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HABITAT USE BY YELLOW-RUMPED WARBLERS AT THE NORTHERN EXTREMITIES OF THEIR WINTER RANGE

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The Presque Isle peninsula, a state park adjacent to the city of Erie, Erie County, Pennsylvania (42°10′N, 80°05′W), has long been known for its unusual floral and faunal characteristics. This narrow peninsula jutting 11.3 km into Lake Erie offers a great diversity of environments (from sandy beaches to climax forests) in a compact space. Many species of migrating birds visit the area, and one is struck also by the richness and unusual nature of the breeding and wintering bird communities (Stull 1965). One unusual feature is the presence of a large population of wintering Yellow-rumped Warblers (*Dendroica coronata*) (See Christmas Counts, Am. Birds, 1957–1977). Numbers reported on Christmas Counts have ranged from 19 (1957) to 297 (1975) and seem to be increasing.

A careful survey of the Christmas Count data underlines the unusual nature of this large population. There is no other area in the Great Lakes region, at least amongst those covered by Christmas Counts, where Yellow-rumped Warblers occur in anything like these numbers. Counts in adjacent areas have yielded no or only a few birds. One has to drop as far south as Tennessee–North Carolina to obtain comparable numbers. Relatively large populations can be found along the Atlantic coast to Massachusetts during midwinter. However, this can be explained by the warming effects of the Gulf Stream, as well as possibly other factors.

Why do these birds overwinter so far north? The Yellow-rumped Warbler is unusual among Parulids in that it is much more of a generalist feeder. Although 78% of its food for the year is animal matter, it also can subsist on various fruits (Palmer and Fowler 1975). Northern bayberry (*Myrica*) has been reported (Hausman 1927) in the diet of Yellow-rumped Warblers and is common on Presque Isle. However, no one has collected regular data over a period of time to link the warblers to this food source and/or to others. We here describe results of a study designed to provide an explanation for this unusual population.

METHODS

Data were collected from 16 January to 18 March 1975 and 13 November 1975 to 8 March 1976. Over 230 hours of observation were accumulated (the majority by Giampa); the peninsula was visited approximately every other day.

Field tactics differed between the seasons. During the first season our approach was

to maximize the time spent in observing the warblers. This meant concentrating on the eastern quarter of the peninsula, since Christmas Count observations and other reports (J. Stull and D. Snyder, pers. comm.) had suggested that the birds were confined mainly to this sector. Within this sector most areas were sampled on a given visit. However, once contact was made the birds were observed sometimes for 30 min or more. Every effort was made to minimize disturbing the birds. Binoculars were used to observe birds and field notes were either written or tape recorded. All aspects of behavior were recorded, including location, number, foods taken, rate of movement, interspecific relations, predation, etc., as well as appropriate weather data. Data were collected during all day-light hours.

During the second season, when the bulk of the data reported here were collected, efforts concentrated on 2 smaller areas in the eastern portion. The first of these, the pine plot or transect, was chosen since it had yielded regular, consistently high counts the previous winter. It seems typical of a stretch of pine-dominated (*Pinus rigida*) habitat that extends to the middle of the northern side of the peninsula. These pines are 15–18 m in height, and the stand averages 95 m wide, with a trail in the middle. The understory is dominated by scattered patches of bayberry averaging 1 m in height. The second area, the cottonwood plot or transect, was directly east of the pines (beginning 230 m from beach house 10); it had yielded irregular, but sometimes high counts the previous winter. This area contains no pine; the canopy is cottonwood (*Populus deltoides*), spaced at intervals of approximately 3.5 m and with heights of 4.5–18 m. The undergrowth contains by far the highest density of bayberry on the peninsula, estimated to be at least 300–400 plants/ha, ranging from .9–3+ m in height. Both areas are subject to little human interference in winter and contain no artificial feeding stations. (For further information on the geography and botany of Presque Isle, see Jennings 1909 and Kormondy 1969.)

