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VARIATION IN THE FORAGING BEHAVIORS OF TWO FLYCATCHERS: ASSOCIATIONS WITH STAGE OF THE BREEDING CYCLE

HOWARD F. SAKAI AND BARRY R. NOON

Abstract. The foraging characteristics of Hammond's and Western flycatchers in northwestern California varied with different stages of the breeding cycle during the breeding seasons (early April–mid August) in 1984 and 1985. The species' behaviors did not always vary in parallel nor were all foraging behaviors distributed equally during the breeding cycle. For example, the direction of aerial foraging movements for both species did not differ between stages. In contrast, the predominant type of foraging activity (either hover-glean or flycatch) differed by stage of the breeding cycle for Western Flycatchers but not for Hammond's Flycatchers. Both birds differed in their use of foraging substrates and plant species among breeding stages. Western Flycatchers did not differ in position (height of foraging bird or distance to the canopy edge) among stages of the breeding cycle, but Hammond's Flycatchers did. Both species foraged in trees with different structural characteristics (diameter-at-breast height, tree height, and bole height) during different stages of the breeding cycle. For both species, differences in foraging patterns within specific stages of the breeding cycle were apparent when compared with data pooled across the breeding stages. Failure to partition the data by stage of the breeding cycle may mask significant sources of variation and preclude important insights into a species' breeding biology.

Key Words: Hammond's Flycatcher; Western Flycatcher; breeding cycle; foraging behavior; northwestern California.

Most studies of avian foraging behavior have estimated foraging patterns by pooling observations within a season even though a species' foraging behaviors may change seasonally. Pooling data may thus mask significant variation, as noted by several authors (Busby and Sealy 1979, Sherry 1979).

Our study of Hammond's (*Empidonax hammondii*) and Western (*E. difficilis*) flycatchers allowed us to test whether tree species selection, forage substrate characteristics, and the overall distribution of foraging behaviors were associated with specific stages of the breeding cycle. Because both Western and Hammond's flycatchers are sexually monomorphic, we were unable to test for intersexual effects which may also provide a significant source of variation. Our objectives are to: (1) test the hypothesis of no difference in the distribution of foraging behaviors between stages of the breeding cycle separately by species; (2) compare our estimates of foraging patterns based on specific stages of breeding cycle with data pooled across the breeding cycle; (3) discuss the insights that arise from information on the within-season variation in foraging pattern; and (4) compare our results with other studies that have ignored sources of variation associated with stage of the breeding cycle.

METHODS

STUDY STANDS

Nine stands, selected to provide three replicates of each combination of three forest development stages (young, mature, and old-growth), were located in Humboldt and Trinity counties of northwestern California (refer to Sakai 1987 for specific details). A young stand was defined as 30–90 years, mature 91–199 years, and old-growth >200 years. Stand age was determined from increment cores of 4–6 dominant Douglas-firs (*Pseudotsuga menziesii*) or by counting annual rings of Douglas-fir stumps found in adjacent clearcuts. The stands were dominated by Douglas-fir and tanoak (*Lithocarpus densiflora*). Pacific madrone (*Arbutus menziesii*) and canyon liveoak (*Quercus chrysophylla*) were the associated hardwoods and incense-cedar (*Calocedrus decurrens*), sugar pine (*Pinus lambertiana*), and whitefir (*Abies concolor*) the associated softwoods.

Study plots ranged in size from 12 to 20 ha and in elevation from 710 to 1235 m. The 12 ha stand contained one transect. The 20 ha plots were rectangular and contained two transects. Located along each transect were six evenly spaced bird census sampling points. These points, located 150 m apart, defined the center of circular plots, which subsequently became the focus for the vegatation and foraging sampling.

FORAGING SAMPLES

To compare variation in foraging behaviors associated with each stage of the breeding cycle across the entire range of habitats occupied by the species in the forests of northwestern California, we pooled data for each species across all study plots. Sakai (1987) discussed, in detail, the association between variation in stand age and vegetation with variation in species' foraging behaviors. In general, he found that variation in foraging behaviors paralleled changes in vegetation structure and floristics associated with stands of varying ages.

