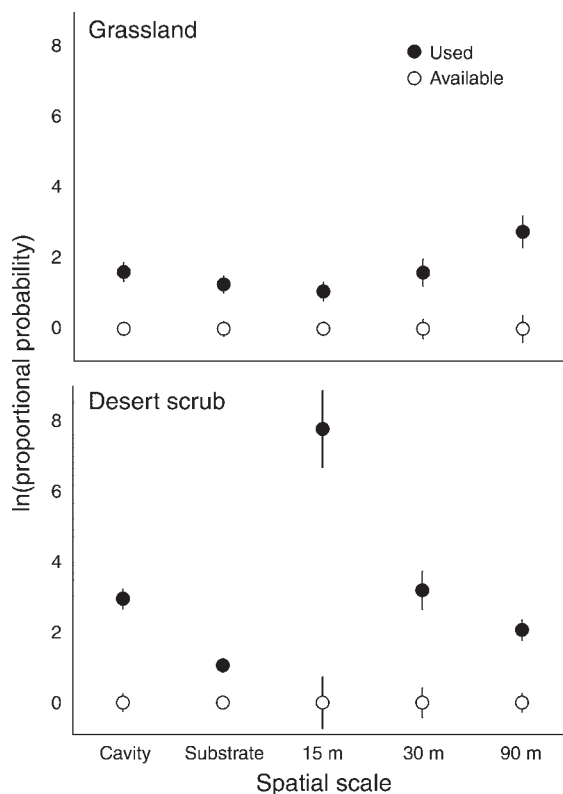


FIG. 8. Proportional probability of use and availability of resources that explained nest site selection by Ferruginous Pygmy-Owls in Sonoran desert scrub ($n = 57$) and semidesert grasslands ($n = 49$) in northern Sonora, Mexico, 2001–2003. Proportional probabilities reflect probability of resource use at each site and were calculated with resource selection functions based on case-controlled logistic regression (Tables 2 and 4), standardized so that availability equals zero for a site with average values of resources, and then log-transformed. Points are means \pm SE computed across all sites within each vegetation community.

distribution, abundance, and relative importance of resources along these gradients.

Environmental gradients

Geographic variation in resource availability was often highest at nest area scales, which affected the type and relative importance of resources that explained nest site selection. In desert scrub, where vegetation structure was often more limited and species composition more variable, owls selected nest areas that were closer to riparian vegetation and that had greater tree density, more mesquite, and less paloverde. Mesquite may be selected over paloverde because its larger leaf area and less variable phenology better mitigates temperature extremes (Suzán et al. 1996) and because it supports dense cover and high abundance of prey (Germano and Hungerford 1981, Lloyd et al. 1998). Overall, patterns of resource selection and nest survival were stronger in desert scrub where environmental conditions were more extreme and where resource availability was more