Within each study area a transect line was established (Emlen 1971, Grubb 1975). They ran through the center, with uniform vegetation along the line as well as on both sides. Each line consisted of 10 45.7 m units, which were sampled 3 times/week (except for 4 in week 1, and 2 in weeks 5 and 6), for a total of 44. Observations started 1 h after sunrise, and the area in which observations began was alternated. At the end all relevant weather data were gathered.

In sampling, the observer(s) walked both directions along the transect line and recorded the number of birds, their transect unit, and other species present (excluding waterfowl). Within a unit, birds judged to be part of an intraspecific flock (Morse 1970) were recorded as such. Side boundaries were set at 45.7 m in each direction. The observations lasted 50.8 ± 12.1 min/transect ($n = 88$). Two observers were used on many counts, but there is no evidence that the second observer significantly affected the scores, except in improving the accuracy of the numbers estimated. In moving from 1 transect unit to the next, birds were not recorded again if they had been "pushed" by the observer(s), or if they had moved spontaneously. By collecting data in passing back through the transect, we recognize that some "double counting" occurred. For many purposes this is of no real consequence since we were interested in relative scores. Also, the birds' rate of movement was great enough that the amount of double counting is not especially high. Finally, we wanted to collect as much information per trip as possible; by disregarding events on the return, much information would have been lost.

Attempts were made to accurately assess food choice in the transect areas. Our method consisted of point observations (Morse 1972). The observer moved slowly within the study area, located a bird, and recorded its first foraging act (actual use of mouth-

parts in pecking at materials). Another individual was then located and recorded; no individual was knowingly recorded more than once. Both habitats were open enough that individuals were located with close to randomness. In most cases 2 observers were used in sampling, and the results were compared to assure that the data were representative. Some feeding data were collected on other species, with particular attention given to those competing for the same resources.

In the cottonwood area bayberry counts were conducted at the end of each week. Ten circular sampling areas were established along the transect line; these had a diameter of 30.5 m and were spaced at 45.7 m intervals. Nine plants were sampled each week. These were chosen using a random numbers generator which identified sampling area, distance from a reference point in the center, and compass direction. Once the plant was selected the berries available to the birds on the plant and on the ground were counted. Counts of ground berries included a .093 m^2 area at the base of the plant. Estimates of bayberry numbers in the pine area were also made weekly.

RESULTS

For the season the Yellow-rumped Warbler was found to be the predominant species in both habitats. We saw 28 species (excluding waterfowl) in the pine plot, but of all birds sighted on the outward and backward censuses 54.5% were Yellow-rumped Warblers, an average of 56.8 birds per census. Similarly, 25 species were detected in the cottonwood sector, but 55.7% were Yellow-rumped Warblers, an average of 48.5 per census. However, there were dramatic fluctuations in numbers over the season, especially in the cottonwood area, and also major differences between the plots. This is shown in Figure 1 which illustrates the relative weekly means for both transects for the entire season. The graph shows that the numbers in the pine area remained reasonably stable, though at a somewhat higher level during mid-winter (December 14–February 14). But in the cottonwoods the warblers were seen in low numbers or not at all except for a period of nearly 5 weeks in the latter part of mid-winter, when there was a dramatic influx. The lower numbers in the cottonwood as compared to the pine plot during early winter (November 23–December 13) and late winter (February 15–March 6) are significant ($p < .02$, Mann-Whitney 2-tailed test, Siegel 1956).