Data were collected during the breeding seasons (early April–mid August) in 1984 and 1985. Four observers (HFS plus three others) and two observers (HFS plus one other) were involved in data collection in 1984

TABLE 1. FREQUENCY OF FORAGING BEHAVIORS OBSERVED FOR HAMMOND'S AND WESTERN FLYCATCHERS BY STAGE OF THE BREEDING CYCLE FOR THE THREE STAND AGE GROUPS, NORTHWESTERN CALIFORNIA

Stage of the breeding cycle	Stand age		
	Young	Mature	Old-growth
	Western Flycatcher		
Pre-incubation	27	47	71
Incubation	54	88	116
Brooding	61	99	131
Post-brooding	54	118	119
	Hammond's Flycatcher		
Pre-incubation	[a]	23	19
Incubation		45	96
Brooding		43	97
Post-brooding		50	57

[a] Did not occur.

and 1985, respectively. In this analysis we pooled data across observers and years as well as study stands. We acknowledge that these factors may contribute additional variation. However, partitioning our data by these additional factors would have greatly reduced the power of our analyses and, for the log-linear analyses, produced more cells than data points. We believe that pooling our data across years was justified because the environmental conditions both years were very similar. This is exemplified by almost identical arrival times for the birds and consistent timing of the breeding stages (Sakai 1988). Pooling across observers was justified on the basis of rigorous training as well as frequent monitoring of observers throughout the period of data collection by the senior author.

Study stands were sampled equally, in terms of visits to each stand, along the bird census transects out to 30 m on either side, in an attempt to obtain 35 foraging birds/flycatcher species/stand/sampling period. Sampling periods for both species were divided into pre-incubation (10 April to 15 May), incubation (16 May to 15 June), brooding (16 June to 15 July), and post-brooding (16 July to 15 August). Despite some individual differences in the timing of the nesting cycle, the populations' nesting behaviors were highly synchronous (Sakai 1988). The dates bounding the periods were chosen such that the majority of the nests were at the same stage of the breeding cycle. Given the degree of synchrony, we feel justified in partitioning the foraging observations by the stage of the species' breeding cycles. Sample sizes for each species by stage of the breeding cycle and stand age are given in Table 1. Hammond's Flycatchers were not found in the younger stands.

Foraging behaviors were recorded from sunrise to late afternoon. The behavior of each flycatcher was recorded from its initial contact for 10–100 s. Once a foraging bird was located, information was taken on its behavior, position in the habitat, and characteristics of the forage substrate (see Table 2). When a bird foraged at more than one location within 100 s, we analyzed only the initial observation. Usually only one observation per individual per day was obtained, but sometimes two were taken on the same individual after 10 min had elapsed. Estimates of specific foraging variables as well as distance and direction of aerial flight movements (Table 2) were collected at those points where a prey was captured. Samples used in individual analyses varied because some data were collected on non-foraging birds (Table 3).

STATISTICAL ANALYSES

The foraging observations of each species could be classified by: stage of the breeding cycle (pre-incubation, incubation, brooding, post-brooding), behavior (flycatch, hover-glean, glean), aerial flight movement (up, down, horizontal), tree species (Douglas-fir, tanoak, Pacific madrone, and other broad-leaf deciduous trees), and substrate (leaf, twig and small branch, medium and large branch, and trunk). The result is a 4 × 3 × 3 × 4 × 4 contingency table with 586 cells. Because (1) this number of cells exceeded our sample size, (2) the expected values within a cell should be >1, and (3) no more than 20% of the cells should have expected values <5 (Cochran 1954), the size of our contingency table had to be reduced to 3-way tables of breeding cycle by tree species by substrate. We used log-linear analyses to examine the interactions among these variables (Bishop et al. 1975). We viewed breeding stage as an explanatory variable and tree species and substrate as response variables. The simplest models that fit the observed data and chi-square test statistics were estimated by algorithms in BMDP program 4F (Dixon et al. 1985).

Tests of the null hypothesis between stage of the breeding cycle and the variables behavior and aerial flight movement were tested by 2-way contingency tables (Sokal and Rohlf 1981:731). By conducting these tests separately from the log-linear analyses we were unable to test for significant interactions between these variables and plant species and substrate. Chi-square values were considered significant at $P < 0.05$. Graphic starplots (Gower and Digby 1981) were used for visual comparisons, by stage of the breeding cycle, of the direction and distance flown by foraging birds that successfully captured prey.

