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HABITAT USE BY THE BLACKPOLL WARBLER

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Habitat use and partitioning by wood warblers in northern coniferous forests have attracted considerable interest (MacArthur 1958; Morse 1968, 1971, 1978). Studies have documented and compared the foraging patterns of several species: Magnolia (*Dendroica magnolia*), Cape May (*D. tigrina*), Yellow-rumped (*D. coronata*), Black-throated Green (*D. virens*), Blackburnian (*D. fusca*), Bay-breasted (*D. castanea*), and Parula (*Parula americana*) warblers. However, little precise information exists upon the exploitation patterns of Blackpoll Warblers (*D. striata*), although they also nest in the northern coniferous forests of eastern North America. At the southeastern limits of their breeding range, Blackpoll Warblers occur on mountaintops, and they also appear on wooded coastal islands of Maine and the Maritime Provinces (Bond 1951, Griscom and Sprunt 1957). Farther north they occur throughout the boreal coniferous forest and breed nearer to the tundra than any other warbler (Todd 1963).

This species is of particular interest, since it is morphologically extremely similar to some of the congeners mentioned above, particularly the Bay-breasted Warbler. Further, it does not appear to nest in many areas frequented by Bay-breasted Warblers, suggesting that these 2 species may exclude each other in most places. I studied the foraging patterns of Blackpoll Warblers on their breeding grounds in the White Mountains of New Hampshire, using techniques similar to those described elsewhere (Morse 1968, 1971) for other warblers. I have supplemented this information with data obtained during spring migration in deciduous forests in Maryland and in spruce forests along the Maine Coast.

STUDY AREAS AND METHODS

Study areas.—Fieldwork on the breeding grounds was carried out on Mt. Osceola, Livermore Twp., Grafton Co., New Hampshire, in June 1971 and June 1977. I gathered foraging observations in forests from about 1050 m to the summit at 1319 m. Balsam fir (*Abies balsamea*) was the predominant tree, with small numbers of white birch (*Betula papyrifera*) and red spruce (*Picea rubens*) (Table 1). The forest ranged from about 3 to 12 m in height, with heavy stunting occurring only at the very top of the mountain (Fig. 1). The only other common warbler in this area was the Yellow-rumped Warbler.

The range of Blackpoll Warblers also extended down Mt. Osceola to about 750 m. Most of this area (down to 825 m) was covered by a dense, second-growth, mixed coniferous-deciduous forest (Fig. 1, Table 1). The lowest area in which apparently breeding Blackpoll Warblers occurred consisted primarily of tall mixed forest (Fig. 1,

TABLE 1

RELATIVE ABUNDANCE (%) OF CANOPY-HEIGHT TREES IN NEW HAMPSHIRE CENSUS PLOTS[1]

Species of tree	Census plot			
	Top (1150 m)	Next to top (950 m)	Next to bottom (850 m)	Bottom (750 m)
Balsam fir (*Abies balsamea*)	97	60	4	12
White birch (*Betula papyrifera*)	3	28	70	14
Red spruce (*Picea rubens*)	–	7	16	25
Pin cherry (*Prunus pensylvanica*)	–	5	9	15
Quaking aspen (*Populus tremuloides*)	–	–	1	–
Yellow birch (*Betula lutea*)	–	–	–	23
Sugar maple (*Acer saccharum*)	–	–	–	6
Mountain maple (*A. spicatum*)	–	–	–	4
Striped maple (*A. pensylvanicum*)	–	–	–	1

[1] The 10 nearest canopy or sub-canopy trees at 10 randomly chosen sites on each census plot.

Table 1). Neither of these areas are typical of the Blackpoll Warbler's commonly reported nesting habitat (Taber 1952, Gross *in* Bent 1953, Todd 1963). Although I did not make systematic foraging observations in these areas, I censused the bird populations there.

I studied the foraging of Blackpoll Warblers in migration in Maryland during May 1977. They occur in large numbers there in mature deciduous forests while in passage, being one of the most abundant of migrants at this time. The profile of the forest in which they were observed (University Park, Prince George's Co.) is shown in Fig. 1. The commonest tree species were red maple (*Acer rubrum*), sweet gum (*Liquidambar styraciflua*), and river birch (*Betula nigra*).

