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DEFENSE OF NECTAR RESOURCES BY MIGRATING CAPE MAY WARBLERS

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Abstract.—Cape May Warblers (*Dendroica tigrina*) were observed foraging at a migratory stopover site near Delta Marsh, Manitoba, in springs with seasonable weather in mid- to late May (1980 and 1981, and 1984–1986) and with below-normal temperatures (1983). During the seasonable springs, arthropods were gleaned (67.1% of 231 prey-capture maneuvers) and aerially hawked (32.9%) from the upper, outer canopy of the deciduous forest and resources were not defended. During the inclement weather in 1983, nectar and possibly pollen were defended at willow catkins. Up to four male Cape May Warblers (two of them color-banded) interacted aggressively with one another, and also dominated Ruby-throated Hummingbirds (*Archilochus colubris*) and Tennessee Warblers (*Vermivora peregrina*) that attempted to forage at the catkins.

DEFENSA DE RECURSOS ALIMENTICIOS POR PARTE DE *DENDROICA TIGRINA*

Resumen.—Individuos de *Dendroica tigrina* fueron observados forrajear en una localidad cercana a Delta Marsh, Manitoba, durante primaveras frescas desde mediados hasta finales de mayo (1980–1981 y 1984–1986) y primaveras frías (1983). Durante las primaveras frescas los artropodos fueron rebuscados (67.1% de 231 presas) y aereamente halconeados (hawking) (32.9%) en la parte superior, externa del docel de un bosque deciduo. Los recursos alimentarios no fueron defendidos. Sin embargo, durante la fría primavera de 1983, las aves defendieron nectar y posiblemente polen de *Salix amygdaloides.* Cuatro aves machos (dos anillados) interaccionaron agresivamente entre sí y dominaron a individuos del zumbador *Archilochus colubris* y a otros de *Vermivora peregrina* que trataron de utilizar los mismos recursos alimenticios.

Many species of North American migrant passerine birds are primarily insectivorous during the breeding season, but subsist largely on nectar or fruit during the remainder of the year (see Keast and Morton 1980). One of these species is the Cape May Warbler (*Dendroica tigrina*). This species seems to be primarily insectivorous while breeding, and MacArthur (1958) and Morse (1978) regarded it as a fugitive species whose population levels on the breeding grounds are influenced by outbreaks of the spruce budworm (*Choristoneura fumiferana*). On the wintering ground, however, this species is an obligate nectarivore. Little is known of the Cape May Warbler's feeding strategy during migration, although anecdotal observations suggest that floral nectar and other plant juices may be among the important sources of energy at this time (e.g., Brooks 1933, Kale 1967, Kilham 1953, Marvel 1948). In the present paper, I report the short-term defense of willow catkins, sources of nectar and possibly pollen, by migrating Cape May Warblers (some of them color-banded) during one spring with unseasonable weather at a stopover site in southern

Manitoba. During springs of five other years with seasonable weather the species generally preyed upon insects in and near tree canopies.

OBSERVATIONS

During mid-May of each year since 1974 we have observed a few migrating Cape May Warblers, most of them males, in the forested dune ridge along the southern shore of Lake Manitoba, Manitoba (area described in MacKenzie 1982). In 1980–1981, and 1984 through 1986, springs without prolonged storms or below-normal temperatures in mid-May, I recorded the prey-capture techniques and foraging location in the ridge forest of 23 individuals (19 males, 4 females) that were feeding alone. Of the 231 prey captures observed, 67.1% were of arthropods gleaned from plant substrates, and 32.9% were of prey aerially hawked. All feeding occurred in the upper, outer canopy of the forest, generally in or from peach-leaved willows (*Salix amygdaloides*), a common tree species in the ridge forest (MacKenzie 1982). No Cape May Warblers were seen interacting aggressively with other Cape May Warblers or individuals of other species in these years, and none occupied a particular site for more than a few minutes. This foraging behavior seemed to be typical of Cape May Warblers during springs with normal weather conditions.

On 19 May 1981, I located four male Cape May Warblers that were foraging 40–110 m apart in isolated, new-growth peach-leaved willows. Single individuals or their replacements foraged in and from these trees over the next 3 d, but all were gone by dawn on 23 May. The birds appeared to feed only on insects, primarily by aerially hawking them from the outer canopies of the willows. After most prey-capture attempts, the individuals returned to the same trees. I did not see any of these individuals interact aggressively with other Cape May Warblers or individuals of other species. Because none of the warblers were banded or otherwise individually distinguishable, I was not certain whether the same birds were observed each day. The weather during May, 1981 was seasonable.

In 1983, one of the willows that was used by a male Cape May Warbler in 1981 was occupied by up to four males at once. This spring was cold (Weatherhead et al. 1985), and the Cape May Warblers fed primarily on nectar and possibly pollen from the catkins of the willow (see Kay 1985). Inter- and intraspecific interactions were frequent. On 18 May, one male was present, along with up to six Ruby-throated Hummingbirds (*Archilochus colubris*) that were also foraging at the catkins. By 22 May, four male Cape May Warblers fed on nectar, although each occasionally hawked flying insects, but returned to the same tree all 14 times this prey-capture maneuver was observed. Typically, the three or four birds were spaced about 1.5–2 m apart in the crown of the tree, and any individual that entered another's "territory" was chased out of it. Seven times I saw individual Cape May Warblers fly 10–20 m and land on an adjacent lawn where they apparently captured arthropod prey amid grass before returning to the same portion of the tree. The Cape May Warblers chased hummingbirds and Tennessee Warblers (*Vermivora peregrina*) nine and three times, respectively, during the 3.5 h I observed them between 18 and 23 May.

