

HABITAT SEGREGATION BETWEEN THE SEXES OF WINTERING HOODED WARBLERS (*WILSONIA CITRINA*)

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ABSTRACT.—Overwintering male and female *Wilsonia citrina* defended exclusive feeding territories in the Yucatan Peninsula, Mexico. Woody vegetation ranging from successional scrub to tall evergreen forest was utilized by the species, but males were most abundant in closed-canopy forest of moderate to tall stature, while females were commonest in lower, more open vegetation. The pattern of plumage variation in female *W. citrina* suggests that females with malelike melanistic plumage tend to locate their territories in the kind of habitat occupied by males. Received 17 September 1984, accepted 8 April 1985.

LACK'S (1971) review of ecological isolation in birds emphasized that spatial proximity is an important determinant of competitive relationships. Lack proposed three nested modes of segregation between ecologically similar (hence, potentially competing) species: geography (two similar species have nonoverlapping ranges, so they do not interact), habitat (two similar species co-occur in the same geographic region, but utilize different habitats within a local landscape), and feeding habits (two similar species co-occur in the same habitat, but differ in their foraging location or food type, or both). Lack acknowledged the difficulty of assigning intermediate cases to these three simple categories, but his system nevertheless is useful, in part because it explicitly recognizes the hierarchical character of ecological segregation. Similar species presently separated by range cannot be said to compete, although competition may have occurred in the past; species separated by habitat may show limited interactions along habitat boundaries, but species that exhibit only within-habitat differences in details of feeding strategy (e.g. prey size, foraging height) have the potential to interact pervasively.

Lack's (1971) primary concern was the ecological-evolutionary interactions among similar species (especially congeners), but a spatially oriented view of competition is also useful in analyzing male-female or adult-immature interactions within species. As an example, Se-

lander's (1966) outline of the mechanisms of ecological separation between the sexes of birds is basically conformable with Lack's interspecific scheme (Table 1), although Selander did not point out the inherently hierarchical relationship between spatial proximity and the intensity of ecological interaction.

Birds have provided a number of well-documented cases of within-habitat feeding differences between the sexes (e.g. Pitelka 1950, Kilham 1965, Selander 1966, Storer 1966, Morse 1968, Williamson 1971, Peters and Grubb 1983). Species showing geographic segregation of the sexes during winter occur among ducks (Bellrose et al. 1961, Nichols and Haramis 1980), woodpeckers (Howell 1953), finches (King et al. 1965, Ketterson and Nolan 1976, Balph 1977), and blackbirds (Dolbeer 1982, James et al. 1984).

Sexual segregation by habitat is the most poorly documented of Lack's three major modes of ecological isolation. For obvious reasons, male and female birds are expected to share the same breeding habitat in most species, but there is no a priori reason that sexual differences in habitat could not be expressed during the non-breeding season. Indeed, Nisbet and Medway (1972) found that overwintering male and female Oriental Reed-Warblers (*Acrocephalus orientalis*) differed in their tendency to utilize reed beds in Malaysia, and Koplin (1973) documented winter habitat differences in male and female American Kestrels (*Falco sparverius*) in California. Interpretation of the latter example

TABLE 1. Hierarchical modes of ecological segregation among similar birds, modified after Lack (1971) and Selander (1966). Defense of exclusive territories is expected to arise where there are no feeding differences (far right of the table), or at the interface between similar habitats or microhabitats on an environmental gradient.

Spatial proximity	Remote	Contiguous	Partially overlapping	Completely overlapping
Mode of segregation				
Lack (1971)	Geography	Habitat	Feeding	None
Selander (1966)	Macrogeographic allopatriy	Microgeographic allopatriy	Microhabitat segregation	Foraging behavior
Potential for competition	None	Low	Moderate	High

was somewhat confounded by the presence of a strong geographic gradient in the relative abundance of the sexes that may supercede habitat differences per se.

