DEMOGRAPHIC AND POPULATION RESPONSES OF CAPE MAY WARBLERS WINTERING IN MULTIPLE HABITATS

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Abstract. Wintering Cape May Warblers (*Dendroica tigrina*) were studied in three habitats along an altitudinal gradient in the Dominican Republic. Results of this study are some of the first to link both population responses and individual condition of nonbreeding birds to prevailing ecological conditions across divergent habitats. Our data suggest that Cape May Warblers are habitat generalists and generally unspecialized resource opportunists, but that differences in food resources result in competitive interactions, sex and age class segregation, and differences in site fidelity and physiological condition among habitats. Diet of the Cape May Warbler varied between habitats: in desert, Cape Mays were primarily insectivores; in dry forest, they foraged primarily on homopteran honeydew; in pine forest, they were principally frugivores. Abundance of warblers as measured by mist-net captures was highest in pine forest sites. Males were more common than females in pine habitat, whereas there was a female-biased sex ratio in other sites. Adult birds were more common in the desert and the pine forest, but there was a bias toward immature birds in dry forest habitat. Overwinter site persistence was 76% in pine, but only 28% and 33% in dry forest and desert, respectively. Annual return rate averaged 57% and did not vary significantly among habitats. Adjusted body mass of site-persistent birds was highest in pine and dry forest and lowest in desert. Pectoral muscle mass scores increased in the pine forest throughout the sampling period, whereas muscle mass scores decreased in the desert. These data suggest that, among the habitats sampled, pine was preferred. It is likely that stability and predictability of resources, particularly fruiting *Trema* trees and nectar sources, attracted dominant Cape May Warblers to pine forests and kept them as site-persistent individuals in good body condition. In contrast, dry forest may have been suboptimal, unless an individual was able to hold and defend a tree with honeydew-producing homopteran scale insects. Desert thorn scrub was seemingly suboptimal because resources were consistently scarce, and conditions became increasingly difficult during the late-winter dry period.

Key words: altitude gradients; Cape May Warbler; demography; Dendroica tigrina; *diet; foraging behavior; habitat generalist; Hispaniola; resource opportunist; site dependence; site fidelity; wintering behavior.*

INTRODUCTION

A fundamental issue in ecology and conservation is the mechanism of population regulation. Identification of the factors that control population size is required to understand the population dynamics of any organism. The determination of regulating factors or processes is a difficult task with most organisms, but is especially so in migrating birds, for which habitat is often thought to play a central role in population regulation. Because migratory birds occur over broader geographic areas than many other organisms, and because breeding and wintering populations probably utilize divergent habitats, population dynamics must be examined on spatial scales that include multiple habitats. Recent models of population regulation of migratory birds in the annual cycle (Sherry and Holmes 1995, 1996, Rodenhouse et al. 1997), based on Fretwell

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(1972) and Morse (1980), suggest the importance of how variation in habitat quality may affect demographics, physiological condition, and survival of migratory birds, and may also impact population size (Rappole and McDonald 1994, Sherry and Holmes 1995, Latta and Baltz 1997).

Studies of the wintering ecology of migratory birds have been used to understand population changes (Rappole et al. 1989, Robbins et al. 1989, Sherry and Holmes 1996) and population limitation (Sherry and Holmes 1995, Marra and Holberton 1998) of a variety of species. Early studies focused primarily on the distribution and abundance of species in Mesoamerica (i.e., Lynch 1989, Hutto 1992) and the Caribbean (Terborgh and Faaborg 1980, Arendt 1992, Wunderle and Waide 1993), often concluding that geographically widespread species, species found in a variety of habitats, or species found in early-successional habitats were habitat generalists on the wintering grounds (Terborgh 1989, Hutto 1992, Lynch 1992). Simultaneously, ecological studies of the foraging behavior of Neotropical migrants often concluded that many wintering

migrants are opportunistic and take advantage of temporarily abundant and spatially unpredictable food resources (Karr 1976, Morse 1989, Levey and Stiles 1992).

More recent studies have focused on the need for habitat-specific demographic data in assessing habitat preferences and population limitation of migratory birds (Holmes et al. 1989, Wunderle 1995, Wunderle and Latta 2000) because a species may segregate by sex and age class, and abundance data alone may be a misleading indicator of population size and habitat preference. Furthermore, various studies have found geographic and temporal variation in habitat use (Hutto 1992, Lynch 1992, Petit et al. 1995) and resource use patterns (Rappole et al. 1983), but these conclusions tend to be drawn from results of compilations of data from various studies over large spatial and temporal scales. Few studies have simultaneously examined the demographics and ecology of those species that are assumed to be habitat generalists and foraging opportunists across a variety of contiguous habitats.

In terms of food resources, habitat generalists are likely to be confronted by a wide array of choices that may vary between habitats or change over time, particularly in a variable environment. Migratory birds in the Caribbean and elsewhere are likely to encounter decreasing opportunities in late winter as droughts associated with the dry season impact food resources (Baillie and Peach 1992, Strong and Sherry 2000), but changes in food abundance associated with dry-season events may also vary between habitats (Parrish and Sherry 1994, Latta and Faaborg 2001).

Among migratory parulines, food limitation has been shown to affect individuals through loss of body mass (Strong and Sherry 2000), delay of northbound migration (Marra et al. 1998), and depressed rate of feather regrowth (Grubb 1989, 1991). The effects of food limitation may also be seen at the population level because food availability may drive dominance mechanisms in winter habitat selection, resulting in sex and age class segregation (Fretwell 1972, Marra et al. 1993). Sherry and Holmes (1995, 1996) have proposed a model of winter population limitation of migratory birds based on Fretwell (1972) that suggests that competitive interactions and sex and age class segregation resulting from between-habitat differences in food resources result in between-habitat differences in physiological condition and site fidelity. The Sherry and Holmes model has been related to the concept of site-dependent regulation (Rodenhouse et al. 1997), which incorporates preemptive site selection and the occupation of heterogeneous environments in providing the negative feedback necessary for population regulation. However, few empirical studies have attempted to link population responses and individual condition of nonbreeding birds to prevailing ecological conditions (Strong and Sherry 2000, Latta and Faaborg 2001), and

none have involved studies of habitat generalists across multiple habitats of varying quality.

The Cape May Warbler (*Dendroica tigrina*) is a Neotropical migratory Parulid warbler that winters in a variety of habitats, principally in the West Indies (Rappole et al. 1983), and may be considered a habitat generalist. Although Wunderle and Waide (1993) concluded from a survey of Caribbean habitats that the species was a ''moderate habitat specialist'' in midsuccessional to mature forest, the species was most abundant in residential areas, and was also recorded in dry forest, coppice, wooded pasture, lowland broadleaf forest, pine, montane broadleaf, and montane second-growth forest. Arendt (1992) also reported the species from nearly every Caribbean habitat in Hispaniola and added open areas, riparian vegetation, wet forests, and wetlands to the list of occupied sites. In most cases, the species defends exclusive territories (Staicer 1992, Baltz and Latta 1998), although it appears to be neither territorial nor site faithful in dry forest in Puerto Rico (Faaborg and Arendt 1984), where it occurs sporadically. In some habitats, territorial Cape May Warblers will occasionally join mixed-species flocks (Staicer 1992, Latta and Wunderle 1996), but in Dominican sites studied here, mixed-species flocks were rarely observed; territoriality was indicated by repeatability of observation of marked individuals in localized areas and aggressive interactions between birds. Although the Cape May Warbler is a spruce budworm specialist in the breeding season (Kendeigh 1947, MacArthur 1958, Crawford and Jennings 1989), it has a broader diet on the wintering grounds, where it is known to forage on insects, fruit, and nectar (Greenberg 1984, Greenberg et al. 1994, Baltz and Latta 1998). The Cape May Warbler has, however, been offered as an example of a migrant morphologically specialized to exploit a distinctive tropical resource (Sealy 1989, Sherry and Holmes 1995); the accuminate bill and semitubular tongue of the Cape May may have evolved for feeding on flowers and fruit and for collecting nectar, which is only available in the winter for this species (Sherry 1990).

In this study, we examined habitat-specific demography and foraging ecology of the Cape May Warbler in three divergent habitats along an altitudinal gradient in the Sierra de Bahoruco, Dominican Republic. Our objective was to test the Sherry and Holmes (1995, 1996) model of winter population limitation of migratory birds by linking population responses and individual condition of this habitat generalist to prevailing ecological conditions, and by showing how demography interacts with habitat quality, mediated by foraging ecology, to limit populations. First, we hypothesized that there are between-habitat differences in the types of resources available to Cape May Warblers, and that these resources determine foraging behavior. Second, we hypothesized that a physiological effect of habitat differences on wintering Cape May Warblers would be observed through changes in adjusted body mass and

PLATE 1. Male Cape May Warblers (*Dendroica tigrina*) frequently feed on *Agave antillana*, especially in high elevation pine forest where relatively predictable food resources attract primarily dominant male and adult overwintering individuals. Photograph by Eladio Fernandez.

in pectoral muscle mass scores. Third, we hypothesized a population response to differences in habitat quality through sex and age class segregation, and between-habitat differences in the survival indices of overwinter site persistence and annual return rate. Finally, we used these data to assess whether the Cape May Warbler is a resource specialist, generalist, or opportunist in the nonbreeding season.

