

AGE-RELATED MIGRATORY BEHAVIOR OF WARBLERS¹

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Many observers of autumn passerine migration have noted a high percentage of immature birds on the oceanic coasts of North America, and this has been termed the "coastal effect" (Ralph, 1975). The proportion of young on coasts is generally over 85-90%, whereas proportions at inland sites usually are about 65-75% (summary in Ralph, 1975). Ralph believes the coastal effect reflects concentrations of inexperienced birds beyond the edges of the species' regular overland migration routes, and that high proportions of young should also be found at the inland edges of these routes. Murray (1966, 1976), although agreeing that most passerines have overland migration routes, believes that normal proportions of adults and young should be found along the coasts. The coastal effect, in his view, is caused by different behavior of adults and young when they return to land after finding themselves over the ocean at the end of a nocturnal migratory flight. Young birds are thought to stop at the first available landfall, whereas adults are more likely to land farther inland (Murray, 1966).

Age ratio data collected around the Great Lakes should help resolve this disagreement because the lakes represent large inland "oceans" that might also cause differential migratory behavior of age classes. The lakes are unlikely to be on the edge of the migration routes of most eastern passerines whose ranges extend well to the west, removing this as a possible explanation of generally high percentages of young which might be found there.

Long Point Bird Observatory (LPBO) is suitably located for collection of Great Lakes age ratio data (Fig. 1). A 33-km peninsula extending from the north shore of Lake Erie, Long Point's eastern tip is 25 km from the northern and 35 km from the southern shores of the lake. LPBO personnel have aged birds at two banding stations on the point since 1965, and at a location 5 km from the shore since 1974. This paper analyzes LPBO's autumn data for 15 species of warblers, as well as data contributed from various other locations in northeastern North America. The hypothesis proposed here is that high percentages of young migrant warblers at coastlines can, at least for the lower Great Lakes, be explained as resulting from differential behavior of adult and immature birds. In addition, lighted man-made structures apparently affect age-related migratory behavior.

METHODS

Table 1 lists the sites from which data were collected. Sites were arbitrarily considered "inland" if they were 5 km or more from a shoreline, because examination of the results showed that high percentages of

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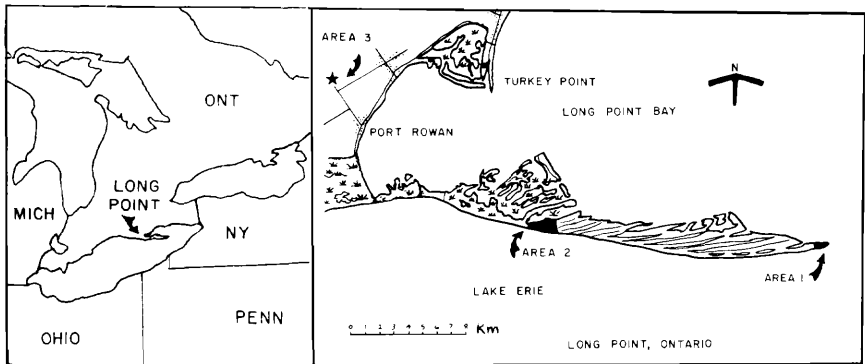


FIGURE 1. Long Point, Ontario, showing the location of the Long Point Bird Observatory's banding stations at the eastern tip of the point (Area 1), midway along the point (Area 2) and on the mainland (Area 3).

young disappeared at very little distance from a coastline. Samples of birds banded at the Long Point lighthouse during the night were combined with those of birds killed. These birds were caught by hand as they fluttered against the light, at the same time that others were being killed by impact (see Hussell, 1969, for further description).

All ages were determined by checking the degree of skull ossification, which separates young of the year from adults (Norris, 1961). Data from LPBO and Leberman and Clench (1969, 1972) show that, in the species covered by this paper, the two age classes migrate more or less synchronously. Thus, the data were considered not to be seriously biased by occasionally interrupted coverage at the contributing banding stations. Ages of birds killed at man-made structures were also considered to be unbiased, because the kills probably occur more or less randomly throughout the migratory season. All the banding stations included began regular autumn coverage by the end of August, and most began early in the month.

Levels of significance of difference between proportions of young in different samples were calculated according to Chi square tests with correction for continuity (Snedecor and Cochran, 1968). "Significant difference" in the text refers to significance at the 5% level or better.

Throughout the paper, abbreviations used for species names are those used by the Long Point Bird Observatory in its banding records (see Table 2).

In comparing age ratios from inland and coastal banding stations and from kills at lighted man-made structures (Fig. 5), all data for a species were combined for each type of site, thus lending most weight to the largest samples. Data from Ralph (1975) and Table 2 show no clear separation of age ratios according to type of location. Part of this is probably real; that is, certain locations may always get a higher or lower

TABLE 1.
Sources of age ratio samples.