The structural characterisitics of the tree in which the bird was foraging and the bird's position (Table 2) were analyzed separately using MANOVA computed using BMDP program 7M (Dixon et al. 1985), with stage of the breeding cycle as the grouping variable. Each MANOVA tested the null hypothesis of equality of the breeding stage centroids (i.e., multivariate means). The relative contributions of the original variables to separation of the stages were based on the magnitude of structure coefficients, which are simple bivariate correlations between the original variables and the canonical variates. Along a canonical variate axis or in a ≥ 2-dimensional canonical space, the origin represents the multivariate mean (centroid) of the pooled sample. To determine whether the sample partitioned by stage of the breeding cycle differs from the pooled sample, one simply needs to determine whether the 95% confidence ellipses about stage centroids overlap a similar ellipse surrounding the origin. If a significant MANOVA resulted, all possible pairwise combinations of stage specific centroids were tested for equality. These a posteriori comparisons were adjusted to maintain an overall experimentwise error rate of $P \leq 0.05$.

TABLE 2. Foraging Variables Recorded for Hammond's and Western Flycatchers in Northwestern California During the Breeding Seasons in 1984 and 1985

Variable	Explanation
Tree species	Tree species in which bird was foraging
Height of foraging bird	Estimate to nearest 1 m. Clinometer used to check estimates
Bird location on forage branch	Estimate to the nearest $\frac{1}{10}$ m of birds' location from the canopy edge
Diameter-at-breast height (dbh) of foraged tree	Measured diameter in cm at 1.1 m height from tree base
Tree height	Estimate to nearest 1 m from ground. Clinometer used to check estimates
Bole height	Estimate to nearest 1 m from ground of first live branch
Types of foraged substrates	Items to which birds direct attention: twigs, <1 cm diameter small branches, 1–5 cm diameter medium branches, 5–15 cm diameter large branches, >15 cm diameter trunks
Distance to prey	Estimate to $\frac{1}{10}$ m from perched bird to prey capture
Foraging behavior	Behaviors such as: flycatch (pursuit of aerial prey) hover-glean (removal of stationary prey while in flight) glean (removal of prey from substrate while perched)
Aerial flight movements	Direction of initial flight from perch (down, up, and horizontal)

RESULTS

Prey Capture and Foraging Activity

The direction of aerial flight movements made in pursuit of prey differed between stages of the breeding cycle in Hammond's (χ^2 = 15.3, df = 6, P = 0.018; Fig. 1a) and Western flycatchers (χ^2 = 16.1, df = 6, P = 0.013). Aerial attack movements of the two species within each stage of the breeding season suggested that both species had almost identical distributions (Fig. 1a). In addition, a comparison of starplots suggested that horizontal attack flights by both species were favored during the pre-incubation and incubation periods, but both birds used vertical attack flights more frequently later in the breeding cycle. There was also an inverse relationship between the proportion of attacks or aerial flight movements in a particular direction and the distance traveled in that same direction to obtain prey (Fig. 1b). We found a significant correlation for Western Flycatchers (r = −0.61, df = 10, P = 0.035), and a marginally significant correlation for Hammond's Flycatchers (r = −0.55, df = 10, P = 0.064). Collectively, the foraging movements of both species suggest that the shortest distance to prey was generally the favored aerial flight direction in all breeding stages (Fig. 1).

Both species gleaned insects from leaves and woody substrates, but too rarely (<2% of the observations) to be included in the contingency analysis. Use of a particular foraging maneuver (either hover-glean or flycatch) by Western Flycatchers differed by stage of the breeding cycle (Table 4). Western Flycatchers hover-gleaned more than expected during the pre-incubation and incubation periods, but flycatched appreciably more than expected during periods with young in nests (χ^2 = 19.9, df = 3, P < 0.01). Hammond's Flycatchers did not differ in use of hover-glean and flycatch activities between the different stages of the breeding cycle (Table 4).

