

## INTERSPECIFIC DEFENSE OF PASTURE TREES BY WINTERING YELLOW WARBLERS

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**ABSTRACT.**—Yellow Warblers (*Dendroica petechia*) defend small territories in isolated patches of trees in cattle pastures in the Lacandon Forest of Chiapas, Mexico. We observed interspecific aggression much more frequently than intraspecific aggression. Although aggression by Yellow Warblers was directed at a minimum of 37 species, resident and migrant alike, attacks on Magnolia Warblers (*Dendroica magnolia*) comprised 35% of the total observed. We found that individual Magnolia Warblers use overlapping home ranges where one warbler tends to be the predominant occupant of a single Yellow Warbler territory. Overlap between neighbors was promoted by the aggressive chasing of Yellow Warblers. Arthropods were twice as abundant in the canopy as in understory shrubs. Exclosure experiments showed that birds harvested approximately 80% of the arthropods available in the canopy and 50% of those available in the understory vegetation. Yellow Warbler defense may be responsible for this difference in density in foliage arthropods between the canopy and understory. To avoid aggression, subordinate species depended on the presence of refugia, comprised of dense understory vegetation. Maintaining the structural heterogeneity of arroyo vegetation may provide critical habitat for many species of migratory birds in cattle pastures. Taken together, the interspecific aggression, intraspecific territoriality, and high rates of resource depletion indicate that competition plays an important role in determining the carrying capacity of second-growth remnants for migratory birds and their use of habitats. Received 27 August 1992, accepted 25 November 1992.

INTERSPECIFIC TERRITORIALITY is generally restricted to a few ecological situations: the breeding territories of closely related species (Johnson 1963, Orians and Willson 1964, Catchpole 1973, Cody 1978, Rice 1978); or the defense of a single, highly productive feeding site, such as a nectar source (Dow 1977, Carpenter 1978, Gill and Wolf 1979), fruiting tree, or the honeydew produced by Homoptera (Loyn et al. 1983, Greenberg et al. 1993). With the exception of aggression at certain flowering or fruiting plants (Kale 1967, Emlen 1973, Schemske 1975), interspecific territoriality or other forms of hostile interactions have not been shown to be important in influencing the distribution of migratory birds in the nonbreeding seasons (Greenberg 1986, Morse 1989). The few studies of interspecific aggression in insectivorous migrants have generally focused on the breeding season (Morse 1966, 1973, 1976, Sherry 1979, Hutto 1981, Sherry and Holmes 1988). Notable exceptions include Willis' (1966) studies of aggressive interactions at army ant swarms and Leisler's (1990) work on certain terrestrial insectivores of the African steppe.

Common sightings of lengthy and occasionally violent interspecific chases by insectivo-

rous Yellow Warblers (*Dendroica petechia* of the migratory subspecies) wintering in tree patches in cattle pastures led us to study more thoroughly the role of such aggression in pasture bird communities. Beyond describing this phenomena, in this study we address three questions about interspecific territoriality that remain incompletely answered. First, is the behavior of the aggressor and the subordinate species adaptive (Murray 1971, Emlen 1973, Sherry and Holmes 1988)? Second, does interspecific aggression and territoriality have an important impact on habitat use (Morse 1976, Sherry 1979)? Finally, does interspecific defense by predators have an effect on other trophic levels? An example of such an effect is provided by Loyn et al. (1983), where the defense of lerp (crystallized honeydew of psyllids) causes the exclusion of insectivorous birds and an increase in both herbivorous insects and plant damage.

### METHODS

*Study site.*—Our study was conducted in the communities (Ejidos) of Chajul and Loma Bonita on the south shore of the Lacantun River opposite the Mon-

tes Azules Biosphere Reserve (300 m elevation, 90°56'W, 16°07'N). The Ejidos, settled in the late 1970s, were cleared for cattle pasture and intensive cultivation of corn and chilies. The natural vegetation (still covering the reserve) was tropical moist forest (30 m canopy, 3,000 mm rainfall/year) with a dry season from January through June. Arboreous vegetation in pastures was found primarily along arroyos and consisted primarily of fast-growing pioneer tree species (*Inga*, *Trichospermum*, *Cecropia*, *Schizolobium*, *Miconia*, *Spondias mombin*, *Xanthoxylum*, *Xylopia*, and *Ceiba*) ranging from 6 to 15 m in height ( $\bar{x} = 10.8 + \text{SE of } 0.2$ ; Salgado unpubl. data) with a shrubby understory of *Miconia*, *Psychotria*, *Piper*, etc. Between winter field seasons, local farmers cleared understory from a small section of arroyo vegetation.

*Ad hoc observations of aggression.*—Aggression involving all migratory birds was recorded during the course of the study, which was conducted over 250 field days between 18 October 1990 and 15 April 1992. Although these data were gathered in an unsystematic manner, they are based on observations from all of the Yellow Warbler habitats visited for a region within 20 km in either direction from Chajul along the Lacantun River, including both disturbed and natural flood-plain vegetation. Thus, they provide a broader overview than the focal observations.