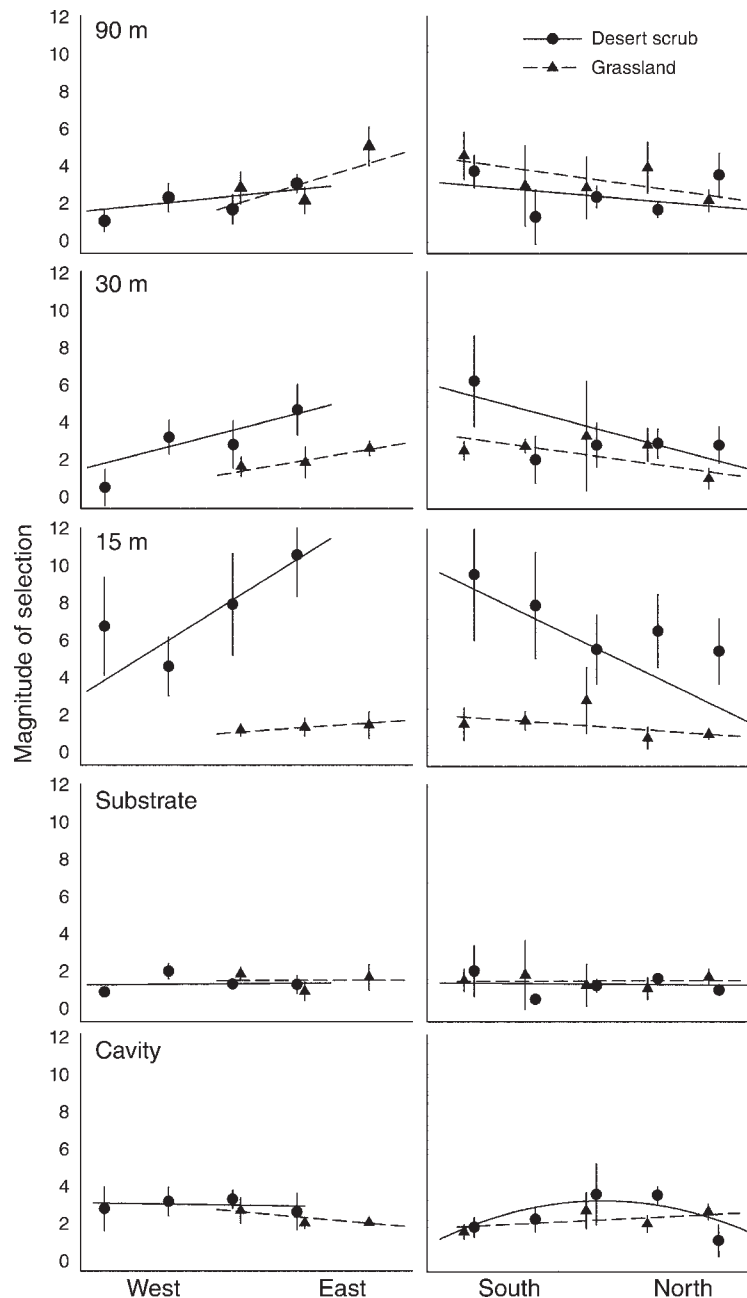


FIG. 9. Geographic variation in magnitude of nest site selection by Ferruginous Pygmy-Owls at five spatial scales and in two vegetation communities in northern Sonora, Mexico, 2001–2003. Geographic axes indicate a 220-km longitudinal gradient (east–west) and 125-km latitudinal gradient (south–north). Lines are based on least-squares regressions within each vegetation community, and points and error bars indicate means \pm SE for points grouped by proximity within each vegetation community. We calculated the magnitude of selection based on resource selection functions (Tables 2 and 4) from which we predicted the proportional probability of use of both used and available resources at each site, and then computed the difference between these probabilities.

variable. Resources with lower availability exert a stronger influence on selection (Orians and Wittenberger 1991).

Cavities that were high above the ground and that had small- to moderate-sized entrances were especially important to nest site selection and reproduction of

pygmy-owls. Availability of these cavities generally increased from north to south and was greatest at middle latitudes where saguaro cacti were more abundant. Although availability of cavity resources varied geographically, use was consistent, suggesting that only a limited range of cavity conditions were suitable for owls.

TABLE 7. Percentage of variation in nest site selection, nest survival, and productivity of Ferruginous Pygmy-Owls explained by decomposing variance explained by resources at the nest cavity, nest substrate, and nest area scales in northern Sonora, Mexico, 2001–2003.

