

How a warbler chooses its habitat: field support for laboratory experiments

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Abstract. During the non-breeding season hooded warblers, *Wilsonia citrina*, defend individual territories and segregate by sex into different habitats. Previous laboratory trials suggested that choice was based upon the verticality of plant features: males prefer habitat with more stems growing vertically, whereas females prefer vegetation predominated by oblique angles. To test the proximate cues used by hooded warblers to assess habitat suitability, the effect of hurricane disturbance on the distribution of the sexes was investigated. Hurricane Gilbert crossed the northern portion of the Yucatan Peninsula, Mexico in mid-September 1988 with 320 km/h winds. The abundance and distribution of each sex was compared before and after the storm. After the storm females appeared in forests previously occupied only by males. Analysis of the angles, size, and density of vegetative stems showed that females were found on territories where the verticality of the vegetation was reduced compared with the verticality of vegetation in territories still defended by males. Vegetative height did not differ in male and female territories. This result supports laboratory predictions that primary cues for habitat segregation are based on the relative amounts of vertical and oblique elements in the habitat.

Habitat selection cues in birds received experimental support some time ago (Klopfer 1965). Partridge (1974) showed that laboratory-raised coal tits, *Parus ater*, and blue tits, *P. caeruleus*, maintained 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.

In contrast to earlier studies, the hooded warbler, *Wilsonia citrina*, provides an opportunity to study factors underlying habitat selection within one species, because the sexes separate into different habitats on non-breeding territories during the over-wintering period. Females occur in shrubby habitats, tree-fall gaps in forests, or forests where prevailing winds cause trees to lean, and males select forests or sapling stands with vertical trunks. There is no territorial overlap and individuals of both sexes defend exclusive territories (Rappole & Warner 1980). Here, we test an a priori hypothesis that the sexes separate by responding differentially

to habitat verticality, the degree to which the plant stems are growing perpendicular to the ground.

This study builds upon previous research on the evolution of this habitat separation. We have shown that this separation arises from a preference or choice and is not due simply to exclusion of one sex by the other from a preferred habitat (Morton et al. 1987). Morton (1990), through laboratory choice trials with hand-raised warblers, documented a sex-specific preference for habitat types that is independent of experience with natural vegetation. He found that females oriented preferentially towards two-dimensional arrays of oblique lines formed from 6.4-cm-wide black crepe paper strips, whereas males oriented preferentially towards vertical strips. This suggested that warblers were more responsive to habitat verticality than vegetative height. The sexes did not respond differently to light intensity, removing this as a potential influence on territorial settlement patterns. Morton (1990) suggested that the different habitat settlement patterns of females and males was related to the oblique angle domination of shrubby habitats preferred by females in contrast to the vertical tree trunk-dominated habitat preferred by males. Both

females and males settle where no large tree trunks exist, such as on recent corn fields allowed to go fallow. These observations supported laboratory studies showing that verticality per se is the important variable. Laboratory studies, however, cannot test the efficacy of all potential cues that warblers might use in natural habitat. Field manipulations should test directly the effect of habitat verticality on habitat use (Morton 1990).

Hurricane Gilbert, whose 320 km/h winds crossed the northern tip of the Yucatan Peninsula in mid-September 1988, provided an opportunity to use hurricane damage in the forest as a 'natural experiment'. For several years prior to the hurricane, we conducted point surveys to census hooded warblers and other species (described in Lynch 1989). We found only males in the extensive coastal forest of Quintana Roo on these prior surveys. Females were found only in areas of dried swamp forest, with distinctive shrubby vegetation, or along edges of roads, cattle pastures, and other disturbed non-forested habitats.

The hurricane's effects on the forest were used to test a two-part hypothesis: (1) that females would now occupy territories in formerly male-only areas, but (2) only where the vegetative structure was relatively non-vertical. Alternatively, only males might be found before and after the hurricane, which might mean that site fidelity could override differences in habitat preference differences between the sexes. If true, this effect could persist for the lifetime of the birds living there before the hurricane struck. Finally, no change in the sex ratio in the forest after the storm might mean that verticality is not used for habitat selection in the field.

METHODS

Study Area

Field research was conducted from 5–12 February 1989 in Quintana Roo, Mexico, in the Yucatan Peninsula, 4–5 months after the hurricane. Hooded warblers do not breed here but overwintered abundantly. They are common by mid-September and continue to arrive from breeding areas in southeastern North America until at least mid-October (personal observation). The study area was accessible from a gravel road, the Vallarta Road, west of Puerto Morelos (described in Morton et al. 1987). Prior to the hurricane, most of the area was covered by mature semi-evergreen forest (see

Lynch 1989). The hurricane defoliated most of the trees, but by our arrival most trees not blown down were sprouting leaves from trunks and remaining lateral branches (Fig. 1). Vine cover was well established in some areas. Descriptions of the hurricane's effects on forest structure are provided by Whigham et al. (1991) for Quintana Roo and by Varty (1991) for Jamaica. Lynch (1991) discusses the hurricane's effects on bird populations in the Yucatan Peninsula.

