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NEST-SITE SELECTION IN THE ACORN WOODPECKER

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ABSTRACT.—Acorn Woodpeckers (*Melanerpes formicivorus*) at Hastings Reservation in central California prefer to nest in dead limbs in large, dead valley oaks (*Quercus lobata*) and California sycamores (*Platanus racemosa*) that are also frequently used as acorn storage trees. Based on 232 nest cavities used over an 18-year period, we tested whether preferred or modal nest-site characters were associated with increased reproductive success (the "nest-site quality" hypothesis). We also examined whether more successful nests were likely to experience more favorable microclimatic conditions or to be less accessible to terrestrial predators. We found only equivocal support for the nest-site quality hypothesis: only 1 of 5 preferred characters and 2 of 10 characters exhibiting a clear modality were correlated with higher reproductive success. All three characteristics of nests known or likely to be associated with a more favorable microclimate, and two of five characteristics likely to render nests less accessible to predators, were correlated with higher reproductive success. These results suggest that nest cavities in this population are built in part to take advantage of favorable microclimatic conditions and, to a lesser extent, to reduce access to predators. However, despite benefits of particular nest characteristics, birds frequently nested in apparently suboptimal cavities. We also found a significant relationship between mean group size and the history of occupancy of particular territories and the probability of nest cavities being built in microclimatically favorable live limbs, suggesting that larger groups residing on more stable territories were better able to construct nests with optimal characteristics. This indicates that there may be demographic, as well as ecological, constraints on nest-site selection in this primary cavity nester. *Received 20 June 1997, accepted 1 May 1998.*

NEST-SITE SELECTION in cavity-nesting birds may affect fitness in at least two ways. First is through nest microclimate, which may be influenced by the size of the cavity, bark type and thickness, density of the surrounding wood, angle of the nest entrance from vertical, and orientation of the nest entrance (Conner 1975, Ricklefs and Hainsworth 1969, Austin 1974, Inouye et al. 1981, Wachob 1996). Second is by reducing predation (Li and Martin 1991) or the likelihood of nest-site usurpation by species such as European Starlings (*Sturnus vulgaris*; Troetschler 1976). These sources of nest loss are likely to be influenced by nest height, the angle of nest entrance, and the smoothness of the bark, all of which may in turn affect the ability of predators to detect and gain access to nest cavities as well as allow birds time to detect and repel predators (Gutzwiller and Anderson 1987). The relative importance of nest microclimate and predation in influencing the construction of nest holes is basic to understanding the environmental and ecological conditions resulting in both annual and individual variation in reproductive success.

A second issue concerning nest-site selection is whether preferred sites are optimal in terms of yielding higher reproductive success. This "nest-site quality" hypothesis has been critically examined in secondary cavity-nesting species where several studies have found that cavities correlated with higher reproductive success are, at least in some cases, neither preferred nor used more frequently. The most common explanation for this discrepancy is that interspecific competition constrains optimal cavity selection (Nilsson 1984, Brawn 1988, Rendell and Robertson 1989, Li and Martin 1991). Whether comparable kinds of constraints occur in primary cavity-nesting species is an open question.

Acorn Woodpeckers (*Melanerpes formicivorus*) are cooperative breeders that live in groups of

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2 to 15 individuals including, in many cases, multiple co-breeders of both sexes (MacRoberts and MacRoberts 1976, Koenig et al. 1995). Regardless of group size or composition, only a single nest is produced at any one time. Groups are permanently territorial and centered on a storage tree or granary in which acorns are stored each autumn. Nests holes are constructed by more than one individual, often over an extended period of time, and are reused frequently (MacRoberts and MacRoberts 1976, Stanback, Hooge, and Koenig unpubl. data).

We measured the characteristics of holes used for nesting by Acorn Woodpeckers in order to examine the following questions: (1) What are the most frequently used nest-site characteristics of Acorn Woodpeckers, and what kinds of nest sites do they prefer? (2) How is reproductive success related to nest site characteristics? In particular, are the most frequently used or preferred nest characters associated with increased reproductive success? (3) Are preferred or more successful characteristics of nest sites those that are likely to be less accessible to nest predators or those likely to have more favorable thermal characteristics? (We assumed that nests less accessible to predators are those built in deeper holes and occurring higher in smooth-barked trees and oriented toward the ground. Nests with more favorable thermal characteristics were those located in large, live limbs that faced east; data supporting these latter two associations are presented below.) (4) Is there any evidence for constraints on nest-site selection in Acorn Woodpeckers?

