

with human urine, and was not eaten by coyotes.) The bird hopped away at my approach and reached the lower branches of a spruce, then hopped up ahead of me from branch to branch. It kept 2 to 3 m ahead of me as I followed. The bird occasionally stopped to peck vigorously at the branches at its feet and to twist off small twigs. Small chips and twigs sometimes fell down. Having gained altitude near the crown the bird flew off when I got close. It (or another bird) returned to the deer remains a day later and this time I ran it down on snowshoes. (The bird accepted meat within seconds of being caught. Its wing muscles were greatly atrophied, but it revived fully after being fed in an aviary for several weeks.) The bird, while captive, snipped all

loose twigs and bark from its perches, and it often hammered the perch in its cage when it saw me coming, first retreating into a corner of the cage away from me.

Perhaps corvids regularly hammer and/or dislodge objects near them as a displacement behavior when they are angry or frustrated. For example, captive Clark's Nutcrackers, *Nucifraga columbiana*, hammer their perches when they are not given food while birds in neighboring cages are being fed (J. Marzluff, pers. comm.). The dislodging of substrate onto intruders could be incidental and a matter of circumstance, rather than serving (consciously or unconsciously) to dissuade intruders.

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## AGGRESSIVENESS IN MIGRATING CAPE MAY WARBLERS: DEFENSE OF AN AQUATIC FOOD SOURCE<sup>1</sup>

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*Key words:* Stopover sites; Cape May Warbler; *Dendroica tigrina*; Manitoba; territoriality; aggressive behavior.

How passerine birds cope with the challenges they face as they move along their migratory pathways has received increasing attention recently (e.g., Rappole and Warner 1976, Bibby and Green 1980, Cherry 1982, Graber and Graber 1983). Undoubtedly, food acquisition influences how these birds decide to use space, because getting enough food to store fat, or merely to survive, is probably the single most important constraint during this time (Hutto 1985). What complicates the decision-making process is that migrating birds sometimes must use resources whose availability fluctuates (Schneider and Harrington 1981, Terrill and Ohmart 1984), often because of unpredictable changes in weather (see Weatherhead et al. 1985, Hobson and Sealy 1987). Nonbreeding birds, including migrants, sometimes find it necessary and economically worthwhile to defend localized food sources, even for a few hours or days. However, the dynamics of this short-term territoriality are poorly known (but see Emlen 1973, Schemske 1975, Rappole and Warner 1976).

During mid-May each year a few migrating Cape May Warblers (*Dendroica tigrina*) stop over on the forested dune ridge (described by MacKenzie 1982) along the southern shore of Lake Manitoba, Manitoba. The number of individuals present during each spring

migration is usually small and only rarely are any captured during routine netting that is conducted daily during the warbler migrations. In some years, however, a few males have been observed defending nectar sources, sometimes over a period of several days (Sealy, unpubl. data). In the present paper I examine a previously undescribed defense of prey on the surface of water by migrating Cape May Warblers.

### RESULTS

Transient individuals of the Cape May Warbler, influenced by a 3-day storm in 1982, suspended their usual arboreal foraging (i.e., foliage gleaning and aerial hawking) and defended fixed areas (territories, sensu Brown 1975) along a water-filled ditch bordered on one side by willows (*S. interior* and *S. amygdaloides*) and on the other by marsh habitat dominated by new shoots of *Phalaris arundinacea* L., about 20 to 25 cm in height. These territories (Fig. 1) were reminiscent of those held by Northern Waterthrushes (*Seiurus noveboracensis*) during migration (Rappole and Warner 1976) and in winter (Schwartz 1964).

The first Cape May Warbler, a male, was seen in 1982 on 10 May; it gleaned and aerially hawked prey from the outer edge of the canopy. Over the next several days more Cape May Warblers were seen, foraging as above. By 17 May the weather had turned inclement, and a severe storm, with high winds, rain, and below-normal temperatures, prevailed through 20 May. In the late afternoon of 17 May I found three males on the ground, each about 8 m apart at the edge of the water in the ditch; they fed on Collembola (Isotomidae) on the water's surface. By noon on 18 May six males were present. The birds walked along the shoreline and

<sup>1</sup> Received 2 September 1987. Final acceptance 2 October 1987.

