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AGE RATIOS AND THEIR POSSIBLE USE IN DETERMINING AUTUMN ROUTES OF PASSERINE MIGRANTS

C. JOHN RALPH

A principal interest of early students of passerine migration was the determination of direction, location and width of migratory routes. In such studies, it was presumed that an area where the species was most abundant was the main migration route. However, during fall, passerine migrants tend to be silent and inconspicuous, rendering censusing subjective at best. Species also differ in preferred habitat, affecting the results of censuses and the number captured by mist netting. In this study, I used the abundance of migrants with another possible criterion, their age ratios, in order to hypothesize possible migratory routes.

Based upon information about species abundance in different areas, a lively debate sprang up in the past between a school favoring narrow routes and one advocating broad front migration. The former suggested that birds followed topographical features ("leading lines") such as river valleys, coast lines and mountain ranges (Baird 1866, Palmen 1876, Winkenwerder 1902, Clark 1912, Schenk 1922). The latter group proposed that a species migrated over a broad geographical area regardless of topographical features (Gätke 1895; Cooke 1904, 1905; Geyr von Schweppenburg 1917, 1924; Moreau 1927). Thompson (1926) and later Lincoln (1935), suggested that both schools were probably right, depending upon the species involved. Early ornithologists were possibly misled because of the differences between easily observable (and often narrow front), diurnal migration and less obvious, but probably more common, nocturnal movements. A species could participate in both and yet be considered only a narrow front, diurnal migrant.

In the last 50 years, the dichotomy was apparently resolved with narrow routes being generally ascribed to diurnal migrants following topographical features, and broad routes ascribed to migrants moving at night, ignoring topographical features (Moreau 1961, Dorst 1962). This view, however, is by no means unanimous (cf. Van Dobben 1935, Deelder 1949). Indeed, Phillips (1951), King et al. (1965), Clench (1969) and Leberman and Clench (1975) have suggested that populations, as well as different age and sex classes of some nocturnal migrants, follow different routes.

On the basis of radar observations, Drury and Keith (1962) have divided fall nocturnal land bird migrants on the Atlantic coast into 2 groups. They suggest that most migrate southwest on a broad front over land, while a few species fly over water from the Atlantic coast of North America to

South America. Among the passerine migrants, only the Blackpoll Warbler (*Dendroica striata*) is known to use this second route (Nisbet et al. 1963, Nisbet 1970).

The "coastal effect."—Interest in age ratios of birds captured during fall migration has focused on the 85–95% incidence of young of most species on the Atlantic coast (Robbins et al. 1959, Drury and Keith 1962, Murray 1966), as compared to 65–70% inland (Nisbet et al. 1963; Barry 1970; Leberman and Clench 1972, 1973). Similarly, high numbers of young prevail on the Pacific coast (Ralph 1971, Stewart et al. 1974). I shall refer to this high percentage of young as the "coastal effect." In Europe, despite much fieldwork, the coastal effect is reported only in passing by Williamson (1959) and Evans (1968).

King et al. (1965:497), Barry (1970) and Leberman and Clench (1975:10) have suggested that the age classes follow different routes, the adults inland, the young along the coast. In view of the substantial number of young inland, even in species with a coastal effect, this interpretation must be incorrect for most species. Most young migrate inland (Ralph 1975). An alternate hypothesis, that high percentages of young denote the periphery of a species' migration route, is a major thesis of this paper.

Use of age ratios.—The rationale for this latter hypothesis is as follows. I assume that a species' main routes are adaptive and take the birds through the most congenial habitats to the most salubrious wintering grounds. Assume then that individuals straying from main routes (see Ralph 1978) will suffer a higher mortality rate than those following them. The next year, strays either will have perished or perhaps have learned a more appropriate orientation. Therefore, by their second fall migration, relatively few individuals should be wandering from the mainstream of the routes. Those individuals at the periphery of routes should be almost entirely young birds on their first trip.

If the coast (with high percentages of young) is the edge of a route, then areas with relatively low percentages of young should represent the actual routes that the species used. In this study, I document age ratios and abundances of migrants and recognize 5 main patterns.

Age ratios from more than 1 site have been compared in the past, giving a geographical perspective (Drury and Keith 1962; Nisbet et al. 1963; Johnson 1965, 1970, 1973; Stewart et al. 1974; Robbins 1976). These authors had few data from sites at any sufficient distance from coasts, and none postulated routes based on age ratio data.

MATERIALS AND METHODS

Sites and species involved.—Data were obtained from records of mist netting and collections of nocturnal migrants killed by colliding with man-made structures (Table 1 and Fig. 1). Certain sites in Massachusetts (Fig. 2) are located on or near the Cape Cod Peninsula,

TABLE 1

LOCATION AND CHARACTERISTICS OF THE SAMPLING STATIONS USED IN THIS STUDY DURING THE FALL MIGRATION

Location	Distance from coast (km)[a]	Source of data	Dates of operation	Type of operation	Additional information
Coastal					
Monomy Is., Mass.	+130	J. Baird (pers. comm.)	1956–70 (21 Aug.–15 Oct., intermittent)	mist nets	
Manomet, Mass.	+60	this study and K. Anderson et al. (pers. comm.)	1970[b]–71 (entire period) (some 1972–73)	mist nets	Manomet Bird Observatory
Boston, Mass.	0	J. Baird (pers. comm.)	1969–70 (entire period)	nocturnal kills at a building	Prudential Center
Island Beach, N.J.	0	B. Murray (1966, pers. comm.)	1963 (2 Aug.–26 Oct.)	mist nets	
Coastal plain					
Sudbury, Mass.	−35	Howard (1967)	1962–66 (1 Sept.–15 Oct., usually)	mist nets	

TABLE 1
CONTINUED

Location	Distance from coast (km)[a]	Source of data	Dates of operation	Type of operation	Additional information
Littleton, Mass.	−50	J. Baird (pers. comm.)	1966–70 (entire period intermittent)	mist nets	
Boylston, Mass.	−60	Baird (1971, 1972)	1970–72 (entire period)	nocturnal kills at a TV tower	
Ashby, Mass.	−80	this study	1971[b] (entire period)	mist nets	Ashby Bird Observatory
Inland					
Carlisle, Penn.	−160	this study	1973–75[b] (1 Sept.–15 Nov.)	mist nets	Reineman Wildlife Sanctuary
Rector, Penn.	−275	Leberman and Clench (1972–73, pers. comm.)	1961–73 (entire period some later)	mist nets	Powdermill Nature Reserve

[a] + indicates east of the coast; − indicates to the west (inland).
[b] Author supervised or made a major contribution of time to operations.

