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NEST-SITE CHARACTERISTICS OF HAMMOND'S AND PACIFIC-SLOPE FLYCATCHERS IN NORTHWESTERN CALIFORNIA[1]

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Abstract. Thirty nests of Hammond's *(Empidonax hammondii)* and 88 nests of Pacific-slope *(E. difficilis)* Flycatchers were located in different-aged Douglas-fir *(Pseudotsuga menziesii)*/tanoak *(Lithocarpus densiflorus)* dominated forests at 12 study sites in northwestern California during the breeding seasons of 1984, 1985, 1987, and 1988. In contrast to Pacific-slope Flycatchers, Hammond's used nest trees that averaged two to three times taller; placed nests three times higher and farther from the tree bole; used only live trees; placed nests only on small- to medium-diameter branches; situated nests in areas with higher foliage cover; and favored nest placement on the northeast and southwest sides of trees. Attributes of nesting habitat also differed between species among different stand development stages. Hammond's Flycatchers in old-growth and mature forests chose nest sites with more open canopy than that found at random sites. Pacific-slope Flycatchers in old-growth and mature forests nested at sites with a lower mid-canopy bole height. In young stands, Pacific-slope Flycatchers selected nest sites with large Douglas-firs and Pacific madrone *(Arbutus menziesii)* trees, higher shrub cover, and fewer medium-size Douglas-fir trees. Hammond's Flycatchers were not found in younger stands. We speculate that if old-growth Douglas-fir/tanoak forests are greatly reduced or eliminated in northwestern California, the density of breeding Hammond's Flycatcher will decrease substantially. However, Pacific-slope Flycatchers would probably be less affected by conversion of old-growth forests to younger-aged classes.

Key words: Hammond's Flycatcher; Pacific-slope Flycatcher; Empidonax hammondii; E. difficilis; *nest-site selection; Douglas-fir forest; northwestern California; old-growth forest.*

INTRODUCTION

Logging practices in northwestern California have drastically reduced the extent of old-growth (200-plus years old) Douglas-fir (*Pseudotsuga menziesii*) forests. Altering stand structure and plant species composition influences the distribution and abundance of birds (Franzreb and Ohmart 1978, Szaro and Balda 1980, Morrison 1982) and their foraging behavior (Mauer and Whitmore 1981, Robinson and Holmes 1982, Franzreb 1983, Sakai 1987). Both Hammond's *(Empidonax hammondii)* and Pacific-slope, formerly Western, *(E. difficilis)* Flycatchers have been shown to occur in higher abundance in old-growth than in younger stands of northwestern California (Raphael 1984, 1988; Sakai 1987). The growing demand for wood products results in an accelerating modification of stand structure and vegetation composition such that old-aged stands are being replaced by younger stands. Published quantitative data on habitat use and nest site selection of Hammond's and Pacific-slope Flycatchers in different-aged stands are insufficient to determine whether their populations will be negatively or positively affected by stand conversion. Increasing the amount of young forest at the expense of old-growth could be a potential problem to the persistence of old-growth habitat specialists (e.g., Spotted Owl, *Strix occidentalis;* Marbled Murrelet, *Brachyramphus marmoratus*) and this type of information is necessary before land managers concerned about the old-growth issue can make sound management decisions.

In this study we quantified nest-habitat features of both species, compared them to each other and to the stands in which they occurred. Our objectives were to test the hypotheses that Hammond's and Pacific-slope Flycatchers do not differ in (1) their selection of nest sites; and (2) their use of nest-site features relative to randomly located, available sites in different-age stands.

METHODS

STUDY STANDS

Candidate stands for inclusion in the study, selected to represent three developmental stages

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(young, mature, and old-growth), were located in Humboldt and Trinity counties of northwestem California. A young stand was defined as 30-90 years; mature, 91-199 years; and old-growth, > 200 years. Mean stand age was determined from increment cores of 4-6 dominant Douglas-firs or by counting annual rings of Douglas-fir stumps found in adjacent clearcuts. All stands were dominated by Douglas-fir and tanoak *(Lithocarpus densiflorus).* Pacific madrone *(Arbutus menziesii*), canyon liveoak *(Quercus chrysophylla),* incense-cedar *(Calocedrus decurrens),* sugar pine *(Pinus lambertiana),* and white fir *(Abies concolor*) were common as associated species.

Final selection of twelve 20-ha stands (five young, four mature, and three old-growth) was based on stand size > 15 ha and accessibility. Several of the selected stands were the same as those used in an earlier old-growth related vertebrate monitoring study (Raphael 1984). The stands occurred between 710 and 1,235 m elevation.

NEST AND HABITAT DESCRIPTION

We studied the nest-site characteristics of both flycatchers between April and August of 1984, 1985, 1987 and 1988. Four observers spent 1,444 person-hours in the field in 1984; two observers spent 2,442 hr in 1985 and 836 hr in 1987; and one observer spent 51 hr in 1988. Pacific-slope Flycatchers were found in all study plots, but Hammond's Flycatchers occurred in only 6 of 12 plots (3 in old-growth and 3 in mature stands).

We located most nests while walking systematically along transect lines and adjacent areas, recording the behavior of foraging birds. Nests were also found during censuses (Sakai 1987) and in 1987 and 1988 during systematic searches.

To establish the location of vegetation sampling points, an imaginary vertical line was projected perpendicularly from the nest site to the ground. All circular vegetation samples were centered at this point. At the end of each breeding season, vegetation at the nest sites and at random points in the stand was measured within two concentric circles (12.6 m radius [0.05 ha] and 25.2 m radius [0.20 ha]). Thirty-one habitat variables, selected to describe floristic and structural forest components believed important for flycatchers, were measured at each nest and random site. We sampled 12-24 random sampling points per stand to compare with flycatcher habitat use at nest sites. Sample points were obtained by choosing random compass directions, pacing between 1 and 99 steps from each systematically placed bird census plots located along each transect, and tossing a stick over the right shoulder with point of impact as plot center.

