Autumn stopover ecology of the Blackpoll Warbler (*Dendroica striata*) in thorn scrub forest of the Dominican Republic

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Abstract: We used mist-netting, color-banding, resighting, and behavioral observations to study the autumn stopover ecology of migrating Blackpoll Warblers (*Dendroica striata*) in coastal thorn scrub forest in the area of Cabo Rojo, Pedernales Province, Dominican Republic. Blackpoll Warblers were the most abundant migrant present in this habitat throughout most of October 1997. Warblers stopping over in this habitat were generally young with moderate to large fat stores. No lean birds (fat score = 0) were captured. Our behavioral observations suggest that Blackpoll Warblers are flexible in terms of social organization, with birds associating in single-species flocks and in mixed-species aggregations, but single birds were also recorded. Foraging activity consisted primarily of gleaning from leaves and was focused on lepidopteran larvae, whose high abundance coincided with Blackpoll Warbler arrival. We suggest that most stopover Blackpoll Warblers were not weakened individuals searching for emergency energy stores but were forced down owing to unfavorable weather conditions for migration; others may have been taking advantage of landfall on the south coast of Hispaniola for daytime rest before continuing across the Caribbean Sea to South America. Coastal thorn scrub forest of Hispaniola appears to be a preferred stopover habitat for a variety of migrants, providing a place to rest and replenish energy reserves following transoceanic flight.

Résumé : Nous avons utilisé plusieurs techniques, filets japonais, marquage à la couleur, observations répétées et études du comportement, pour étudier l'écologie d'étape en automne chez des Parulines rayées (Dendroica striata) migratrices dans la forêt de buissons épineux de la région de Cabo Rojo, province de Pedernales, en République dominicaine. La Paruline rayée a été le migrateur le plus abondant dans cet habitat pendant presque tout le mois d'octobre 1997. Les parulines en arrêt à ce site étaient généralement des oiseaux jeunes avec des réserves de graisse modérées ou importantes. Aucun oiseau maigre (indice des graisses = 0) n'a été capturé. L'étude du comportement des oiseaux a révélé de la flexibilité sur le plan de l'organisation sociale, puisque certains oiseaux voyageaient en vols d'une seule espèce, d'autres se joignaient à des groupes d'espèces diverses et certains volaient seuls. La quête de nourriture se faisait surtout par sondage des feuilles et la recherche était concentrée sur les larves de lépidoptères dont l'abondance maximale coïncidait avec l'arrivée des parulines. Nous croyons que la plupart des parulines qui ont fait étape n'étaient pas des individus affaiblis à la recherche de réserves énergétiques d'urgence, mais des oiseaux qui ont été forcés de se poser, probablement à cause de trop mauvaises conditions de migration; d'autres ont pu profiter d'un atterrissage pour se reposer à Hispaniola pendant le jour avant de continuer leur migration au-dessus des Antilles, en route vers l'Amérique du Sud. La forêt côtière de buissons épineux d'Hispaniola semble constituer un habitat de prédilection pour faire étape chez bon nombre d'oiseaux migrateurs, leur permettant de se reposer et de refaire leurs réserves d'énergie après leur vol transocéanique.

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Introduction

Understanding the ecology and behavior of Neotropical migrant landbirds in stopover habitat is important in understanding the annual cycle of migratory birds (Moore et al. 1990; Hagan and Johnston 1992) and may be important in understanding the apparent declines of some migrant populations (Robbins et al. 1989; Latta and Baltz 1997). Stopover habitat is crucial to migrants, because it provides a place to

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rest and replenish energy reserves, often for short (1–2 days) stays prior to or following the crossing of significant ecological barriers (Wood 1982; Bairlein 1985*a*; Biebach et al. 1986). Stopover habitat also accommodates birds that may be weak and forced to interrupt migration and birds forced down because of unfavorable weather (Moore and Kerlinger 1987). Most studies of the stopover biology of migrant passerines in the Western Hemisphere have focused on northbound spring migrants on the north coast of the Gulf of Mexico (Moore and Kerlinger 1987; Loria and Moore 1990; Kuenzi et al. 1991), but birds may face different pressures during spring and fall migrations, especially since natural selection favors a timely arrival on the breeding grounds (Francis and Cooke 1986).

Stored fat is the primary energy source for migration. Because lean birds that are able to replenish their fat stores in migration have a better chance of completing migration successfully (Moore and Simm 1985; Bairlein 1985*b*), the

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selection of stopover sites in appropriate habitat is important (Martin and Karr 1986). At some sites, some birds replenish fat reserves at a rate of close to 10% of their body mass per day (Bairlein 1985a; Biebach et al. 1986; Moore and Kerlinger 1987), while at other sites birds appear to move on after only a daytime rest without depositing additional fat or increasing their mass (Safriel and Lavee 1988; Winker 1995). This may be a result of how different individuals or species balance the benefits and risks of stopover (Biebach et al. 1986; Safriel and Lavee 1988); feeding during migration meets energy demands and reduces the risk of starvation, but foraging migrants may incur other costs, such as a slower pace of migration and increased rates of predation. Since differences in stopover biology among species can be quite remarkable (Morris et al. 1996), studies of individual species are needed.