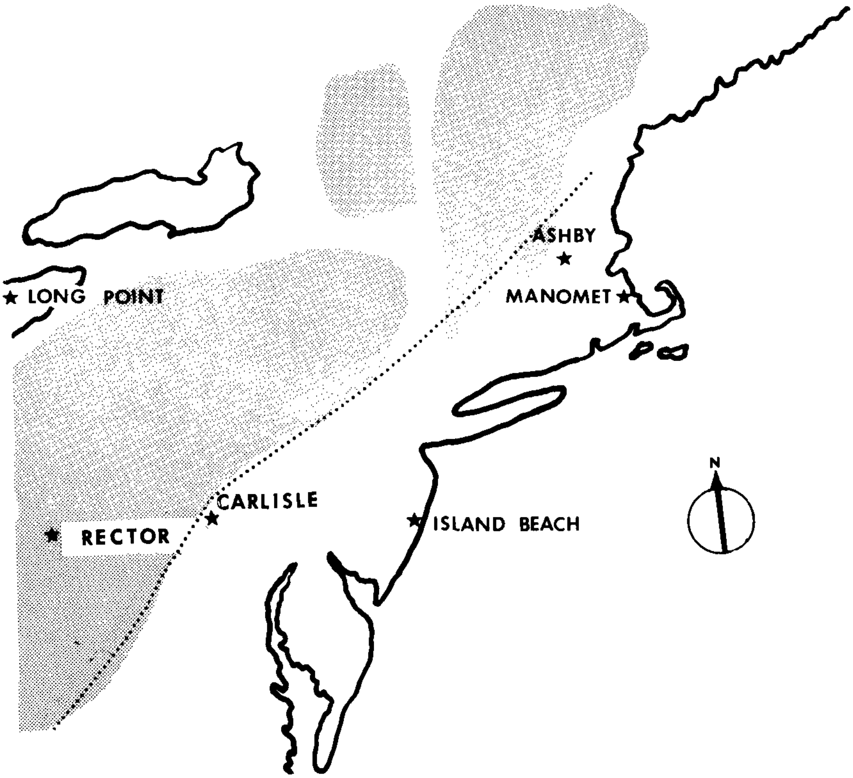

FIG. 1. Map of the northeast United States showing principal sources of data outside of Massachusetts. Shaded areas indicate mountainous regions, and the dotted line indicates the western boundary of the coastal plain.

which extends some 130 km out into the Atlantic. In this study, I consider the Monomoy station to be 130 km beyond the main coast line, Manomet approximately 60 km out, and Boston on the coast line. Carlisle lies at the junction of the coastal plain and the Appalachians and perforce should usually yield age ratios and abundances intermediate between those characteristic of coastal plain stations and those of Rector, the station on the western side of the Appalachians. I considered only those species with samples of $N \geq 20$ in at least 2 locations. On this basis, data for 61 species of autumn migrants (out of a possible 150+) were available, representing 42,219 individuals. The 61 species comprised 90–95% of the passerine migrants.

The period of fall migration was considered to be from 1 August to mid-November. Use of this time period helped to minimize bias caused by including local residents. Some post-breeding wandering occurring in early August is not "true" migration, and usually involves relatively few birds. Such movements are overshadowed by true fall migration (Ralph, unpubl.). Furthermore, many migratory movements begin as early as the first week in August and should be included. Migration occurring after mid-November involves relatively few individuals (Leberman and Clench 1972, 1973, 1975).

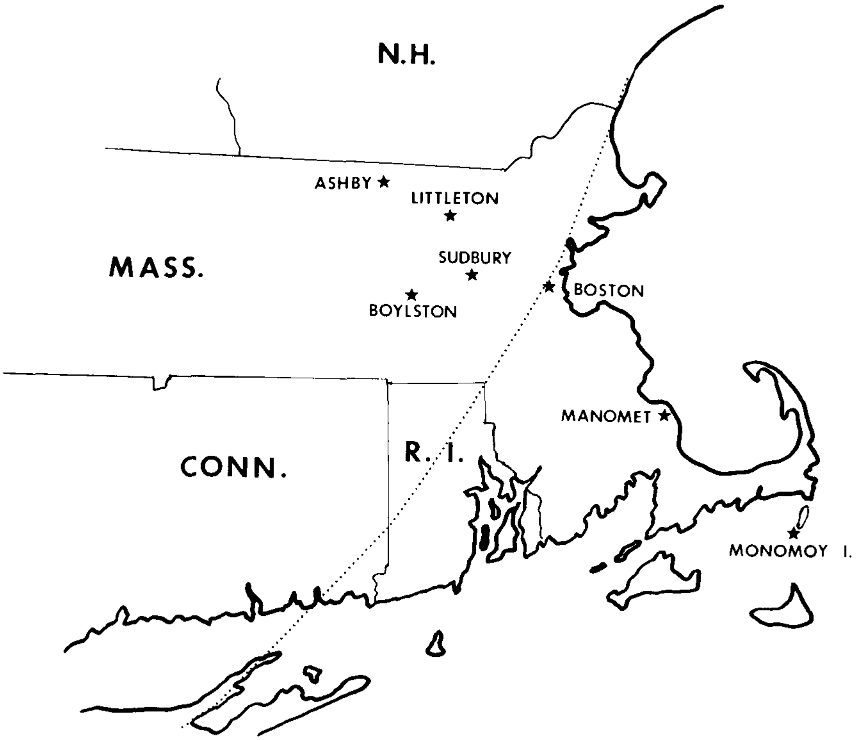

FIG. 2. Map of the stations located in Massachusetts. The dotted line indicates the coast as it is considered in this paper. Stations to the east were considered coastal stations, and those to the west were considered coastal plain stations.

Age ratios, abundances and timing of migration.—Age was usually determined by assessing degree of skull ossification (see Miller 1946, Norris 1961). This technique could be reliably employed through at least mid-November. Age was also determined in a few species on the basis of diagnostic plumage characters (e.g., White-crowned Sparrows [*Zonotrichia leucophrys*]).

Significance levels between percentages of young were calculated using an arcsine transformation (Sokal and Rohlf 1969:607–8). I examined the year-to-year variability of age ratio data at Rector, Pennsylvania, and found that two-thirds of the species vary by less than 10% annually with regard to percentage of young in the sample (Ralph 1975). After 2 years of data collection, more than 95% of the age ratios of all species are within 5% of a long-term (e.g., 10 years) average. I have at least 2 years of data for all but 2 stations; the average was 3.3 years. For rarer species at Rector and Manomet, data from additional years (so labeled in Table 1) were used.

To compare species abundances between sites, I determined the percentage each species comprised of the total number of all passerine birds at that location. At most stations abundance values were calculated on the basis of previously uncaught birds, in order to help eliminate residents. At Rector and Manomet, abundance values were based only on those years in which data from all species were tabulated.