Location	Years in sample	Source
Coastal banding stations		
1. Long Point, Ont. (eastern tip)	1965-1977	Long Point Bird Observatory
2. Long Point, Ont. (midway on point)	1965-1977	Long Point Bird Observatory
3. Prince Edward Point, Ont.	1977	Kingston Field Naturalists
4. Presque Isle, PA	1975-1978	Ronald and Mary Leberman
5. Monomoy Island, MA	1956-1970 (intermittent)	Ralph (1975)
6. Manomet, MA	1970-1973	Ralph (1975)
7. Island Beach, NJ	1963	Ralph (1975)
Inland banding stations		
8. Port Rowan, Ont.	1974-1977	Long Point Bird Observatory
9. Aberfoyle, Ont.	1973-1976	A. D. Brewer
10. Grant County, WV	1977	G. A. Hall
11. Rector, PA	1961-1973	Ralph (1975)
12. Carlisle, PA	1973-1975	Ralph (1975)
13. Sudbury, MA	1962-1966	Ralph (1975)
14. Littleton, MA	1966-1970 (intermittent)	Ralph (1975)
15. Ashby, MA	1971	Ralph (1975)
Nocturnal kills		
16. Illinois (various TV towers)	1958-1960, 1962 and 1972	Graber and Graber (1962) and R. R. Graber (pers. comm.)
17. Long Point, Ont. (coastal lighthouse)	1965-1977	Long Point Bird Observatory
18. Nanticoke, Ont. (coastal lighted stack)	1972 and 1977	Long Point Bird Observatory
19. Kingston, Ont. (coastal lighted stack)	1973, 1974 and 1977	Kingston Field Naturalists
20. Youngstown, OH (TV tower)	1974-1976	Carnegie Mus. Nat. Hist.
21. Boylston, MA (TV tower)	1970-1972	Ralph (1975) and pers. comm.
22. Boston, MA (coastal lighted building)	1969-1970	Ralph (1975) and pers. comm.

percentage of young than others, and some species likely will not conform to the pattern of high percentage of young at coasts and lower at inland sites. But at least some of the variation in age ratios must be due to annual differences. For example, the percentage of young Yellow-rumped Warblers at Long Point varies markedly from year to year, sometimes significantly so (Table 3). Similar results are noted for other species. In addition, certain weather conditions may bring large influxes of birds of unusual age ratios (Stewart et al., 1974). Because many of