The Blackpoll Warbler (Dendroica striata) breeds in coniferous forests across northern Canada and the northeastern United States and winters in northern South America (American Ornithologists' Union 1998). Stopover habitat and stopover ecology of migrating Blackpoll Warblers is virtually unknown. Nisbet et al. (1963) and Murray (1989) presented age composition and bird mass data of in-flight transients from Bermuda and two sites in Florida, respectively; and Morris et al. (1996) and Parrish (1997) presented some sitepersistence data from stopover sites in coastal New England, but the birds studied had only completed a small fraction of their presumed migration; but otherwise, the literature on migrating Blackpoll Warblers has been limited to a 30-year debate over the migratory route of this species (summarized by Nisbet et al. 1995). One hypothesis (Murray 1965, 1989) suggests that Blackpoll Warblers leave North America from the southeast Atlantic coastal plain south of Cape Hatteras N.C., and fly directly to South America. An alternative hypothesis suggests that most Blackpoll Warblers make a long transoceanic flight from the northeastern United States and southeastern Canada, passing over Bermuda, Puerto Rico, and the Lesser Antilles, to wintering areas in South America (Nisbet 1970). Nonstop flights from as far north as Nova Scotia to the north coast of South America are expected to be made in <100 h by small passerines (Stoddard et al. 1983). Support for the transoceanic-flight route includes observations with radar (Nisbet 1970; Williams et al. 1977; Williams and Williams 1978), mist-netting, and sighting data (Nisbet 1970; McNair and Post 1993), together with observations of birds passing these Atlantic and Caribbean islands without landing (Richardson 1976; Williams and Williams 1978).

Despite the more than 30 papers that have addressed Blackpoll Warbler migration (see Nisbet et al. 1995 for review), there has been little mention of the regular presence of Blackpoll Warblers on Hispaniola or of the use of coastal dry forest as stopover habitat on an annual basis. The species is described as scarce in the Greater Antilles (Wetmore and Swales 1931; Bond 1950), uncommon in Hispaniola (Wetmore and Swales 1931), and "irregular everywhere except perhaps in Puerto Rico and the Virgin Islands" (Nisbet 1970). Some regional field guides acknowledge that Blackpoll Warblers migrate through Hispaniola (Dod 1981; Raffaele et al. 1998), but there are no data on abundance or the importance of Hispaniola to migrating birds. Here we present for the first time observations on the use of coastal thorn scrub forest by migrating Blackpoll Warblers in extreme southern Hispaniola. We provide census data as well as habitat-use data and behavioral observations to quantify many aspects of Blackpoll Warbler stopover ecology in this region, and speculate on possible controls on the incidence of Blackpoll Warbler stopover on Hispaniola. We conclude with some comments on the importance of stopover habitat and what these data suggest in terms of the migration-route debate.

Materials and methods

Study site

We studied the stopover ecology of migrating Blackpoll Warblers from 4 to 21 October 1997 in coastal thorn scrub forest in the area of Cabo Rojo, Pedernales Province, Dominican Republic (18°0'N, 71°38'W). Coastal thorn scrub forest has been studied at this site by Fisher-Meerow and Judd (1989). They found common broadleaf tree species, including Capparis cynophallophora, Capparis ferruginea, Guaiacum officinale, Haitiella ekmanii, Metopium brownei, Opuntia moniliformis, Phyllostylon brasiliensei, and Plumiera obtusa. Common shrubs found included Croton origanifolius, Croton discolor, and Lippia alba, while succulents included Agave brevipetala, Cephal cereus, Ilarrisia nashii, Melocactus communis, Opuntia caribeae, and Opuntia dillenii. Very little soil is present on these sites. Rather, the forest floor is mostly made up of "dogtooth" limestone rock (Howard and Briggs 1953). The area normally has two dry seasons annually (December-March and July-August), but September-November is usually fairly wet and vegetation is green. Rainfall recorded at this site in September and October 1997 fell within the 10-year average recorded at Cabo Rojo, 4 km away (S.C. Latta, unpublished data).

The methods we used to study Blackpoll Warbler stopover ecology in this thorn scrub forest follow.

Vegetation structure

We measured vegetation structure in 12 randomly selected circular plots (radius 11.3 m; 0.02 ha). Within each plot, all stems >3 cm in diameter at breast height (DBH) were measured. Foliage heights were determined at 20 points located at 1.6-m intervals along each cardinal radius of each plot, by counting the number of foliage touches along a 3 m tall pole marked at 0.5-m intervals placed at each sampling point. For height intervals above 3 m, we sighted along the pole and recorded the presence or absence of foliage in each height class. We recorded the number of foliage touches within each of the following height classes: 0-0.5, 0.5-1.0, 1.0-1.5, 1.5-2.0, 2.0-2.5, 2.5-3.0, 3.0-4.0, 4.0-6.0, and 6.0-8.0 m. Foliage touches were classified as either forbs, cactus and succulents, or broadleaf trees and shrubs. For each height interval, percent cover was calculated by dividing the number of points in which foliage was present in that height interval by the total number of sample points (240) and multiplying by 100. We determined canopy height by measuring the heights of the 10 tallest trees in the circle and calculating the mean, and measured canopy cover with a spherical densiometer at the midpoint of each cardinal radius.