Nest orientations, to the nearest compass degree, were measured from the center of the tree bole to nest location. For analysis, nest orientations were grouped into eight 45° subdivisions. Graphic procedures were adapted from Silverman (1986:4).

ANALYSES

The null hypotheses of no difference (1) between species in their patterns of nest-site selection; and (2) within species between random sites and nest sites, were tested separately by seral stage. To compare nest sites between species and nest sites with random sites, we used step-wise discriminant function analysis (BMDP program 7M [Dixon et al. 1985]). Some variables were transformed prior to statistical analysis in order to increase their fit to a normal distribution. For the majority of discriminant analyses, our data violated the assumption of equality of the group covariance matrices. This result was not surprising nor did it preclude the possibility of discovering important ecological relationships from the analyses. Lack of equality of covariance matrices between species can arise, for example, if one species is more specialized in its nest-site selection than another species. In the context of our analyses, tests of the equality of covariance matrices provided useful biological insights into a species' relative degree of habitat specialization as well as the specificity of its nest-site selection relative to random locations. The degree of specialization within a group was inferred from the determinant of a group's covariance matrix which is a measure of the generalized variance (Morrison 1976:253) within the group. In general, if the null hypothesis of covariance equality was rejected, the group with the smaller covariance matrix was considered to be significantly less variable. Statistical inference from discriminant analysis is generally believed to be robust to violations of the covariance assumption (Cooley and Lohnes 1971). In the two-group case the null hypothesis is accepted more frequently when the covariance matrices are unequal (Green 1978: 170), but there is little evidence that moderate violations significantly change classification success (Williams 1983). Biological interpretation

TAI3LE 1. Two-group stepwise discriminant analysis of Hammond's Flycatcher and Pacific-slope Flycatcher use of specific nest-site characteristics (all nest sites) in old-growth and mature Douglas-fir/tanoak dominated forests of northwestern California. Group means and standard deviations of variables included in the model are presented.

Variable[a]	Old-growth group means (SD)		Structure coeffi-	Mature group means (SD)		Structure
	Hammond's	Pacific-slope	cients	Hammond's	Pacific-slope	coefficients
Nest height (m)	21.1 (4.2)	5.9 (5.3)	0.975	19.8 (4.3)	5.9 (4.8)	0.921
Percent foliage surrounding 0.5 m circumference of nest	26.1 (13.3)	9.1 (17.0)	0.531	22.3 (8.8)	5.4 (7.9)	0.788
Nest distance to nearest water (m)	–	–	–	130.5 (60.2)	166.0 (56.5)	-0.311
Sample size	19	42		11	29	
Wilk's lambda	0.327			0.352		
Approximate F-statistics	121.36***			69.95***		
Cohen's kappa	0.85**			1.00**		
$\ln \lvert\Sigma\rvert$	16.60	17.76		15.11	15.27	
χ^2	9.67			3.79		

[a] Only variables whose structure coefficients had an absolute value > 0.30 are presented.
** Significant at $P < 0.001$; *** significant at $P < 0.0001$.

of the canonical variate was based on the magnitude of structure coefficients (bivariate correlations between the original variables and the canonical variate scores). Variables with structure coefficients less than 0.30 were considered relatively unimportant and are not discussed. Classification results were used to estimate the magnitude of group separation. Cohen's kappa statistics (Z value) was computed for each discriminant model to test whether the model classified the observations significantly better than chance alone (Titus et al. 1984).

To determine whether flycatcher nests were oriented nonrandomly, we tested the goodness of fit of each species' observed circular frequency distribution of nest orientations to a uniform distribution (Zar 1984:441).

RESULTS

NEST-SITE SELECTION: CHARACTERISTICS OF NEST TREES

Pacific-slope Flycatcher nests were found in all three seral stages, but Hammond's Flycatchers occurred and nested only in stands >90 years old. As a consequence, seral stage comparisons between species were restricted to mature and old-growth stands. All Hammond's Flycatcher nests located were in live trees. In contrast, the Pacific-slope Flycatcher nested in live trees as well as in snags and in ground nests located in exposed root wads of fallen trees. Given the greater variability in nest-site selection of the Pacific-slope Flycatcher, we felt that two separate analyses comparing the species' nest sites were meaningful; one based on all nests, and one restricted to nests located within live trees. The variables available for selection in a stepwise discriminant analysis are restricted to those measured on all observations. As a result, analyses based on the complete sample of nests were restricted to fewer variables than analyses based on the live tree samples.

Based on the sample of all nests, the nest sites of the two flycatcher species differed significantly in both mature and old-growth stands (Wilk's lambda = 0.352 and 0.327, respectively; $P < 0.001$ in both cases; Table 1). In both mature and old-growth stands, Hammond's Flycatcher nested significantly higher and in areas with greater concealment of the nest by foliage (Fig. 1). The percent of correct classification of the species' samples were much higher than that based on a chance classification. The models classified 100% better than chance in mature stands (Cohen's kappa $Z = 1.23$, $P < 0.001$) and 85% better than chance in old-growth stands (Cohen's kappa $Z = 0.94$, $P < 0.001$). Based on the set of variables common to all nest sites, the species' covariance matrices were not significantly different in either mature or old-growth stands ($\chi^2 = 3.79$ and 9.67, respectively; $P > 0.05$ in both cases; Table 1). Thus, in terms of these variables, there was no evidence of greater nest-site specialization by one species relative to the other.

