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HABITAT SEGREGATION BY SEX IN THE HOODED WARBLER: EXPERIMENTS ON PROXIMATE CAUSATION AND DISCUSSION OF ITS EVOLUTION

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Ecologists often study habitat selection in highly mobile animals, such as birds, by describing habitat use rather than by exploring underlying mechanisms. Several underlying mechanisms have been suggested. Food assessment may control and continually adjust habitat selection (habitat selection as a branch of optimal-foraging theory; Rosenzweig 1985). Habitat may be selected largely innately or, as Hutto suggested (1985), by the use of innate cues coupled with varying degrees of modification by food assessment and other means. Habitat imprinting, habitat use governed through an age-dependent learning period, has also been suggested (see, e.g., Wecker 1963).

Experimental tests of mechanisms are rare (Morse 1985), even though the contribution of innate mechanisms to habitat selection received experimental support some time ago (see, e.g., Klopfer 1965; Wiens 1972). More recently, Partridge (1974) showed that laboratory-raised coal tits (*Parus ater*) and blue tits (*P. caeruleus*) maintain species-typical preferences for the foliage types they prefer in nature: pine and oak, respectively. Furthermore, she showed that each species was best at exploiting the type of food encountered in its natural habitat (Partridge 1976). By using congeners, genetic and morphological differences between the two species were reduced to produce a meaningful comparison. Greenberg (1983, 1984*a*,*b*, 1987*a*,*b*) extended the discussion of innate influences in habitat selection to the use of foraging microhabitats. He showed that *Dendroica* warblers differ in their fear responses toward foraging substrates not experienced previously (neophobia). Greenberg viewed neophobia as a simple proximate mechanism controlling an individual's tendency to explore new microhabitats: as neophobia increases, foraging plasticity decreases. Although the cues underlying habitat choice may necessarily be simple if they are controlled genetically (Lack 1971; Partridge 1978), the importance of genetically based mechanisms compared with other causes of habitat selection remains little known but highly relevant to theory in ecology and evolution.

In contrast to previous studies, the hooded warbler (*Wilsonia citrina*) provides an opportunity to study factors underlying habitat selection through intraspecific

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comparisons. In the Neotropics, males and females occupy nonbreeding (wintering) territories (Rappole and Warner 1980) that differ markedly in physiognomy (Lynch et al. 1985). Females' territories are located in late-successional shrub or brushy fields, often in dry, deciduous habitat. In contrast, males defend territories in second-growth or mature forests. Individual birds defend their territories against conspecifics of either sex (Rappole and Warner 1980; pers. obs.).

What proximate factors cause this habitat segregation? Hooded warblers breed in deciduous forest in southeastern North America. The wintering habitats used by males appear more similar to breeding habitats (in the sense of James 1971) than do the female wintering habitats. This suggested an initial hypothesis that forest habitat would be the "preferred" habitat for overwintering territories. Therefore, the observed habitat segregation might be due to an active exclusion of females from forests by the larger males (Lynch et al. 1985). Support for this hypothesis would suggest that competitive displacement had occurred (Slatkin 1984) and unite closely the proximate and ultimate causation of this habitat segregation.

This hypothesis was not supported by a field removal experiment in Mexico, which showed no effect of the absence of males on habitat use by females (Morton et al. 1987). Females appeared to choose shrub habitat over forest, even without males present to exclude them from it. Importantly, this preference was not associated with the different foraging substrates present in the two habitats (e.g., males have potential access to forest canopy; females do not). We found no difference in foraging height, rate, or maneuvers between the sexes in their respective habitats (Morton et al. 1987).

Here, I test an alternative hypothesis concerned with proximate causation, that the sex difference in habitat preference by hooded warblers is largely innate. Hand-raised hooded warblers, with no experience in choosing natural habitats, were used to determine if the sexes differentiated between artificial habitats in the laboratory. The laboratory experiments were designed to simulate the differences in habitat between the sexes as observed in nature. If the laboratory-raised birds demonstrated such differentiations in one or both sexes, a strong innate contribution to the habitat segregation discovered through field observations would be supported.

In addition, field observations of males and females using habitat that appeared atypical for their sex provide insight into the way in which habitat-selection cues interact with complex natural habitats to produce sexual segregation. This approach provided an independent means of testing the efficacy of the cues identified in the laboratory to predict habitat use in nature.

