

# DIURNAL, INTRASEASONAL, AND INTERSEXUAL VARIATION IN FORAGING BEHAVIOR OF THE COMMON YELLOWTHROAT<sup>1</sup>

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**Abstract.** Foraging characteristics of breeding Common Yellowthroats (*Geothlypis trichas sinuosa*) on the central California coast varied between early morning and midday periods, among periods within the nesting season, and between sexes. From early morning to midday, yellowthroats increased their use of vegetation at heights below 1 m and above 3 m, but reduced their use of vegetation at heights of 2-3 m. A midseason increase in the use of vegetation at heights above 3 m occurred after 3 May. Male yellowthroats foraged at significantly greater heights, on average, were more likely to choose flycatching over other maneuvers, and were possibly better adapted, morphologically and behaviorally, to exploit spatiotemporal changes in prey abundance than were females. Singing males occurred at greater heights, on average, than either foraging males or females, but did not differ from foraging birds in their use of substrates or plant species. We evaluated the use of plant species for foraging in comparison with availability within 10 m of foraging individuals and over the entire study area, and found significant diurnal and intraseasonal patterns of selection. Common Yellowthroats actively selected arroyo willow (*Salix lasiolepis*) at both spatial scales of availability during all diurnal and seasonal periods. Use of foraging maneuvers varied intraseasonally but was independent of diurnal period. We found no significant interaction between diurnal and intraseasonal patterns of foraging. Our results suggested that Common Yellowthroats alter their foraging behavior in response to changes in foraging conditions associated with diurnal and intraseasonal dynamics of freshwater marsh ecosystems. Pooling of foraging data over diurnal or intraseasonal periods, or between sexes, may mask significant differences that are important in understanding foraging characteristics.

**Key words:** foraging; habitat selection; niche; diurnal; intraseasonal; Common Yellowthroat; *Geothlypis trichas*.

## INTRODUCTION

Studies of avian foraging behavior have generally pooled data across diurnal periods even though activity patterns, foraging behavior, and availability of prey species can vary among times of day (Verner 1965, Voigts 1973, Holmes et al. 1978, Hutto 1981, Gray 1993). Although researchers have also commonly pooled foraging observations within seasons, some authors have cautioned that such pooling may conceal important sources of foraging variation (Hejl and Verner 1990, Sakai and Noon 1990). Foraging behavior has been shown to vary between sexes in several species (Selander 1966, Holmes 1986, Grub and Woodrey 1990) including some wood warblers (Parulinae; Morse 1968, Morrison 1982; Hanowski and Niemi 1990). Therefore, accounting for diurnal, intraseasonal, and intersexual variation may avoid masking of important behavioral differences and thus improve studies of

avian foraging behavior. Further, comparisons of pooled sets of data should be justified by appropriate sampling of such variation to avoid incorrect interpretations of foraging relationships.

Common Yellowthroats (*Geothlypis trichas*) forage primarily by gleaning (Eckhardt 1979, Hutto 1981), but also use other maneuvers including sally-hover (Eckhardt 1979), sally-strike (on aerial prey and stationary substrates), and flutter-chase of flushed prey (pers. observ.; terminology follows Remsen and Robinson 1990). Hutto (1981) found that feeding activities of Common Yellowthroats are more constrained by midday increases in insect activity than are those of species that sally for aerial insects more frequently, presumably because active (flying) insects are less available to birds that forage primarily by gleaning. In freshwater marshes along the central California coast, water levels decline gradually through spring and summer, and vegetation structure changes with the seasonal growth of perennial and annual plant species. Such habitat changes, along with differences in phenolo-

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gies of terrestrial and aquatic-emergent insect populations, are associated with dramatic spatial and temporal variation in the abundance and distribution of invertebrate prey (Orians and Horn 1969, Voigts 1973, Voigts 1976, Weller 1978, 1986, Orians 1980). Therefore, if Common Yellowthroats forage optimally, they can be expected to vary their use of marsh vegetation and food resources in response to complex conditions that vary over time and space.

Our objectives in this study were to (1) quantify the foraging niche of breeding Common Yellowthroats (*G. t. sinuosa*; Grinnell 1901, Grinnell and Miller 1944) in a coastal freshwater marsh, (2) determine the extent of diurnal, intraseasonal, and intersexual variation in yellowthroat foraging behavior, and (3) compare patterns of foraging substrate use with availability.

## METHODS

### STUDY AREA

The study area was Olema Marsh, a 17.5-ha freshwater marsh at the confluence of Bear Valley Creek and Lagunitas Creek, in Marin County, California. Some brackish water influence existed along the lower (northwest) edge, upland annual grasses bordered the northeast side, and riparian forest dominated by red alder (*Alnus rubra*), arroyo willow (*Salix lasiolepis*), and yellow willow (*Salix lasiandra*) bordered the southern edges of the marsh. Marsh vegetation was dominated by cattail (*Typha* spp.) and bulrush (*Scirpus* spp.). Scattered arroyo willow thickets covered approximately 9% of the marsh. Together, three open water ponds covered approximately 0.75 ha.