STUDY SITE AND METHODS

We studied a color-banded population of Acorn Woodpeckers in and around Hastings Natural History Reservation in central coastal California (36°22'N, 121°32'W), a population that has been under continuous study since 1971 (MacRoberts and MacRoberts 1976, Koenig and Mumme 1987). Data were collected on nests used between 1972 and 1987. The vegetation at Hastings consists of oak woodland interspersed with grassland, oak savanna, riparian woodland, and chaparral (Griffin 1974). Valley oaks (*Quercus lobata*), blue oaks (*Q. douglasii*), and coast live oaks (*Q. agrifolia*) are common throughout the reserve, and California black oaks (*Q. kelloggii*) and canyon live oaks (*Q. chrysolepis*) are largely restricted to higher elevations. California sycamores (*Platanus racemosa*) and willows (*Salix* spp.) are common in the riparian woodland, and madrones (*Arbutus menziesii*) and California buckeyes (*Aesculus californica*) are found in the more heavily forested areas. European Starlings, which are known to usurp Acorn Woodpecker nest cavities (Troetschler 1976), were present during the study but generally not sufficiently abundant to conflict with the nesting activities of the woodpeckers.

Nest-site characters were measured for 232 nest cavities representing 463 nesting attempts in 16 years of the study. Eleven parameters of nest holes were recorded: tree species, diameter at breast height (dbh), diameter of limb at nest height (dnh), nest height, relative height in tree (nest height/tree height), depth of nest cavity, compass orientation of entrance hole, hole angle from horizontal (measured with a clinometer), distance to primary granary tree, tree viability (whether tree was alive), and limb viability (whether nest limb was alive). Not all measurements were available for all nests. Group and reproductive success parameters measured included clutch size, number of fledglings (estimated by the number of nestlings banded on day 21 of the 30-day nestling period), nesting success (whether the nest fledged young), territory occupancy (proportion of years territory was occupied), and group size at the time of nesting attempts.

In order to confirm the presumed effects of nest orientation on nest microclimate, temperature fluctuations in insulated nest boxes designed to approximate the thermal characteristics of Acorn Woodpecker nests were recorded in June 1986. Four insulated nest boxes were mounted on a utility pole at the same height; each box faced one of the four cardinal directions. Temperatures were measured simultaneously in all four boxes using thermocouples placed in the center of the box. An additional thermocouple was used to measure ambient temperature. Thermocouples were attached to a Campbell Micro Data Logger that recorded the five temperatures every 5 s and averaged readings at 5-min intervals. Thermocouples were also used to record temperatures in Acorn Woodpecker nest cavities in five matched pairs of live and dead limbs in June 1986. Each thermocouple was placed at the bottom of the nesting cavity approximately 2 cm above the floor of the nest, and the temperatures were averaged as above. Each pair of replicated cavities was in the same tree and was matched as closely as possible for direction, surrounding vegetation, height, and dnh.

Availability of trees was estimated from vegetation surveys performed throughout the study area in suitable woodpecker habitat between 1977 and 1979. Surveys consisted of 0.04-ha circular plots in the center of a 60-m grid overlaid on the study area. The estimated proportion and size distribution of each tree species, as well as the number of snags present, were based on all 631 vegetation plots (corresponding to a sampled area of 227 ha) covering approximately 76% of the study area over which nests were sampled. We estimated the proportion of suitable nest sites that were in dead limbs based on 100 randomly chosen limbs (4 each from 25 trees) that were the size typically used by nesting woodpeckers. All of the trees were large and were distributed across species in the same approximate frequency as actual nest cavities.

Because nest holes are often reused, we used nest holes rather than nest attempts as independent samples. In order to deal with annual differences in reproductive success, which can be considerable (Koenig and Mumme 1987), clutch size and fledging success for each year were standardized by subtracting the mean and dividing by the standard deviation of the same variables averaged across all groups studied for that year. These standardized values were then averaged across all nesting attempts in the same cavity, which ranged from 1 to 12 ($\bar{x} = 2.0 \pm$ SD of 1.7 attempts).

