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SOCIALITY AND FORAGING BEHAVIOR OF THE CERULEAN WARBLER IN VENEZUELAN SHADE-COFFEE PLANTATIONS¹

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Abstract. We examined the use of Venezuelan shade-coffee plantations by the Cerulean Warbler (*Dendroica cerulea*) and other Neotropical migrants. Cerulean Warblers were commonly observed as pairs in mixed-species flocks. Average (\pm SE) flock size was 13 ± 2 species with 22 ± 3 individuals. Average flock territory size was 2.5 ± 0.2 ha. No differences were detected in foraging behavior (maneuvers, location, or success) among adult males, adult females, and immature birds. Adult males were often observed visiting flowers of canopy trees. The results of this study indicate that shade coffee plantations may provide suit-

able wintering habitat for Cerulean Warblers although comparisons with other habitats are needed.

Key words: *Cerulean Warbler, Dendroica cerulea, foraging behavior, mixed-species flocks, Neotropical migrants, shade coffee plantations, Venezuela.*

The North American population of Cerulean Warblers (*Dendroica cerulea*) is declining faster than that of any other species of wood-warbler (Robbins et al. 1992, Sauer et al. 1997). Despite the growth of research efforts on the breeding grounds, little has been published on their wintering habits and habitats (Robbins et al. 1992, Parker 1994).

Cerulean Warblers winter on the eastern slope of the Andes Mountains of South America. Individuals have most often been observed within a narrow elevation range of 500–2,000 m (Robbins et al. 1992), although they have been sighted at over 3,000 m (J. Jones, pers. observ.). This elevation range corresponds with the

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mature, humid evergreen forest zone and is a landscape that is ideal for human settlement and agriculture, notably the production of coffee, cacao, tea, hill rice, and coca (Robbins et al. 1992, Stotz et al. 1996). Other than the Atlantic Forests of Brazil, the humid montane forests of South America have been altered more drastically than any other South American forest type (Robbins et al. 1992, Stotz et al. 1996). These factors contribute to the conclusions of some researchers that the degradation of habitats in the northern Neotropics is a major cause of the decline of migratory songbird populations (Morse 1980, Robbins et al. 1989, Rappole and McDonald 1994).

The goal of our research was to assess the use of shade coffee plantations by Cerulean Warblers in Venezuela. First, we examined the social behavior of Cerulean Warblers within shade coffee avian-species assemblages. Cerulean Warblers are known to occur in mixed-species flocks during migration and on the wintering grounds (Robbins et al. 1992, Parker 1994). Second, we documented the wintering foraging behavior of Cerulean Warblers. We paid special attention to birds foraging in *Erythrina poeppigiana* due to this tree's high wildlife value (Feinsinger et al. 1979, Morton 1979, Toledo and Hernández 1979). We documented foraging behavior as the first step to understanding how Cerulean Warblers use managed forests.

METHODS

STUDY AREA

This study was undertaken in January–February 1997 in the states of Mérida and Barinas, Venezuela; these two states are within the most northerly stretch of the contiguous Andes Mountains in South America. Study sites were selected on the basis of Cerulean Warbler sightings by other ornithologists. All study sites were areas of shade coffee cultivation that ranged in elevation from 675 to 1,230 m. Thirteen of the 14 surveyed plantations were actively managed, and 1 was abandoned. The average (\pm SE) size of the shade coffee plantations (herein referred to as cafetales) was 3.3 ± 0.3 ha ($n = 14$). Tree species found in the canopy of these sites included *Inga* spp., *Erythrina poeppigiana*, *Cedrela mexicana*, *Heliocarpus popayanensis*, and *Persea americana*. The cafetales were surrounded by a mixture of second-growth forest, cattle pasture, and cropland.

MIXED-SPECIES FLOCK OBSERVATIONS

Mixed-species flocks within the cafetal boundaries were followed and observed if they contained at least one Cerulean Warbler. Birds were considered to be members of a flock if they were seen foraging with at least one other species and moving with them for at least 15 m (Powell 1989, Hutto 1994). Flock territory boundaries were inferred by antagonistic interactions with other flocks (Jullien and Thiollay 1998) or by habitat discontinuities, such as roadsides, beyond which the flock did not pass. Territory sizes were determined by transcribing territory boundaries onto detailed maps of the regions and measuring the area directly using the map scale.