### VEGETATION

To assess the availability of foraging substrates, we measured overall vegetation structure in October of 1990 and 1993 at 146 points spaced at 10-m intervals along four random transects across the marsh. At each point, we measured the height and species of all vegetation that contacted a vertical pvc pole (diam. = 2.65 cm). We also visually estimated the percent cover of each dominant species within a 10-m radius around every third sampling point. As foraging birds move through the environment, the availability of resources should change at each bird location (Raphael and Maurer 1990). Therefore, to further assess foraging habitat available to Common Yellowthroats, we visually estimated the percent

cover of each dominant plant species within a 10-m-radius habitat patch surrounding each foraging individual.

## BIRDS

Foraging data were collected from early morning to mid-afternoon (05:20–14:00, Pacific Standard Time) during the breeding seasons (11 March to 10 June) of 1990, 1992, and 1993. We searched the entire study area for Common Yellowthroats and mapped each individual encountered; the maps were used to ensure even sampling of foraging behaviors across the study area (Beal and Khamis 1990). When a yellowthroat was encountered, we visually followed the individual until a foraging maneuver was observed. Most observations were conducted from portable ladders, 1.6–1.9 m tall, to increase the visibility of birds in the marsh vegetation.

We recorded the following information associated with the moment a foraging maneuver was performed and the specific point where the maneuver was directed: type of foraging maneuver, including glean, aerial glean (sally-hover-glean or sally-strike on stationary substrates), and flycatch (sally on aerial prey or flutter-chase of prey flushed from stationary substrates; Remsen and Robinson 1990); perch and foraging substrates, including twig (diam. < 1 cm), branch (diam. > 1 cm), leaf, air, flower, and floating debris; perch and foraging height above ground (m); perch and foraging plant species; and perch and foraging distance to edge of foliage (m). We collected additional data on singing males that were *not* foraging by recording microhabitat data identical to those collected on foraging individuals but directed at perching rather than foraging substrates. Observations were separated by at least 10 minutes or 10 meters.

Because of sample size limitations, we pooled foraging data across years. Such pooling could bias results by concealing annual differences in foraging behaviors (Miles 1990, Szaro et al. 1990, Schooley 1994). However, we believe pooling across years did not bias our results because (1) breeding season water levels were similar among years (pers. observ.); (2) distribution of dominant plant species cover did not differ significantly between 1990 and 1993 ( $\chi^2 = 0.97$ ,  $df = 2$ ,  $ns$ ); (3) the number of Common Yellowthroat territories was similar among years ( $\chi^2 = 0.14$ ,  $df = 2$ ,  $ns$ ); (4) the timing of first singing males, individuals carrying nest material, and females car-

rying food was similar among years (unpubl. data); and (5) breeding bird communities (Evens and Stallcup 1991, Evens and Stallcup 1993, Evens and Stallcup 1994) were identical in composition and species richness ( $\chi^2 = 0.00$ ,  $df = 2$ ,  $ns$ ), and very similar with regard to relative species abundances among years ( $\chi^2 = 8.19$ ,  $df = 30$ ,  $ns$ ).

We partitioned observations into early morning and midday periods to account for diurnal differences in the relative availabilities of prey species that were likely to result from differences in emergence phenologies of aquatic insects and activity cycles of adult (flying) insects (Taylor 1966, Orians and Horn 1969, Holmes et al. 1978, Orians 1980). We used a chronologically constrained cluster analysis (Legendre et al. 1985) to identify temporal structure in the foraging data. The method requires that foraging observations be contiguous in time to be fused into a cluster. It does this by combining an agglomerative algorithm with tests of group differences and removal of aberrant observations at each step. Chronological clustering identified an overall shift in foraging behavior at approximately 09:30, with a probability of  $< 0.001$  that the resulting early morning and midday groups did not differ.

To examine behavioral responses to within-season differences in prey availability, foraging habitat, and or foraging needs related to breeding cycle, we divided the foraging data into intraseasonal groups. We were not able to identify within-season periods of differing prey availabilities because (1) we did not measure prey abundances or emergence rates, and (2) aquatic emergent insect species exhibit a wide range of within-season emergence phenologies, such that numerous potential peaks in insect emergence staggered throughout the nesting season precluded prediction of intraseasonal availability (Orians 1980; J. Haffernik, L. Serpa, pers. comm.). Further, gradual within-season changes in vegetation did not result in discrete periods of habitat composition or structure (pers. observ.). The breeding cycle of Common Yellowthroats could not be used to identify within-season periods related to foraging needs (Sakai and Noon 1990) because Common Yellowthroats produce multiple broods (Stewart 1953, Hofslund 1959, pers. observ.) and different stages in the breeding cycle occurred simultaneously among nesting pairs (pers. observ.). Therefore, we used temporal structure of the foraging data itself to guide our

investigation of intraseasonal patterns. Chronological clustering (see above) identified early (11 March–3 May), middle (4–27 May), and late (28 May–10 June) intraseasonal foraging periods; probabilities that temporally adjacent groups did not differ were  $< 0.10$  and  $< 0.001$ , respectively.