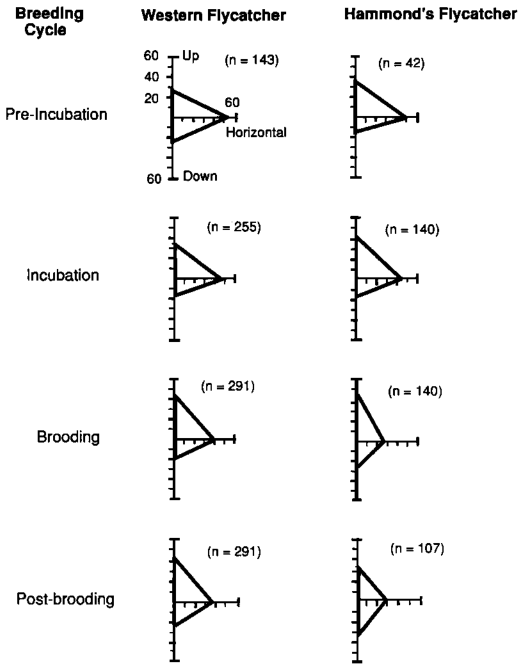
Variation in Plant Species and Substrate Use

For both the Western Flycatcher and the Hammond's Flycatcher, the only log-linear model that

TABLE 3. Range of Sample Sizes Used in Analyses of Western and Hammond's Flycatchers Foraging Behavior by Stage of the Breeding Cycle, Northwestern California

	Stage of breeding cycle			
Species	Pre-incubation	Incubation	Brooding	Post-brooding
Western Flycatcher	120–140	226–255	219–284	228–281
Hammond's Flycatcher	32–40	110–133	95–133	78–100

(a)
Aerial Flight Movement (%)



(b)
Distance to Prey Capture (m)

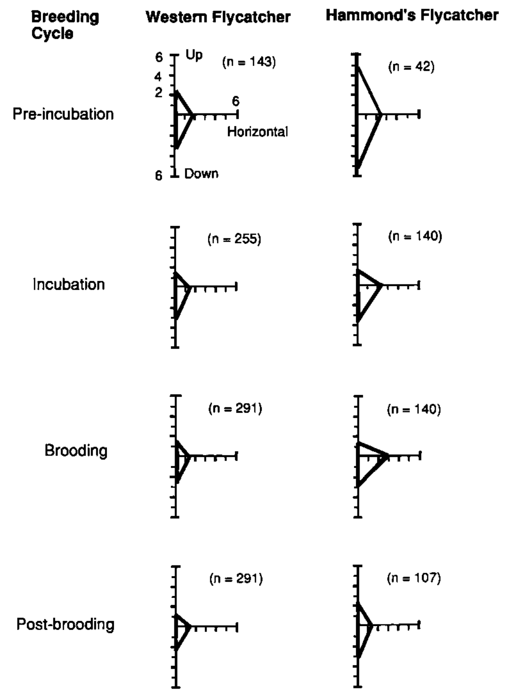


FIGURE 1. Percent of prey attacks (a) and the average distance flown (b) in each of three directions for Western and Hammond's flycatchers by stage of the breeding cycle in northwestern California. The direction of aerial flight movements made in pursuit of prey did not differ between stages of the breeding cycle by Hammond's ($\chi^2 = 15.3$, df = 6, $0.01 < P < 0.025$) or Western ($\chi^2 = 16.1$, df = 6, $0.01 < P < 0.025$) flycatchers.

←

adequately fit the observed data was one containing the 3-factor interaction term. Tests of the null hypothesis that the 3-way interaction term equaled zero were rejected with $P < 0.01$ for both species. Thus, the degree of association between any pair of variables (breeding stage, tree species, use of forage substrates) depended on the specified level of the third variable (Table 5). Given this result, we did not attempt to fit any simpler models (see Sokal and Rohlf 1981:749), but rather made separate 2-way tests of independence for the association between breeding stage and plant species and between breeding stage and foraging substrate.