Point counts

We conducted 10-min, 25 m radius point counts at 12 points in thorn scrub forest every 3–4 days from 4 to 21 October, to document the abundance, arrival dates, and departure dates of Blackpoll Warblers and other permanent resident and migratory bird species. Points were situated in a grid pattern, which partially encompassed our mist-netting site (see below), with each point 150 m from the closest point. We also conducted point counts in dry forest (24 points), moist broadleaf forest (12 points), and pine forest (36 points) at various times during the same migratory period, to establish the breadth of habitats used by Blackpoll Warblers. All sites were within 31 km of each other along an altitudinal gradient (elevation 18–1465 m). All point counts were conducted by the same observer (S.C. Latta), begun at sunrise, and completed by 09:30. No point counts were conducted in inclement weather.

Mist-netting and condition of birds

We sampled birds by mist-netting in two banding sessions: 14– 16 and 23–25 October 1997. The first of these netting sessions was timed to coincide with the expected peak of Blackpoll Warbler abundance, while the second banding session was timed to coincide with the expected decline in numbers of both banded and unbanded Blackpoll Warblers. We placed 24 mist nets (12×2.6 m, 30-mm mesh) in a single line covering approximately 300 linear metres. For each netting session, nets were open between 16:00 and 19:45 on day 1, between 06:00 and 12:00 and 16:00 and 19:45 on day 2, and between 06:00 and 10:30 on day 3, for a total of 432 net-hours. Nets were closed during the hot midday hours, when bird activity was greatly reduced, to minimize the possibility of bird mortalities.

All mist-netted birds were identified to species, age, and sex by plumage characteristics (Pyle 1997), when possible, and banded with both a numbered metal band and color bands for identification in the field. We measured wing chord (unflattened), tarsus length, and bill length, and weighed birds to the nearest 0.1 g on a 30-g Pesola scale. All migrants were scored for the presence of fat, using a scale of 0-5 (0, no fat; 1, trace; 2, fat covers bottom of furculum; 3, fat covers bottom and sides of furculum; 4, fat fills furculum; 5, fat mounded and spreading over breast muscle), and for pectoral muscle mass, using a scale of 0-2 (0, muscle concave and sternum prominent; 2, muscle convex and sternum not detectable; Gosler 1991).

All birds were cared for in accordance with the principles and guidelines of the Canadian Council on Animal Care.

Site persistence

Whereas previous studies of site persistence of stopover migrants assumed that the absence of a recapture indicated departure of the bird from the study site (Rappole and Warner 1976; Bairlein 1985*a*; Biebach et al. 1986; Safriel and Lavee 1988), we assumed that some birds still present on the site might be net shy and not be recaptured. From 15 to 25 October, we attempted to relocate banded birds by slowly walking through an area approximately 600×500 m that surrounded our net line. Resight effort equaled 18.0 person-hours/day (4 individuals searching from 06:30 to 11:00). Each bird encountered was identified to species and the color-band combination recorded if it was banded.

Behavioral observations

While searching for color-banded birds, we also recorded behavioral observations on each Blackpoll Warbler encountered. We recorded the "social organization" in which we found each individual, noting whether each bird was foraging singly, in a mixedspecies flock, in a single-species flock, or within an aggregation of mixed species. A bird was said to belong to a mixed-species flock if the flock consisted of at least two birds of different species within 25 m of one another that were moving together for at least 5 min (Latta and Wunderle 1996). A bird was said to belong to a single-species flock if the group moving together consisted only of Blackpoll Warblers. We defined an aggregation as a mixed-species group that did not move together within the first 5 min of observation. Most behavioral observations were made on individuals that were not color-banded, so all behavioral observations may not be independent. However, because we made observations on multiple days in habitat containing many birds and while moving systematically through the habitat, we feel that independence of observations was not significantly compromised.

Foraging behavior

For each Blackpoll Warbler encountered, we recorded the first foraging event 5 s after the bird was detected, to avoid a bias toward the more conspicuous feeding techniques and to reduce the problem of autocorrelation inherent in sequence data (Wagner 1981). We used the methods of Remsen and Robinson (1990) and recorded foraging maneuver (glean, reach, jump, sally, or other), location of the food item or foraging substrate, height of the bird above the ground, canopy height (estimated height of the tallest tree within 15 m), horizontal position of the bird (inner one third of tree, middle one third of tree, or outer one third of tree), and foliage density at the foraging site. Foliage density was estimated as the amount of light passing through an imaginary 2.0 m diameter sphere surrounding the foraging site (light, 75-100% of light passes through; moderate, 25-74%; dense, 0-24%). We identified the prey encountered as often as possible. We also recorded the bird species of the nearest neighbor to foraging individuals and estimated the distance between the birds.

We recorded foraging rates as the average time between feeding attempts, as long as there was a minimum of four consecutive attempts visible to the observer. We also recorded handling time, i.e., the time a bird took to capture and consume a lepidopteran larva; handling time is the time elapsed from the moment prey is captured to the completion of ingestion.

Arthropod abundance

Finally, we quantified changes in the apparent preferred prey of stopover Blackpoll Warblers (caterpillars; S.C. Latta, personal observation; this study). We quantified the abundance of nonvolant arthropods by shaking 10 randomly selected, similarly sized, marked trees for 5 s and collecting all arthropods that fell from the tree on a bedsheet. We also visually inspected branches and leaves for arthropods that may not have been released by the shaking. These arthropods were counted and identified to order. Arthropod abundance was quantified on 14 October, at the peak of Blackpoll Warbler abundance. We again quantified the abundance of non-flying arthropods on 24 October.

Statistical analyses

The software package systat version 5.2 (Wilkinson 1992) was used to perform various statistical tests described by Sokal and Rohlf (1981). A probability of Type I error of 0.05 or less was accepted as significant, but greater values are shown for descriptive purposes. Data presented are means \pm SE 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.