STUDY SITES AND METHODS

We studied winter-resident migratory birds from 1 October to 1 April 1996–1997 and 1997–1998, and from 8 January to 15 February 1999. Three study sites of 12–15 ha each were established in each of three habitats: low-elevation desert thorn scrub (20–50 m elevation), mid-elevation dry forest (300–745 m elevation), and high-elevation pine forest (1100–1475 m elevation) near Cabo Rojo and the Sierra de Bahoruco, Dominican Republic (18°0′ N, 71°38′ W).

Desert thorn scrub sites.—Low-elevation desert thorn scrub, found on a characteristic dogtooth limestone substrate, has been studied by Fisher-Meerow and Judd (1989). Vegetation consists of widely scattered broadleaf trees which are partially deciduous, small broadleaf shrubs, and various cacti. Common broadleaf tree species include *Capparis cynophallophora*, *C. ferruginea*, *Guaiacum officinale*, *Haitiella ekmanii*, *Metopium brownei*, *Phyllostylon brasiliensei*, and *Plumeria obtusa*. Common shrubs include *Croton origanifolius*, *C. discolor*, and *Lippia alba*.

A foliage height profile (Latta and Brown 1999) shows a low, open canopy with an understory dominated by broadleaf shrubs. Few forbs are present, and

although cacti and succulents are also sparse, they do occasionally extend into the canopy. Canopy cover is spare, at $22.0 \pm 28.4\%$ (all data are expressed as mean $\pm$ 1 SD), with greatest cover in the 2–4 m height categories and a maximum height of only 6 m. Mean and median broadleaf tree heights are 1.4 ± 1.0 m and 1.2 m, respectively.

Mean temperature is 25.0°C in January in desert thorn scrub habitat; mean rainfall is <500 mm/yr (Fisher-Meerow and Judd 1989), with two pronounced dry seasons annually (December–March and July–August); December–March is normally exceedingly dry.

Dry-forest sites.—The most abundant trees in dry forest are from the Malvaceae, Euphorbiaceae, and Fabaceae, and include *Capparis ferruginea*, *Zizyphus rignoni*, *Bursera simaruba*, *Cameraria angustifolia*, *Cordia buchii*, and *Plumeria obtusa*; in disturbed areas, *Acacia macracantha*, *Prosopis juliflora*, and *Cassia atomaria* may be found (see Plate 1; Fisher-Meerow and Judd 1989).

A foliage height profile shows a moderately low, mostly closed canopy, a few large emergent trees, and an understory dominated by broadleaf shrubs. Only low forbs are present, and cacti and succulents are sparse. Canopy cover averages $93.9 \pm 16.6\%$, with greatest cover in the 4–8 m height categories and a maximum height of 22 m. Mean and median broadleaf tree heights are 10.6 ± 4.6 m and 8.0 m, respectively.

Mean temperature is 25.0°C in January; rainfall is estimated at 750–1000 mm/yr, with two pronounced dry seasons annually: December–March and July–August (Fisher-Meerow and Judd 1989).

Pine sites.—Pine forest is dominated by Hispaniolan

Pine (*Pinus occidentalis*); the only other common tree is the palm *Coccothrinax scoparia*. In some areas, particularly those disturbed by road cuts, burning, or natural forces, *Trema lamarckiana* may be prominent. A well-developed shrub layer is present, and common broadleaf species include *Cestrum brevifolium*, *Chamaescrista glandulosa*, *Coreopsis buchii*, *Hypericum hypericoides*, *Lyonia truncata*, *L. microcarpa*, *Myrica picardae*, and *Senecio picardae*, as well as the succulent *Agave antillana* (Fisher-Meerow and Judd 1989). The ground is covered by a thick layer of grasses.

A foliage height profile (Latta and Sondreal 1999) shows a fairly open canopy, a sparse intermediate layer of pine, and a dense mixed-broadleaf and pine understory. Canopy cover averages $51.1 \pm 26.4\%$, with greatest cover in the 6–15 m height categories and a maximum pine height of 23 m. Mean and median pine heights are 17.7 ± 4.9 m and 19.0 m, respectively. The intermediate layer also consists solely of pine. Broadleaf trees and shrubs form a dense ground cover and understory, with broadleaf trees extending to 2.5 m in height.

Mean annual temperature in pine forest is ~15°C and mean rainfall is ~1700 mm/yr (Fisher-Meerow and Judd 1989), normally with two dry seasons annually (December–March and July–August). The dry season in pine is less pronounced than that at lower elevations.

Bird abundance.—We used both point counts and mist netting as complementary indices of abundance of Cape May Warblers (Ralph and Scott 1981, Ralph et al. 1993). We conducted 10-min, 25 m radius point counts at six points in each study site in October, January, and March 1996–1998 and January 1999. Points were situated in a grid pattern except in the linear dry-forest study sites, where points were placed along a transect. In all cases, each census point was 150 m from the closest point. All point counts were conducted by the same observer, begun at sunrise, and completed by 0930 hours. No point counts were conducted in inclement weather. We calculated the mean number of detections of birds ($\times 100$) within 25 m of each site during each month sampled, and the mean number of detections across each habitat each year. A second measure of abundance was made by counting the number of birds captured in mist nets, and calculating the number of captures per net-hour of effort ($\times 1000$) in each habitat.

Sampling birds.—Birds were sampled with mist nets (12 m $\times$ 3 m $\times$ 30 mm mesh) set in three parallel rows (150 m apart) of 11–16 nets each; nets in the dry-forest sites were placed in a single line of 31–39 nets over ~700 m. Birds were sampled three times annually: November, January, and March 1996–1998, and again in January 1999. All mist-netted birds were identified to species, age (immature = HY/SY, hatching year/second year; adult = AHY/ASY, after hatching year/after second year), and sex by plumage characteristics (Pyle et

al. 1987). We used midwinter mist net captures to determine demographic structure and assumed that captures were representative of the sex and age classes resident in each habitat. Only midwinter captures were used to avoid the inclusion of wandering birds which are much more prevalent in the early- and late-winter periods.

We measured wing chord and weighed birds to the nearest 0.1 g on a 30-g Pesola scale. All migrants were scored for pectoral muscle mass using a scale of 0–3 (0, muscle concave and sternum prominent; 3, muscle convex and sternum not detectable; Gosler 1991), and furcular fat deposits using a scale of 0–5 (0, no fat; 5, fat bulging and spilling out of furcular cavity; Holmes et al. 1989). All birds were banded with both a numbered metal band and color bands for identification of individuals in the field.

Following each banding session, color-banded birds were relocated through extensive resighting efforts. We spent a mean of 57.2 ± 41.1 person-hours relocating color-banded birds at each site in each banding session. Resighting effort varied somewhat between sites, but continued until all previously identified site-faithful birds were relocated, or until no more newly resighted banded birds were identified after >10 person-hours of searching a site.

Site fidelity.—We describe both within-year (overwinter site persistence) and between-year (annual return rate) site fidelity. The former is defined as those birds banded in November and subsequently recaptured or resighted in January or March of the same field season. We quantify overwinter site persistence during early winter (November–January) and late winter (January–March), as well as for the entire November–March winter period. Annual return rate is defined as any of the within-year site persistent birds (from a previous field season) that were captured or resighted in a subsequent field season.

Wanderers.—Wanderers are individuals without a territory that are thought to adopt a wandering strategy because of the presence of territorial conspecifics in all suitable habitat (Fretwell 1972, Wunderle 1995). Color-banded birds that were never seen >24 h after banding were assumed to be nonterritorial wanderers.

Foraging behavior.—We recorded a single foraging event for each Cape May Warbler encountered each day. We used the methods of Remsen and Robinson (1990) to record the location of the food item or foraging substrate and the foraging maneuver used in each foraging event. All near-perch maneuvers were combined into a single category and included glean, reach, and probe. Similarly, all aerial maneuvers were combined into a single category. We identified the food item taken as often as possible. In many cases, however, we assumed that: (1) a bird probing into a flower is consuming nectar; (2) an individual gleaning or reaching to vegetation is consuming arthropods; and (3) a bird repeatedly gleaning or reaching to *Bursera* bark

TABLE 1. Abundance of Cape May Warblers in three habitats as determined by fixed-radius point counts and mist-net captures.