Restricting the comparison to live nest trees still detected significant, though less extensive, differences in the species' nest sites in both ma-

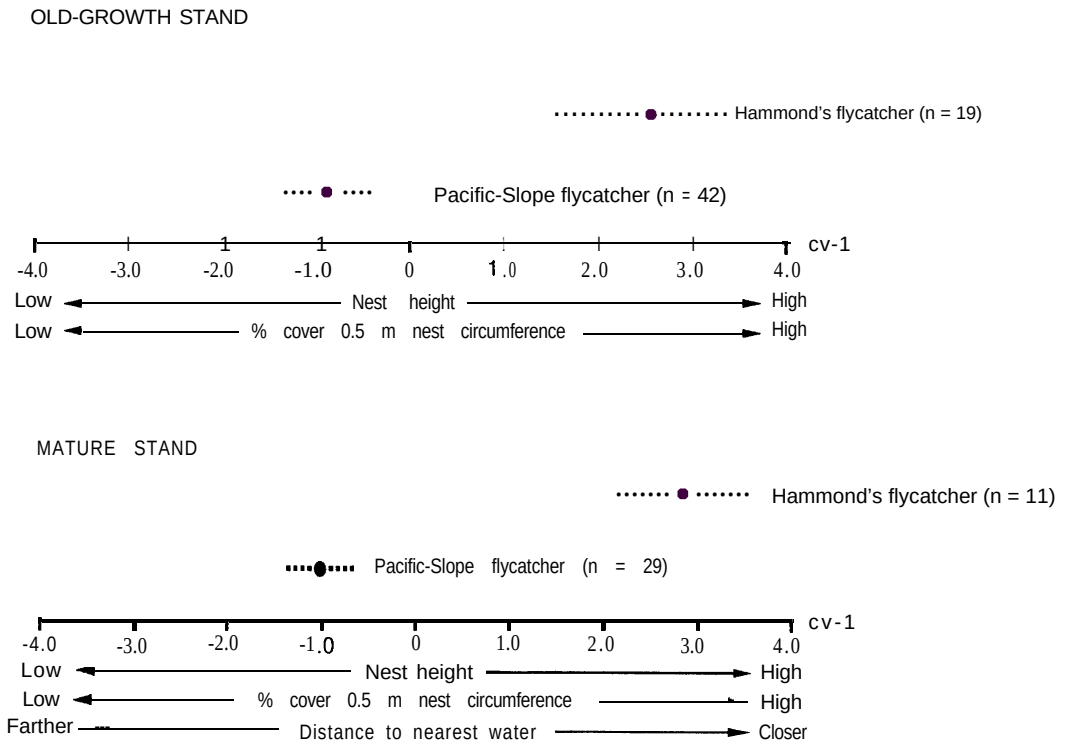

FIGURE 1. Means and 95% confidence intervals of canonical variate (CV) scores and variables which discriminate between Hammond's and Pacific-slope Flycatcher nest sites in mature and old-growth forest stands in Douglas-fir/tanoak dominated forests of northwestern California. Analyses based on all nest-sites.

TABLE 2. Two-group stepwise discriminant analysis of Hammond's Flycatcher and Pacific-slope Flycatcher use of specific nest-site characteristics (live trees only) in old-growth and mature Douglas-fir/tanoak dominated forests of northwestern California. Group means and standard deviations of variables included in the model are presented.

Variable[a]	Old-growth group means (SD)		structure coefficients	Mature group means (SD)		Structure coefficients
	Hammond's	Pacific-slope		Hammond's	Pacific-slope	
Distance of nest to tree trunk (m)	5.3 (1.8)	0.7 (1.2)	0.939	4.3 (1.8)	0.7 (1.5)	0.793
Nest height (m)	21.1 (4.2)	7.0 (5.9)	0.895	19.8 (4.3)	7.3 (5.1)	0.850
Nest tree height (m)	44.9 (10.0)	24.2 (16.0)	0.674	44.6 (6.9)	1.8 (10.5)	0.877
Diameter-at-breast-height of nest tree (cm)	104.2 (32.9)	54.9 (44.7)	0.587	84.5 (18.7)	47.9 (36.2)	0.543
Percent foliage surrounding 0.5 m circumference of nest	26.1 (13.3)	12.8 (19.3)	0.406	22.3 (8.8)	4.9 (6.0)	0.826
Nest branch diameter (cm)	7.3 (2.7)	31.0 (44.0)	-0.376	7.2 (3.0)	20.5 (10.7)	-0.647
Distance of nest to canopy edge (m)	2.3 (0.9)	3.2 (1.9)	-0.309	–	–	–
Sample size	19	25		11	19	
Wilk's lambda	0.282			0.331		
Approximate F-statistics	106.86***			56.49***		
Cohen's kappa	0.73**			0.58**		
ln $\lvert\Sigma\rvert$	28.57	34.66		22.20	29.98	
χ^2	111.84***			59.69**		

[a] Only variables whose structure coefficients had an absolute value >0.30 are presented.
** Significant at $P < 0.01$; *** significant at $P < 0.001$.

