

**INTERSEXUAL AND INTERSPECIFIC DIFFERENCES IN
THE FORAGING BEHAVIOR OF RUFOUS-SIDED TOWHEES,
COMMON YELLOWTHROATS AND PRAIRIE WARBLERS IN
THE PINE BARRENS OF SOUTHEASTERN MASSACHUSETTS**

DAVID C. MORIMOTO

*Biology Department
Regis College
235 Wellesley Street
Weston, Massachusetts 02193 USA*

FRED E. WASSERMAN

*Biology Department
Boston University
5 Cummington Street
Boston, Massachusetts 02215 USA*

Abstract.—Interspecific differences in the foraging behavior of the three most abundant breeding birds in the southeastern Massachusetts pine barrens were more pronounced than intersexual differences. Significant and relevant intersexual differences did exist, however, and help to explain how this community is organized. The foraging behavior of female Prairie Warblers (*Dendroica discolor*) was more similar to Common Yellowthroats (*Geothlypis trichas*) than to male Prairie Warblers. Of the three species, male and female Rufous-sided Towhees (*Pipilo erythrophthalmus*) showed the least amount of intersexual foraging differences. Male and female Common Yellowthroats foraged at different heights, but did not differ in the use of plant species or foraging maneuvers. The intersexual differences that existed are best explained by the hypothesis that sex-related reproductive activities constrain the behavior of individuals. Male Common Yellowthroats and Prairie Warblers often sang at heights above 3 m. The nests of these species were typically built in shrubs near the ground. Consequently, males of both species may have been foraging higher than females because of related male singing and female nesting activity. Male Rufous-sided Towhees may have been constrained morphologically to forage on the ground, because no intersexual differences in foraging height occurred despite the fact that males often sang well above the ground.

**DIFERENCIAS INTERESPECÍFICAS E INTERSEXUALES EN LA
CONDUCTA DE FORRAJE O DE PIPILO ERYTHROPHTHALMUS,
GEOTHLYPIS TRICHAS Y DENDROICA DISCOLOR EN PINARES
DEL SURESTE DE MASSACHUSETTS**

Sinopsis.—Diferencias interespecíficas en la conducta de forrajeo de las tres especies residentes más abundantes de los pinares del sureste de Massachusetts resultaron ser más marcadas que diferencias intersexuales. Sin embargo, se encontraron diferencias intersexuales significativas y relevantes que ayudan a explicar como esta organizada esta comunidad considerada pobre. La conducta de forrajeo de hembras de *Dendroica discolor* resultó ser más similar a la conducta exhibida por *Geothlypis trichas*, que a los machos de su propia especie. De las tres especies estudiadas, *Pipilo erythrophthalmus*, exhibió la menor diferencia intersexual de forrajeo. Los sexos de esta especie forrajearon a diferente altura, pero no difirieron en el uso de especies particulares de plantas o en las maniobras de forrajeo. Las diferencias intersexuales existentes pueden ser explicadas con la hipótesis que indica que las actividades reproductivas relacionadas a los sexos impone límites a la conducta de los individuos. Los machos de *G. trichas* y de *D. discolor* a menudo cantan a alturas superior a los 3 m. Los nidos de estas especies típicamente son construídos en arbustos pero cerca del suelo. Consecuentemente, los machos de ambas especies pueden haber estado forrajearo a

mayor altura que las hembras debido a actividades relacionados con el canto y el anidamiento de estos, respectivamente. Los machos de *P. erythrophthalmus* pueden haber estado limitados morfológicamente a forrajear en los suelos. En estos no se encontró diferencia intersexual en la altura de forrajeo, aunque usualmente cantan a una altura considerable del suelo.

Knowledge of intersexual and interspecific differences in the foraging behavior of coexisting species, and of the factors responsible for these differences, can provide valuable insight into how and why birds select the habitats that they do and, ultimately, how communities are organized.

Intersexual differences in the foraging ecology of birds have been well documented (e.g., Franzreb 1983, Holmes 1986) and may sometimes be more pronounced than those between species (Holmes 1986, Noske 1986). There are generally two explanations given for intersexual differences: (1) males and females partition resources to reduce competition (Noske 1986, Rand 1952, Selander 1966) or (2) energetic constraints on foraging differ for males and females due to sex-related reproductive activities such as singing in males and nesting in females (Franzreb 1983, Holmes 1986, Morse 1980, Nolan 1978, Wasserman 1986).