During the early intraseasonal sampling period, some catkins were still present on the arroyo willows, willow leaves were newly formed (soft), willow canopies were relatively sparse, cattail leaves were  $< 1.5$  m tall, most plant species were not flowering, and fledgling Common Yellowthroats were not observed. During the mid-season period, most willow catkins were gone, *Potentilla anserina* was flowering, *Oenanthe sarmentosa* was beginning to flower, and Common Yellowthroat fledglings and evidence of second broods (birds carrying nest material) were observed. After 27 May, willow canopies were fully developed with dense foliage, willow leaves were more leathery, cattails were 1.5–2.5 m tall, and cattails, *P. anserina*, *O. sarmentosa*, and other forbs were flowering.

#### STATISTICAL ANALYSES

We developed log-linear models (Bishop et al. 1975), using diurnal period and intraseasonal period as explanatory variables to examine temporal patterns in the other variables. Response variables were foraging substrate (leaf, twig, branch, other), foraging species (cattail/bulrush, willow, air, forb), foraging maneuver (glean, aerial glean, flycatch), and foraging height ( $< 1$  m, 1–2 m, 2–3 m,  $> 3$  m). Because expected values within cells should be  $> 1$  and no more than 20% of the cells should have expected values  $< 5$  (Cochran 1954), we were limited to three-way contingency tables that did not include multiple response variables. Therefore, we examined each response variable separately and did not examine relationships among response variables. We pooled use of cattail (85% of pooled category) and bulrush (15%) because of small sample sizes and structural similarity of the plants.

Log-linear models were selected using stepwise procedures to remove all interaction terms that were not significantly different from zero, and choosing the simplest models (fewest interaction terms) that best fit the data ( $P > 0.05$ ). For each chosen model, we estimated the loglinear parameters, or  $u$ -terms, to assess the sign and magnitude of each component of each variable in each interaction term (Bishop et al. 1975); the sign

and magnitude of the  $u$ -terms indicate the direction and importance, respectively, of each effect.

We tested for intersexual differences in foraging behavior and use of perch sites by foraging males and females and singing males by using chi-square values derived from two-way contingency tables. Foraging males were classified as singing males if they sang from the same perch from which they foraged. To reduce unknown sex-related bias in the analysis of temporal differences, and time or period bias in the analysis of intersexual differences, we randomly omitted observations of foraging males or females, or singing males, within diurnal and intraseasonal periods until proportions of each sex class within each cell were as close as possible to the overall proportions in the data (43% foraging males, 23% females, 34% singing males).

We tested for differences between use of foraging substrate species and availability of plant species within a 10-m radius of foraging birds with Wilcoxon's signed-ranks tests. We compared the results of these tests among categories related to sex, diurnal period, and intraseasonal period; sampling distributions among categories of each level were held constant with regard to the other two, as described above. We used  $t$ -tests to evaluate differences between plant species cover within bird-centered foraging areas and (1) overall frequency of each plant species recorded at random sample points in 1993 (1-sample tests) and (2) percent cover within a 10-m radius of random sample points in 1993 (2-sample tests).

## RESULTS

Three-way log-linear interactions involving diurnal and intraseasonal effects on foraging behaviors were not necessary to adequately represent the structure of our data. Therefore, we selected simpler models involving two-way interactions between diurnal or intraseasonal effects and each of the foraging behaviors measured (Table 1).

### FORAGING HEIGHTS

Common Yellowthroats foraged at different heights during different diurnal and intraseasonal periods, as indicated by significant two-way log-linear interactions between foraging height and both diurnal and seasonal period (Table 1). The magnitudes and signs of parameter values suggested that yellowthroats reduced their use of

TABLE 1. Log-linear models selected for foraging height, foraging maneuver, foraging substrate, and foraging substrate species of Common Yellowthroats in coastal freshwater marsh.

Model I: foraging height	
$\ln x_{ijk} = u + D_i + S_j + F_k + DS_{ij} + DF_{ik} + SF_{jk}$	
Likelihood-ratio $\chi^2 = 11.63$ , $df = 6$ , $P = 0.07$	
Model II: foraging substrate species	
$\ln x_{ijk} = u + D_i + S_j + F_k + DF_{ik} + SF_{jk}$	
Likelihood-ratio $\chi^2 = 13.89$ , $df = 8$ , $P = 0.08$	
Model III: foraging maneuver	
$\ln x_{ijk} = u + D_i + S_j + F_k + DS_{ij} + SF_{jk}$	
Likelihood-ratio $\chi^2 = 9.26$ , $df = 6$ , $P = 0.16$	
Model IV: foraging substrate	
$\ln x_{ijk} = u + D_i + S_j + F_k + DF_{ik} + SF_{jk}$	
Likelihood-ratio $\chi^2 = 13.84$ , $df = 8$ , $P = 0.09$	
Parameters	
$D_i$ = diurnal period	$i = 1, 2$
$S_j$ = intraseasonal period	$j = 1, 2, 3$
$F_k$ = foraging effect:	
foraging height	$k = 1, 2, 3, 4$
foraging substrate species	$k = 1, 2, 3, 4$
foraging maneuver	$k = 1, 2, 3$
foraging substrate	$k = 1, 2, 3, 4$
$x_{ijk}$ = expected cell frequency in the $ijk^{\text{th}}$ cell	
$u$ = mean of logarithm of expected cell frequencies	