FORAGING OBSERVATIONS

To document foraging behavior of Cerulean Warblers, each individual encountered was followed for as long as possible. No maneuver was recorded during the first 30 sec of observation to minimize bias towards more obvious maneuvers (Hejl et al. 1990, Noon and Block 1990). Observation units were 1 min in length separated by 1 min of no recording. Each maneuver was classified as a glean, sally, or lunge (Remsen and Robinson 1990). Each maneuver observed during the 1-min observation periods was noted, as was the success or failure of each maneuver, if discerned. To maximize statistical independence, only the first maneuver from each observation period was used in the analyses (Hejl et al. 1990). Foraging heights were measured using a clinometer and measuring tape. Substrates were not recorded. Sample size considerations limited our analyses to foliage gleans only.

All species observed foraging in *Erythrina poeppigiana* were documented with careful attention paid to whether or not the birds investigated flowers. A flower was considered "visited" if the bird placed its head inside the corolla. Flowers were gathered by hand from low branches to examine any fauna living inside the flower.

DATA ANALYSES

All variables were tested for normality and homoscedasticity, and no transformations were necessary. Statistical tests were considered significant at $P \leq 0.05$. Values reported are means \pm SE.

RESULTS

Cerulean Warblers were detected at all sites and were the fourth most common Neotropical migrant in the cafetales. The three most common Neotropical migrants were American Redstart, Bay-breasted Warbler, and Blackburnian Warbler, in decreasing order of abundance (scientific names in Table 1).

MIXED-SPECIES FLOCK OBSERVATIONS

Sixteen mixed-species flocks containing Cerulean Warblers were surveyed (Table 1). Sixty-three species participated in these flocks with an average number of species of 13 ± 2 (range 6–23). The average number of individuals was 22 ± 3 (range 8–40). Only once was a Cerulean Warbler observed outside of a mixed-species flock. On average, two individual Cerulean Warblers (range one to four) were detected in each flock, usually one male and one female. The average flock territory size was 2.5 ± 0.2 ha (range 1.6–3.4 ha). All flock territories were contained within the boundaries of the cafetales.

FORAGING BEHAVIOR

We limited our analysis of foraging behavior to 104 foraging observations made on 31 individual Cerulean Warblers. Adult males ($n = 14$ individuals; 52 observations) foliage gleaned 65% of the time, sallied 19%, and lunged 16%. Adult females ($n = 11$; 31 observations) foliage gleaned 68% of the time, sallied 19%, and lunged 13%. Immature birds ($n = 6$; 21 observations) foliage gleaned 76% of the time, sallied 19%, and lunged 5%. There were no sex/age differences in the distribution of observed foraging maneuvers (χ^2 ,

TABLE 1. Bird species occurring in 16 Cerulean Warbler mixed-species flocks, ranked in decreasing frequency of occurrence. Only species sighted in $\geq 25\%$ of flocks are listed. Mean values are based only on flocks in which a given species was detected.

