

MIGRATION OF AGE AND SEX CLASSES OF PASSERINES ON THE ATLANTIC COAST IN AUTUMN

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THERE seems to be general agreement that in many species of birds the adults and immatures, and perhaps males and females, migrate at different times or by different routes in autumn. However, there is less than general agreement on what the order of migration is—do adults precede the immatures, or vice versa? Tordoff and Mengel (1956), after reviewing the work on this problem, concluded that “the whole subject is still unsettled.”

The lack of agreement results from inadequate data, which are usually obtained sporadically from birds killed at lighthouses, ceilometers, and television towers. The use of mist-nets at selected locations makes it possible to capture and examine migrants daily throughout the migratory period. During the autumn of 1963, I had the opportunity to determine the age of several thousand passerine migrants at the Island Beach Operation Recovery Station in New Jersey. The data obtained form the basis of this paper.

METHODS

From 2 August to 26 October 1963 birds were mist-netted almost daily at Island Beach State Park, Ocean County, New Jersey. Due to inclement weather no netting was done on 5 and 20 August, 16 September, and 22 October. The period of study spanned the migration periods of most species.

Until 22 August I worked alone. On 23 August I was joined by the first of many banders and assistants who took part in this study. The large number of migrants captured precluded examination of all birds, but an attempt was made to see as many as possible of most passerine species. James Baird examined some birds from 19 to 22 September, and Jeff Swinebroad did the same on 28 September; otherwise, the birds were examined by me.

Except as noted below, age was determined by examining the stage of ossification of the skull, using the method of Miller (1946), as modified by Baird (*in* Norris, 1961). A bird with a clear, pinkish, unspckled area on the skull was called immature, and a bird with the entire roof of the skull whitish and speckled was called adult.

The age and sex of some individuals were determined by plumage or soft part coloration as noted below (Dwight, 1900, Roberts, 1955, and mimeographed sheets from the Bird-Banding Office present more detailed descriptions).

Nuthatches.—The sexes in the Red-breasted Nuthatch¹ can be distinguished by the color of the pileum: black in males and bluish in females. The race of the White-breasted Nuthatch (*cookei*) that is most likely to occur in New Jersey has a similar sexual dimorphism. All skulls were examined.

Thrushes.—Some individuals were called immature on the basis of buffy tips on

¹ With few exceptions, scientific names of species mentioned in the text appear in Tables 1, 2, or 3. Otherwise, scientific names appear in the text.

the greater secondary wing coverts. Skulls of birds without buffy tips were examined; some were adult and some were immature.

Red-eyed Vireo.—The age of some birds was determined by eye color: red in adults and brown to reddish-brown in immatures. Eye color was determined to be completely reliable in the many birds whose skulls were examined.

Black-and-white Warbler.—Males have sharp black streaks on the breast, whereas females have dull streaks and a brownish cast to the plumage. A few males were aged by plumage characteristics: adults have a broad black patch around the eye and immatures have a black stripe through the eye. Skulls of all females were examined.

Cape May Warbler.—Males were distinguished by the broad white wing-bar and generally brighter aspect, and females were distinguished by a narrow wing-bar and duller aspect.

Black-throated Blue Warbler.—Black-throated, blue birds were called males, and greenish birds were called females.

Prairie Warbler.—The skulls of most birds were examined, but a few were aged and sexed by plumage characteristics. The adult male has black face markings, the adult female has olive-green face markings, and immatures have grayish face markings. Immatures were sexed by the general brightness of males and dullness of females.

Scarlet Tanager.—Males have black greater and lesser secondary coverts, and females have greenish coverts. Skulls of all females and most males were examined, but in some cases males were called adults on the basis of black primaries.

Rose-breasted Grosbeak.—Few skulls were examined. Males have pinkish under wing coverts, and females have yellowish under wing coverts. Adult males were distinguished by black primaries, as well as more extensive black in body plumage.

White-crowned Sparrow.—Some immatures were identified by the dark brownish lateral and light brownish median crown stripes.

RESULTS

Several thousand passerine migrants of 80 species were aged, but data on only 44 species are presented. Of the 80 species, 5 are common breeding birds at Island Beach: Catbird (*Dumetella carolinensis*), White-eyed Vireo (*Vireo griseus*), Yellowthroat (*Geothlypis trichas*), Rufous-sided Towhee (*Pipilo erythrophthalmus*), and Song Sparrow (*Melospiza melodia*). They are not included in this analysis because of the difficulty of separating migrants from residents. Also, 31 species that were represented by fewer than 25 individuals each are excluded because I consider these samples too small for useful analysis.