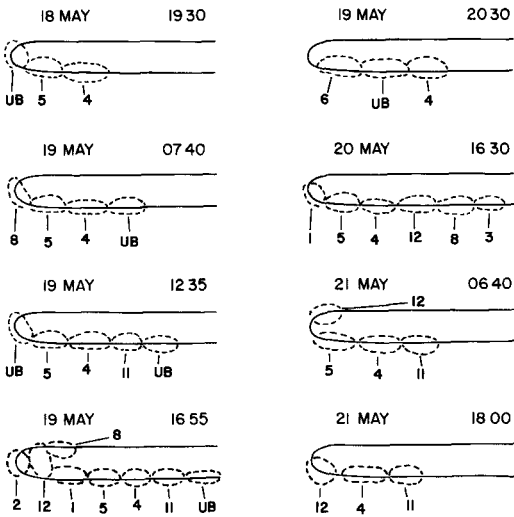


FIGURE 1. Boundaries of Cape May Warbler territories along the edge of a water-filled ditch in the dune-ridge forest, Delta Marsh, Manitoba, 18 to 21 May 1982. Dashes (—) = territory boundary; UB = unbanded bird; numbers refer to specific individuals.

gained access to the prey on the water's surface by perching on bent-over and floating branches. Aggressive interactions between Cape May Warblers and other species suggested that they were defending specific areas. By late afternoon that day I had color-marked 11 males, and by noon the next day another individual had been marked. Three of these individuals were not seen again.

Up to nine males, eight marked and at least one unmarked, held territories along the side of the ditch with trees for hours and in some cases for up to at least 4 days (Fig. 1). Each male defended his territory against intrusion by other male and female Cape May Warblers (Table 1). The proportion of interactions in each category did not change between territory owners and nonterritorial opponents (Table 1,  $\chi^2 = 0.047$ ,  $P \gg 0.25$ ). The territorial Cape May Warblers dominated most of the individuals of the 10 other species with which they interacted. Of these the Swainson's Thrush (*Catharus ustulatus*), Yellow-rumped Warbler (*Dendroica coronata*), and Northern Waterthrush were large

in body size (Table 2). Solitary Sandpipers (*Tringa solitaria*), considerably larger, were tolerated in their territories and the two interactions that involved the Cape May Warbler-sized Least Flycatcher (*Empidonax minimus*) saw the Cape May Warblers chased (Table 2). The primary means of territorial defense seemed to be overt aggression, with intruders being chased away. I did not hear any call notes that might have been involved in defense (see Rappole and Warner 1976). Territorial neighbors occasionally crossed each other's boundaries but most hostile interactions were directed toward intruders from elsewhere (Table 1). Attacks on these birds were frequent and usually saw the intruder chased away. Some fights occurred that involved physical contact; twice, two Cape May Warblers fell into the water. When two individuals were removing prey from the water's surface and found themselves confronting one another, a visual display often was given by one or both of them. The birds crouched slightly, raised their tails, and walked rapidly toward one another.

Figure 1 shows the arrangement of Cape May Warbler territories along the ditch at various times from 18 to 21 May. The territory holders remained on their territories throughout 19 May, during the height of the storm. Foraging apparently involved taking only surface insects. None of the birds spent the night on its territory; by 20:40 on 18 and 19 May, respectively, all territory holders had moved into the tree portion of the ridge forest. Some of the males had returned to their territories by 06:30 (Fig. 1). By noon on 20 May the wind had died down somewhat and although it remained cold, some of the territory holders began to fly across the ditch to the marsh where they foraged amid *Phalaris*. Such trips were infrequent on 19 May but increased over 20 and 21 May as the storm subsided (Table 3). Also, aerial hawking of flying prey gradually became more frequent on 20 and 21 May (Table 3), with less time being spent feeding and defending territories. All of the territorial males were gone by 22 May and none was encountered elsewhere on the study area. The last Cape May Warbler, an unmarked male, was seen on 23 May foraging in the upper canopy of a tree in the ridge forest.

#### DISCUSSION

The defense of an aquatic food supply by Cape May Warblers reveals a previously unrecognized plasticity in this species' selection of prey and the methods it uses to obtain it. The habitat shift observed is perhaps not too surprising for a migratory species such as this, considering the myriad of habitats it must encounter

TABLE 1. Interactions involving territorial male Cape May Warblers with conspecifics.

Status of opponent	Visual displays	Chases	Fights
Territory owner	4 (33%) <sup>a</sup>	8 (32%) <sup>b</sup>	2 (29%) <sup>c</sup>
Nonterritorial bird <sup>d</sup>	8 (67%) <sup>a</sup>	17 (68%) <sup>b</sup>	5 (71%) <sup>c</sup>
Total	12	25	7

<sup>a</sup>  $\chi^2 = 1.33$ ,  $P > 0.1$ .

<sup>b</sup>  $\chi^2 = 3.24$ ,  $P < 0.05$ .

<sup>c</sup>  $\chi^2 = 1.29$ ,  $P > 0.1$ .

<sup>d</sup> Includes unbanded females.

TABLE 2. Species of birds with which territorial male Cape May Warblers did or did not interact, 18 to 20 May 1982.