TABLE 2

ASSIGNED ROUTES, PERCENTAGE OF YOUNG, NUMBERS AND PERCENTAGE OF TOTAL OF PASSERINE MIGRANTS

Species name	Diel timing[c]	Rector % young	Rector N	Rector % Σ	Significance[a]	Carlisle % young	Carlisle N	Carlisle % Σ	Significance[a]	Coastal plain % young	Coastal plain N	Coastal plain % Σ	Significance[a]	Coast % young	Coast N	Coast % Σ	Winter range[a]
Broad front migrants																	
Eastern Phoebe	0.20	0.603	214	0.0091	***	0.119	34	0.0084	***	0.728	77	0.0050	***	1.000	186	0.0063	1
Blue Jay	0.00	0.619	86	0.0021	—	—	16	0.0039	—	0.663	216	0.0139	***	0.810	339	0.0114	1
Red-eyed Vireo	0.95	0.631	1015	0.0225	***	0.786	229	0.0563	*	0.680	195	0.0125	***	0.930	612	0.0206	3
Connecticut Warbler	1.00	0.678	118	0.0034	—	—	4	0.0010	—	0.667	27	0.0017	***	0.950	99	0.0033	3
Mourning Warbler	0.88	0.539	143	0.0030	NS	0.591	44	0.0108	—	—	6	0.0004	—	1.000	82	0.0028	3
Canada Warbler	0.75	0.790	224	0.0051	NS	0.773	122	0.0300	+	0.661	84	0.0054	***	0.965	228	0.0077	3
Purple Finch	0.00	0.717	434	0.0066	NS	0.637	32	0.0079	NS	0.707	33	0.0021	+	0.850	174	0.0059	1
Swamp Sparrow	0.70	0.692	1208	0.0319	***	0.183	21	0.0052	***	0.613	53	0.0034	***	0.940	513	0.0173	1
Dark-eyed (Slate-colored) Junco	0.65	0.432	1814	0.0548	***	0.642	132	0.0324	**	0.747	499	0.0321	***	0.971	858	0.0289	1
Field Sparrow	0.36	0.695	1879	0.0609	NS	0.589	52	0.0128	NS	0.703	64	0.0041	***	0.918	282	0.0095	1
White-throated Sparrow	0.69	0.566	2103	0.0592	***	0.464	361	0.0887	***	0.645	656	0.0422	***	0.916	1445	0.0487	1
Fox Sparrow	0.78	0.508	122	0.0044	—	—	3	0.0007	—	0.541	43	0.0028	***	0.980	152	0.0051	1
Tentative broad front migrants																	
Ruby-crowned Kinglet	0.34	0.401	674	0.0411	***	0.188	245	0.0602	***	0.575	400	0.0257	NS	0.533	169	0.0057	1
Yellow Warbler	0.70	0.780	59	0.0017	—	—	0	0.0000	—	0.800	20	0.0013	+	0.932	236	0.0080	3
Song Sparrow	0.62	0.689	2125	0.0746	NS	0.677	42	0.0103	*	0.825	267	0.0172	NS	0.861	697	0.0235	1
Coastal migrant																	
Red-breasted Nuthatch	0.32	—	0	0.0000	—	—	0	0.0000	—	0.937	30	0.0019	***	0.718	732	0.0247	1
Tentative coastal migrant																	
Black-capped Chickadee	0.00	0.898	303	0.0390	—	—	13	0.0032	—	0.923	562	0.0362	*	0.946	4282	0.1443	1

TABLE 2
Continued

Species name	Diel timing[c]	Rector % young	Rector N	Rector % Σ	Significance[a]	Carlisle % young	Carlisle N	Carlisle % Σ	Significance[a]	Coastal plain % young	Coastal plain N	Coastal plain % Σ	Significance[a]	Coast % young	Coast N	Coast % Σ	Winter range[a]
Coastal and coastal plain migrant																	
Tennessee Warbler	0.87	0.949	1616	0.0233	—	0.934	56	0.0138	***	0.732	128	0.0082	NS	0.660	97	0.0033	3
Coastal plain migrants																	
Gray Catbird	0.56	0.862	1271	0.0533	***	0.676	253	0.0622	*	0.774	228	0.0147	***	0.940	2149	0.0724	1
American Robin	0.32	0.927	167	0.0071	—	—	10	0.0025	—	0.524	202	0.0130	***	0.926	1016	0.0342	1
Wood Thrush	0.75	0.879	91	0.0035	+	0.743	32	0.0079	NS	0.790	105	0.0068	***	0.949	79	0.0027	3
Hermit Thrush	0.55	0.937	222	0.0073	***	0.674	25	0.0061	NS	0.751	203	0.0131	***	0.942	294	0.0099	1
Swainson's Thrush	0.87	0.875	527	0.0274	***	0.766	173	0.0425	***	0.555	283	0.0182	***	0.935	602	0.0203	3
Gray-cheeked Thrush	0.81	0.827	127	0.0084	+	0.647	23	0.0057	***	0.443	51	0.0033	***	0.916	155	0.0052	3
Veery	0.94	0.938	32	0.0010	**	0.660	32	0.0079	NS	0.591	77	0.0050	***	0.843	204	0.0069	3
Brown Thrasher	0.00	0.821	78	0.0034	—	—	10	0.0025	—	0.516	25	0.0016	**	0.786	103	0.0035	1
Black-and-white Warbler	0.80	0.875	80	0.0025	*	0.643	26	0.0064	—	0.621	310	0.0199	***	0.868	449	0.0151	2
Parula Warbler	0.88	—	10	0.0002	—	—	4	0.0010	—	0.600	117	0.0075	**	0.807	62	0.0021	3
Magnolia Warbler	0.85	0.818	1258	0.0287	***	0.421	140	0.0344	***	0.674	192	0.0124	***	0.919	296	0.0100	3
Black-throated Blue Warbler	0.95	0.912	57	0.0011	—	0.875	49	0.0120	NS	0.802	140	0.0090	***	0.933	270	0.0091	3
Palm Warbler	0.53	0.920	388	0.0129	—	—	5	0.0012	—	0.787	65	0.0042	***	0.988	479	0.0161	2
Ovenbird	1.02	0.875	255	0.0073	***	0.621	69	0.0170	*	0.773	283	0.0182	***	0.925	308	0.0104	3
Northern Waterthrush	0.76	0.722	187	0.0046	NS	0.737	26	0.0064	**	0.430	54	0.0035	***	0.844	532	0.0179	3
Common Yellowthroat	0.95	0.788	1606	0.0487	*	0.643	57	0.0140	NS	0.533	150	0.0097	***	0.782	836	0.0282	2
American Redstart	0.79	0.849	523	0.0123	**	0.685	47	0.0115	NS	0.653	406	0.0261	***	0.968	721	0.0243	3
Scarlet Tanager	0.90	0.900	251	0.0082	***	0.714	65	0.0160	NS	0.702	45	0.0029	***	0.938	113	0.0038	3
Rose-breasted Grosbeak	0.77	0.774	124	0.0061	NS	0.732	80	0.0197	NS	0.589	22	0.0014	**	0.899	50	0.0017	3
Rufous-sided Towhee	0.21	0.791	492	0.0108	***	0.418	62	0.0152	***	0.709	170	0.0109	***	0.910	304	0.0102	1

