COMPETITIVE RELATIONSHIPS BETWEEN PARULA WARBLERS AND OTHER SPECIES DURING THE BREEDING SEASON

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IN comparison with most other warblers, and particularly the ones with which it most frequently comes in contact, the Parula Warbler (*Parula americana*) is characterized by its small size. In view of its foraging habits, suggestive both of kinglets and of larger warblers, studies of this species were pursued to determine any effects which its interspecific relationships might have upon its breeding ecology and behavior.

The Parula Warbler breeds throughout a wide geographic area in North America, frequenting a variety of habitats ranging from boreal spruce forests to sweet gum–oak swamps. It demonstrates a strong affinity for epiphytic growth on its breeding grounds—beard lichen (*Usnea* sp.) in the north and Spanish moss (*Tillandsia usneoides*) in the south.

The major part of the work reported in this paper was conducted on Hog Island (Todd Wildlife Sanctuary), Bremen, Lincoln County, Maine, in the spring and summer of the years 1962 to 1966. Supplementary observations were made in other areas along the coast of Maine as well as inland. Several pairs of this species were followed through a complete breeding season in a forest south of Baton Rouge, East Baton Rouge Parish, Louisiana. Surveys were made in both Maine and Louisiana to determine the density and distribution of Parula Warblers. Foraging data were obtained in a manner similar to that used for other passerine species by Gibb (1954, 1960). The habitat was divided up into a number of foraging stations and note was taken of exactly where each individual was feeding when first observed. An attempt was made to survey the trees evenly from their tops to the ground, so that any bias caused by the differential conspicuousness of individuals in the various parts of the habitat would be minimized. Usually no more than one observation was taken on an individual per day. As far as was possible, I also observed the birds' activities, food obtained, and the method used in procuring it. Observations on interactions between different species were made whenever possible.

Hog Island is 330 acres (132 hectares) in size and lies immediately adjacent to the mainland. It is covered with a mature red and white spruce (*Picea rubens* and *P. glauca*) forest, most trees ranging in height between 18 and 25 m. Where undisturbed the foliage is dense, only scattered patches of ground being illuminated by sunlight, virtually no undergrowth occurring, and limbs of the lower three to five m being

TABLE 1
RELATIVE ABUNDANCE OF *USNEA* IN MAINE[1]

Area	*Area covered by* Usnea *(in per cent)*			*Length of growth (in cm)*
	Trunk	*Large limbs*	*Foliage*	
East shore, dense forest	7 (0–11)	11 (1–25)	8 (1–24)	3.8 (2.3–5.8)
West shore, dense forest	0	1 (0–5)	1 (0–1)	1.8 (0.0–2.5)
East shore, blowdown	10 (1–26)	18 (2–44)	5 (0–12)	4.3 (2.3–6.6)
West shore, blowdown	2 (0–4)	3 (1–11)	1 (0–5)	2.8 (2.0–3.8)
East shore, birch grove	2 (1–3)	4 (0–11)	1 (0–1)	2.8 (2.5–3.0)
Interior, dense forest	2 (0–5)	7 (0–25)	10 (0–43)	3.0 (2.0–4.6)
Interior, about outcroppings of rock	1 (0–3)	10 (0–26)	7 (0–26)	3.8 (2.8–5.3)
Dead spruces, all areas above	no data	14 (7–21)	—	4.1 (2.8–5.3)
Mainland, exposed area	17 (10–33)	25 (14–39)	no data, but low	3.8 (3.6–4.6)
Mainland, unexposed area	2 (0–3)	1 (0–2)	no data, but low	2.3 (0.0–3.8)

[1] Means are given, with extremes in parentheses.

dead. Where slightly more sun strikes the ground there is often a dense growth of young spruces less than 30 cm high. Openings in the forest resulting from fallen trees are rapidly repopulated by young trees. Groves of white birches (*Betula papyrifera*) up to 3 or 4 hectares in size occur on a few parts of the island. *Usnea* grows extensively on trunks and limbs of the spruces and birches, being most dense where there is exposure to easterly and southeasterly winds that prevail during foggy weather.

