NEST-SITE PREFERENCES OF FLAMMULATED OWLS IN WESTERN NEW MEXICO[1]

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Abstract. We studied nest-site preferences of Flammulated Owls (*Otus flammeolus*) in the Zuni Mountains of western New Mexico and used multivariate analyses of the nest cavity, nest tree, and surrounding woody vegetation to ask if and then how the birds select nest sites. Significantly reduced variance in used compared to unused sites for both cavity/ nest-tree and vegetation data indicates that the used sites are a nonrandom subset of the source pool (i.e., the birds are selective). Preferred cavities are modal in the source pool, but preferred vegetation is characterized by low shrub density, high canopy height, and high importance of mature *Pinus edulis*. Preferred vegetation characteristics appear more limited than preferred cavity/nest-tree characteristics. Nest sites have fewer shrubs in front of than behind the cavity entrance. This is consistent with the species' habit of flying at shrub level upon approaching and leaving the nest. The suggestion that Flammulated Owls have increased in abundance with increasing vegetative density is not supported.

Key words: Flammulated Owl; nest sites; New Mexico; site selection; habitat selection; Zuni Mountains.

INTRODUCTION

The Flammulated Owl (*Otus flammeolus*) is a small, migratory, cavity-nesting insectivore of coniferous forest vegetation in western North America (Marshall 1967, Ross 1969). Between the time of its discovery in 1852 and the mid-20th century it was considered rare (e.g., Bendire 1892, Miller 1936, Winter 1974). More recently it has been found to be common in some areas of California and Colorado (e.g., Marshall 1939, Winter 1974, Marcot and Hill 1980, Richmond et al. 1980). The species is also quite numerous in parts of the Zuni Mountains, New Mexico, where we have observed it intermittently for over three decades.

While the apparent change in abundance may reflect additional, modern observers locating this inconspicuous species more frequently (Richmond et al. 1980), habitat change may be a contributing factor. The physiognomy of western coniferous woodland and forest has been altered dramatically in the past century. In much of the species' range, production of seedlings and fire suppression, following extensive logging, have replaced open stands of old-growth timber, especially *Pinus ponderosa,* with young, even-aged, closed stands (Wright and Bailey 1982).

Several authors (e.g., Marshall 1967, Bull and Anderson 1978) suggest that a brushy understory characterizes Flammulated Owl habitat. If this reflects a true preference or requirement, the species may have increased as brush (closed) vegetation increased. To test this hypothesis, we used multivariate statistical techniques to compare various habitat features of known nest sites with those of unused but potential nest sites. We asked (1) whether nest-site occupation patterns indicate selection or merely random occupation of minimally acceptable sites and (2) if selection is indicated, what criteria the birds seem to be using.

We applied this mode of inquiry to two different scales of resolution, the vegetation around the nest site because of its relevance to the foregoing hypothesis, and the cavity and nest tree because secondary cavity nesters, like this owl, may be most strongly limited by availability of suitable cavities (von Haartman 1957, Hildén 1965). Greater importance of one dimension of the nesting niche could mean that the birds are

more selective at this scale than the other. Partitioning our analysis allows us to test this possibility.

METHODS

The study area was Cottonwood Gulch, 12 km south of Thoreau, McKinley County, New Mexico, at 2,230 to 2,277 m elevation. Vegetation of the 200-ha site is open woodland to closed-canopy forest, dominated by Colorado pinyon (*Pinus edulis*) with subdominant junipers (*Juniperus monosperma, J. scopulorum, and J. deppeana*) and oaks (*Quercus gambelii, Q. undulatus*) in the uplands. Ponderosa pine (*P. ponderosa*) codominates the drainages and north-facing slopes of the rocky, rolling terrain. Narrow-leaf cottonwoods (*Populus* × *acuminata*) and willows (*Salix* spp.) dominate a riparian zone along Sawyer Creek.