Data on nest orientation and entrance angle were analyzed using angular statistics (Zar 1984). The tightness of the dispersion around the mean vector is represented by a relative index (r) in which 1.0 indicates the same orientation for all points and 0 indicates random orientation. The significance of r was determined using the Rayleigh test (Batschelet 1965). The nonparametric two-sample Watson U^2 test (Zar 1984) was used to compare differences in mean vectors. Skewness was tested using the t statistic (Sokal and Rohlf 1981). To test for the relationship between the most frequently used nest-site characteristics and reproductive success, nests were divided into two or three categories depending on the variable and the shape of the frequency distribution with respect to the character. Statistical tests were two-tailed when possible.

RESULTS

Nest-site preferences.—The six species of trees in which we found woodpecker nest cavities constituted more than 90% of the trees in the study area. Based on the estimated abundance of tree species, Acorn Woodpeckers clearly preferred valley oaks and sycamores and avoided blue oaks and coast live oaks (Fig. 1). Of 222 trees used for nesting, only 7 (3.1%) were in snags. However, this number was significantly higher than expected based on the estimated availability of snags (0.65%; $\chi^2 = 21.3$, df = 1, $P < 0.001$).

Despite the rarity of dead trees, 49.8% of nest cavities ($n = 221$) were in dead limbs, which was significantly higher than expected based on our sample of randomly chosen limbs (12% dead; $\chi^2 = 291$, df = 1, $P < 0.001$). Forty-two percent of nest cavities were located in trees used as granaries, also far more than expected ($P < 0.001$) given that granaries comprised only about 0.12% of trees in our study site.

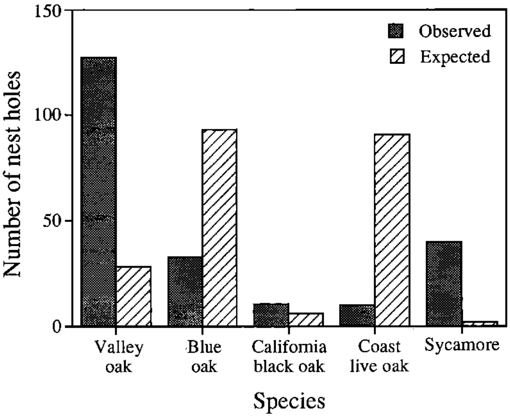

FIG. 1. Distribution of Acorn Woodpecker nests across tree species (excluding one nest built in a willow) compared with the average numerical abundance of the five tree species in the study area. Nests were found significantly more often than expected in valley oaks and sycamores and less often than expected in blue and coast live oaks ($\chi^2 = 1{,}134$, df = 4, $n = 221$, $P < 0.001$).

Nests invariably occurred in relatively large trees: of all trees in the study area, an estimated 76.3% were smaller than the smallest tree in which a nest was located (i.e. 35.6 cm dbh). However, even if the analysis is restricted to the subset of trees larger than 35.6 cm dbh, birds preferred larger trees for nest cavities (Mann-Whitney U-test, $z = 15.1$, $P < 0.001$, $n = 202$ nest trees vs. 414 randomly selected non-nest trees).

Characteristics of nests.—Descriptive statistics of nest sites are summarized in Table 1, and frequency distributions for characters are plotted in Figures 2 and 3. Nest height was positively correlated with tree height ($r_s = 0.45$, $n = 126$, $P < 0.001$); 13% of nests were located in the top 20% of the tree, and no nests were in the bottom 20%. The frequency distribution of nest-hole orientation was biased toward the east (67.2% were oriented between 0° and 180°; binomial test, $z = 5.2$, $n = 232$, $P < 0.001$; Fig. 2A) and was significantly nonuniform (Rayleigh test, $z = 5.0$, $n = 194$, $P < 0.01$). Almost all of the nest holes (95.4%) faced downward (Fig. 2B).

Correlates of reproductive success.—Four measures of reproductive success were recorded for nest cavities and averaged over all known

TABLE 1. Descriptive statistics for nest cavities used by Acorn Woodpeckers at Hastings Reservation, 1972 to 1987.