foraging heights of 2–3 m and increased their use of both lower (0–1 m) and upper (> 3 m) heights from early morning to midday (Figure 1A, Table 2). This vertical stratification of foraging activity was probably not the result of a within-period shift because midday foraging heights were independent of diurnal timing ( $r = 0.13$ ,  $df = 77$ ,  $P > 0.05$ ). Similarly, parameters related to intraseasonal effects on foraging height suggested a midseason increase in foraging above 3 m and below 1 m that was independent of date within the second period ( $r = 0.09$ ,  $df = 225$ ,  $P > 0.05$ ; Fig. 1A, Table 2).

### USE OF PLANT SPECIES

Significant log-linear interaction terms indicated that Common Yellowthroats used plant species differently for foraging between diurnal periods and among intraseasonal periods (Table 1). Parameter values reflected a diurnal pattern of greater use of cattail/bulrush in midday compared to early morning (Fig. 1B, Table 2). Although cattails and bulrushes were not actively selected as foraging sites within habitat patches, yellowthroats foraged in patches with significantly more cattails than generally available in midday but not in early morning (Table 3).

Intraseasonal effects on use of foraging substrate species resulted in greater use of forbs and decreased use of cattail/bulrush and willow after 27 May (Fig. 1B, Table 2). In all intraseasonal

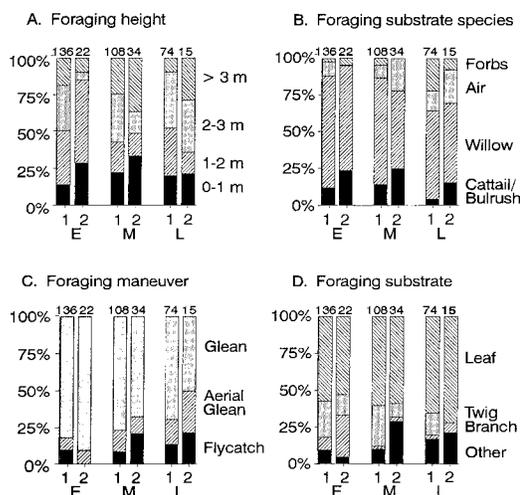


FIGURE 1. Relative frequencies of use of foraging heights, foraging substrate species, foraging maneuvers, and foraging substrates by breeding Common Yellowthroats within (1) early morning and (2) midday diurnal periods and (E) early, (M) middle, and (L) late intraseasonal periods in central California coastal freshwater marsh.

periods, yellowthroats used cattail, bulrush, and forbs in significantly smaller proportions than available in the surrounding habitat patch (Table 3). However, random cover estimates suggested that until late May birds used areas with significantly more cattail cover than generally available in the marsh; random point estimates were not significant (Table 3). These habitat areas were further characterized by significantly fewer bulrushes and forbs than generally available (Table 3).

Foraging Common Yellowthroats actively selected willows at two spatial scales. In all diurnal and intraseasonal periods, yellowthroats consistently used foraging areas with more willows than generally available in the marsh (Table 3). Within those areas, in all diurnal and intraseasonal periods measured, yellowthroats foraged in willows more often than expected.

#### FORAGING MANEUVERS

The use of foraging maneuvers was independent of diurnal period; therefore the interaction term did not enter the model. However, Common Yellowthroats significantly altered their use of foraging maneuvers among intraseasonal periods (Table 1). Parameter values suggested reduced

gleaning as the season progressed, with a concomitant increase in aerial gleaning (Fig. 1C, Table 2).

#### FORAGING SUBSTRATES

Yellowthroats used foraging substrates differently between diurnal periods and among intraseasonal periods (Table 1). Parameter values suggested that birds decreased their use of leaves and twigs, and increased their use of branches and other foraging substrates from early morning to midday. As the season progressed, yellowthroats foraged more frequently on leaves and "other" substrates (included air, flowers, and floating debris), and less frequently on twigs and branches (Fig. 1D, Table 2).