FIELDWORK

We found two to five nests annually (May to June 1981 to 1986) by checking all suitably-large woodpecker cavities. Seventeen of 21 nests were "independent" uses, in that they did not constitute reoccupation of a cavity by either member of a banded pair. These 17 comprise our sample of used sites. They were located in live and dead pinyons (5), ponderosas (10), and live cottonwoods (2). Their distribution among dominant tree species differed from the availability of the same species, based on 266 trees sampled randomly across the three vegetation types (chi-square = 7.6, $P = 0.02$, see below).

After the young fledged, we measured nest-cavity height, true bearing of the cavity, cavity depth, minimum linear dimension of the cavity entrance and floor, relative height (absolute cavity height subtracted from mean canopy height based on the three closest canopy trees), and cavity-tree diameter (dbh 1.3 m above ground). These seven parameters comprised our cavity/nest-tree data set at each used site.

Also, 15 m in front of and 15 m behind cavity entrances, we measured distance to and dbh of the nearest tree (>2 m tall) and shrub in each of four quarters and figured densities and basal areas (Cottam and Curtis 1956). Woody species counts contributed to a diversity index (H' = $-\Sigma p_i \log_2 p_i$), and species importance values (IVs) were relative density + relative basal area + relative frequency. Pinyon IV-ponderosa IV was calculated because pinyons outnumbered ponderosas in the general vegetation, but more nests were in ponderosas (Fisher's exact $P = 0.01$). Tree and shrub densities, total basal area, diversity, canopy height, and IV difference between the two species of pine comprised our vegetation data set.

For comparison with each nest site, the same data were obtained at each nearest, concurrently-available, unused cavity. (Tree species frequency of these cavities was the same as that of the used cavities, chi-square = 2.1, $P = 0.34$.) The cavity had to be large enough to admit and conceal a Flammulated Owl (minimum entrance >5 cm, depth >12 cm), which restricted sites to those excavated by Hairy Woodpeckers (*Picoides villosus*) or Northern Flickers (*Colaptes auratus*), sometimes enlarged by Abert's squirrels (*Sciurus aberti*). Further, the cavity had to be empty or used by a bluebird (*Sialia currucoides, S. mexicana*, 27 to 30 g) or smaller species, as we found unattended bluebird eggs in an active owl nest and assumed larger birds and rodents deterred Flammulated Owls ($\bar{x} \pm$ SD weight of eight nesting males = 52.6 ± 1.26 g and 14 nesting females = 65.9 ± 1.55 g).

The other environmental measurements were chosen as potentially important to successful nesting after observing the breeding biology of the species (cf. Holmes 1981, Whitmore 1981). Samples of woody vegetation employing four instead of two points per cavity tree (measurements of 32 rather than 16 surrounding trees and shrubs) did not change our results in trials designed to streamline the fieldwork.

ANALYTICAL TECHNIQUES

To demonstrate that the owls choose nonrandomly from the source pool of nest sites, it is necessary to show that used and unused sites differ in variance and/or mean along at least one dimension of habitat. We suggest that choice is indicated if the variance of any feature of used sites is significantly lower than that of unused sites, even if means of the two data sets are equal. This test has not been used in previous, similar studies (e.g., Kroll 1980, Clark et al. 1983, Marks 1986, Brooks and Davis 1987, Speiser and Bosakowski 1987).

We could not test for the equality of variances and means simultaneously, so we split the alpha = 0.05 of Type I error available for our hypothesis of choice among a variance test, a means test, and a separate test of cavity entrance bearing (Bonferroni adjustment, Harris 1985). Other-

TABLE 1. Environmental features at Flammulated Owl nest sites and nearest available, unused sites ($n = 17$ per group for all vegetation features and dbh of the nest tree, cavity bearing, height, and relative cavity height; $n = 16$ per group for cavity entrance and 15 for cavity depth and floor).