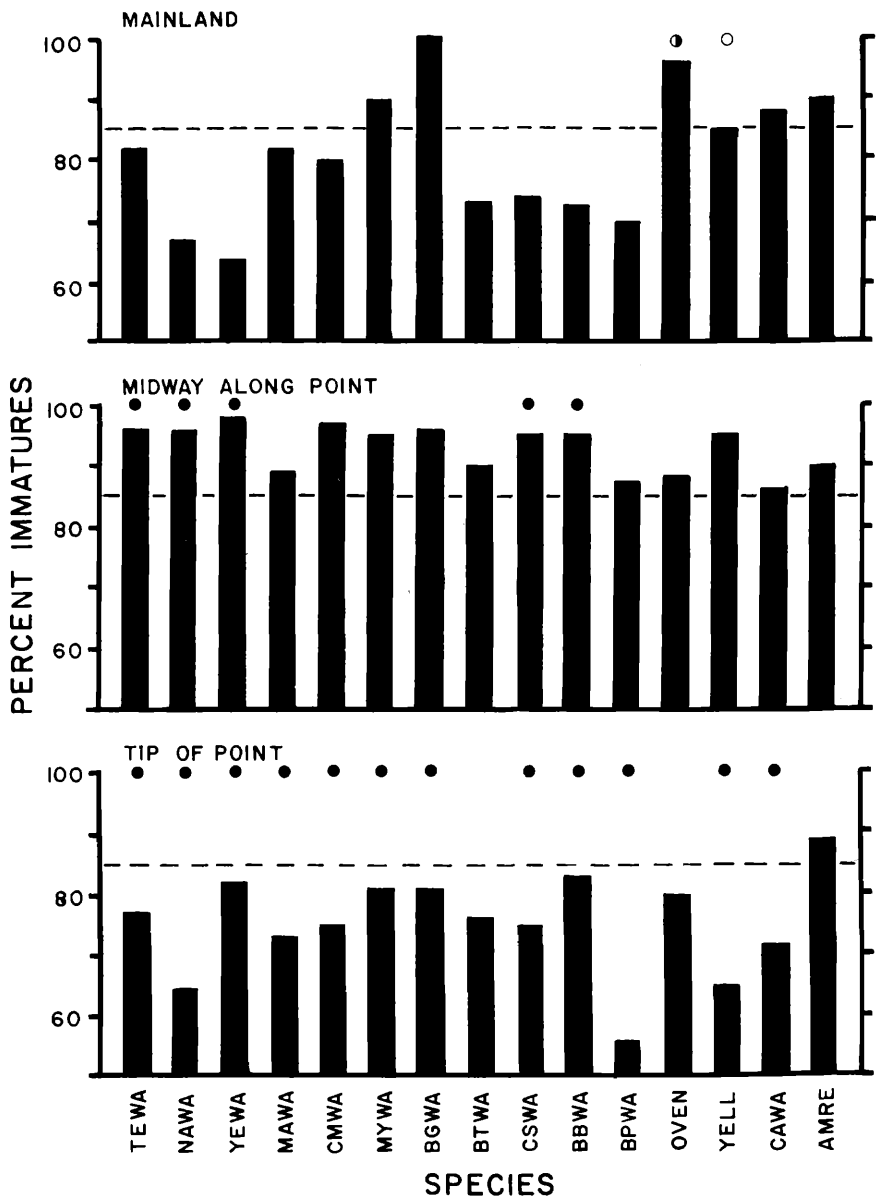


FIGURE 2. Age ratios of warblers at LPBO's three banding stations (see Fig. 1). Dots indicate significant differences between the age ratios above and below (the two at the top of the figure show differences between the inland station and that at the tip of the point). Significance levels of 0.5, 1 and 5% are indicated, respectively, by solid, half-solid and open circles. The dashed line gives the approximate level above which an age ratio is believed to show a coastal effect (85%). For sample sizes and species codes, see Table 2.

TABLE 2.
Continued.

Species and code (see Figs.)	Location (see Table 1)																					
	Coastal stations ¹						Inland stations ¹						Nocturnal kill sites									
	1	2	3	4	8	9	10	16	17	18	19	20	21	22								
Chestnut-sided Warbler <i>D. pensylvanica</i> CSWA	75.0 (96)	94.7 (75)	90.7 (129)	90.5 (21)	73.9 (46)	100.0 (13)	88.2 (51)	9.1 (33)	44.7 (85)	54.7 (64)	86.5 (89)	60.0 (25)	66.7 (3)									
Bay-breasted Warbler <i>D. castanea</i> BBWA	83.2 (220)	95.3 (593)	85.3 (347)	61.6 (185)	72.1 (43)	97.4 (38)	71.7 (508)	23.9 (67)	50.2 (275)	75.9 (116)	62.7 (308)	63.0 (81)	88.9 (9)									
Blackpoll Warbler <i>D. striata</i> BPWA	55.4 (918)	87.0 (460)	67.8 (152)	58.5 (94)	70.0 (20)	100.0 (8)	46.9 (1,088)	57.1 (7)	53.7 (473)	66.1 (59)	30.8 (13)	61.5 (52)	36.9 (149)	90.0 (10)								
Ovenbird <i>Seiurus aurocapillus</i> OVEN	80.3 (127)	87.7 (106)	88.3 (60)	75.0 (64)	95.7 (70)	100.0 (1)	52.1 (219)	45.6 (342)	78.2 (119)	59.7 (243)	49.0 (61)	41.0 (89.5)										
Common Yellowthroat <i>Geothlypis trichas</i> YELL.	64.6 (209)	94.7 (38)	76.5 (17)	0 (3)	84.8 (33)	100.0 (3)	31.0 (29)	58.6 (401)	78.2 (202)	85.3 (204)	73.5 (34)	45.5 (22)	75.0 (4)									
Canada Warbler <i>Wilsonia canadensis</i> CAWA	71.9 (224)	85.9 (163)	72.9 (107)	90.0 (11)	88.4 (43)		38.9 (18)	78.7 (75)	100.0 (1)	14.3 (7)												
American Redstart <i>Setophaga ruticilla</i> AMRE	89.1 (192)	89.8 (167)	88.6 (177)	75.0 (8)	90.0 (30)	71.0 (100)	7.2 (69)	45.7 (81)	67.8 (149)	74.3 (136)	68.8 (16)	45.8 (59)	55.6 (9)									

¹ Data for locations 5-7 and 11-15 can be found in Ralph (1975). Locality 21 (Boylston, MA) has been removed from Ralph's "coastal plain" group (13-15) and 22 (Boston, MA) from his "coastal" group (5-7), because they represent nocturnal kill sites rather than banding stations.

² Percent hatching-year (HY) birds.

³ Number aged in parentheses.

⁴ Data collected at Morgantown, WV. Includes data for 1967-1977.

TABLE 3.

Annual variation in percentage of immature Yellow-rumped Warblers banded at the eastern tip of Long Point.

Year	Number banded	Percent immature ¹
1965	161	84
1966	97	86
1967	188	83
1968	210	74*
1969	98	65*
1970	44	91***
1971	19	100
1972	73	70*
1973	10	70*
1974	—	—
1975	38	84
1976	103	86
1977	77	96

¹ Significant differences between years are indicated as * ($P < .05$) and *** ($P < .005$).

the sample sites contributed data for one or only a few years, and because the larger samples tended to come from stations with most years covered, combining data from all stations of a given type, weighted by sample size from each, should give the best "average" percentage of immature birds for that type of station.