METHODS

I obtained 22 nestling hooded warblers, 4–5 days of age, from eight nests found in June and July of 1984 and 1985 at a breeding site in northwestern Pennsylvania. Sex was determined after the post-juvenal molt began 2–3 wk after fledging, when males began to acquire black feathers on their heads and throats. The sex ratio was 4.4 males to each female, and, since entire broods were collected for handraising, this was a natal sex ratio. This male-biased sex ratio resulted in an imbalance in the sex ratio of experimental subjects. In the two years, 17 young (13 males, 4 females) were raised to independence. At fledging, the birds were divided randomly by sex among five indoor aviaries (2 × 3 × 3 m) provided with wooden dowels and branches for perches. Mealworms (*Tenebrio* sp.) and a blended mixture of meat, boiled eggs, carrots, baby cereal, and vitamins were fed ad libitum from food cups. The birds were kept on the breeding-season (ambient) light regime until late September, when a photoperiod of 12 h light and 12 h darkness, resembling that of their tropical wintering range, was maintained. Experiments began at this time and lasted until late March of 1985 and 1986.

A separate room (3.4 m long × 3.2 m high × 2.7 m wide) was used for all experiments. Walls and ceiling were covered with acoustic tile; the floor was covered with wood chips to produce a uniform background. Light was provided by four 200-watt bulbs evenly arrayed over the length of the room. The birds were observed from an adjacent room through a window fitted with one-way glass. In all experiments, a single bird was removed from its "home" cage and carried in a paper bag to the experimental room. The paper bag was placed on the floor in the center of the experimental room, the observer entered the adjacent room, and the bird was allowed to "escape" from the paper bag. No food was provided during the experiment. Data on the bird's location were taken for 20 min. The bird was then recaptured and returned to its "home" cage in the holding room. A bird was tested with at least 1 wk separating each 20-min trial. All but one of the birds were used at least twice. Some individuals were used only two times and then released during the migration period, because there was insufficient cage space for housing all birds throughout the winter.

Experiment 1

The field measurements of male and female winter territories suggested that males might prefer taller vegetation than females. Experiment 1 was designed to test the null hypothesis that males and females would show no preferences in their use of two three-dimensional habitats. The artificial habitats were constructed to reflect two major physiognomic differences in natural territories, height and density (Lynch et al. 1985). Because of the limited size of the experimental room, both habitats contained plants within the size range of vegetation found in nonbreeding territories of wild females. The habitats differed in this way: the "tall" habitat consisted of 10 2.29-m-tall stems (ca. 3.8 cm in diameter) of Japanese bamboo (*Polygonum cuspidatum*) stuck vertically in a 1-m^2, 15-cm-thick piece of Styrofoam, and the "short" habitat consisted of 18 1.07-m-tall stems (ca. 1.9 cm in diameter) of Japanese bamboo stuck in a separate piece of 1-m^2, 15-cm-thick Styrofoam. The tall habitat, with branches and leaves starting 0.9 m up the stems, resembled a small stand of upright saplings; the short habitat resembled a dense shrub. The two habitats were set on the floor against opposite walls, separated by 0.75 m. Time spent in each habitat (in seconds) was recorded during each 20-min trial. In all, 85 trials were run with 15 birds. After all birds had been tested once or twice, the positions of the habitats were switched to control for any possible preference for habitat location rather than structure. The results of all trials were averaged for each bird and analyzed using the Wilcoxon matched-pairs, signed-ranks test (Siegel 1956; Owen 1962).

Experiment 2

Experiment 2 was designed to test whether the sexes differentiate between forest and shrub habitats using cues provided by the angles that the branches and trunks formed relative to the ground. Forests have many vertical elements (tree trunks), whereas shrub habitats have more-oblique visual elements and lack vertical tree trunks. To represent these differences, I placed identical lengths of 6.4-cm-wide black crepe paper on sections (2.1 × 2.4 m) of opposite walls of the room. On one wall, the crepe-paper strips ran vertically; on the other, they were placed at oblique angles. Two perches, 1 m above the floor, ran parallel to and 1 m away from each wall. I used 20-min trials to test the null hypothesis that males and females would not differ in their orientation toward the two-dimensional "habitats." A bird was said to be oriented toward a given wall if the bird's bill pointed toward that wall or within 90° of the perpendicular to it. The number of seconds a bird oriented itself toward each wall was timed with a stopwatch by an observer blind to the hypothesis being tested. The "habitats" were switched to opposite walls to control for position effects. Trials for each bird were averaged, and Mann-Whitney *U*-tests were used to compare sexes.

In addition to the habitat-preference experiments, I used naive birds from year one to test for the presence of a preferred light intensity (Klopfer 1967). Unlike habitat segregation, which has been well documented among wild hooded warblers, habitat preference based on a light-intensity cue has not been shown. Indeed, male territories in the highly deciduous, second-growth forests of Yucatán are often as sunlit as the shrubby fields used by females. In the laboratory, a light-intensity gradient was produced by unscrewing some light bulbs and by blocking the side of the remaining lights facing the "dark" end of the room. Six perches, running the width of the room and perpendicular to the light-intensity gradient, were equally spaced. In each 20-min trial, the time spent on each numbered perch was recorded. I reversed the light-intensity gradient to control for position effect.