Features	Nest sites		Unused sites	
	$\bar{x} \pm SD$	CV	$\bar{x} \pm SD$	CV
Cavity/nest tree				
Cavity height (m)	4.9 ± 1.6	32.7	4.9 ± 3.2	65.3
Relative cavity height (m)	5.3 ± 2.2	41.5	3.5 ± 4.3	122.9
Cavity depth (cm)	21.2 ± 5.2	24.5	12.9 ± 11.8	91.5
Cavity entrance (cm)	5.9 ± 0.9	15.3	6.0 ± 1.5	25.0
Cavity floor (cm)	13.5 ± 2.8	20.7	12.4 ± 4.3	34.7
Tree dbh (cm)	46.2 ± 10.7	23.2	45.7 ± 14.8	32.4
Surrounding woody vegetation				
Tree density/ha	504.0 ± 416.0	82.5	1,706.0 ± 4,044.0	237.0
Shrub density/ha	442.0 ± 619.0	140.0	1,528.0 ± 3,033.0	198.5
Basal area (m²/ha)	525.0 ± 310.0	59.0	876.0 ± 851.0	97.1
Pinyon IV–Ponderosa IV	102.0 ± 196.0	192.2	95.0 ± 154.0	162.1
Canopy height (m)	10.1 ± 1.8	17.8	8.5 ± 2.1	24.7
Species diversity (H')	1.5 ± 0.3	20.0	1.3 ± 0.5	38.5

wise, the probability of a Type I error would have been higher than the conventional 5%. We decided a priori to allocate 0.025 to variance, 0.02 to mean, and 0.005 to bearing for cavity/nest-tree variables. Alpha was 0.03 for variance and 0.02 for mean in the vegetation data and was allocated in like manner to the search for particular criteria of choice (see below).

To avoid further division of the Type I error rate, we used multivariate statistics to test for differences among variances and means. For the equal-variance hypothesis, a test of homogeneity of covariance matrices was employed. We used multivariate analysis of variance (MANOVA) to test the means hypothesis, and Rayleigh's R to assess the significance of mean bearings. The circular standard deviation was the measure of bearing dispersion. These techniques are not very graphic, so we examined nest-site selection graphically with principal components analysis (PCA). Used and unused sites were plotted on the first two PC axes, which explained the majority of the variation (see below).

If nest-site choice was suggested by significantly reduced variance in the used-site data, PCAs were reemployed to identify the criteria of choice. Scores of each of the first three unrotated axes were subjected to a one-tailed, F-test of equality of variances. We then attempted to interpret significant PC axes. Because each F-test tested the same hypothesis, it was necessary to subdivide the already reduced alpha level equally among them. Finally, after finding significantly

different means, we used stepwise discriminant function analysis (DFA) to identify particular criteria of choice. Classification performed by this analysis enabled identification of anomalous sites. Because three were used one year but were nearest available, unused sites in another year, we expected three misclassifications.

RESULTS

Visual inspection of the untransformed data suggests that there are differences between used and unused sites in both variability (cavity and vegetation features) and means (vegetation features especially) (Table 1). However, all linear variables except species diversity were nonnormally distributed, so we normalized these data with $\log_{10}$ transformation. The two relative measures were also transformed with additive codes in order to preclude taking the logarithm of 0.

Cavity bearings show no pattern. Neither used nor unused sites have significant mean angles (used: Rayleigh's R = 1.94, $P > 0.5$; unused: R = 6.80, $0.10 > P > 0.05$). Also, the dispersion of bearings at used sites (circular SD = 119.32) exceeds that of unused sites (77.52), so the direction a cavity faces apparently is not involved in nest-site selection.

MULTIVARIATE TESTS OF CHOICE

Multivariate tests indicate that Flammulated Owls are nevertheless selective. For both cavity/ nest-tree and vegetation data, the covariance matrices are significantly heterogeneous (chi-square

TABLE 2. Principal component analysis (PCA) of variation of nest-tree and cavity characteristics (log-transformed) of used and unused nest sites. Only the first three principal components are reported, because they explain the majority of variation.