RESULTS

Age data for LPBO's three banding stations on Lake Erie are shown in Figure 2. The relatively small samples (Table 2) for LPBO's mainland site indicate that 9 of the 15 species analyzed have "low" percentages of immature birds (<85–90%) suggesting that it should be classified as an inland site. The station midway along the point, however, shows high percentages of young birds in all 15 species, 5 of them significantly higher than at the inland location, in spite of smaller sample sizes there. Thus, this site appears to exhibit a classic coastal effect, and we would expect similar percentages at the eastern tip of the point. As is obvious from Figure 2, however, age ratios from the tip of the point are similar to those inland. Because of the larger sample sizes involved, more of the age ratios from the tip of the point are significantly different from the percentages midway along the point (12 of 15). For most species (13 of 15), the age ratios from the tip of the point do not differ significantly from those at the inland site, reinforcing the conclusion that the mainland site and the tip of the point both show typical "inland" ratios, while the station midway along the point truly shows a coastal effect.

It is noteworthy that Ovenbird and Common Yellowthroat are the two species for which the proportions of immature birds at the mainland station are significantly higher than at the tip of the point. Both of these

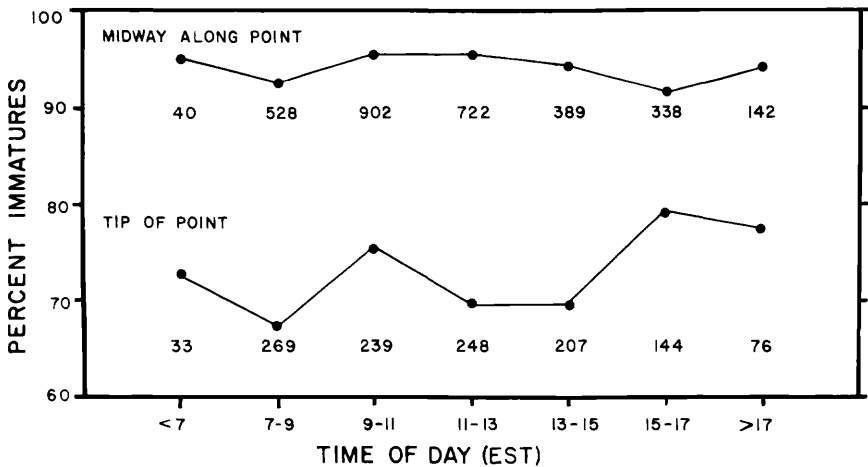


FIGURE 3. Percentages of immature warblers at LPBO's two coastal banding stations according to time of day (EST). Data for nine of the most commonly banded warblers were combined for the years 1975-1977. Species represented are TEWA, NAWA, MAWA, CMWA, MYWA, CSWA, BBWA, BPWA and YELL (see Table 2). Sample sizes are given under each point.

breed in the vicinity of the mainland site, and the age ratios may, therefore, be biased away from those in the migrant population. Of the three species whose age ratios do not differ significantly between the two coastal stations on Long Point, one (Black-throated Blue Warbler) is represented by small sample sizes, and the others (Ovenbird and American Redstart) are, again, local breeders. These complications, combined with those discussed in the methods, suggest that analysis of age ratios for a small number of species or from small sample sizes may give misleading results.

Two possible interpretations emerge for the LPBO age ratio data. The high percentage of young birds midway along the point may be anomalous, an artifact of the particular geography of Long Point, such that no true coastal effect exists. Alternatively, the results from the tip of the point may be the ones needing explanation. At the station midway along the point, a common observation of banding personnel (including the authors) is that birds seem to be moving through the area from east to west, often not appearing in large numbers until mid-morning. Perhaps birds land along the point in "normal" proportions (i.e., those typical of inland areas), but young birds move along the point during the day, swamping the numbers of adults remaining in any one area.

To test this hypothesis, age data from both stations on the point were divided into time periods throughout the day. If movements by young birds were swamping adults midway along the point, we would expect normal proportions of young there early in the morning, and high pro-