An independent samples *t* test (two tailed) was used to test for differences in the means of adjusted bird mass, pectoral muscle mass score, and fat score when grouped by time of capture (mid-October versus late October) and to test for differences in the means of bird mass, adjusted bird mass, pectoral muscle mass score, and fat score when grouped by age (hatching year (HY) versus after hatching year (AHY)) and length of stopover (<1 day vs. >1 day). A Mann–Whitney *U* test was used to test for differences in the means of bird mass of Blackpoll Warblers that were captured in mid-October versus late October mist-netting sessions. A 2 × 2 test of independence with a χ^2 statistic was used to test for independence in the age of birds among samples. Regression was used to relate body mass to fat score and body mass to pectoral muscle mass score.



Fig. 1. Vegetation profile of coastal thorn scrub forest at Cabo Rojo, Pedernales, Dominican Republic, based on twelve 11.3 m radius circular plots (0.02 ha).

Results

Vegetation structure

The vegetation profile for coastal thorn scrub forest (Fig. 1) shows a low fairly open canopy with a sparse understory dominated by broadleaf trees. Few forbs are present on the rocky floor and, while cacti and succulents are also sparse, they do occasionally extend into the canopy.

Point counts

Point-count results showed a dramatic increase in Blackpoll Warbler numbers in mid-October (Fig. 2) in thorn scrub forest. The mean number of birds recorded per point (\times 100) rose from 16.7 on 4 October to 108.3 on 7 October and dropped on 10 October, but rose to a high count of 200.0 birds on 14 October before rapidly declining. Only 1 week later, relatively few (25.0) birds were recorded. The numbers of Blackpoll Warblers present appeared to be related to barometric pressure readings (Fig. 2), with increased numbers coinciding with the presence of low pressure systems in the region.

Throughout the month, Blackpoll Warblers were more common than any other migrant in the thorn scrub forest; other migrants included the Palm Warbler (*Dendroica palmarum*), normally the most abundant migrant species in this habitat from November to March, and the Prairie (*Dendroica discolor*) and Cape May (*Dendroica tigrina*) Warblers, which are also abundant winter residents at this site (S.C. Latta, unpublished data). The mean number of individuals of each of these species recorded per point (×100) was no greater than 33.3 at any time. No Blackpoll Warblers were ever recorded in adjoining dry forest habitat, moist broadleaf forest, or pine forest.

Fig. 2. Mean number of Blackpoll Warblers recorded per point (×100) in coastal thorn scrub forest at Cabo Rojo, Pedernales, Dominican Republic, in October 1997, compared with the midday barometric pressure (1 in. (25.4 mm) of Hg (20° C) = 3.374 kPa) reading in the central Caribbean Basin, as recorded at 11:00 at Mayaguez, Puerto Rico.



Mist-netting and condition of birds

Mist net capture data showed a pattern of Blackpoll Warbler abundance similar to that of the point count data (Table A1). Blackpoll Warblers were the single most common species in this habitat (26.0% of all net captures) in **Fig. 3.** Frequency distributions of body masses and, in parentheses, of body masses adjusted for body size (body mass/wing chord), of Blackpoll Warblers captured in coastal thorn scrub forest at Cabo Rojo, Pedernales, Dominican Republic, in October 1997.



mid-October but, by late October, Blackpoll Warbler captures had declined to only 5.2% of all captures. In the early netting period at the peak of Blackpoll Warbler abundance, among the migratory species, 62 of 158 (39.2%) migrants captured were Blackpoll Warblers. By the late netting period, only 10.0% of migrants captured were Blackpoll Warblers. Also, between the two netting sessions, the total number of migrants captured declined 43% (from 158 to 90 birds). Although it may be argued that the decline in net captures of warblers reflected net shyness, especially given that the netting sessions were only 10 days apart, the capture of resident individuals stayed nearly constant (Table A1). This suggests that the decline in migrants captured in general, and in Blackpoll Warblers captured in particular, was not the result of net shyness but was due to many birds moving out of the study site entirely. There was no significant difference in age ($\chi^2 = 1.288$, df = 1, P = 0.256), mass (U = 333.5, P = 0.150), adjusted mass (t = 2.074, P = 0.053), mean fat score (t = -0.628, P = 0.540), or mean pectoral muscle mass score (t = 1.446, P = 0.174) between birds captured in the early and late mist-netting sessions, so all captures were combined for further analyses of age effects on body condition.

Young Blackpoll Warblers dominated the net captures. Of the Blackpoll Warblers captured, 73% (N = 52) were HY birds, 10% (N = 7) were AHY males, and 17% (N = 12) were AHY females. A frequency distribution of bird-mass data (Fig. 3) shows a normal distribution with a slight preponderance of relatively heavier birds. The same trend is seen when bird mass is adjusted for body size (Fig. 3). Age differences did not explain this slight skewing. There was no significant difference in body mass between HY and AHY birds (t = 0.974, P = 0.340; Table 1). Bird mass averaged 12.6 g (SE = 0.23 g) for HY birds and 13.1 g (SE = 0.44 g) for AHY birds. Similarly, there was no difference in adjusted body mass between HY and AHY birds (t = 0.571, P = 0.574).