Variable	$\bar{x} \pm$ SD	Range	n
dbh (cm)[a]	98.3 ± 36.8	35.6–254.6	203
dnh (cm)[b]	31.1 ± 13.4	13.1–114.0	167
Hole depth (cm)	37.9 ± 9.8	22.0–70.0	105
Nest height (m)	8.1 ± 2.7	2.3–18.0	196
Relative nest height[c]	0.58 ± 0.17	0.21–0.99	126
Distance to granary (m)	140.9 ± 217.5	0–1,080	161
Nest-hole orientation (°)	78.5 ± 109.5	—	194
Nest-hole angle[d]	−34.2 ± 22.5	−87 to +30	175

[a] Diameter of tree at breast height.
[b] Diameter of limb at nest height.
[c] Nest height divided by tree height.
[d] Relative to horizontal.

times that individual cavities were used: (1) mean standardized clutch size (mean clutch size), (2) mean standardized number of young fledged from all nests (total mean fledged), (3) mean standardized number of young fledged from successful nests only (successful mean fledged), and (4) proportion of nests in the cavity that successfully fledged young (cavity success). Nest holes that were relatively higher in trees were more successful ($r_s = 0.23$, $n = 120$, $P < 0.01$) and fledged more young (total mean fledged, $r_s = 0.30$, $n = 111$, $P < 0.001$; successful mean fledged, $r_s = 0.28$, $n = 92$, $P < 0.01$) than holes that were relatively lower in trees. In addition, cavities in live limbs tended to fledge more young than those in dead limbs (Mann-Whitney U-test, $z = 2.3$, $n = 193$, $P < 0.05$), relatively successful cavities were oriented differently than relatively unsuccessful cavities (Watson test, $U^2 = 0.26$, $n = 182$, $P < 0.05$), and holes close to granaries tended to have relatively smaller clutches ($r_s = 0.19$, $n = 111$, $P < 0.05$). No measure of reproductive success differed between nests in trees used as granaries and those in trees not used as granaries (Table 2).

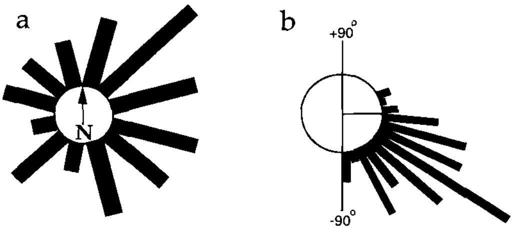

FIG. 2. Circular frequency histograms for (A) nest-hole orientation ($n = 194$) and (B) nest-hole angle ($n = 175$).

Relationship between optimal and most frequently used nest characteristics.—Five marginally significant results ($P < 0.05$) emerged from analyses testing whether the most frequently used category for a particular nest characteristic was related to increased reproductive success; three of these indicated that the modal category was the most successful (Table 2). For dnh, both mean clutch size and mean total young fledged were largest for intermediate-sized limbs 20 to 30 cm dnh, which were also the most frequently used in the population (Fig. 3). Both of these effects were due primarily to poor success of nests in limbs <20 cm dnh (Fig. 4). Also, east-facing holes (0° to 180°) were more successful and were used more frequently than were

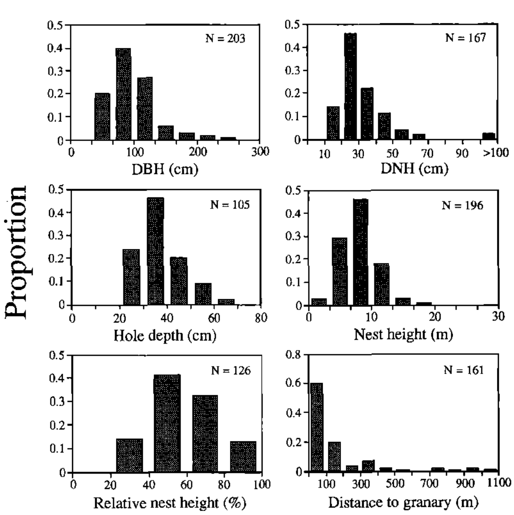

FIG. 3. Frequency distribution for six characteristics of cavities used by nesting Acorn Woodpeckers.

TABLE 2. Relationships between nest-site characteristics and four measures of reproductive success in Acorn Woodpeckers. Characteristics are divided into categories based on the frequency distributions in Figures 1–3 and listed in the far-right column; modal categories are listed in bold. Listed are test statistics with sample sizes in parentheses; values are z-scores (Mann-Whitney tests) for two-category variable and χ^2 (Kruskal-Wallis) for three-category variables. For clutch size and number of young fledged, values are the average of standardized values for all years a particular cavity was used.