Component of variation and scale	Nest site selection†			Nest survival‡			Productivity§		
	15 m	30 m	90 m	15 m	30 m	90 m	15 m	30 m	90 m
Total variation	76.0	76.6	84.5	26.9	31.1	26.9	21.4	25.1	23.9
Cavity¶	53.2	53.2	53.2	20.2	20.2	20.2	10.4	10.4	10.4
Substrate¶	28.6	28.6	28.6	6.4	6.4	6.4	4.9	4.9	4.9
Area	38.1	43.8	49.5	6.9	14.9	1.2	3.2	6.4	4.9
Pure variation	43.6	42.6	52.0	20.1	21.0	26.9	13.4	16.7	17.1
Cavity	26.5	22.9	26.0	13.1	11.1	19.3	8.9	9.0	10.7
Substrate	4.0	6.1	4.4	1.3	0.0	1.9	1.2	0.7	0.5
Area	13.1	13.6	21.6	5.7	9.9	5.7	3.3	7.0	5.9
Shared variation	32.4	33.9	32.5	9.2	10.1	0.0	8.0	8.4	6.9
Cavity and substrate	7.5	3.8	4.6	5.6	5.1	4.5	5.9	4.9	4.8
Cavity and area	7.8	11.4	8.3	1.6	3.6	−4.5	1.1	1.1	0.7
Substrate and area	5.7	3.6	5.3	−0.3	1.0	−0.9	−0.1	0.4	0.6
Cavity, substrate, and area	11.5	15.1	14.3	−0.2	0.4	0.9	0.9	2.0	2.1

Notes: Within nest areas, we considered each scale separately when combining these factors with those at cavity and substrate scales. Total variation was that explained by full models that included all relevant factors within and among scales, pure components were explained only by factors at individual spatial scales, and shared components were those that could not be explained by any individual scale because of correlation among scales.

† Based on deviance from case-controlled logistic regression comparing nests with paired available sites.

‡ Based on deviance from logistic-exposure models comparing nests that survived and failed.

§ Based on total sum-of-squares from ordinary least-squares regression where the response was number of young within one week of fledging.

¶ Values are the same across all nest area scales because different area scales were not considered.

In desert environments, birds select nest orientations that moderate temperatures within nests (Ricklefs and Hainsworth 1969). As temperatures increased toward the western portion of our study area, use of west-facing nest cavities decreased and use of north-facing cavities increased (Fig. 5). Because summer temperatures are lower in north- vs. west-facing saguaro cavities (Soule 1964), these changes in nest orientation likely offer thermoregulatory advantages to owls and could explain lower rates of nest failure in cavities with cooler microclimates. Gila Woodpeckers (*Melanerpes uropygialis*; Inouye et al. 1981, Korol and Hutto 1984) and Elf Owls (*Micrathene whitneyi*; Hardy and Morrison 2001), two common cavity nesters in the region, also select north-facing nest cavities in the hotter western portion of the study area, whereas nest orientations are more variable in the east (Goat and Mannan 1987, Kerpez and Smith 1990). Although nonrandom selection by pygmy owls could be an artifact of selection by cavity excavators, orientations of available cavities did not vary (Fig. 5).

Populations of many species can become smaller and more dispersed near the margins of their geographic ranges due to resource limitations (Brown et al. 1995, Holt et al. 2005). For pygmy-owls, nest spacing increased toward the western edge of the study area as vegetation structure became progressively sparser. Accordingly, probability of selection at nest area scales declined to near zero, providing evidence of an important resource threshold that delineates the western margins of the owl's distribution (Russell and Monson

1998). Toward the south and east, however, vegetation structure became increasingly well developed and probability of selection at nest area scales continued to increase without reaching asymptotes (Figs. 7 and 9), patterns that likely continue into more tropical environments where resources thresholds are more complex.

Studies restricted to small portions of a species' geographic range may fail to identify resources that are important to populations when these resources are abundant or not locally available. As abiotic and biotic components of the environment vary, different ecological processes and changing resource availabilities may result in variable patterns of resource selection and importance. Consequently, studying resource selection across a broad range of environments can help differentiate the relative importance of resources and identify thresholds that explain the distribution of species and abundance of populations.