The hurricanes of 1954 and winds of following years have damaged the forest severely on many parts of the island. Several areas of .5 to 15 hectares formerly covered with mature spruces have been thus completely denuded of tall trees or contain only scattered survivors. In many other places openings of less than .5 hectare have been formed, or trees have been greatly thinned. This wind damage has lengthened the total edge of the spruce forest on Hog Island, which before 1954 was largely concurrent with the shore line.

Estimates were made to determine the approximate density of *Usnea* lichen on various parts of Hog Island. For each division of the habitat (see Table 1), evenly spaced points were plotted on a map and six points from each division were chosen randomly as areas for censusing *Usnea* growth on trees. The chosen points were then located in the field, and the nearest large tree (15 m or taller) was analyzed. Visual estimates were made on the percentage of area covered by *Usnea* on trunks, large limbs, and foliage, as well as the average length that the lichen trailed below its point of attachment (Table 1).

The study area in Louisiana, about four km south of Baton Rouge, is a mature oak–gum forest. Though containing small numbers of several species of trees, Nuttall oaks (*Quercus nuttallii*) and sweet gums

TABLE 2
DISTRIBUTION OF PARULA WARBLERS ON HOG ISLAND

Area	*Length of shoreline (km)*	*Number of territories*	*Territories/km of shoreline*
West shore, spruce forest	1.4	4	2.9
West shore, blowdown	1.1	11	10.0
East shore, spruce forest	1.3	5	3.8
East shore, blowdown	0.7	7	10.0
East shore, birch forest	0.5	3	16.7
Blowdowns in interior of island	–	2	–
Natural openings in forest[1]	–	2	–
Total	5.0	34	–

[1] Resulting from outcroppings of rock.

(*Liquidambar styraciflua*) are the commonest of the large trees in the area, sometimes exceeding heights of 30 m. A well formed understory occurs in which American hornbeam (*Carpinus caroliniana*) is the principal member. This forest supports a heavy growth of Spanish moss, many plants trailing to over one m below their place of attachment. Study was concentrated in a 10-hectare area.

DISTRIBUTION AND DENSITY OF THE BIRDS

In Maine, Parula Warblers foraged most frequently at medium heights and sang at elevations ranging from foraging level to treetops. On Hog Island individuals of this species were confined to the periphery of spruce forests, as they were in other areas studied along the coast of Maine. Only rarely did these birds venture into the unbroken spruce forest. Graber and Graber (1951) also noted that this species was confined to edges of forests during the breeding season in Michigan. The distribution of breeding Parula Warblers on Hog Island during the 1965 season is indicated in Table 2. Few natural openings occur in the forest on Hog Island, but on some of the more offshore islands nearby, extensive openings occur as a result of outcroppings of granitic rock. Parula Warblers nest frequently about such openings.

Although Parula Warblers construct their nests of *Usnea*, no direct relationship between the density of the warblers and the density of the lichen was noted. A higher per cent of *Usnea* covering occurred along the east shore than the west shore, both in heavily forested areas and blowdowns (Table 1), but there were comparable frequencies of Parula Warblers on the east and west shores (Table 2). Samples taken in the largest white birch area (on the east shore) indicate an abundance of *Usnea* intermediate to that of east and west shores, yet there were three pairs of Parula Warblers in this relatively small area. Undisturbed areas in the interior of the island were variable in the density of *Usnea*

TABLE 3
HEIGHT (IN METERS) OF FORAGING ON HOG ISLAND[1]

Species	*Number of observations*	*Observed range of height*	*Mean ± standard error*	*Standard deviation*
Golden-crowned Kinglet	251	0.0–16.8	8.0 ± 0.23	3.6
Parula Warbler	240	1.5–18.3	10.0 ± 0.25	3.9
Magnolia Warbler	115	0.0–13.7	7.3 ± 0.30	3.2
Myrtle Warbler	130	0.0–13.7	7.8 ± 0.27	3.0
Black-throated Green Warbler	304	0.0–19.8+	11.8 ± 0.31	5.5
Blackburnian Warbler	96	10.7–19.8+	15.2 ± 0.32	3.2