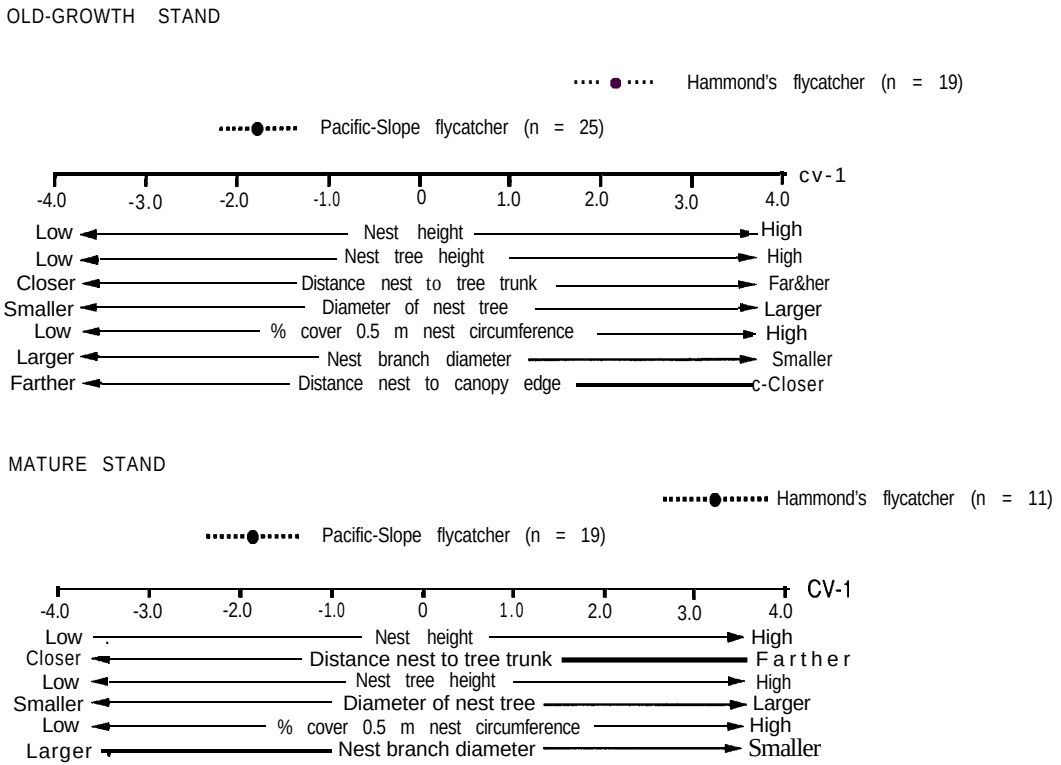

FIGURE 2. Means and 95% confidence intervals of canonical variate (CV) scores and variables which discriminate between Hammond's and Pacific-slope Flycatcher nest sites in mature and old-growth forest stands in Douglas-fir/tanoak dominated forests of northwestern California. Analyses based only on nest sites located in live trees.

ture and old-growth stands (Wilk's lambda = 0.331 and 0.282, respectively; $P < 0.001$ in both cases; Table 2). In both seral stages, Hammond's nests were significantly further from the trunk of the nest tree, located on smaller branches, located further above the ground, more concealed by foliage, and located in trees that were both taller and of greater diameter than nests of the Pacific-slope Flycatcher (Fig. 2). Classification success remained significantly better than chance in both mature and old-growth stands (58% improvement, $Z = 0.75$, $P < 0.001$, and 73% improvement, $Z = 0.75$, $P < 0.001$, respectively), though substantially less in mature stands than when all nest sites were analyzed. Based on a larger set of nest-site variables, the determinant of the covariance matrix for the Hammond's Flycatcher was significantly smaller than for the Pacific-slope Flycatcher in both mature and old-growth stands ($\chi^2 = 56.7$ and 111.8, respectively, $P < 0.001$ in both cases; Table 2). This difference suggests that the Hammond's Flycatcher was significantly more specialized than the Pacific-slope Flycatcher in its selection of nest sites in live trees.

Distribution of nest orientations differed significantly from a uniform distribution for Hammond's ($G = 19.60$, df = 7, $P < 0.0l$), but not for Pacific-slope Flycatchers ($G = 9.45$, df = 7, $P > 0.05$). Hammond's placed their nests with northeast and southwest exposures; the Pacific-slope Flycatcher showed no preference (Fig. 3).

WITHIN AGE-CLASS PATTERNS OF NEST-SITE SELECTION

Hammond's Flycatchers showed evidence of nest-site selection in old-growth (Wilk's lambda = 0.315, $P < 0.001$) and mature (Wilk's lambda = 0.344, $P < 0.001$; Table 3) stands. Hammond's Flycatcher used nest trees of significantly larger diameter than what was available in the general population for old-growth ($t = -8.37$, df