#### INTERSEXUAL DIFFERENCES

Although nonparametric analysis failed to detect a significant association between the sex of foraging Common Yellowthroats and their use of 1-m height intervals ( $\chi^2 = 6.72$ ,  $df = 3$ ,  $P = 0.08$ ), one-way analysis of variance revealed that males foraged at significantly greater heights, on average, than females ( $F = 6.51$ ,  $df = 1, 360$ ,  $P = 0.01$ ). Male Common Yellowthroats generally sang from greater heights than they foraged ( $\chi^2 = 9.58$ ,  $df = 3$ ,  $P = 0.02$ ). Males were also more likely to choose flycatching over other foraging maneuvers than were females (Yates corrected  $\chi^2 = 9.76$ ,  $df = 1$ ,  $P < 0.005$ ), although gleaning represented 72.7% and 84.1% of foraging maneuvers by males and females, respectively. Male and female Common Yellowthroats did not differ with regard to choice of vegetation foraging substrates ( $\chi^2 = 1.65$ ,  $df = 3$ ,  $P = 0.64$ ) or substrate species ( $\chi^2 = 0.35$ ,  $df = 2$ ,  $P = 0.84$ ); singing males did not differ significantly from foraging birds in their overall use of plant species ( $\chi^2 = 0.87$ ,  $df = 2$ ,  $P = 0.65$ ) but were more likely than foraging birds to perch on twigs compared to other substrates (Yates corrected  $\chi^2 = 5.54$ ,  $df = 1$ ,  $P = 0.02$ ).

Common Yellowthroats actively selected willows at two spatial scales for singing as well as foraging. Singing males, foraging males, and foraging females selected habitat areas with more willows than generally available in the marsh (Table 3). Within those areas, singing males, foraging males, and foraging females, each used willows more often than expected by chance (Table 3). Male and female yellowthroats both tended to use forbs in proportions comparable to or less

TABLE 2. Estimated log-linear parameter values (and ratio to their standard errors) for significant interactions involving Common Yellowthroat foraging variables (Table 1).

	Diurnal period			Seasonal period		
	Morning	Midday	Early	Middle	Late	
<b>Model I: Foraging height</b>						
0-1 m	-0.215 (-1.856)	0.215 (1.856)	-0.200 (-1.436)	0.153 (1.159)	0.046 (0.298)	
1-2 m	-0.004 (-0.036)	0.004 (0.036)	0.350 (3.022)	-0.421 (-3.233)	0.071 (0.514)	
2-3 m	0.374 (2.830)	-0.374 (-2.830)	-0.132 (-1.122)	-0.087 (-0.729)	0.219 (1.676)	
> 3 m	-0.155 (-1.297)	0.155 (1.297)	-0.012 (-1.124)	0.354 (2.590)	-0.336 (-1.900)	
<b>Model II: Foraging substrate species</b>						
Cattail/bulrush	-0.371 (-2.373)	0.371 (2.373)	0.401 (2.022)	0.424 (2.192)	-0.825 (-3.255)	
Willow	0.109 (0.850)	-0.109 (-0.850)	0.318 (2.315)	0.003 (0.019)	-0.321 (-2.258)	
Air	-0.199 (-1.171)	0.199 (1.171)	-0.116 (-0.578)	0.023 (0.120)	0.093 (0.467)	
Forbs	0.462 (1.631)	-0.462 (-1.631)	-0.603 (-2.067)	-0.449 (-1.634)	1.052 (4.580)	
<b>Model III: Foraging maneuver</b>						
Glean	- <sup>a</sup>	- <sup>a</sup>	0.309 (2.286)	-0.021 (-0.188)	-0.288 (-2.423)	
Aerial glean	- <sup>a</sup>	- <sup>a</sup>	-0.211 (-1.319)	0.028 (0.186)	0.184 (1.182)	
Flycatch	- <sup>a</sup>	- <sup>a</sup>	-0.097 (-0.584)	-0.007 (-0.044)	0.104 (0.627)	
<b>Model IV: Foraging substrate</b>						
Leaf	0.055 (0.515)	-0.055 (-0.515)	-0.250 (-2.034)	0.091 (0.632)	0.159 (1.048)	
Twig	0.546 (3.140)	-0.546 (-3.140)	0.040 (0.260)	0.312 (1.813)	-0.352 (-1.731)	
Branch	-0.370 (-2.097)	0.370 (2.097)	0.792 (3.223)	-0.613 (-1.831)	-0.179 (-0.531)	
Other	-0.231 (-1.631)	0.231 (1.631)	-0.582 (-3.203)	0.210 (1.132)	0.372 (1.894)	

<sup>a</sup> Interaction term not included in the model.

TABLE 3. Temporal and sex-specific use of dominant plant species as foraging sites and habitat patches (10-m radius around bird) by Common Yellowthroats at Olema Marsh, California. Symbols indicate habitat used significantly more (+) or less (-) than expected by availability ( $P < 0.05$ ); ns = not significantly different from availability ( $P > 0.05$ ).

Sites within patches <sup>a</sup>	Diurnal period				Intraseasonal period			Intersexual group		
	Early morning	Midday	≤3 May	4-27 May	≥28 May	Singing males	Foraging males	Foraging females		
Cattail	-**	ns	-**	-**	-**	-**	-**	-**		
Bulrush	-**	-*	-**	-**	-*	-**	-**	-*		
Willow	+	+	+	+	+	+	+	+		
Forbs	-	-	ns	-*	-	ns	-*	ns		
Patches within Olema Marsh <sup>b</sup>										
Cattail	ns/-*	+/+*	+**/ns	+ /ns	ns/-**	ns/ns	ns/-*	ns/ns		
Bulrush	-**/-**	-**/-**	-*/-**	-*/-**	-**/-**	-*/-**	-**/-**	-**/-**		
Willow	+/+**	+/+**	+/+**	+/+**	+/+**	+/+**	+/+**	+/+**		
Forbs	-*/-**	-*/-**	-**/-**	-**/-**	ns/ns	-*/-**	ns/-**	ns/-**		

<sup>a</sup> Wilcoxon signed-ranks test; \*  $P < 0.01$ , \*\*  $P < 0.001$ .