[1] Height of forest averaged 21.3 m.

growth, ranging from sparse to very heavy. No Parula Warblers were found there. *Usnea* cover on trees surrounding outcroppings of rock in the middle of the island was sparser than in some heavily wooded areas, yet Parula Warblers did nest at the edge of two of the larger openings. Dead spruces characteristically had a heavy covering of *Usnea*, and only an occasional dead tree in an area would result in the presence of a luxuriant local station. Supplemental censuses were made in two areas of primarily deciduous forest in Bremen, two km from the ocean. Two pairs of Parula Warblers nested within a plot of two hectares in an exposed location with a local, unusually heavy concentration of *Usnea*; none was found in an adjacent sheltered area of comparable size, nor in a large surrounding area.

All nests observed were situated in *Usnea*, as were those found by Cruickshank (1956) on this island (combined N = 81). Thus, the presence of the plant is important, but its abundance appears to be of minor importance as compared with other factors. Birds of the mainland sometimes nested where only small tufts of this plant were available.

In Louisiana, Parula Warblers remained largely in the main canopy 15 m or more up. They ranged widely through this stratum of the nearly undisturbed forest, showing no apparent tendency to be restricted to edges. Each nest found was in Spanish moss (N = 5); eight pairs probably nested on the 10-hectare main study plot.

COMPARISON OF FORAGING

While Parula Warblers appear to minimize overlap in foraging with other warblers by feeding heavily in the extreme tips of the foliage, this very practice subjects them to considerable potential overlap with unrelated species. In the northern spruce forests such an overlap with Golden-crowned Kinglets (*Regulus satrapa*) and Ruby-crowned Kinglets (*R. calendula*) may be heavy. Both kinglets are very small, work frequently on the tips of spruce foliage, and hover for protracted periods at

tips of spruce foliage. The circumboreal distribution of *Regulus*, the considerable proliferation of its races (see A.O.U. Check-list, 1957: 452–454; Vaurie, 1959: 298–303), and its heavy utilization of spruce (and other coniferous) forests suggests that species of *Regulus* are highly adapted to forage in such areas, and that they have inhabited these forests for a long period of time. Both local kinglets were typically birds of the interior parts of the forest, as were potential warbler competitors, Myrtle (*Dendroica coronata*), Black-throated Green (*D. virens*), and Blackburnian (*D. fusca*) warblers. None of these species nested in heavily disturbed areas as did Parula Warblers; the total amount of activity in heavily disturbed areas of each of these other species on Hog Island represented only a small percentage of their total activity. Magnolia Warblers (*D. magnolia*) also were found inside these forests, though more abundant in mixed coniferous–deciduous growth than in the spruces. The foraging of Golden-crowned Kinglets and Parula Warblers (Table 3) at the same time (June) showed many similarities, as well as a number of differences, the latter probably being partly the result of the slightly different habitats most frequently used by the two species.

The Golden-crowned Kinglet was a common nesting species on Hog Island. Birds of this species foraged more heavily on the inner parts of spruce trees than did Parula Warblers, frequently working on dead limbs and dead twigs of live branches proximal to live growth. Over 20 per cent of their foraging on the tips of vegetation was performed on the delicate shade leaves of the inner foliage, while only 6 per cent of foraging at tips by Parula Warblers was done in this inner region. Shade leaves are an adaptation to a low incidence of sunlight upon the needles (Spurr, 1964: 29); hence, the trees in a dense forest have more of this growth than do ones along the edge of the forest. Golden-crowned Kinglets concentrated their foraging at a somewhat lower height than did Parula Warblers, though substantial overlap in height occurred among all species studied. As a result, a considerable amount of foraging was done by the kinglets in the same areas worked by Parula Warblers, and the former also used some of the movements commonly used by Parula Warblers for foraging in the tips of the foliage.

Ruby-crowned Kinglets were too uncommon on Hog Island to allow adequate comparison with other species, but occasional observations indicated that they foraged heavily on tips of spruce foliage and hovered frequently. In spruce forests at Tremont, Hancock County, Maine, both species of kinglets are common, and observations there confirmed the impressions gained from observations on Hog Island.