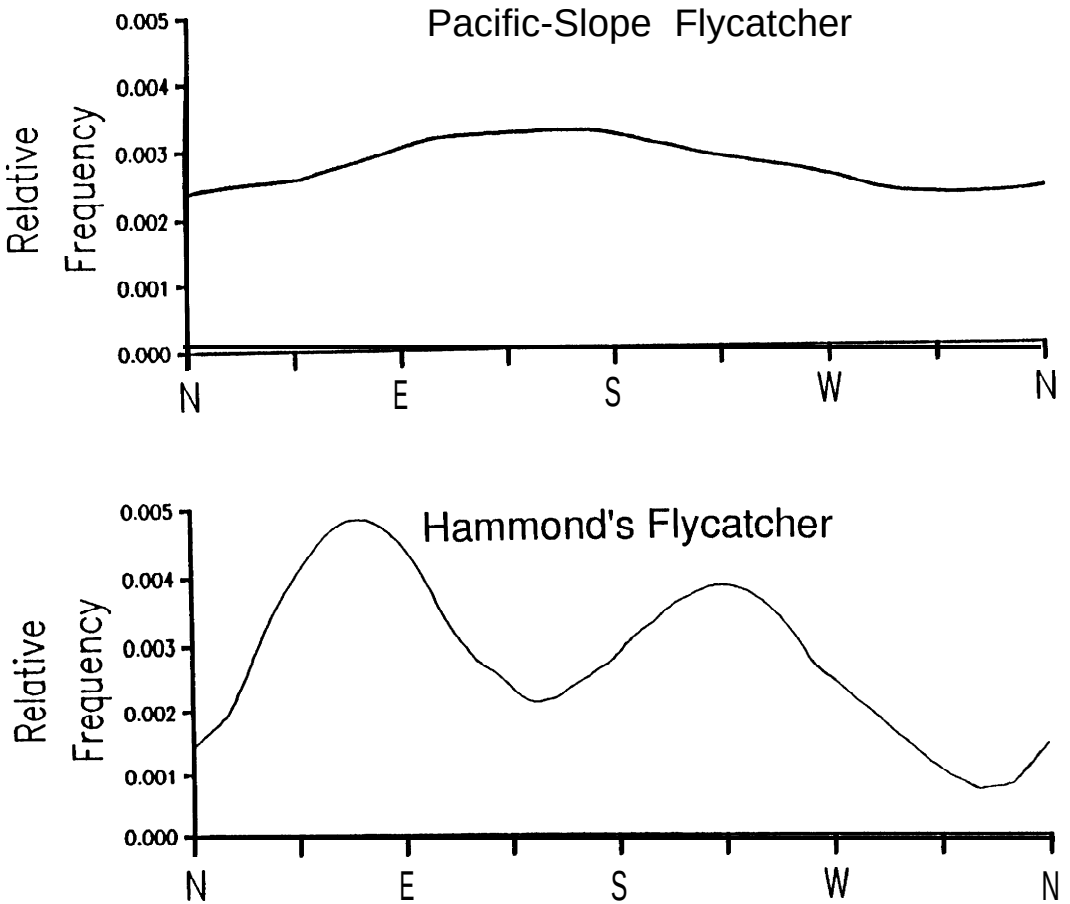

FIGURE 3. Frequency of placement of nests by Hammond's and Pacific-slope Flycatchers in relationship to the tree bole and azimuth. The x-axis displays the data points of measured azimuths taken from the center of the tree bole to nest location.

= 21, $P < 0.0001$) and mature (t = -10.55, df = 10, $P < 0.0001$) stands. In old-growth stands, Hammond's Flycatchers nested in areas with more open canopy, fewer small (1 to 10 cm diameter-at-breast-height [DBH]) tanoaks but more large (50 to 100 cm DBH) tanoaks, and selected areas with a higher canopy bole height (Fig. 4). Hammond's Flycatchers in mature stands used nest sites closer to water with more open airspace in the canopy resulting from a higher canopy bole height (Fig. 4). The percentage of correct classifications of nest-centered and random vegetation samples was much higher than that based on a chance classification (Fig. 4). The models classified 80% better than chance in old-growth stands ($P < 0.001$, Cohen's kappa Z = 8.12), and 94% better than chance alone in mature stands (Z = 13.0). As judged by the covariance test, the generalized variance of nest sites and random sites were not significantly different in either mature or old-growth stands (Table 3).

Pacific-slope Flycatchers also showed evidence of nest-site selection in old-growth (Wilk's lambda = 0.169, $P < 0.001$), mature (Wilk's lambda = 0.341, $P < 0.001$), and young (Wilk's lambda = 0.267, $P < 0.001$) stands (Table 4). The diameters of Pacific-slope Flycatcher nest trees were not significantly different than what was available in the general population for old-growth (t = -1.57, df = 46, P = 0.12), mature (t = -2.02, df = 22.6, P = 0.056) or young (t = -2.05, df = 16, P = 0.058) stands. In the older stands, structural, rather than floristic, components were more important in nest-site selection.

In old-growth stands, nest sites had lower mid-canopy bole heights, more closed canopies but with higher canopy bole heights, and a higher density of large (> 50 cm DBH and > 15 m height) snags (Fig. 3). Nest sites in mature stands occurred in areas with a lower mid-canopy bole height, more ground cover (0 to 0.5 m height), and higher numbers of small (1 to 10 cm DBH) Pacific madrone trees (Fig. 3). Nest sites in young stands were characterized by larger (> 50 cm DBH) Douglas-fir and Pacific madrone trees, fewer medium (10 to 50 cm DBH) size Douglas-firs, and higher shrub cover (Fig. 3). The percentage of correct classifications of nest-centered and random vegetation samples was much higher than that based on chance classification (Fig. 3). The model classified 84% better than chance in young stands (Cohen's kappa $Z = 9.85$, $P < 0.001$), 80% better than chance in mature stands ($Z = 8.72$, $P < 0.001$), and 96% better than chance in old-growth stands ($Z = 9.11$, $P < 0.001$) (Table 4). Based on the covariance test results and the relative magnitudes of the group covariance matrices, nest sites were significantly less variable than random sites in mature and old-growth forest but not in young forest (Table 4).

TABLE 3. Two-group stepwise discriminant analysis of Hammond's Flycatcher nest-site characteristics as compared with those of available sites in different seral stages of Douglas-fir/madrone dominated forests of northwestern California. Group means and standard deviations of variables included in the model are presented.

Variable[a]	Old-growth group means (SD)		Structure coefficients	Mature group means (SD)		Structure coefficients
	Nest site	Random site		Nest site	Random site	
Canopy bole height (m)	17.4 (2.2)	13.1 (1.7)	−0.829	16.3 (1.5)	13.2 (2.4)	−0.560
Density of tanoak 1–10 cm DBH	352.6 (199.8)[b]	615.4 (258.4)[b]	0.508	–	–	–
Percent canopy closure	82.4 (5.8)	86.6 (3.8)	0.456	–	–	–
Density of tanoak 50–100 cm DBH	25.5 (21.5)[b]	10.3 (14.7)[b]	−0.408	–	–	–
Distance to nearest water (m)	–	–	–	130.9 (72.2)	190.0 (30.0)	0.599
Percent cover 17–50 m height	–	–	–	52.8 (13.1)	66.2 (13.8)	0.415
Sample size	19	48		11	60	
Wilk's lambda	0.315			0.344		
Approximate F-statistics	33.69***			20.33***		
Cohen's kappa	0.80***			0.94***		
ln $\lvert\Sigma\rvert$	−282.89	−83.44		−355.55	−22.40	
χ^2	0.000			0.000		

[a] Only variables whose structure coefficients had an absolute value >0.40 are presented.
[b] Units for density are stems/ha.
*** Significant at $P < 0.001$.