*Focal observations.*—Focal observations were made on a single pasture in the Chajul Ejido. During the period 1 February to 2 April 1991, six male and one female Yellow Warblers were followed during a single 3-h watch (0700 to 1000 CST) by two observers. The observation session of one male was interrupted by heavy rain for an hour, so that male was followed during a second session; thus, there were eight total sessions. One observer recorded the location and activity of the Yellow Warbler every 5 min, as well as the distance and object of all chases. Three Yellow Warblers were color banded. Other individual Yellow Warblers were readily identified and followed because of their small territories and their distinct pattern of red striping. The second observer recorded locations (height and tree) of all other visitors. Yellow Warblers commonly left the tree patch to feed or rest in the understory shrubbery. Due to wind and rains, the actual observation time per bird was reduced to an average of 170 min.

Focal observations were made on five territories in the same study area during the second winter. These observations were designed primarily to examine seasonal changes in behavior. Each territorial bird was followed for 3 h during the period from September through October 1991 and for another 3 h in February 1992. One female territory was abandoned and only four territorial birds were followed in the second season.

*Social system of a subordinate species.*—Since Yellow Warbler aggressive interactions predominantly involved Magnolia Warblers, we focused on this species

to examine the spacing system of a social subordinate. During the period of arrival for the Magnolia Warbler (15–25 October) in year 2 of the study, we netted and color banded nine individuals. Unique patterns of streaking were used to identify three additional individuals. Several times a week we walked through each of the 11 Yellow Warbler territories in the pasture and searched for individually identifiable Magnolia Warblers; the positions of these birds were then recorded.

*Foraging rate.*—Individual Yellow and Magnolia warblers were followed for 2-min periods during which time all foraging maneuvers were recorded along with the number of large arthropods captured. Large arthropods, in all cases caterpillars, were defined as those observed to extend outside the edges of the mandible after capture. Such observations were made on at least 10 different Yellow Warbler territories.

*Exclosures to measure impact of avian predation on arthropods.*—During the period 5 to 10 October 1991, we set up 15 exclosures on branches in Yellow Warbler territories. Exclosures consisted of 2.4 m<sup>2</sup> of black plastic crop netting with 3.5-cm squares. Use of crop netting to study avian impact on arthropods was pioneered by Holmes et al. (1979), and is generally assumed to exclude bird and other large vertebrate predators, while allowing the free passage of arthropods. We observed few other vertebrate arboreal foliage insectivores and, therefore, assume that the experiment is measuring primarily bird predation. Furthermore, the large mesh size has essentially no effect on microclimate or air movement. Eight exclosures were set up in the lowest branches of canopy trees (*Inga*), and seven were set in understory shrubs (*Miconia*, *Psychotria*, *Piper*). For each paired exclosure and control treatment, we selected two sets of branches and randomly assigned one to be the exclosure. Before tying the netting around the branches, we counted insects and compared the number of arthropods per 100 leaves. During the period 8 to 12 December we harvested both the control and experiments in large clear plastic bags, which were then fumigated with ethyl acetate and searched for arthropods. All arthropods were identified to order or family, and the length was measured. The sample of leaves was dried overnight in a propane-powered plant drier and weighed. We compared the samples for the number of arthropods per 100-g dry mass of leaves.

## RESULTS

*Ad hoc observations of aggression.*—During the period mid-September through April we recorded 350 chases involving Yellow Warblers (apart from focal surveys); in all but four of the chases, Yellow Warblers were the aggressor. Both sexes were observed to chase other species,

TABLE 1. Frequencies of chases ( $n = 314$  total) of different species by Yellow Warblers observed (not including intraspecific aggression, nor chases observed during focal observations). Number of chases given, with percent of total chases in parentheses.

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Magnolia Warbler (*Dendroica magnolia*), 90 (31%); Wilson's Warbler (*Wilsonia pusilla*), 30 (10%); Least Flycatcher (*Empidonax minimus*), 24 (8%); Blue-gray Gnatcatcher (*Poliophtila cerulea*), 24 (8%); American Redstart (*Setophaga ruticilla*), 19 (7%); Black-and-White Warbler (*Mniotilta varia*), 17 (6%); Lesser Greenlet (*Hylophilus decurtatus*), 13 (4%); Philadelphia Vireo (*Vireo philadelphicus*), 9 (3%); Common Yellowthroat (*Geothlypis trichas*), 9 (3%); Paltry Tyrannulet (*Tyranniscus villisimus*), 9 (3%); White-collared Seedeater (*Sporophila torquatus*), 6 (2%); Yellow-olive Flycatcher (*Tolmomyias sulphureus*), 5 (2%); Tennessee Warbler (*Vermivora peregrina*), 5 (2%); Nashville Warbler (*V. ruficapilla*), 4 (2%); Black-throated Green Warbler (*Dendroica virens*), 3 (1%); Greenish Elaenia (*Myiopagis viridicata*), 3 (1%); Sepia-capped Flycatcher (*Leptopogon amaurocephalus*), 2 (1%); Ochre-bellied Flycatcher (*Mionectes olivacea*), 2 (1%); Dusky-capped Flycatcher (*Myiarchus tuberculifer*), 2 (1%); Yellow-rumped Warbler (*Dendroica coronata*), 2 (1%); Warbling Vireo (*Vireo gilvus*), 2 (1%); Green-breasted Mango (*Anthracothorax prevostii*), 1 (<1%); White-bellied Emerald (*Amazilia candida*), 1 (<1%); Yellow-throated Vireo (*Vireo flavifrons*), 1 (<1%); White-eyed Vireo (*V. griseus*), 1 (<1%); Northern Parula (*Parula americana*), 1 (<1%); Indigo Bunting (*Passerina cyanea*), 1 (<1%); Variable Seedeater (*Sporophila americana*), 1 (<1%); Blue-black Grosbeak (*Cyanocopsa cyanooides*), 1 (<1%); Unidentified (not included in percent), 31.