Black-throated Green Warblers showed more similarities in foraging to Parula Warblers than did any other warblers in the spruce forest on

TABLE 4

FREQUENCY (IN PER CENT) OF FORAGING POSITIONS IN SPRUCE FOREST

Position	*Golden-crowned Kinglet*	*Parula Warbler*	*Magnolia Warbler*	*Myrtle Warbler*	*Black-throated Green Warbler*	*Blackburnian Warbler*
Spruce						
Tip of foliage	38.2	48.3	9.6	14.6	26.3	19.8
Gleaning	25.9	32.9	3.5	10.8	14.1	16.7
Stretching	1.2	5.0	0.9	–	1.3	–
Hovering	9.5	7.5	5.2	3.8	10.9	3.1
Hover-walking	0.4	2.1	–	–	–	–
Hanging	1.2	0.8	–	–	–	–
Small live twigs (up to 5 mm)	9.2	23.3	46.1	17.7	38.2	48.9
Dead twigs	13.9	2.9	5.2	0.8	0.7	2.1
Gleaning	9.9	2.5	4.3	0.8	0.7	2.1
Hovering	3.2	0.4	0.9	–	–	–
Hanging	0.8	–	–	–	–	–
Dead branch	30.3	2.1	13.0	30.0	8.2	2.1
Gleaning	29.1	2.1	13.0	29.2	7.5	2.1
Hovering	0.8	–	–	0.8	0.7	–
Hanging	0.3	–	–	–	–	–
Usnea-covered branch	–	5.0	0.9	–	0.7	–
Branch (distal)	5.2	3.8	3.5	1.5	3.9	4.2
Branch (proximal)	1.6	6.3	12.2	12.3	14.4	15.6
Trunk	–	–	–	–	0.7	–
Flycatching	–	2.5	2.6	19.2	2.0	3.1
Deciduous growth	0.8	5.8	5.2	0.8	3.9	4.2
Ground	0.8	–	1.7	3.1	1.0	–
Number of observations	251	240	115	130	304	96

Hog Island (Table 4). They foraged at the most similar height (Table 3) and part of the foliage as Parula Warblers, hovered more frequently than other resident *Dendroica* warblers, and attained the highest density of any warbler in the study area (Cadbury and Cruickshank, 1937; Morse, 1967). The population density of this species, the Blackburnian Warbler, and Myrtle Warbler appears closely correlated with the volume of foliage in an area (MacArthur, 1958; Morse, 1967). Hence, there would be less opportunity for interactions between Parula Warblers and the three *Dendroica* warblers along the edges of forests (especially around newly formed openings in which low-level foliage is limited) than in the undisturbed forest. Neither Black-throated Green Warblers nor any of the other *Dendroica* warblers in this forest used the tips of the foliage as frequently as did Parula Warblers (Table 4). Nevertheless, the use of this part of the habitat by the combined *Dendroica* warblers was heavy. Blackburnian Warblers foraged more similarly to Parula and to Black-throated Green warblers than did Magnolia and Myrtle warblers, but did not use the tips of the foliage as frequently, partly the result of a

low frequency of hovering (Table 4). Blackburnian Warblers usually foraged at greater heights than Parula Warblers (Table 3).

During the breeding season only two other species that foraged at all similarly to Parula Warblers occupied the spruce forest. Black-capped Chickadees (*Parus atricapillus*) nested in areas where birches were frequent, and did not appear daily in the spruce forest until after many of the young Parula Warblers were fledged (about 10 July). Then they fed frequently upon spruce foliage. Red-breasted Nuthatches (*Sitta canadensis*) nested commonly in this forest, but confined the majority of their foraging to trunks and large limbs, though foraging regularly in the spruce foliage. The potential competition for a food source presented by these two species probably was negligible in comparison to that of kinglets and other warblers.