In this study we examined the foraging ecology of the three most common bird species, Rufous-sided Towhee (*Pipilo erythrophthalmus*), Common Yellowthroat (*Geothlypis trichas*) and Prairie Warbler (*Dendroica discolor*), in the southeastern Massachusetts pine barrens. These species comprise approximately 49–70% of the individuals in this habitat (see below). Therefore, this study provides a comprehensive analysis of an avian community consisting of primarily three species. The study was designed to determine (1) if these three common species selectively foraged at certain heights or on certain plant species, (2) if males and females differed in selectivity, (3) if intersexual foraging patterns were related to either singing behavior of males or nest height and (4) if interspecific differences in foraging behavior were more pronounced than intraspecific differences.

METHODS

This study was conducted on eight 7–9-ha strip transects in the pine barrens of the towns of Plymouth (5 transects), Bourne (1 transect) and Mashpee (2 transects), in southeastern Massachusetts. The pine barrens occur on well-drained, sandy soils of the glacial outwash plain and are characterized by an open canopy of pitch pine (*Pinus rigida*) and a dense shrub layer dominated by scrub oak (*Quercus ilicifolia*) and several ericaceous species, including black huckleberry (*Gaylussacia baccata*), sheep laurel (*Kalmia angustifolia*) and blueberry (*Vaccinium angustifolium* and *V. vacillans*). Deciduous trees are relatively uncommon and primarily include black oak (*Q. velutina*) and white oak (*Q. alba*). The ground layer is dominated by the perennial herbs, wintergreen (*Gaultheria procumbens*) and bearberry (*Arctostaphylos uva-ursi*).

Vegetation was sampled on 165 randomly located 0.04-ha circular plots (20–23 plots/transect) in 1985 and 1986 to provide a basis for comparing the foraging distributions of birds. A 5-m pole (2.54 cm diameter) was

vertically positioned every 2.25 m along two perpendicular lines crossing the center of each plot. At each of the 20 sampling points per plot, the number of vegetation contacts and the species making contact were recorded in six height intervals (0–0.5, 0.5–1.0, 1.0–1.5, 1.5–3.0, 3.0–6.0 and >6.0 m). The heights of contacts above 5 m were estimated. Vertical vegetation structure was characterized by calculating the proportion of total vegetation contacts in each height interval. Floristic composition was characterized by determining the proportions of contacts with pitch pine (PPINE), deciduous trees (DECID), scrub oak (SOAK), ericaceous shrubs (ERIC) and herbs (HERB).

Foraging and singing activities were quantified between late May and mid July in both 1985 and 1986. All observations were made within 5 h after sunrise while walking along the center of each strip transect and during regular walks through various sections of the transects. Each transect was visited 7–8 times per year. Each foraging individual was observed for up to 2 min (i.e., a foraging episode). This method was chosen over an interval sampling method to include rare behaviors and to minimize the bias toward conspicuous behaviors (Morrison 1984, Tacha et al. 1985). For each foraging episode, foraging height and foraging maneuver were recorded and the substrate and plant species of the event were noted. Similarly, for each singing male encountered, singing height and, when applicable, the location within a tree were recorded. For each foraging or singing episode, the number of observations in each category was calculated and converted to a percentage. Thus, the sample sizes given represent the number of observed foraging or singing episodes. In total, we observed birds on the territories of 257 Rufous-sided Towhees, 251 Common Yellowthroats and 187 Prairie Warblers. The locations of foraging and singing birds were divided into the six height categories used to measure vegetation contacts.

Foraging maneuvers included gleaning (taking prey while perched), hovering (taking prey while in flight), hawking (flying from a perch to take aerial prey) and ground movement (all ground-directed maneuvers).

Substrates to which foraging maneuvers were directed included foliage, twigs less than 1 cm in diameter, branches more than 1 cm in diameter, tree trunks, ground and air. Foraging maneuvers and substrates were considered jointly in all analyses. Hovering behaviors directed toward banches and trunks were extremely rare and were not included in any analyses. The location of foraging or singing in trees was recorded as proximal (along the inner half of the tree canopy) or distal (along the outer half of the tree canopy).