The very large influx of Yellow-rumped Warblers into the cottonwood-bayberry area coincided with heavy snow that accumulated during most of January and early February. Snow cover seemed to be a major variable affecting habitat choice. A comparison of the number of birds in the cottonwoods during mid-winter on days of partial or no snow cover with days of complete ground cover yields strikingly different means: 7.7 and 31.2 respectively ($n = 8$ and 14). This difference is significant at the .02 level (Mann-Whitney 2-tailed test). Temperature and wind, in contrast, could not be established as factors which significantly influenced habitat choice, though wind did seem to influence the height at which the birds foraged in the

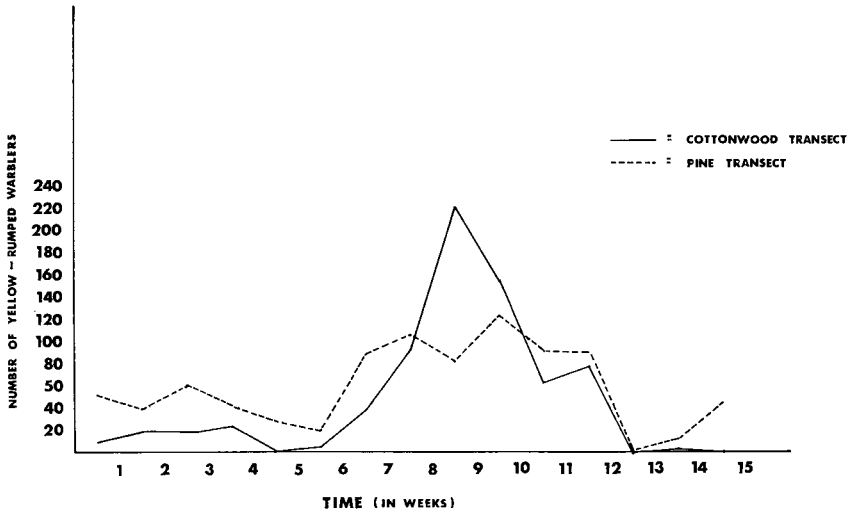

FIG. 1. Fluctuation in estimated numbers of Yellow-rumped Warblers over the season for both transect areas (weeks running consecutively starting week of November 23 [November 23–March 6]).

more exposed cottonwood habitat. (The mean temperature for the winter of 1975–76 was .9°C, with early winter at 5.6°C, mid-winter at −2.7°C, and late winter at 2.3°C. Wind along the lake was substantially greater than inland, an average of 16.2 knots in January, 1975 and 13.4 knots in February, 1975 as compared to 10.2 and 9.7 for the same periods at Youngstown, Ohio [data courtesy of U.S. Department of Commerce and U.S. Coast Guard].)

During the period of heavy snow cover, data were collected on the feeding behavior of the Yellow-rumps in the cottonwood area. Of 254 independent observations over a period of days, 89% of foraging was on bayberry fruit. These results are consistent with those collected the previous year where individual birds were followed for a period of time. Figure 2 shows the 3-week means of warblers plotted against the 3-week means of bayberries per plant over the season in the cottonwood area. The numbers of warblers foraging on the bayberries do not correlate with the berries available. However, the graph does indicate that a low number of (available) bayberries can support a large population of Yellow-rumped Warblers.

In the pine area the feeding choice of the warbler was much more diversified. A single flock sometimes included individuals clinging to the bark of pines, picking at pine needles, fluttering on the tree trunks, eating bayberries from bushes, and moving about on the ground. Of 195 sample