Despite the high frequency of foraging on spruce foliage by *Dendroica* warblers and kinglets, Parula Warblers also foraged heavily there through most of the breeding season, even in territories where deciduous growth was readily available. In one area of several hectares that was composed of approximately 50 per cent spruces and 50 per cent birches, Parula Warblers were seen foraging over five times as frequently on spruce as on birch growth (119 times to 23 times) during the first half of June. The difference of these enumerated data is highly significant in a binomial test ($P < .001$). Kinglets and the spruce-forest *Dendroica* warblers were less abundant in coniferous–deciduous forests than in spruce forests, but the preference of Parula Warblers for conifers at this season was also noted when this species foraged in areas containing white birches with only occasional spruces. In limited observations made in predominantly deciduous forests on the adjacent mainland, Parula Warblers foraged a disproportionately great amount of the time in coniferous growth during the first half of June.

Later in the season this preference for conifers decreased until on Hog Island, where equal opportunities to forage in coniferous and deciduous growth were available, Parula Warblers worked in deciduous growth somewhat more frequently than they did in coniferous growth (66 times to 51 times by 15 July). This difference from the condition described in the first half of June was highly significant in a chi-square test ($P < .001$). At this time the birds had just fledged their young, and the increased demand for food probably contributed to the extension of their range of foraging. Family groups of spruce-forest *Dendroica* warblers (except Myrtle Warblers) also moved into the deciduous growth frequently at this season, resulting in very heavy use of these areas. However, the frequent infestations of microlepidopterous larvae and leaf miners (Hymenoptera: Tenthredinidae) on birches at this season that often even

TABLE 5

SONG PATTERN OF PARULA WARBLERS FOLLOWING INTERSPECIFIC FIGHTS, CHASES, AND OTHER INSTANCES OF CLOSE CONTACT

Species opposing	*Accented Ending Song*	*Unaccented Ending Song*	*Muted or incomplete songs*
Black-capped Chickadee	1	–	–
Golden-crowned Kinglet	–	1	3
Magnolia Warbler	2	–	–
Myrtle Warbler	3	1	–
Black-throated Green Warbler	2	3	1
Blackburnian Warbler	2	2	1

caused their partial defoliation probably resulted in a temporarily superabundant food source. Golden-crowned Kinglets, which were feeding large families of recently fledged young at this time, seldom left the spruces; thus, the number of birds foraging in the deciduous growth did not rise even higher.

HOSTILE BEHAVIOR

In spite of the close similarities in foraging between some of the species, displays of overtly hostile behavior among them were not common. Relatively few observations of this nature were made during the course of this study. The analysis of songs of Parula Warblers proved to be the most valuable source of information on interspecific hostile behavior. Songs accompanied or followed all encounters observed between male Parula Warblers and other species during the summer season. Apparent instances of antiphonal singing were noted between Parula Warblers and Golden-crowned Kinglets, as well as between the Parula Warbler and *Dendroica* warblers.

Male Parula Warblers possess two distinct song patterns, referred to here as Accented Ending Songs and Unaccented Ending Songs, which are sung under different circumstances. Peterson (1947) describes them respectively as follows: a buzzy climbing trill snapping over the top, and a series of notes ending in a climbing trill. Robbins, Bruun, and Zim (1966) provide a sonogram of the Accented Ending Song. These songs were superficially similar in the two areas studied. The contexts in which these two songs are sung by Parula Warblers appear comparable to those of Yellow Warblers, *Dendroica petechia* (Morse, 1966), with Accented Ending Songs occurring in situations associated with a low level of aggression, Unaccented Ending Songs in situations associated with a somewhat higher level of aggression, and muted and incomplete songs in situations associated with a still higher level of aggression.

The small sample size (Table 5) prevents adequate analysis of these phenomena. However, the most frequent level of aggression exhibited by

TABLE 6
FREQUENCY (IN PER CENT) OF FORAGING POSITIONS OF PARULA WARBLERS IN DECIDUOUS FORESTS

Position	*Oak-gum (Louisiana)*	*White birch (Maine)*
Tips of foliage	67.4	59.8
Gleaning	58.1	50.0
Stretching	1.6	–
Hovering	4.6	8.6
Hover-walking	3.1	1.2
Small live twigs (up to 5 mm)	10.1	32.9
Dead branch	3.1	–
Spanish moss	4.6	–
Branch (distal)	11.6	3.7
Branch (proximal)	1.6	1.2
Flycatching	1.6	2.4
Number of observations	129	82

Parula Warblers (measured by the songs) appeared to be directly related to the amount of similarity in foraging between them and the other species involved. Thus, Golden-crowned Kinglets elicited a strong response most frequently, and Black-throated Green and Blackburnian warblers usually elicited a weaker response, while Myrtle and Magnolia warblers elicited progressively weaker responses.