TABLE 2
Continued

Species name	Diel timing[c]	Rector % young	Rector N	Rector % Σ	Significance[a]	Carlisle % young	Carlisle N	Carlisle % Σ	Significance[a]	Coastal plain % young	Coastal plain N	Coastal plain % Σ	Significance[a]	Coast % young	Coast N	Coast % Σ	Winter range[a]
Tentative coastal plain migrants																	
Brown Creeper	0.30	0.721	86	0.0015	—	—	0	0.0000	—	0.620	68	0.0044	***	0.819	541	0.0182	1
Yellow-rumped (Myrtle) Warbler	0.82	0.765	1645	0.0464	—	—	18	0.0044	—	0.662	1455	0.0936	***	0.924	3690	0.1243	1
Savannah Sparrow	0.94	—	49	0.0010	—	—	0	0.0000	—	0.610	36	0.0023	***	0.944	714	0.0241	1
Appalachian migrant (Carlisle and west)																	
Least Flycatcher	0.34	0.790	391	0.0249	NS	0.804	44	0.0108	—	—	12	0.0008	—	0.931	131	0.0044	3
Eastern Wood Pewee	0.61	0.856	299	0.0087	NS	0.798	39	0.0096	—	—	10	0.0006	—	0.793	29	0.0010	3
Nashville Warbler	0.76	0.690	393	0.0102	**	0.478	52	0.0128	***	0.896	144	0.0093	**	0.973	111	0.0037	3
Wilson's Warbler	0.65	0.556	306	0.0073	NS	0.591	21	0.0052	*	0.857	21	0.0014	*	0.988	171	0.0058	3
Indigo Bunting	0.72	0.784	365	0.0153	**	0.875	198	0.0486	—	—	7	0.0005	—	—	11	0.0004	3
American Goldfinch	0.00	0.480	1762	0.0671	***	0.589	747	0.1835	+	0.723	45	0.0029	NS	0.686	35	0.0012	1
Tentative Appalachian migrant (Carlisle and west)																	
House Wren	0.30	0.873	221	0.0177	***	0.534	20	0.0049	***	0.929	28	0.0018	NS	0.985	68	0.0023	2
Appalachian migrants (Rector and west)																	
Black-throated Green Warbler	0.83	0.765	372	0.0086	*	0.902	38	0.0093	NS	0.927	121	0.0078	NS	0.967	91	0.0031	2
White-crowned Sparrow	0.64	0.676	105	0.0032	—	—	1	0.0002	—	—	18	0.0012	—	0.918	110	0.0037	1
Lincoln's Sparrow	0.69	0.775	493	0.0174	—	—	13	0.0032	—	0.973	38	0.0024	NS	0.938	81	0.0027	2

TABLE 2
Continued

Species name	Diel timing[c]	Rector % young	Rector N	Rector % Σ	Significance[a]	Carlisle % young	Carlisle N	Carlisle % Σ	Significance[a]	Coastal plain % young	Coastal plain N	Coastal plain % Σ	Significance[a]	Coast % young	Coast N	Coast % Σ	Winter range[a]
Tentative Appalachian migrant (Rector and west)																	
Golden-crowned Kinglet	0.44	0.608	181	0.0100	—	—	13	0.0032	—	0.772	119	0.0077	*	0.870	264	0.0089	1
West of Appalachian migrants (high percentage young at all stations)																	
Yellow-bellied Flycatcher	0.38	0.952	333	0.0080	—	0.929	51	0.0125	—	—	12	0.0008	—	0.955	112	0.0038	3
Solitary Vireo	0.39	0.900	108	0.0019	—	0.930	35	0.0086	NS	1.000	21	0.0014	*	0.932	74	0.0025	2
Cape May Warbler	0.68	0.893	512	0.0084	—	—	9	0.0022	—	0.928	46	0.0030	NS	0.937	559	0.0188	3
Chestnut-sided Warbler	0.92	0.850	200	0.0047	NS	0.771	26	0.0064	NS	0.882	52	0.0033	NS	0.905	63	0.0021	3
Bay-breasted Warbler	0.98	0.921	229	0.0030	NS	0.872	54	0.0133	NS	0.826	66	0.0042	NS	0.843	89	0.0030	3
Western Atlantic migrant																	
Blackpoll Warbler	0.81	0.785	233	0.0082	—	—	3	0.0007	—	0.607	6519	0.4194	***	0.798	2056	0.0693	3
Uncertain routes (species whose routes could not be determined)																	
White-breasted Nuthatch	0.00	—	83	0.0016	—	—	3	0.0007	—	0.846	26	0.0017	NS	0.932	59	0.0020	1
Blackburnian Warbler	0.96	0.952	62	0.0011	—	—	13	0.0032	—	0.834	38	0.0024	NS	0.912	34	0.0011	3
Chipping Sparrow	0.42	0.863[d]	373	0.0073	—	—	14	0.0034	—	0.897	29	0.0019	NS	0.942	94	0.0032	2

[a] Between percentage of young in adjacent areas are: — = insufficient data (N < 20, or not available); NS = not significant ($P > 0.10$); + = not significant ($P < 0.10$); * = $P < 0.05$; ** = $P < 0.01$; *** = < 0.001.
[b] Winter ranges are designated as northernmost area commonly wintering in: 1 = Central Atlantic States; 2 = Southeastern United States; 3 = South of United States.
[c] Diel timing of migration from Ralph (1975) are: 1.02 = most nocturnal; 0.00 = most diurnal (see text for explanation).
[d] Based on 51 individuals.

Each netting station differed from others in vegetation, location of nets, net height and operation schedule. These variables affect the capture rate of certain species; they probably do not significantly affect the age composition. Certainly the pooling of data from several sites and years tends to reduce potential biases from this source. At 2 stations, Carlisle and Ashby, it was possible to use techniques previously described (Ralph 1976) to correct the number of captures for varying number of nets and time of operation. This method provides a somewhat more accurate data set, but does not alter the comparisons between stations.

To define nocturnal and diurnal migrants, an index to the diel timing of migration was determined from data taken at Long Point Bird Observatory, Ontario (Bradstreet and Woodford 1970, Woodford 1970). In this analysis (Ralph 1975), a ratio was calculated between the natural logarithms of the number taken during nocturnal flight at a lighthouse and the number taken during the day at netting and trapping operations. The Ovenbird (*Seiurus aurocapillus*) had the highest ratio (1.02), with 1142 at the lighthouse and 1005 caught in nets and traps. Most Ovenbirds apparently migrate at night. A value approaching 0.00 indicated the most diurnal of the migrants (species with no individuals at the lighthouse were assigned the value 0.00).

Assignment of routes.—I regarded a station to be in the mainstream of a species' migratory route if, compared to other stations: (1) adults of that species were more abundant (i.e., the percentage of young was lower), and (2) the species made up a higher percentage of the total catch of passerine birds. Conversely, a station with a relatively high percentage of young and low abundance of that species was considered to be on the periphery of the species' route. These determinations are, of necessity, subjective. Three factors were weighed in making the determinations: (1) the relative magnitude of differences between age ratios and abundances at different stations, (2) the level of significance of differences between stations, and (3) the sample sizes involved. I gave greater weight to age ratios than to abundances, since I assumed that there would be more site bias in the abundance of a given species.