Field Methods

We visited forested sites along the Vallarta Road that contained only males before the hurricane and performed point counts to survey for hooded warblers. We avoided shrubby areas that females had occupied before the hurricane. Methods used are discussed in detail in earlier publications (Lynch et al. 1985; Lynch 1989). The same techniques were used here to generate comparable data. We played back territorial chip notes of hooded warblers, using a Uher 4000 Report Monitor tape-recorder. Imitations of the distress 'squeak' call of a small passerine and the whistled call of a ferruginous pygmy-owl, *Glaucidium brasilianum*, were used to elicit responses. We counted all hooded warblers heard or seen from the census point during 10–12 min.

R.G. conducted population surveys of hooded warblers wintering in the Sian Ka'an Biosphere Reserve, before and after Hurricane Gilbert passed to the north. This area was on the southern fringe of the hurricane, 150 km south of our Vallarta Road site, and was little affected by it. Therefore, his surveys control for year-to-year variation in warbler numbers not due to the hurricane (e.g. poor breeding success the preceding summer, lower overall populations). R.G. used a transect method to estimate numbers and his data are presented in detail elsewhere (Greenberg 1992). Each transect was 1 km in length and birds were recorded within 40 m of either side of the transect.

Testing the Two-part Hypothesis

Because females are readily distinguishable from males by plumage features in the field (Morton 1989), we sexed all individuals observed.

We photographed each territory to determine whether female territories would include habitat

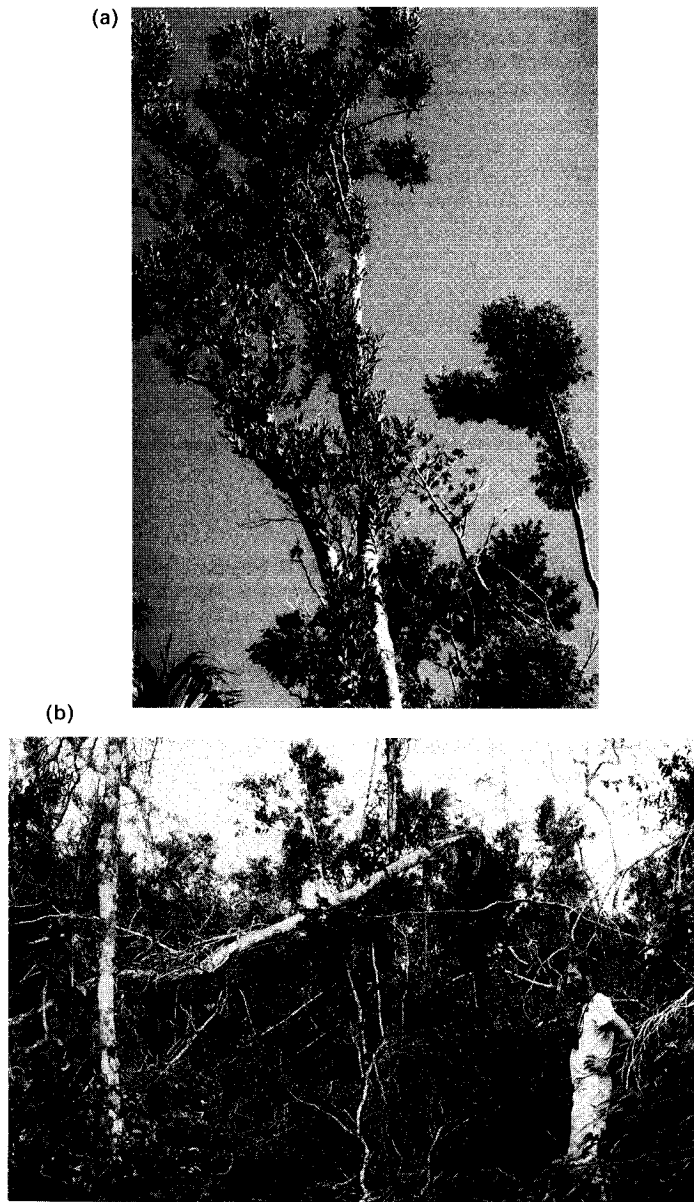


Figure 1. Photographs showing the condition of the Quintana Roo, Mexico forest during our study, in February 1989, 4-5 months after it was struck by Hurricane Gilbert. (a) Depicts the regrowth of leaves along the remaining main tree branches, and (b) shows the accumulation of canopy branches blown to the ground.