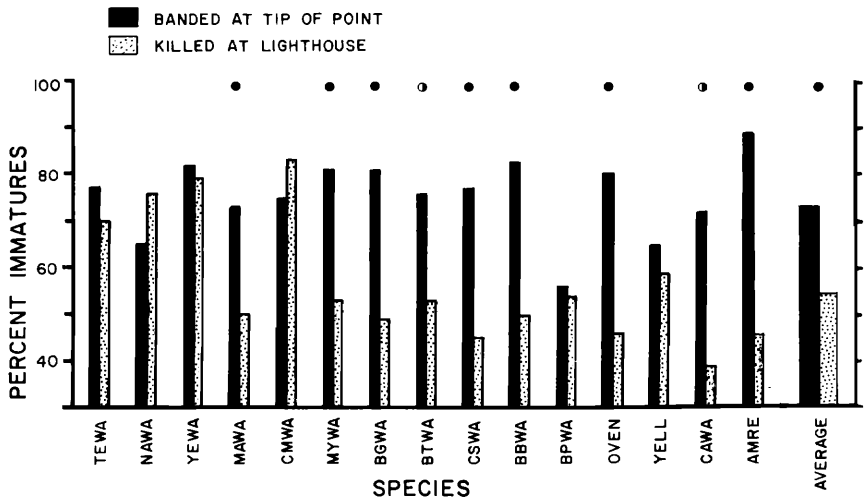


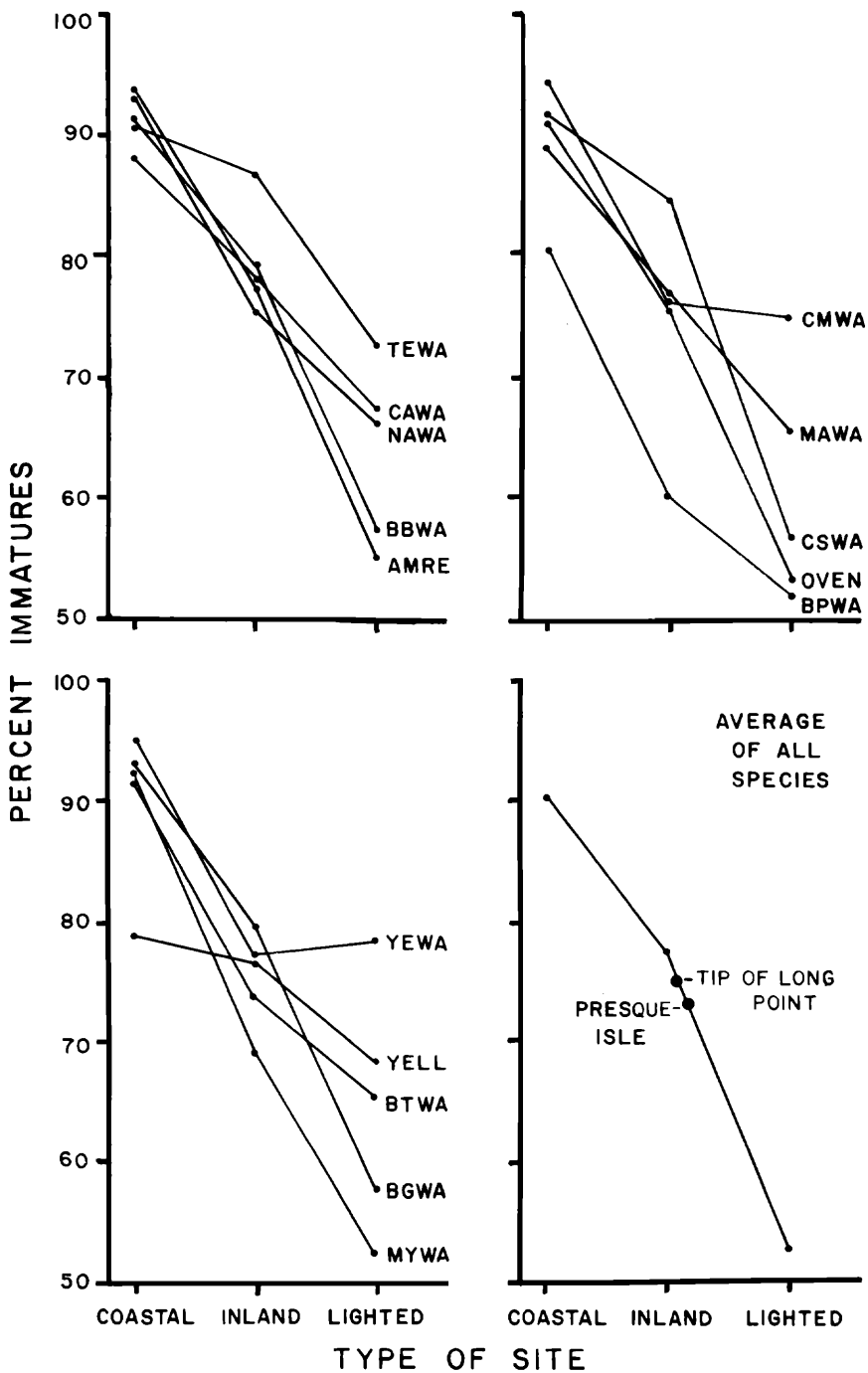
FIGURE 4. Percentages of immature birds caught at the banding station at the tip of Long Point (solid bars) compared to those from the sample killed or banded at the lighthouse at night (shaded bars). Significant differences between bars for each species are indicated as in Fig. 2. See Table 2 for sample sizes and species codes.

portions later. As is shown in Figure 3, this does not occur. Instead, the percentages at both sites are relatively stable throughout the day. Sample sizes for individual species were small, but because each species showed a similar pattern of age ratio with time, data for all species were pooled. Apparently the proportion of young increases at the tip of the point later in the day, but the percentage of young in the first three time periods of the day does not differ significantly from that in the last three periods. The increase results mainly from the capture of high proportions of young Yellow-rumped Warblers late in the day. (This species is probably more of a diurnal migrant than the others; Ralph, pers. comm.).