		Mean no. of young fledged			
Variable	Mean clutch size	All nests	Successful nests only	Cavity success	Categories
Tree species	−0.1 (142)	−0.4 (179)	0.6 (145)	−0.1 (197)	**Valley oak + sycamore** vs. others
Nest tree a granary	1.5 (111)	−0.6 (137)	1.0 (114)	−0.7 (155)	Granary vs. **non-granary**
Tree viability	1.0 (149)	−0.9 (194)	0.0 (159)	−0.6 (210)	**Alive** vs. dead
dbh	−3.4 (143)	−1.3 (178)	0.3 (145)	−3.8 (191)	<66.7, **66.7–100**, >100 cm
dnh	7.0 (131)*	8.2 (151)*	4.3 (127)	4.7 (156)	<20, **20–30**, >30 cm
Nest-hole depth	0.0 (89)	0.8 (98)	0.0 (84)	1.3 (99)	<30, **30–40**, >40 cm
Nest height	0.3 (144)	−2.0 (177)	−2.1 (148)	−0.3 (186)	<6.7, **6.7–10**, >10 m
Relative nest height	−3.6 (91)	−8.7 (111)*	−4.7 (92)	−5.8 (120)*	<0.4, **0.4–0.6**, >0.6
Nest-hole orientation	−0.2 (140)	2.2 (177)*	1.1 (148)	1.5 (185)	**0 to 180°** vs. 180 to 360°
Nest-hole angle	−1.3 (136)	−1.6 (160)	−5.1 (133)	−1.1 (165)	<−40°, **−40 to −20°**, >20°

*, $P < 0.05$.

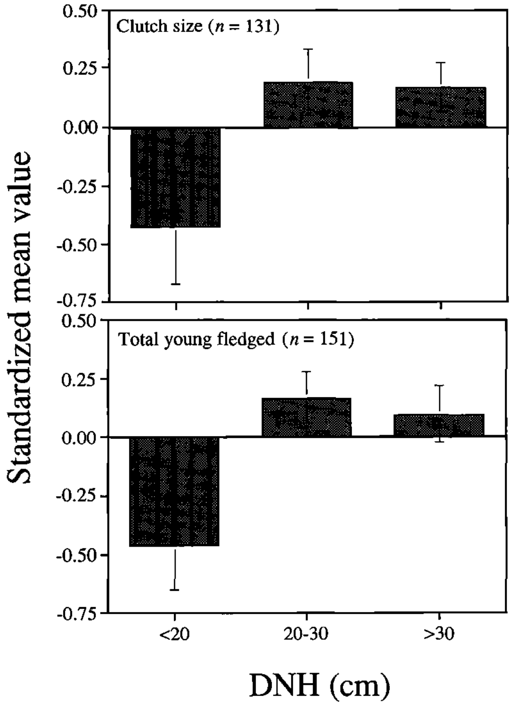

FIG. 4. Standardized mean (±SE) clutch size (upper panel) and total mean number of young fledged (lower panel) from nest cavities built in various limb diameters (dnh). Differences are significant (Kruskal-Wallis tests, clutch size, $\chi^2 = 7.0$, df = 2, $P < 0.05$; young fledged, $\chi^2 = 8.2$, df = 2, $P < 0.05$).

west-facing holes (Table 2). However, nests in the upper 40% of trees fledged more total young and were the most successful, whereas cavities occurred most often in the middle 20% of trees (Table 2).

Factors influencing nest microclimate.—From temperature measurements in artificial nest cavities, east-facing cavities warmed up faster in the mornings and maintained warmer temperatures until early afternoon than did holes facing in other directions (Fig. 5). We determined how microclimate was influenced by nest-hole orientation by averaging temperatures throughout the daylight hours (0600 to 1800) and then comparing these means and their standard deviations for the five days of data. East-facing holes were warmer than either west-facing or north-facing holes on all five days (Wilcoxon matched-pairs signed-rank test, both $P < 0.05$) and were warmer than south-facing holes on four of five days ($P = 0.08$). Similarly, on all five days the standard deviations of daytime temperatures for east-facing holes were smaller than those for either south-facing or west-facing holes (both $P < 0.05$) and smaller than north-facing holes on three of five days ($P = 0.22$). Thus, east-facing holes generally were warmer and experienced lower overall temperature fluctuations than holes facing the other directions.