Habitat and year	Point count†	Mist-net captures‡	
		Per net-hour × 1000	Total
Desert thorn scrub			
1997	0.0	5.8	28
1998	5.6	4.0	25
1999	0.0	6.4	10
Mean (1 SE)	1.9 (0.6)	5.4 (0.7)	
Dry forest			
1997	5.0	6.6	26
1998	41.5	7.4	34
1999	50.0	6.2	9
Mean (1 SE)	32.2 (13.8)	6.8 (0.4)	
Pine forest			
1997	16.5	3.6	18
1998	8.4	9.1	32
1999	25.0	9.8	15
Mean (1 SE)	16.6 (4.8)	7.5 (2.0)	

† Point count data are: (no. birds/25 m radius circle) × 100. Sample sizes (no. point counts per habitat per year) are $n = 54$ point counts for 1997 and 1998, and $n = 18$ point counts in 1999.

‡ Mist-net capture data are: (no. birds captured per net hour) × 1000 and the total number of captures.

or limbs is foraging on honeydew. For analysis, all food items were classified as nectar, fruit and seeds, arthropods, or homopteran honeydew. Because the sex of the foraging bird was not consistently recorded, foraging data were pooled across sex.

Flower and fruit abundance.—We used the methods of Hilty (1980) and Blake et al. (1990) to document flower and fruit abundance. Ten individuals of each species of flowering or fruiting plant known to be commonly used by foraging Cape May Warblers were randomly selected along a transect, marked, and scored monthly for flowers and fruit. Scores are an index of flowering or fruiting activity and are based on a scale of 0 to 4 (0, no flowers or fruit; 1, ≤25% of crown in flowers or fruit; 2, 26–50%; 3 = 51–75%; 4, 76–100%). A mean score of flowering or fruiting activity was then calculated for each month in each site. Flowering and fruiting species were not ranked or weighted by bird preference because only commonly used species were included in the analyses. Plants selected for studies of flowering included *Guaiacum officinale*, *Agave brevipetala*, and *Opuntia moniliformis* in the desert thorn scrub; *Bursera simaruba* and *Guaiacum sanctum* in dry forest; and *Coccothrinax scoparia*, *Agave antillana*, and *Trema lamarckiana* in pine forest. Plants selected for studies of fruiting included *Bursera simaruba* in dry forest and *Trema lamarckiana* in pine forest; no fruiting trees were known to be used by Cape May Warblers in desert thorn scrub habitat.

Statistical analyses.—The software package SYSTAT Version 5.2.1 (Wilkinson 1992) was used to perform various statistical tests described by Sokal and Rohlf (1995). Data are presented as mean ± 1 SD unless otherwise stated. Data were tested for normality using normal probability plots and tests of skewness and kurtosis. When data were not normally distributed, nonparametric statistics were used.

A Spearman correlation was used to compare point-count data to mist-net capture data, fruit and flower abundances to abundance of Cape May Warblers in mist-net captures, and fruit and flower abundance to the percentage of birds wandering. A 2 × 2 test of independence with a χ^2 statistic or a row × column test of independence with a G statistic was used to test for independence in the age and sex of birds between habitats; the age and sex of wandering birds, site-persistent individuals, and birds returning the following year; the percentage of wandering birds among habitats; and the percentage of various food items in the diet.

We used ANOVA to examine the effects of year and habitat on the number of birds detected in point counts and the number of birds captured in mist nets. ANOVA was also used to examine the effects of habitat and sampling period (early-winter; mid-winter; late-winter) on adjusted body mass (body mass/wing chord), and the effect of sampling period on adjusted body mass within each habitat. Differences in the mean abundance of flower and fruit were analyzed among years, habitat types, and sampling periods using a three-way ANOVA. ANOVA was also used to test for interactions and to test for differences in flower and fruit abundance among years and sampling periods within each habitat. Finally, we used ANOVA on ranked data (Conover and Iman 1981) to examine the interaction between habitat and winter time period in terms of pectoral muscle mass score and fat score.

TABLE 2. Percentage of midwinter captures of Cape May Warblers distributed by sex and age class across three habitats: HY, immature birds including HY/SY birds; AHY, adult birds including AHY/ASY birds.

Year	N	Males			Females		
		HY	AHY	All males	HY	AHY	All females
Desert thorn scrub							
1997	(9)	0.0	44.4	44.4	0.0	55.6	55.6
1998	(6)	16.7	16.7	33.4	33.3	33.6	66.6
1999	(10)	20.0	10.0	30.0	50.0	20.0	70.0
Total	(25)	12.0	24.0	36.0	28.0	36.0	64.0
Dry forest							
1997	(8)	37.5	25.0	62.5	37.5	0.0	37.5
1998	(9)	0.0	44.4	44.4	44.4	11.2	55.6
1999	(8)	25.0	0.0	25.0	50.0	25.0	75.0
Total	(25)	20.0	24.0	44.0	44.0	12.0	56.0
Pine forest							
1997	(5)	20.0	20.0	40.0	0.0	60.0	60.0
1998	(14)	14.3	35.7	50.0	21.4	28.6	50.0
1999	(15)	13.3	46.7	60.0	33.3	6.7	40.0
Total	(34)	14.7	38.2	52.9	23.5	23.5	47.1

We used logistic regression to test for interactions between habitat and sampling period in terms of the percentage of wandering birds. We also used logistic regression to test for interactions between habitat and year in terms of the percentage of birds returning the following year, and in terms of site persistence in the three winter sampling periods. Because it was necessary to reduce the number of parameters in the logistic regression model (Noon and Block 1990), the percentage of wandering birds in a habitat was summed across years, and the age and sex of wandering birds were not included in the model. Similarly, in the model for site persistence, both age and sex were excluded to reduce the number of parameters. In all analyses, if two-way interactions were not present, we then tested for main effects.

RESULTS

Bird abundance.—The abundance of Cape May Warblers as measured by fixed-radius point counts (Table 1) was highest in dry forest sites and lowest in desert thorn scrub, but varied significantly by habitat and year ($F_{2, 147} = 80.96$, $P < 0.001$). The abundance of Cape May Warblers as measured by mist net captures (Table 1) was highest in pine forest sites and lowest in desert thorn scrub, but also varied significantly by habitat and year ($F_{2,52} = 31.63$, $P < 0.001$). There was a low correlation between point count and mist net capture results ($r_S = 0.234$), and low correlations of both the number of birds recorded in point counts and the number of birds recorded in mist nets with the index of flower abundance ($r_S = -0.390$ and $r_S = 0.318$, respectively) and the index of fruit abundance ($r_S = -0.136$ and $r_S = 0.005$, respectively).

Demographic structure.—We found a marginally statistically significant difference, summed across years, in sex ratios between habitats ($G = 5.89$, df = 2, $P = 0.053$; Table 2). Males occurred slightly more frequently than females in pine habitat (52.9% male, $\chi^2 = 0.72$, df = 1, $P = 0.396$), and females were more frequent than males in dry forest (56.0% female, $\chi^2 = 2.89$, df = 1, $P = 0.089$), but these sex ratios were not significantly different. However, in desert thorn scrub there was a significant female bias (64.0% female, $\chi^2 = 15.89$, df = 1, $P < 0.001$), which was consistent between years. We also found a significant difference in age class ratios between habitats ($G = 16.94$, df = 2, $P < 0.001$; Table 2). Immature birds were more common than adults in dry forest habitat (64% immature, $\chi^2 = 15.89$, df = 1, $P < 0.001$), but there was a bias toward adult birds in desert thorn scrub (60.0% adult, $\chi^2 = 8.05$, df = 1, $P = 0.004$) and pine forest (61.7% adult, $\chi^2 = 11.63$, df = 1, $P < 0.001$). However, differences in age class ratios varied between years and with sex. For example, 68.7% of the immature birds in the dry forest were females, and 61.9% of the adult birds in the pine forest were males.

Overwinter site persistence.—Summed across years,

TABLE 3. Overwinter site persistence of Cape May Warblers in three habitats and three time periods in the Dominican Republic.

Habitat and year	Percentage of warblers persisting over winter (N)		
	Nov–Jan	Jan–Mar	Nov–Mar
Desert thorn scrub			
1996–1997	60 (5)	67 (6)	50 (4)
1997–1998	71 (7)	60 (5)	25 (8)
Total	67 (12)	64 (11)	33 (12)
Dry forest			
1996–1997	36 (11)	86 (7)	18 (11)
1997–1998	43 (7)	83 (6)	43 (7)
Total	39 (18)	85 (13)	28 (18)
Pine forest			
1996–1997	67 (6)	100 (6)	50 (6)
1997–1998	100 (11)	100 (21)	91 (11)
Total	88 (17)	100 (27)	76 (17)

overall site persistence (Table 3) was higher in the late-winter period (88%) than the early-winter period (64%), with site persistence of 47% for the entire over-winter period. Site persistence was significantly higher for adult birds (52%) than immature birds (38%; $\chi^2 = 3.97$, df = 1, $P = 0.046$), and was significantly higher for females (54%) than males (37%; $\chi^2 = 5.86$, df = 1, $P = 0.016$). In the early-winter period, site persistence varied significantly only with habitat ($\chi^2 = 6.73$, df = 2, $P = 0.034$) and was highest in pine forest and lowest in dry forest; in the late-winter period, site persistence did not vary significantly with either habitat ($\chi^2 = 1.49$, df = 2, $P = 0.476$) or year ($\chi^2 = 0.06$, df = 1, $P = 0.802$). For the entire overwintering period (November–March), we found a significant interaction between habitat and year ($\chi^2 = 6.08$, df = 2, $P = 0.048$).

