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INTERSPECIFIC AGGRESSION BY YELLOW WARBLERS IN A SUN COFFEE PLANTATION[1]

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Non-breeding habitat use is mediated infrequently by interspecific aggression in migratory birds. Such aggression occurs most commonly among birds exploiting rich resource patches such as nectar, fruit, or other similar resources (Greenberg et al. 1994). Interspecific territoriality and dominance is less commonly noted among insectivorous species (Rappole and Warner 1980, Greenberg et al. 1994). One such system of interspecific territoriality was recently reported for Yellow Warblers (*Dendroica petechia*) overwintering in riparian trees in cattle pastures (Greenberg and Salgado-Ortiz 1994). Greenberg and Salgado-Ortiz present data suggesting that such patches constitute rich resource islands in an otherwise inhospitable habitat. Furthermore, consistent with the hypothesis of Orians and Willson (1964), the transformation of structurally diverse forest to more open agricultural habitats and the concomitant reduction in abundance and diversity of birds should increase the defensibility of resources. Based on these considerations we hypothesize that interference competition could be important in other tropical agroecosystems where tree cover is substantially reduced. One such agroecosystem is "sun" coffee plantation. Sun coffee plantations have taken hold recently and replaced traditional shaded coffee plantations throughout much of Latin America (Perfecto et al., in press). In this note we provide some support for the hypothesis by presenting our observations of interspecific aggression by Yellow Warblers defending isolated trees in a sun coffee plantation in Guatemala.

STUDY SITE AND METHODS

Observations were made during February and March 1995 on a large (4,000 ha) coffee plantation (Finca Concepción) and smaller adjoining plantations—Delicia and Dulcé Nombré—in Tucurú, Guatemala (15° 8′N, 90° 14′W, 450–600 m elev.). The habitat consisted of rows of coffee approximately 2 meters in height with a scattering of small trees (*Inga, Gliricidia, Erythrina, Citrus,* etc.) generally 4–5 meters in height. Bird densities were low (Greenberg et al., unpubl. data) and the most common species were either temperate migrants or resident species characteristic of agricultural habitats. The following were the 15 most common species based on point counts (Greenberg et al., unpubl. data) in descending order of abundance: Wilson's Warbler (*Wilsonia pusilla*), Magnolia Warbler (*Dendroica magnolia*), Rufous-capped Warbler (*Basileuterus rufifrons*), Yellow-faced Grassquit (*Tiaris olivacea*), Blue-black Grassquit (*Volatinia jacarina*), Least Flycatcher (*Empidonax minimus*), Indigo Bunting (*Passerina cyanea*), Black-headed Saltator (*Saltator atriceps*), Black-throated Green Warbler (*Dendroica virens*), Great-tailed Grackle (*Cassidix mexicanus*), Chestnut-headed Oropendola (*Psarocolius wagleri*), Clay-colored Robin (*Turdus grayi*), Melodious Blackbird (*Dives dives*), and Yellow Warbler.

Yellow Warblers were found commonly in sun and semi-shade coffee plantations, as well as those with a light deciduous shade of the small-leafed legume *Gliricidia sepium,* but were absent from forest, coffee plantations with substantial shade, and shrubby habitats. Although we had no marked birds, the behavior of the Yellow Warbler was consistent with the defense of small territories. Birds repeatedly patrolled the same small area, and engaged in counter-calling with neighboring Yellow Warblers at boundary trees. Throughout the study we observed birds with similar patterns of red markings in the same set of trees.

As in the cattle pasture study, one or (more commonly) two people followed each of 11 Yellow Warblers for 3 hours (7:00–10:00). Information on location and behavior of individuals refers to this time period throughout the paper—we have no data on birds during the mid-day or afternoon. Each bird was watched for one session, with the exception of one individual that was followed for two 90-min periods. Birds were actually only in view for 26 of the 33 possible hours of observation. In addition to occasions when birds were lost, there were frequent periods of inclement weather. Observers recorded the location of the bird, the distance of all between-tree flights, and the distance and target of any chase. At the end of the period the area covered by the Yellow Warbler was mapped and estimated. Mapping and distance estimations were facilitated by the farmer's practice of planting purple ornamental plants at 10-meter intervals, forming a highly visible grid system. Because territories were larger than in the previous study, we were unable to keep track of all intruders onto coffee plantation territories.