Blackpoll Warblers are uncommon spring migrants in the spruce forests along the Maine Coast. I made a limited number of observations upon them there in white spruce (*Picea glauca*) forests from 1966 to 1972. The foliage profiles of these forests (illustrated in Morse 1971, 1973) are rather similar to those of the fir forest censused on Mt. Osceola (Fig. 1), although the forest is somewhat taller.

Methods.—In gathering foraging data I followed techniques described in earlier studies (Morse 1968, 1971, 1978). Briefly, I measured the time that different individuals foraged at different heights and in different parts of the tree (tips of foliage,

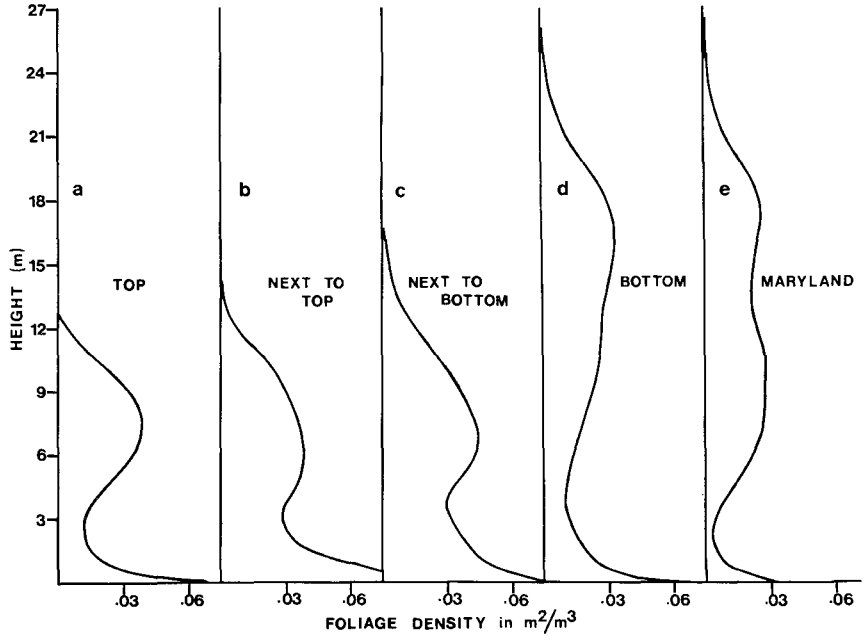

FIG. 1. Profiles of foliage in 4 census areas on Mt. Osceola (a–d); profile of foliage in Maryland study site (e). All profiles measured using techniques of MacArthur and MacArthur (1961).

inner part of limbs, etc.). I recorded a maximum of 5 min of foraging per individual, although it usually was not possible to obtain that much information before a bird was lost. I made an effort not to gather foraging data from the same general location more than once, and the results obtained come from a minimum of 25 individuals in both New Hampshire and Maryland and 8 individuals in Maine. Most of the observations were made upon males. Since I located several individuals by their songs, I checked for possible bias in the locations recorded. Data from the first min of foraging observations were compared with those gathered after the first min. Since no significant difference occurred ($P > 0.05$, χ^2), the data were pooled.

I censused the densities of birds in the undisturbed fir forest, using a plot of 3.3 ha (8.3 acres) (Table 2). Eight counts of about 1 h were made in this area between 06:00 and 11:00 during the last 2 weeks of June 1977. If individuals held territories at the edge of a plot, I counted the number of observations made inside and outside of this plot and assigned the pair an appropriate fraction of total occupancy. Additionally, I made censuses of a plot in the same way at each of 3 sites at lower elevations; 950 m (second growth dominated by conifers), 850 m (second growth dominated by deciduous growth), and 750 m (tall mixed forest).