Fieldwork on hooded warbler wintering territoriality has been published elsewhere (Lynch et al. 1985; Morton et al. 1987). Additional observations of several female warblers when no males were present were made in Panama in 1987, and breeding-season and postbreeding, premigration observations were obtained in northwestern Pennsylvania from 1985 to 1987. The field observations are discussed following the results of the laboratory tests.

RESULTS

Experiment 1: Three-Dimensional, Artificial, Tall and Short Habitats

Males spent more time in the tall artificial habitat ($T = 2.93$; $P < 0.002$, comparing $\bar{X}$ s/trial with the Wilcoxon matched-pairs, signed-ranks test), whereas females showed a nonsignificant tendency ($T = 1.83$; $P < 0.50$) to use the short

TABLE 1

Experimental Habitat Preference of Eleven Male and Four Female Hooded Warblers, in Seconds per Twenty-Minute Trial

Bird No.	Males: Tall Habitat	Males: Short Habitat	Males: *N*	Females: Tall Habitat	Females: Short Habitat	Females: *N*
1	1157 ± 29	28 ± 23	5	300 ± 300	900 ± 300	4
2	972 ± 107	144 ± 32	3	518 ± 167	682 ± 166	4
3	767 ± 266	392 ± 275	4	1200 ± 0	0	4
4	510	0	1	290 ± 205	901 ± 202	6
5	983 ± 217	272 ± 243	5			
6	841 ± 286	16 ± 16	4			
7	1180 ± 20	0	4			
8	828 ± 284	358 ± 286	4			
9	1110 ± 10	19 ± 6	2			
10	1076 ± 124	124 ± 124	2			
11	730 ± 470	24 ± 165	2			

Note.—Values are means ± one standard error. *N*, The number of trials run on the bird.

TABLE 2

Preference for Vertical or Oblique Lines by Three Male and Three Female Hooded Warblers, in Seconds per Twenty-Minute Trial

Bird No.	Males: Vertical	Males: Oblique	Males: *N*	Females: Vertical	Females: Oblique	Females: *N*
1	1121	79	3	722	479	2
2	845	298	3	307	727	4
3	993	130	4	0	1200	3

Note.—Warblers faced two-dimensional arrays of vertical and oblique black crepe-paper strips mounted on walls. Values are seconds. *N*, The number of trials run on the bird.

habitat (table 1). Males spent 12 times as many minutes in the tall habitat as in the short habitat. Mean time per trial spent in either habitat, as opposed to the floor or wall, was nearly the same for males and females (17.05 vs. 19.96 min, respectively). I conclude that males either were averse to using the short habitat or preferred the tall habitat. Females as a group showed no clear preference for one over the other.

Experiment 2: Orientation to Vertical versus Oblique Stripes in Two Dimensions

With the experimental room empty except for the wire perch, males and females differed significantly in their orientation toward the two patterns of black stripes ($U = 0$; $P < 0.05$). Females tended to face the wall with crepe-paper stripes aligned obliquely, whereas males faced the wall with vertical stripes (table 2). This significant difference in orientation persisted regardless of the perch used by the bird (i.e., the birds did not simply orient toward the wall either closest to or farthest from their perch).

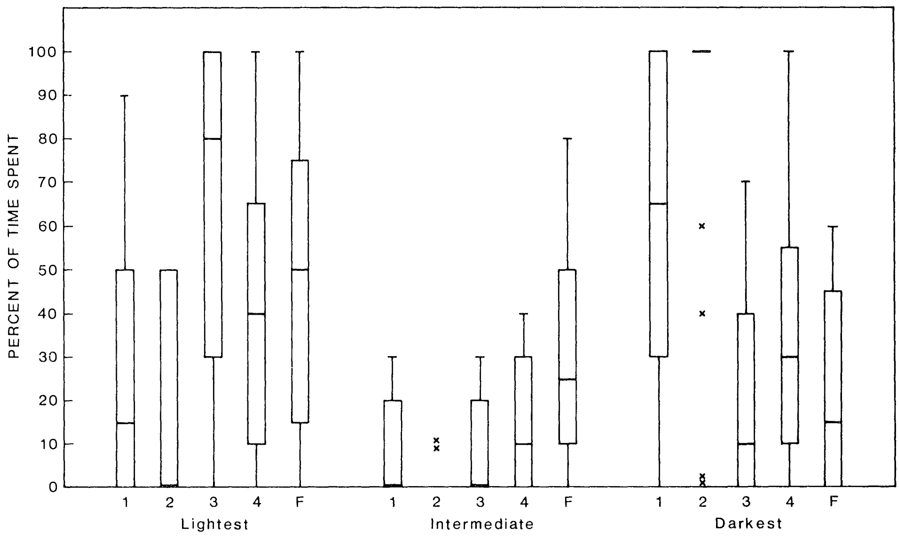

FIG. 1.—Box plot (Emerson and Strenio 1983) of time spent by four male (1–4) and one female (*F*) hooded warblers (12 trials per bird) in portions of the experimental room with varying light intensities. *Middle horizontal line*, Median time; *upper and lower ranges of boxes*, upper and lower quartiles; *vertical line*, range among trials; X, outlying values.