The two flycatcher species differed in the type of foraging substrates used at different stages of the breeding cycle (Fig. 2). During pre-incubation, Hammond's Flycatchers foraged more on leaf surfaces, switched to greater use of air during incubation and brooding, and showed a slight tendency to use woody substrates more during brooding and post-brooding ($\chi^2 = 24.2$, df = 9, $P < 0.01$). In contrast, during the pre-incubation and incubation periods, Western Flycatchers foraged more from leaf surfaces, switched to foraging more in air during brooding, and used small branches and twigs more than expected during post-brooding ($\chi^2 = 39.8$, df = 12, $P < 0.01$).

Both species also used different foraging plant species during different stages of the breeding cycle (Fig. 3). Both Western and Hammond's flycatchers shifted from extensive use of Douglas-fir in early breeding cycle stages to heavy use of tanoak and Pacific madrone in later stages. During the post-brooding period, Western Flycatchers used Douglas-fir much less than expected (and much less than in the previous three stages) and used other tree species, such as tanoak and Pacific madrone, more than expected ($\chi^2 = 70.7$, df = 8, $P < 0.01$). Further insights are precluded because differences in the breeding stage distributions are complex. During the pre-incubation and incubation periods, Hammond's Flycatchers used Douglas-fir more than expected, and used other tree species, such as tanoak and Pacific madrone, less than expected ($\chi^2 = 41.6$, df = 9, $P < 0.01$). However, during the later breeding stages (brooding and post-brood-

TABLE 4. NUMBER OF FORAGING BEHAVIORS OBSERVED BY STAGE OF THE BREEDING CYCLE FOR HAMMOND'S AND WESTERN FLYCATCHERS IN NORTHWESTERN CALIFORNIA

Bird species	Foraging behavior	Pre-incubation	Incubation	Brooding	Post-brooding
Hammond's Flycatcher	Flycatch	10	45	47	20
	Hover–glean	32	93	90	87
	Glean	0	2	3	0
Western Flycatcher	Flycatch	17	38	80	53
	Hover–glean	121	213	210	234
	Glean	4	4	1	4

ing periods), Hammond's Flycatchers used tanoak more than expected with less than expected use of the other tree species.

The shift in plant species use was associated with a change from the predominant use of overstory vegetation (dominated by Douglas-fir) early in breeding to increased use of the understory strata (dominated by various hardwood species) later. Thus, the change in the pattern of plant species used for foraging is reflected by a corresponding shift in the vertical distribution of foraging bouts (Fig. 4).

VARIATION IN FORAGING POSITION

The position of Western Flycatchers did not differ by height of foraging or distance to the canopy edge during the various stages of the breeding cycle (Fig. 5). Considering these variables simultaneously in a discriminant model, we also failed to detect significant separation by breeding stage. However, the position of Hammond's Flycatchers in the canopy during the post-brooding stage differed significantly from their positions during all other stages (MANOVA, $F = 10.1$, df = 2,401, $P < 0.01$; Fig. 6). All other pairwise comparisons of Hammond's Flycatchers position by breeding stage, except for the pre-incubation–incubation comparison, were significantly different. According to structure coefficients, variation in the heights of foraging birds contributed most to the observed differences in Hammond's Flycatchers position between stages of the breeding cycle.

VARIATION IN FORAGE TREE STRUCTURE

We detected significant differences in the use of structural characteristics of trees during different stages of the breeding cycle for both species. The structural characteristics of trees selected by Western Flycatchers during post-brooding differed significantly from those used during the pre-incubation and incubation stages (MANOVA, $F = 9.5$, df = 2,788, $P < 0.01$; Fig. 7). All other comparisons between stages were non-significant. Based on the structure coefficients, tree height and diameter of the forage tree were equally important to Western Flycatchers in their selection of forage trees during different stages of the breeding cycle.