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and interspecific aggression was observed in all habitats occupied by Yellow Warblers, including pioneer vegetation along the naturally disturbed north shore of the Rio Lacantun. During this period, Yellow Warblers chased other Yellow Warblers only 12 times (3%). However, during the initial month (September and early October), intraspecific interactions comprised 50% (13/36) of the total. Twenty-nine species were chased (Table 1) with an additional four observed on focal watches but, in general, attacks were more common against smaller ( $\leq 10$  g, 81% of total chases), migratory (75%) species. Wood-warblers (Parulinae) received 63% of the attacks, tyrant flycatchers 18%, and vireos 8%. The Orchard Oriole (*Icterus spurius*), which flocked in the *Ingas* during the flowering period of March and April, was the only species that consistently chased Yellow Warblers.

The distance from which the attack on target birds was initiated averaged  $9.0 \pm 0.7$  m (range 5–30 m). Attacks were classified as strikes, direct flights, and fly-ins. In strikes, which were rare (5% of all attacks;  $n = 100$ ), an aggressor flew directly at and contacted the victim, occasionally grappling to the ground. Strikes could result in injury (e.g. when a Magnolia Warbler dropped to the ground with a sprained or broken wing). Direct flights, in which an aggressor flew directly at, but did not physically contact, its target individual were common (86% of the interactions). Fly-ins, in which Yellow Warblers flew rapidly into a tree and landed a meter or two shy of the target individual, comprised 9% of interactions. If a target bird failed to leave, the Yellow Warbler followed with a short chase. In addition to these specific dyadic interactions,

Yellow Warblers often flew a loop around a tree causing subordinate individual to drop below the canopy.

*Focal watches.*—Territories of the 12 focal birds (7 in year 1 and 5 in year 2) averaged 520 m<sup>2</sup> and contained an average of  $6.7 \pm 1.2$  trees. Because Yellow Warblers show sexual habitat segregation, and males are more common in the taller riparian trees characteristic of our primary study site, 10 of 12 territorial focal birds were males.

Yellow Warblers moved repeatedly among these few canopy trees, changing trees once every  $2.7 \pm 0.7$  min on average. The rate of chasing was high but variable among focal watches, with averages ranging from 0 to 10 chases per hour ( $\bar{x} = 5.4 \pm 1.1$ ; Fig. 1). The frequency of invasion by birds (20 g or less) was a major correlate of attack frequency (Fig. 1; Pearson's  $r = 0.97$ ). These frequencies are for the total time followed including periods when Yellow Warblers were in nearby grass or shrubbery. Yellow Warblers were in the tree patches an average of  $77.7 \pm 5.2\%$  of the time, and in low shrubbery or grass  $22.3 \pm 3.6\%$ .

Overall, 17 species were attacked during focal watches; Magnolia Warbler was the most common target species (Table 2) followed by Least Flycatcher (*Empidonax minimus*) and Wilson's Warbler. Furthermore, Magnolia Warblers were consistent targets, chased in 14 of 17 focal watches. The only three watches without chases to Magnolia Warblers were those conducted in late September, prior to the arrival of the species.

Species varied considerably in the likelihood that a visit to a canopy tree within a Yellow

Warbler territory would evoke a chase (Table 3). Species the size of Yellow Warblers or smaller ( $\leq 10$  g) were chased significantly more often than larger species (Mann-Whitney  $U = 15$ ,  $n = 5$  and  $6$ ,  $P < 0.01$ ). Furthermore, the results of chases differed markedly (Table 3); the small birds either dropped to the shrubbery (median of species = 16.5%) or flew to the next Yellow Warbler territory (50%), whereas larger birds rarely left the tree in which the attack took place. The difference in body size corresponds to a taxonomic classification as well; most of the small birds were wood-warblers and the larger birds tyrannid flycatchers. By attacking small birds at a higher rate, Yellow Warblers tended to chase species they were more successful in excluding. There was a significant correlation between the proportion of individuals of a species chased and the proportion chased that were forced out of the territory ( $r = 0.7$ ,  $P < 0.05$ ,  $n = 11$ ).