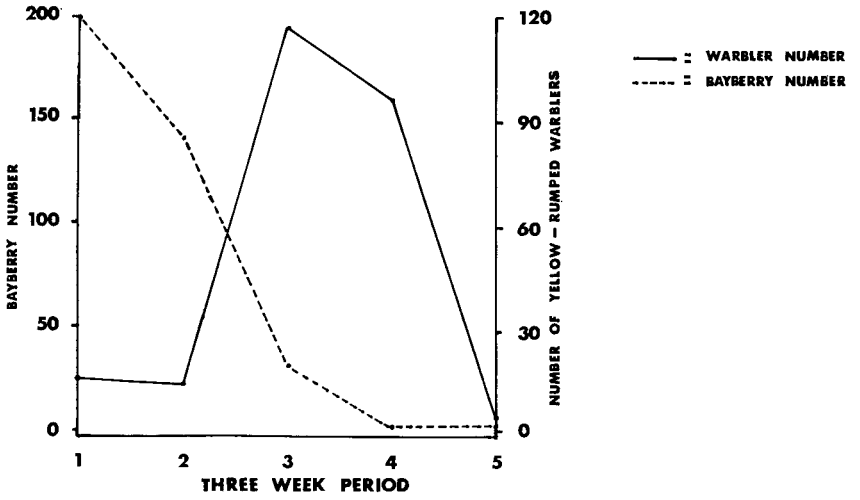

FIG. 2. Seasonal numbers of Yellow-rumped Warblers in relation to the number of bayberries available/plant (November 23–March 6).

feeding observations (middle February of 1975, ground open, mild temperature) 56% were of birds in pines, 37% were in bayberry bushes or on the adjacent ground (where it was assumed that bayberry fruit was the primary food), almost 6% were of birds in deciduous trees, with 1% in the "other" category. Of the pine feeding about 45% was within 3 m of the ground along the main trunk. In the pine area by mid- to late winter the supply of bayberries on the plants was very low. Ground feeding seemed to be more important then. On 21 and 27 February 1976 of 6 flocks of 10 or more located in the pines to the west of the study area, 4 were observed to be feeding wholly on the ground for the duration of observation.

The flexibility of the warbler's feeding tactics was also illustrated by the fact that they were observed feeding at fallen, partly decayed logs and feeding on spider eggs while hovering under the eaves of a beach house. This latter activity was observed only once, during heavy snow cover. We noted no active invertebrates in either season during the mid-winter period.

There seemed to be only 2 other sites where the warblers could be located with regularity. One was an extension (westward) of the pine transect. The other was to the south in the immediate area of Beach 11, where there was a small amount of pine and bayberry. At no time were birds seen feeding outside the range of the bayberry plant during mid-winter. Our estimate of total birds on the peninsula for the winter of 1975–76 is 500, somewhat higher than the 20 December 1975 Christmas Count.

Of the 4635 Yellow-rumped Warbler observations along both transects, 93.1% were flocking with 1 or more Yellow-rumped Warblers, with an average flock size of 9.6 ± 1.3. The rate of movement of a foraging flock was brisk and almost constant. Some flocks appeared quite cohesive, though flocks were often loosely organized, with individuals and/or small groups joining or leaving. Agonistic behavior was almost completely absent during mid-winter, though it occurred some in early spring. Also, as spring approached flocks seemed to become less stable, resulting in a more dispersed population.

The warblers commonly were part of larger interspecific associations. At the beginning of the season loose flocks were composed of many species, but by the middle of winter they were reduced to a nucleus of Yellow-rumped Warblers, Black-capped Chickadees (*Parus atricapillus*), and Downy Woodpeckers (*Picoides pubescens*). Quantitative analyses of these interspecific associations, based on the transect unit in which birds were located, show that these flocks were formed with equal regularity in both habitats. Downy Woodpeckers consistently were "absolute followers" (Morse 1970) within these flocks; there were about as many unambiguous cases of warbler following chickadee as vice versa. As with Yellow-rump social interactions, no instances of direct competition for food during mid-winter were noted. This was the case despite the fact that the feeding habits of the chickadees seemed quite similar to that of the warblers. In addition to warblers and chickadees, Common Flickers (*Colaptes auratus*), Downy Woodpeckers, Starlings (*Sturnus vulgaris*), and Tree Sparrows (*Spizella arborea*) fed on bayberry fruit with some regularity.

Six predatory bird species were recorded during each season. Of these the American Kestrel (*Falco sparverius*) and Northern Shrike (*Lanius excubitor*) were seen regularly, with 3 instances each of active pursuit of the warblers during the second season alone. Of these all but one took place in the more open cottonwood area.