Light Intensity

I predicted that, if light had an influence on habitat choice, males would prefer darker portions, and females would prefer lighter portions, of the experimental room. A box plot (Emerson and Strenio 1983) of time spent by the five warblers available in year one (four males and one female) in the lightest, intermediate, and darkest parts of the experimental room showed no tendency for such a difference in males (fig. 1). Light intensity alone would not produce habitat segregation by precluding males from using the open habitat used by females. Furthermore, males in winter territories are seen commonly in leafless, sunlit, deciduous-forest habitat, and, conversely, females often use heavily foliaged, dark habitat (pers. obs.). Therefore, the laboratory results for males are in agreement with field observations. The field observations also suggest that naive females are unlikely to respond differentially to light cues in the laboratory, but this remains to be tested. It should be pointed out, however, that the experimental birds had not experienced a strong light gradient previously, their holding cages being evenly lit relative to the experimental room. Thus, a learned association between light intensity and appropriate habitat in wild birds cannot be ruled out.

DISCUSSION

Experiments on Cues Used by Naive Warblers

Taken together, the experiments showed that hooded warblers exhibited a sexual difference in habitat preference paralleling that found in wild warblers.

This difference occurred even though the birds were raised in captivity from the nestling stage, inexperienced with natural habitats, and without the influence of social learning from adults that might produce sex-biased habitat imprinting. The use of habitat-naive subjects shows that their nonrandom habitat choice in the laboratory is based on innate, not experientially derived, preferences (Partridge 1978). Experiment 1 showed that males avoided the low, shrubby habitat but that females showed no preference for either the tall or short artificial habitat. Females were not predicted to make a choice in this experiment, since both habitats were within the range of vegetative physiognomy used by wild females for nonbreeding territories. Males were predicted to choose the tall habitat, and this was confirmed.

Special attention was given to the behavior of the birds being tested to justify the assumption that they were assessing the artificial habitats. First, the birds made choices because they moved between the artificial habitats an average of 4.9 times per trial. They did not simply remain within the first habitat encountered. Second, if the preference shown was based on a simple comparison of the volume of the two habitats, with the birds occurring in the more voluminous one solely by chance, the tall habitat would have been used more than the short one by both sexes. That females did not choose between habitats on the basis of relative volume suggests strongly that they used other cues. Leaf shape, density, and arrangement on stems were ruled out, since the same plant species was used in both habitats, although stem thickness did differ, as described above.

However, the differences in structure of the artificial habitats (see also the next subsection) suggested that the cues used by wild birds may be structurally simple ones. Experiment 2 supported the idea that, in choosing territorial habitat, birds cue on the predominance of vertical visual elements of forest vegetation (tree trunks) and of oblique visual elements in shrubby field plants. The relative verticality of plant growth form provides a minimum, yet sufficient, cue to underlie the wintering and postbreeding habitat segregation in hooded warbler sexes.

Support for the Use of Minimal Cues from Field Observations

The use of simple proximate cues for habitat choice by birds does not imply inflexible habitat selection. Habitats used by both sexes of hooded warblers encompass a wide range of the forest-to-field continuum (Lynch et al. 1985) because a simple cue may occur in a variety of habitats. The cues uncovered by the laboratory trials (that males prefer vertical and females prefer oblique vegetative growth forms) were further tested by examining field sites that did not seem to fit the general finding that males inhabit forests and females inhabit scrub. For example, a narrow band of forest on the coast of central Quintana Roo, Mexico, consists of dense trees about 6 m tall; I predicted that this habitat would be occupied by males. Surprisingly, it was occupied almost exclusively by females (Lynch et al. 1985). The laboratory study provides an answer to the mystery of this seeming exception in habitat use: prevailing onshore winds (and hurricanes) caused the vegetation to grow at an angle about 25° from vertical. The experiments suggest that, since few vertical elements were present, females predominated. Similarly, on Isla Bastimentos, Bocas del Toro Province, Panama, female

hooded warblers occupy territories in virgin forest, but only near the coast, where rainstorms frequently blow down trees. Although the trees grow back, many live vine tangles are left at ground level, increasing oblique growth forms in this forest. Conversely, males predominate in dense, short (2-m) stands of vertical saplings that sprouted from fallow cornfields near Chichén Itzá, Yucatán, Mexico (fig. 2). The habitat designations ''forest'' and ''shrubby field,'' while generally predictive of where the sexes are found, thus have many exceptions. These field observations, together with the laboratory results, suggest that the birds respond to cues based on the relative verticality of the vegetation.