Attacks were always directed towards birds

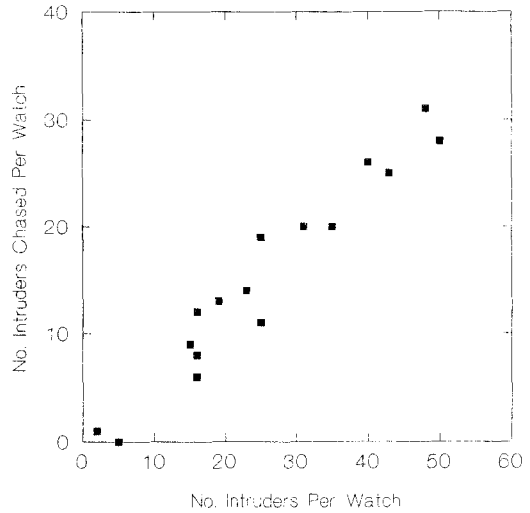


Fig. 1. Scatter plot showing number of interspecific chases versus number of visitors to Yellow Warbler territory ( $Y = -0.45 + 0.62X$ ;  $r = 0.97$ ) during 3-h focal observations.

TABLE 2. Chases per hour ( $\bar{x} \pm SE$ ) of different species during 3-h watches at focal territories.

Species	February-April 1991	September-October 1991	February 1992	Grand mean
Magnolia Warbler	6.6 ± 1.4	3.2 ± 2.0*	4.0 ± 0.5	4.6
Least Flycatcher	2.1 ± 0.6	0.4 ± 0.2	2.0 ± 0.7	1.5
Wilson's Warbler	1.4 ± 0.8	1.6 ± 1.4	0.8 ± 0.5	1.3
Yellow Warbler	0	2.4 ± 0.7	1.5 ± 0.6	1.3
Canada Warbler <sup>b</sup>	0	1.8 ± 1.4	0	0.6
Black-and-White Warbler	0.9 ± 0.4	0.5 ± 0.1	0	0.5
Yellow-bellied Flycatcher <sup>b</sup>	0.6 ± 0.7	1.0 ± 1.0	0	0.5
American Redstart	0.4 ± 0.4	0.8 ± 0.6	0.3 ± 0.3	0.5
Bananaquit <sup>b</sup>	0.1 ± 0.1	1.0 ± 0.8	0.3 ± 0.3	0.5
Sepia-capped Flycatcher	1.0 ± 0.8	0	0	0.3
Yellow-olive Flycatcher	0.5 ± 0.3	0	0.3 ± 0.3	0.3
Red-legged Honeycreeper <sup>b</sup>	0	0.2 ± 0.2	0.3 ± 0.3	0.2
Paltry Tyrannulet	0.6 ± 0.7	0	0	0.2
Rufous-tailed Hummingbird <sup>b</sup>	0.6 ± 0.4	0	0	0.2
Dusky-capped Flycatcher	0.5 ± 0.3	0	0	0.2
Lesser Greenlet	0.5 ± 0.3	0	0	0.2
Common Tody Flycatcher <sup>b</sup>	0.4 ± 0.4	0	0	0.1
Warbling Vireo	0.3 ± 0.3	0	0	0.1
Eastern Wood-Pewee <sup>b</sup>	0	0.2 ± 0.2	0	0.1
Hooded Warbler <sup>b</sup>	0	0.2 ± 0.2	0	0.1
Greenish Elaenia	0	0	0.3 ± 0.3	0.1
Philadelphia Vireo	0	0	0.3 ± 0.3	0.1
Tennessee Warbler	0	0	0.3 ± 0.3	0.1
Ochre-bellied Flycatcher	0.1 ± 0.1	0	0	<0.1
Blue-gray Gnatcatcher	0.1 ± 0.1	0	0	<0.1
Northern Parula	0.1 ± 0.1	0	0	<0.1
Unidentified	2.8 ± 0.7	0.2 ± 0.2	0.5 ± 0.3	1.2
Total	19.6	13.5	10.6	11.9

\* Magnolia Warblers arrived after first three focal surveys.

<sup>b</sup> Scientific names for these species: Canada Warbler (*Wilsonia canadensis*), Yellow-bellied Flycatcher (*Empidonax flaviventris*), Rufous-tailed Hummingbird (*Amazilia tzacatl*), Common Tody Flycatcher (*Todirostrum cinereum*), Bananaquit (*Coereba flaveola*), Red-legged Honeycreeper (*Cyanerpes cyaneus*), Eastern Wood-Pewee (*Contopus virens*), and Hooded Warbler (*Wilsonia citrina*).

TABLE 3. Percentage of visitors chased by Yellow Warblers and percentage of individuals chased that left tree canopy, dropped into understory, or remained in place.