Single-axis niche breadths for each sex and species were calculated for foraging height, use of plant species and foraging maneuver using the Shannon-Weaver (Shannon and Weaver 1949) index. This index was scaled from 0 to 1 by dividing by the maximum niche breadth obtained when all categories are equally used (Airola and Barrett 1985). Single-axis niche overlap between sexes and species was calculated using the formula for proportional similarity (Sabo and Holmes 1983).

To determine if foraging-height and plant-use distributions differed from foliage height and plant species distributions goodness-of-fit G -tests were performed (Sokal and Rohlf 1981) comparing foraging-height and plant-use distributions to vegetation structure and composition. As many statistical tests were performed, the significance level chosen was $P = 0.01$. Differences in foraging distributions between sexes and between species were determined with separate G -tests for foraging height, foraging maneuver, foraging location and plant species use. G -tests were also performed to compare singing-height distributions to foraging-height distributions and vegetation structure.

To evaluate intraspecific foraging relationships with respect to those between species on both single-dimensional and multi-dimensional niche axes, the matrix of species and sexes by foraging variables was subjected to hierarchical cluster analysis (average-linkage-between-groups method using Euclidean distances; Norusis 1985). Separate cluster analyses were performed using the eight foraging maneuver variables, the 11 combined foraging-height-plant species variables, and all 19 variables combined. Foraging location observations were not included in these analyses.

RESULTS

Although 31 breeding bird species were detected at the study sites, the avifauna was dominated by Rufous-sided Towhees, Common Yellowthroats and Prairie Warblers, which comprised 49–70% of the total density of breeding birds in the eight study areas.

Comparisons with vertical vegetation structure (Fig. 1) revealed that both male and female Rufous-sided Towhees selectively foraged on or near the ground ($G = 59.24$ for males, $G = 78.32$ for females; both $P < 0.001$, $df = 5$), whereas male and female Prairie Warblers selectively foraged at heights greater than ground level ($G = 100.36$ for males, $G = 26.86$ for females; both $P < 0.001$, $df = 5$). Female Common Yellowthroats foraged at lower heights, when compared to the vertical vegetation structure, avoiding heights 1.5–3.0 and >6.0 m ($G = 15.50$, $P < 0.01$, $df = 5$). In contrast, male Common Yellowthroats appeared to be more opportunistic, using vegetation at different heights in proportion to its availability ($G = 9.43$, $P > 0.05$, $df = 5$). In all three species, males tended to forage higher than females (Fig. 1). These differences were statistically significant only in Common Yellowthroats and Prairie Warblers, however (Table 1).

As a result of the obvious differences in the foraging-height distributions of Rufous-sided Towhees compared to the other two species, interspecific foraging differences were quantified only for Common Yellowthroats and Prairie Warblers. These comparisons revealed that Prairie Warbler males differed significantly from Common Yellowthroats in foraging height, use of plant species, foraging maneuver, and location in a tree (Table 2; $P < 0.01$). Female Prairie Warblers and male Common Yellowthroats were most similar with foraging height, foraging maneuver and location in tree being statistically indistinguishable ($P > 0.01$, Table 2). Common Yel-