In the present study we test the hypothesis that well-defined habitat segregation between the sexes exists in nonbreeding populations of the Hooded Warbler (*Wilsonia citrina*), a long-distance migrant whose winter distribution in Middle America does not overlap its breeding range in eastern North America (A.O.U. 1983). This hypothesis originated from the results of a regional survey of the nonbreeding biology of overwintering migratory birds that we conducted in Mexico's Yucatan Peninsula. We observed that male Hooded Warblers were abundant in heavily forested habitats, where females rarely were observed. In contrast, females were relatively common in scrubby, low-stature woodlands and brushy old fields, habitats where males were rare or absent. Overwintering male and female *W. citrina* defend individual feeding territories (Rappole and Warner 1981), and we attempted to verify our impressions of habitat segregation by quantifying characteristics of the vegetation within a representative sample of male and female territories.

METHODS

Fieldwork was conducted from mid-February to early March 1982 in the Mexican states of Yucatan and Quintana Roo. More than 100 forested sites were surveyed for the presence of *W. citrina*, using prerecorded tapes of the Hooded Warbler's aggressive "chip" note played back on a Uher 4000 Report Monitor tape recorder. The tape was played intermittently for 3-5 min at each site, after which time one of us emitted an imitation of a distress "squeak," and another whistled an imitation of the Ferruginous

Pygmy-Owl (*Glauclidium brasilianum*), a diurnal predator on small birds that is common throughout Middle America (pers. obs.). Hooded Warblers of both sexes reacted vigorously to these calls, typically approaching to close range and emitting the distinctive metallic "chip" note. In areas where *W. citrina* were abundant, it was not unusual for us to detect the aggressive call notes of two or even three territorial individuals from a single survey point. We were able to determine the sex of all *W. citrina* that approached closely enough for us to obtain an unobstructed view. Females that were observed at sufficiently close range were assigned a plumage score based on the amount of malelike black pigmentation in the head region (Table 2).

Physiognomic and floristic characteristics of 28 *W. citrina* territories (15 male, 13 female) were quantified using a modified version of the method of James and Shugart (1970). We attempted to avoid bias in our selection of territories by deciding in advance on a given day that we would measure all male and female territories that were encountered, and by including territories from both Quintana Roo and Yucatan for both sexes. We do not claim that our sample ratio of 15:13 male to female territories accurately reflects the true regional sex ratio, although Rappole and Warner (1981) found male and female Hooded Warblers to be essentially equal in abundance during migration in southern Veracruz, Mexico.

The following characteristics were counted or measured within a 0.04-ha circular plot that was centered on the first place we detected an individual *W. citrina* within its territory: mean and maximum canopy height (estimated with the aid of an optical rangefinder device), percent canopy closure (based on 25 vertical sightings through a 10-cm diameter tube), abundance and diameter at 1.5 m height (DBH) of all trees >10 cm DBH, number of woody stems <10 cm DBH (counted in two 22.5 × 1.5-m transects through the center of the plot), and percentage cover of herbaceous vegetation (based on 25 vertical sightings through a 10-cm diameter tube). In addition, we recorded the numbers of the following three widespread and easily identified tree species in each plot:

TABLE 2. Index of melanism in female *W. citrina*. Class 5 individuals are similar to males, except for the presence of some yellow feathers on the chin and upper throat and some greenish feathers on the crown. Frequency of each class based on examination of 198 female museum skins of all ages.

Melanism class	n	(%)	Description
0	81	(41)	No black pigmentation
1	61	(31)	Narrow, often discontinuous black border along posterior edge of auricular region; little or no black in crown
2	18	(9)	Some black on crown; black coloration extends partway across throat
3	16	(8)	Black extends around edges of crown and posterior auricular region, forming a bib across lower throat; upper throat and chin yellow
4	18	(9)	Like class 3, but black covers most of cap and lower throat, with scattered flecks of black feathers on upper throat and chin
5	4	(2)	Like class 4, but upper throat and chin with considerable black coloration

Manilkara zapota, a dominant canopy species in mesic forests; *Thrinax radiata*, an abundant understory palm in humid forests; and *Bursera simaruba*, a widespread species characteristic of midsuccessional forests, tree fall gaps, and other sites with high light intensity. Summary statistics computed from the primary data included the total basal area of all trees (DBH > 10 cm) and the mean basal area of the five largest trees on each plot.