Apparently then, mainly immature birds land on the greater part of Long Point at the end of a migratory flight. Any birds moving west during the day are proportionally no different in age than the ones that originally landed at the station midway along the point. The question, then, is why the tip of the point does not also show the expected high percentage of immature birds.



FIGURE 5. Average percent immature warblers at inland and coastal banding stations and from kills at lighted man-made structures (see methods). All sites in Table 1 are included except the banding stations at the tip of Long Point and at Presque Isle, PA. The averages for all species at these two localities are shown against the unweighted averages for all other sites.



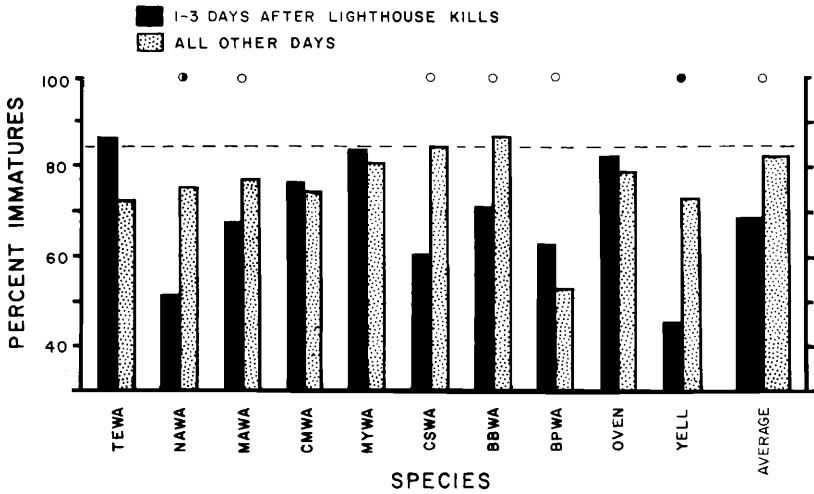


FIGURE 6. Percentages of immature birds banded at the tip of Long Point 1 through 3 days after a lighthouse kill (solid bars), compared to those from birds banded on all other days (shaded bars), 1965–1977. Significant differences between bars for each species are indicated as in Fig. 2.

The main feature of the eastern tip of Long Point which differs from every other place is the presence of a lighthouse. A comparison of the age ratios of birds killed at the lighthouse (or banded there during the night) with those from the regular banding station showed that, in 9 of 15 species, the lighthouse samples had significantly lower percentages of young birds than did those caught during regular banding. None had a significantly higher percentage of young (Fig. 4). The average for all 15 species (weighted by sample size) also showed significantly more adults in the killed sample. Data from other banding sites and tower kills (Table 1) indicate that the Long Point lighthouse is not peculiar in this regard, but that birds killed at lighted structures in general have the lowest percentages of immatures found anywhere (Fig. 5; see also Tordoff and Mengel, 1956; Johnston and Haines, 1957; Brewer and Ellis, 1958; Goodpasture, 1963; Taylor, 1972, 1973). Data from the banding station at the tip of Long Point, however, are very different than would be expected for a coastal station. Our conclusion is that the presence of the lighthouse alters the behavior of the migrants such that adults are more likely to be captured there than at a normal coastal banding site.

Possibly the lighthouse could alter age ratios only under certain conditions. For example, high percentages of young birds might be banded on most days, but when weather conditions are of the kind that cause migrants to be killed at the lighthouse, large “falls” of adult birds might occur. This would obscure the normally high percentage of young.