Are These Habitat Cues Used Only in the Nonbreeding Season?

Since male and female hooded warblers both live in forests in the breeding season, do habitat cues change seasonally for males and females, perhaps converging? Two lines of evidence suggest that the answer is no.

The first is illustrated in the niche-gestalt analysis by James (1971). She presented outline drawings of vegetative structural elements that were consistently present in the breeding territories of six warbler species. The hooded warbler was the only species whose breeding habitat contained the combination of dense shrubs and forest that occurs where tree falls provide light gaps for shrub and blackberry (*Rubus* sp.) growth. Apparently, habitat cues that cause territorial separation between the sexes in the nonbreeding season must be found combined (in unknown proportions) in breeding territories.

The second line of evidence derives from observations of habitat use in the breeding and postbreeding season in northwestern Pennsylvania (pers. obs.). During the pairing and incubation stages of reproduction, males sing and forage from subcanopy positions, but they also forage at their usual stations near the ground. When feeding nestlings and fledglings, and during postbreeding molt, males forage near the ground, as in the nonbreeding season. They use subcanopy posts not so much for foraging as for singing; the acoustics are better there (Wiley and Richards 1982; Morton 1986). Males remain near the ground and do not use song for the defense of winter territories (Morton et al. 1987). Females forage and place nests about 45 cm above the ground in thickets. After breeding, four color-marked females left their forested breeding territories and established feeding and molting territories in adjacent shrub habitat. By mid-to-late August, females were found in dense brush along nonforested portions of streams and in *Rubus* patches at the forest edge. In contrast, their mates remained within the forest in their breeding territories throughout postbreeding molt. I do not know why the females

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FIG. 2 (*facing page*).—*Upper*, The interior of a territory of female hooded warblers within virgin rain forest on Isla Bastimentos, Bocas del Toro Province, Panama. No males were found on the island. Note the abundance of oblique branching caused by canopy vines that fell to the forest floor in past storm blowdowns. *Lower*, A mist-net lane through short, dense trees, approximately 7 yr old, growing in an abandoned Mayan cornfield near Chichén Itzá, Yucatán, Mexico. Although not ''forest-like'' in appearance, only male hooded warblers used this habitat. Note the predominant verticality of the trunks, which are less than 9 cm in diameter.

TABLE 3

MECHANISMS AND POSSIBLE CONSEQUENCES OF ASYMMETRIES IN INTERSEXUAL COMPETITION FOR WINTER TERRITORIES

Trait	Mechanism	Evolutionary Consequences
Size dimorphism	unequal competition	habitat segregation geographical separation nonterritoriality of one sex size convergence
Age	unequal competition	all of the above nonterritoriality, floating
	equal competition	none
Foraging habit		
Generalism	unequal competition	all of the above foraging divergence sexual dichromatism
	equal competition	sexual monochromatism
Specialization	unequal competition	geographical separation nonterritoriality of one sex sexual dichromatism
	equal competition	sexual monochromatism

moved out. No aggression was observed between former breeding partners that might have caused the females' exodus.

This premigration separation suggests that the more complete habitat separation observed in the tropics results from sex differences in habitat preference combining with nonoverlapping, individual territoriality. Theoretically, in an area large enough to hold many territories, male and female territories would be randomly dispersed if vertical and oblique habitat cues were equally common. Apparently, obligate territoriality has made vertical separation or differential niche utilization unlikely as intersexual-avoidance mechanisms (Selander 1966; Bell 1986). Conversely, cohabitation during the breeding season necessitates habitats that contain both vertical tree trunks and oblique shrub elements. The resulting mixture restricts the hooded warbler to a subset of the forest habitat available for breeding, as described by James (1971).

The Ultimate Causation of the Evolution of Nonbreeding Habitat Segregation by Sex

The habitat segregation in hooded warblers discussed here is a form of sexual dimorphism. Slatkin (1984) suggested that the extent of genetic correlation between the sexes does not affect the likelihood that a species will evolve sexual dimorphism. If true, habitat segregation may evolve rapidly and is not likely to be restricted to hooded warblers. If nonbreeding males and females compete territorially for identical habitat, any asymmetry in the probability that one sex will win over the other results in selection favoring those individuals of the losing sex that adopt other tactics. Table 3 lists the likely causes of initial asymmetries and some alternative tactics. One prediction is that a species having sexes equal in size will not exhibit habitat segregation. Furthermore, such a species is more likely to be sexually monochromatic, an adaptation resulting from intersexual competition for winter territories (see the following subsection).