A frequency distribution of fat-class scores showed a more skewed but still normal distribution, with more fat scores at the high end (Fig. 4). No birds were scored as lean (fat score = 0). Again, age differences did not explain this skewing. We found no significant difference in mean fat scores between HY and AHY birds (t = 0.433, P = 0.668; Table 1). Fat score was significantly related to body mass (F = 36.33, P < 0.0001, R = 0.60), with heavier birds having a higher average fat score.

Similarly, a frequency distribution of pectoral muscle mass scores (Fig. 4) shows a normal curve only slightly skewed towards a low muscle score. Age of the bird was found to be significant in explaining these results. We found a significant difference in pectoral muscle mass scores between HY and AHY birds (t = 2.405, P = 0.022; Table 1). Pectoral muscle mass scores were also highly related to body mass (F = 15.69, P < 0.0001, R = 0.58), with heavier birds having a higher average muscle score.

Site persistence

The results of our resighting efforts suggest that few Blackpoll Warblers remain more than a few days in this area. On days 1 and 2 post banding, we were able to resight only 8 of 62 (12.9%) banded birds each day. On day 3 post banding, only 8.1% of banded birds were resighted, and on days 4 and 5 post banding, only 3.2 and 1.6% were resighted, respectively. No banded birds were seen more than 5 days after banding.

Of the eight birds identified as having remained at the stopover site for more than 1 day, seven were HY birds (Table 1). We found no significant difference between birds that remained more than 1 day and those that moved off site, in terms of age (HY vs. AHY: $\chi^2 = 1.218$, df = 1, P = 0.270), mass (t = 1.237, P = 0.253), adjusted mass (t = 1.217, P = 0.257), fat score (t = 0.520, P = 0.618), or pectoral muscle mass score (t = 0.647, P = 0.535). However, sample sizes are very small.

Behavioral observations

Our behavioral observations suggest that Blackpoll Warblers are flexible in terms of social organization at this stopover site. The birds associated primarily in single-species flocks (N = 50, 44% of observations), the average size of which was 3.25 birds. Single Blackpoll Warblers were also common (N = 41, 36% of observations), as were Blackpoll Warblers in mixed-species aggregations (N = 23, 20% of observations). Blackpoll Warblers were not recorded in mixedspecies foraging flocks. Of the 23 feeding aggregations encountered in which Blackpoll Warblers were present, Prairie and Cape May warblers were the migratory species most often present (39.1 and 26.1% of aggregations, respectively). The resident Bananaquit (Coereba flaveola, 17.4% of aggregations), Black-crowned Palm Tanager (Phaenicophilus palmarum, 13.0% of aggregations), and Northern Mockingbird (Mimus polyglottos, 8.7% of aggregations) were also commonly present in feeding aggregations. Inter- and intraspecific aggression within these flocks and aggregations was rarely observed.

Table 1. Comparison of the energetic condition of HY and AHY Blackpoll Warblers mist-netted 14–16 and 24–26 October 1997, and of Blackpoll Warblers mist-netted 14–16 October 1997 that either remained near the capture site >1 day or showed no site persistence.

	Ν	Age (HY:AHY)	Mass (g)	Adjusted mass (g)	Fat score	Pectoral muscle mass score
Age			(8)			
nge						
HY	52		12.6±0.23	0.176 ± 0.003	3.2 ± 0.1	0.8 ± 0.1
AHY	19		13.1±0.40	0.181±0.006	3.4±0.3	1.2±0.1*
Site persistence						
>1 day	8	7:1	12.2±0.56	0.169 ± 0.008	3.0±0.6	0.8±0.2
None	54	37:17	12.9 ± 0.03	0.181 ± 0.004	3.3±0.1	1.0 ± 0.1

Note: Values given are the mean \pm SE.

*P = 0.022 (two-tailed independent samples t test); P < 0.05.

Fig. 4. Frequency distribution of accumulated-fat and pectoral muscle mass scores of Blackpoll Warblers captured in coastal thorn scrub forest at Cabo Rojo, Pedernales, Dominican Republic, in October 1997.



Nearest-neighbor distance was calculated for 122 individual Blackpoll Warblers in 46 flocks or aggregations. In 92.6% of observations, the nearest neighbor to a Blackpoll Warbler was another Blackpoll Warbler. Nearest-neighbor distance for these birds averaged 1.40 m (SE = 0.10 m).

Foraging behavior

Blackpoll Warblers were active foragers and focused their activity on caterpillars during this migration stopover; caterpillars were the focus of 51% of 209 feeding observations. The presence of the Blackpoll Warblers coincided with a tremendous emergence of caterpillars, primarily of the lepidopteran family Pieridae. Because much of the foraging was for these caterpillars, 78% of Blackpoll Warbler foraging attempts occurred on broadleaf-tree leaves, with another 17% of attempts occurring on broadleaf-tree branches or twigs. Among broadleaf trees, foraging was concentrated on acacia (25% of attempts) and sea grape (*Coccoloba uvifera*; 17% of attempts) trees, which appeared to be particularly favored by the caterpillars. Many individual trees were, in fact, largely or entirely defoliated by caterpillar activty by mid-October.

As is typical of gleaning insectivores, Blackpoll Warblers used the near-perch maneuvers of gleaning and reaching for 88% of observed feeding attempts (N = 184), and only rarely did they use jumps (4.3% of observed attempts) or sallies (4.3% of observed attempts). Most foraging took place in the middle third (52.6% of observations) and outer third (38.3%) of the tree, where foliage density was moderate (48.8% of observations) or light (33.5% of observations).

