SEXUAL SEGREGATION BY HABITAT IN MIGRATORY WARBLERS IN QUINTANA ROO, MEXICO

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ABSTRACT.—We determined habitat preferences for males and females of nine species of dichromatic warblers in the Sian Ka'an Reserve, Quintana Roo, Mexico. We found significant habitat segregation in the American Redstart (*Setophaga ruticilla*), Common Yellowthroat (*Geothlypis trichas*), Magnolia Warbler (*Dendroica magnolia*), and Northern Parula (*Parula americana*), and we confirmed previously reported habitat segregation in the Hooded Warbler (*Wilsonia citrina*). Possible differences in habitat distribution were found in the Black-and-white Warbler (*Mniotilta varia*), Prothonotary Warbler (*Protonotaria citrea*), and Black-throated Green Warbler (*Dendroica virens*). Only migratory Yellow Warblers (*Dendroica petechia*) showed no sign of sexual segregation. In all five cases where there is a significant difference between successional stages, males occupied the more mature habitat. The overall frequency and spatial pattern of recaptures were similar between sexes. *Received 29 March 1989, accepted 26 January 1990.*

HABITAT segregation between the sexes was first described for American Kestrels (*Falco sparverius*, Mills 1976) and Eastern Great Reed Warblers (*Acrocephalus orientalis*, Nisbet and Medway 1972). More recently the first species of Neotropical migrant land bird was found to display intersexual segregation. Male and female Hooded Warblers (*Wilsonia citrina*) defend territories in different habitats (Lynch et al. 1985, Morton et al. 1987). Males were common in mature forest, and females occurred in a variety of scrub habitats. However, the overall frequency of habitat segregation among Neotropical migrants has not been established. Sexual habitat segregation has important implications for understanding the life history and demography of particular species and for assessing the possible effects of habitat alteration. We report the results of a survey of the most common dichromatic migratory wood warblers found in the Northeastern Yucatan Peninsula. The results summarize two different surveys; each author conducted one survey. We used two techniques (mist-netting and visual-auditory surveys), which produced complementary data sets. Where the data can be compared, the results are generally in agreement. The data sets together provide information on all of the common dichromatic warblers in the Sian Ka'an Reserve, Quintana Roo, Mexico.

METHODS

Study area.—The fieldwork was conducted in the Sian Ka'an Biosphere Reserve and surrounding *ejidos* (rural land cooperatives) in the northeast coastal region of the Yucatan Peninsula. The reserve receives 1,200 mm/yr of rainfall, primarily during a rainy season from June to November. The area supports a high abundance and diversity of Nearctic migrants during the nonbreeding season (Waide 1980, Lynch 1989). We conducted surveys in coastal dune scrub, mangrove scrub, seasonally flooded scrub, low forest, medium-height subdeciduous forest, medium-height subperennial forest, pasture, and postclearing successional scrub. These habitats represent the major vegetation types of the eastern Yucatan Peninsula (Miranda 1958, Olmsted et al. 1983).

Within each habitat where we mist-netted, the vegetative cover was categorized and estimated for an imaginary circle centered at each of 24 net sites. The categories include (a) herb, grass, or fern; (b) scrub (1-4 m); and (c) trees (4 m+). Cover was estimated to one of five classes, each representing 20% (e.g. cover class 1 = 1-19%, class 2 = 20-39%). A quantitative description of the habitats is presented (Table 1). Medium-height subperennial forest was not sampled in an equivalent fashion, but it has greater stature (mean canopy height = 13-15 m), fewer deciduous canopy trees, and a moister, shadier understory than subdeciduous forest.

To analyze the bird survey data, we pooled the

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TABLE 1. Habitat structure measurements of study plots. Numbers are means (±SD) based on 24 points per plot.