We tested for the effect of limb viability on nest microclimate by pairing five live and five

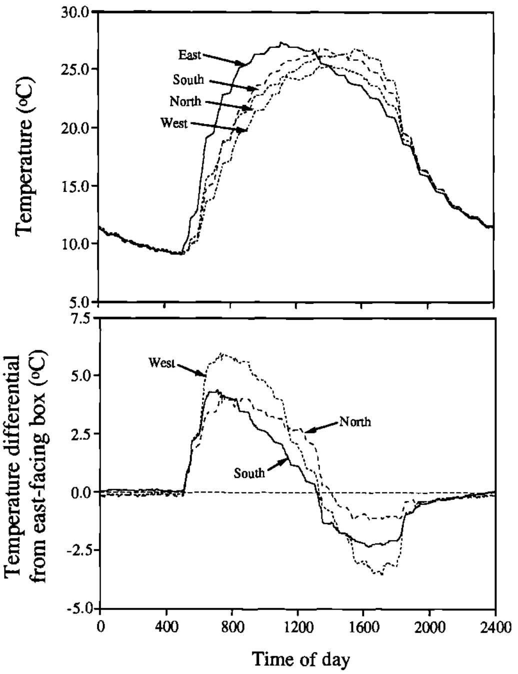

Fig. 5. Effects of orientation on daily temperature patterns in artificial nest boxes at Hastings Reservation. Graphed are mean temperatures of boxes facing the four cardinal directions, averaged over five days in June 1986 (upper panel) and differences between east-facing boxes and matched boxes facing the other three cardinal directions (lower panel). In the lower panel, positive values indicate that east-facing boxes are warmer, negative values the reverse.

dead limbs while controlling for nest orientation, exposure, and height. Temperatures were significantly higher in live limbs during the non-daylight hours over a five-day period (Wilcoxon matched-pairs signed-rank test, $z = 2.02$, $P < 0.05$). Averaging all temperatures recorded during the five days of measurements, the overall variance in temperature was considerably lower in live limbs (variance = 26.0°) than in dead limbs (variance = 161.3°).

Factors affecting predation.—Neither nest depth, absolute nest height, nor nest angle varied linearly with the incidence of nesting failure. When tested against a normal distribution, nest depth and nest height were significantly skewed toward smaller values (depth: $\bar{x} = 0.84$ ± SE of 0.24 for skewness, $t_s = 3.7$, $P < 0.001$; height: $\bar{x} = 0.38 \pm 0.17$, $t_s = 2.2$, $P < 0.05$; Fig. 3), indicating that birds tended to use holes lower in trees and in shallower limbs more than the converse. The mean angle of nest holes was well below horizontal (Table 1) and was not skewed significantly ($\bar{x} = -0.02 \pm 0.18$, $t_s = 0.1$, $P > 0.5$, Fig. 2B).

Two variables that were likely to be associated with greater protection from predators were positively associated with increased success: smooth bark and relative nest height. Of the nest trees used by Acorn Woodpeckers, only sycamores have relatively smooth bark that makes them more slippery than oaks. Nests in sycamores tended to fledge more young than did nests in all other tree species combined (Mann-Whitney *U*-test, $z = 1.96$, $n = 188$, $P = 0.05$) and contained a higher proportion of nests that were successful ($z = 2.2$, $n = 206$, $P < 0.05$). Regardless of the species, nests that were relatively (but not absolutely) high in trees fledged significantly more young and were more likely to be successful than nests that were relatively low in trees.

Relationship between nest-site selection and group/territory characteristics.—The ability to build suitable nests cavities potentially could be influenced by group size and continuity of territory occupation. We examined the relationship between these two variables and the five characteristics of nesting cavities associated with differences in reproductive success (i.e. limb viability, nest orientation, relative nest height, dnh, and tree species). Group size was averaged over all occasions the cavity was used, and territorial occupancy was categorized into those occupied continuously versus those not occupied continuously. Nest-hole orientation, relative nest height, and dnh did not differ significantly with group size or continuity of territory occupation. However, mean group size was significantly larger when cavities were in live limbs ($\bar{x} = 4.5$ ± SD of 1.0, $n = 101$) versus dead limbs ($\bar{x} = 3.8 \pm 1.7$, $n = 95$; $z = 2.5$, $P = 0.01$) and when cavities were in sycamores ($\bar{x} = 4.8 \pm 2.0$, $n = 37$) versus other species of trees ($\bar{x} = 4.0 \pm 1.8$, $n = 156$; $z = 2.2$, $P < 0.05$). Also, the proportion of holes built in live limbs was significantly higher in territories that were continuously occupied (60.2%, $n = 128$) than in those that were not continuously occupied (40.5%, $n = 74$; $\chi^2 = 6.5$, df = 1, $P < 0.05$).