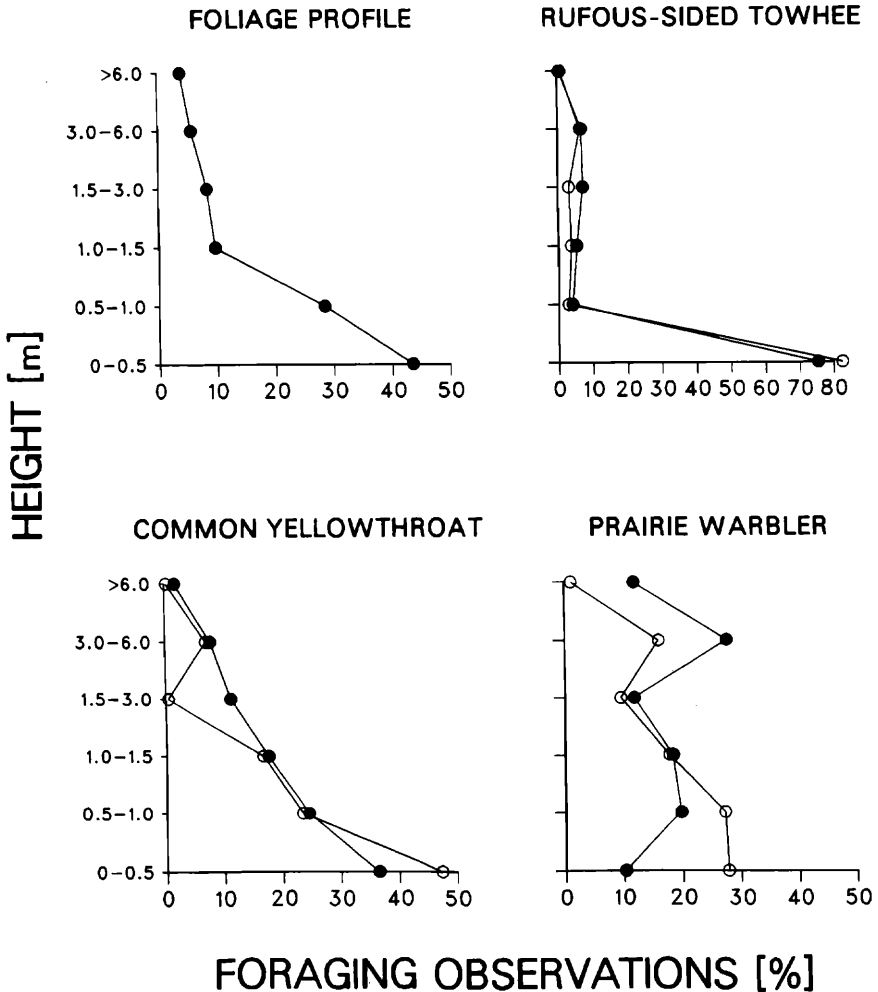


FIGURE 1. Foliage height profile and foraging height profiles for males (solid circles) and females (open circles) of the three most common pine barrens birds.

lowthroats generally foraged more often in herbs and less often in pitch pine than Prairie Warblers (Fig. 2). These differences were most pronounced between Common Yellowthroats and male Prairie Warblers.

Males and females of all three species used plants in proportions significantly different from their availability (Fig. 2, all $P < 0.001$). Although Rufous-sided Towhees foraged mostly on the ground (Table 3, Fig. 1), when they foraged above the ground they preferred pitch pines, deciduous trees (primarily oaks) and scrub oak, and avoided ericaceous shrubs and herbs. Male and female Common Yellowthroats and female Prairie Warblers exhibited the most pronounced preferences for scrub oak (Fig. 2).

TABLE 1. Niche breadth and intersexual overlap for foraging height and use of plant species. Significance of differences between sexes was determined using goodness-of-fit *G*-tests.

Species	Sex	N	Foraging height		Plant species	
			Breadth	Overlap	Breadth	Overlap
Rufous-sided Towhee	M	491	0.51	0.93	0.75	0.09
	F	409	0.40		0.69	
Common Yellowthroat	M	263	0.86	0.87*	0.63	0.94
	F	141	0.68		0.61	
Prairie Warbler	M	248	0.96	0.75*	0.64	0.77*
	F	72	0.89		0.59	

* $P < 0.01$.

No intraspecific intersexual differences in plant species use were found for Rufous-sided Towhees or Common Yellowthroats (Table 1). Male Prairie Warblers, however, divided their foraging more evenly between pitch pines and scrub oak than did female Prairie Warblers (Fig. 2).

All three species were rather specialized in their foraging maneuvers and substrate, as indicated by the low breadth indices (Table 3). Rufous-sided Towhees were predominantly ground foragers, whereas Common Yellowthroats and Prairie Warblers most often gleaned prey from foliage. No significant intersexual differences in foraging maneuvers were found for any species (Table 3).