	Plot size (ha)	Canopy ht. (m)	Vegetative cover			Mist-net hours
			Trees	Shrubs	Herbs	
Second growth						
1-2 yr	1.5	1.1 ± 0.3	0	2.6 ± 0.9	2.6 ± 1.6	1,105
3-4 yr	1.5	1.6 ± 0.6	0.4 ± 0.6	3.1 ± 1.0	2.0 ± 1.0	1,230
7-8 yr	3.0	3.7 ± 1.1	2.6 ± 1.0	1.5 ± 0.7	1.2 ± 1.0	1,250
Mangrove scrub	1.5	2.1 ± 1.2	1.6 ± 0.8	4.0 ± 0.8	0.4 ± 0.6	576
"Sabana"	1.5	2.1 ± 1.5	1.2 ± 1.6	2.0 ± 1.3	2.7 ± 1.0	1,656
Low forest	1.5	5.5 ± 1.6	3.6 ± 0.5	1.6 ± 0.9	0.6 ± 0.6	1,728
Medium forest	2.5	11.0 ± 1.6	4.1 ± 0.6	0.9 ± 0.3	0.2 ± 0.1	1,404

habitats in two ways. The mist-netting data (Table 2) are compared for open habitats (second growth 3-4 yr of age or younger and sabana, a marshlike habitat), scrub (7-8-yr-old second growth and mangrove scrub), low forest (seasonally flooded low forest), and medium forest. To analyze the broad-scale visual survey, we contrasted scrub habitats (from pasture to 7-8-yr-old second growth), subdeciduous, and subperennial forests.

Mist-netting.—In each of the vegetation types (except subperennial forest), we established grids that consisted of 3 parallel lines with 8 mist nets (2 × 12 m, 30 mm mesh) on each line. Nets were spaced 15-25 m apart along the lines, and 50-70 m between the lines. The total areas netted varied between habitats from 1.5 to 3.0 ha. Nets were opened at dawn (ca. 0600) and closed 6 h later. Nets were opened for at least three consecutive days in each habitat during the autumn, winter, and spring of 1985/1986 and of 1986/1987 for a total of 9,372 net hours. All of the habitats were sampled each year in midwinter. Additional netting was done in September-October and April in some habitats. Because only ground-level mist nets were used, the relative numbers of individuals captured do not reflect differences in species' abundance between different habitats (Lynch 1989).

Visual surveys.—The Sian Ka'an Reserve and nearby areas were surveyed during the winter of 1987/1988 and of 1988/1989. The surveys were designed only to determine sex ratios, not to estimate relative abundance. A particular habitat patch or trail was selected for each survey, and the sex of each dichromatic warbler was recorded. Effort was made to select sites that were away from edge situations and could be unambiguously assigned to one of three major habitats: scrub, subdeciduous, or subperennial forests. Each site was visited only once each winter.

Criteria used to distinguish sexes.—Sex was determined for all species by plumage characteristics. The criteria were developed from the USFWS banding manual (1984) and supplements from Pyle et al. (1987). There is a likelihood of some error for subtle distinctions (such as between first-year male and female American Redstarts, and male and female Magnolia Warblers. For participants in the visual surveys, interobserver consistency was tested both with mist-netted and observed birds, and it was found to be high for both. For Magnolia Warblers, observer classification from plumage characters was checked independently against wing chord (using a cutoff of 58 mm or greater for males), and they were consistent 97% of the time. Resident Yellow Warbler females were distinguished from migratory females by their grayer upperparts and duller yellow underparts.

TABLE 2. Ratio of males to females in mist-netted samples of warblers. Data were pooled to conduct Chi-square contingency test for heterogeneity in sex ratio.[a]

	Open	Scrub	Low forest	Medium forest	P
Black-and-white Warbler	8:7	0:3	5:15	1:1	NS
Prothonotary Warbler	15:6	1:2	4:2	1:2	NS
Yellow Warbler	4:6	6:7	0:0	0:0	NS
American Redstart	2:19	6:3	4:10	4:3	<0.025
Hooded Warbler	3:11	1:20	9:10	8:1	<0.01
Common Yellowthroat	25:27[b]	22:12	8:0	0:0	<0.025

[a] Data were pooled to make the following comparisons: Black-and-white Warbler, American Redstart, and Hooded Warbler open+scrub habitat vs. forest; Prothonotary Warbler and Common Yellowthroat open habitat vs. scrub+forest; and Yellow Warbler open habitat vs. scrub.

[b] Significant heterogeneity exists between the recently cleared fields (11:24) and the *sabana* or marsh-like habitat (14:3).

TABLE 3. The percentage of males that comprises sightings of dimorphic warblers in scrub and forest habitats (sample size in parentheses).