<sup>b</sup> Two-sample *t*-test against random cover estimate of availability/one-sample *t*-test against random point estimate of availability; \*  $P < 0.01$ , \*\*  $P < 0.001$ .

than availability (Table 3). Therefore, increasing use of forbs as the season progressed (Table 2) was probably a result of seasonal differences in forb cover and associated prey.

DISCUSSION

Our results show significant variation in foraging behavior of Common Yellowthroats related to diurnal and intraseasonal timing. Diurnal patterns of behavior were generally consistent across intraseasonal periods; intraseasonal patterns did not differ significantly between diurnal periods. Such variation reflects complex temporal processes associated with marsh ecosystems (Voigts 1976, Weller 1978, Orians 1980, Mitsch and Gosselink 1986, Weller 1986), including changes in temperature (Taylor 1966), weather (Orians 1980), hydrologic conditions (Gosselink and Turner 1978), arthropod distributions (Voigts 1973, Orians 1980), vegetation structure (Voigts 1976, Weller 1978), emergence phenologies of aquatic insects (Orians and Horn 1969, Voigts 1973, Orians 1980) and arthropod activity cycles (Taylor 1966, Holmes et al. 1978, Hutto 1981). However, investigation of how such processes might influence yellowthroat behavior was beyond the scope of this study.

We found an overall diurnal pattern suggesting that foraging Common Yellowthroats focused on willows, with increasing use of cattail/bulrush and sites below 1 m and above 3 m from early morning to midday. Because of temperature effects, flying adult insects are more active in midday than early morning (Taylor 1966), and may therefore be less available in midday to birds that forage primarily by gleaning, such as yellowthroats (Hutto 1981). Common Yellowthroats feed on a wide variety of aquatic-emergent insects and terrestrial arthropods, including Arachnida, Ephemeroptera, Odonata, Hemiptera, Diptera, Lepidoptera, and others (Beal 1907, Bent 1953, Hofslund 1959, Foster 1977). Prey availability can be influenced by diurnal emergence patterns of aquatic insects. Emergence of odonates; for example, can be pronounced in late morning after rapid rise in ambient temperature that allows metamorphosis to occur more rapidly, thus minimizing vulnerability to predation (Orians 1980).

Diurnal differences in yellowthroat foraging behavior were strongest at approximately 09:30 (see Methods). This coincided with the time when rising air temperatures in the marsh began to

level off (unpubl. data). Orians and Horn (1969) reported that teneral (newly emerged) insects in marshes are most available to Red-winged Blackbirds (*Agelaius phoeniceus*), Yellow-headed blackbirds (*Xanthocephalus xanthocephalus*), and Brewer's Blackbirds (*Euphagus cyanocephalus*) in late morning and midday. Although we did not directly measure prey availability, we speculate that the observed patterns of foraging behavior reflected improved foraging opportunities in midday at (1) sites below 1 m in cattail/bulrush that could have resulted from midday increases in emergence rates of aquatic insects (Orians and Horn 1969, Voigts 1973, Orians 1980) and (2) sites in or near the upper canopies of willows as temperatures and insect activity increased and adult (stationary or flying) insects concentrated at greater heights in or above the vegetation (Taylor 1966, Holmes et al. 1978). The choice between these two responses may have partly depended on whether willows were present as preferred substrates within a habitat patch, although in 36% of observations in patches that included both willows and cattails yellowthroats chose to forage in cattails. Other explanations could involve diurnal shifts in foraging height related to intersexual differences (see below). However, because of sample size limitations, we did not evaluate temporal effects on interactions among foraging heights, plant species, substrates, and maneuvers used by yellowthroats. Such analyses could reveal additional foraging variation.

Common Yellowthroats actively selected willows for foraging throughout the breeding season. Our results also suggested increased foraging above 3 m in midseason, and trends of decreased foraging in cattail/bulrush, greater use of forbs, less gleaning and more frequent aerial gleaning as the season progressed. These observations suggest an hypothesis that foraging yellowthroats (1) increase their use of forbs passively, without active selection, as a result of intraseasonal increases in the availability of annual forbs and (2) respond to changes in distribution and or abundance of flying insects. That yellowthroats apparently preferred habitat patches with cattails until late in the season even though they did not actively select cattails for foraging suggests that cattail areas were selected for other reasons, such as nesting cover. Alternatively, differences in conspicuousness of birds foraging in cattails and willows could have biased comparisons of plant

species use. However, differences in visibility among potential foraging sites were generally consistent across diurnal, intraseasonal, and sex-related categories and therefore should not bias our overall results.