Species	Frequency (%)	Mean \pm SE individuals per flock
American Redstart (<i>Setophaga ruticilla</i>)	88	2.2 \pm 0.2
Blue-gray Tanager (<i>Thraupis epsicopus</i>)	67	2.0 \pm 0.0
Tennessee Warbler (<i>Vermivora peregrina</i>)	44	1.1 \pm 0.1
Blackburnian Warbler (<i>Dendroica fusca</i>)	44	1.6 \pm 0.2
Bay-breasted Warbler (<i>Dendroica castanea</i>)	44	1.9 \pm 0.3
Streak-headed Woodcreeper (<i>Lepidocolaptes souleyetii</i>)	38	1.5 \pm 0.2
Black-and-white Warbler (<i>Mniotilta varia</i>)	38	1.8 \pm 0.2
Guira Tanager (<i>Hemithraupis guira</i>)	38	2.2 \pm 0.2
Red-crowned Woodpecker (<i>Melanerpes rubricapillus</i>)	31	1.4 \pm 0.1
Bananaquit (<i>Coereba flaveola</i>)	31	1.8 \pm 0.2
Blue-necked Tanager (<i>Tangara cyanicollis</i>)	31	1.6 \pm 0.2
Burnished-buff Tanager (<i>Tangara cayana</i>)	31	1.6 \pm 0.2
Buff-throated Saltator (<i>Saltator maximus</i>)	31	1.4 \pm 0.2
Yellow-bellied Elaenia (<i>Elaenia flavogaster</i>)	25	1.3 \pm 0.3
Slaty-capped Flycatcher (<i>Leptopogon superciliaris</i>)	25	1.5 \pm 0.3
Yellow-legged Thrush (<i>Platycichla flavipes</i>)	25	1.8 \pm 0.3
Rufous-browed Peppershrike (<i>Cyclarhis gujanensis</i>)	25	1.8 \pm 0.3
Scrub Greenlet (<i>Hylophilus flavipes</i>)	25	1.3 \pm 0.3
Slate-throated Redstart (<i>Myioborus miniatus</i>)	25	1.8 \pm 0.3
Bay-headed Tanager (<i>Tangara gyrola</i>)	25	1.8 \pm 0.3

= 1.6, $P > 0.5$), nor was any sex/age group more likely to succeed at a given foraging attempt (foliage gleaned only, males 66% successful, females 74%, immatures 50%; $\chi^2 = 1.82$, $P = 0.40$). Cerulean Warblers primarily gleaned from canopy and midstory foliage, although male Cerulean Warblers ($n = 7$) also were observed foraging in dead leaf clusters in bromeliad epiphytes. Cerulean Warblers were never observed foraging on coffee plants. The majority of the sallies were mostly to air. Identified prey items included lepidopteran larvae, spiders, and large flies. No significant difference (ANOVA, $F_{27,101} = 0.64$, $P > 0.5$) was found in foraging heights for adult males (12.4 \pm 0.58 m; range 6.5–17.4), adult females (11.8 \pm 0.82 m; range 6.3–15.2), and immature birds (11.2 \pm 0.56 m; range 7.4–15.3).

Of the 109 bird species observed in *Erythrina poeppigiana*, 57% were observed foraging on the flowers, including Cerulean Warblers. The average visitation rate by Cerulean Warblers was 17 \pm 2 flowers min^{-1} ($n = 7$ adult males). Other Neotropical migrants observed foraging in *E. poeppigiana* flowers were Tennessee Warbler, Bay-breasted Warbler, Blackpoll Warbler (*Dendroica striata*), American Redstart, and Rose-breasted Grosbeak (*Pheucticus ludovicianus*). Examination of the flowers revealed that 6.7% (5/75) of flowers contained insects and these were either micro-dipterans or microcoleopterans.

DISCUSSION

It appears that Cerulean Warblers may be tolerant of a degree of habitat disturbance and manipulation on the wintering grounds. Although Cerulean Warblers regularly occur in undisturbed forest (J. Jones, pers. observ.), they also are relatively common in cafetales in

Venezuela. In other areas of the Neotropics, Neotropical migrants are commonly observed using cafetales during the winter season (Greenberg et al. 1997a, 1997b, Johnson 1999, Moguel and Toledo 1999). However, as density is not always a reliable indicator of habitat suitability (Van Horne 1983), estimates of overwinter survival and comparisons with undisturbed habitats are needed to fully assess the quality of cafetales as nonbreeding habitat for Cerulean Warblers and other Neotropical migrants (Conway et al. 1995). Johnson (1999) found that the overwinter persistence of American Redstarts was higher in Jamaican shade coffee and citrus plantations than in natural habitats.

Most of the flocks in our study area which contained Cerulean Warblers contained at least two individuals, usually an adult male and female. Whereas Parker (1994) reported seeing as many as six individuals in one flock during spring migration in Belize, Robbins et al. (1992) reported that never more than two individuals were present in mixed-species flocks in Peru. It appears that, once on the nonbreeding grounds, Ceruleans adopt a sociality similar to that of the resident species that exist in mixed-flocks—that is, a single male and single female per flock (Powell 1980, Jullien and Thiollay 1998). Despite their abundance (both within and across flocks), none of the northern migrant species appeared to be acting as nuclear species (Powell 1980).