DISCUSSION

SELECTION OF NEST SITES

Potential factors influencing differences in nest-site selection by Hammond's and Pacific-slope Flycatchers in our study area include, for example, a combination of avoidance of competition, different thermoregulatory requirements, and varying responses to predation pressure. When sympatric, the two congeneric flycatcher species appear to use nest sites that differ in vegetation structure and floristics. No other studies have compared the nest sites of these two species where sympatric in a Douglas-fir/hardwood dominated forest. These differences in nest-site selection may be a function of avoidance of competition. Although our study was not designed to test the effects of competition between the two flycatchers, we believe that some competition between the sympatric flycatchers in our study area does occur but does not result in the competitive exclusion of one species by the other. Behavioral interactions observed between both species were evident when territories were being established and during the nesting period (Sakai

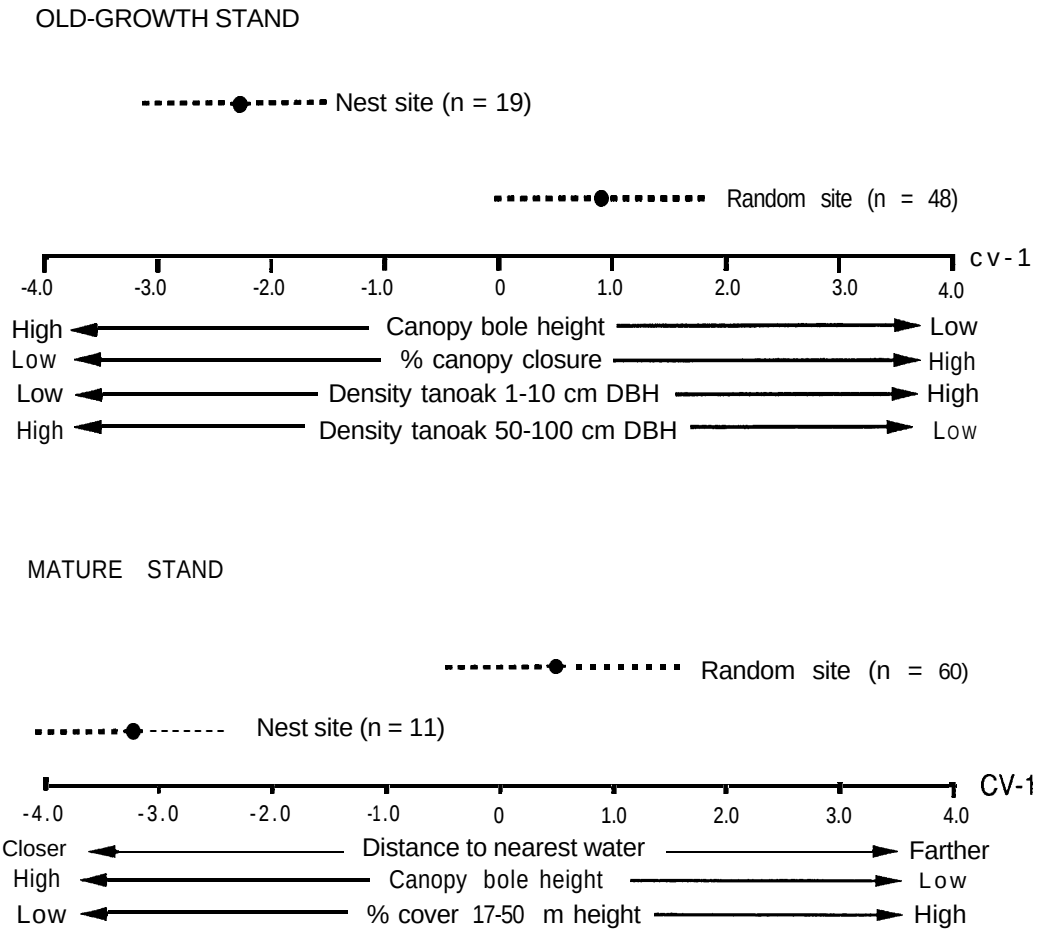

FIGURE 4. Means and 95% confidence intervals of canonical variate (CV) scores and variables which discriminate between Hammond's Flycatcher nest sites and randomly available sites in mature and old-growth forest stands in Douglas-fir/tanoak dominated forests of northwestern California.

1987). This speculation supports Johnson's (1966) comment that competition between Hammond's and Pacific-slope Flycatchers is very likely when they are found in sympatry. Our speculation also supports the statement by Beaver and Baldwin (1975) that each species of flycatcher has a slightly different habitat preference which ultimately affects the coexistence of both species. Differences between the species in our study occurred for nest height, diameter of nest tree, height of nest tree, distance of nest from the bole, nest location, condition of nesting substrate, and amount of foliage cover surrounding the nest.