Species	Scrub	Subdeciduous	Subperennial
Black-and-white Warbler	58 (12)	55 (20)	48 (62)
Northern Parula[a]	37 (83)	59 (27)	67 (48)
Black-throated Green Warbler	47 (30)	50 (40)	63 (72)
Magnolia Warbler[a]	36 (99)	55 (64)	60 (101)
American Redstart[a]	35 (113)	74 (90)	80 (139)
(adult males)[a]	16	48	47
Hooded Warbler[a]	11 (72)	67 (83)	89 (97)

[a] Significant ($P < 0.05$) heterogeneity based on Chi-square contingency test pooled forest vs. scrub data.

Statistical tests.—Testing for differences in the proportion of males in different habitats was by a Chi-square contingency test. For the visual data, tests compared forest and scrub habitats. Because of variable and sometimes small sample sizes, the mist-net data were also grouped. In all cases, adjacent habitats along the successional gradient were pooled. However, because of the differences in distribution across the successional gradient, habitats were grouped in different ways.

RESULTS

Prothonotary Warbler.—The Prothonotary Warbler (*Protonotaria citrea*) was a common transient (mainly in autumn). The few mist-net captures in scrub and forest habitat showed no skew in sex ratio. However, most birds captured in open habitats were males. The difference in sex ratio between open and other habitats was not significant.

Black-and-white Warbler.—Black-and-white Warblers (*Mniotilta varia*) were found primarily in forests. The mist-nets yielded a high proportion of females in the low forest, but sample sizes for other habitats were generally small and the difference between pooled forest and open-scrub samples was not significant. Visual surveys indicated an even sex ratio for scrub and forest habitats.

Northern Parula.—Northern Parulas (*Parula americana*) were found in most terrestrial habitats in Sian Ka'an, but were most common in older secondary-scrub with a substantial number in the canopy of the subperennial forest. Few were mist-netted. Based on the visual surveys, Northern Parulas had a significantly female-biased sex ratio in scrub and male-biased sex ratio in the taller forests (Table 3).

Yellow Warbler.—During winter most of the Yellow Warblers (*Dendroica petechia*) in the Sian Ka'an area were migrants. Yellow Warblers were common, but had a very restricted habitat distribution. They were most common in the natural scrub vegetation (mangrove and coastal scrub), and uncommon in postclearing succession. In the open and scrub habitats considered here, Yellow Warblers displayed an overall even sex ratio with no indication of interhabitat variation. When additional data from coastal scrub were included, the overall sex ratio was also equal (30:32).

Magnolia Warbler.—Magnolia Warblers (*D. magnolia*) were common in every habitat except recently cleared fields, although they were more common in forest than scrub. They were categorized only by sex in the visual surveys (Table 3). There was a small but significant bias towards females in the scrub and towards males in the forest habitats.

Black-throated Green Warbler.—Black-throated Green Warblers (*D. virens*) were most common in forest, and were uncommon in secondary scrub with high densities of *Acacia* and other leguminous trees. Based on the visual surveys (Table 3), we found a nonsignificant trend towards an increased proportion of males in taller forest habitat.

Hooded Warbler.—Hooded Warblers were in every habitat except mangrove scrub. Based on mist-netting (Table 2), we found 8 times as many males as females in medium forest, but only 13% as many males as females in open and scrub habitats ($P < 0.001$). The structurally intermediate low forest had an intermediate sex ratio. Similar results were obtained in the visual survey (Table 3) with the proportion of males ranging from 11% in scrub to 89% in tall forest habitat (overall Chi square, $P < 0.001$).

American Redstart.—American Redstarts (*Setophaga ruticilla*) were numerous in all habitats with at least some woody vegetation. Mist-netting data (Table 2) show that almost all birds in the open habitat were females, whereas males made up 29-67% of the small samples captured in scrub to subdeciduous forest. There was no consistent trend within scrub and forest habitats. Perhaps, because of a larger sample size (particularly for forest habitats), the difference in sex ratio was clearer with the visual survey data. Males made up 74-80% of the forest observations, and only 35% of the scrub observations ($P < 0.001$). The proportion of adult males, where no problem in accurate determination by plumage should exist, also increased dramatically between scrub and forest habitat.