Species	Mean body mass (g) <sup>1</sup>	No. of interactions	No. interactions initiated by Cape May Warbler/no. initiated by other species
Solitary Sandpiper ( <i>Tringa solitaria</i> )	51.2	0	—
Least Flycatcher ( <i>Empidonax minimus</i> )	10.3	2	0/2
House Wren ( <i>Troglodytes aedon</i> )	10.9	2	2/0
Swainson's Thrush ( <i>Catharus ustulatus</i> )	30.8	1	1/0
Orange-crowned Warbler ( <i>Vermivora celata</i> )	9.0	1	1/0
Yellow Warbler ( <i>Dendroica petechia</i> )	9.8	6	6/0
Yellow-rumped Warbler ( <i>D. coronata</i> )	12.3	8	8/0
Black-and-white Warbler ( <i>Mniotilta varia</i> )	11.0	2	2/0
American Redstart ( <i>Setophaga ruticilla</i> )	8.5	7	7/0
Northern Waterthrush ( <i>Seiurus noveboracensis</i> )	17.8	4	4/0
Wilson's Warbler ( <i>Wilsonia pusilla</i> )	7.7	1	1/0

<sup>1</sup> Body mass data from Dunning (1984); mean mass of Cape May Warbler ( $n = 102$ , sexes combined) = 11.0 g.

on its migratory pathway (see also Zumeta and Holmes 1978). Cape May Warbler foraging behavior on the breeding grounds has been characterized as occurring consistently near the tops of trees, where, in addition to gleaning insects from the foliage, it frequently aerially hawks flying insects (MacArthur 1958). Its movements in the trees are generally vertical, causing the feeding zone to be restricted to the outer shell of the tree (MacArthur 1958). This picture of Cape May Warbler foraging behavior, however, changes when other workers' observations and those of the present study are considered. Although Cape May Warblers have been reported foraging in upper and outer canopies in winter (Skutch 1967; Lack 1976; Post 1978; Sealy, pers. observ.), this trait may not be characteristic during that season. Eaton (1953) and Bond (1957) noted that overwintering Cape May Warblers often foraged near the

near the ground, and during inclement weather on the breeding grounds, MacArthur (1958) sometimes found them foraging in low shrubs, often amid flowers. Morse (1980) reported them foraging amid grass on beaches. In addition, Cape May Warblers have been observed feeding on localized concentrations of food such as insects at flowers, fruit, and sap in addition to nectar (Foster and Tate 1966, Kale 1967, Leck 1972, Emlen 1973, Lack 1976).

Nectar feeders, such as hummingbirds and sunbirds, tend to chase all competitors of the same or smaller size with equal vigor (e.g., Wolf et al. 1975). This observation is consistent with Morse's (1974) conclusion that interspecific dominance is generally based upon size, for larger species are either difficult or impossible to chase from a territory. Although most of the individuals that the territorial Cape May Warblers chased in the present study were of the same or smaller size, three species were slightly to considerably larger (Table 2). One of these species, the Northern Waterthrush, apparently was excluded from foraging along the ditch, a habitat that this species uses frequently during migratory stopovers in the ridge forest. The observations also showed that Cape May Warblers chased conspecifics from their territories more often than they did other species (Table 1), a finding consistent with Wunderle's (1978) observations of a Palm Warbler (*Dendroica palmarum*) defending a nectar source. The true significance of the present observations, however, cannot be appreciated fully because the relative abundance of Cape May Warblers and individuals of the other species was not known (see Post 1978).

The observations in the present study and those reported in the literature shed light on the results of Grant's (1966) analysis of the relative tarsus lengths of landbirds. In contrast to seven other groups of passerine birds, Grant found that *Dendroica* warblers did not show a correlation between relative tarsus length and foraging position. Because Cape May Warblers had been characterized by MacArthur (1958) as a species that foraged the highest and most peripherally in the canopy, they therefore were presumed to use rigid

TABLE 3. Extra-territorial foraging trips taken by male Cape May Warblers, 19 to 21 May 1982. Observations were made between 09:40 and 12:40 of males 4, 5, and 11, holders of contiguous territories.

Extra-territorial foraging	Male number		
	4	5	11
No. of trips to forage in marsh			
19 May	6	3	2
20 May	9	9	7
21 May	17	11	13
	$\chi^2 = 6.07^a$	$4.52^a$	$8.28^b$
No. of aerial hawks			
19 May	1	0	2
20 May	5	3	3
21 May	6	7	9
	$\chi^2 = 3.50^c$	$7.40^d$	$6.14^a$

<sup>a</sup>  $P < 0.05$ .

<sup>b</sup>  $P < 0.005$ .

<sup>c</sup> Not significant.

<sup>d</sup>  $P < 0.025$ .

perches the least. Thus, Grant predicted that this species would have the smallest tarsus/wing length ratio. In fact, he found that the Cape May Warbler has the second largest ratio. This result is perhaps not so surprising in light of this species' now-known diverse use of foraging stations. Indeed, as Grant pointed out, its representation as the species that uses rigid perches least seems to be incorrect.

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