All three species foraged significantly more often along the distal half of tree branches compared with an equal distribution of proximal and distal foraging (Table 4). This pattern was most pronounced for male Prairie Warblers, which foraged distally significantly more frequently than female Prairie Warblers. In Rufous-sided Towhees, females foraged distally significantly more often than males.

The singing-height distributions of all three species differed significantly from vertical vegetation structure, with all three species, particu-

TABLE 2. Interspecific overlap between Common Yellowthroats and Prairie Warblers.

Species-sex pair		Foraging height	Plant species	Foraging maneuver	Location in tree
Common Yellowthroat	M	0.69*	0.69*	0.94*	0.93*
Prairie Warbler	M				
Common Yellowthroat	F	0.59*	0.63*	0.92*	0.94*
Prairie Warbler	M				
Common Yellowthroat	M	0.89	0.90*	0.93	0.99
Prairie Warbler	F				
Common Yellowthroat	F	0.80*	0.86*	0.95	0.97*
Prairie Warbler	F				

* $P < 0.01$.

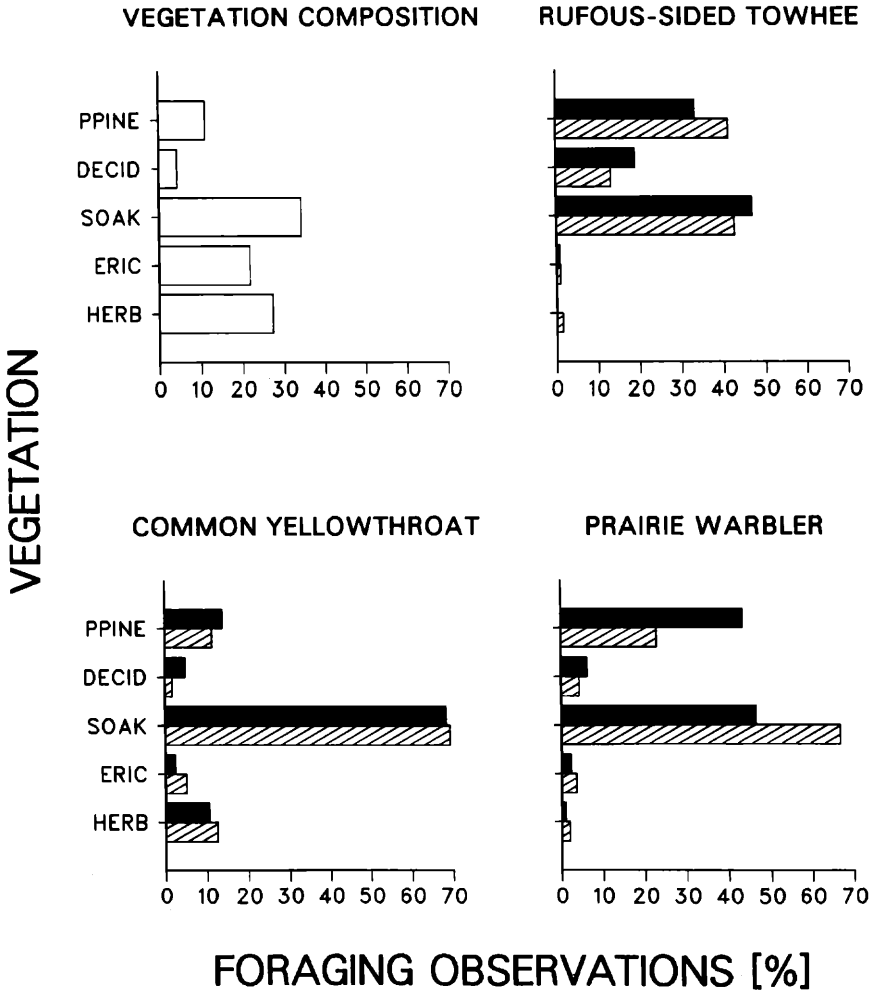


FIGURE 2. Vegetation composition and use of vegetation by males (solid bars) and females (shaded bars) of the three most common pine barrens birds. Vegetation categories include pitch pine (PPINE), deciduous trees (DECID), scrub oak (SOAK), ericaceous shrubs (ERIC), and herbaceous vegetation (HERB). Males and females of all three species used plants in proportions significantly different from their availability ($P < 0.001$).