RESULTS

All of the focal Yellow Warblers (indeed, all Yellow Warblers observed in the sun coffee plantation) were

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males, based on the presence of red streaking on the underparts (Pyle et al. 1987). Most of the Yellow Warbler activity occurred in the canopy of small trees, with individuals found only 17.9% of the time (10% SD, n = 11) in the coffee layer. Yellow Warbler territories averaged 0.5 ha ± 0.25 SD (n = 11). Yellow Warblers moved frequently between trees on the territory, averaging 16.7 flights between tree or bushes per hr, covering 219 ± 79 m SD. Chases occurred an average of 2.20 times per hr (2.5 SD, range 0–8.9, 52 total) with a mean distance of 7.5 ± 1.4 m between the site of chase initiation and the target bird. Of the 50 instances when the target bird was identified, 40% were Magnolia Warblers, 20% Tennessee Warblers, 12% Black-throated Green Warblers, 8% Least Flycatchers, 6% Yellow Warblers, 4% Indigo Buntings, 2% Philadelphia Vireos (*Vireo philadelphicus*), 2% Solitary Vireos (*V. solitaria*), 2% Wilson's Warblers, and 2% House Wrens (*Troglodytes aedon*). Overall, 97% were to heterospecific individuals, 98% were to migrants, and 86% were to species that are approximately the same size or smaller than Yellow Warblers. Yellow Warblers chased a non-random subset of the birds in a plantation. We compared the proportion of chases directed to common (> 0.10 individual per point count, Greenberg et al., unpubl. data) small (< 15 g) birds to the proportional abundance of these species (Table 1). Although the point counts were distributed over a larger area than the focal territories, we regard them as our best quantitative estimate of the abundance of birds that have a potential of interacting with the Yellow Warblers. With this caveat in mind, we found a large and significant difference between the frequency of chases to a species and its relative abundance (χ^2 = 39.9, df = 7, $P < 0.001$). The largest deviations were found in Magnolia and Tennessee Warblers, which were chased more frequently, and Wilson's and Rufous-capped Warblers and the grassquits, which were chased less frequently than expected on the basis of abundance. Overall, small birds that commonly forage in trees were the preferred targets for Yellow Warbler attacks (Table 1). All but 10 of the chases (19%) involved displacing the target bird from a tree rather than a coffee shrub. Nearly all (90%) of the chases resulted in the target bird leaving a particular tree. However, only three chases resulted in birds leaving the entire Yellow Warbler territory.

DISCUSSION

Yellow Warbler aggression in coffee plantations was similar to that reported from gallery vegetation in cattle pastures (Greenberg and Salgado-Ortiz 1994) in several ways. At both sites birds involved in the interspecific aggression were predominantly males. Previously we had found that primarily male Yellow Warblers are found in tall trees, whereas females occupy scrubby habitats with small trees. It is interesting, therefore, that male Yellow Warblers are characteristically found in sun coffee plantation—a scrubby habitat. Interspecific aggression was far more common than intraspecific at both sites. Most intraspecific territorial interactions involved counter-calling or individuals perching in adjacent trees at territorial boundaries. Most aggression was directed towards small insectivorous migratory species, with Magnolia Warblers being by far the most frequent victim (40% in coffee plantation and 35% in riparian pasture trees). Aggression against small birds was usually successful in displacing birds out of trees into the shrub layer. Patrolling behavior was similar, with 16.7 inter-tree flights per hr compared to 22.2 in the cattle pasture territories. Chases were initiated from a similar distance from the target bird (7.5 ± 1.4 vs. 9.0 ± 0.7m SE).

However, some notable differences between sun plantation and riparian pasture trees were observed. Yellow Warblers spent considerable time (17.8%) in the shrub (coffee) layer, whereas they spent virtually all of their time in the riparian pasture trees. This may relate to the small stature and isolated distribution of the plantation trees which provides poor cover for protection from predators and insolation. Territory size was considerably larger in the sun plantation (0.5 ha versus 0.05 ha, $U_{11,12}$ = 132, $P < 0.001$), and interspecific chases were much less frequent there (2.2 ± 2.5 SD per hr versus 4.9 ± 3.1 SD per hr, $U_{11,16}$ = 150, $P < 0.002$), probably because of the much lower frequency of intruders, associated with the overall low density of birds in sun coffee plantations. We recorded 2.0 migrants and 4.0 total birds per 10-min point count (n = 110 points) in sun coffee (Greenberg et al., unpubl. data), and 4.7 migrants and 12.2 total birds in gallery vegetation in lowland cattle pasture in Chiapas (n = 212 points, Warkentin et al. 1995). This amounts to approximately double the number of migrants and tri-

TABLE 1. Percentage chases involving small (<15 g) birds versus their relative abundance in a sample of 110 point counts in sun coffee plantations for species with greater than 10 detections on point counts (Greenberg et al., unpubl. data).