Blackpoll Warblers foraged at a mean height of 2.60 m (SE = 0.14 m), under a mean canopy height of 5.2 m. Thus, the relative foraging height of the birds (foraging height/ canopy height) was 0.50 (SE = 0.03).

Feeding rates varied widely. Among 25 birds in which feeding rates were recorded, a food item was taken on average every 21.4 s (SE = 3.1 s; range = 2.5-55.0 s). Differences in feeding rates likely primarily reflected differences in prey-handling time, which in turn reflected differences in prey (caterpillar) size. The handling times of 23 caterpillars ranged from 5 to 33 s (mean = 14.0 ± 1.5 s).

Arthropod abundance

The abundance of caterpillars in the diet was reflected in the mid-October arthropod survey, in which 86.8% of collected arthropods were caterpillars. However, caterpillars were not uniformly distributed among tree species (mean = 22.1 ± 14.3 caterpillars/sampled tree): in our sample, large numbers were found principally on acacia trees. By 24 October, caterpillars had declined in abundance by 85% overall and only 32.2% of collected arthropods were caterpillars (mean = 3.6 ± 1.1 caterpillars/sampled tree). Variation in the numbers of caterpillars between trees was much lower in the later sample, and coleopterans, hymenopterans, and other insects were relatively more abundant.

Discussion

In October 1997, Blackpoll Warblers stopping over in coastal thorn scrub habitat were generally young (HY), fat (fat score > 0), and apparently capable of continuing migration. Data presented here on distribution and abundance, energetic condition, and foraging behavior suggest that these birds did not arrive as a fallout of generally stressed and weak birds searching for emergency energy stores. Weather conditions unfavorable for continued flight probably

prompted Blackpoll Warbler stopover on Hispaniola, but the opportunity to take advantage of landfall for daytime rest before continuing across the Caribbean Sea to South America may also have played a role in the use of thorn scrub by migrating Blackpoll Warblers.

Distribution and abundance

In mid October, Blackpoll Warblers are regularly found in large numbers across the south coast (and possibly the north coast) of Hispaniola. Blackpoll Warblers are known to Dominican birdwatchers as locally common passage migrants, more common in the fall than in the spring (Dod 1981; A.R. Keith, J. Wiley, A. Ottenwalder, and S.C. Latta, in preparation²). Few reports exist from the island's north coast, although Schwartz and Klinikowski (1965) reported that the species was a common migrant in dry and mesic forests from Monte Cristi to Sosua. Migrants are regularly found in large numbers on the south coast of the island, where they have been recorded in dry scrub forest or other broadleaf habitats from Cumayasa in the east, through San Pedro de Macoris, Santo Domingo (botanical gardens), Las Salinas de Bani, Azua, and Oviedo, and at least as far west as Pedernales on the Haitian border (A.R. Keith, J. Wiley, A. Ottenwalder, and S.C. Latta, in preparation, see footnote 2). In 1996, large numbers of Blackpoll Warblers were recorded in the area of Cabo Rojo from 13 to 17 October (S.C. Latta, personal observation). Although we did not formally census these birds, we noted that they were the most common species in this habitat at the time. However, by mid November, when we mist-netted at this site, no Blackpoll Warblers were encountered.

Data from this study also indicate the continued presence of Blackpoll Warblers throughout much of October 1997. However, all Blackpoll Warblers did not arrive simultaneously and few remained at our study site >24 h. We recorded pronounced peaks in abundance of Blackpoll Warblers in point counts (7 and 14 October) followed by declines of nearly 80% within the next 3 days. Resighting data from color-banded birds showed a similar decline of 87% in 1-2 days.

These peaks and lows in abundance would seem to suggest the arrival and departure of waves of migrants rather than the continuing presence of a relatively constant number of birds, which might be expected if nonterritorial Blackpoll Warblers were wandering over large areas of contiguous thorn scrub habitat for extended periods of time. Data presented here suggest that large numbers of Blackpoll Warblers coincide with low pressure troughs in the Central Caribbean, with smaller numbers of birds perhaps continuing to arrive daily, but few birds staying beyond 24 h. Richardson (1976) also noted the relationship between local weather conditions in the Greater Antilles and increased densities of migrants and recorded particularly large numbers of migrants when low pressure systems were present and trade winds abated. Low pressure systems such as these are not uncommon in the Caribbean and may be expected to occur regularly during the migratory period (August-November; Williams et al. 1977). A similar study on a habitat island would clarify this pattern of stopover, as would longer-term correlations of migrant abundance in the Greater Antilles with weather patterns in the Caribbean Basin.

A short stopover period in thorn scrub is consistent with the results of Morris et al. (1996) and Parrish (1997), who found that, during migration, very few Blackpoll Warblers were recaptured >1 day after banding (<3% in each study) on islands in coastal New England, when only a fraction of the way through their autumn migration. However, they did not color-band or resight banded birds, so net shyness cannot be entirely ruled out as an explanation of their low recapture rates. Many other studies have shown that stopovers tend to be of short duration for a variety of other passerines. Loria and Moore (1990) found that only 15% of Red-eyed Vireos stayed >1 day at a Gulf Coast stopover site, and Moore and Kerlinger (1987) found that migrants completing a trans-Gulf flight most often stayed only 1-2 days on the north coast of the Gulf of Mexico. Length of stay among stopover migrants has been shown to be related to suitability of habitat (Moore and Kerlinger 1987) and, for a few species, to the extent of fat depletion on arrival (Bairlein 1985a; Biebach et al. 1986; Moore and Kerlinger 1987; Loria and Moore 1990), with lean birds staying longer than fat birds (Cherry 1982; Safriel and Lavee 1988; Morris et al. 1996).