Wanderers.—Summed across all years and habitats, males (49.5%) were as likely as females (50.5%) to be wanderers, and immature birds (50.5%) were as likely as adult birds (49.5%) to wander. Summed across years, there was a significant difference in the percentage of wandering birds among habitats ($G = 38.37$, df = 2, $P < 0.001$; Table 4) with fewer wanderers in pine (26%) than in dry forest (59%) or desert (67%). Using a logistic regression, we found a moderately significant interaction between habitat and winter time period of wandering birds ($\chi^2 = 8.35$, df = 4, $P = 0.080$), but the percentage of wandering birds varied significantly by both habitat ($\chi^2 = 16.30$, df = 2, $P < 0.001$) and winter sampling period ($\chi^2 = 12.69$, df = 2, $P = 0.002$). We found no significant correlation between the proportion of birds wandering and flower or fruit abundance ($r_S = -0.311$ and $r_S = -0.025$, respectively).

Annual return rate.—The percentage of birds returning to previously occupied sites (Table 5) was higher in 1997 (65%) than in 1998 (51%); summed across years, annual return rate was 57%. Annual return rate

TABLE 4. Percentage of Cape May Warblers wandering in each habitat in early winter, midwinter, and late winter, 1996–1997 and 1997–1998. Results are pooled across sexes and two age classes (immature, adult).

Habitat and year	Percentage of warblers wandering in winter periods (N)			
	Early	Mid	Late	Total
Desert				
1996–1997	73 (11)	12 (8)	78 (28)	57 (47)
1997–1998	79 (29)	28 (7)	79 (14)	72 (50)
Total	78 (40)	20 (15)	78 (42)	67 (97)
Dry forest				
1996–1997	31 (16)	38 (8)	100 (2)	38 (26)
1997–1998	83 (18)	67 (9)	62 (8)	74 (35)
Total	59 (34)	53 (17)	70 (10)	59 (61)
Pine forest				
1996–1997	50 (12)	0 (5)	0 (1)	33 (18)
1997–1998	33 (12)	21 (14)	0 (6)	22 (32)
Total	42 (24)	16 (19)	0 (7)	26 (50)

TABLE 5. Percentage of Cape May Warblers that are site persistent in the midwinter to late-winter period in year x and that return to the same site in year $x + 1$.

Habitat and year	Percentage of site-persistent returning warblers (N)		
	Male	Female	All
Desert thorn scrub			
1997	100 (2)	40 (5)	57 (7)
1998	0 (0)	0 (2)	0 (2)
Total (1997 and 1998)	100 (2)	29 (7)	44 (9)
Dry forest			
1997	80 (5)	33 (3)	63 (8)
1998	60 (5)	100 (3)	75 (8)
Total (1997 and 1998)	70 (10)	67 (6)	69 (16)
Pine forest			
1997	60 (5)	100 (3)	75 (8)
1998	55 (11)	42 (12)	48 (23)
Total (1997 and 1998)	56 (16)	53 (15)	55 (31)

was significantly higher for males (64%) than females (50%; $\chi^2 = 4.01$, df = 1, $P = 0.045$), but the difference in return rates of adult birds (60%) and immature birds (52%) was not significantly different ($\chi^2 = 1.30$, df = 1, $P = 0.254$). Using a logistic regression, we found no statistically significant difference in return rates among habitats ($\chi^2 = 3.70$, df = 2, $P = 0.158$) or years ($\chi^2 = 0.22$, df = 1, $P = 0.640$).

Body condition.—Body mass adjusted for body size (Table 6) varied significantly between habitats when summed across years and winter sampling periods ($F_{2,89} = 3.71$, $P = 0.028$). Mean adjusted mass was highest in pine forest and dry forest, and lowest in desert thorn scrub. Fat scores did not vary among habitats ($F_{2,89} = 1.80$, $P = 0.171$) or winter time periods ($F_{2,89} = 0.44$, $P = 0.648$), but there was a significant interaction between habitat and time period on pectoral muscle class scores ($F_{4,89} = 3.20$, $P = 0.017$). This interaction was the result of a trend toward increasing muscle mass scores in the pine forest through the sampling periods, and a concurrent trend toward decreasing muscle mass scores in the desert thorn scrub. This contrast in body condition of birds in the pine forest with those in the desert is supported by a comparison of the mass of individual birds captured in consecutive sampling periods. Although sample sizes are small, 83% of six birds in the pine forest showed mass gains; in the desert, 70% of 10 birds lost mass.

Foraging behavior.—Cape May Warblers fed on a variety of food types (Table 7), which varied significantly among habitats ($\chi^2 = 197.4$, df = 6, $P < 0.001$). Arthropods were the most frequent food item in desert thorn scrub habitat, homopteran honeydew made up the largest percentage of food items in dry forest, whereas arthropods and fruit and seeds were the greatest contributor to the diet in the pine forest. Diets, however, varied significantly in the desert habitat through the

winter ($\chi^2 = 23.95$, df = 2, $P < 0.001$), with nectar contributing more to the diet in late winter. In dry forest, diets also varied significantly through the winter ($\chi^2 = 14.40$, df = 6, $P = 0.025$); honeydew increased as a food item while fruit and seeds decreased. There was, however, no significant difference across time periods in the percentage of each food type to the diet of Cape May Warblers in pine forest ($\chi^2 = 6.09$, df = 4, $P = 0.193$). Cape May Warblers exhibited stereotyped foraging behavior; near-perch maneuvers were used in 94.9% of 730 foraging observations.

Flower and fruit abundance.—The abundance of flowers varied between years, winter sampling periods, and habitats (Fig. 1). A significant three-way interaction occurred between years, winter sampling periods, and habitats in terms of flower abundance ($F_{4,13} = 6.19$,

TABLE 6. The mean (and 1 SD) adjusted mass (body mass/ wing chord), fat class score (range 0–3), and pectoral muscle mass score (range 0–5) of site-persistent Cape May Warblers mist-netted in three habitats and three time periods.

Habitat and period	N	Adjusted mass	Fat	Muscle	
Desert thorn scrub					
Early winter	16	0.144 (0.008)	1.44 (1.04)	1.44	(0.72)
Midwinter	12	0.141 (0.010)	1.75 (1.16)	1.58	(0.95)
Late winter	8	0.147 (0.011)	1.38 (1.30)	0.87	(0.35)
Mean	36	0.144 (0.012)	1.53 (1.14)	1.36	(0.78)
Dry forest					
Early winter	15	0.149 (0.012)	1.47 (0.72)	0.867	(0.50)
Midwinter	7	0.150 (0.011)	2.14 (1.21)	1.00	(0.58)
Late winter	3	0.155 (0.010)	1.33 (0.58)	1.00	(0)
Mean	25	0.150 (0.010)	1.64 (0.91)	0.92	(0.50)
Pine forest					
Early winter	14	0.145 (0.007)	1.50 (0.75)	1.14	(0.67)
Midwinter	17	0.148 (0.008)	1.82 (0.73)	1.24	(0.56)
Late winter	6	0.152 (0.010)	2.00 (1.26)	1.83	(0.41)
Mean	37	0.148 (0.900)	1.73 (0.85)	1.30	(0.61)

TABLE 7. Diet of Cape May Warbler based on foraging observations in three habitats and early winter (October–November), mid-winter (December–January), and late winter (February–March) time periods.

Habitat and food type	Percentage of diet, by winter period			
	Early	Mid	Late	Combined
Desert thorn scrub	($n = 34$)	($n = 0$)	($n = 30$)	($n = 64$)
Nectar	0	⋯	16	8
Fruit/seeds	6	⋯	7	6
Arthropods	94	⋯	77	86
Honeydew	0	⋯	0	0
Dry forest	($n = 108$)	($n = 132$)	($n = 148$)	($n = 388$)
Nectar	10	11	8	10
Fruit/seeds	25	13	10	15
Arthropods	27	19	27	24
Honeydew	38	57	55	51
Pine forest	($n = 39$)	($n = 78$)	($n = 161$)	($n = 278$)
Nectar	21	23	27	25
Fruit/seeds	46	31	36	36
Arthropods	33	46	37	39
Honeydew	0	0	0	0

$P = 0.005$), indicating different patterns of flowering activity in all habitats. Within each habitat, however, there was no significant conditional interaction between year and winter sampling period in terms of flower abundance (desert, $F_{2,3} = 0.42$, $P = 0.690$; dry forest, $F_{2,3} = 0.47$, $P = 0.665$; pine forest, $F_{2,3} = 0.56$, $P = 0.623$). There were also no statistically significant main effects in the desert habitat (year, $F_{1,2} = 1.33$, $P = 0.369$; sampling period, $F_{2,2} = 2.91$, $P = 0.256$), dry forest habitat (year, $F_{1,2} = 0.28$, $P = 0.650$; sampling period, $F_{2,2} = 3.05$, $P = 0.247$), or pine forest habitat (year, $F_{1,2} = 1.58$, $P = 0.335$; sampling period, $F_{2,2} = 1.90$, $P = 0.344$).