OBSERVATIONS IN LOUISIANA

In Louisiana, Parula Warblers were studied in a mature oak–gum forest. Several other species of warblers nested in the study area, including Prothonotary (*Protonotaria citrea*), Swainson's (*Limnothlypis swainsonii*), Kentucky (*Oporornis formosus*), and Hooded (*Wilsonia citrina*) warblers, and the Yellowthroat (*Geothlypis trichas*), but none foraged regularly above the understory, while Parula Warblers seldom foraged below the main canopy. The majority of the latter species' foraging occurred at the bases of leaves and even on leaves (Table 6). Two to three pairs of Carolina Chickadees (*Parus carolinensis*) nested in the main study area, fed frequently on the outer parts of the trees, and foraged more similarly to Parula Warblers than did any other species present. Yellow-throated (*Vireo flavifrons*) and Red-eyed (*V. olivaceus*) vireos were among the most important foragers on the larger branches at this height.

Parula Warblers in Louisiana also foraged most widely when their young were nearly fledged, probably because of increased food demands at the time. Not until young were fledged did the adults appear regularly in the understory. Simultaneously, Prothonotary Warblers extended their range of foraging upward, and then infrequent fights and chases occurred between the two species, in which Prothonotary Warblers prevailed in each observed instance.

DISCUSSION

Crombie (1947: 66) defined competition as being the demand at the same time by more than one organism for the same resources of the environment in excess of the immediate supply. His definition will be followed here. Indirect evidence of two sorts suggests that species of warblers nesting in spruce forests maintain a population level near or at the maximum limit possible with the available food supply. Failure to attain a higher level probably is the result of competition. Observations by a number of workers in other northern coniferous forests (Kendeigh, 1947; Stewart and Aldrich, 1952; Morris *et al.*, 1958) indicate that populations of warblers increase at times of spruce budworm outbreaks, when a superabundant food supply is available. Secondly, many (though not all) of the species studied on Hog Island extended their foraging range noticeably into available deciduous growth at the time of maximum food demands, which occurred after their young were fledged. These movements frequently coincided with the appearance of an abundant insect food source in the deciduous trees, though in 1964 this source never materialized to its usual dimensions.

Not only is overlap in foraging with other species less severe for the Parula Warblers of the southern forest, but the species' small size probably is of greater advantage to it there than in spruce forests. The low weight facilitates the foraging by these birds at bases of leaves and on leaves with long petioles, being less of an advantage in the tips of spruce foliage. Little if any young growth has appeared upon the red spruces along the Maine coast when the warblers return in the spring, and the stiff growth of the preceding year is strong enough to support much larger birds than Parula Warblers. The young growth of white spruce is less rigid than that of red spruce, but even its young shoots will support a greater load than will petioles and leaves of many deciduous trees. White spruces are most often associated with the edge of the forest and subclimax conditions (the areas frequented by Parula Warblers) than are red spruces.

The apparent adaptation of the Golden-crowned Kinglet (and probably the Ruby-crowned Kinglet) to forage in the tips of the foliage and small dead limbs probably makes these birds effective competitors of the Parula Warbler in an unbroken spruce forest. The kinglets' most frequently used foraging motion, hovering, is performed with considerable agility, and the average period of foraging per hover appears to be in excess of that of the warblers studied, though it was not measured. Many Golden-crowned Kinglets doubtlessly are dependent upon conifers throughout the year. *Dendroica* warblers also share foraging habits with Parula Warblers to varying degrees.