Common Yellowthroat.—The Common Yellowthroat (*Geothlypis trichas*) was the most common warbler in open habitats, but it was absent from all forest types except seasonally flooded low forest. Mist-net captures were significantly skewed towards females in the open pastures and fields (11:24), and male-biased for the older second-growth scrub habitats (30:12). In the natural open habitat, "sabana," males were more common (14:3).

Recaptures.—Of the individual warblers from four species (Table 4), 21% ($n = 223$) were recaptured after at least 30 days from their first capture. Although there was considerable interspecific variation, there was no significant difference in site tenacity between the sexes. Females were recaptured at a slightly and nonsignificantly higher rate (males, 16%; females, 24%). The mean distance between captures and recaptures (activity radius, Table 4) was similar for both sexes in all species, with the possible exception of the American Redstart.

DISCUSSION

Some degree of habitat segregation by sex is the rule for dimorphic warblers that migrate through or winter in the northeastern Yucatan Peninsula. In all five species where there is a significant pattern, males occupy the more mature habitat along the successional gradient. In addition, the Black-throated Green Warbler showed a nonsignificant trend in the same direction. The one exception was in migratory populations of the Prothonotary Warbler. This exception is noteworthy because Prothonotary Warblers have been found commonly in male-female pairs during winter in Panama (Morton 1980, pers. obs.). However, although the sex ratio is female-biased in open habitats, it is not significantly different from the samples from other habitats. Furthermore, sex ratio was based on a small sample of transient individuals.

In the Hooded Warbler, Morton (1990) has argued that the proximate mechanism for sexual habitat segregation is an innate difference in the response to simple cues. Support for this hypothesis comes from two experiments. In one, a removal experiment, females failed to occupy mature forest when the resident males were removed (Morton et al. 1987). In a laboratory experiment, naive hand-reared males and females showed distinct preferences for plant height and habitat structure (Morton 1990). Innate differences in habitat preference should lead to relatively invariant differences in habitat occupied. Habitat segregation in this species is, in fact, nearly complete, particularly when fine-scaled habitat measures are analyzed with multivariate techniques (Lynch et al. 1985). However, few of the species show habitat segregation that is as clearly defined as in the Hooded Warbler. In the case of Magnolia Warblers and Northern Parulas, the magnitude of the segregation was small, although statistically significant. In these situations, the role of dominance interactions between the sexes may be more important. Experiments similar to those conducted on Hooded Warblers would make an interesting comparison. We found no support for the idea that females behave as "floaters" in the nonforest habitat. The overall frequency and pattern of recaptures was similar between the sexes.

Perhaps a more facultative basis for habitat segregation explains the apparent differences between studies for the same species. Holmes et al. (1989) reported no consistent habitat segregation between the sexes of American Redstart in four Jamaica study areas. Another explanation is that the same degree of habitat segregation occurs in Jamaica and Mexico, but the study in Jamaica focused on a more narrow and structurally intermediate range of habitats.

Two possibilities have been presented for the evolution of habitat segregation in Hooded Warblers (Lynch et al. 1985). One explanation holds that differences in sex roles during the breeding season may lead to asymmetrical dominance relationships in the winter. Males, the larger and more aggressive sex, are able to exclude females from the better habitat. An alternative hypothesis is that the two habitats represent different adaptive peaks. Males and females are best adapted for feeding and avoid-

TABLE 4. Activity radius (mean [±SD] intercapture distance) and recaptures for four species of warblers. The sex ratio of recaptures is not significantly different from the sex ratio of captures in any species (Chi-square contingency test); sample sizes are in parentheses.

Species	Sex	Activity radius (m)	Captures	Recaptures
Black-and-white Warbler	M	87 ± 44 (33)	14	3
	F	65 ± 32 (39)	26	9
American Redstart	M	37 ± 21 (16)	16	3
	F	93 ± 35 (47)	35	10
Hooded Warbler	M	100 ± 81 (33)	21	6
	F	82 ± 40 (42)	42	9
Common Yellowthroat	M	80 ± 37 (43)	41	3
	F	57 ± 38 (33)	36	4

ing predators in their preferred habitats. We cannot help distinguish these two hypotheses. However, these observations and others (for Black-throated Blue Warblers, *Dendroica caerulescens;* Wunderlie pers. comm.) suggest that habitat preference is not an arbitrary feature of a particular sex for a particular species. Rather, there seems to be a repeated pattern: male warblers are associated with forest and females with more open habitats.

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