The abundance of fruit varied only between habitats (Fig. 1). No significant three-way interaction occurred between years, winter sampling periods, and habitats in terms of fruit abundance ($F_{2,9} = 0.60$, $P = 0.570$).

There were also no significant conditional interactions (year × habitat, $F_{1,6} = 0.38$, $P = 0.562$; year × sampling period, $F_{2,6} = 0.02$, $P = 0.979$; habitat × sampling period, $F_{2,6} = 0.62$, $P = 0.572$). There was a significant main effect of habitat on fruit abundance ($F_{1,7} = 7.07$, $P = 0.032$), but neither year ($F_{1,7} = 0.39$, $P = 0.551$) nor sampling period ($F_{2,7} = 3.27$, $P = 0.099$) was statistically significant. Within each habitat, there was no significant conditional interaction between year and winter sampling period in terms of fruit abundance (dry forest, $F_{2,3} = 0.92$, $P = 0.489$; pine forest, $F_{2,3} = 0.24$, $P = 0.797$). There were also no statistically significant main effects in the dry forest habitat (year, $F_{1,2} = 2.68$, $P = 0.243$; sampling period, $F_{2,2} = 0.29$, $P = 0.773$), or pine forest habitat (year, $F_{1,2} = 0.10$, $P = 0.785$; sampling period, $F_{2,2} = 6.07$, $P = 0.141$).
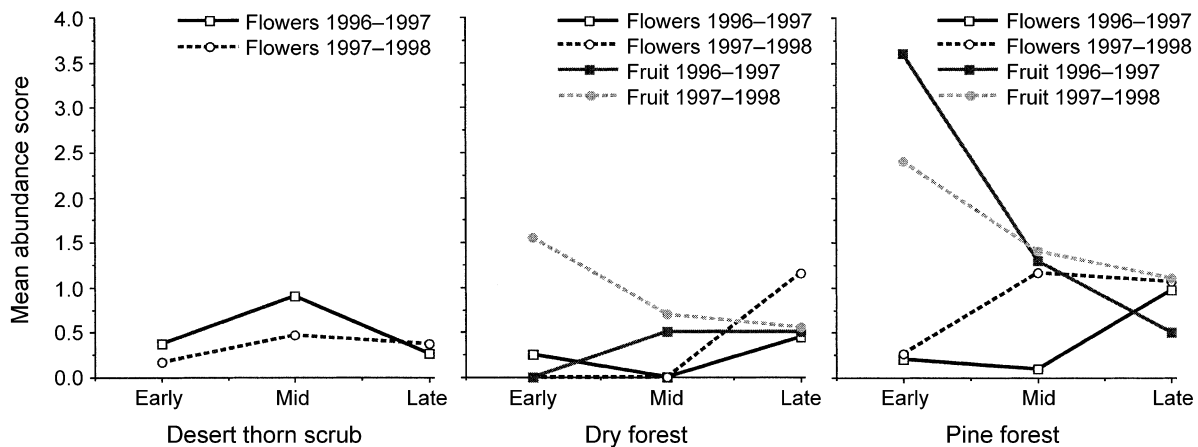

FIG. 1. Scores of flower and fruit abundance in each habitat during early winter (November), midwinter (January), and late winter (March) 1996–1997 and 1997–1998. Scores are an index of flowering or fruiting activity and are based on a scale of 0–4 (0, no flowers or fruit; 1, ≤25% of crown in flowers or fruit; 2, 26–50%; 3, 51–75%; 4, 76–100%) and represent a mean of 10 individual plants per species that were marked and scored monthly.

Discussion

This study provides data on demographies, site fidelity, physiological condition, and foraging ecology to link, for the first time, both population responses and individual condition of a wintering Neotropical migratory bird species to prevailing ecological conditions across divergent habitats. Our results support models of winter population limitation of migratory birds that suggest that between-habitat differences in food resources result in competitive interactions and sex and age class segregation, as well as differences in site fidelity and physiological condition, resulting in age- and sex-specific survival characteristics among habitats (Sherry and Holmes 1995, 1996). These data also support the concept of site dependence (Rodenhouse et al. 1997), which may have application in describing the population dynamics of this species.

Abundance and demography.—Cape May Warblers are common winter residents in pine forest and dry forest, and are fairly common in desert thorn scrub habitat in the Dominican Republic. Although Cape Mays are most common in mist net captures in pine forest, point counts show higher rates of detection in dry forest. This is probably a result of differences in forest structure and foraging practices. In dry forest, Cape Mays may be more visible, but less prone to capture, because they favor foraging on homopteran honeydew high in *Bursera* trees (Latta et al. 2001), which are generally leafless in winter. In pine forest, Cape May Warblers may be less visible foraging in the dense foliage of the scattered *Trema* trees, but tend to be more easily captured as they descend to forage on *Agave* and other flowers, which they use consistently throughout the winter. However, the absolute number or density of birds between habitats is less important in assessing habitat quality or population dynamics than demographics (Winker et al. 1990, Wunderle 1995, Marra and Holmes 2001).

Among at least some species of wintering migrants that defend distinct territories, male and adult birds are generally thought to be dominant over female and immature birds, and are thus expected to occupy the optimal habitats (Fretwell 1972, Holmes et al. 1989, Marra and Holberton 1998). The tendency for male and adult Cape May Warblers to occur in pine forest suggests that this habitat is relatively better for this species, but interannual differences in sex ratios suggest that factors other than broad habitat types may also influence demographics. Our results suggest that dry forest and desert thorn scrub may be relatively suboptimal habitats with a female bias, but we also found a heavy skew toward adult birds in desert. This pattern may be expected if a dominance hierarchy is not operating among Cape May Warblers and females preferentially select desert thorn scrub habitat (Morton 1990). However, the lower levels of site persistence, and poor body condition of desert birds especially, argue against sex-

specific differences in habitat preferences. Alternatively, the presence of Cape May Warblers in habitats where they generally fare poorly may be the result of habitat heterogeneity. In previous work (Latta and Faaborg 2001), Prairie Warblers (*Dendroica discolor*) were shown to discriminate between narrow desert wash sites within the desert thorn scrub matrix. Cape May Warblers may also discriminate between these vegetation types and segregate by sex or age class. Unfortunately, a small sample size prevents an analysis of this type.

Site fidelity.—In models of winter population regulation (Sherry and Holmes 1995, 1996, Rodenhouse et al. 1997), site fidelity is used as an index of survival and as an indication of habitat quality. Data on site fidelity offer the broadest measure of habitat suitability and also suggest that, among the habitats sampled, pine forest is optimal for wintering Cape May Warblers. Overwinter site persistence of Cape May Warblers has not been measured previously except by Staicer (1992), who calculated a 75% rate of site persistence for the species in Puerto Rican second-growth thorn scrub and dry forest, but did not define the length of time that birds were site persistent. Broad patterns of site persistence presented here are consistent with studies of other species showing that site persistence is generally higher in the late-winter period than the early-winter period (Holmes et al. 1989, Wunderle and Latta 2000). The mean overwinter site persistence of 76% in pine forest is relatively high compared to the overall site persistence of other Parulid warblers wintering in native forests and shade coffee plantations, but the percentages of site-persistent birds in dry forest (28%) and desert thorn scrub (33%) are unusually low. For example, overall site persistence ranges are 52–80% for the American Redstart *Setophaga ruticilla* (Holmes et al. 1989, Sherry and Holmes 1996, Wunderle and Latta 2000), 42–76% for the Black-throated Blue Warbler *D. caerulescens* (Holmes et al. 1989, Wunderle 1995, Wunderle and Latta 2000), and 61–77% for the Black-and-white Warbler *Mniotilta varia* (Wunderle and Latta 2000).