TABLE 2

DENSITY OF SMALL PASSERINE BIRDS ON STUDY SITE IN PAIRS/40 HA (100 ACRES)

Species	Census plot			
	Top (1150 m)	Next to top (950 m)	Next to bottom (850 m)	Bottom (750 m)
Yellow-bellied Flycatcher (*Empidonax flaviventris*)	–	22	30	–
Brown Creeper (*Certhia familiaris*)	–	–	–	12
Winter Wren (*Troglodytes troglodytes*)	–	9	9	–
Swainson's Thrush (*Catharus ustulatus*)	–	34	42	11
Gray-cheeked Thrush (*C. minimus*)	22	23	9	–
Ruby-crowned Kinglet (*Regulus calendula*)	–	10	–	–
Solitary Vireo (*Vireo solitarius*)	–	–	–	10
Red-eyed Vireo (*V. olivaceus*)	–	–	–	35
Nashville Warbler (*Vermivora ruficapilla*)	2	6	18	–
Magnolia Warbler (*Dendroica magnolia*)	–	57	–	–
Black-throated Blue Warbler (*D. caerulescens*)	–	–	–	20
Yellow-rumped Warbler (*D. coronata*)	31	12	–	–
Black-throated Green Warbler (*D. virens*)	–	–	–	50
Blackburnian Warbler (*D. fusca*)	–	–	–	21
Blackpoll Warbler (*D. striata*)	47	101	92	6
Ovenbird (*Seiurus aurocapillus*)	–	–	–	38
Canada Warbler (*Wilsonia canadensis*)	–	–	31	15
American Redstart (*Setophaga ruticilla*)	–	20	–	10
Purple Finch (*Carpodacus purpureus*)	–	12	–	–
Dark-eyed Junco (*Junco hyemalis*)	23	12	20	12
White-throated Sparrow (*Zonotrichia albicollis*)	23	25	–	–
TOTAL	148	342	252	238

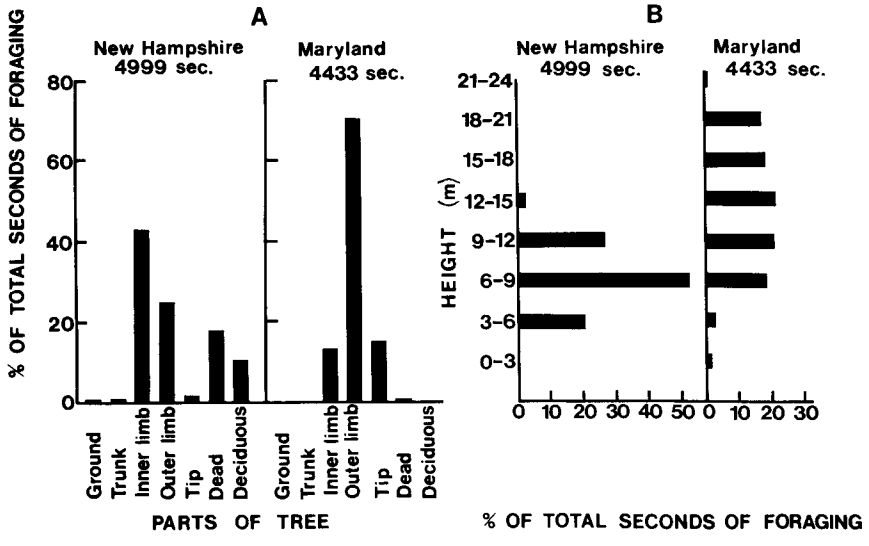

FIG. 2. Percentages of time spent foraging in different parts of tree; heights at which foraging took place.

RESULTS

Foraging observations on the breeding grounds.—Blackpoll Warblers usually foraged at medium heights in conifers, using the inner parts of the limbs most frequently. The heights foraged (Fig. 2) did not differ significantly from the profile of the forest (Fig. 1) ($P > 0.05$ in a 2-tailed Spearman Rank Correlation Test). In addition to the predominant foraging motion of gleaning, individuals occasionally hawked for insects and fed while hovering next to vegetation (Table 3). In the relatively few observations made on deciduous (white birch) foliage on the breeding grounds, Blackpoll Warblers showed a stronger tendency to forage on small outer parts of limbs than they did in the adjacent firs. In 40 foraging observations totalling 443 sec there, they foraged 32% of the time on the inner parts of limbs, 61% on the outer parts, 4% on tips of foliage, and 3% on dead limbs.