Principal component	I	II	III
Eigenvalue	2.664	1.521	0.781
Cumulative % explained	44.4	69.7	82.7
Variables	Eigenvectors (loadings)		
Cavity depth	0.522	−0.220	−0.028
Cavity height	0.461	−0.318	0.118
Cavity entrance	0.407	0.457	−0.224
Nest-tree dbh	0.360	0.268	0.781
Cavity floor	0.309	0.533	−0.457
Relative cavity height	−0.348	0.533	0.338

$= 50.0$, df $= 21$, $P < 0.001$; and chi-square $= 38.4$, df $= 21$, $P = 0.01$, respectively). This is nicely illustrated by the PCAs (Tables 2, 3), especially in the tighter clusters of points representing nest sites (Fig. 1).

The means test of vegetation also demonstrates that Flammulated Owls are selective. Although the MANOVA of cavity/nest-tree variables is not significant (Wilk's lambda $= 0.86$, $F = 0.60$, df $= 6,27$, $P = 0.72$), the vegetation MANOVA is (Wilk's lambda $= 0.46$, $F = 5.22$, df $= 6,27$, $P = 0.001$). Unequal variances can lead to significant F-tests when means are not different. The insignificant result of the cavity/nest-tree MANOVA is dependable, therefore, while the slight inequality of variances of vegetation data does not compromise the highly significant result of the MANOVA (Ito and Schull 1964).

CRITERIA OF CHOICE

Flammulated Owls apparently select nest sites on the basis of all six cavity/nest-tree features.

Only PC I of these data showed significant variance reduction ($F = 11.85$, df $= 14, 14$, $P < 0.001$), and it is a composite of all six variables that seems to represent an overall size gradient (Table 2). The insignificant MANOVA (see above) showed that no means test would reveal criteria of choice, so we did not perform DFA on these variables.

The owls in our study area also select nest sites on the basis of the openness and maturity of the vegetation surrounding the nest. Only PC I of the vegetation data revealed significant variance reduction ($F = 3.76$, df $= 16, 16$, $P < 0.01$). It is a gradient of decreasing tree and shrub density and basal area, together with increasing canopy height and importance of pinyon pine (Table 3). This is essentially a successional gradient from immature, dense stands to mature, open ones.

Discriminant function analysis of the six vegetation features pinpoints a linear combination of shrub density, canopy height, and the relative importance of pinyon as a criterion of choice (Table 4). Shrub density is correlated at the 0.01

TABLE 3. Principal component analysis (PCA) of variation of vegetation characteristics (log-transformed except species diversity) of used and unused nest sites. Only the first three principal components are reported, because they explain the majority of variation.

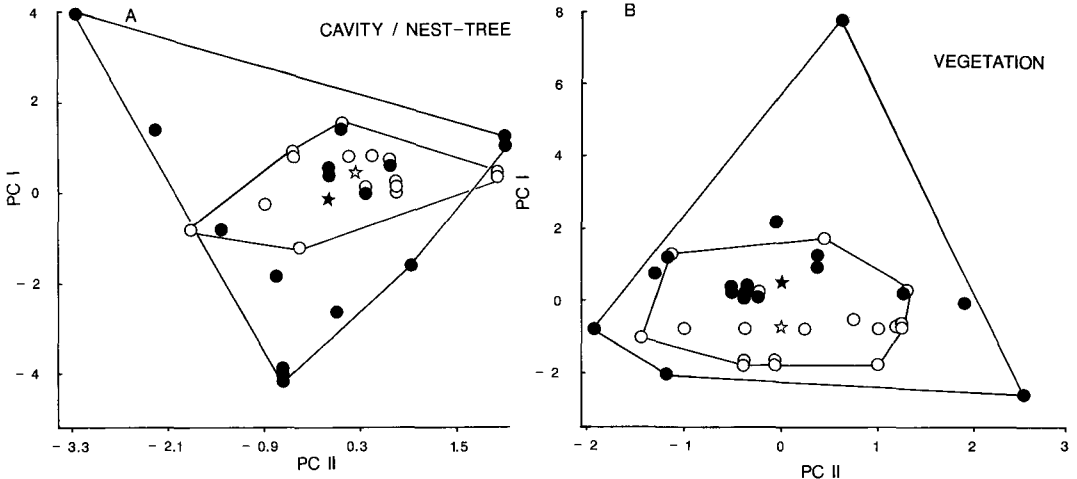| Principal component	I	II	III
Eigenvalue	3.208	1.075	0.889
Cumulative % explained	53.5	71.4	86.2
Variables	Eigenvectors (loadings)		
Tree density	0.532	−0.087	−0.041
Basal area	0.504	−0.150	0.074
Shrub density	0.445	0.213	0.318
Pinyon IV–Ponderosa IV	−0.430	−0.302	−0.153
Canopy height	−0.267	0.108	0.903
Species diversity	−0.082	0.906	−0.225