Many species of migrant birds exhibit an important ingredient of selection that might favor sexual habitat segregation—territoriality in the nonbreeding season (Rappole et al. 1983). For example, wintering adult male American redstarts (*Setophaga ruticilla*) predominate in mature forests, whereas females and subadult males are common in brushy second growth (pers. obs.; Lynch, unpubl. data).

The hooded warbler illustrates several attributes that are likely to have led to its habitat segregation. Males, since they are heavier than females, are more likely to win in aggressive encounters. Hooded warblers visually detect prey at distances ranging from a few centimeters to 2 m and then chase or glean it. This generalized foraging style would not pose as much of an obstacle to selective pressures favoring habitat segregation as would foraging methods tied to specific habitats or microhabitats. (In contrast, a worm-eating warbler [*Helmitheros vermivorus*], which feeds by probing in dead leaves caught in foliage, might find less to forage in shrubby fields than in forests.) Since male hooded warblers could forage in a greater vertical range in their habitat, but do not differ from females in this respect, it seems unlikely that new foraging opportunities contributed directly or indirectly to habitat segregation in this species.

Conditions favoring habitat segregation might just as easily favor geographical displacement (Ketterson 1979). However, for unknown reasons, geographical separation between the sexes in birds that migrate from North America to the tropics may be rare, having been suggested for only one species so far (Pearson 1980; Greenberg 1986).

Ultimate Causation, Proximate Cues, and Female Plumage Variation

Plumage coloration reflects complex sources of selection often derived largely from social interaction. Attention to plumages has emphasized males (Lyon and Montgomerie 1986; Rohwer and Butcher 1988). Hooded warbler plumages are particularly variable in the female, uniform in the male. Here, I hypothesize that this variability is correlated with a recent change, caused by humans, in the distribution and abundance of female wintering habitat.

In their first winter, male hooded warblers obtain a complete black "hood" and cannot be readily differentiated from older males by plumage. The situation is quite different for females. The first prebasic molt in females results in a yellow-green plumage devoid of melanism. Birds overwinter and breed in this subadult plumage. Before their second overwintering period, the female prebasic molt results in a plumage that varies greatly in melanism. Females range from being nearly completely yellow-green to being almost indistinguishable from males in the degree to which the black "hood" is developed. The extremely melanistic females are rare, constituting about 1%–6% of museum skins, a figure representative of field observations (Lynch et al. 1985). Because they are less common, highly melanistic females were assumed to be the oldest individuals, the premise being that females become more melanistic with age. However, observations of captive females and recaptured wild females show that females do not change in the extent of melanism after their second prebasic molt (Morton 1989). The highly variable adult female plumage does not represent an age-related change. What could explain the uniformity and existence of the subadult plumage, the variation in adult female plumage, and the uneven distribution of the amount of black "hood" coloration in females, particularly the rarity of the most highly melanistic females?

Rohwer and Butcher (1988) suggested that subadult plumages in males may evolve rapidly because between-population differences in the occurrence of such a plumage were discovered in two species. Rapid evolution may also characterize female hooded warbler plumage. Could the relatively low proportion of adult females with male-like melanism reflect anthropogenic habitat changes in the primary wintering grounds?

Perhaps, before the extensive development of swidden agriculture by the Maya, selection favored females, in their first winter, that did not compete for territories in forest habitat. This seems likely since this age class lacks both site dominance and experience, and it is competing against both larger males and experienced, older females. Hooded warblers return to previously held winter territories (Rappole and Morton 1985). With the odds against them, those subadult females that avoided territorial conflicts with adults should have been favored by natural selection. The distinctive non-melanistic subadult female plumage in hooded warblers may be an adaptation to reduce conspicuousness in open habitats or, alternatively, to help subadult females avoid conflicts with wintering adults. This latter function has been ascribed to the dull plumage color in some populations of yellow warblers (*Dendroica petechia*; Morton 1976). The black throat is displayed by males in an upright, aggressive posture (Rappole and Warner 1980), and females also use this upright throat display.

Before the advent of slash-and-burn agriculture approximately 4000 years ago (Harrison and Turner 1978), it is likely that adult female hooded warblers interacted with males more extensively than they do now. Forest habitat must have been more continuous, commonly interrupted by tree falls, a feature typical of mature tropical forests (Brokaw 1982). If wintering females avoided forests then, as they do today, they may have been restricted to tree-fall gaps. But females using tree-fall gaps would have been surrounded by males. Even now, females interact more with males where forests are extensive and mature (Rappole and Warner 1980; Rappole, pers. comm.). Thus, male-female interactions must have been extensive before Mayan agriculture began. I suggest that a higher probability of male-female interactions would produce selection favoring the black throat in females, as long as females settled in habitats less preferred by males. In habitats less preferred by males, females are able to defend territories against intrusion by males (pers. obs.; Rappole and Warner 1980). If females encounter males commonly, a black throat should enhance the threat of the females' upright throat display against the males. Because of this source of selection favoring a common threat-signaling system, I speculate that hooded warblers may have been less sexually dichromatic before swidden agriculture than they are at present.

