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EFFECTS OF UNKNOWN SEX IN ANALYSES OF FORAGING BEHAVIOR

JOANN M. HANOWSKI AND GERALD J. NIEMI

Abstract. Foraging data were collected on Yellow-rumped (*Dendroica coronata*) and Palm (*D. palmarum*) warblers, both of which nest in spruce bogs of northern Minnesota. Male and female Palm Warblers cannot be distinguished, whereas sexes of the Yellow-rumped Warbler are dichromatic. We used our data to examine effects of unknown sex in analyses of foraging data. Male Yellow-rumped Warblers foraged higher than females. When data from sexes were combined, the mean was closer to the value for males because the sample size was larger for that sex. It follows that foraging data for sexually monochromatic species may not be representative for either sex. In addition, interspecific comparisons of foraging behavior may not be appropriate when sexes are unknown. Appropriate statistical tests may compensate for unknown sexes. Analysis of frequencies (chi-square or G-test) may eliminate this bias because means are not compared. However, this test does not compensate for the unknown proportion of male and female observations, which obviously skews the frequency distribution.

Key Words: Warbler; foraging behavior; date analysis

MacArthur's (1958) study of foraging behavior in spruce-woods warblers initiated a voluminous literature on avian foraging behavior. Nevertheless, little attempt had been made to standardize collection or analysis of such data. One topic that is rarely considered is how observations of birds of unknown sex affect the results of foraging analyses. Our objectives were to: (1) quantify foraging height and tree height used by two spruce-woods warblers, the monochromatic Palm Warbler (*Dendroica palmarum*) and the sexually dichromatic Yellow-rumped Warbler (*D. coronata*); (2) determine the consequences of unknown sex in interspecific comparisons of foraging and tree heights; and (3) examine statistical tests that best quantify interspecific differences or similarities in foraging behavior when sexes are unknown.

STUDY AREA AND METHODS

We studied birds in a black spruce (*Picea mariana*) bog in 1980 and 1981 (Hanowski 1982). The study area, located within the Red Lake Peatland in northwest Minnesota, is relatively homogeneous, with 95% of the trees black spruce and 5% tamarack (*Larix laricina*) (Niemi and Hanowski 1984). Mean tree height was 5.7 m (Hanowski 1982) and the stand age was 150–200 yr (Heinselman 1963). Labrador tea (*Ledum groenlandicum*) and leatherleaf (*Chamaedaphne calyculata*) were common in the understory and the ground was covered with mosses (*Sphagnum* spp., *Dicranum* spp., and *Polytrichum* spp.).

We collected foraging data three times weekly from early May through early July in two 17.5-ha study areas (500 × 350 m) (Niemi and Hanowski 1984), primarily in the morning (04:30–12:00 CDT). Data for several foraging variables (e.g., method, substrate size) also were collected, but here we concentrate on data for height of tree and height of foraging bird in 1-m intervals. The relatively short stature of trees allowed us to record heights accurately. We recorded data at 30-s intervals for up to five observations/sighting. Height means (t-test; $P < 0.05$) or frequencies (chi-square; $P < 0.05$) for the first observation in a series were not different from subsequent observations in a series for any bird group. We used only the initial observation in all statistical analyses.

Foraging data were analyzed by comparing means (parametric tests) and frequencies (nonparametric tests). Mean bird and tree heights were first compared with a three-group (male Yellow-rumped, female Yellow-rumped, and Palm warblers) analysis of variance (ANOVA). If a significant ($P < 0.05$) difference was found, Scheffe's test (Sokal and Rohlf 1981) was used to compare individual group means. Frequencies of bird and tree heights were compared with a 3 × 12 chi-square contingency-table test. Paired comparisons were also computed with chi-square tests if the initial three-group test was significant ($P < 0.05$).

RESULTS

The three-group ANOVA indicated that these two species selected trees of different heights and also foraged at different heights ($P < 0.05$; Table 1). Scheffe's multiple comparisons showed that the male Yellow-rumped Warblers foraged higher than females ($P < 0.01$) but did not select taller trees (Table 2, Fig. 1). The Palm Warbler (Fig. 2) foraged lower and selected shorter trees than the yellow-rumps ($P < 0.01$; Table 2). However, no difference ($P > 0.05$) existed between foraging height or height of trees selected by the Palm and female Yellow-rumped warblers (Table 2). By contrast, when we combined data for male and female yellow-rumps, we found that yellow-rumps selected taller trees (Fig. 3, Table 2) but that the height of the foraging bird did not differ between species.