FIGURE 1. Plots of nest sites used by Flammulated Owl (open circles) and nearest available unused sites (closed circles) on the first two Principal Component (PC) axes of separate PC analyses of (A) cavity/nest-tree and (B) vegetation variables. Lines connecting data points indicate boundaries of PC space occupied by the used and unused samples, and stars show the positions of group means (open star = used sites, closed star = unused sites). See Tables 2 and 3 for the contributions of the variables to each axis.

level with both tree density ($r = 0.54$) and basal area ($r = 0.47$), two features which are also correlated ($r = 0.88$), so the failure of these other measures to enter the discriminant function does not represent a loss of information. Both the discriminant function and PC I describe the same gradient of closed to open vegetation. Flammulated Owl nests are concentrated toward the mature, open end of this gradient (Figs. 1, 2).

The discriminant function correctly classifies 28 of 34 sites (82.4%), not including the three expected misclassifications. In only two of 17 cases did an owl choose a site less desirable, according to the discriminant function, than the nearest alternative. In one of these, both the used and unused sites were comparatively undesirable, and neither site was used again. The other case involved a pair that moved 10 m to its previous alternative site in a year following much human disturbance in front of its first-chosen site.

HABITAT PREFERENCES AT DIFFERENT SCALES

The selection we have detected implies that Flammulated Owls have preferred values on both the cavity/nest-tree and vegetation scales of habitat resolution. These preferences suggest that vegetation may be more nearly limiting than cavity/nest-tree characteristics. The preferred cavity/nest-tree characteristics are modal in the source

pool, as indicated by the greatly reduced variance of used sites about a mean that is not significantly different from the mean of the unused sites. On the other hand, preferred vegetation is rather rare in the source pool, as indicated by the position of the mean for used sites in the tail of the distribution for unused sites (Fig. 2).

BIOLOGICAL SIGNIFICANCE

The flight behavior of Flammulated Owls supports our findings that open vegetation is preferred over dense vegetation. When they leave a nest, the owls dive steeply, then level off and fly 1 to 2 m above ground. This is also true of Eastern Screech-Owls (*O. asio,* Gehlbach, unpubl.), and both species sometimes fly low into the nest area and rise abruptly to the cavity. Similar be-

TABLE 4. Summary of stepwise discriminant analysis of log-transformed vegetation variables at Flammulated Owl nest sites and nearest available, unused sites ($n = 17$ per group; no variables removed from model).

Step	Entered	Wilk's lambda	P	Coefficient[a]
1	Shrub density	0.802	0.009	3.346
2	Canopy height	0.685	0.003	−0.730
3	Pinyon IV–Ponderosa IV	0.579	0.001	−1.081