RESULTS

The coastal effect.—Fifty-two of 59 (88.1%) species ($N \geq 20$) at coastal sites (Table 2) had a higher proportion of young on the coast than at the nearest inland (coastal plain or Carlisle) location with adequate data. Of these, 40 species had a significantly ($P \leq 0.05$) higher percentage of young than the age ratio at the inland location.

Patterns of age ratios and abundances.—Data in Table 2 were grouped according to distance from the coast into 4 general regions. The route taken by a species could encompass one or more regions. I outline below the 5 patterns of age ratios and abundances that emerged in the area under consideration. Additional data from other areas, when available, will undoubtedly alter these assignments. No attempt was made to integrate the information on "known" migratory routes from other publications, as these are usually based on somewhat subjective information.

(1) *Possible broad front migrants.*—A species migrating through the northeastern United States in a general southwesterly direction, regardless of topography, is considered to be a broad front migrant. According to my hypothesis, the percentage of young should be higher and abundance lower on the coast than inland. Twelve species appeared to fit this pattern, 20.0% of the total (Table 2).

Three additional species were tentatively assigned to this pattern, the Ruby-crowned Kinglet (*Regulus calendula*), Yellow Warbler (*Dendroica petechia*) and Song Sparrow (*Melospiza melodia*). Skull ossification is completed in this kinglet somewhat earlier than in most species (Leberman 1970), potentially biasing age data. Therefore, kinglet data from Carlisle, mostly from later in the migratory period, were excluded. The Yellow Warbler (an early migrant) was uncommon at all sites, so I disregarded its absence at Carlisle and classified it in the broad front pattern. A high percentage of young in Song Sparrows prevailed until Carlisle, but the species was abundant on the coastal plain.

(2) *Possible coastal migrants.*—A species concentrating its migration along the coast would be more abundant and have a lower percentage of young there than on the coastal plain and inland. Only the Red-breasted Nuthatch (*Sitta canadensis*) showed this pattern clearly (Table 2).

The Black-capped Chickadee (*Parus atricapillus*) also probably follows this route through the northeast. Although it had high percentages of young at all sites, its exceptional abundance (14% of the total) on the coast, suggests this is the main path. Chickadee populations frequently irrupt, and first-year birds are the ones that move (Ralph, unpubl.), so that they would predominate at all sites. In contrast, the nuthatch, also an irruptive species, had substantial numbers of adults in the coastal migration.

The Tennessee Warbler (*Vermivora peregrina*) appears to use both the coast and the coastal plain. However, the high percentage of young (94.9%) and great abundance at Rector, making up 2.3% of the total catch of all species, suggest that this warbler probably has a major route to the west.

(3) *Possible coastal plain migrants.*—This category includes those species that would avoid both the coast and the Appalachian Mountains. Such species would be most common and have the lowest percentage of young on the coastal plain. They would decline in abundance and increase in percentage of young on the coast and also at Carlisle on the boundary of the coastal plain and the Appalachians (and certainly at Rector). Twenty species (32.8%) were assigned to this group.

An additional 3 species were tentatively regarded as coastal plain migrants. The Brown Creeper (*Certhia familiaris*) showed a relatively low percentage of young at Rector, indicating it may fit the broad front pattern, but its high abundance at the coast, coupled with the relatively low percentage of young on the coastal plain, suggests that its route may lie in the latter area. The Yellow-rumped Warbler (*Dendroica coronata*) was common at Rector, but had a significantly ($P < 0.01$) higher percentage of young there than on the coastal plain. This higher incidence at Rector, in addition to the relative scarcity of this species at Carlisle, indicated its pattern fits the coastal plain one. The Savannah Sparrow (*Passerculus sandwichensis*) is more abundant on the coast than the coastal plain, but the low percentage of young at the latter location would indicate its route is on the coastal plain.

(4) *Possible Appalachian and west migrants.*—If a route of a species lay in and to the west of the Appalachians, one would expect the species to be most common and have the lowest percentage of young at Rector, on the western side of the Appalachians. Towards the coast, the percentage of young would increase either at Carlisle or the coastal plain, and the species would decline in abundance. Fourteen species (23.0%) appeared to fit this pattern. Six species (possibly 7) apparently had routes west of Carlisle. Three (possibly 4), had a pattern indicating a route west of Rector.

Five additional species were tentatively considered to have a route west of Rector. These were species having equally high percentages of young at all stations. The House Wren (*Troglodytes aedon*) seemingly belonged to this group, with a possible route through the region including Carlisle, where the lowest percentage of young (53.4%) was found. At Rector, the percentage of young was significantly higher (87.3%), indicating that this wren might concentrate its route in the Appalachians, although this cannot be determined from available data.

The Golden-crowned Kinglet (*Regulus satrapa*) had its lowest percentage of young at Rector, suggesting that its main migration route is from here to the west. However, nowhere were very high percentages of young found, and the species may actually be a broad front migrant. As with the Ruby-crowned Kinglet, many young birds had ossified skulls early in the season, so age ratios are not reliable, further compounding the problem.

(5) *Possible western Atlantic migrants (the Blackpoll route).*—Blackpoll Warblers, after apparently pausing on the eastern coastal plain, leave North America and head south over water to tropical America (Nisbet 1970). Their main route thus crosses the coast, explaining the relatively low percentages of young at the coast and on the eastern coastal plain. The lowest percentage of young was on the coastal plain rather than the coast (Table 2). This might be expected because most individuals apparently begin their long flight somewhat inland (Nisbet et al. 1963; Richardson, in press). Most species (70.4%) of migrants wintering south of the United States have more than 90% young at the coast (Table 2). However, a few species, like the blackpoll, had relatively low percentages of young (<85%) at the coast. I will consider these species with those that Drury and Keith (1962) suggested as potential overwater migrants (Table 3). They based their list on subjective impressions of density at Bermuda.

Young make up 79.8% of the blackpolls on the coast, more than 10% below the average for all warbler species (90.4%). Of the species with 80% young along the coast, only 2 are on Drury and Keith's (1962) list (Table

TABLE 3

POSSIBLE WESTERN ATLANTIC MIGRANTS, THEIR ASSIGNED ROUTES, THE PERCENT YOUNG FOUND AT COASTAL STATIONS, AND THE NUMBER KILLED AT TV TOWERS IN FLORIDA AND TENNESSEE IN THE AUTUMN

Species	Assigned route	% young on coast	Number in Florida[2]	Number in Tennessee[2]
Palm Warbler[1]	Coastal Plain	98.4	1944	60
American Redstart[1]	Coastal Plain	96.8	1099	229
Yellow Warbler[1]	Tent. Broad Front	93.2	63	11
Ovenbird[1]	Coastal Plain	92.5	1128	2140
Myrtle Warbler[1]	Tent. Coastal Plain	92.4	1006	16
Black-and-white Warbler[1]	Coastal Plain	86.8	502	362
Northern Waterthrush[1]	Coastal Plain	84.4	484	110
Veery	Coastal Plain	84.3	668	3
Bay-breasted Warbler	App. and W.	84.3	157	409
Parula Warbler[1]	Coastal Plain	80.7	1041	8
Blackpoll Warbler[1]	W. Atlantic	79.8	11	20
Eastern Wood Pewee	App. and W.	79.3	34	3
Common Yellowthroat[1]	Coastal Plain	78.2	3477	97
Tennessee Warbler	Coastal and Coastal Plain	66.0	331	1242

[1] Species in Drury and Keith (1962).
[2] Sources given in text.