Blackpoll Warblers spent a considerable part of their time perching motionless or singing while perched motionless. In addition to the 4999 sec of foraging observations, 5288 sec were recorded in which individuals were stationary; therefore, foraging took up only 49% of the total time observed. These figures probably are conservative, since I frequently searched for

TABLE 3

FORAGING MOTIONS OTHER THAN GLEANING

Motion[1]	New Hampshire	Maryland
Hawking for insects	1.8 (9)	4.1 (18)
Hovering at vegetation	1.0 (5)	0.5 (2)
Retrieving fallen food	–	0.9 (4)

[1] Number/1000 sec of foraging, with total number of observations in parentheses.

considerable periods before locating singing birds. Probably I did not sight them sooner because they were not moving.

Foraging observations in migration.—All foraging in deciduous forests took place in the canopy. The heights exploited (Fig. 2) did not differ significantly from the foliage profile of the canopy (Fig. 1) ($P > 0.05$ in a 2-tailed Spearman Rank Correlation Test). Individuals foraged significantly more peripherally here than in the fir forests in New Hampshire ($P = 0.05$ in a 1-tailed test), but this difference probably resulted partly from differences in the location of foliage in deciduous and coniferous trees. The area treated as the inner parts of the branches here consisted of limbs of 3 cm diameter or more, which in Maryland typically did not support leaves, bark, or lichens that would be likely to provide hiding places for insects. However, a minority of the birds' time was also spent foraging in new leaf clusters, a pattern that did not parallel the one seen in the conifers. These birds hawked for insects somewhat more frequently than did individuals in the breeding area (Table 3), although the difference was not significant ($P > 0.05$, χ^2). These birds also occasionally hovered at the tips of vegetation (Table 3).

Intermittent observations were also made on Blackpoll Warblers during spring migration on several spruce-clad islands off the Maine Coast from 1966 to 1972. These observations were made on Thief, Crane and Franklin islands, which have a white spruce cover resembling the fir forest near the top of Mt. Osceola. Since a total of only 1101 sec of foraging observations was recorded on 3 islands of slightly differing foliage characteristics (see Morse 1971), a detailed comparison is inappropriate. However, here, too, Blackpoll Warblers made very heavy use of the inner parts of the limbs (64%) and only occasional use of the tips of the vegetation (4%). Individuals on these islands made minimal use of dead limbs (4%), which may be a function of the small number of dead limbs in the trees exploited on these islands. Neither did these individuals forage in deciduous growth, which could result solely from the virtual lack of deciduous trees on these

islands. These birds concentrated their activities in the 6–9 m height category (79%), which is slightly higher than that recorded from Mt. Osceola (Fig. 1). However, this difference, too, may result from slight differences in the height of the forests on the islands and the upper parts of Mt. Osceola. In general, these migrants foraged very similarly to the breeding birds on Mt. Osceola.

Censuses on the breeding grounds.—In addition to their usually noted locations on mountain tops, Blackpoll Warblers occurred commonly down the mountainsides in largely second-growth habitats. In fact, their overall densities in these locations were as much as twice as high as those near the summit of Mt. Osceola (Table 2). However, they made up approximately the same proportion of the overall bird fauna at each of the top 3 study areas (30–36%), and the low density near the top correlates with a low overall density of birds (Table 2). Only in the lowest census area was the Blackpoll Warbler not the most abundant bird species (Table 2). It was the only warbler found in all 4 census plots. Among other warblers, only the Nashville Warbler (*Vermivora ruficapilla*) was found in 3 of the 4 plots.

DISCUSSION

Foraging patterns.—While marked differences in foraging exist between Blackpoll Warblers in coniferous and deciduous vegetation, they may not be as great as they appear at first glance. The difference in height seems to be a function of the height of the forest, with the birds in all situations concentrating their activities in the middle parts of the canopy, although they were seen at times in the top of the canopy in the deciduous forest in migration. While individuals concentrated their activities on the inner parts of the limbs on conifers and the outer parts on the deciduous trees, their position relative to the foliage was probably quite similar, as a result of the differences in leaf distribution in conifers and deciduous trees. In no situations did they frequently exploit the tips of the foliage. Foraging patterns of migrant and breeding individuals in conifers were very similar. Therefore, the impression gained in each area is one in which individuals concentrate their activities well in from the extremities of the vegetation and at modest heights.