Species	n	Percent chased	Percent individuals chased that		
			Left	Dropped	Remained
<b>Small birds (<math>\leq 10</math> g)</b>					
Magnolia Warbler	65	75	33	59	9
Wilson's Warbler	16	69	19	82	0
Black-and-White Warbler	10	50	100	0	0
American Redstart	8	63	67	33	0
Common Tody Flycatcher	5	60	0	0	100
Paltry Tyrannulet	8	50	100	0	0
Median		61.5	50	16.5	0
<b>Large birds (<math>&gt; 10</math> g)</b>					
Least Flycatcher	27	37	0	20	80
Sepia-capped Flycatcher	13	38	0	13	87
Yellow-bellied Flycatcher	11	45	0	0	100
Yellow-olive Flycatcher	13	31	0	0	100
Dusky-capped Flycatcher	10	40	0	4	0
Median		38	0	4	87

in the canopy of trees (bird height  $\bar{x} = 7.1 \pm 0.4$  m;  $\bar{x}$  tree height =  $10.4 \pm 0.6$  m). Warblers and other birds smaller than Yellow Warblers were significantly lower in the tree when chased than were larger birds (relative height bird/tree = 0.64 versus 0.75, Mann-Whitney  $U = 4432$ ,  $n = 125$  and  $93$ ,  $P < 0.01$ ). Warblers were generally chased from the tree after climbing from its lowest branches. For example, when the Yellow Warbler was on territory, Magnolia Warblers that were not chased averaged  $5.4 \pm 0.5$  m ( $n = 16$ ), whereas Magnolia Warblers that were chased were foraging at  $8.1 \pm 0.6$  m ( $n = 49$ , Mann-Whitney  $U = 206$ ,  $n = 16$  and  $49$ ,  $P < 0.01$ ). During periods when the Yellow Warbler was off territory for more than 5 min, Magnolia Warblers averaged  $8.0 \pm 0.4$  m ( $n = 15$ ).

The average frequency of chasing during year 2 was only slightly greater than one-half (54%) the frequency observed in year 1 during the same season. Vegetation on the pasture was extensively modified with the removal of much of the shrubby understory, possibly reducing habitat for subordinate species. With the exception of a single female Yellow Warbler, all Yellow Warbler territories were similar in size and location throughout the winter. Three color-banded birds were observed to defend the same set of trees all winter. We found no significant difference in the overall frequency of aggression between early and late winter in year 2. The species chased were generally similar. Dur-

ing the early period there were more intraspecific chases and chases of passage migrants such as Canada Warbler (*Wilsonia canadensis*).

*Spacing behavior of Magnolia Warbler.*—Although individual Magnolia Warblers were observed in up to seven different Yellow Warbler territories, each focused on one territory (referred to as a core area). Further, there was a strong tendency for different individuals to occupy different Yellow Warbler territories (Fig. 2).

Overall, the array of Magnolia Warbler home ranges was stable, with only a few disappearances and substitutions. Figure 2 illustrates the banded or recognizable birds during October through December of year 2. Even though banding was conducted during the period of arrival for the species, only one banded Magnolia Warbler was known to be a nonresident (floater or migrant). The yellow-banded Magnolia Warbler was observed off the study area and, thus, its 100% occurrence in territory 1 (Fig. 2) is an artifact of the location of this territory at the edge of the plot. "Yellow" disappeared in January, leaving "Green" as the principal occupant of territory 1. "Black-Orange" was observed in two territories (9 and 10) until January, when an unmarked adult male arrived in territory 10 and restricted Black-Orange to territory 9. The major exception to the one-to-one correspondence was the sharing of Yellow Warbler territories 4 and 5 by Red-Green and Or-