The comparable incidence of foraging motions in Louisiana and in Maine suggests that Parula Warblers occupy a comparable niche in these two extremely different habitats. When Parula Warblers foraged in deciduous trees in the north (Table 6), it was in a manner similar to that employed early in the season in conifers. These observations suggest a low degree of flexibility in the foraging behavior of the species. Despite this situation, Parula Warblers nest over a wide geographical range and perhaps have exploited the only available opening in the spruce forest.

Thus, in Maine, Parula Warblers appear to operate less effectively than do individuals of this species in Louisiana. Individual factors contributing to this situation in Maine include apparent competition with kinglets and several other warblers for food, interspecific hostile activities, and a method of foraging that is less advantageous in the spruce forest than in deciduous trees. These factors may be responsible in large part for the Parula Warbler being a species of the edge of the forest in the climax spruce forests and reaching its northern limit south of the St. Lawrence drainage on the eastern seaboard (A.O.U. Check-list, 1957), south of the other species with which it is potentially in competition and far south of the northern limit of these tree species.

The Parula Warbler is the only warbler of these spruce forests that is primarily southern in range, and the similarity of its foraging under various vegetational conditions points to a primarily deciduous adaptation. Continual swamping by the large southern population may prevent the acquisition of a more nearly perfect adaptation to the spruce habitat by the northern population. The deciduous adaptation, large southern population, and existence of congeners only of exclusively southern distribution suggest that this species is a relative newcomer to the northern forests. As indicated by Mengel (1964: 37), the presence of a large number of species of warblers in the spruce forest potentially makes colonization of that habitat a formidable task.

The similarity of foraging behavior and the intensity of hostile behavior displayed both suggest that the Golden-crowned Kinglet is the strongest potential competitor of the Parula Warbler in the spruce forest where the study was conducted. Although Golden-crowned Kinglets do not reach as high a breeding density in most years as do Black-throated Green Warblers on Hog Island (Cadbury and Cruickshank, 1937–58), and, because of their small size, would not require as much food per individual, this difference is partly negated by the extremely large families that the kinglet raises (see Bent, 1949: 387). The abundant Black-throated Green Warbler is probably the next most important in this regard, followed by the Blackburnian Warbler. Magnolia and Myrtle warblers appear much less important as potential competitors, and the effect of any other species

of birds upon Parula Warblers in this forest is probably negligible. Though no other species forage in a manner nearly identical to the Parula Warbler, kinglets and other warblers have exploited the habitat so heavily that collectively they probably are a major factor limiting Parula Warblers to the edges of the spruce forest.

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SUMMARY

The foraging of Parula Warblers (*Parula americana*) and of their potential competitors was studied in Maine and in Louisiana during the breeding season. Parula Warblers inhabited the edges of spruce forests in Maine, and in Louisiana they occurred uniformly through an oak-gum forest. Most foraging occurred in tips of the foliage, where the birds' low weight appeared advantageous. Methods of foraging were quite similar in both coniferous and deciduous growth and suggest a primarily deciduous adaptation.

Kinglets and *Dendroica* warblers overlapped Parula Warblers widely in their foraging in spruces. Golden-crowned Kinglets (*Regulus satrapa*) foraged heavily on foliage tips, but worked on inner foliage and small dead limbs more often than did Parula Warblers. Black-throated Green Warblers (*D. virens*) used the tips of live foliage more than any other *Dendroica* warbler, but not as often as Parula Warblers and Golden-crowned Kinglets. Blackburnian Warblers (*D. fusca*) worked these tips less frequently, and usually foraged higher than any others. Magnolia (*D. magnolia*) and Myrtle (*D. coronata*) warblers shared even fewer foraging similarities with Parula Warblers. Though no species foraged in a manner nearly identical to the Parula Warbler, their over-all usage of the habitat was heavy. Nevertheless, Parula Warblers showed a definite preference for coniferous growth at this season. As young were about to fledge they extended their foraging range into neighboring deciduous growth, as did most *Dendroica* warblers.

Several other warblers shared the Louisiana study area with Parula Warblers, but none regularly occurred in the upper canopy with them. Only when the Parula Warblers extended their foraging range as young were fledged did contact with others occur regularly.

It is concluded that kinglets and other warblers are an important factor limiting the distribution of Parula Warblers in the spruce forest.

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