Hammond's Flycatchers tended to use trees with very different structural characteristics during the post-brooding and brooding periods than they did during the pre-incubation and incubation periods (MANOVA, $F = 13.2$, df = 2,310, $P < 0.01$; Fig. 8). All other comparisons between different stages were nonsignificant. Based on the structure coefficients, tree diameter and height were equally important to the separation of

TABLE 5. THE CHOSEN LOG-LINEAR MODELS FOR TREE SPECIES AND SUBSTRATE FOR THE WESTERN AND HAMMOND'S FLYCATCHERS

Western Flycatcher:

$\ln X_{ijk} = \mu + S_i + T_j + I_k + ST_{ij} + SI_{ik} + TI_{jk} + STI_{ijk}$

Hammond's Flycatcher:

$\ln X_{ijk} = \mu + S_i + T_j + I_k + ST_{ij} + SI_{ik} + TI_{jk} + STI_{ijk}$

Parameters:

μ = mean of the logarithm of the expected cell frequencies
S_i = breeding stage $i = 1, 2, 3, 4$
T_j = tree species $j = 1, 2, 3, 4$
I_k = substrate $k = 1, 2, 3$
X_{ijk} = expected cell in frequency in the ijk^{th} cell

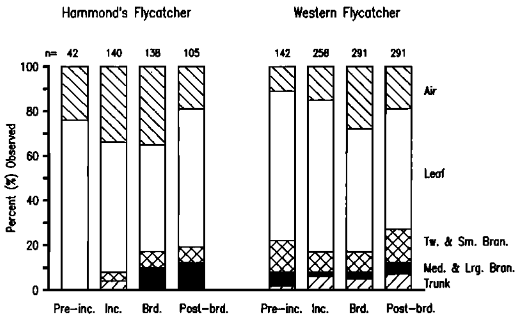


FIGURE 2. Percent of substrates used by foraging Western and Hammond's flycatchers for each of the four stages of the breeding cycle in northwestern California. Breeding cycle codes are: Pre-inc. = pre-incubation period, Inc. = incubation period, Brd. = brooding period, and Post-brd. = post-brooding period.

Hammond's Flycatcher forage tree characteristics by breeding stage.

COMPARISONS WITH POOLED BREEDING CYCLE DATA

Differences in foraging pattern for each species were apparent when patterns based on specific stages of the breeding cycle were compared with data pooled across the breeding stages. For the categorical data these comparisons are indirect. From the log-linear analyses we found that the variables tree species and substrate were significantly associated with stage of the breeding cycle. Also, removal of the variable categorizing breeding stage cycle caused a significant lack of fit of observed to expected values for both species. In addition, the two-way contingency analyses detected significant associations between stage of the breeding cycle and the distribution of other aspects of foraging behavior for almost all analyses.

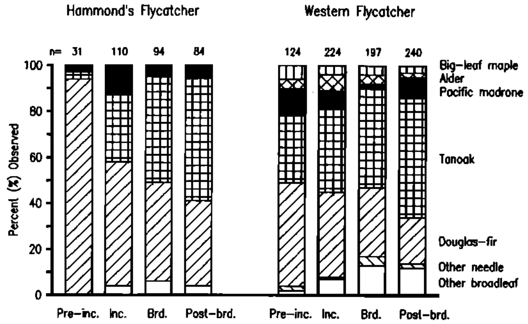


FIGURE 3. Percent of plants used by foraging Western and Hammond's flycatchers for each of the four stages of the breeding cycle in northwestern California. Breeding cycle codes are: Pre-inc. = pre-incubation period, Inc. = incubation period, Brd. = brooding period, and Post-brd. = post-brooding period.

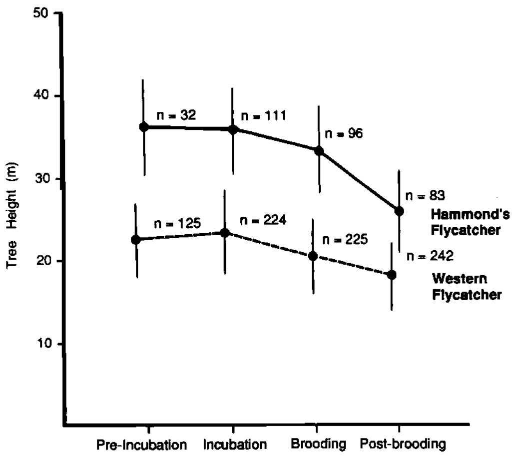


FIGURE 4. Mean tree height used by foraging Western and Hammond's flycatchers for each of the four stages of the breeding cycle in northwestern California. Ninety-five percent confidence intervals are shown.