3) and 4 are not. Five of Drury and Keith's species—Palm (*Dendroica palmarum*), Yellow-rumped and Yellow warblers, American Redstart (*Setophaga ruticilla*) and Ovenbird—have more than 90% young along the coast. In view of the strong coastal effect which these 5 species show, it seems unlikely that they follow a western Atlantic route.

Species using primarily an overwater route would be expected to be rare in the southeastern U.S. in migration. Indeed, the Blackpoll Warbler largely bypasses the southern states in migration (Nisbet 1970). TV tower kills in Florida (Stoddard and Norris 1967, Taylor and Anderson 1973) and in Tennessee (Laskey 1969a, b) show that of the species in Table 3, only Eastern Wood Pewee (*Contopus virens*), Blackpoll and Yellow warblers are apparently rare in both areas. The pewee may actually be more common but may not be susceptible to nocturnal accidents. The Veery (*Catharus fuscescens*), Yellow-rumped and Parula (*Parula americana*) warblers, relatively uncommon in Tennessee, are common in Florida kills. Their principal route might lie to the east of Tennessee.

Abundance in Bermuda would be a good indicator of birds flying between the northeast and South America, since this island group is almost midway in this flight. Adults should comprise a substantial percentage of

TABLE 4
PERCENTAGE OF YOUNG, AND THE NUMBER CAUGHT, OF WARBLERS AND VIREOS CAPTURED IN BERMUDA DURING THE AUTUMN

Species	Percent young	Number caught	Species	Percent young	Number caught
Black-and-white Warbler	96.4	28	Bay-breasted Warbler	66.7	3
Worm-eating Warbler	100.0	6	Blackpoll Warbler	44.4	234
Swainson's Warbler	100.0	1	Prairie Warbler	100.0	2
Prothonotary Warbler	100.0	9	Palm Warbler	100.0	9
Blue-winged Warbler	100.0	1	Ovenbird	89.5	19
Tennessee Warbler	92.3	13	Northern Waterthrush	100.0	30
Nashville Warbler	83.3	6	Kentucky Warbler	100.0	1
Orange-crowned Warbler	100.0	2	Connecticut Warbler	0.0	2
Parula Warbler	85.7	21	Mourning Warbler	100.0	1
Yellow Warbler	100.0	5	Common Yellowthroat	100.0	24
Magnolia Warbler	100.0	23	Yellow-breasted Chat	100.0	2
Cape May Warbler	100.0	5	Hooded Warbler	100.0	8
Black-th. Blue Warbler	100.0	8	Wilson's Warbler	100.0	1
Myrtle Warbler	100.0	1	Canada Warbler	100.0	1
Black-th. Green Warbler	100.0	5	American Redstart	98.8	87
Blackburnian Warbler	100.0	4	Red-eyed Vireo	100.0	43
Chestnut-sided Warbler	100.0	6	Philadelphia Vireo	100.0	4

birds passing through there. Records of warblers and vireos from occasional mist netting in Bermuda by J. Baird and D. Wingate (pers. comm.) show that only the blackpoll is both common and represented by high numbers of adults (Table 4). Thus, it would appear that only the blackpoll, among passerines, uses an overwater route as its major pathway.

Undetermined routes.—It was not possible to determine the route taken by the White-breasted Nuthatch (*Sitta carolinensis*), Blackburnian Warbler (*Dendroica fusca*) and Chipping Sparrow (*Spizella passerina*). Too few data were available for age ratio assessments, and no coastal effect was found. Perhaps additional capture data would clarify the type of routes for these 3 species.

Association of routes with other species characteristics.—To determine if particular routes were associated with the distance migrated, I divided the species in this study according to the northernmost area in which they are found commonly in winter (Table 2, last column): (1) the central Atlantic states, (2) the southeastern Unites States, or (3) south of the United States. Of all species for which I determined a route, nearly half (48.1%) of those wintering south of the United States are coastal plain migrants (Table 5). One-half of the species wintering in the central Atlantic

TABLE 5
NORTHERNMOST WINTERING AREA OF SPECIES PROBABLY AND POSSIBLY (IN PARENTHESES) ASSOCIATED WITH DIFFERENT ROUTES

Route	Central Atlantic States	Southeastern United States	South of United States	Totals
Broad front	8 (2)	0 (0)	4 (1)	12 (3)
Coastal	1 (1)	0 (0)	1 (0)[a]	2 (1)
Coastal Plain	5 (3)	3 (0)	13 (0)[a]	21 (3)
West of Appalachians	2 (1)	3 (1)	9 (0)	14 (2)
Western Atlantic	0 (0)	0 (0)	1 (0)	1 (0)
Undetermined	1	1	1	3
Totals	17 (7)	7 (1)	28 (1)	61

[a] One species had its route on both the coast and the coastal plain.

states showed a broad front migration pattern, while 5 (31.3%) were coastal plain migrants.

Migrant species using the coastal plain tended to have more individuals migrating at night than those using other routes (Table 2), but not significantly so ($P > 0.10$, Mann-Whitney U-test). The average coastal plain migrant had a diel timing index value of 0.717, while broad front migrants averaged 0.575, and Appalachian and west migrants averaged 0.583.

When I grouped the migrants by taxa and compared their routes, more than half of the warblers (52.4%) used the coastal plain, as did the 6 thrush species (Table 2). These relationships were weak, but significant ($P < 0.05$). No other correlations of routes with taxa were found.

DISCUSSION

Possible causes of the coastal effect.—Evidence marshalled in this paper supports the existence of the "coastal effect" and indicates that a high percentage of young in a local sample indicates that a site is on the edge of the main migration route. I previously discussed some of the hypotheses that have been advanced to explain the coastal effect (Ralph 1971). However, additional published data, as well as this study's thorough documentation of the phenomenon, have shed new light on the hypotheses. They fall into 5 main categories.