The vegetation data were subjected to stepwise discriminant function analysis (DFA), using BMDP computer program P7M (Dixon 1981). Each territory was classified a priori as either "male" or "female," and the DFA procedure then computed the weighted combination of habitat features that best differentiated the two classes of territories.

To determine whether or not habitat differences between male and female Hooded Warblers are associated with morphological differences, we examined study skins in the collections of the National Museum of Natural History and the American Museum of Natural History. Sexual dimorphism was assessed by comparing the length of the exposed culmen, tarsus, and unflattened wing chord in 25 male and 25 female specimens. In addition, summaries of weight data for 89 males and 115 females (all collected during migration) were obtained from Dunning (1984). Within-sex variation in plumage was quantified for 198 female museum specimens. We relied on the collector's determination of the sex, although only about 15% of the specimen labels indicated that gonads had been examined. The extent of malelike melanism in females was scored on a 6-part ordinal scale (Table 2). Class 0 females lacked black pigmentation, whereas class 5 females had a malelike black cap and bib.

RESULTS AND DISCUSSION

Male vs. female territories.—The results of DFA (Fig. 1) strongly confirmed our initial impres-

sion of consistent differences between the territories of male and female *W. citrina*: the 15 male and 13 female territories showed essentially no overlap in their discriminant scores based on 7 of the original 12 habitat characteristics ($F_{7,20} = 6.93, P < 0.01$). In comparison with male territories, territories of females contained more shrubs ($\bar{x} = 3.2$ vs. 1.8 stems/m²), fewer trees (525 vs. 875/ha), smaller trees (mean basal area of largest trees = 280 vs. 849 cm²), and a lower canopy (mean height = 5.6 vs. 8.2 m). Female territories often were located within tracts of brushy successional woods ("acahuales") that quickly regenerate when agricultural fields are abandoned in the typical slash-and-burn rotation employed by local Maya farmers. Females also established territories within various natural habitats, including stands of naturally stunted, often deciduous, woodland that occur within seasonally flooded shallow depressions. These forests were completely dry at the time of our 1982 study, which was midway through the annual winter dry season. In wet years (e.g. 1983–1984) these depressions may retain water year-round, and thus remain unavailable as habitat for terrestrially foraging birds. Female *W. citrina* are also present in large numbers in the dense, stunted forest that occurs along the coast of central Quintana Roo (pers. obs.). The physiognomy (if not the floristic composition) of this natural association closely resembles that of the successional acahuales.

Geographic patterns.—Both the stature of the natural forest and the intensity of human disturbance change radically from east to west across the northern portion of the Yucatan Peninsula. Except for the immediate coastal strip

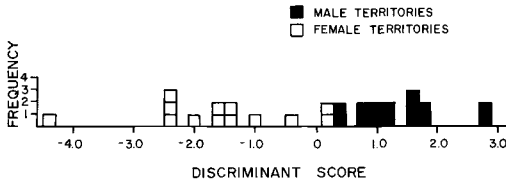


Fig. 1. Scores for discriminant function separating territories of male vs. female *W. citrina* on the basis of vegetational characteristics. Characters with the strongest positive (i.e. "male") loadings were the number of tree species, the basal area of the largest trees in the plot, the abundance of *Manilkara zapota*; characters with strong negative ("female") loadings were degree of canopy closure, percent ground cover, shrub density, and total basal area of all woody plants.

along the Caribbean, the lightly populated eastern section (Quintana Roo) supports a dense growth of medium to tall, mostly evergreen forest (Fig. 2), much of which has persisted to the present time (Fig. 3). By comparison, the western section of the peninsula (the state of Yucatan) receives considerably less rainfall and supports deciduous or partly deciduous forest that tends to be lower in stature. The natural vegetation in the state of Yucatan has been profoundly altered by the relatively dense population of Maya agriculturalists that has inhabited the region for more than 2,000 yr. Little, if any, old-growth forest survives in the state (Bequaert 1935), although numerous patches of secondary forest, some of them fairly extensive, dot the region. Given the observed association of female *W. citrina* with lower, drier woodlands within a local mosaic of successional habitats, one might also expect to find a higher female:male ratio in Yucatan, as opposed to Quintana Roo. The ratio of females to males in 153 documented feeding territories within Quintana Roo was found to be 1:3.4; this ratio increased to 1:2.0 in 67 Yucatan territories, but the difference is not statistically significant at the 0.05 level ($\chi^2 = 2.37; 0.10 > P > 0.05, 1 \text{ df}, 1\text{-tailed test}$). As noted above, we do not claim that these figures necessarily represent the actual ratio of the sexes in the two states, because our habitat sampling was not strictly random at the regional level. Nevertheless, females do appear to be relatively more abundant in the drier scrubby woodlands of the interior than in the tall, humid forests of the Caribbean versant. This difference most likely reflects re-