Data on site persistence for the entire overwinter period (November–March) show two interesting patterns. First, although there was no significant difference in site persistence among habitats or years in the late-winter months (January–March) when site persistence was uniformly quite high (>60%), site persistence varied significantly with habitat in the early winter (November–January). Second, birds that were site persistent in the early winter in pine forest and dry forest tended to be site persistent for the entire November–March overwinter period. This is seen in the relatively small change in site persistence from the early winter to the entire winter in these habitats. In contrast, desert thorn scrub birds that were site persistent in the early winter were much less likely to be site persistent for the entire winter. This low site persistence in late winter

TABLE 8. Summary of habitat-specific findings of population responses and individual condition of nonbreeding Cape May Warblers in three habitats in the Dominican Republic.

| Habitat | Captures/ net hr (× 1000) Mean ± 1 SE | Midwinter captures (%) | | Percentage of birds† | | | Adjusted mass Mean ± 1 SE | Change in pectoral muscle score | Observed diet‡ | Mean abundance score, yr 1/yr 2 | |
		Male	Adult	SP	W	R				Flower	Fruit
Desert	5.4 ± 0.7	36	60	33	67	44	0.144 ± 0.002	−0.570	arthropods 86%	0.5/0.3	0.0/0.0
Dry forest	6.8 ± 0.4	44	36	28	59	69	0.150 ± 0.002	0.133	honeydew 51%	0.2/0.4	0.2/0.9
Pine forest	7.5 ± 2.0	53	62	76	26	55	0.148 ± 0.001	0.690	arthropods 39% fruits/seeds 36% nectar 25%	0.4/0.8	1.8/1.6

† SP = percentage of birds that are site persistent from November to March; W = percentage of captured birds that are nonterritorial wanderers, averaged across all time periods; R = percentage of site persistent birds that return to the same site in the following winter.

‡ Percentage of all feeding observations in that diet category.

in desert thorn scrub is similar to that seen in these same sites for Prairie Warblers, which were shown to be most impacted by late-winter dry season events, when many birds were apparently forced out of their territories or died (Latta and Faaborg 2001).

Birds that are not site persistent are classified as wanderers. Results presented here suggest that, especially in early winter, many Cape May Warblers may be wandering, perhaps assessing various habitats or territories in search of a stable food supply (see *Foraging behavior*). Proportionately more wanderers were captured in dry forest, and especially in desert thorn scrub, than in pine forest, but the moderately significant interaction that we found between habitat and winter time period of wandering birds results from different patterns of wandering in each habitat through the winter. Data support the hypothesis that resources for Cape May Warblers are consistently scarce in the dry forest (unless an individual is able to hold and defend a tree with honeydew), and that conditions become increasingly difficult in the desert thorn scrub during the late-winter dry period. The higher frequency of wanderers in the drier habitats is consistent with the model of ideal despotic distribution (Fretwell 1972), which predicts the highest incidence of wandering in the lowest quality habitats.

Body condition.—Aside from indices of survival just described, body condition data have been used in models of winter population limitation as indicators of habitat quality (Wunderle 1995, Marra and Holberton 1998, Wunderle and Latta 2000). Data on body condition of Cape May Warblers support the hypothesis that pine and desert thorn scrub habitats are of contrasting quality. Although adjusted body mass was not significantly different between habitats, birds tended to be heavier in the pine and dry forest habitats than in the desert. Pectoral muscle mass scores varied significantly; the data showed a significant increase in muscle mass scores in pine forest and a corresponding decrease in muscle mass scores in the desert thorn scrub. Muscle scores in the dry forest were more stable. This is the

most direct evidence for physiological effects of habitat differences on wintering Cape May Warblers, and suggests again that the pine forest is relatively better habitat and desert thorn scrub is suboptimal. Dry forest appears to be adequate habitat only for site-persistent birds that can maintain territories that include honeydew sources.

Flower and fruit abundance and foraging behavior.—Differences in site fidelity and body condition of Cape May Warblers in different habitats may be understood in terms of contrasts in resource abundance and foraging behavior, such that foraging ecology mediates between demographics and habitat quality to limit populations (Sherry and Holmes 1995, 1996, Rodenhouse et al. 1997). Although food abundance is notoriously difficult to measure (Smith and Rotenberry 1990), data presented here suggest that between-habitat differences in the types of resources available determine foraging behavior, and suggest that the amount and stability of food resources affect body condition and site persistence of Cape May Warblers (Table 8). For example, in desert thorn scrub, Cape May Warblers are primarily insectivores; appropriate fruit seems to be unavailable to this species, and flower abundance is relatively low and peaks in mid-winter. In this habitat, Cape May Warblers show low rates of site persistence, high rates of wandering (especially in the late-winter dry season), and decreasing pectoral muscle mass scores.

At dry forest sites, the diet of Cape May Warblers is dominated by a unique resource: homopteran honeydew. Honeydew at this site is produced by a scale insect (Family Margarodidae) associated with the tree *Bursera simaruba*. This is a locally widespread, but patchy, resource that is vigorously defended by Cape May Warblers against both conspecifics and other species (Latta et al. 2001). Data suggest that honeydew may be a critical component of the diet of this species, especially during the late-winter dry season. Foraging by the Cape May Warbler on honeydew increased significantly over the winter, so that by mid- and late

winter, >55% of Cape May foraging observations were on honeydew. Data presented here showing very low site persistence and a very high percentage of wandering birds suggest that individuals do not remain in dry forest if they are unable to maintain a territory that encompasses trees bearing homopteran honeydew. Body condition data of site-persistent birds suggest that those individuals that are able to hold territories do well in maintaining body mass and pectoral muscle scores (Table 8).

The increase in use of honeydew over the winter may suggest a decrease in availability of other resources (principally nectar), but flower counts do not decrease in late winter. Rather, increased honeydew use in the diet may signal shifts in dietary needs of individuals (Greenberg 1984, Levey and Stiles 1992), and honeydew may best fulfill the increased energetic needs of birds preparing for migration. This may be an ideal food source for the Cape May Warbler, in particular, because the same morphological adaptations that make nectarivory possible (the semitubular tongue) would also allow the consumption of honeydew. Fruit, which fills high-energy needs in some other migratory species (Levey and Stiles 1992, Moore et al. 1995), is less available to Cape May Warblers in dry forest habitats. The principle fruit used by this species in dry forest, *Bursera*, has a long fruiting period and a low rate of fruit ripening and is thus available in low to moderate quantities throughout the winter (Greenberg et al. 1995). The fruits are too large, however, to be consumed whole by Cape May Warblers; rather, the birds appear to feed occasionally on the juice that may seep from ripe or injured fruit, or the small insects that may be attracted to the juice.

Finally, in pine forest, Cape May Warblers are primarily frugivores and take advantage of *Trema* trees, which generally flower and fruit continuously (S. C. Latta, *unpublished data*). Cape May Warblers vigorously defend individual trees or groups of closely spaced trees and are the most frequent visitors to this resource (S. C. Latta, *unpublished data*). Complementing the nearly continual availability of this fruit are relatively plentiful and consistently available sources of nectar, which tend to increase in abundance in late winter. It is likely that it is this stability and predictability of resources that attract dominant Cape May Warblers to pine forests, help to maintain body condition, and allow site persistence (Table 8).

Although data are lacking to accurately assess sexual differences in use of food resources, previously published data on aggressive interactions around honeydew support the hypothesis that there are intersexual dominance hierarchies operating among Cape May Warblers. Latta et al. (2001) showed that honeydew sources in dry forest were most actively defended by the Cape May Warbler (58.0% of aggressive acts), and that male individuals were dominant and significantly more aggressive than females; males were involved in 91% of the acts of aggression by this species. Similar patterns of aggression may be expected around *Trema* sources in pine habitat, where Cape May Warblers were the aggressors in 98% of aggressive actions ($n = 98$) even though at least 12 avian species consumed *Trema* (S. C. Latta, *unpublished data*). Among the Cape May Warblers involved in these aggressive actions, females were more common than males (67% female), suggesting female dominance of *Trema*. However, male aggression targeted females (63% of intraspecific interactions) proportionally more often than females targeted males (16% of intraspecific interactions). These data suggest that males do dominate females, but that males are less likely to be defending *Trema* trees than are females. Although similar data are lacking, we suggest that males in pine habitat may prefer nectar sources such as *Agave* and palm flowers, which were also important food resources in pine habitat.

Beyond intersexual dominance, these aggression data also emphasize the role of interspecific aggressive interactions in mediating habitat use, and support the assertion of Greenberg et al. (1994) that interspecific territoriality may be a regular feature of some species such as the Cape May Warbler. These data support the notion that interspecific defense focuses on keystone resources (Terborgh 1986) and patchy resources such as nectar and fruit (Greenberg et al. 1994) or honeydew (Greenberg et al. 1993, Latta et al. 2001) that may be especially important for maintaining migratory bird populations in particular habitats.

Habitat generalists and resource opportunists.—Recent reviews of habitat use by Neotropical migrants (Hutto 1992, Lynch 1992, Petit et al. 1995) indicate a clear preponderance of many species in early-successional or disturbed habitats, including agricultural sites. Although some agriculture, such as shade coffee plantations, may mimic specialized habitats in structure and function (Wunderle and Latta 1996), relatively few species have been shown to be habitat specialists in the winter season. This includes the Cape May Warbler, which is commonly found in a wide variety of habitats in winter, and may thus be considered a habitat generalist. This species does, however, respond to variation in habitat quality, as seen in sex and age class segregation, differences in site persistence, and changes in body condition among habitats.