With the advent of swidden agriculture, a mosaic of forest and shrub habitat was created. For thousands of warbler generations, these unnatural, adjacent patches of forest and shrub provided more habitat for female territories. Most importantly, male-female interactions in these patches were much reduced relative to female-female interactions. With females competing more among themselves, selective pressure favoring the females' signaling via a male-like melanistic throat would be reduced. This should not imply that melanistic females prefer tree-fall gaps in the forest for winter territories. Breeding-season events might contribute by favoring sexual dichromatism to speed pairing. Alternatively, with a reduction in nonbreeding male-female interactions, the adult female may be converging toward the subadult female plumage, perhaps because the yellow-green plumage is more cryptic in open habitats. I view the current variability in adult female melanism, and the rarity of the fully developed hood, as representative of a change in the "best solution" to the ultimate source of selection that favored habitat separation, the greater fighting ability of the larger males.

SUMMARY

Although habitat choice has been shown to have an innate basis in some vertebrates, few experimental studies have been performed, and these most often relied on interspecific comparisons. Male and female hooded warblers (*Wilsonia citrina*) defend territories in markedly different habitats while wintering in the tropics. Males use forests; females use shrub or field habitats. I used naive hand-raised warblers in experiments designed to test for sex-related innate differences in habitat selection. Choosing between two three-dimensional artificial habitats, males chose the tall habitat with separated stems over the short habitat with dense stems, whereas females showed no preference. Field observations and a laboratory experiment with the naive birds showed no habitat preferences based on light intensity. Finally, naive warblers were exposed to a two-dimensional array of black stripes on opposite walls of an experimental room, one wall with the black stripes arranged vertically and the other with the stripes arranged at oblique angles to the floor. Males oriented toward the vertical stripes, whereas females oriented toward the oblique stripes. Since forests have more vertical structures than shrubby fields, an innate preference for cues based on vertical or oblique cues is a sufficient proximate mechanism to bring about the observed habitat segregation between the sexes in wild birds.

I discuss possible sources of selection favoring the evolution of intraspecific habitat segregation by sex. A hypothesis is presented to explain the presence of a subadult female plumage and a highly variable adult female plumage as they relate to habitat segregation in the hooded warbler. I suggest that this unusual plumage variability in females resulted from changes in the habitat available to females after swidden agriculture began in their main wintering area.

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LITERATURE CITED

Bell, H. L. 1986. Sexual differences in the behavior of wintering golden whistlers *Pachycephala pectoralis* at Wollomombi, N.S.W. Emu 86:2–11.

Brokaw, N. V. L. 1982. Treefalls: frequency, timing, and consequences. Pages 101–108 *in* E. G. Leigh, A. S. Rand, and D. M. Windsor, eds. The ecology of a tropical forest, seasonal rhythms and long-term changes. Smithsonian Institution Press, Washington, D.C.

Emerson, J. D., and J. Strenio. 1983. Boxplots and batch comparison. Pages 58–96 *in* D. C. Hoaglin, F. Mosteller, and J. W. Tukey, eds. Understanding robust and exploratory data analysis. Wiley, New York.

Greenberg, R. 1983. The role of neophobia in determining the degree of foraging specialization in some migrant warblers. Am. Nat. 122:444–453.

———. 1984*a*. The role of neophobia in the foraging site selection of a tropical migrant bird: an experimental study. Proc. Natl. Acad. Sci. USA 81:3778–3780.

———. 1984*b*. The winter exploitation systems of bay-breasted and chestnut-sided warblers in Panama. Univ. Calif. Publ. Zool. 116:1–107.

———. 1986. Competition in migrant birds in the nonbreeding season. Curr. Ornithol. 3:281–308.

———. 1987*a*. Development of dead leaf foraging in a tropical migrant warbler. Ecology 68:130–141.

———. 1987*b*. Seasonal foraging specialization in the worm-eating warbler. Condor 89:158–168.

Harrison, P. D., and B. L. Turner. 1978. Pre-Hispanic Maya agriculture. University of New Mexico Press, Albuquerque.

Hutto, R. L. 1985. Habitat selection by nonbreeding, migratory land birds. Pages 455–476 *in* M. L. Cody, ed. Habitat selection in birds. Academic Press, New York.