with low verticality relative to male territories, an a priori hypothesis derived from the laboratory experiment (Morton 1990). We avoided observer bias by photographing the position where the bird was first seen and from a direction 180° to that from which the bird arrived. The latter protocol assured

that the camera was focused into the bird's territory. One of us stood where the territorial warbler had first been seen and provided a size standard for the vegetation measurements. Next, a 35-mm slide photograph was taken from 10 m away with the person photographed on the left side of the picture.

Table I. Mean number of hooded warblers per transect count through six habitats in Sian Ka'an Biological Reserve before and after Hurricane Gilbert (from Greenberg 1992)

Habitat*	1988 (before hurricane) (<i>N</i> = 25 censuses)	1989 (after hurricane) (<i>N</i> = 16 censuses)
Pasture	0.1	0
Milpa	0.1	0.5
Grazed acahual	1.5	1.4
Ungrazed acahual	2.1	2.3
Subdeciduous forests	4.0	4.4
Subperennial forests	3.1	2.8
Mean total per census	10.9	11.4

No difference in hooded warbler abundance, comparing before and after the hurricane (sign test, $P = 0.50$).

*See Lynch (1989) for habitat descriptions.

All features were in focus. The camera's perspective covered the ground to within 3 m, the foraging zone used by hooded warblers (Morton et al. 1987).

Each slide of a hooded warbler territory was assigned a number and the sex of the bird holding it was unknown to the person performing the analysis of the slides. The slide was projected on an Osram Diastar 200 35 mm slide viewer, enlarging the image to 19.5×13 cm. A grid divided into six 6.5×6.5 cm blocks was overlain on each image. Plant stems were then traced on the grid using red marking for stems greater than 10 cm in diameter, orange for those from 3.1 to 10 cm, and blue for stems 3 cm or less in diameter. After tracing all six blocks, each block was treated separately and each stem within a block was assigned three variables: the stem's angle (placed in one of 18 categories of 5° increments from horizontal (0°) to vertical (90°), the stem's diameter class as described above, and the stem's length. Three categories of stem length were used: stem tracing greater than 3.25 cm (< 0.5 length or width of a grid block), greater than 3.25 but less than 6.5 cm, and greater than 6.5 cm in length on the projected image. The number of individual territories measured was 39. All tracing values ($N = 10\ 859$) were analysed via the Statistical Analysis System (PC-SAS) package (SAS 1985) and averaged for each territory. Mann-Whitney *U*-tests were used to compare median stem angles, median stem diameters, and median numbers of total stems on male and female hooded warbler territories. A step-wise discriminant function analysis (DFA, SAS 1985) was used to determine

Table II. Number of point counts at the Vallarta Road site with positive responses from at least one hooded warbler compared with counts with no response, before and after Hurricane Gilbert

	Before hurricane	After hurricane	<i>P</i>
Positive response	59	37	0.01*
No response	15	31	
Single bird responded	45	35	0.02†
Two or three birds responded	14	2	

*Hooded warblers were present at significantly more point counts before the hurricane ($\chi^2 = 10.44$, $df = 1$).

†Hooded warblers were more densely packed before than after Hurricane Gilbert ($\chi^2 = 5.58$, $df = 1$).

the overall separation of these territories by the sexes with different combinations of these variables.

RESULTS

Population Changes Before and After the Hurricane

The Sian Ka'an Reserve showed no annual difference in hooded warbler numbers in any of the six habitats surveyed by R.G. in 1988 and 1989 (Table I).

The Vallarta Road area showed reduced numbers of hooded warblers between 1983 and 1989.

Table III. A comparison of vegetative features of male and female hooded warbler territories in the Vallarta Road forest

	Male (<i>N</i> = 26)	Female (<i>N</i> = 13)	<i>P</i> *
Mean stem angle above horizontal	11.93 ± 0.17 (SE)	10.54 ± 0.30	< 0.01
Mean stem diameter index	1.67 ± 0.06	1.50 ± 0.06	NS
% Small diameter	50.25	62.28	NS
% Medium diameter	32.73	25.43	NS
% Large diameter	17.03	12.30	NS
No. stems	171.54 ± 13.04	199.31 ± 27.40	NS
Index of stem length	1.19 ± 0.02	1.14 ± 0.02	NS

*Mann-Whitney *U*-tests.