Male Common Yellowthroats foraged at significantly greater heights, on average, than females. Males were also more likely, on average, to choose flycatching over gleaning than were females. Such differentiation in habitat use between sexes is most simply explained as a consequence of foraging near centers of activity which differ in the breeding season (Morse 1968, Franzreb 1983, Holmes 1986). Differences in foraging heights could result from intersexual competition for preferred sites (Petit et al. 1990), but a large overlap in foraging heights, the predominant use of gleaning in both sexes, and a lack of clear differences in substrate use or habitat preferences suggests that competition-based partitioning of resources does not occur. In marshes, where polygyny is unusually prevalent among passerines (Verner and Willson 1966, Orians 1980), and can occur in Common Yellowthroats (Stewart 1953, Powell 1978), enhanced intersexual differentiation of breeding behaviors associated with polygyny (Selander 1966, Orians 1980) might contribute to intersexual differences in foraging behavior.

Morphological differences between male and female yellowthroats reflect these differences. Female yellowthroats have shorter wings, on average, than males (Eckhardt 1979, Pyle et al. 1987); consequently, they are better suited for shorter flights in low, dense vegetation near the nest site, whereas males have longer wings suited for longer rapid flights in more open habitat at heights used for singing and territorial defense. Activity patterns of insects and some wood warblers (Parulinae), including Common Yellowthroats, have been shown to be inversely related, probably because active (flying) insects are less available to birds that forage primarily by gleaning (Hutto 1981). Therefore, male yellowthroats may be better adapted to exploit temporal and spatial changes in prey abundance related to availability patterns of flying insects.

We suggest that Common Yellowthroats breeding in freshwater marshes respond independently to diurnal and intraseasonal changes in foraging conditions. We conclude that diurnal, intraseasonal, and intersexual differences in foraging behavior are important sources of varia-

tion that can influence studies of songbird foraging relationships in freshwater marsh habitats. Effective management of songbird populations in freshwater marshes may depend on accurate assessment of foraging habitat. Therefore, studies of foraging behavior should account for such variation to avoid misleading interpretations of habitat and foraging relationships.

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#### LITERATURE CITED

- BEAL, K. G., AND H. J. KHAMIS. 1990. Statistical analysis of a problem data set: correlated observations. *Condor* 92:248-251.
- BEAL, F. E. 1907. Birds of California in relation to the fruit industry. U.S. Biol. Surv. Bull. 30.
- BENT, A. C. 1953. Life histories of North American wood warblers. U.S. Natl. Museum Bull. 203.
- BISHOP, Y. M. M., S. E. FEINBERG, AND P. W. HOLLAND. 1975. Discrete multivariate analysis: theory and practice. MIT Press, Cambridge, MA.
- COCHRAN, W. G. 1954. Some methods for strengthening the common  $\chi^2$  tests. *Biometrics* 10:417-441.
- ECKHARDT, R. C. 1979. The adaptive syndromes of two guilds of insectivorous birds in the Colorado Rocky Mountains. *Ecol. Monogr.* 49:129-149.
- EVENS, J. G., AND R. W. STALLCUP. 1991. Coastal riparian marsh. *J. Field Ornithol.* 62 (Suppl.):75-76.
- EVENS, J. G., AND R. W. STALLCUP. 1993. Coastal riparian marsh. *J. Field Ornithol.* 64 (Suppl.):91-92.
- EVENS, J. G., AND R. W. STALLCUP. 1994. Coastal riparian marsh. *J. Field Ornithol.* 65 (Suppl.):105-106.
- FOSTER, M. L. 1977. A breeding season study of the Salt Marsh Yellowthroat (*Geothlypis trichas sinuosa*) of the San Francisco Bay area, California. M.S. thesis, San Jose State Univ., CA.
- FRANZREB, K. E. 1983. Intersexual habitat partitioning in Yellow-rumped Warblers during the breeding season. *Wilson Bull.* 95:581-590.
- GOSELINK, J. G., AND R. E. TURNER. 1978. The role of hydrology in freshwater wetland ecosystems, p. 63-78. *In* R. E. Good, D. F. Wingham, and R. L. Simpson [eds.], *Freshwater wetlands*. Academic Press, New York.
- GRAY, L. J. 1993. Response of insectivorous birds to emerging aquatic insects in riparian habitats of a tallgrass prairie stream. *Am. Midl. Nat.* 129: 288-300.
- GRINNEL, J. 1901. The Pacific Coast yellowthroats. *Condor* 3:65-66.
- GRINNEL, J., AND A. H. MILLER. 1944. The distribution of the birds of California. *Pacific Coast Avifauna* 27:1-608.
- GRUBB, T. C., AND M. S. WOODREY. 1990. Sex, age, intraspecific dominance status, and the use of food by birds wintering in temperate-deciduous and cold-coniferous woodlands: a review. *Stud. Avian Biol.* 13:270-279.
- HANAOWSKI, J. M., AND G. J. NIEMI. 1990. Effects of unknown sex in analysis of foraging behavior. *Stud. Avian Biol.* 13:280-283.
- HEJL, S. J., AND J. VERNER. 1990. Within-season and yearly variations in avian foraging locations. *Stud. Avian Biol.* 13:202-209.
- HOFSLUND, P. B. 1959. A life history study of the Yellowthroat, *Geothlypis trichas*. *Proc. Minnesota Acad. Sci.* 27:144-174.
- HOLMES, R. T. 1986. Foraging patterns of forest birds: male-female differences. *Wilson Bull.* 98:196-213.
- HOLMES, R. T., T. W. SHERRY, AND S. E. BENNET. 1978. Diurnal and individual variability in the foraging behavior of American Redstarts (*Setophaga ruticilla*). *Oecologia* 36:141-149.
- HUTTO, R. L. 1981. Temporal patterns of foraging activity in some wood warblers in relation to the availability of insect prey. *Behav. Ecol. Sociobiol.* 9:195-198.
- LEGENDRE, P., S. DALLOT, AND L. LEGENDRE. 1985. Succession of species within a community: chronological clustering, with applications to marine and freshwater zooplankton. *Am. Nat.* 125: 257-288.
- MILES, D. M. 1990. The importance and consequences of temporal variation in avian foraging behavior. *Stud. Avian Biol.* 13:210-217.
- MITSCH, W. J., AND J. G. GOSELINK. 1986. *Wetlands*. Van Nostrand Reinhold, New York.
- MORRISON, M. L. 1982. The structure of western warbler assemblages: ecomorphological analysis of the Black-throated Gray and Hermit Warblers. *Auk* 99:503-513.
- MORSE, D. H. 1968. A quantitative study of foraging of male and female spruce-woods warblers. *Ecology* 49:779-784.
- ORIAN, G. H., AND H. S. HORN. 1969. Overlap in foods and foraging of four species of blackbirds in the Potholes of central Washington. *Ecology* 50: 930-938.
- ORIAN, G. H. 1980. Some adaptations of marsh-nesting blackbirds. Princeton Univ. Press, Princeton, NJ.
- PETTIT, L. J., D. R. PETTIT, D. E. PETTIT, AND W. J. FLEMING. 1990. Intersexual and temporal variation in foraging ecology of Prothonotary Warblers during the breeding season. *Auk* 107: 133-145.
- POWELL, G. V. N. 1978. An observation of polygyny in the Common Yellowthroat. *Wilson Bull.* 90: 656-657.
- PYLE, P., S. N. G. HOWELL, R. P. YUNICK, AND D. F. DESANTE. 1987. Identification guide to North American passerines. Slate Creek Press, Bolinas, CA.