Categorizing the Cape May Warbler as a resource specialist, generalist, or opportunist can be difficult because of the need to place the species along a hypothetical continuum of foraging behaviors (Sherry 1990), and because categorization can be further confused by consideration of different temporal and spatial scales (Ellis et al. 1976, Sherry 1990). From an evolutionary perspective, Cape May Warblers must be considered resource specialists because they have a semitubular tongue (Gardner 1925) that is unique among other Parulid warblers, and that may have evolved as an adaptation to a seasonally predictable supply of nec-

tar on the wintering grounds (Sherry 1990). This hypothesis is difficult to accept, however, at least when viewed against this population of Cape May Warblers, because of the relatively low use of nectar in all habitats. Moreover, seasonally predictable foods in winter, especially nectar and fruit, are not very common in the Neotropics because of variation within and between winters in flowering and fruiting phenologies (Morton 1973, Levey and Stiles 1992). The possibility remains, however, that in the past (or even in other contemporary habitats), nectar may have been a much more important and predictable part of the Cape May winter diet, and that changes in resource abundance may have altered the foraging habits of this species. Nectar may have been of particular importance in the late-winter dry season, when insect abundance is depressed and when there may be a strong selective advantage to those individuals that can best utilize nectar or honeydew sources. Support for this idea is seen in our data showing a general increase in nectar resources in the dry season (especially in desert), the suggestion that males may preferentially defend nectar sources in pine, and the increased use of honeydew in the late winter in the dry forest.

From an ecological perspective, Cape May Warblers may be seen as specialists because foraging maneuvers are stereotyped and consist almost entirely of near-perch gleaning, reaching, and probing, thus suggesting a narrow niche breadth (Colwell and Futuyma 1971). However, Cape May Warblers may best be considered classic dietary opportunists because of their broad use of arthropods, fruit, nectar, and homopteran honeydew both within and between winter seasons. Greenberg (1979) argues persuasively that the Cape May Warbler is among a suite of large-bodied, low-agility, conifer-breeding species that are opportunistic in foraging in the nonbreeding period because they evolved as generalists in association with coniferous forests and were preadapted for roles as opportunists on their wintering ranges. These species, which principally exploit spruce budworms in conifers through simple perching and gleaning, lack a specialized feeding technique such as aerial attacks that would increase their foraging radius. Eaton (1953) made a similar observation when he noted that warblers wintering in the West Indies use the same foraging maneuvers in the winter as in the summer, even though the habitats bear no obvious similarity. Hence, physical limitations make the Cape May Warbler and other conifer-breeding parulids more likely to be opportunistic on the nonbreeding grounds (Greenberg 1979). In this study, birds that appear to specialize on different resources in each habitat (insects in desert thorn scrub, honeydew in dry forest, and fruit and nectar in pine forest) are opportunistically selecting the most profitable foraging substrates available to them. This pattern of local specialization by the Cape May Warbler is not surprising, as the degree of dietary specialization often depends critically on resource abundance (Ford et al. 1990). However, individual birds would also be expected to shift between substrates as resource abundance changes between habitats (Rosenberg 1990) or over time. Thus, between-habitat differences in resources result in competitive interactions, sex and age class segregation, and differences in site fidelity and physiological condition.

Literature Cited

Arendt, W. J. 1992. Status of North American migrant landbirds in the Caribbean: a summary. Pages 143–171 *in* J. Hagan and D. Johnston, editors. Ecology and conservation of Neotropical migrant landbirds. Smithsonian Institution Press, Washington, D.C., USA.

Baillie, S. R., and W. J. Peach. 1992. Population limitation in Palearctic–African migrant passerines. Ibis **134**:120–132.

Baltz, M. E., and S. C. Latta. 1998. Cape May Warbler (*Dendroica tigrina*). *In* A. Poole and F. Gill, editors. The Birds of North America, Number 332. The Academy of Natural Sciences, Philadelphia, Pennsylvania, and the American Ornithologists' Union, Washington, D.C., USA.

Blake, J. G., B. A. Loiselle, T. C. Moermond, D. J. Levey, and J. S. Denslow. 1990. Quantifying abundance of fruits for birds in tropical habitats. Studies in Avian Biology **13**: 73–79.

Colwell, R. K., and D. J. Futuyma. 1971. On the measurement of niche breadth and overlap. Ecology **52**:567–576.

Conover, W. J., and R. L. Iman. 1981. Rank transformations as a bridge between parametric and nonparametric statistics. American Statistician **35**:124–129.

Crawford, H. S., and D. T. Jennings. 1989. Predation by birds on spruce budworm *Choristoneura fumiferana*: functional numerical and total responses. Ecology **70**:152–163.

Eaton, S. W. 1953. Wood warblers wintering in Cuba. Wilson Bulletin **65**:169–174.

Ellis, J. E., J. A. Wiens, C. F. Rodell, and J. C. Anway. 1976. A conceptual model of diet selection as an ecosystem process. Journal of Theoretical Biology **60**:93–108.

Faaborg, J., and W. J. Arendt. 1984. Population sizes and philopatry of winter resident warblers in Puerto Rico. Journal of Field Ornithology **55**:376–378.

Fisher-Meerow, L. L., and W. S. Judd. 1989. A floristic study of five sites along an elevational transect in the Sierra de Baoruco, Provincia Pedernales, Dominican Republic. Moscosoa **5**:159–185.

Ford, H. A., L. Huddy, and H. Bell. 1990. Seasonal changes in foraging behavior of three passerines in Australian eucalyptus woodland. Studies in Avian Biology **13**:245–253.

Fretwell, S. D. 1972. Populations in a seasonal enviroment. Princeton University Press, Princeton, New Jersey, USA.

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Gardner, L. L. 1925. The adaptive modifications and taxonomic value of the tongue in birds. Proceedings of the U.S. National Museum **67**:1–49.

Gosler, A. G. 1991. On the use of greater covert moult and pectoral muscle as measures of condition in passerines with data for the Great Tit *Parus major*. Bird Study **38**:1–9.

Greenberg, R. 1979. Body size, breeding habitat, and winter exploitation systems in *Dendroica*. Auk **96**:756–766.

Greenberg, R. 1984. The winter exploitation systems of Bay-breasted and Chestnut-sided Warblers in Panama. University of California Publications in Zoology **116**:1–107.

Greenberg, R., C. M. Caballero, and P. Bichier. 1993. Defense of homopteran honeydew by birds in the Mexican highlands and other warm temperate forests. Oikos **68**:519–524.

Greenberg, R., M. S. Foster, and L. Marquez-Valdelamar. 1995. The role of the white-eyed vireo in the dispersal of *Bursera* fruit on the Yucatan Peninsula. Journal of Tropical Ecology **11**:619–639.

Greenberg, R., J. Salgado-Ortiz, and C. Macias-Caballero. 1994. Aggressive competition for critical resources among migratory birds in the Neotropics. Bird Conservation International **4**:115–127.

Grubb, T. C., Jr. 1989. Ptilochronology: feather growth bars as indicators of nutritional status. Auk **106**:314–320.

Grubb, T. C., Jr. 1991. A deficient diet narrows growth bars on induced feathers. Auk **108**:725–727.

Hilty, S. L. 1980. Flowering and fruiting periodicity in a premontane rain forest in Pacific Columbia. Biotropica **12**: 292–306.

Holmes, R. T., T. W. Sherry, and L. Reitsma. 1989. Population structure, territoriality, and overwinter survival of two migrant warbler species in Jamaica. Condor **91**:545–561.

Hutto, R. L. 1992. Habitat distributions of migratory landbird species in western Mexico. Pages 211–239 *in* J. Hagan and D. Johnston, editors. Ecology and conservation of Neotropical migrant landbirds. Smithsonian Institution Press, Washington, D.C., USA.

Karr, J. R. 1976. On the relative abundance of migrants from the north temperate zone in tropical habitats. Wilson Bulletin **88**:433–458.

Kendeigh, S. C. 1947. Bird population studies in the coniferous forest biome during a spruce budworm outbreak. Ontario Department of Lands and Forests, Biological Bulletin **1**:1–100.

Latta, S. C., and M. E. Baltz. 1997. Population limitation in Neotropical migratory birds: comments on Rappole and McDonald (1994). Auk **114**:754–762.

Latta, S. C., and C. Brown. 1999. Autumn stopover ecology of the Blackpoll Warbler (*Dendroica striata*) in thorn scrub forest of the Dominican Republic. Canadian Journal of Zoology **77**:1147–1156.

Latta, S. C., and J. Faaborg. 2001. Winter site fidelity of Prairie Warblers in the Dominican Republic. Condor **103**: 455–468.

Latta, S. C., H. A. Gamper, and J. R. Tietz. 2001. Revising the convergence hypothesis of avian use of honeydew: evidence from Dominican subtropical dry forest. Oikos **93**: 250–259.