For the continuous variables, comparisons with the pooled sample can be illustrated graphically. The mean foraging position within trees for Hammond's Flycatchers differed significantly among pre-incubation, incubation, and post-brooding periods. All stages, except for the brooding period, differed significantly from the

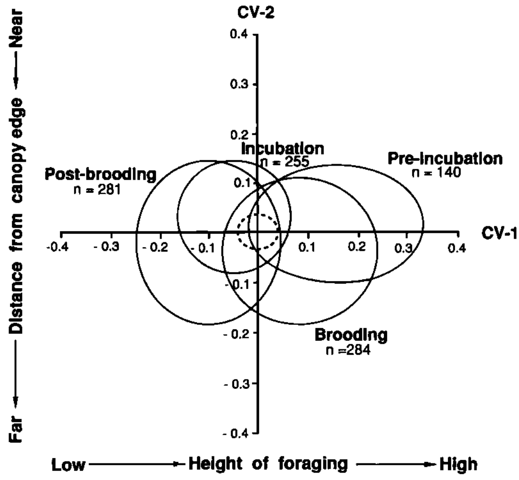


FIGURE 5. Mean canonical variate scores characterizing Western Flycatchers' position in the forage trees for each of the four stages of the breeding cycle in northwestern California. The canonical variate represents variation in the height of the foraging bird. Ninety-five percent confidence intervals are shown.

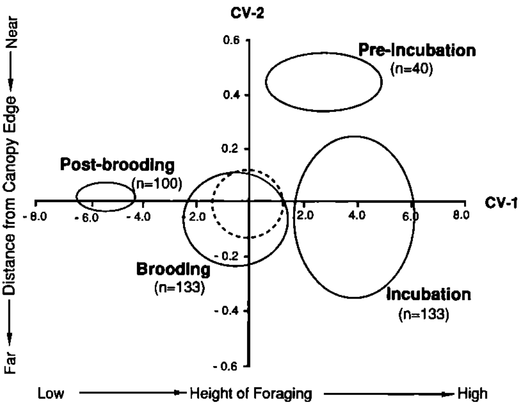


FIGURE 6. Mean canonical variate scores characterizing Hammond's Flycatchers' position in the forage trees for each of the four stages of the breeding cycle in northwestern California. CV-1 represents variation in the height of the foraging bird, CV-2 variation in distance from the canopy edge. Ninety-five percent confidence ellipses are shown.

centroid of the pooled sample (Fig. 6). In contrast, the mean foraging position of Western Flycatchers within trees did not differ among stages of the breeding cycle, nor did these means differ from data pooled across the breeding stages (confidence intervals around canonical variate scores all overlapped with the confidence ellipse around the origin, Fig. 5).

The structural characteristics of trees used by Hammond's Flycatchers differed significantly from early to late stages and all stages differed significantly from the pooled sample centroid (Fig. 8). Structural features of trees used by Western Flycatchers were significantly distinct in the post-brooding stage. In addition, the positions of the pre-incubation, incubation, and post-brooding periods differed significantly from the pooled sample centroid (Fig. 7).

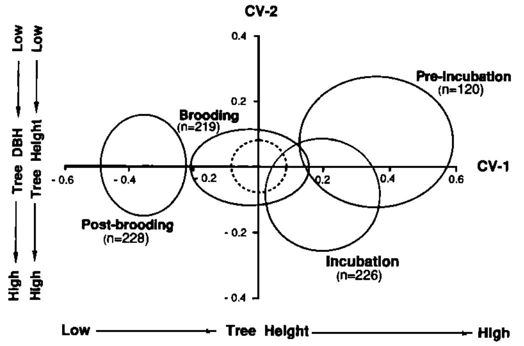


FIGURE 7. Mean canonical variate scores characterizing the structural characteristics of the forage trees used by Western Flycatchers during four stages of the breeding cycle in northwestern California. CV-1 represents variation in tree height, CV-2 variation in tree dbh and tree height. Ninety-five percent confidence ellipses are shown.