- RAPHAEL, M. G., AND B. A. MAURER. 1990. Biological considerations for study design. *Stud. Avian Biol.* 13:123-125.
- REMSEN, J. V., JR., AND S. K. ROBINSON. 1990. A classification scheme for foraging behavior of birds in terrestrial habitats. *Stud. Avian Biol.* 13:144-160.
- SAKAI, H. F., AND B. R. NOON. 1990. Variation in the foraging behaviors of two flycatchers: associations with stage of the breeding cycle. *Stud. Avian Biol.* 13:237-244.
- SCHOOLEY, R. L. 1994. Annual variation in habitat selection: patterns concealed by pooled data. *J. Wildl. Manage.* 58:367-374.
- SELANDER, R. K. 1966. Sexual dimorphism and differential niche utilization in birds. *Condor* 68:113-151.
- STEWART, R. E. 1953. A life history study of the Yellowthroat. *Wilson Bull.* 65:99-115.
- SZARO, R. C., J. D. BRAWN, AND R. P. BALDA. 1990. Yearly variation in resource-use behavior by ponderosa pine forest birds. *Stud. Avian Biol.* 13:226-236.
- TAYLOR, L. R. 1966. Analysis of the effect of temperature on insects in flight. *J. Anim. Ecol.* 32:99-117.
- VERNER, J. 1965. Time budget of the male Long-billed Marsh Wren during the breeding season. *Condor* 67:125-139.
- VERNER, J., AND M. F. WILLSON. 1966. The influence of habitat on mating systems of North American passerine birds. *Ecology* 47:143-147.
- VOIGTS, D. K. 1973. Food niche overlap of two Iowa marsh ictrids. *Condor* 75:392-399.
- VOIGTS, D. K. 1976. Aquatic invertebrate abundance in relation to changing marsh vegetation. *Am. Midl. Nat.* 95:313-322.
- WELLER, M. W. 1986. Marshes, p. 201-224. *In* A. Y. Cooperrider, R. J. Boyd, and H. R. Stuart [eds.], *Inventory and monitoring of wildlife habitat*. U.S. Dept. Inter., Bur. Land Management. Service Center, Denver, CO.
- WELLER, M. W. 1978. Management of freshwater marshes for wildlife, p. 267-284. *In* R. E. Good, D. F. Wingham, and R. L. Simpson [eds.], *Freshwater wetlands*. Academic Press, New York.