(1) *Differential timing of migration.*—This hypothesis explains the coastal effect as an artifact of sampling. Brewster (1887), noting that few adults were collected in autumn, postulated that the post-breeding adults migrated in July before the young and before the collectors were active. Differences between adults and young of about 30 days between peaks of

passage were shown in the Least Flycatcher (*Empidonax minimus*) at Long Point (Hussell et al. 1967, Ely 1970) and in the Western Flycatcher (*E. difficilis*) (Johnson 1973, Stewart et al. 1974). However, Clench (1969) found synchronous migration in *E. minimus* at Rector. Also, few inland data were available for the Western Flycatcher, making conclusions necessarily tentative. Murray (1966) and Leberman and Clench (1973) showed as many as 15 days difference at Rector in average migration dates between adults and young for a few species, including the Red-eyed Vireo (*Vireo olivaceus*) and White-throated Sparrow (*Zonotrichia albicollis*). In most species, however, the age classes migrate more or less in synchrony. Certainly, in no known case (with the possible exception of the Western Flycatcher) is the migration asynchronous enough to explain the coastal effect. That is, it does not appear that adults of any species migrate so early as to be missed by netting beginning in August. Finally, the high percentage of adults of most species at inland locations also precludes Brewster's (1887) explanation, which would require that young predominate at both inland and coastal sites during the latter part of the migration.

Alternatively, perhaps adults fly greater distances without stopping and so would not be captured as often. This hypothesis may obtain for those few species with a high percentage of young at all localities, both coastal and far inland, considered above to be migrating west of the Appalachians. I know of no published discussions for or against this hypothesis.

(2) *Adults overflying the coast.*—In discussing Blackpoll Warblers, Murray (1966) postulated that both adult and young nocturnal migrants regularly stray offshore. Both age classes return to the mainland, with the young stopping at landfall, whereas the adults fly farther inland, perhaps seeking more suitable habitat. Thus, the adults pass over the coast but do not land. This hypothesis requires that any bird offshore at dawn (1) have enough energy reserves, (2) have offshore winds slower than its airspeed, and (3) be able to relocate land. I doubt whether a substantial fraction of birds offshore fulfill these conditions.

Kills of several species of migrants at tall structures contradict Murray's hypothesis. The kills at the Prudential Center on the coast in Boston would likely include adults if they were flying over the coast. However, 90.6% of all birds here were young (N = 427). At the Boylston TV tower, 60 km inland, only 46.6% of the kill were young (N = 682). Apparently, the age composition of migrants in the airspace above the coast is similar to that on the ground. Adults are overflying the coast in much lower proportions than they are overflying inland locations.

(3) *Different routes.*—Clench (1969) postulated that adult Least Flycatchers migrate along the Appalachians (as I found), and the young to the east and along the coast, which was not confirmed by this study. I found

5 species that might have different routes used by different age classes. Yellow-bellied Flycatcher (*Empidonax flaviventris*), Solitary Vireo (*Vireo solitarius*), and Cape May (*Dendroica tigrina*), Chestnut-sided (*D. pensylvanica*) and Bay-breasted (*D. castanea*) warblers. These species had high percentages of young at all stations in the area of study, suggesting that the adults might have a route to the west. However, data are lacking that show a preponderance of adults at any location.

(4) *Learning.*—Drury and Keith (1962) have hypothesized that young on their first autumn flight learn to avoid the hazards (e.g., dehydration and depletion of energy reserves) of an overwater flight. As adults, they do not repeat a route taking them to the coast.

Supporting this hypothesis, migrants offshore have been observed by radar to reorient, at times towards land (Myres 1964, Richardson 1978). Indeed, it appears that there is a mechanism allowing migrants with energy reserves to regain land. Those lacking these reserves would perish. Whether the returning birds could learn from their experience, and not repeat their offshore flight, is problematical.

Although the learning hypothesis has considerable merit, it does require many individuals to experience an offshore flight. The hypothesis may not hold for those beginning their flight near the coast and going southeast offshore within the first few hours of night. (Many individuals also head SSW-SW along the shore.) Since individuals offshore observed by radar do not normally change their direction during the night (Richardson 1975), by dawn they would be too far out to return, given normal energy reserves (e.g., Odum et al. 1961) and a definitely offshore direction. With the northeast-southwest orientation of the eastern U.S. coast, even a southward orientation would lead a bird too far offshore to return. Emlen (1969, 1970) has shown that the orientation of Indigo Buntings (*Passerina cyanea*) is defined at an early age, and thus is probably not easily modified by experience. Finally, nocturnal migrants are often reported far offshore, indicating that some individuals persist in flying offshore, with fatal results.

(5) *Maladaptive orientation.*—Drury and Keith (1962) suggested that "the birds which live to be adults are those inheriting a tendency to move on courses which keep them over the mainland." This suggests that birds surviving to become adults generally move on overland routes that avoid the coast because they have proper orientation (Ralph 1971, 1978), adequate compensation for wind drift (Baird and Nisbet 1960) and/or begin migration under conditions not leading to wind displacement from the normal route (Evans 1968). In contrast, the birds along the coast would be largely immature birds not possessing these abilities, as shown in Ralph (1978). They have been, or will be, exposed to the hazards of overwater flight.

Some data support this explanation. The literature abounds with references to land bird migrants at sea, apparently persisting in flying in directions leading potentially to their death. These include observations from ships at sea (e.g., Sprunt 1931, Buckley 1946, Kuroda 1955, Scholander 1955, Hubbs and Banks 1966, Jenson and Livingstone 1969, Williams et al. 1977), on offshore islands (e.g., Howell 1959; Kuroda 1961, 1964; Ralph 1968) and with radar (Williams et al. 1977). Most critical to this hypothesis is that these birds often appear exhausted and sometimes quite emaciated. This has been quantified on an offshore island by Eliassen and Hjelmtvedt (1958) and on the coast by Murray and Jehl (1964) and Ralph (unpubl.).

Williams et al. (1977) provides evidence for offshore mortality, and they ". . . suggest significant mortality for at least some groups of birds." All of these points argue strongly that many individuals do persist in flights involving offshore directions, often with fatal conclusions.

The first 3 hypotheses discussed above may well account for some of the young along the coast. However, the last two are the most tenable, and in my opinion the last has special merit and is probably the cause of the majority of young that reach the coast. The learning and disorientation hypotheses are not necessarily mutually exclusive. Disoriented young that reach the coast and survive might learn to avoid the coast during subsequent migrations.

Species showing little or no coastal effect.—My analysis suggests that the Blackpoll Warbler is possibly the only passerine species using a route over the western Atlantic. It was the only species with all of the following characteristics: (1) relatively low percentage of young along the coast and in Bermuda, (2) uncommon in both Florida and Tennessee, and (3) relatively abundant in Bermuda.