larly Prairie Warblers, selecting higher song perches and avoiding lower ones (Fig. 3). The song-height distributions of all three species also differed significantly from their foraging-height distributions ($G = 100.35$ for Rufous-sided Towhees; $G = 83.03$ for Common Yellowthroats; $G = 41.79$ for Prairie Warblers; all $P < 0.001$, $df = 5$) and from the foliage-height distributions ($G = 54.52$ for Rufous-sided Towhees; $G = 110.12$ for Common Yellowthroats; $G = 223.97$ for Prairie Warblers; all $P < 0.001$, $df = 5$). Thus, although Rufous-sided Towhees often sang at

TABLE 3. Percentages of foraging maneuvers and substrate use by three dominant species in the Southeastern Massachusetts Pine Barrens. All overlap values were nonsignificant.

Species	Sex	Foliage		Twig		Branch		Trunk		Air		Ground		Foraging substrate/ maneuver	
		Hover	Glean	Hover	Glean	Glean	Glean	Glean	Glean	Hawk	All	Breadth	Overlap		
Rufous-sided Towhee	M	0.5	22.5	0	2.2	0.8	0.3	0	0	73.5	0.35	0.93			
	F	0.2	16.3	0.1	1.5	1.1	0.4	0	0	80.4	0.30				
Common Yellowthroat	M	0.4	88.9	0.6	6.4	0.4	0.6	0.5	0.5	2.2	0.24	0.94			
	F	0.1	84.4	0.1	8.4	0.9	0	0.3	0.3	5.7	0.28				
Prairie Warbler	M	3.9	85.3	0.5	5.9	0.7	0.2	3.1	0.4	0.30	0.94				
	F	2.4	83.0	0.3	7.5	2.1	0	1.3	3.4	0.34					