Species	% Birds chased (n = 45 ind.)	% Census (n = 238 ind.)	Strata
Magnolia Warbler	40	15	shrub/canopy
Tennessee Warbler	20	4	canopy
Black-throated Green Warbler	12	8	canopy
Least Flycatcher	8	10	canopy
Indigo Bunting	4	10	shrub
Wilson's Warbler	2	16	shrub
Rufous-capped Warbler	0	13	shrub
Yellow-faced Grassquit	0	13	shrub
Blue-black Grassquit	0	10	shrub

ple the total number of birds. This magnitude of difference corresponds well with the 2.2 times greater frequency of chasing, particularly because Yellow Warblers chased mainly migrants. One could argue that territory size is 10 times larger in sun coffee, thus the number of intruders should be higher than in the cattle pasture territories. However, the similar distance from which attacks were initiated suggests that at both sites, Yellow Warblers displaced only birds in a small, local area.

Perhaps because of the large size of plantation territories, Yellow Warblers rarely chased subordinates entirely from their territory. In addition, chases were focused on birds in a small portion of the territory at any one time. Therefore, the behavior of Yellow Warblers in sun coffee plantations cannot clearly be defined as interspecific territoriality (although these complications occur to varying degrees in most territorial systems). However, because the area defended by the Yellow Warbler moved with the warbler, the behavior is not similar to interspecific site dominance found commonly in some nectarivorous species (Lyon 1976). Still, whatever the phenomenon is labelled, Yellow Warblers invest considerable energy in displacing potential competitors from the limited number of small trees found in their territories. Because coffee shade trees support a much higher biomass of arthropods than do coffee plants themselves (Greenberg et al., unpubl. data), the aggression of Yellow Warblers may be an important factor in reducing the access of subordinate species to food resources in sun coffee plantations. In three years of research in shaded coffee plantations we have obtained no evidence of a similar system of interspecific interference competition. This suggests that above and beyond the reduction in resources caused by the conversion of shade to sun coffee, some migratory species incur the additional cost of being harassed while foraging in the few productive trees in sun plantations.

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LITERATURE CITED

GREENBERG, R., AND J. SALGADO-ORTIZ. 1994. Interspecific defense of pasture trees by wintering Yellow Warblers. Auk 111:672–682.

GREENBERG, R., J. SALGADO-ORTIZ, AND C. MACIAS-CABALLERO. 1994. Aggressive competition for critical resources among migratory birds in the Neotropics. Bird Conserv. Int. 4:114–127.

LYON, D. L. 1976. A montane hummingbird territorial system in Oaxaca, Mexico. Wilson Bull. 88: 281–299.

ORIANS, G. H., AND M. F. WILLSON. 1964. Interspecific territories of birds. Ecology 45:736–745.

PERFECTO, I., R. RICE, R. GREENBERG, AND M. VAN DER VOORT. In press. Shade coffee: a disappearing refuge for biodiversity. BioScience.

PYLE, P., S. N. G. HOWELL, R. P. YUNICK, AND D. F. DESANTE. 1987. Identification guide to North American passerines. Slate Creek Press, Bolinas, CA.

RAPPOLE, J., AND D. WARNER. 1980. Ecological aspects of migrant bird behavior in Veracruz, Mexico, p. 353–393. In A. Keast and E. S. Morton [eds.], Migrant birds in the Neotropics: ecology, behavior, distribution, and conservation. Smithsonian Institution Press, Washington, DC.

WARKENTIN, I., R. GREENBERG, AND J. SALGADO-ORTIZ. 1995. Songbird use of gallery woodland in recently cleared and older settled landscapes of the Selva Lacandona, Chiapas, Mexico. Conserv. Biol. 9:1095–1106.