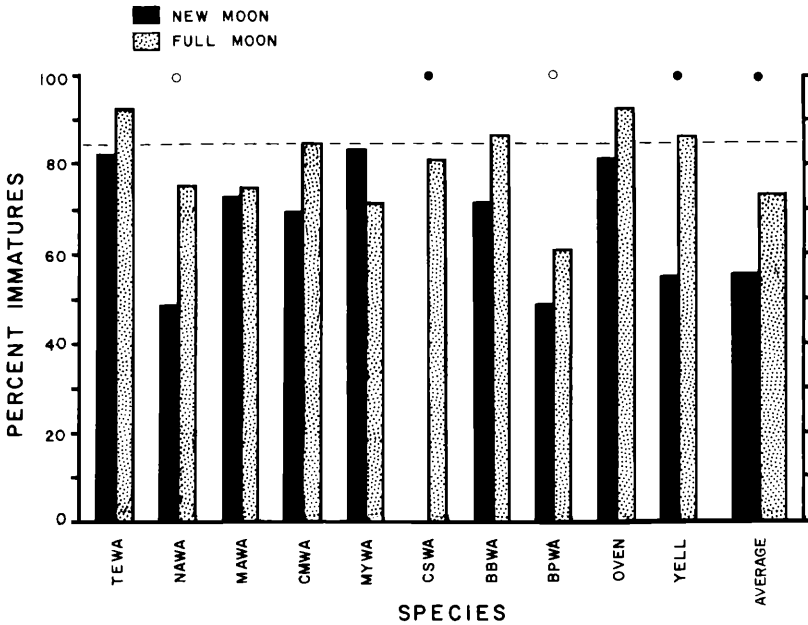


FIGURE 7. Percentages of immature birds banded at the tip of Long Point in the 5-day periods surrounding a new moon (solid bars) compared to those from periods of full moon (shaded bars), 1965–1977. Significant differences between bars for each species are indicated as in Fig. 2.

To test this possibility, the sample of birds banded in regular operations at the tip of Long Point was divided into birds banded 1–3 days after a lighthouse kill and birds banded on all other days. (A similar test was done comparing the first day after kills to all other days, but the split described here gave higher significance levels with similar overall results.) For half of the species analyzed, significantly more adults were caught in the three days after lighthouse kills than on other days (Fig. 6). One species, Blackpoll Warbler, shows a significant trend in the opposite direction, but the overall results suggest that the lighthouse does tend to attract adults at certain times more than at others.

Most bird kills at electrical generating station stacks in Ontario occur on moonless nights (D. Broughton, pers. comm.), so perhaps darkness rather than poor weather alone causes migrating adult warblers to land near the lighthouse. Figure 7 shows the age ratios of warblers banded during 5-day periods at the time of new moon versus those banded at the time of full moon. Four of the 10 species showed significantly more adults in the dark periods, as did the weighted average for all 10 species. During periods of full moon, half the species showed more than 85% immatures, similar to the age ratios found midway along the point.

This analysis was necessarily crude, not taking into account time of

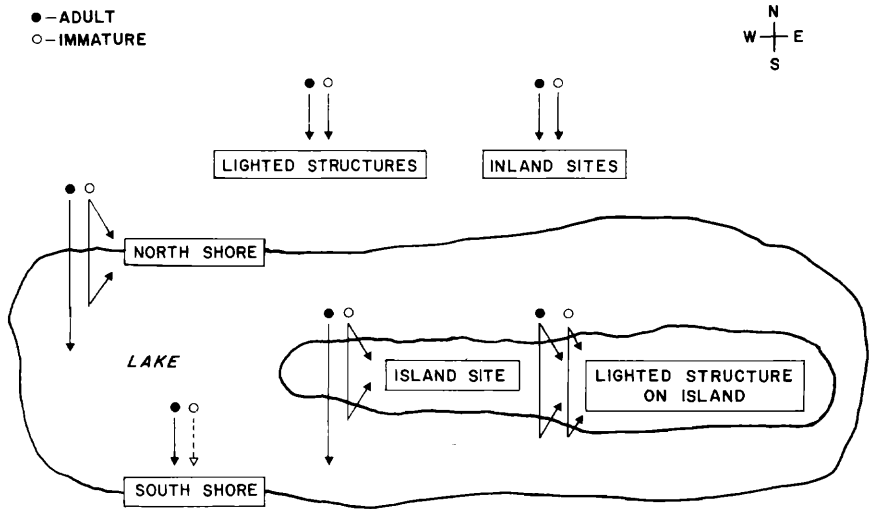


FIGURE 8. Illustration of our hypothesis to explain age ratios around the lower Great Lakes. Solid and open circles represent adult and immature birds, respectively, whereas the arrows denote the hypothesized direction of movement during migratory flight.

moonrise and moonset or other factors, such as weather, contributing to overall darkness. Nonetheless, the evidence presented in Figures 4, 6, and 7 suggests that the unexpectedly high proportion of adults captured at the tip of Long Point results from influxes of adults under certain conditions. Because darkness is involved in attracting adults, the lighthouse is implicated as the feature causing the adults to alter their migratory behavior.

DISCUSSION

The pattern of age ratios documented here can be summarized as follows. Lighted structures normally kill a relatively low percentage of young birds, whereas inland banding stations yield samples with low or moderate percentages. Coastal age ratios vary according to location. In most cases (on the north shores of the lower Great Lakes and on islands or peninsulas such as Long Point), normally a high percentage of young birds is found. Near lighted structures, however, the percentages of young drop. Although only one rather small sample is known from the south shore of Lake Erie, apparently a relatively low percentage of young birds also occurs there (see Presque Isle, Fig. 5).