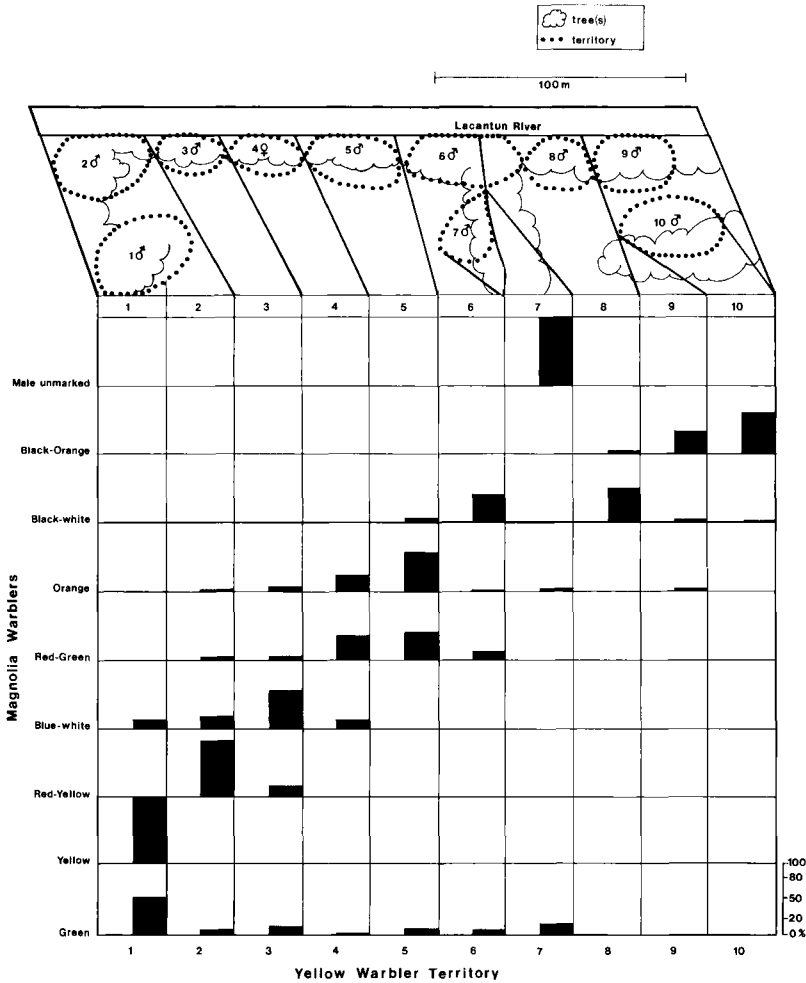


Fig. 2. Linear array of Yellow Warbler territories. Graph displays relative proportion of resightings for marked or otherwise recognizable Magnolia Warblers. Colors on ordinate indicate color-band combinations. Figure illustrates tendency for given Magnolia Warbler to be associated with one Yellow Warbler territory.

ange. Territory 4 was a scrubby area defended by a female Yellow Warbler. Orange abandoned this area for a new territory outside of the study plot in January, leaving territory 4 as a buffer area largely unoccupied by a Magnolia Warbler. Blue-White was observed in territory 3 until early November, when it disappeared and was rapidly replaced by an unmarked immature female. This female and Red-Green moved into the scrubby female territory when chased off the trees by the male Yellow Warbler.

As a result of movements and replacements, in January there was a one-to-one correspondence between Magnolia Warbler core areas and male Yellow Warbler territories (i.e. those with

canopy trees). During followings of focal birds we never saw more than one Magnolia Warbler at a time. Aggression between Magnolia Warblers was rarely observed. However, Magnolia Warbler individuals Red-Green and Orange (which shared two territories) frequently were observed chasing each other. On two occasions aggression was elicited when two warblers were called in with a playback tape. The dominant birds were themselves immediately chased by the local Yellow Warbler.

*Arthropod abundance.*—The total number of arthropods per 100 leaves in *Inga* canopy was approximately double that of the nearby understorey shrubbery ( $5.0 \pm 0.8$  vs.  $2.3 \pm 0.2$ ;

TABLE 4. Number of arthropods per 100 g dry-mass foliage (actual number observed per sample in parentheses) in enclosure and control treatments in canopy versus understory shrub vegetation in Yellow Warbler territories.

Plant type	Enclosure	Control	Percent reduction
<b>Canopy</b>			
<i>Inga</i>	25.2 (21)	22.0 (18)	12
<i>Inga</i>	20.3 (35)	16.5 (29)	17
<i>Inga</i>	34.9 (21)	9.6 (9)	73
<i>Inga</i>	27.2 (29)	13.4 (13)	50
<i>Inga</i>	40.3 (19)	23 (19)	43
<i>Inga</i>	79.8 (40)	7.3 (6)	81
<i>Inga</i>	31.8 (47)	5.0 (7)	84
Unidentified tree	30.9 (17)	7.6 (4)	57
$\bar{x} \pm SE$	$36.2 \pm 6.6$	$13.0 \pm 2.4$	$52 \pm 1.7$
<b>Understory</b>			
<i>Piper</i>	15.8 (20)	1 (2)	94
<i>Piper</i>	69.2 (36)	8.6 (8)	88
<i>Miconia</i>	58.2 (32)	15.9 (9)	73
<i>Apocynacea</i> sp.	58.1 (25)	3.4 (2)	94
Unidentified shrub	30.9 (17)	7.6 (4)	75
<i>Psychotria</i>	17.0 (12)	5.4 (3)	69
$\bar{x} \pm SE$	$41.5 \pm 9.4$	$6.9 \pm 2.1$	$82 \pm 4.5$

Mann-Whitney  $U = 0$ ,  $n = 4$  and  $4$ ,  $P < 0.05$ ). Similarly, there were significantly more large arthropods ( $> 5$  mm length;  $0.4 \pm 0.1$  vs.  $0.2 \pm 0.1$ , Mann-Whitney  $U = 0$ ,  $n = 4$  and  $4$ ,  $P < 0.05$ ).

**Feeding rate.**—We found no significant difference in foraging attack rates between Yellow and Magnolia warblers on Yellow Warbler territories ( $\bar{x} = 3.5 \pm 0.2$  vs.  $4.2 \pm 0.2$ , respectively, Mann-Whitney  $U = 1,772$ ,  $n = 70$  and  $50$ ,  $P > 0.05$ ). However, Yellow Warblers captured large arthropods, primarily 2-cm caterpillars, during 30% of the 70 2-min watches. Magnolia Warblers were only observed to capture large prey during 4% of the 50 watches. This difference was significant ( $X^2 = 12.7$ ,  $df = 1$ ,  $P < 0.001$ ). With an ingestion rate of large arthropods almost an order of magnitude greater in Yellow Warblers compared with Magnolia Warblers, it is likely that their energy intake was considerably higher as well.