Important resources

Characteristics of nest cavities often influence selection and reproductive performance of cavity-nesting birds (Nilsson 1984, Sonerud 1985), and in our study system these included cavity height, entrance area, volume, and orientation. Height of nest cavities influenced selection, nest survival, and productivity of pygmy-owls, potentially due to lower predation risk higher above ground (Nilsson 1984, Li and Martin 1991). Coachwhip snakes (*Masticophis flagellum*), for example, a common tree-climbing predator that we observed depredating fledgling pygmy-owls, may not

search cavities high above ground. Although predation is often thought to drive selection of cavities that are higher above ground, thermoregulatory factors may also be important in desert environments because temperatures within saguaro cavities decrease with increasing height (Soule 1964). Presence of large trees near nests strongly influenced nest site selection and nest survival likely because they provide protection from predators and temperature extremes.

Resource partitioning among coexisting species can promote selection of cavities with smaller entrances if they exclude larger species and reduce competitive interactions and predation (Nilsson 1986, Sonerud 1985). In the Sonoran Desert, pygmy-owls coexist with American Kestrels (*Falco sparverius*), Elf Owls and Western Screech-Owls (*Megascops kennicottii*), Gilded Flickers (*Colaptes chrysoides*), Gila Woodpeckers, flycatchers (*Myarchis* sp.), and Purple Martins (*Progne subis*), all of which we observed nesting near pygmy-owls. Western Screech-Owls seem especially likely to affect resource selection by pygmy-owls in areas where abundance of cavities are low. Perhaps as a consequence of these and other interactions, pygmy-owls selected nest cavities that had smaller entrance areas than those used by Western Screech-Owls (Hardy and Morrison 2003).

Spatial scale

Although pygmy-owls exhibited evidence of selection at all spatial scales, magnitude of selection and the influence of resources on selection and reproductive performance varied among scales. Selection was greater at the cavity scale than at the substrate and most nest area scales (Fig. 8), suggesting the importance of cavity resources that strongly affected reproductive performance (Fig. 6). Magnitude of selection did not vary geographically at the cavity scale, but did vary at area scales, suggesting that only a narrow range of cavity conditions are suitable for pygmy-owls. Further, magnitude of selection in desert scrub, where temperatures are higher and vegetation structure is lower, was greatest immediately around nests. Ultimately, patterns of resource selection vary with scale because the consequences of some ecological processes also vary with scale (Pribil and Picman 1997). Cavity resources, for example, explained more variation in nest survival than in productivity because predation and competition for nest sites likely drive selection at this scale and typically affect only whether or not entire nests survive. In contrast, nest area resources explained more variation in productivity because they have a greater influence on the number of young that can be produced.

To assess the effects of spatial scale on resource selection, most studies evaluate numerous scales independently without investigating the strength of selection or correlation among resources across scales (Lawler and Edwards 2006). Determining the relative influence of resources among scales is complex biologically, given the hierarchical nature of selection decisions made by

animals, as well as statistically, given correlations in resource characteristics among scales that result from their inherently hierarchical structure. Although cavity resources may drive selection decisions by pygmy-owls, choices at small scales are not independent of those at larger scales. If resources most closely linked to reproductive performance drive selection, then our results suggest that cavity resources are fundamental determinants of selection by pygmy-owls because they explained larger proportions of pure variation in productivity and nest survival than resources at other scales. In contrast, substrate factors explained little pure variation in selection (Table 7).

Habitat selection is thought to be a hierarchical decision-making process that occurs from large to small spatial scales (Hutto 1985). If, however, resources at small scales have a stronger and more consistent influence on reproduction and survival, and animals perceive resources at multiple scales simultaneously (Hildén 1965), then selection could involve “bottom-up” decisions. In these circumstances, an important resource at small scales could trigger animals to investigate resources at larger scales especially if resources at small scales affect reproduction and survival most and animals sample resources near ground level. Lower plasticity in resource selection at small vs. large scales, strong patterns of selection and reproductive performance explained purely by resources at the cavity scale, and flight and natal dispersal behaviors that occur exclusively near ground level (Flesch et al. 2010) suggest a bottom-up process by pygmy-owls.