[a] Standardized (by pooled within variances) canonical discriminant function coefficient.
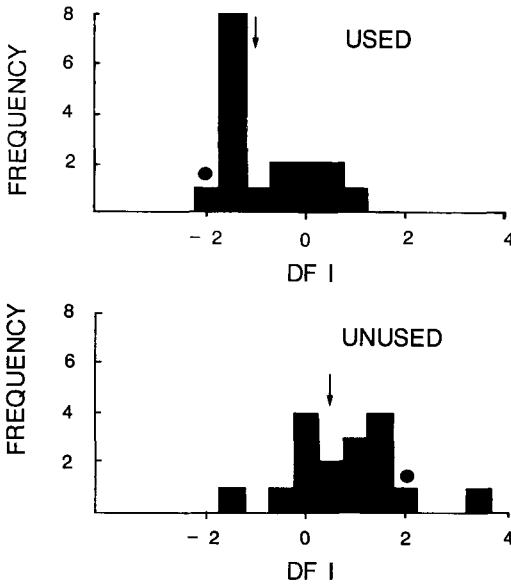
FIGURE 2. Frequency of scores of nest sites used by Flammulated Owls and nearest available unused sites on a canonical discriminant function of decreasing shrub density, taller canopy, and increasing importance of pinyon pine toward the negative end of the vegetational gradient (a successional gradient toward more mature woodland and forest). Arrows indicate mean scores, and closed circles indicate the scores on DF I of the sites illustrated in Figure 3. See Table 4 for details of the discriminant function.

havior is recorded in the Boreal Owl (*Aegolius funereus*, Norberg 1970) and Eurasian Sparrowhawk (*Accipiter nisus*, Newton 1986). Certainly, an open area around the nest allows unobstructed, low-level flight. Figure 3 shows a highly favored nest site of *O. flammeolus*, according to its score on the discriminant function, and its nearest available alternative, which had a very unfavorable score. The vegetation contrast is obvious.

If Flammulated Owls choose nest sites based on a clear flight path at 1 to 2 m, they should be concerned with reduced plant density, especially shrub density, in front of the cavity entrance rather than behind the nest tree. Therefore, we recalculated shrub and tree density for the front and back of each site separately and compared values within and between used and unused sites (Bonferroni-adjusted P for each one-tailed Wilcoxon's signed-ranks test = 0.02). Shrub densities in front of used trees are significantly lower in all comparisons ($P < 0.01$). Tree densities are not lower in front of used sites, except possibly

in comparison with the back of unused sites ($P = 0.02$). These results support our post hoc hypothesis of biological significance.

Cottonwood Gulch was logged of ponderosa pine in the 1920s and has not experienced fire since that decade. Several very dense stands of ponderosa seedlings have become thickets of stunted saplings, "doghair" (cf. Fig. 3.). Of course such thickets around a potential nest cavity increase shrub density and its correlates, tree density and basal area. Since these thickets are homogeneous, we considered them as canopy at some sites, so the canopy sometimes was quite low and the comparative importance of pinyon reduced accordingly (Fig. 3).

REPRODUCTIVE SUCCESS

We obtained reproductive data at 10 successful nests ($\bar{x} \pm$ SD of clutch size = 2.3 ± 0.5, brood size = 2.2 ± 0.6, number of fledglings = 1.8 ± 0.7), but the limited variation precludes meaningful tests of reproductive-environmental relationships. No correlations are evident among any feature of nesting success and corresponding PC I cavity/nest-tree or PC I vegetation scores. Furthermore, reduced woody plant density is not linked to reduced frequency of nest predation as in the Boreal Owl (Sonerud 1985, but see Korpimäki 1987). Cause of failure of two of 15 Flammulated Owl nests is uncertain, but both were surrounded by very open vegetation (64, 156 shrubs and 239, 334 trees/ha, cf. Table 1).

DISCUSSION

We have shown that occupied nest sites are a nonrandom subset of those available to Flammulated Owls in our study area. We concluded that the attributes of the used sites reveal the preferences of the birds. Several extrinsic factors, however, may impinge on translation of habitat preferences into realized habitat occupancy patterns (Svärdson 1949, Hildén 1965, Wiens 1985). Intraspecific competition can force birds into suboptimal habitat, resulting in their selection of sites that do not accurately reveal their preferences. We doubt that this is the case in our study, though, because no more than five of the 14 acceptable sites were used at any one time (i.e., the population was unsaturated, see below).