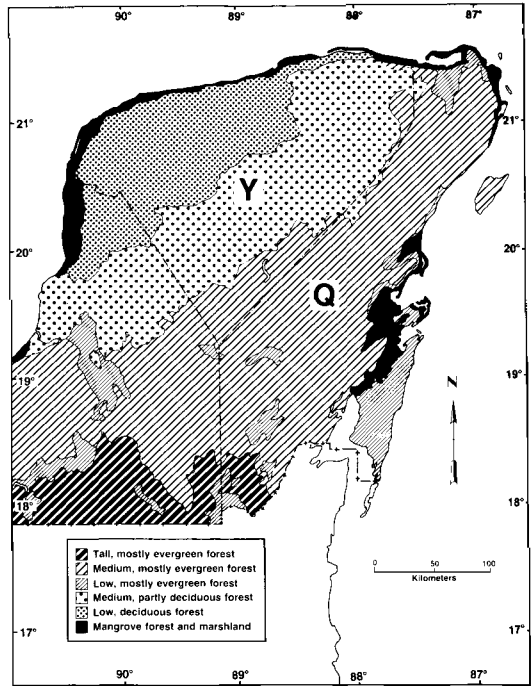


Fig. 2. Map of natural vegetation types in the northern Yucatan Peninsula. Male *W. citrina* were relatively more abundant in the humid, taller forests of Quintana Roo (Q) than in the drier, short-statured woodlands of Yucatan (Y). Data extracted from the 1:1,000,000 vegetation map (Merida sheet) issued by the Direccion General del Territorio Nacional, Mexico City (1981).

gional differences in the distribution of habitats used by males vs. females, and is not the result of some independent mode of geographic segregation of the sexes.

Dimorphism in external morphology.—Hooded Warblers are monomorphic in bill length and tarsal length, but males are heavier than females and have significantly longer wings (Table 3). Our limited observations of foraging by the two sexes during the breeding season suggest that females often glean insects on or near the ground, whereas males frequently hawk insects or sally to the ground from an elevated perch. This apparent difference is not, however, maintained on the wintering grounds (E. S. Morton unpubl. data). If confirmed by additional observations, sexual differences in foraging tactics could be functionally related to the observed differences between males and females in wing length and body weight. A sim-

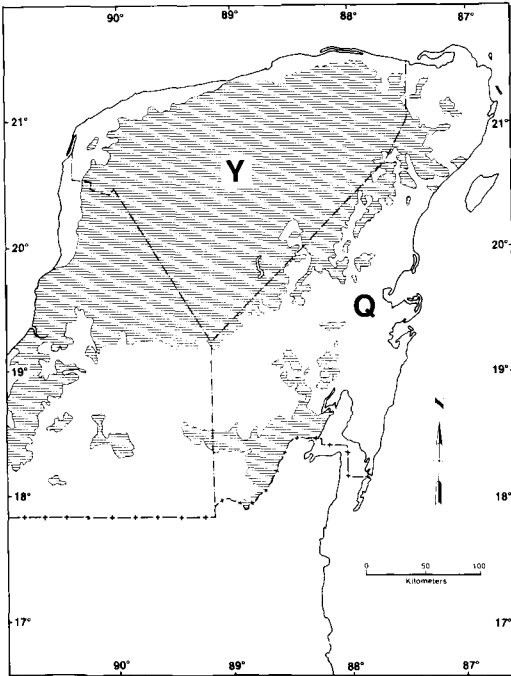


Fig. 3. Map showing the extent of croplands, pastures, and other human-related disturbance (cross-hatched) in the northern Yucatan Peninsula (Y = Yucatan, Q = Quintana Roo). Source of data as in Fig. 2.

