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Received 17 March 1986, accepted 28 August 1986.

Do Male Hooded Warblers Exclude Females from Nonbreeding Territories in Tropical Forest?

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Male and female Hooded Warblers (*Wilsonia citrina*) defend exclusive feeding territories in the nonbreeding season (Rappole and Warner 1980). Rappole and Warner (1980) showed that individuals remain on their territories for the duration of the overwintering period, and return to the same winter territory each year. These authors presented data suggesting that females are rare or absent in mature forest, but also demonstrated that females are fully capable of defending their territories from intrusions by males. Lynch et al. (1985) documented clear-cut habitat segregation between the sexes of Hooded Warblers during the nonbreeding season. Surveying hundreds of Hooded Warbler territories in the Mexican states of Quintana Roo and Yucatan, they found males in canopied mature and second-growth forests and females in shrubby, low-stature woodlands and brushy old fields. The nonbreeding habitat of males appears more similar to the breeding habitat (*sensu* James 1971) than does the female nonbreeding habitat. Despite the large physiognomic differences between habitats used by males and females, the sexes do not differ substantially in foraging maneuvers or foraging heights (Table 1).

One hypothesis to explain the intersexual habitat segregation is that the larger males are behaviorally dominant over females and tend to exclude them from the preferred forest habitat in the nonbreeding period (Lynch et al. 1985). Any such behavioral dominance might be expressed most strongly when the birds first arrive on their tropical nonbreeding grounds. From 9 to 23 October 1984, we tested the "male dominance" hypothesis by mapping territories of color-banded Hooded Warblers and then removing males from territories adjacent to female territories. We then observed the females for any increase in their use of forest habitat in the absence of defending males.

Our study area straddled a gravel road ca. 3.5 km west of Puerto Morelos, Quintana Roo, Mexico. Hooded Warblers begin to arrive in the area by mid-August, and are abundant there by late September (pers. obs.). Most of the study area is covered by mature semi-evergreen forest dominated by *Manilkara*

TABLE 1. Foraging heights and movements of male and female Hooded Warblers at the Quintana Roo study site.

	Males ($n = 8$)	Females ($n = 7$)	P
Foraging heights			
>0.7 m	849 min (47%)	545 min (40%)	NS[a]
<0.7 m	943 min (53%)	822 min (60%)	
Foraging moves per second			
Hops	0.18 ± 0.07[b]	0.18 ± 0.08	NS
Flights	0.08 ± 0.03	0.08 ± 0.03	

[a] NS = no significant difference ($P > 0.05$).
[b] Mean ± SD.

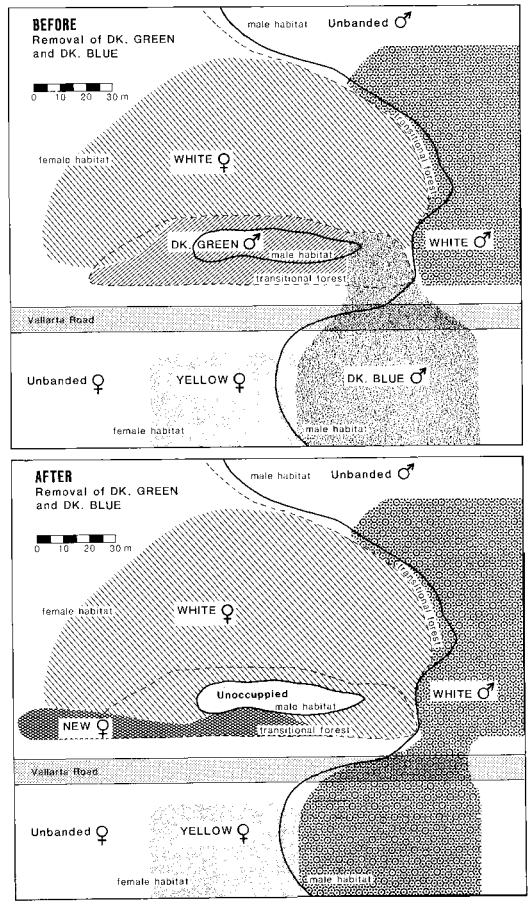

Fig. 1. Territorial configurations of male and female Hooded Warblers before and after males dark green and dark blue were removed. "Female" habitat refers to dry tintale scrub and "male" habitat refers to canopied forest as described by Lynch et al. (1985). Transitional forest refers to second-growth forest and scrub ecotones.

zapota, interspersed with seasonally flooded shallow depressions called "tintales." The tintales support a characteristic shrubby vegetation with scattered deciduous trees (e.g. *Hematoxylon campechianum, Mimosa bahamensis, Erythroxylon areolatum*) and various species of shrubs, sedge (*Dichrema* sp.), and grasses. Female Hooded Warblers maintain territories in the tintales, which tend to be dry during most of the overwintering period. We color-banded 15 Hooded Warblers (8 males, 7 females) and could individually recognize 5 additional females through their distinctive black head markings (Lynch et al. 1985). For intensive study we selected two nearly adjacent tracts where several female and male territories abutted, and where at least one male territory was surrounded by female territories. We spent 126 man-hours observing individuals and mapping territorial boundaries before any experimental manipulations (9–15 October) and a similar period making observations after removing 4 males from their territories (16–23 October). Territory borders were located by observing border defenses, which are marked by a change in vocalizations from the common "chink" bark to a rapid "chippity-chup" call similar to that given by nearly independent fledglings (Morton pers. obs.). A distinctive low, harsh "zrrr" call was given by attacking individuals. The configurations of territories before the removal experiment are shown in the "before" portions of Figs. 1 and 2.