Interspecific competition also appears slight. No other small, cavity-nesting owl was present in our study area during the study, so competition for food or nest sites with nocturnal pred-

FIGURE 3. Nearest available unused (left) and used (right) nest sites of Flammulated Owls on a north-facing slope at 2,277 m in the Zuni Mountains, New Mexico. Cavities indicated by arrows are 8.2 and 6.7 m above ground, respectively, in ponderosa pines. Note the vegetation gradient from dense, shrubby ponderosas around the unused site (5,270 stems/ha) to a more open shrub stratum on the right, particularly in front of the used site (396 stems/ha in contrast to 927 stems/ha behind this tree).

ators is unlikely. Among potential competitors for cavities (i.e., those larger than bluebirds, see Methods), Hairy Woodpeckers do not reuse old cavities (pers. observ.), and American Kestrels (*Falco sparverius*) are too rare to have a major effect. Only Abert's squirrels and Northern Flickers have occupied cavities previously used by the owls, and are large enough to restrict their options. Their impact is a matter deserving further study.

Because of tradition or habit, individuals may continue to reuse a previously used site after it has become unsuitable by the populaton's standards ("time-lags" of Wiens 1985). We minimized the effect of this complication by using only "independently" selected sites (see Methods section). Only the nests found in 1981–1982, at the beginning of the study, may have represented reuse of a site previously used by the same pair. For all these reasons we are confident that the utilization patterns in our study area reveal preference patterns, at least for the local population.

There is no perfectly objective way to test statistically for nest-site selection, because statistical significance is influenced by the controls one uses. If, for example, we had allowed cavities of any size, or vegetation found in the interstices of the occupied territories, into the null data set, we might have found results that were statistically significant but biologically trivial. In restricting our null data set to cavities that owls might reasonably be expected to use, and to vegetation surrounding such cavities, we reduced the likelihood of finding significant differences, but increased the realism of the tests.

By using as controls only the nearest, simultaneously available sites meeting these minimal criteria, we increased the likelihood that unused sites represented those selected against rather than those unoccupied because the habitat was not saturated with owls. Identifying the habitat preferences of a population requires that the population be unsaturated, while identifying the extremes of acceptable habitat requires that it be

supersaturated. Because our controls were realistic and the owl population was sparse, we are confident that our statistical findings reveal real selection and hence preference for the selected values, rather than being artifacts of our methods.

Our results do not support the hypothesis that cavities are more important than appropriate vegetation to these secondary cavity nesters. Of course cavities are absolutely limiting in a way that vegetation may not be. But high selectivity, which we found in the form of greatly reduced variance of used sites, is to be expected when highly preferred sites are abundant (Stephens and Krebs 1986). Had cavities been in short supply, we should have found much greater variability in cavity/nest-tree attributes of used sites, because some pairs would have been forced to use less-preferred sites. Instead, it appears, almost all of the pairs were able to find sites with highly-preferred cavity/nest-tree attributes. Thus, an increasing population of owls might exhaust the supply of preferred vegetation before occupying all preferred cavities. Of course territoriality and food availability might limit the population to an even lower density. Additionally, our two habitat scales do not describe orthogonal axes, so site selection on them is not independent.

The preference of the Flammulated Owls in our study area for open, mature forest with low shrub cover does not support the hypothesis that the species has increased in abundance in response to expansion of second-growth habitats. Indeed, if the Flammulated Owl has increased, it may have been in spite of thicket proliferation. Doghair stands of ponderosa pine are a major contributor to undesirable, high-density vegetation (Fig. 3). Such stands are widespread in the Zuni Mountains and elsewhere in the range of *O. flammeolus* (pers. observ.). The current silvicultural practices of thinning doghair and controlled burning should benefit the owl.

Nevertheless, we add a proviso, because dense vegetation has been noted in the territories of Flammulated Owls (Hanna 1941, Marshall 1967, Bull and Anderson 1978, Marcot and Hill 1980). Although dense shrubbery does not characterize nest sites in the Zuni Mountains, thickets are present near all used and unused sites in our study area, and could be a criterion of territorial or home-range selection, as opposed to nest-site selection. Such thickets are used for roosting and calling (pers. observ.), possibly because of pre-

dation pressure (Marshall 1939, but see Marcot and Hill 1980), and the same is true of *O. asio* (Gehlbach, unpubl.).

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