See Methods for description of stem angle categories, stem diameter and stem length indices.

Absolute numbers were significantly lower (Table II). Response rates per point count averaged 84 and 70% in counts performed in 1982 and 1983, whereas in 1989, more than 4 months after the hurricane struck, only 54% of the point counts resulted in a positive response from a hooded warbler. Furthermore, two or three warblers were counted at 24% of the census points before the hurricane but only 5% of the point counts after the hurricane resulted in more than a single warbler (Table II).

Female Hooded Warblers in the Forest

During the pre-hurricane censuses, no females were observed in the forest areas of the Vallarta Road site (*N* = 34 warblers identified to sex, all males). Post-hurricane censuses in the same locations revealed 13 females and 26 males in the same areas, a significant difference ($\chi^2 = 11.61$, *df* = 1, *P* < 0.001, corrected for continuity).

Differences in the vegetation in male and female territories

Male and female territories differed significantly in the angle of vegetation, with males occupying territories with more vertical stems compared with female territories (Table III). The photographs of male and female territories did not differ in measures of stem density or in stem length. Stem density reflects the density of the habitat whereas stem length reflects the vertical height of the vegetation, with tree trunks and branches longer than those of more shrubby plants. Although there was

also no significant difference in stem diameter there was a non-significant tendency for female territories to include more small-diameter stems, while male territories contained more larger-diameter stems. Since large stems were those greater than 10 cm in diameter (see Methods), this would indicate that males had more tree trunks in their territories, but not significantly so, than did females.

In summary, males occupied territories with greater verticality in the vegetative stems than did females. There were no statistically significant differences in the height, density, diameter, or length of the vegetative stems in the territories.

The discriminant function derived from all four variables was significant with an r^2 of 0.62 ($F_{4,34} = 5.2$, *P* = 0.002). Males and females were separated significantly as a function of all four variables ($\chi^2 = 8.67$, *df* = 1, *P* < 0.01, based on a posteriori classification), but the standardized canonical coefficients for the four variables indicated that most of the variation was explained by the angle variable (angle = 0.97, length = 0.40, diameter = 0.06, and density = 0.42).

DISCUSSION

In the laboratory, using hand-raised and habitat-naïve hooded warblers, we showed that males preferred to face black crepe paper strips arrayed vertically on a wall, whereas females preferred an oblique array of strips (Morton 1990). These experiments, and field observations of females in forest and males in shrubby habitat, led to the conclusion

that while most hooded warbler males are in forest and most females are in shrub and field habitat, the birds base their choice of habitat on a minor subset of the physical differences between forest and fields. Hurricane Gilbert's effects on the forest were to leave the trees standing, but to increase the oblique angles of vegetation in a patchy manner. Thus the forest trees remained but the smaller canopy branches were blown down. These branches, and more non-vertical tree trunks, lowered the overall verticality of this forest vegetation.

The difference in verticality between territories selected by males and females differed in the direction predicted by the laboratory trials. Female hooded warblers settled in places where no females had been observed since our studies began in the late 1970s. Vegetation on female territories averaged 7° less vertical from that of males. We conclude that females moved into the forests used previously by males.

Our photographic method provided one view of a bird's territory but did not allow quantification of relative use. Playbacks may have induced birds to leave preferred areas. Because we used our first visual contact as the criterion for positioning the camera at each territory the resulting photographs may depict relatively open portions of the territory. These factors, however, would tend to bias results in favour of the null hypothesis, i.e. no difference between females and males in the habitat structure of their territories.

An alternate hypothesis to account for the advent of female territories in the forest is that the hurricane reduced density in the forest by killing the males. According to this hypothesis, females or males arriving after the hurricane, from late September on, found little resistance from other warblers and could settle relatively easily. This alternative is made less plausible by field experiments, performed in 1986 in the same site as the present study, designed to test the male exclusion of females hypothesis (Morton et al. 1987). When we experimentally removed males from territories in forested areas surrounding female territories in shrub habitat, females did not enter this immediately adjacent and undefended forest. Therefore, females chose shrub habitat even though they were not being excluded from 'preferred' forest habitat by socially dominant males. Female preference for shrub habitat supported the notion that the ultimate reason for females to separate from males is to increase over-wintering survival in females. This would be

accomplished by avoiding territorial aggression with males, which are larger than females (Morton 1990). In the proximate timeframe, individuals use a simple cue, habitat verticality, differing according to their sex, to separate. For cues to habitat selection to have some genetic basis, as suggested by the laboratory studies (Morton 1990), a minor subset of habitat complexity should be used (Lack 1971; Partridge 1978).

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