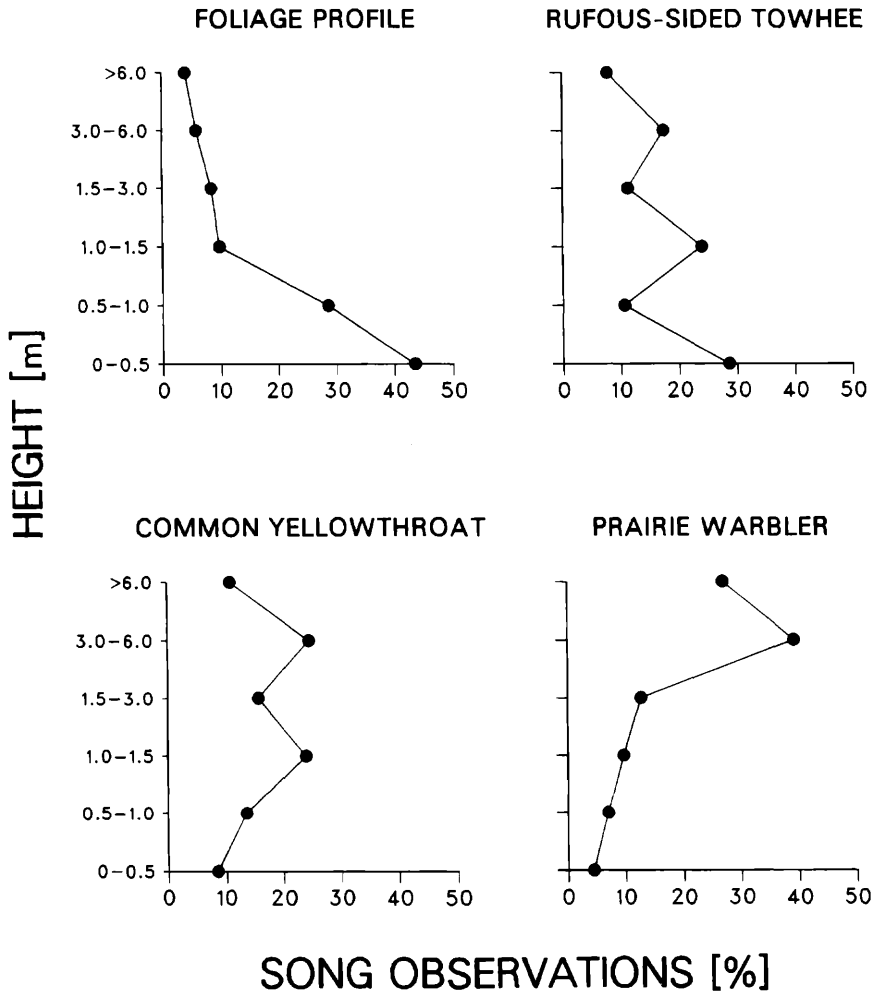


FIGURE 3. Foliage height and singing height profiles for the three most common pine barrens birds.

heights greater than 1.5 m, they most often foraged on the ground. Prairie Warblers preferred to sing at heights greater than 3 m and also foraged frequently at these heights. Common Yellowthroats frequently sang at a variety of heights greater than 0.5 m. Common Yellowthroats, in addition to singing while perched, often performed flight songs (9.25 ± 2.91 m (mean \pm SE) above ground in 1986, $n = 16$), always flying from the shrub layer and usually, but not always, landing in shrubs (Kowalski 1983).

All three species, particularly Prairie Warblers, sang from the distal portions of branches more often than expected in an equal distribution

TABLE 4. Frequency of prey captures occurring in the distal half of tree branches. All species foraged significantly more in distal than in proximal branches ($P < 0.01$).

Species	Sex	N	Distal (%)	Overlap
Rufous-sided Towhee	M	83	57.9*	0.92*
	F	54	73.8*	
Common Yellowthroat	M	74	69.0*	0.99
	F	30	71.6*	
Prairie Warbler	M	163	82.7*	0.92*
	F	30	66.2*	

* $P < 0.01$.

(Table 5). Prairie Warblers and Rufous-sided Towhees sang distally more frequently than they foraged distally, whereas the reverse was true for Common Yellowthroats.

The cluster analysis of foraging maneuver frequencies revealed that interspecific differences were more pronounced than intersexual differences (Fig. 4). The cluster analyses of the combined foraging height and plant species frequencies and of all foraging variables together revealed that female Prairie Warblers were more similar to Common Yellowthroats (especially males) than they were to male Prairie Warblers, however (Fig. 4).

DISCUSSION

The foraging behavior of birds is the result of a complex of interacting factors including diurnal (Holmes et al. 1978), seasonal (Brush and Stiles 1986, Conner 1979) and annual (Holmes 1986, Holmes and Schultz 1988) prey availability; the presence or absence of competitors (Hutto 1981, Peters and Grubb 1983, Sherry 1979), vegetation structure (Maurer and Whitmore 1981, Sabo and Holmes 1983); and the interacting effects of floristic composition and plant architecture (Holmes and Robinson 1981; Jackson 1979; Robinson and Holmes 1982, 1984). In addition, the energetic constraints placed on individuals by sex-related activities and morphology are important.

The results of this study illustrate the importance of considering in-

TABLE 5. Frequency of songs and overlap of singing and foraging in the distal half of tree branches. All three species sang from the distal portions of branches more often than expected in an equal distribution ($P < 0.01$).

Species	Distal (%)	Overlap with foraging
Rufous-sided Towhee	67.9*	0.95*
Common Yellowthroat	62.0*	0.96*
Prairie Warbler	87.1*	0.98*

* $P < 0.01$.