Energetic condition

Data on body mass suggest that Blackpoll Warblers stopping over in this thorn scrub habitat were generally not stressed. The mean mass of HY (12.6 \pm 0.2 g) and AHY $(13.1 \pm 0.4 \text{ g})$ birds was several grams higher than the fatfree mass reported for Blackpoll Warblers (10.34 \pm 0.78 (SD) g; Dunning 1993). Masses recorded at Cabo Rojo were higher than those recorded for Blackpoll Warblers captured on an island in the Gulf of Maine (Morris et al. 1996) when birds had just begun migration. In that study, the mean mass of HY birds was 11.1 g (SD = 1.2 g, N = 130) and the mean mass of AHY birds was 11.5 g (SD = 0.9 g, N = 40). As with our data, there was no significant difference in mean mass between HY and AHY birds from these Maine sites. Masses recorded at Cabo Rojo were lower, though, than masses of autumn migrating Blackpoll Warblers from Bermuda (mean mass of 141 Blackpolls = 14.0 g, range = 7.7-20.5 g; Nisbet et al. 1963) and Florida (mean mass of HY birds = 16.5 g, range = 11.3-19.7 g, N = 133; mean mass of AHY birds = 16.4 g, range = 10.4-19.8 g, N = 96; Murray 1989). A geographic comparison of masses and an interpretation of these differences is difficult, however, because of different capture or recovery techniques and lack of knowledge about whether the individuals were arriving, dispersing, or fattening (Nisbet et al. 1995).

Accumulated-fat and pectoral muscle mass scores from Blackpoll Warblers at Cabo Rojo also indicate that these birds were not deficient in energetic reserves. Fat scores and pectoral muscle mass scores were both normally distributed. AHY birds had a higher pectoral muscle mass score than HY birds, but this may reflect developmental differences more than energetic deficiencies, as changes in fat accumulation would be expected to occur before changes in flight musculature in energy stressed birds (Loria and Moore 1990). Surprisingly, no birds were lean (fat score = 0). Simi-

²A.R. Keith, J. Wiley, A. Ottenwalder, and S.C. Latta. An annotated checklist to the birds of Hispaniola. In preparation.

lar data from other migrant stopover sites frequently show much lower fat scores. For example, Moore and Kerlinger (1987) and Loria and Moore (1990) recorded that close to 40% of the spring migrants arriving on the north coast of the Gulf of Mexico were lean, and Morris et al. (1996) found that >50% of autumn migrants in the Gulf of Maine were lean. Lean birds are expected at stopover sites, since various studies suggest that, for several passerine species, stopover is determined by fat reserves (Biebach 1985; Bairlein 1985a; Biebach et al. 1986) or a combination of fat reserves and weather conditions (Rappole and Warner 1976). Our data indicating the absence of emaciated birds at Cabo Rojo suggest that these were not fatigued birds that had fallen out of larger migratory flights. Rather, the presence of fat birds may indicate that migrants landed after encountering unfavorable weather conditions, as migrants forced down by weather are, on average, fatter than migrants that land when weather is favorable for continuing migration (Moore and Kerlinger 1987), or that migrants simply landed for a daytime rest (Biebach et al. 1986). The lack of lean birds may also suggest that Blackpoll Warblers are in fact exceptionally well-adapted for long distance flights, as suggested by Hussell and Lambert (1980); they were unable to apply a mass-loss standard to the Blackpoll Warbler that could be applied to nine other migrant passerines.

Foraging behavior

In this migratory season, Blackpoll Warbler stopover coincided with a tremendous abundance of lepidopteran larvae, which are a rich source of energy for birds. This abundance of caterpillars was not seen again throughout the winter (S.C. Latta, unpublished data). While we do not know if the Blackpoll Warbler stopover coincides annually with high caterpillar abundances, lepidopteran phenologies in dry forest habitat generally follow the rainfall cycles, which appear to be fairly regular in this region (S.C. Latta, unpublished data). Blackpoll Warbler foraging behavior reflected a preference for caterpillars, and warbler social organization reflected a dependence on this typically aggregated food source. Because caterpillars were not distributed evenly between trees, Blackpoll Warblers were nonterritorial, displayed little intraspecific aggression, and tended to forage in aggregations and in flocks that moved between these rich food sources. The intensity of foraging behavior suggests that replenishing energy reserves is more important to stopover Blackpoll Warblers than rest, but this conclusion may be biased, because birds are more easily seen when foraging than when resting.

The intraspecific sociality of the Blackpoll Warbler during stopover supports a prediction made by Greenberg (1979), who argued that *Dendroica* warblers that breed in coniferous forests are more likely to be social during migration and on the wintering grounds than closely related species that breed in deciduous forests or mixed deciduous and coniferous forests. Greenberg argued that the conifer-adapted *Dendroica* species are more generalized and opportunistic in their foraging behavior during the nonbreeding season in nonconiferous habitats and that these foraging attributes should be correlated with within-species sociality. This was shown to be true for the Bay-breasted Warbler (*Dendroica castanea*) and now appears to be true for *D. striata* as well.