**Effect of bird predation on arthropods in Yellow Warbler territories.**—During the pre-experiment census we found an average of  $2.7 \pm 0.06$  arthropods/100 leaves in the area to be enclosed and  $2.7 \pm 0.02$  in the control branches (Wilcoxon signed-rank test  $W = 51$ ,  $n = 14$ ,  $P > 0.05$ ). After the experiments, arthropod numbers were consistently reduced outside versus

inside the bird enclosures by an average of  $64.6 \pm 6.9\%$  (Table 4). The greatest difference was observed in the understory shrubs:  $82 \pm 4.5\%$  versus  $52 \pm 1.7\%$  in the canopy trees (Mann-Whitney  $U = 7.5$ ,  $n = 8$  and  $6$ ,  $P < 0.05$ ). Although the number of arthropods in the understory was only 53% that of the canopy, a result similar to the insect censuses, the number of arthropods in enclosures was similar between the two strata.

Arthropod reductions also were nonrandom with respect to taxa. The greatest differences were found for Orthoptera (84%,  $n = 80$ ) and Lepidoptera (80%,  $n = 24$ ). Other groups showed moderate levels of reduction (Homoptera = 54%,  $n = 19$ ; Araneae = 47%,  $n = 173$ ; and Coleoptera = 43%,  $n = 107$ ). Only the Hemiptera showed no significant reduction in numbers outside the enclosure (4%,  $n = 42$ ).

## DISCUSSION

**Inter- versus intraspecific territoriality.**—Our observations of long-term territoriality in Yellow Warblers are consistent with those of other observers (Morton 1976). Morton argued that the bright yellow coloration found throughout the year in most Yellow Warblers functions primarily as an aggressive signal for territorial defense. He established that individuals in populations lacking bright coloration tended to be nonterritorial participants in mixed-species flocks.

We found that, after the initial period of territory establishment, Yellow Warblers displayed far more overt aggression towards members of other species than towards conspecifics. Interspecific aggression remained high throughout the entire seven-month winter season. Interactions with conspecifics, at least during the late fall and winter, primarily involved counter-calling and border patrolling in close proximity. In contrast, the frequent chases of other species were never accompanied by chipping.

**Determinants of the frequency of interactions.**—Long-distance chases averaging one every 12 min represent a high energetic investment in interspecific defense. The frequency of interactions resulted from two different factors: the high rate of response of Yellow Warblers; and the high frequency of "testing" of Yellow Warblers' territories by subordinate species. Individuals of subordinate species often spent much of their time in shrubbery, hedgerows, or the

lowest branches of trees. Subordinates would only enter the canopy when the Yellow Warbler left the tree or the patch of trees.

However, the frequency of attacks on a particular species was not simply a function of intrusion frequency; the probability of attack was different among species. The contrast could best be seen between interactions involving other small birds (primarily wood-warblers) versus interactions with larger birds (tyrant flycatchers). Warblers were more frequently attacked, driven out of the tree canopy or territory more often, and attacked at lower heights in the tree than were flycatchers.

*Resources in canopy of pasture trees.*—Both the low threshold for aggression and the high frequency of testing by subordinates suggest that the canopy of pasture trees represents a resource with rich food resources. This suggestion is logical and consistent with the observation that pasture vegetation is dominated by fast-growing "pioneer" species, which are relatively productive and have relatively palatable leaves (Coley 1982). The hypothesis that Yellow Warblers are defending an area of high food density is supported by the high density of insects in canopy versus understory vegetation on Yellow Warbler territories. The 5.0 arthropods per 100 leaves is considerably higher than numbers obtained using similar methods in other habitats and regions at the same time of year. Greenberg and Gradwohl (1980) reported 1.2 arthropods per 100 leaves in Panamanian forest understory, Greenberg (1992, in prep.) found 0.8 to 2.5 arthropods per 100 leaves in second growth and forest in the lowlands of Chiapas and Quintana Roo, Mexico. Further evidence of high food abundance in Yellow Warbler territories comes from the frequency with which Yellow Warblers captured large caterpillars.

The enclosure experiments provide evidence that the territorial behavior of the birds acts to increase the standing crop of arthropods (Loyn et al. 1983). If one accepts the assumption that the enclosures primarily affect levels of bird predation on arthropods, then without bird predation the densities of arthropods are similar. With bird predation, arthropod densities in the canopy are twice that of the understory. This may be a result of the exclusion of large numbers of foliage-gleaning birds by a single territorial Yellow Warbler. Presumably, Yellow Warblers are able to accomplish this because of the particular structure of solitary tree canopies. If this hypothesis proves to be correct, then the

interspecific territoriality occurs in response to both the locally high resource levels in forest patches and the defensibility of the canopy. The importance of habitat structure and the ability of the defender to detect and drive out intruders in shaping avian territories has recently received empirical support (Eason 1992).

*Possible influence of interspecific aggression on habitat use and home-range overlap in subordinate species.*—Our study does not establish how widespread interspecific territoriality is in wintering Yellow Warblers. Previous workers on Yellow Warblers in particular (Wiedenfield 1992), and on migrants in general, have not reported interspecific aggression. However, we believe the behavior is easily overlooked. Since discovering its importance in the Lacandon Forest, we have made numerous observations of interspecific aggression by Yellow Warblers in other parts of Chiapas and Las Tuxtlas, Veracruz. Other observers have reported aggressive Yellow Warblers from the Peruvian Amazon (J. Sterling pers. comm.) and Guanacaste, Costa Rica (R. Fleischer pers. comm.). Furthermore, T. Sherry and P. Marrer (pers. comm.) found resident Yellow Warblers to be highly interspecifically aggressive in the mangroves of Jamaica.