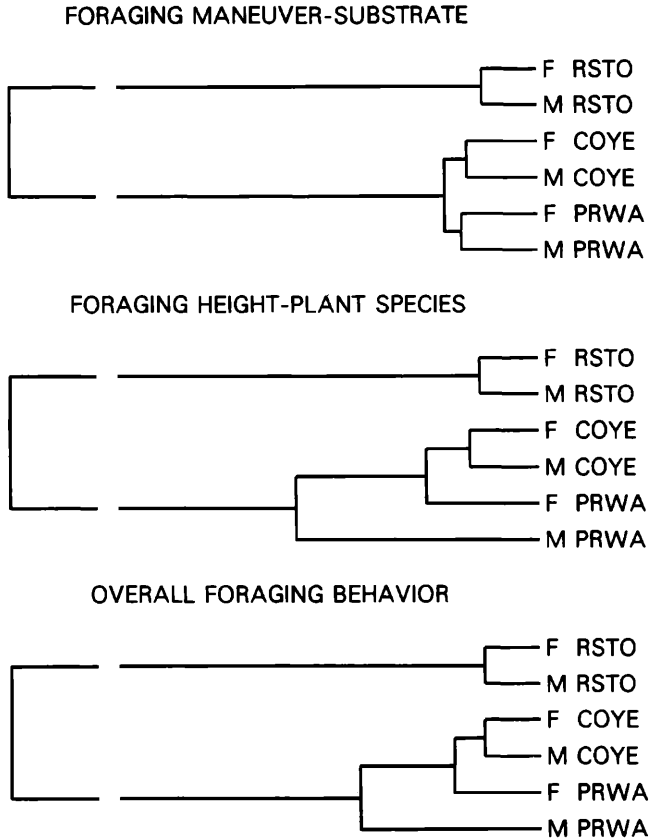


FIGURE 4. Cluster dendrograms showing Euclidean distances between male (M) and female (F) Rufous-sided Towhees (RSTO), Common Yellowthroats (COYE), and Prairie Warblers (PRWA) with respect to foraging maneuver-substrate use, foraging height-plant use and overall foraging behavior.

tersexual foraging differences in studies of niche relationships in birds. There was considerable variability in the extent to which intersexual differences in foraging behavior existed in these three abundant bird species. Male and female Rufous-sided Towhees exhibited few differences, whereas Prairie Warblers exhibited pronounced differences between males and females. Intersexual differences in Common Yellowthroats were intermediate between these two species.

Foraging constraints due to sex-related activities.—One hypothesis proposed to explain intersexual foraging differences is that individuals are constrained by sex-related activities: singing in males and nest-building and incubating in females (Franzreb 1983; Holmes 1986; Holmes et al. 1978; Morse 1980; Nolan 1978; Wasserman 1982, 1986). From several results of this study we suggest that the intersexual foraging differences observed may be associated with such sex-related activities.

The widely scattered trees in this open habitat were important to male Prairie Warblers as song posts. Thus male Prairie Warblers were constrained by their singing activities to forage where they could send long distance signals more effectively. As female Prairie Warblers place their nests in the upper portions of shrubs, typically at heights less than 2 m (Bent 1963, Nolan 1978), they most often foraged in scrub oak at heights less than 1.5 m, where they remained relatively inconspicuous. The findings that male Prairie Warblers sang most often from the distal portions of tree branches and foraged distally more than females support the hypothesis that Prairie Warbler foraging is constrained by sex-related activities.

Male Common Yellowthroats were less dependent on pitch pines for song posts and distributed their singing and foraging among heights in a more opportunistic fashion. Alternatively, females restricted their foraging primarily to heights of less than 1.5 m. This may be explained by the fact that Common Yellowthroats typically nest a few centimeters above the ground (Bent 1963, Harrison 1975) and correspondingly, females were foraging closer to their nests. Thus, it appears that the constraints of sex-related activities are sufficient to account for the intersexual differences in foraging behavior in Common Yellowthroats.

The intersexual differences in the frequency of foraging by Rufous-sided Towhees at the 1.5–3-m height interval might be explained similarly, although no overall intraspecific differences in foraging behavior were found for this species despite the finding that males often sang at heights greater than 3 m. It appears that both sexes of this species were constrained, most likely by morphology, to forage primarily on the ground.

The resource partitioning hypothesis.—The second hypothesis proposed to account for intersexual foraging differences is that they evolved to reduce intersexual competition (Rand 1952, Selander 1966). The results of this study can not refute this hypothesis. More detailed studies of foraging behavior, for example involving manipulations (Peters and Grubb 1983), are required before conclusive statements can be made regarding the importance of intraspecific competition in these three species. Insight into the causes of intersexual differences in foraging behavior also would be provided by additional detailed field studies of individual pairs at different stages of the breeding season (Wasserman 1986), laboratory studies of intrinsic foraging behaviors (Emlen and DeJong 1981), and studies on the ontogeny of foraging behavior (Greenberg 1984, 1987).

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