Migration route

It is unclear whether these data can help clarify the Blackpoll Warbler migration route debate. The proponents of the southeastern U.S. route have not postulated a regular stopover of migrants in the Greater Antilles, despite the fact that their route would bring the bulk of the population directly over the island (see Murray 1989 for maps of hypothetical routes). The proponents of the alternative, the transoceanic route (Nisbet et al. 1995), have made a stronger case, but their proposed migration route projects the bulk of the migration going far to the east of Hispaniola, with only the western limit of the migration passing within perhaps 100 miles (1 mile = 1.609 km) of the Florida coast (Nisbet 1970) and crossing over Hispaniola. In fact, Nisbet (1970) characterizes Blackpoll Warbler abundance in Hispaniola as "irregular."

The presence of large numbers of Blackpolls on Hispaniola, however, should not be surprising. Williams and Williams (1978), using radar and visual data, have shown that birds leave the coast of North America following the passage of a strong cold front, and then simply maintain a constant southeast heading in flight. When they encounter the northeast trade winds in the area of the Sargasso Sea, their track shifts to a southwest one, by virtue of wind drift, but the birds maintain a southeast heading. Arrival over Hispaniola may depend primarily on the individuals departure point, wind drift, and the strength of the trade winds (Richardson 1976). Once over Hispaniola, maps of habitat associations suggest that there are approximately 10 890 km² of thorn forest habitat in the Dominican Republic (DIRENA 1998) and, if maximum point count results are extrapolated across the landscape, there is potential stopover habitat for up to 11 million Blackpoll Warblers at any given time. However, the proportion of all migrant Blackpoll Warblers that stop is unknown.

Habitat importance

Finally, our data suggest that coastal thorn scrub is important stopover habitat for migrating Blackpoll Warblers. Acacia trees found in this habitat, with their abundant insect populations, may be of particular importance to migratory birds. Greenberg et al. (1997) found that acacia trees and related mimosoid legumes also supported a high density and diversity of migratory birds in southern Mexico, and discussed the importance of acacias to stopover migrants in coastal cheniers of Louisiana and Texas and the importance of the related mesquite (Prosopis juliflora) to foliagegleaning warblers in Puerto Rico. Greenberg et al. (1997) hypothesize that insect herbivores are abundant on acacia and related species, because these trees have invested in mechanical defenses (thorns) against large grazing herbivores rather than in chemical defenses against small insect herbivores. While our data suggest that both lepidopteran larvae and migratory birds favor acacia trees in thorn scrub forest, a more rigorous test of temporal and spatial variation in arthropod abundance across tree species is warranted.

Thorn scrub forest is not only of importance to Blackpoll Warblers. Other species also use this habitat as a stopover site. Northern Waterthrushes (*Seiurus noveboracensis*) were very abundant in mid-October, although by November few are mist-netted. Prairie Warblers and Cape May Warblers were also more abundant here in October than they were in later months, even though both are winter residents in this habitat. In addition, we caught surprising numbers of Connecticut Warblers (*Oporornis agilis*) and Prothonotary Warblers (*Protonotaria citrea*), which are seldom, if ever, encountered later in the winter (Latta and Brown 1998). Other thorn scrub sites may be equally important to migrating passerines for shelter, daytime rest, and refueling during the migratory period.

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Appendix

Common name	Scientific name	Early	Late
Mourning Dove	Zenaida macroura	0	1
Zenaida Dove	Zenaida aurita	2	0
White-winged Dove	Zenaida asiatica	0	1
Common Ground Dove	Columbina passerina	21	17
Yellow-billed Cuckoo	Coccyzus americanus	1	1
Mangrove Cuckoo	Coccyzus minor	2	0
Antillean Mango	Anthracothorax dominicus	5	19
Broad-billed Tody	Todus subulatus	1	0
Hispaniolan Woodpecker	Melanerpes striatus	1	0
Gray Kingbird	Tyrannus dominicensis	1	1
Stolid Flycatcher	Myiarchus stolidus	7	1
Northern Mockingbird	Mimus polyglottos	1	3
Prothonotary Warbler*	Protonotaria citrea	4	1
Yellow Warbler	Dendroica petechia	4	3
Magnolia Warbler*	Dendroica magnolia	0	1
Cape May Warbler*	Dendroica tigrina	12	19
Chestnut-sided Warbler*	Dendroica pensylvanica	1	0
Bay-breasted Warbler*	Dendroica castanea	1	1
Blackpoll Warbler*	Dendroica striata	62	9
Prairie Warbler*	Dendroica discolor	44	27
Palm Warbler*	Dendroica palmarum	0	9
Northern Waterthrush*	Seiurus noveboracensis	21	16
Connecticut Warbler*	Oporornis agilis	3	0
American Redstart*	Setophaga ruticilla	8	2
Common Yellowthroat*	Geothlypis trichas	2	4
Ground Warbler	Microligea palustris	8	3
Warbler (hybrid)* ^{<i>a</i>}	Dendroica sp.	0	1
Black-crowned Palm Tanager	Phaenicophilus palmarum	4	6
Bananaquit	Coereba flaveola	12	17
Greater Antillean Bullfinch	Loxigilla violacea	10	10

Table A1. Species and numbers of birds mist-netted in the coastal thorn scrub forest of Pedernales Province,

Note: Early, 14–16 October 1997; late, 24–26 October 1997; *, migratory species. "Formal description in preparation (with K.C. Parkes).