Although this summary is based in some cases on rather few data, assume that it shows the true pattern of age ratios around the Great Lakes. What is the best explanation? Our hypothesis, illustrated in Figure 8 and outlined below, is followed by further details and suggestions of tests which could be made to verify it.

1. At inland banding locations and in lighted man-made structure kills, age ratios approximate true ratios in the migrating population.

2. On the north shores of the lower Great Lakes, immature birds are more likely than adults to hesitate at flying over the lakes and/or are more likely to turn back and land on the shore if they find themselves over water at the end of migratory flight. The same situation holds for islands or peninsulas out in the lake. Adults are more likely to fly on to the south shore, and this is why a relatively low percentage of immatures is found there.

Farther inland from the south shore, we would expect normal inland ratios. Most young birds probably cross the lakes normally, and it may be only those birds caught over water at the end of a migratory flight that cause the anomalies in shoreline age ratios.

3. At a lighted structure on a northern shore or on an island, adults behave as if the site were inland (although this may occur only under certain conditions of weather and moon phase). That is, adults are likely to land near the light rather than continue on to the south shore of the lake. This would explain the moderate to low percentages of young found in the banding sample from the eastern tip of Long Point.

Although lighted structures, on the average, show lower percentages of young than elsewhere (Figs. 4, 5), we have suggested that both inland banding samples and tower kills represent approximately "true" age ratios. This is because the ranges in age ratios from these sites overlap (Table 2). It is possible, however, that inland banding samples really do have consistently higher percentages of young birds than samples from tower kills. To demonstrate this possibility, samples from inland stations would have to be taken in the same years as at inland lighted structures, from areas far enough away not to be influenced by the light but close enough to be sampling the same population of migrants. If a consistent difference were found, we would have to hypothesize either that adults are preferentially attracted to lighted structures, or that immatures are easier to capture in regular banding operations. At present insufficient data are available to speculate further on these possibilities.

Point 2 of our hypothesis, suggesting differential behavior of adults and immatures when faced with large bodies of water, could be strengthened with more data, particularly from the southern shores of the Great Lakes. In addition, it might be possible to use a ceilometer at northern shores to determine whether some birds actually turn back towards land at the end of a migratory flight, and whether some go farther inland than others, as predicted by Murray (1966). (The fact that an apparent concentration of adults occurs on the south shore of Lake Erie, however, suggests that adults also stop at the first available land.)

Our third point, on the possible effects of lighted structures on adult behavior, should be tested with controlled laboratory experiments. Ralph (1978) and others (Emlen, 1967) have found that sky glow alters preferred migratory direction of some species in cages, although this

effect is not found in certain radar studies (T. Williams, pers. comm.). Further investigation of this topic might prove fruitful.

Although this paper contends that the coastal effect on the Great Lakes is caused by differential behavior of adult and young birds when faced with large bodies of water, it does not mean that the high percentages of immatures along oceanic coasts occur for the same reason. Ralph (1975) believes that the Atlantic coast is the edge of most species' migration routes, and that birds caught there are off course and, therefore, likely to be immatures. Murray (1966) feels the explanation is similar to ours for the Great Lakes, although his views differ in detail. The crux of the difference between Murray's and Ralph's hypotheses is that Murray believes that adults regularly fly over coastal areas, although not captured there in proportion to their true numbers, whereas Ralph feels that adults of most species simply are not present over coastlines. Examination of age ratios of birds landing on ships or islands offshore will not resolve the question, because our data have shown that even when adults are present, they may not land at such sites. If lighted man-made structures, however, kill samples of birds actually migrating, then tower kills from along the oceanic coasts might show whether adults are normally there in migratory flight. The one sample available for warblers, from the Prudential Tower in Boston, MA (Table 2), has far too few birds in it to support any conclusions, although other species present (largely sparrows) show a high percentage of immatures.

Considering the large numbers of people banding birds and collecting tower kills (Weir, 1976), it is regrettable that so few reliable age data are available to test the hypotheses discussed in this paper. We urge people to make accurate age determination a routine part of their field procedure.

SUMMARY

Age data for 15 species of warblers from Long Point, Ontario and from other sites throughout northeastern North America were analyzed. The results suggest that immature warblers are more likely than adults to turn back to the nearest land when finding themselves over the Great Lakes at the end of a migratory flight, and/or are more likely to hesitate at starting off over the water. It cannot as yet be determined whether high percentages of immatures at oceanic coasts can be explained in the same manner. Adult birds figure more prominently in samples of birds killed at lighted structures than elsewhere, and apparently land near them after migratory flight even if at a coastal site, in contrast to the behavior hypothesized at coastal areas with no lights. This behavior is more obvious in conditions of darkness (poor weather and no moon). Further tests of these hypotheses are suggested. Controlled experiments of the effects of lights on migration might prove particularly interesting.

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