Resource choices and consequences

To assess whether the decisions animals make when choosing resources are adaptive, studies often attempt to identify innate resource preferences, and then assess the influence of preferred resources on survival or reproduction (Brown and Shine 2004, Doak et al. 2006). When comparing resource use and availability, however, innate preferences can only be distinguished from their realized expression in nature (i.e., selection) if resources that are assumed to be available are both accessible and procurable on an equal basis. For wild vertebrates, this assumption is rarely met because factors that can constrain ideal patterns of resource selection (i.e., preference) such as territoriality (Kluyver and Tinbergen 1953), predator avoidance (Werner et al. 1983), and interspecific competition (Davis 1973) are difficult to address in natural settings (Robertson and Hutto 2006).

At smaller spatial scales, we observed a general correspondence between resources that explained selection and those that explained reproductive performance especially in desert scrub. At larger scales and in grasslands, however, fewer resources explained reproductive performance and some resources that were selected by the population had no apparent influence on reproduction. This lack of correspondence may not

indicate these resources were unimportant or that selection had no consequences on fitness for several reasons. First, resources may confer advantages to individuals that are expressed by other parameters such as mate attraction, offspring condition, and recruitment probability (Alatalo et al. 1986, Brown and Shine 2004). Second, if selection reflects an accumulation of past responses to environmental pressures, then these behaviors may have already been optimized (Williams and Nichols 1984). Consequently, short-term variation in reproductive performance may not reflect choices that have proven optimal over the long term, especially for resources that are temporally dynamic. Finally, if innate preference is inferred based on unrealistic assumptions of availability, resource choices may seem decoupled from performance.

Although correspondence between resource choices and demographic performance suggests these behaviors are adaptive, other processes may better explain these patterns. For highly territorial animals such as pygmy-owls, conspecific interactions may force subordinate individuals into areas of lower quality (Fretwell and Lucas 1970, Pulliam 1988) where observed variation in reproductive performance results from differences in habitat quality rather than inherent differences in fitness or preference among individuals (Johnson 2007). Regardless, assessing the demographic consequences of resource choices across broad resource and spatial gradients may be a better approach for identifying resources that are important for management because factors that constrain ideal resources choices may also vary along these gradients.

Conservation implications

Strategies to conserve and recover wildlife populations should ensure that resources important to species are maintained at appropriate levels. The importance of resources, however, may change as abundance, availability, quality, and necessity for a particular resource varies. When studies of resource selection are limited to small, homogenous portions of a species' range and to a narrow subset of spatial scales, use-availability studies may not provide an ideal basis for identifying important resources for species that inhabit a wide range of environments. For these species, prioritizing the relative importance of resources requires information on how resource use and availability changes across a full range of environmental conditions and spatial scales (e.g., Collins 1983, Cunningham and Johnson 2006) and how resource choices affect demographics (Hobbs and Hanley 1990, Garshelis 2000).

Resources that are systematically important to a species across its geographic range are fundamental for developing broad-based strategies for conservation and management. For pygmy-owls, nest cavity resources proved important across a range of environments and spatial scales and therefore should be an important focus for managers. Although resources at the substrate

scale also were important, these patterns may have been artifacts of correlations with resources at the cavity scale. In contrast, resources that vary in importance geographically may require site-specific prescriptions. For pygmy-owls inhabiting arid, lower elevation areas, vegetation cover immediately around nests is critical given its low availability. In contrast, at higher elevations, where availability of tall trees and woodland vegetation are higher, resources at larger scales should be a focus. Knowledge of resource trade-offs among spatial scales can also inform management. For pygmy-owls in areas where availability of high-quality cavities is low, but resources at larger scales are abundant, increasing the abundance of cavities with nest boxes or by translocating mature saguaros should aid recovery, especially in areas where other important resources are available (Tables 1–4). Assessing how selection and demographic performance change in response to underlying changes in resource availability and importance can help optimize conservation strategies.

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