The relatively low percentages of young along the coast in 7 other species (Table 3), could be explained in one of two ways. One would be that the coast is not actually the edge of the route of these species. These apparent exceptions to the principal generalization of this study could have evolved strategies allowing some individuals to survive, despite a tendency to migrate near or even beyond the coast. Richardson's (1978) radar observations of nocturnal passerines migrating off the Atlantic coast of Canada are particularly relevant to this point. In addition to those flying overland (southwest or west), some fly over water and parallel the coast (southwest or south southwest). At dawn, with following winds, they usually kept that course, probably intersecting shore near Virginia. In contrast, those individuals flying under unfavorable winds with a head or side component often changed direction and flew northwest toward the coast during the morning hours. This strategy would enable some of those flying in a generally southwesterly direction near land to survive. Bay-breasted and Tennessee warblers (west of the Appalachian migrants) with relatively low percentages of young at the coast and no coastal effect, may use this strategy. A change in flight direction may also be in the repertoire of the other 5 long-distance migrants with relatively low percentages of young along the coast.

Determining routes of migration.—Using age ratios and abundances of birds at a given capture station to hypothesize routes of migration is subject to many potential sources of error. It is not the purpose of this paper to explore them all, but it is my judgment that the effect of these variables is relatively minor and does not affect my basic interpretations of the overall picture to any significant degree.

This study, although essentially restricted to northeastern North America, supports Thompson's (1926) suggestion that some species probably migrate over a broad front, while others may follow more narrow paths. In the area studied, 43% of the species apparently avoid the mountains, channeling their flight down the coastal plain or coast. This group does not appear to be restricted to diurnal migrants, as has been suggested. It seems unlikely that these birds would fly over the Appalachians without being detected there. Habitats in the Appalachian Mountains are rather similar to neighboring, lower areas, and these species would be expected to land if they were present. Few of the coastal plain migrants breed only to the north of this area. Undoubtedly, other populations of these species also have routes to the west of the area of this study.

Independent evolution of routes.—I had expected to find strong relationships between routes and other factors, such as diel timing of migration, taxa and distance to wintering grounds, among others. Only weak relationships were found. Most long-distance migrants moving along the coastal plain are insectivorous. This route is near the stabilizing influence of the ocean, perhaps allowing a more dependable food source than a more inland route. Even a slight temperature differential could be a selective force if, for instance, early frosts occasionally decimated insect populations. Those more hardy bird species wintering in the central Atlantic states, by contrast, apparently tended to be broad front migrants in our area, passing through the slightly colder mountains, as well as the coastal plain.

The lack of an association between routes and other characteristics of migration suggests independent evolution of routes by each species. It also indicates that other aspects, such as timing of migration (on both a seasonal and daily basis), have also evolved independently to meet the particular selective pressures acting on each species.

CONCLUSIONS

These data and the resulting hypotheses will, I hope, stimulate further investigations. Most especially, I would urge that the following avenues of research and predictions be explored and tested: (1) Accurate age ratio data be accumulated from stations to the south and west of the area in this paper. Far too many banders fail to ensure that 95% of captured birds are accurately aged. (2) The limited recovery data available on passerines should be compiled and published, with due regard to the fact that recoveries are usually of birds which have been selected against. (3) If a banding station is on the edge of a migratory route of a species, individuals there may be of lower weight, and with less fat reserves than in the hypothesized central part of a route. (4) If the hypothesis is correct, quantitative data from offshore ships and from islands, at some distance from a "main" route, should include records of lighter birds. (5) It is logical that mist net capture in an area of a given species should be an accurate assessment of the amount of migration of the species in that area. In this paper I held that, due to site bias, they perhaps are not. Several stations or nets set over a wider area than is usually the case should confirm or deny this supposition.

SUMMARY

Age ratios and abundance of 61 migrant passerine species comprising more than 42,000 birds were analyzed in an attempt to determine patterns of migration. The data were collected at 10 stations from coastal Massachusetts to inland Pennsylvania. Age ratios are thought to be useful in determining routes of migration. The principal criteria for the edge of a species' route are suggested to be a higher proportion of young and a lower density of the species than in other areas. Almost all species in this area fell readily into 1 of 5 patterns that suggest 5 possible routes: (1) immediately along the coast (3 species); (2) on the coastal plain (24 species); (3) west of the Appalachians (17 species); (4) overwater, direct to South America (only the Blackpoll Warbler); and (5) an unconfined, broad front, encompassing the entire area (14 species). For 3 species, no route could be determined.

Almost all species showed the "coastal effect," a higher percentage of young along the coast than elsewhere. By the criteria given, this indicates that the coast is the edge of the migratory route of most species. Most probably the young found near the coast lack some navigational capabilities and are off course; many of them probably perish.

In general, a given route was not strongly associated with either diurnal or nocturnal migration, distance to wintering grounds, or with any genus or family of birds. I speculate that this is evidence that routes have evolved independently in each species.

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APPENDIX A

SCIENTIFIC NAMES OF SPECIES IN TABLES NOT MENTIONED IN TEXT

Eastern Phoebe (*Sayornis phoebe*)
Blue Jay (*Cyanocitta cristata*)
Gray Catbird (*Dumetella carolinensis*)
Brown Thrasher (*Toxostoma rufum*)
American Robin (*Turdus migratorius*)
Wood Thrush (*Catharus mustelina*)
Hermit Thrush (*C. guttata*)
Swainson's Thrush (*C. ustulata*)
Gray-cheeked Thrush (*C. minima*)
Philadelphia Vireo (*Vireo olivaceus*)
Black-and-white Warbler (*Mniotilta varia*)
Prothonotary Warbler (*Protonotaria citrea*)
Swainson's Warbler (*Limnothylypis swainsonii*)
Worm-eating Warbler (*Helmitheros vermivorus*)
Nashville Warbler (*Vermivora ruficapilla*)
Blue-winged Warbler (*V. pinus*)
Orange-crowned Warbler (*V. celata*)
Magnolia Warbler (*Dendroica magnolia*)
Black-throated Blue Warbler (*D. nigrescens*)
Black-throated Green Warbler (*D. virens*)
Prairie Warbler (*D. discolor*)
Northern Waterthrush (*Seiurus noveboracensis*)
Kentucky Warbler (*Oporornis formosus*)
Mourning Warbler (*O. philadelphia*)
Connecticut Warbler (*O. agilis*)
Common Yellowthroat (*Geothlypis trichas*)
Yellow-breasted Chat (*Icteria virens*)
Wilson's Warbler (*Wilsonia pusilla*)
Hooded Warbler (*W. citrina*)
Canada Warbler (*W. canadensis*)
Scarlet Tanager (*Piranga olivacea*)
Rose-breasted Grosbeak (*Pheucticus ludovicianus*)
Purple Finch (*Carpodacus purpureus*)
American Goldfinch (*Spinus tristis*)
Rufous-sided Towhee (*Pipilo erythrophthalmus*)
Dark-eyed Junco (*Junco hyemalis*)
Field Sparrow (*Spizella pusilla*)
Fox Sparrow (*Passerella iliaca*)
Lincoln's Sparrow (*Melospiza lincolnii*)
Swamp Sparrow (*M. georgiana*)

INSTITUTE OF PACIFIC ISLANDS FORESTRY, U.S. FOREST SERVICE, 1151 PUNCHBOWL STREET, HONOLULU, HAWAII 96813. ACCEPTED 8 JULY 1980.