The orientation of flycatcher nests in our study area differed considerably between species. Our results suggest that Hammond's Flycatchers, but not Pacific-slope Flycatchers, select nest sites in response to environmental factors, possibly solar heat and wind. Selective orientation of nests is generally attributed to thermal influences (McEllin 1979, Inouye et al. 1981, Finch 1983). Hammond's Flycatcher nests were placed midway in live trees, oriented primarily NE and SW, located close to the canopy edge, and concealed by foliage cover. Given these factors, Hammond's Flycatcher nest sites would receive maximum solar heat in the early morning and late afternoon, when temperatures are cooler, and would be relatively shaded from the midday sun. In the summer, prevailing winds in our study area blow from the north and west. The primary orientation of Hammond's Flycatcher nest sites

TABLE 4. Three-group stepwise discriminant analysis of Pacific-slope Flycatcher nest-site characteristics as compared with those of random sites in different seral stages of Douglas-fir/tanoak dominated forests of northwestern California. Group means and standard deviations of variables included in the model are presented.

Variable[a]	Old-growth			Mature			Young		
	Nest site	Random site	Structure coefficient	Nest site	Random site	Structure coefficient	Nest site	Random site	Structure coefficient
Mid-canopy bole height (m)	5.6 (2.2)	9.4 (1.0)	0.806	6.0 (2.0)	8.7 (1.4)	0.762	–	–	
Canopy bole height (m)	16.7 (2.3)	13.1 (1.7)	-0.719	–	–	–	–	–	–
Percent canopy closure	92.2 (5.5)	86.6 (3.8)	-0.557	–	–	–	–	–	–
Density of snag >50 cm DBH and >15 m height	3.7 (4.2)[b]	0.81 (1.9)[b]	-0.451	–	–	–	–	–	–
Percent cover 0-0.5 m height	–	–	–	25.1 (28.9)	11.3 (9.6)	-0.418	–	–	–
Density of Pacific madrone l-10 cm DBH	–	–	–	15.2 (31.0)[b]	3.7 (10.1)[b]	-0.303	–	–	–
Density of Douglas-fir >50 cm DBH	–	–	–	–	–	–	35.0 (26.9)[b]	33.0 (22.0)[b]	-0.604
Density of Pacific madrone >50 cm DBH	–	–	–	–	–	–	1.5 (1.8)[b]	2.1 (2.6)[b]	-0.376
Density of Douglas-fir 10-50 cm DBH	–	–	–	–	–	–	95.7 (134.9)[b]	80.0 (82.9)[b]	0.412
Percent cover 0.5-2 m height	–	–	–	–	–	–	25.9 (12.7)	25.3 (14.7)	-0.322
Sample size	42	48		29	60		17	60	
Wilk's lambda	0.169			0.341			0.267		
Approximate F-statistics	49.854***			19.372***			20.402***		
Cohen's kappa	0.96***			0.80***			0.84***		
ln |Σ|	– 121.95	-85.75		-201.51	-24.31		-312.56	– 122.00	
χ^2	1,718.09***			612.91***			0.000		

[a] Only variables whose structure coefficients had an absolute value >0.40 for old-growth sites and >0.30 for mature and young sites are presented.
[b] Units for density are stems/ha.
*** Significant at $P < 0.001$.