One possible consequence of this latter result is that the fitness advantages of nesting in live limbs and in sycamores might be due to the confounding effects of group composition rather than any microclimatic advantage of live limbs. We checked for this by performing ANCOVAs with mean group size (the covariate) entered prior to the main factor (limb viability or tree species). Even after controlling for the effect of mean group size ($F = 5.2$, df = 1 and 172, $P = 0.02$), fledging success was influenced by limb viability ($F = 4.3$, df = 1 and 172, $P = 0.04$). Similarly, nest cavities in sycamores fledged more young ($F = 7.5$, df = 1 and 190, $P < 0.01$) and were more successful ($F = 4.2$, df = 1 and 190, $P < 0.05$) even after controlling for mean group size. Thus, cavities in live limbs and in sycamores were more successful even after controlling for the generally larger groups with which they were associated.

DISCUSSION

Acorn Woodpeckers at Hastings Reservation prefer to build nests in large valley oaks and sycamores, which also are frequently used as granaries for storing acorns. Snags are rare in our study area but are preferred when present, a result also found for several cavity-nesting species in central Arizona (Li and Martin 1991). Birds also use dead limbs far in excess of their availability. This almost certainly is due to choice of limbs that are easily excavated by the birds; we have no evidence that limbs die owing to the excavating activities of the birds.

Nest-site quality hypothesis.—Out of the five preferred nest-site characteristics, only one (tree species) was associated with higher reproductive success: nests in sycamores fledged more young and were more successful than nests in other tree species. However, the combined reproductive success for nests in valley oaks and sycamores (both of which were used in excess of their relative abundance) did not differ from that in all other tree species (Table 2). Moreover, even though Acorn Woodpeckers preferred to nest in larger trees, trees that were dead, and trees that were used as granaries, these characteristics did not have a significant positive influence on reproductive success. Dead limbs were actually associated with lower reproductive success despite being preferred relative to their availability.

We obtained similar mixed results in tests of association between reproductive success and nest-site characteristics that were used most frequently in our population (Table 2). Two preferred characteristics (nest limbs 20 to 30 cm dnh and holes facing east) were associated with slightly increased reproductive success. The effect of limb size was due primarily to relatively low clutch size and fledging success in cavities in very small limbs, an effect comparable to that found in several other cavity-nesting species (Löhrl 1973, Ludescher 1973, Karlsson and Nilsson 1977).

Of the eight additional variables exhibiting a clear modality, seven were not associated with differences in reproductive success. The eighth, relative nest height, was highly significantly associated with increased reproductive success, but only 13% of the nests were in the reproductively most successful upper 20% of the trees. These results indicate that neither modal nest characteristics nor nest characteristics chosen by birds more frequently than expected by chance are necessarily associated with increased reproductive success. A similar lack of concordance among preferred, modal, and most successful nest-site characteristics has been reported in other studies of both secondary (Brawn 1988) and primary (Li and Martin 1991) cavity nesters.

The role of nest microclimate.—A favorable nest microclimate may increase reproductive success by decreasing the energetic costs of incubation (White and Kinney 1974) and by preventing death by exposure and/or increasing the growth rate of young (Quinney et al. 1986). Data relevant to the hypothesis that nest microclimate plays an important role in nest-site selection in our population are summarized in Table 3. All three variables known or likely to be associated with improved nest microclimate were also associated with higher reproductive success. Two of these (larger limbs and east-facing cavities) were also modal characteristics of nest cavities. In contrast, live limbs were not preferred relative to availability and were used in the same frequency as dead limbs, despite being microclimatically favorable and associated with increased total fledging success. However, for two of three variables, the data suggest that nest cavities with more favorable microclimatic characteristics are associated with increased reproductive success and are used most frequently by Acorn Woodpeckers.