If the phenomenon is of common occurrence, it has implications for habitat use and social system of migrants in patches of second growth. Several recent studies have pointed out the potential value of such habitat for overwintering forest migrants (Greenberg 1992, Powell et al. 1992). However, based on fieldwork in Veracruz, Mexico, Rappole and Morton (1985) argued that forest migrants that maintained small populations in cleared areas tended to have nonterritorial spacing systems. Floaters predominate because resources levels are low or unpredictable. At our Chiapas site, observations of Yellow Warblers defending small long-term territories belie this explanation (see also Rappole and Warner 1980). If Yellow Warblers are able to maintain small territories throughout the winter, there is nothing inherently unstable or unpredictable in the resource base that would prevent other species, such as Magnolia Warblers, from maintaining territories as well. Furthermore, we were unable to find evidence of large numbers of floaters belonging to any of the subordinate species (Salgado Ortiz 1993). High turnover and nonterritoriality do not characterize the behavior of the Magnolia Warbler, the most common forest migrant in the



patches of tree. Also, we did not find them in other predominantly forest migrants (Black-and-White Warbler and American Redstart; Salgado Ortiz 1993).

For Magnolia Warblers we found a pattern of regular dispersion with respect to Yellow Warblers. In the single case where two individuals commonly overlapped, much of the shared area was a patch of shrubby area defended by a female Yellow Warbler. Overt aggression was commonly observed between the two Magnolia Warblers. It appears that Magnolia Warblers maintain territories through a mechanism of passive avoidance, perhaps mediated by their frequent use of call notes. Overt aggression may be subdued by the threat of aggression by Yellow Warblers. The pattern of a near one-to-one correspondence between Magnolia and Yellow warbler territories is unusual in birds and has only been reported for species that associate in mixed-species flocks (Munn and Terborgh 1979, Gradwohl and Greenberg 1980). This may be an artifact of the patchiness of the habitat, or could be because Magnolia Warblers that remain resident on a single territory learn both the activity patterns of the dominant Yellow Warbler and possible escape paths to use when attacked.

The winter habitat for Yellow Warblers contrasts with breeding habitat in generally having a clear open understory (city parks, pastures, villages, etc.). A survey of forest patches in the pastures of the Marquez de Comillas shows that Yellow Warblers achieve their highest densities where the understory has been removed (Greenberg et al. unpubl. data). Yellow Warblers may avoid vegetation with a developed understory because dense vegetation provides a critical refuge for subordinate, migratory birds. The great reduction in interactions between years on our study site was probably a result of the clearing of the understory shrubbery in the Yellow Warbler territories.

Given the great extent of cattle pasture in lowland Middle America, small changes in habitat management on pastures may have a large effect on the carrying capacity for migratory birds. The observations in this study suggest that the maintenance of hedgerow vegetation should provide a critical refuge for many migratory species and allow them some access to the highly productive canopy trees.

*Adaptive significance of interspecific strife in Yellow Warblers.*—Because we studied interspecific

aggression in Yellow Warblers in anthropogenic pastures, it may be inappropriate to invoke adaptive hypotheses for its occurrence. However, we observed the phenomena in all habitats used by Yellow Warblers, including second growth in the natural flood plain.

Several hypotheses have been proposed for the function (or lack thereof) of interspecific territorial behavior (Murray 1971, Sherry and Holmes 1988). Because the Yellow Warblers we studied are defending winter feeding territories, those relating to breeding and nesting do not apply. Two major hypotheses remain: (1) interspecific aggression benefits Yellow Warblers by maintaining high food levels with the increase in standing crop of food offsetting the energetic cost of chasing (Carpenter 1978, Gill and Wolf 1979); or (2) the behavior is a non-adaptive carry-over from situations where aggression is adaptive (Murray 1971, Emlen 1973). Several observations argue against the latter explanation: (1) intraspecific chasing was very rare compared to interspecific; (2) the rate of interspecific chasing remained high throughout the winter, despite the rarity of intraspecific chasing; (3) a range of species, very different in appearance from Yellow Warblers, was attacked; and (4) high rates of chasing, either intra- or interspecific, have not been reported for other times of year (Morse 1989). In addition, attacks were more commonly aimed at trespassing warblers and other small foliage-gleaning birds, than against flycatchers. However, this comparison is almost completely confounded by size and the inability of Yellow Warblers to scare off larger birds.

The high frequency of capture of large caterpillars by Yellow Warblers and the high density of arthropods found on canopy leaves suggest that Yellow Warblers are defending rich patches of food. This is the circumstance in which overt, adaptive interference competition should occur (Maurer 1984). In fact, we believe that Yellow Warbler aggression represents a likely example of the importance of interspecific competition in determining habitat use by migratory birds in the nonbreeding season.

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