Females did not occupy the vacated male habitat in either site (Figs. 1 and 2, "After"). Of particular interest were the former territories of two males, "dark green" (Fig. 1) and "unbanded" (Fig. 2), which were surrounded by females. With the exception of a narrow band of 3–4-m-tall second-growth "transition" habitat, these areas remained unoccupied for the duration of the study. Female red/orange (Fig. 2) expanded her territory around the vacated male habitat, but she remained in the crescent-shaped basin that defined her original tintale habitat. The unbanded male had defended a narrow strip of tintale habitat (Fig. 2) between the mature forest portions of his territory. Upon his removal, female red/orange displaced "new" female, who attempted to set up a new territory in the 0.5–1-m-tall cut shrubs bordering the road (Fig. 1, "After," and Fig. 2, "Before"). Male white (Fig. 1) expanded his territory southward across the 35-m-wide road, and was first seen interacting with female yellow at the same border site she had defended against male dark blue. These territory boundary changes took place within 2 days of male removal. The former territories of the four removed males were occupied wholly by two males, one territory remained vacant (male dark green, Fig. 1, "After"), and one territory was partially used by a new male (Fig. 2, "After").

When the area was resurveyed on 1–3 December

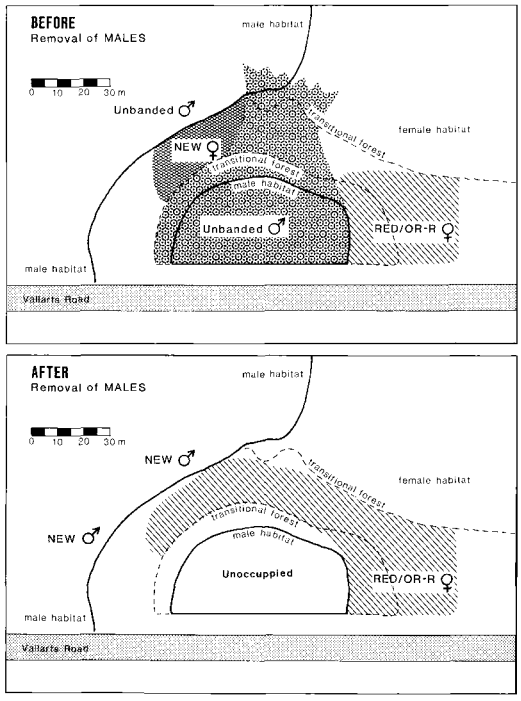

Fig. 2. Territorial configurations of male and female Hooded Warblers at site 2, located ca. 30 m west of the site in Fig. 1, before and after removal of two unbanded males. Other designations are the same as in Fig. 1.

1984, the former territory of the unbanded male (Fig. 2) remained unoccupied. Female red/orange remained in the crescent-shaped tintale habitat and did not use the vacant forest habitat. Also, she did not enter the forest habitat in response to playbacks of Hooded Warbler "chips" from within the forest habitat. Male white remained south of the road (Fig. 1) in the former territory of male dark blue, but had abandoned his original territory north of the road. The latter was occupied by an unbanded male.

We conclude that direct male exclusion of females from forest habitat is not a sufficient proximate explanation of habitat segregation between the sexes in Hooded Warblers. An alternative explanation is that the birds are simply sedentary and would not move into areas they did not occupy previously. However, our study was conducted at a time, just following migration, when territories were being occupied and boundaries were being defended actively, more so than is the case later in the season (J. F. Lynch pers. obs.). Also, both males and females (some of which may have been "floaters") were shown to move into areas vacated by our removal of males, but the original habitat segregation between the sexes was maintained nevertheless. Finally, the apparent reluctance of females to enter mature forest habitat, even when the latter was not defended by a male and was surrounded by female-occupied shrub habitat, is evidence that females and males "prefer" the different habitats in which we find them.

We are grateful to Enrique Carrillo, Director General of the Centro de Investigaciones de Quintana Roo, for facilitating our research, and to Ingrid Olmsted for identifying plant species. The study was supported by a Scholarly Studies grant from the Smithsonian Institution to Lynch and Morton.

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Received 15 May 1986, accepted 4 September 1986.

A New Technique for Releasing Migrants from Orientation Cages

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In recent years, studies of orientation in migratory birds have proceeded along two largely independent routes. On the one hand, investigators taking advantage of Kramer's (1950) discovery have placed migrants in orientation cages of various designs and examined their behavior under a variety of conditions. On the other, fieldworkers have used radar and visual techniques to observe the orientation behavior of free-flying migrants under natural environmental conditions. The ability to systematically control potentially relevant variables has enabled those employing orientation cages to demonstrate a number