One of our motivations behind exploring mixed-species flock composition in cafetales was to examine the interplay between migrant sociality and habitat carrying capacity of managed landscapes (Jullien and Thiollay 1998). The average shade cafetal size in our study sites was 3.3 ha. This is representative of shade cafetal sizes throughout the Andean region of Venezuela (P.

R. Perazzi, pers. observ.). Venezuelan cafetales are smaller than sizes documented for Guatemala (8.7 ha; Greenberg et al. 1997a) and slightly smaller than those in Costa Rica (3.5 ha; Perfecto 1996). When average cafetal size is compared with average mixed-flock territory size (~2.5 ha), it appears that shade cafetales in Venezuela may be capable of only supporting a single mixed-species flock. This translates to an average of two Cerulean Warblers per cafetal. The same physical area can support three to four breeding pairs in eastern Ontario, Canada (J. Jones, unpubl. data). Consequently, mixed-species flocking behavior in wintering Cerulean Warblers may indirectly contribute to population limitation. Individual species densities were possibly limited by the multi-species territorial system below the level that would be allowed by single-species territoriality (Jullien and Thiollay 1998). Cerulean Warblers that inhabit other habitat types also participate in mixed-species flocks and the territory sizes of these flocks are similar to those found within cafetales (J. Jones, pers. observ.).

The foraging activities of Cerulean Warblers were concentrated in the midstory of the cafetales (as evidenced by average foraging heights), except for time spent foraging in the flowers of *Erythrina poeppigiana*. Although we did not quantify substrate use, Cerulean Warblers, especially adult males, often were observed foraging on the foliage of epiphytes and in dead leaf clusters collected in bromeliad epiphytes. The removal of epiphytes from canopy trees is a common management tool in Venezuelan cafetales and may have adverse effects on Cerulean Warbler ecology.

The lack of sex or age differences in foraging location, maneuver distribution, and maneuver success parallels findings from the breeding grounds (J. Jones, unpubl. data), although low sample sizes likely limited our statistical power. Although Cerulean Warblers were never observed foraging on coffee plants, they often were observed in shrubby undergrowth surrounding coffee plantations. These behaviors are similar to the opportunistic use of the understory observed on the breeding grounds (J. Jones, unpubl. data).

All species of *Erythrina* are pollinated by birds (Bruneau 1997), and *E. poeppigiana* is thought to be primarily passerine pollinated with occasional hummingbird assistance (Feinsinger et al. 1979, Bruneau 1997). The peak flowering period of *E. poeppigiana* coincides with the arrival of northern migrants (Feinsinger et al. 1979). Several, primarily insectivorous, migrant species were observed visiting *E. poeppigiana* flowers in Venezuela, including Cerulean Warbler, Tennessee Warbler, Bay-breasted Warbler, Blackpoll Warbler, and American Redstart. As the examination of flowers revealed very little arthropod biomass within the flowers, we believe that these Neotropical migrants were visiting the flowers for nectar or pollen. Diet augmentation on the wintering grounds is a relatively common behavior in Neotropical migrants (Leck 1972, Emlen 1973, Morton 1980). Indeed, the reliance of certain Neotropical migrants on nectar food-resources may have led to remarkable instances of coevolution (e.g., Orchard Orioles *Icterus spurius*, and *Erythrina fusca* in Panama; Morton 1979). To our knowledge, use of nectar or pollen has not previously

been reported for Cerulean Warblers or Blackpoll Warblers.

Our results indicate that shade coffee plantations may offer Cerulean Warblers suitable wintering habitat in South America. Given the trends in habitat degradation throughout the nonbreeding range of this species, this is a positive sign. Much work remains to be done, however, before we can truly assess the value of these managed landscapes for Neotropical migrants. Of primary importance is the sampling of habitats other than managed landscapes to determine whether the densities of individuals supported in shade coffee are indicative of overall densities. The next step is to address site tenacity at these managed sites, both within and across seasons, and to explore differences in overwinter survivorship between managed and undisturbed habitats. Finally, we need to explore the effects of cafetal canopy management such as manipulation of *Erythrina* abundance or bromeliad removal on habitat use and habitat selection by Neotropical migrants.

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