ilar interpretation has been advanced to explain sexual dimorphism in wing length for *Vireo olivaceus* (Williamson 1971). During the breeding season, the longer-winged males of this species tend to forage higher in the forest than do females. It should be noted that, unlike *W. citrina*, *V. olivaceus* is monomorphic in body weight, despite substantial sexual variation in wing length (Williamson 1971, Dunning 1984), so these two morphological traits can show a certain degree of independent variation (cf. Grant 1968).

Hooded Warblers usually exhibit strong sexual dimorphism in plumage. All males possess a black cowl that contrasts strikingly with the bright yellow face (Fig. 4). Males also use distinctive postures to enhance the visual impact of the head pattern in aggressive interactions, which typically occur under the low light conditions of the forest understory (Rappole and Warner 1981). Typical females lack the striking head pattern of males, but Chapman (1907) long ago noted that there is considerable variation in the degree to which females approach the

TABLE 3. Comparison of external morphology of male and female *W. citrina*. Table values are means \pm 2 SE. Weight data are from Dunning (1984).

Character	Male	Female	Significance level of difference
Bill length (mm)	9.2 \pm 0.2 (n = 25)	9.3 \pm 0.2 (n = 25)	NS
Tarsus length (mm)	19.6 \pm 0.6 (n = 25)	19.1 \pm 0.2 (n = 25)	NS
Wing chord (mm)	66.3 \pm 0.9 (n = 25)	62.2 \pm 0.8 (n = 25)	0.001
Body weight (g)	10.8 \pm 0.1 (n = 89)	10.1 \pm 0.1 (n = 115)	0.001

male color pattern. Of 30 adult female study skins examined by Chapman, 9 (30%) lacked all black pigmentation (corresponding to a score of 0 on our melanism scale), 1 (3%) showed nearly as much black coloration as do males (4 or 5 on our scale), and the remaining 20 specimens (67%) exhibited various intermediate degrees of melanism. Rappole and Warner (1981) did not distinguish degrees of melanism in the plumage of female *W. citrina*, but they did note that less than 5% of the overwintering and transient females were "male-plumaged."

Our results, based on examination of museum specimens, are consistent with those of Chapman (1907) and of Rappole and Warner (1981). We scored 18 of 55 (33%) designated "adult" female museum skins of *W. citrina* as 0, 3 skins (6%) as closely similar to males (scored as 4 or 5), and 18 skins (33%) as exhibiting a trace of black coloration along the border between the crown and cheeks (scored as 1). Clearly, adult females with little or no melanism predominate in *W. citrina*.

Chapman (1907) noted that young female Hooded Warblers often show less black pigmentation than do adult females, and speculated that the tendency to develop a malelike black hood is age-dependent. Our data support Chapman's interpretation: of 25 museum specimens designated as immature by the original collectors, 24 (96%) fell into melanism class 0, the single exception being a class 2 individual. This difference in the relative frequency of completely nonmelanic immature vs. adult females (96% vs. 33%) was statistically highly sig-

nificant ($P < 0.01$, binomial test). There are no known morphological criteria for aging females beyond their first year, so we cannot determine whether individual females tend to become more melanistic with successive annual molts after year 1. However, our observations of study skins, captive birds, and free-living individuals show that males develop a complete black hood before their first migration and that the distribution of female color morphs in museum collections is reasonably representative of the natural distribution.

Possible functions of sexual dimorphism.—Summarizing our results to this point, we have shown that: (1) male Hooded Warblers are heavier and have longer wings than females, but the sexes do not differ in tarsal or bill length; (2) most females have little or no black pigmentation, but some individuals approach the male condition in the development of a striking black "hood"; (3) wintering males defend feeding territories within relatively tall closed-canopy forest, whereas the majority of female territories are located in shorter, more open successional scrub and deciduous woodland; and (4) young females tend to have less melanistic plumage than older individuals.