The three-group chi-square test, like the t-test, showed that the male and female yellow-rumps and the Palm Warbler differed from each other in their use of tree and foraging heights (P <

TABLE 1. Mean, Variance, Sample Size and Results of ANOVA and Chi-square Tests for Bird and Tree Heights Selected by Male and Female Yellow-rumped and Palm Warblers (Sexes Combined) while Foraging

Species	N	Bird height $\bar{X}$	Bird height s^2	Tree height $\bar{X}$	Tree height s^2
Male Yellow-rumped Warbler	46	5.6	2.9	7.5	3.5
Female Yellow-rumped Warbler	22	3.3	2.8	6.8	1.9
Palm Warbler	82	4.1	4.9	6.2	4.1
Male and female Yellow-rumped Warbler[a]	68	4.8	3.6	7.2	2.9
Overall ANOVA		$P < 0.01$		$P < 0.04$	
Overall chi-square		$P < .0.02$		$P < 0.01$	

[a] Not included in overall ANOVA or chi-square test.

0.05; Table 1). Two of eight paired chi-square tests comparing foraging data had different results from Scheffe's test. In both situations, the chi-square test was significant when the Scheffe's test was not (Table 2). The two tests that were not in agreement concerned tree height between female yellow-rumps and the other two groups (male yellow-rumps and Palm Warblers).

DISCUSSION

If the goal of foraging analyses is to assess resource use by a species, distinguishing sexes may not be critical. Frequency distributions of a species' use of trees and its height when foraging will provide an adequate indication, although the space used by males will probably be over-represented due to their conspicuousness. In contrast, if the objective is to define and separate microhabitat use for species that are close, both morphologically and in the habitat that they occupy, ignorance of sexual differences may obscure ecologically important differences between species.

The inability to distinguish between sexes is a problem because approximately 50% of North American passerine species are sexually monochromatic. Furthermore, when sexes have been distinguished, studies have found that males and females forage at different heights and select different heights of trees for foraging (Morse 1968, 1971a, 1973, 1980b; Morrison 1982; Franzreb 1983b; Holmes 1986; Grubb and Woodrey, this volume). For example, our data for yellow-rumps agree with a previous study by Franzreb (1983b), who showed that males foraged higher than females. Nevertheless, in other studies male and female data have been combined with little consideration for the consequences of this procedure.

We have shown that neither a comparison of mean heights (t-test) or frequency of heights (chi-square or G-test) may be appropriate when sexes cannot be distinguished because: (1) interspecific and intraspecific sexual differences will not be detected, and (2) means compared will be skewed toward the sex with the larger sample size. For example, t-tests are not appropriate because the mean is skewed toward the sex with the larger sample. Combining data from Yellow-rumped Warbler sexes obscured the actual difference between female yellow-rumps and Palm Warblers. If the ratio of male to female observations in the sample is not equal for both species, interspecific comparisons will be inaccurate.

The alternative test is nonparametric comparisons of frequency distributions. Where sexes are unknown, these comparisons should be more appropriate because means are not compared. Indeed, most investigators have used them (Sturman 1968, Balda 1969, Hertz et al. 1976, Morse 1979). Our nonparametric tests detected more differences between species groups than the ANOVAs or Scheffe's test. Chi-square tests indicated that male yellow-rumps selected taller trees

TABLE 2. Results of Scheffe's (P-values) and Paired Chi-square (χ^2) Tests between Male and Female Yellow-rumped Warblers and Palm Warblers for Bird and Tree Heights Selected while Foraging

Comparison	Bird height Scheffe's	Bird height χ^2	Tree height Scheffe's	Tree height χ^2
Male versus female Yellow-rumped Warbler	0.01	0.01	0.18	0.03
Male Yellow-rumped versus Palm Warbler	0.01	0.01	0.01	0.01
Female Yellow-rumped versus Palm Warbler	0.08	0.01	0.16	0.01
Yellow-rumped (sexes combined) versus Palm Warbler (sexes combined)	0.29	0.39	0.02	0.01

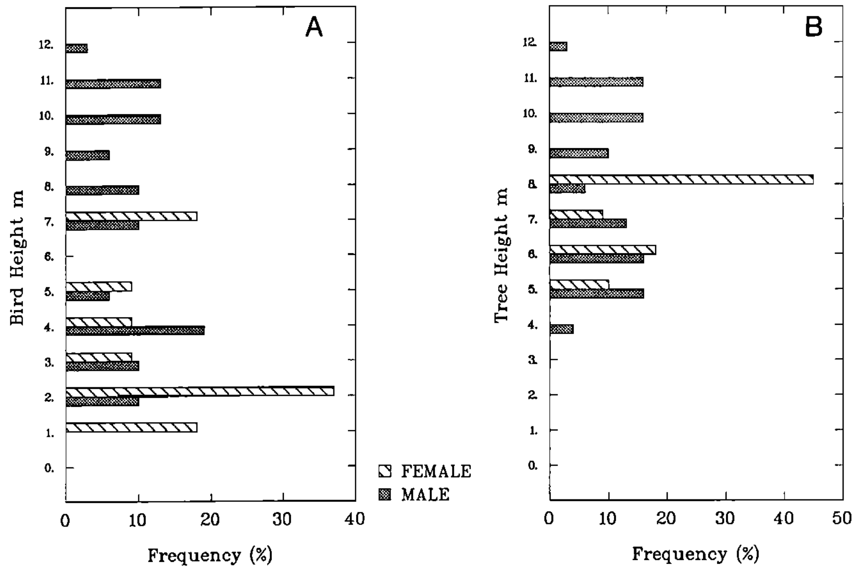

FIGURE 1. Distribution (relative percent) of (A) bird height (m) and (B) tree height (m) selected for foraging by male (N = 46) and female (N = 22) Yellow-rumped Warblers.

than females and that females selected taller trees than Palm Warblers. Neither of these differences was detected with Scheffe's test. However, as in Scheffe's test, combining the yellow-rumped sexes masked the difference in foraging height between species.