Latta, S. C., and M. L. Sondreal. 1999. Observations on the abundance, site persistence, home range, foraging, and nesting of the Pine Warbler on Hispaniola, and first record of ground nesting for this species. Ornitología Neotropical **10**:43–54.

Latta, S. C., and J. M. Wunderle, Jr. 1996. The composition and foraging ecology of mixed-species flocks in pine forests of Hispaniola. Condor **98**:595–607.

Levey, D., and F. G. Stiles. 1992. Evolutionary precursors of long-distance migration: resource availability and movement patterns in Neotropical landbirds. American Naturalist **140**:447–476.

Lynch, J. F. 1989. Distribution of overwintering Nearctic migrants in the Yucatan Peninsula, I: general patterns of occurrence. Condor **91**:515–544.

Lynch, J. F. 1992. Distribution of overwintering Nearctic migrants in the Yucatan Peninsula, II: use of native and human-modified vegetation. Pages 178–196 *in* J. Hagan and D. Johnston, editors. Ecology and conservation of Neotropical migrant landbirds. Smithsonian Institution Press, Washington, D.C., USA.

MacArthur, R. H. 1958. Population ecology of some warblers of northeastern coniferous forests. Ecology **39**:599–619.

Marra, P. P., K. A. Hobson, and R. T. Holmes. 1998. Linking winter and summer events in a migratory bird by using stable-carbon isotopes. Science **282**:1884–1886.

Marra, P. P., and R. L. Holberton. 1998. Corticosterone levels as indicators of habitat quality: effects of habitat segregation in a migratory bird during the non-breeding season. Oecologia **116**:284–292.

Marra, P. P., and R. T. Holmes. 2001. Consequences of dominance-mediated habitat segregation in American Redstarts during the nonbreeding season. Auk **118**:92–104.

Marra, P. P., T. W. Sherry, and R. T. Holmes. 1993. Territorial exclusion by a long-distance migrant warbler in Jamaica: a removal experiment with American Redstarts (*Setophaga ruticilla*). Auk **110**:565–572.

Moore, F. R., S. A. Gauthreaux, Jr., P. Kerlinger, and T. R. Simons. 1995. Habitat requirements during migration: important link in conservation. Pages 121–144 *in* T. E. Martin and D. M. Finch, editors. Ecology and management of Neotropical migratory birds. Oxford University Press, New York, New York, USA.

Morse, D. H. 1980. Population limitation: breeding or wintering grounds. Pages 505–516 *in* A. Keast and E. S. Morton, editors. Migrant birds in the Neotropics: ecology, behavior, distribution and conservation. Smithsonian Institution Press, Washington, D.C., USA.

Morse, D. H. 1989. American warblers. Harvard University Press, Cambridge, Massachusetts, USA.

Morton, E. S. 1973. On the evolutionary advantages and disadvantages of fruit eating in tropical birds. American Naturalist **107**:8–22.

Morton, E. S. 1990. Habitat segregation by sex in the Hooded Warbler: experiments on proximate causation and discussion of its evolution. American Naturalist **135**:319–333.

Noon, B. R., and W. M. Block. 1990. Analytical considerations for study design. Studies in Avian Biology **13**:126–133.

Parrish, J. D., and T. W. Sherry. 1994. Sexual habitat segregation by American Redstarts: importance of resource seasonality. Auk **111**:38–49.

Petit, D. R., J. F. Lynch, R. L. Hutto, J. G. Blake, and R. B. Waide. 1995. Habitat use and conservation in the Neotropics. Pages 145–197 *in* T. E. Martin and D. M. Finch, editors. Ecology and management of Neotropical migratory birds. Oxford University Press, New York, New York, USA.

Pyle, P., S. N. G. Howell, R. P. Yunick, and D. F. Desante. 1987. Identification guide to North American passerines. Slate Creek Press, Bolinas, California, USA.

Ralph, C. J., G. R. Geupel, P. Pyle, T. E. Martin, and D. F. DeSante. 1993. Handbook of field methods for monitoring landbirds. U.S. Forest Service General Technical Report **PSW-GTR-144**. Pacific Southwest Research Station, U.S. Forest Service, Albany, California, USA.

Ralph, C. J., and J. M. Scott, editors. 1981. Estimating numbers of terrestrial birds. Studies in Avian Biology **6**.

Rappole, J. H., and M. V. McDonald. 1994. Cause and effect in population declines of migratory birds. Auk **111**:652–660.

Rappole, J. H., E. S. Morton, T. E. Lovejoy, and J. L. Ruos.

1983. Nearctic avian migrants in the Neotropics. U.S. Department of the Interior, U.S. Fish and Wildlife Service, Washington, D.C., USA.

Rappole, J. H., M. A. Ramos, and K. Winker. 1989. Wintering Wood Thrush movements and mortality in southern Veracruz. Auk **106**:402–410.

Remsen, J. V., and S. K. Robinson. 1990. A classification scheme for foraging behavior of birds in terrestrial habitats. Studies in Avian Biology **13**:144–160.

Robbins, C. S., J. R. Sauer, R. S. Greenberg, and S. Droege. 1989. Population declines in North American birds that migrate to the neotropics. Proceedings of the National Academy of Sciences (USA) **86**:7658–7662.

Rodenhouse, N. L., T. W. Sherry, and R. T. Holmes. 1997. Site-dependent regulation of population size: a new synthesis. Ecology **78**:2025–2042.

Rosenberg, K. V. 1990. Dead-leaf foraging specialization in tropical forest birds: measuring resource availability and use. Studies in Avian Biology **13**:360–368.

Sealy, S. G. 1989. Aggressiveness in migrating Cape May Warblers: defense of an aquatic food source. Condor **90**: 271–274.

Sherry, T. W. 1990. When are birds dietarily specialized? Distinguishing ecological from evolutionary approaches. Studies in Avian Biology **13**:337–352.

Sherry, T. W., and R. T. Holmes. 1995. Summer versus winter limitation of populations: what are the issues and what is the evidence? Pages 85–120 *in* T. E. Martin and D. M. Finch, editors. Ecology and management of Neotropical migratory birds. Oxford University Press, New York, New York, USA.

Sherry, T. W., and R. T. Holmes. 1996. Winter habitat quality, population limitation, and conservation of Neotropical–Nearctic migrant birds. Ecology **77**:36–48.

Smith, K. G., and J. T. Rotenberry. 1990. Quantifying food resources in avian studies: present problems and future needs. Studies in Avian Biology **13**:3–5.

Sokal, R. R., and F. J. Rohlf. 1995. Biometry. Third edition. W. H. Freeman, New York, New York, USA.

Staicer, C. A. 1992. Social behavior of the Northern Parula, Cape May Warbler, and Prairie Warbler wintering in second-growth forest in southwestern Puerto Rico. Pages 308–320 *in* J. M. Hagan III and D. W. Johnston, editors. Ecology and conservation of Neotropical migrant landbirds. Smithsonian Institution Press, Washington, D.C., USA.

Strong, A. M., and T. W. Sherry. 2000. Habitat-specific effects of food abundance on the condition of ovenbirds wintering in Jamaica. Journal of Animal Ecology **69**:883–895.

Terborgh, J. W. 1986. Keystone plant resources in the tropical forest. Pages 330–344 *in* M. E. Soule, editor. Conservation biology. Sinauer Associates, Sunderland, Massachusetts, USA.

Terborgh, J. W. 1989. Where have all the birds gone? Princeton University Press, Princeton, New Jersey, USA.

Terborgh, J. W., and J. R. Faaborg. 1980. Factors affecting the distribution and abundance of North American migrants in the Eastern Caribbean region. Pages 145–156 *in* A. Keast and E. S. Morton, editors. Migrant birds in the Neotropics: ecology, behavior, distribution, and conservation. Smithsonian Institution Press, Washington, D.C., USA.

Wilkinson, L. 1992. SYSTAT: the system for statistics. SYSTAT, Evanston, Illinois, USA.

Winker, K., J. H. Rappole, and M. A. Ramos. 1990. Population dynamics of the Wood Thrush in southern Veracruz, Mexico. Condor **92**:444–460.

Wunderle, J. M., Jr. 1995. Population characteristics of Black-throated Blue Warblers wintering in three sites on Puerto Rico. Auk **112**:931–946.

Wunderle, J. M., and S. C. Latta. 1996. Avian abundance in sun and shade coffee plantations and remnant pine forest in the Cordillera Central, Dominican Republic. Ornitología Neotropical **7**:19–34.

Wunderle, J. M., Jr., and S. C. Latta. 2000. Winter site fidelity of Nearctic migrant birds in isolated shade coffee plantations of different sizes in the Dominican Republic. Auk **117**:596–614.

Wunderle, J. M., Jr., and R. B. Waide. 1993. Distribution of overwintering Nearctic migrants in the Bahamas and Greater Antilles. Condor **95**:904–933.