DISCUSSION

A large population of Yellow-rumped Warblers remains throughout the winter in the eastern portion of Presque Isle near Erie, Pennsylvania. Such a population is remarkable considering the latitude and the wind chill factor. Probably the most important factor in allowing its presence is the large amount of bayberry. The local distribution of the warblers matches that of the bayberry. Also, during times of heavy snow cover and low temperatures, large numbers of warblers can be found in the area of the highest bayberry density where the warblers concentrated almost totally on bayberry fruit for food. For the bayberry to be used as almost the exclusive food during in-

clement weather, it must be of high nutritional value to support the warbler's high metabolic rate (Emlen 1966). Hausman (1927) reports that the waxy substance on the bayberry is a fat composed of glycerides of steric, palmitic, myrtistic, and oleic acids. Also, the berry contains traces of protein and carbohydrate.

Apparently heavy snow, by eliminating feeding on the ground and at the base of trees and shrubs, makes the cottonwood-bayberry area the most efficient one in which to forage. Without snow, even when bayberries were abundant, this area was little used. Gottfried and Franks (1975) reported substantial shifts in feeding locale of Dark-eyed Juncos (*Junco hyemalis*) with varying weather conditions, especially snow cover (see also Morse 1970, Heppleston 1971, Grubb 1975). Heavy snow occurred fairly late in the season when the invertebrate supply was likely depleted by earlier foraging activity (see Gibb 1960). It is possible that similar weather conditions earlier in the winter would not have produced the same shift.

Feeding away from the cottonwood area (mainly in the pines) has several advantages. One is a greater protection from predators. Indeed, the constant movement and lack of a small home range may in itself serve as a defensive mechanism (e.g., Gibb 1960). A greater protection from the wind is also important (Gottfried and Franks 1975). Also, in the pines feeding behavior was very diversified. Thus, it is probable that a greater variety of foods was taken, allowing for better nutritional balance. Morse (1970, 1971) has referred to the foraging plasticity in this species.

During both seasons the bayberry numbers on the branches were very low by early February even in the best areas. Probably a good proportion of this loss can be attributed to the "harvesting" by birds. There appears to be a small margin of error, at least so far as bayberry as a food resource is concerned. Gibb (1954, 1960) also reported a substantial decline in food availability by late winter. Pulliam and Enders (1971) reported it probable that 75% or more of the total seed crop was eaten by finch species in central North Carolina during a typical winter. West (1967), on the other hand, found that a much smaller proportion of available food was required by wintering Tree Sparrows in Illinois.

The benefit of interspecific flocking has been the subject of much attention (Wilson 1975). In our case protection from predators would appear to be an important biological advantage, since much foraging must be done in the open. Siegfried and Underhill (1975) have recently shown experimentally the importance of numbers in detecting predators. Several authors (Morse 1970, Austin and Smith 1972, Kricher 1975) report that members of the genus *Parus* form the nucleus to which other species are drawn. This was not the case in our study; chickadees often were seen following the warblers.

A possible reason for this is the dominance in numbers of the warblers. Our data are also at variance with reports of substantial fighting amongst individuals of a flock, and the resulting partitioning of food niches (Morse 1967, 1972). Our data agree more with that of Pulliam and Enders (1971) who found substantial overlap in food use among finch species and Austin and Smith (1972) who found very low levels of aggression in flocks of wintering birds in southern Arizona.

SUMMARY

The Yellow-rumped Warbler (*Dendroica coronata*) is a common winter resident on Presque Isle, a peninsula jutting into Lake Erie, Pennsylvania. This population was studied during the winters of 1974–75 and 1975–76 with the intent of exposing the factors which enable the warblers to remain this far north. Foraging behavior was found to be highly diversified and habitat selection was strongly influenced by weather variables and food accessibility. Bayberry was found to be the major food resource during periods of inclement weather. Though numbers fluctuated greatly in the study areas, the warblers remained on the peninsula throughout the winter. They were normally in flocks, which regularly included several other species.

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