An important question is whether sexual differences in morphology are directly linked with the ecological differences we have documented. One working hypothesis is that males, perhaps by virtue of their greater size, are behaviorally dominant over females, and that overwintering males tend to exclude females from deep forest, the preferred habitat during the breeding season (Todd 1940, Sprunt 1957). We know that sexual dominance, if indeed it exists in this species, cannot be absolute, for we have observed territorial female Hooded Warblers chase off intruding males (see also Rappole and Warner 1981). However, the larger males may tend to prevail over females early in the overwintering period, when territorial limits are initially established.

If, as suggested by Rohwer (1975, 1977) for Harris' Sparrow (*Zonotrichia querula*), the degree of melanism in *W. citrina* is correlated with social dominance, one might expect malelike female Hooded Warblers, which tend to be older individuals, to be more successful in defending choice feeding territories. Our data are insufficient to rigorously test this crucial prediction, but it is noteworthy that the two females whose territories most resembled those

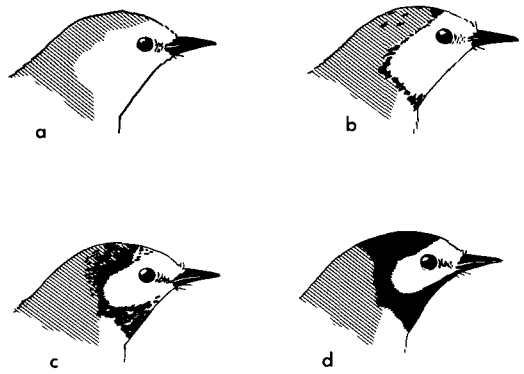


Fig. 4. Variation in plumage melanism of female *W. citrina*, showing class 0 (a), class 3 (b), and class 5 (c) individuals. Class 5 females are similar to males (d), but females show considerable yellow pigmentation in the upper chin region and a moderate amount of olive coloration (cross-hatched) in the dark cap.

of males according to the discriminant function analysis (Fig. 1) were by far the most melanistic of the 13 females whose territories we studied. We could not assign precise melanism scores to these females on the basis of our field observations, but both would have scored 4 or 5, whereas none of the remaining 11 individuals scored higher than 2.

An alternate possibility, which would be consistent with (but would not require) a basic pattern of male dominance, is that there is no difference in the "quality" of male and female territories. In this connection, Rohwer and Ewald (1981) have suggested that pale-colored Harris' Sparrows (which tend to be socially subordinate) may be more successful than dominant melanistic individuals at harvesting diffuse food resources, but that this success is reversed when food is found in localized concentrations. Rohwer and Ewald's "social ecomorph" hypothesis might also apply to *W. citrina* if male and female territories could be shown to be equally productive, or if probabilities of mortality due to predation, physiological stress, etc. do not differ (or differ in compensatory fashion) as a function of habitat stature and openness.

A variant of the "social ecomorph" hypothesis proposes that sexual differences in habitat use by Hooded Warblers developed in response to the social dominance of males over females, but that subsequent morphological and individual behavioral adaptations have tended to increase female efficiency at exploiting the

suboptimal habitats to which they have been relegated. This adjustment may or may not have been completely effective, in the sense that male territories may remain more productive (or safer) than female territories, but females may have assumed at least some characteristics of ecomorphs. In contrast to Rohwer and Ewald (1981), we would emphasize morphological adaptations and improvement in individual foraging behavior, rather than changes in social behavior, in the "adjustment" of females to what initially may have been less desirable habitats. However, the underlying idea that the subordinate sex (or morph) will tend to evolve mechanisms to "make the best of a bad bargain" is common to both our formulation and that of Rohwer and Ewald (1981). The role of malelike females in such a social system remains uncertain, but it is tempting to speculate that melanistic plumage acts as a status signal for older and (perhaps) more aggressive females. The fact that these malelike females appear to occupy malelike habitat is evidence that typical "female" habitat is not preferred by the older, hence more experienced, females that tend to develop male plumage characteristics. Slatkin (1984) argued on theoretical grounds that ecological differences between males and females can help maintain sexual dimorphism, even if the dimorphism initially arose through some other mechanism (e.g. sexual selection).

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