These observations closely parallel those of Parnell (1969) in a number of habitats in North Carolina, where he found them typically to be birds of the mid-crown. Sick (1971) has also reported upon the habitat choices and foraging patterns of Blackpoll Warblers on their wintering grounds in Brazil. There, these birds made heavy use of tamarind trees (*Tamarindus indicus*), which superficially resemble conifers, by virtue of their needle-like leaflets.

In particular, blackpolls showed a strong tendency to exploit the shaded interior parts of these trees—similar to their exploitation of conifers.

Habitat distribution on the breeding grounds.—While the Blackpoll Warbler is often considered a mountaintop bird at the southern limit of its range (Griscom and Sprunt 1957), the altitudinal gradient of these birds on Mt. Osceola is high, with apparently breeding individuals ranging down to as low as 750 m, and with high densities being recorded as low as 850 m in second-growth vegetation. The altitudinal range of these birds on the mountain was greater than that of any other warbler and greater than that of any other species except the Dark-eyed Junco (*Junco hyemalis*) (Table 2). Able and Noon (1976) noted similarly wide gradients of Blackpoll Warblers in the Adirondack Mountains of New York and Green Mountains of Vermont.

Relationships with Bay-breasted Warblers.—Blackpoll and Bay-breasted warblers are very similar morphologically. Perhaps not generally appreciated is the fact that these 2 species apparently infrequently overlap in their breeding sites, although their composite geographic ranges show high degrees of overlap (Griscom and Sprunt 1957, AOU Check-list 1957). In New England, the Blackpoll Warbler is usually a species of relatively high elevations. The Bay-breasted Warbler, on the other hand, typically occurs at low elevations in spruce-fir forests and is associated with outbreaks of the spruce budworm (*Choristoneura fumiferana*) as well. Of the many breeding-bird censuses run in northern coniferous forest habitats (see Erskine 1971, 1972, 1976), Blackpoll and Bay-breasted warblers have been recorded together at the same site (several census plots) only in the Green River watershed of northern New Brunswick. Further investigation of the 2 species there would be profitable.

One possible explanation for this largely contiguous distributional pattern is that these species are too similar to each other to coexist. That interpretation is supported by the similarities in their foraging patterns (Morse 1978, this paper). Both concentrate their activities toward the centers of coniferous trees at moderate heights. The similarities in foraging patterns of these species are greater than those of any other members of the coexisting complex of *Dendroica* warblers (MacArthur 1958; Morse 1968, 1971). It is tempting to conclude that the boundaries of limiting similarity have been violated in this case. Although these species were studied in different forests with modestly differing foliage profiles, thus making a direct measurement of overlap impractical, the tendency of Blackpoll Warblers to shift their foraging height somewhat in response to the height of the canopy suggests that if they did occur with Bay-breasted Warblers at a site, they would exhibit a foraging pattern extremely similar to that species.

SUMMARY

Foraging patterns of Blackpoll Warblers were studied on their breeding grounds in mountain fir forests of New Hampshire and during migration in Maryland and Maine. Populations were also censused at several altitudes in New Hampshire. Blackpoll Warblers spent most of their time foraging on inner parts of vegetation at medium heights, although their placement in deciduous trees was more peripheral than that in conifers, probably a result of differences in the distribution of foliage. Blackpoll Warblers were the commonest species of bird in mountaintop fir forests, but their density there was lower than that found in some mixed coniferous-deciduous, second-growth areas on the mountainsides. They showed the widest altitudinal gradient of any warbler and a wider one than any other passerine except the Dark-eyed Junco.

Blackpoll Warblers forage very similarly to Bay-breasted Warblers, and only 1 of the 2 appears to breed at most sites. I suggest that their habitat use patterns are so similar that they cannot coexist under most circumstances.

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NEW LIFE MEMBER

Ms. Kathy Martin has become a life member of the Wilson Ornithological Society. Ms. Martin is presently conducting a research project on waterfowl as a part of the Dunk River Interdisciplinary Research Project. Her principal research interest is in population dynamics of upland game and passerine species. With a number of scientific and popular publications to her credit, Ms. Martin is also active in natural history and environmental organizations, recently serving as representative from P.E.I. to the Canadian Environmental Advisory Council Conference. In addition to her ornithological interests, Ms. Martin enjoys scuba diving, writing, photography, and is active in a variety of sports.