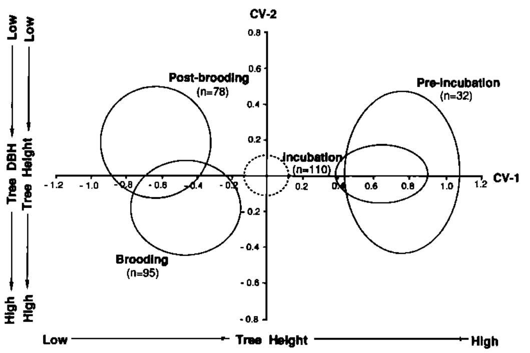


FIGURE 8. Mean canonical variate scores characterizing the structural characteristics of the forage trees used by Hammond's Flycatchers during four stages of the breeding cycle in northwestern California. CV-1 represents variation in tree height, CV-2 variation in tree dbh and tree height. Ninety-five percent confidence ellipses are shown.

DISCUSSION

EFFECTS OF POOLING DATA ACROSS THE BREEDING CYCLE

Because foraging behaviors vary significantly between stages of the breeding cycle, pooling data across the breeding stages may mask significant variation in foraging behavior. Intraspecific variation in foraging behaviors between sexes or between seasons is well known. And our research has shown that variation associated with stage of the breeding cycle may also be pronounced (see also Brennan and Morrison, this volume). As a result, partitioning of a species' foraging niche by sex or season is essential to increase our understanding of its life history.

Pooling data may be justified for some variables. For example, Hammond's and Western flycatchers direction of flight movements by stage of the life cycle did not vary significantly between breeding stages; therefore, pooling the data would not have changed our inferences. In contrast, comparison of bird position (height in tree and distance to the canopy edge) showed no difference between pooled data and stages of the life cycle for Western Flycatchers but did for Hammond's Flycatchers. Further, both species showed evidence of significant changes in the use of tree structural characteristics when the data were compared by stage of the life cycle. We conclude that whenever sample size is adequate, analysis by stage of the breeding cycle should be carried out.

HETEROGENEITY OF FORAGING BEHAVIORS WITHIN THE BREEDING CYCLE

For both Western and Hammond's flycatchers, direction of foraging movements while pursuing prey was not related to stage of the breeding cycle. However, for both species the shortest distance to prey was generally the favored flight movement direction in all breeding stages. Because nearby prey are easier to detect and require less energy to capture, on average, this is not surprising and explains the inverse relationship between attack frequency and attack distance.

Note that this consistent relationship between aerial flight movement and distance occurred in the context of an otherwise variable foraging repertoire, with both species changing aspects of their distribution of foraging behaviors (positions within the forage trees, frequency of use of different tree species, tendency to forage lower) as the breeding cycle progressed. We speculate that these changes were due to changes in prey availability, as reflected in the inverse relationship of vector movement and distance to prey.

Western and Hammond's flycatchers differed intraspecifically in foraging activity and substrate use throughout their breeding cycles, but both species essentially used the same substrates during the same stages of the breeding cycle. Overall, the variation in forage activity, substrate use, and vertical distribution by the flycatchers suggests differences in their food resources throughout the breeding cycle. Both species hover-gleaned off leaves more often during the early breeding stages and switched later to flycatching insects from the air or gleaning off woody substrates.

Hammond's Flycatchers consistently selected taller trees and foraged higher in the canopy and subcanopy than Western Flycatchers. However, both species were similar in that they used Douglas-fir more in the early stages of the breeding cycle and tanoak and Pacific madrone in the later stages. Douglas-fir, tanoak, and Pacific madrone, the most common tree species in the study areas, had a high insect density (Sakai 1987). Even assuming a strong relationship between plant species and their associated arthropods, we can not determine if shifts in utilized plant species were caused by within-season shifts in prey availability or by necessary dietary changes.

Changes in use of tree species for foraging in our study area could also be associated with differences in the tree structural characteristics as Robinson and Holmes (1982, 1984) found in New Hampshire, or the amount of air-space available for flycatching (Sakai 1987), since these factors ultimately influence the foraging opportunities and the bird's position in the vegetation. The primary causes for the stage-specific changes in foraging cannot be determined from our data set. However, the simplest explanation is that the observed differences occurred as a result of within-season changes in prey availability coupled with a need to maintain high foraging efficiency.

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