On 23 May 1983 I color-banded two of the male Cape May Warblers (A and B) observed above between 0730 h and 0940 h; both of these males and two unbanded individuals remained in the tree the rest of that day and all of the next, but were gone on 24 May. Males A and B foraged consistently in about 3 m^2 of the upper and outer canopy, but on different sides of the tree. Occasionally, they hawked prey or foraged on the lawn, but soon returned to their "territories" in the willow. Eleven times male A supplanted B and each time male B moved to another part of the crown or to another tree nearby. It was when one of the males returned that most of the interactions occurred.

Using sweep nets, we sampled the arthropod biomass on tree foliage in the ridge forest from mid-May through mid-August every year from 1975 through 1987. The biomass has fluctuated greatly each year (Busby and Sealy 1979, Guinan and Sealy 1987), but in general it was low until the end of May or early June when emergences of adult midges (Diptera: Chironomidae) began. In 1981, the weather during May was normal, and the Cape May Warblers gleaned and aerially hawked arthropods, and none was seen interacting aggressively or behaving in other ways that suggested food resources were defended. In 1983, when below-normal temperatures prevailed in mid-May, nectar was sought and its source was defended. The behavior of some other species of migrant and resident species also changed during this period in 1983, presumably in response to depleted food reserves. Swallows huddled in species-specific nest sites, and many died (Weatherhead et al. 1985). Yellow Warblers (*D. petechia*), including banded residents and migrants, foraged on the beach of Lake Manitoba and in Delta Marsh. Color-banded males deserted their territories in the ridge forest to join the warbler feeding flocks.

DISCUSSION

Selection should favor the defense of a food source, even temporarily, when the energy gained from its exclusive use exceeds the energy expended in the defense (Myers et al. 1979, Wolf et al. 1975). Evidence suggests that defending nectar sources is energetically worthwhile (Cruden and Hermann-Parker 1977, Tramer and Kemp 1979). The defense of a food supply by migrating, male Cape May Warblers has been observed generally under circumstances where regional shortages of natural foods were suspected. Kale (1967) reported a migrating Cape May Warbler over three consecutive days on Dry Tortugas, Florida, that repeatedly attacked and repelled warblers of its own and other species whenever they approached a certain blossom of a century plant (*Agave braceana*). Kale also summarized M. Hundley's observations of aggressive behavior by migrating Cape May Warblers, in peninsular Florida, but no indication was given whether localized sites were defended. On the wintering grounds, Leck (1972) observed a Cape May Warbler in Puerto Rico that exhibited long-term territorial behavior at a *Cecropia* tree. The warbler chased Bananaquits (*Coereba flaveola*) and Black-throated Blue Warblers (*D. caeurulescens*) when they came near the flowers. Away from the tree, the Cape May Warbler was subordinate to the Bananaquit and of equal dominance with the other warbler species. Emlen (1973) reported a Cape May Warbler that dominated throughout one day the flower head of an agave on Grand Bahama Island, where it chased Palm Warblers (*D. palmarum*), Common Yellowthroats (*Geothlypis trichas*), and Cuban Emeralds (*Chlorostilbon ricordii*). Wunderle (1978) reported a Palm Warbler defending the flowers of a Tiger's Claw (*Erythrina* sp.) in Florida. The warbler spent more time chasing conspecifics from the tree than it spent chasing either of two other species of wood warblers. During lengthy pursuits of conspecifics, both Yellow-rumped Warblers (*D. coronata*) and Northern Parulas (*Parula americana*) flew into the unguarded tree and fed on nectar until the Palm Warbler returned and chased them. Wunderle reasoned that shorter pursuits of conspecifics should permit the tree to be guarded more efficiently from other warblers. Although I did not time the pursuits by Cape May Warblers in the present study, conspecifics were indeed chased more frequently (see also Sealy 1988). However, this may have been because the aggressive individuals were side by side in the same tree. Also, the relative abundance of Cape May Warblers and individuals of the other species was not known.

Tramer and Kemp (1979) reported Tennessee Warblers, over-wintering in Costa Rica, that tolerated conspecifics when they fed on insect larvae but became intolerant of them when they sought nectar (but see Morton 1980). The migrating Cape May Warblers, in the ridge forest, similarly shifted their behavior when they fed on nectar during inclement weather in 1983. The nectar source was defended against conspecifics and individuals of at least two other species, but arthropod prey taken in the forest canopy in years with normal weather conditions apparently was not defended. Interestingly, during a storm in 1982, Cape May Warblers sought neither arboreal prey nor nectar, but instead defended "territories" along water and fed on tiny insects from its surface (Sealy 1988). The Cape May Warbler's plasticity in its short-term use of food resources permits individuals to exploit a wide variety of food types often under unpredictable environmental conditions. This plasticity is not surprising because the adaptations of migrants represent compromises due to different selection pressures on the breeding grounds, wintering grounds, and at migration stopover sites (Rappole and Warner 1976).

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