Chi-square tests are not an adequate solution to the problem because the proportion of male and female observations in the sample is still unknown. The frequency of height observations in data that identified sexes had two unimodal normal distributions (Wilk's-Shapiro test; Sha-

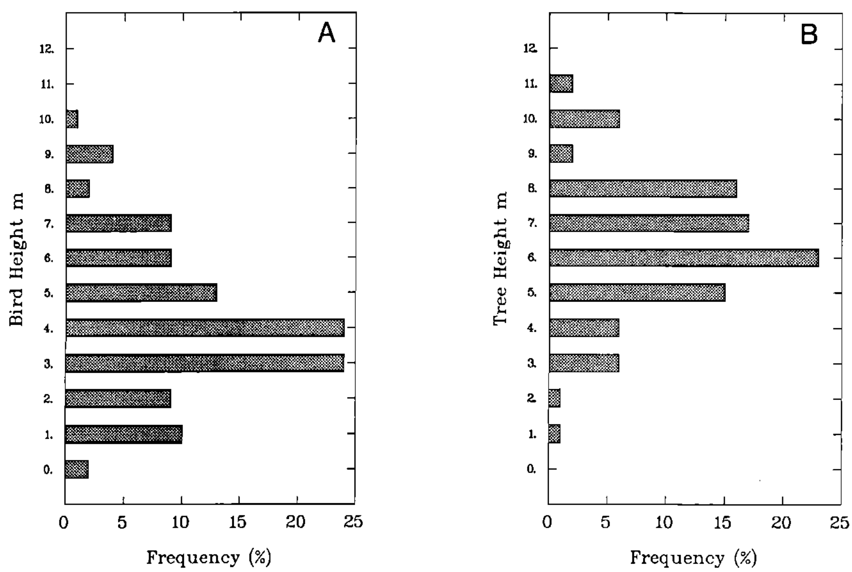

FIGURE 2. Distribution (relative percent) of (A) bird height (m) and (B) tree height (m) selected for foraging by Palm Warblers (N = 82).

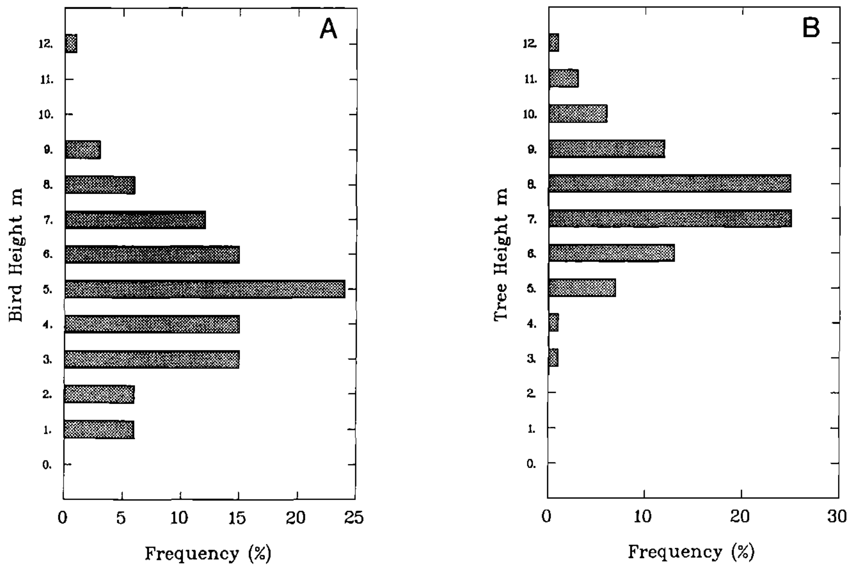

FIGURE 3. Distribution (relative percent) of (A) bird height (m) and (B) tree height (m) selected for foraging by Yellow-rumped Warblers sexes combined (N = 68).

piro and Wilk [1965]), which is expected if males forage higher than females. However, when we combined data between sexes, the frequency distribution remained unimodal and normal (Fig. 3), due to the overlap of observations in the center of the distribution. Similarly, we would not expect the frequency distribution of Palm Warbler foraging heights to show two unimodal distributions, because data were a combination of heights for both sexes. Therefore, nonparametric tests are not a remedy if the goal is to identify interspecific differences.

One cannot assume that random foraging observations for sexually monochromatic species will contain similar proportions of males and females because males are usually more conspicuous than females (pers. obs.; Holmes 1986). This assumption is not a solution to the problem of unknown sex.

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