James, F. C. 1971. Ordinations of habitat relationships among breeding birds. Wilson Bull. 83:215–236.

Ketterson, E. D. 1979. Aggressive behavior in wintering dark-eyed juncos: determinants of dominance and their possible relation to geographic variation in sex ratio. Wilson Bull. 91:371–383.

Klopfer, P. H. 1965. Behavioral aspects of habitat selection. Wilson Bull. 77:376–381.

———. 1967. Behavioral stereotypy in birds. Wilson Bull. 79:290–300.

Lack, D. 1971. Ecological isolation in birds. Blackwell, Oxford.

Lynch, J. F., E. S. Morton, and M. E. Van der Voort. 1985. Habitat segregation between the sexes of wintering hooded warblers (*Wilsonia citrina*). Auk 102:714–721.

Lyon, B. E., and R. D. Montgomerie. 1986. Delayed plumage maturation in passerine birds: reliable signaling by subordinate males? Evolution 40:605–615.

Morse, D. H. 1985. Habitat selection in North American parulid warblers. Pages 131–158 *in* M. L. Cody, ed. Habitat selection in birds. Academic Press, New York.

Morton, E. S. 1976. The adaptive significance of dull coloration in yellow warblers. Condor 78:423.

———. 1986. Predictions from the ranging hypothesis for the evolution of long distance signals in birds. Behaviour 99:65–86.

———. 1989. Female hooded warbler plumage does not become more male-like with age. Wilson Bull. 101:460–462.

Morton, E. S., J. F. Lynch, K. Young, and P. Mehlhop. 1987. Do male hooded warblers exclude females from nonbreeding territories in tropical forest? Auk 104:133–135.

Owen, D. B. 1962. Handbook of statistical tables. Addison-Wesley, Reading, Mass.

Partridge, L. 1974. Habitat selection in titmice. Nature (Lond.) 247:573–574.

———. 1976. Field and laboratory observations on the foraging and feeding techniques of blue tits (*Parus caeruleus*) and coal tits (*Parus ater*) in relation to their habitats. Anim. Behav. 24:534–544.

———. 1978. Habitat selection. Pages 351–376 *in* J. R. Krebs and N. B. Davies, eds. Behavioural ecology: an evolutionary approach. Sinauer, Sunderland, Mass.

Pearson, D. L. 1980. Bird migration in Amazonian Ecuador, Peru, and Bolivia. Pages 273–284 *in* A. Keast and E. S. Morton, eds. Migrant birds in the Neotropics: ecology, behavior, distribution, and conservation. Smithsonian Institution Press, Washington, D.C.

Rappole, J. H., and E. S. Morton. 1985. Effects of habitat alteration on a tropical avian forest community. Pages 1013–1021 *in* P. A. Buckley, M. S. Foster, E. S. Morton, R. S. Ridgely, and F. G. Buckley, eds. Neotropical ornithology. Ornithol. Monogr. 36. American Ornithologists' Union, Washington, D.C.

Rappole, J. H., and D. W. Warner. 1980. Ecological aspects of migrant bird behavior in Veracruz, Mexico. Pages 353–393 *in* A. Keast and E. S. Morton, eds. Migrant birds in the Neotropics: ecology, behavior, distribution, and conservation. Smithsonian Institution Press, Washington, D.C.

Rappole, J. H., E. S. Morton, T. E. Lovejoy, and J. L. Ruos. 1983. Nearctic avian migrants in the Neotropics. U.S. Department of the Interior, Fish and Wildlife Service, Washington, D.C.

Rohwer, S., and G. S. Butcher. 1988. Winter versus summer explanations of delayed plumage maturation in temperate passerine birds. Am. Nat. 131:556–572.

Rosenzweig, M. L. 1985. Some theoretical aspects of habitat selection. Pages 517–540 *in* M. L. Cody, ed. Habitat selection in birds. Academic Press, New York.

Selander, R. K. 1966. Sexual dimorphism and differential niche utilization in birds. Condor 68:113–151.

Siegel, S. 1956. Nonparametric statistics for the behavioral sciences. McGraw-Hill, New York.

Slatkin, M. 1984. Ecological causes of sexual dimorphism. Evolution 38:622–630.

Wecker, S. C. 1963. The role of early experience in habitat selection by the prairie deermouse *Peromyscus maniculatus bairdi*. Ecol. Monogr. 33:307–325.

Wiens, J. A. 1972. Anuran habitat selection: early experience and substrate selection in *Rana cascadae*. Anim. Behav. 20:218–220.

Wiley, R. H., and D. G. Richards. 1982. Adaptations for signal transmission and signal detection. Pages 131–170 *in* D. E. Kroodsma and E. H. Miller, eds. Acoustic communication in birds. Vol. 1. Academic Press, New York.