The role of nest predation.—Nesting success in our population exceeds 70% (Koenig and Mum-

TABLE 3. Summary of evidence for the importance of nest microclimate and accessibility to predators in nest-site selection by Acorn Woodpeckers.

Variable	Preferred?	Most frequent?	Most successful?	Related to success?
Variables known or likely to influence nest microclimate				
Larger limb	—	Yes	Yes	Yes
Live limb	No	No	Yes	Yes
East-facing hole	—	Yes	Yes	Yes
Variables known or likely to influence accessibility to nest predators				
Smooth-barked tree	Yes	No	Yes	Yes
Hole relatively high in tree	—	No	Yes	Yes
Deeper hole	—	No	No	No
Higher hole	—	No	No	No
Nest oriented vertically	—	Yes	No	No

me 1987). However, predation seems to be the main cause of nest loss (M. T. Stanback unpubl. data). Gopher snakes (*Pituophis melanoleucus*) are the most common nest predators (Eichholz and Koenig 1992), and our data support the hypothesis that nest sites are chosen to reduce accessibility to snakes (Table 3). Nests in sycamores, which have relatively smooth, slippery bark except when very old, were preferred when available and tended to have higher fledging success and lower nest failure than nests in other species of trees. More significantly, nesting success increased as relative height of nests increased. Why relative nest height (vs. absolute) showed this effect is unclear.

We found no relationship between reproductive success and either hole depth, absolute nest height, or angle of the hole relative to the ground, factors that are also likely to influence accessibility to predators. Nonetheless, these results suggest that choosing relatively inaccessible nests is a factor in nest-site selection in Acorn Woodpeckers, despite the low incidence of nest predation relative to that of many open-nesting species.

Constraints on optimal nest-site selection.—If predictable features of nest sites are associated with higher reproductive success, what prevents birds from selecting sites and constructing cavities with those characteristics? Conversely, why are certain nest characteristics preferred or used more frequently when they do not appear to be associated with higher reproductive success?

Most likely, the answer to both of these questions is that nest-site selection is constrained in some manner. One commonly invoked constraint is interspecific competition for nest sites (Nilsson 1984, Brawn 1988, Rendell and Robertson 1989, Li and Martin 1991). However, because Acorn Woodpeckers construct their own cavities, they are presumably not significantly constrained by other species' nest preferences. More likely constraints are of two kinds. First are "ecological" constraints that limit the ability of birds to choose nest sites with particular characteristics. Examples include the species of tree in which nests can be built (which is constrained by the absence of certain species in particular territories), and the rarity of snags (which limits the number of nests that can be excavated in dead trees). An additional example is relative nest height. Despite a highly significant reproductive advantage in nests located relatively high in trees, the vast majority of nests were located in the "upper middle" of trees (Fig. 3). The most likely explanation for this discrepancy is that relative nest height is determined primarily by the location of large, dead limbs, which inevitably decrease in number as one ascends a tree.

More interesting are "demographic" constraints that limit the ability of birds to excavate cavities with optimal characteristics. Our best example of such a constraint is the relatively low incidence of nests in live limbs (51.2% vs. an estimated availability of 88.0%) despite their microclimatic advantages and correlation with high total mean fledging success. Most likely, this reflects the difficulty of excavating in live wood, especially hardwoods such as the oaks that dominate our study site. That excavation difficulty constitutes a demographic constraint is supported by the difference in mean group size of birds nesting in live versus dead limbs (group size is higher when nesting in live limbs) and by the difference in the probability of nests being in live limbs in territories that are continuously occupied versus those that are not continuously occupied (continuous occupancy is associated with nesting in live limbs). Apparently, larger and more stable groups allow the increased cost of nest construction in live limbs to be shared among multiple individuals and over multiple years.

These results indicate that significant ecological and demographic constraints exist on optimal nest-site selection in Acorn Woodpeckers, despite the relatively strong nest-building capabilities of this species. This conclusion has important implications for the conservation of primary cavity nesters. For example, although Acorn Woodpeckers apparently prefer to nest in snags and dead limbs, to provide dead limbs as artificial nesting habitat would be to offer suboptimal nesting sites. Instead, providing live limbs with potential nest cavities partially excavated would be more likely to enhance the reproductive output of the population. Because the relationships among preferred, modal, and optimal nest-site characteristics are complex, assumptions about nest-site choice should not be made without careful evaluation, even for species that excavate their own cavities.

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