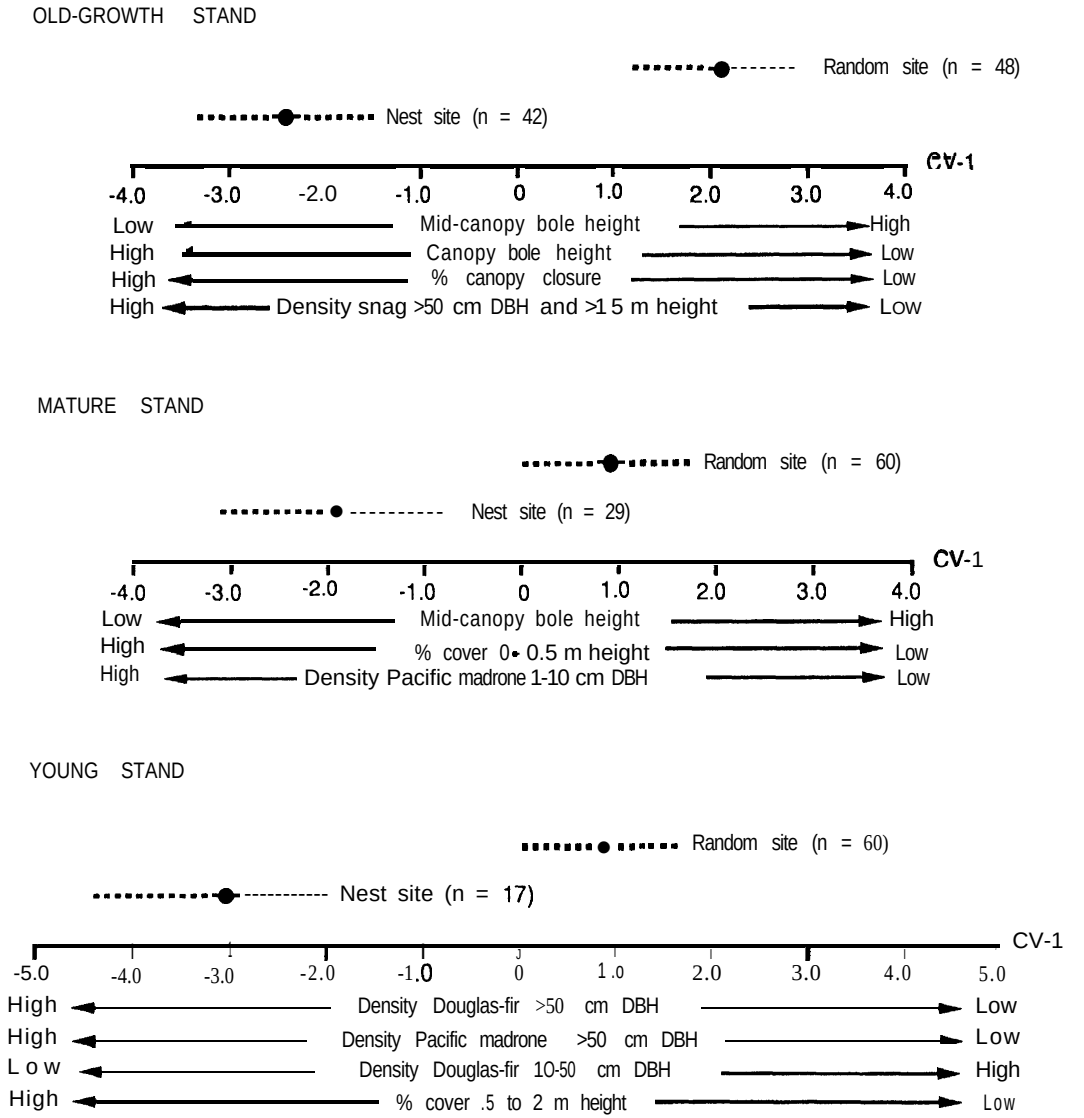

FIGURE 5. Means and 95% confidence intervals of canonical variate scores and variables which discriminate between Pacific-slope Flycatcher nest sites and randomly available sites in young, mature and old-growth forest stands in Douglas-fir/tanoak dominated forests of northwestern California.

faced away from prevailing wind, perhaps aiding thermoregulation. The influences of solar heat on nest placement is further supported by comparing the nesting habits of Hammond's and Pacific-slope Flycatchers. Pacific-slope Flycatchers nested mainly in the subcanopy layer, were catholic in their choice of nest sites and plant species, and showed no selection in terms of nest orientation.

Another explanation for Hammond's Flycatchers' nest-site specificity is concealment from predators. Eastern Kingbird (*Tyrannus tyrannus*) nests placed at mid-heights in the tree, midway between the center of the tree and canopy edge, and with higher vegetation cover around the nest had a higher nest success (Murphy 1983). Hammond's Flycatcher selected nest sites in similar conditions, perhaps to avoid predators such as Steller's Jays (*Cyanocitta stelleri)* which were common in our study areas (Sakai 1988). There-

fore, we speculate that a combination of predator avoidance, avoidance of competition, and thermoregulation may be a plausible explanation for selection of nest sites by Hammond's Flycatcher in our study area.

Most species of birds are not restricted to a particular type of nesting substrate. Species with general nest requirements include Pacific-slope Flycatchers (Bent 1942:248, Davis et al. 1963: 351, and this study), House Sparrows *(Passer domesticus)* (Welty 1975:27l), Western Wood-Pewee *(Contopus sordidulus)* (Bent 1942:280), and others. However, bird species that rely on tree cavities often prefer large snags and are thus more site-specific, e.g., woodpeckers (Mannan et al. 1980, Raphael and White 1984). In our study area Hammond's Flycatchers were significantly more selective than Pacific-slope Flycatchers in the size of their nest trees. All Hammond's Flycatcher nests located were found in live, tall, and large-diameter trees. The difference in abundance or presence of live, tall, and large-diameter trees like Douglas-firs, white firs, and tanoaks in northwestern California may account for the absence of Hammond's Flycatchers in younger stands.

WITHIN AGE-CLASS PATTERN OF NEST-SITE SELECTION

Although Mannan's study area in northeastern Oregon differed in vegetation composition from our study area, some patterns of nest-site selection for 11 Hammond's Flycatcher nests that he reported were similar to those in our study. Mannan (1984) reported Hammond's Flycatchers selecting nest sites with fewer understory trees, and overstory trees with large, well-developed canopies. In our study area, Hammond's Flycatchers selected as nest sites the taller, larger-diameter trees with open canopies, higher mid-canopies, and high canopy bole height. Other variables such as fewer numbers of small tanoaks in old-growth nest sites, and nests found closer to water in mature stands also distinguished Hammond's Flycatchers' nest sites from random sites.

Pacific-slope Flycatchers were found to use a diversity of nest sites, in agreement with other studies (Bent 1942, Johnson 1980). Past accounts of Pacific-slope Flycatcher breeding habitat suggest that nearby water is an important component in selection of nest sites (Bent 1942:247, Johnson 1980:9). Our analyses did not select distance to water as a discriminating variable between nest and random sites. In contrast, we computed average distances of more than 100 m from water for 88 Pacific-slope Flycatcher nests representing all three seral stages. As found in other studies of temperate bird species (MacArthur and MacArthur 1961, Wiens 1969, Anderson and Shugart 1974, Whitmore 1977, Noon 1981, Sabo and Holmes 1983), our analyses indicate that structural characteristics (e.g., canopy closure) strongly influenced habitat selection.

Comparing species occurrence and nest-site selection patterns across seral stages allowed us to identify the Hammond's Flycatcher as a species likely to be negatively affected by the conversion of mature and old-growth stands in younger age classes. Within mature and old-growth stands, the Hammond's Flycatcher showed greater nest-site specialization, particularly in live trees, than the Pacific-slope Flycatcher. Thus, even in the absence of stand conversion, the Hammond's Flycatcher may be more sensitive to human-induced disturbance of these seral stages. Based on our findings, if old-growth Douglas-fir/tanoak forests are greatly disturbed, reduced or eliminated in northwestern California, we predict the density of breeding Hammond's Flycatchers will decrease substantially. We further speculate that leaving clearings with scattered large, old Douglas-fir/hardwood trees will not benefit Hammond's Flycatchers, but probably will benefit Dusky-Flycatchers *(E. oberholseri).* Intact older stands, probably no smaller than 15 ha, will be of greater benefit for Hammond's Flycatchers than stands with openings having scattered large trees. However, Pacific-slope Flycatchers, being less selective in locating their nest sites, would probably be less affected by the conversion of old-growth forests to younger-age classes.

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