Of the species analyzed, 22 were represented by over 100 individuals (Tables 1 and 3). The percentage of adults in these species ranged from 0.8 to 28.6. In 18 of these 22 species adults occurred throughout most of the migratory period, and the peak capture of adults usually coincided with the peak capture of immatures. In one species, the Red-eyed Vireo, adults predominated during the first few weeks of migration. In the remaining three species, Palm Warbler, Yellow-breasted Chat, and Canada Warbler, few adults were caught. The three adult Palm Warblers were caught on one day, as were the two adult Canada Warblers. Three adult

TABLE 1
NUMBERS OF SOME PASSERINES AT ISLAND BEACH, NEW JERSEY, AUTUMN, 1963
(SAMPLES OF 100 OR MORE INDIVIDUALS)

Group	Period ¹												Totals	Per cent adult
	August					September				October				
	2	10	17	24	31	7	14	21	28	5	12	19-26		
<i>Brown Creeper (Certhia familiaris)</i>														
Adult	0	0	0	0	1	1	5	17	8	3	5	0	40	15.3
Immature	0	0	0	1	5	21	2	123	43	12	7	8	222	
<i>Hermit Thrush (Hyalocichla guttata)</i>														
Adult	0	0	0	1	0	0	0	0	0	0	4	2	7	4.3
Immature	0	0	0	0	0	0	0	0	17	23	91	24	155	
<i>Swainson's Thrush (H. ustulata)</i>														
Adult	0	0	0	0	0	2	2	14	4	0	0	0	22	5.3
Immature	0	0	0	1	18	91	46	138	77	12	7	3	393	
<i>Gray-cheeked Thrush (H. minima)</i>														
Adult	0	0	0	0	0	0	3	2	4	0	1	0	10	8.3
Immature	0	0	0	0	0	1	4	45	49	6	3	3	111	
<i>Veery (H. fuscescens)</i>														
Adult	0	0	1	1	16	2	2	0	0	0	0	0	22	16.4
Immature	0	0	1	13	78	13	3	3	1	0	0	0	112	
<i>Red-eyed Vireo (Vireo olivaceus)</i>														
Adult	0	0	0	4	9	16	3	2	0	0	0	0	34	10.1
Immature	0	0	0	2	16	68	75	70	57	4	7	1	300	
<i>Magnolia Warbler (Dendroica magnolia)</i>														
Adult	0	0	0	0	0	1	3	7	5	4	0	0	20	9.2
Immature	0	0	0	2	19	56	58	29	30	3	1	0	198	
<i>Myrtle Warbler (D. coronata)</i>														
Adult	0	0	0	0	0	0	0	0	14	9	58	21	102	8.2
Immature	0	0	0	0	0	0	0	15	133	208	564	227	1147	
<i>Blackpoll Warbler (D. striata)</i>														
Adult	0	0	0	0	1	4	15	24	14	1	2	2	63	9.6
Immature	0	0	0	0	2	49	95	231	171	27	17	3	595	
<i>Palm Warbler (D. palmarum)</i>														
Adult	0	0	0	0	0	0	0	0	3	0	0	0	3	0.8
Immature	0	0	0	0	0	6	25	66	122	19	102	33	373	
<i>Ovenbird (Seiurus aurocapillus)</i>														
Adult	0	0	0	0	8	3	1	1	1	0	0	0	14	7.7
Immature	0	1	0	2	56	44	21	28	11	2	3	0	168	
<i>Northern Waterthrush (S. noveboracensis)</i>														
Adult	1	3	1	1	24	2	4	4	0	0	0	0	40	13.1
Immature	15	6	5	44	44	40	34	65	10	1	1	0	266	
<i>Yellow-breasted Chat (Icteria virens)</i>														
Adult	0	0	0	3	0	0	0	0	0	0	1	0	4	2.7
Immature	0	1	4	14	38	39	9	22	11	3	5	0	146	
<i>Canada Warbler (Wilsonia canadensis)</i>														
Adult	0	0	0	2	0	0	0	0	0	0	0	0	2	1.7
Immature	1	3	3	46	37	12	6	4	1	0	0	0	113	
<i>Slate-colored Junco (Junco hyemalis)</i>														
Adult	0	0	0	0	0	0	0	0	1	1	4	6	12	2.1
Immature	0	0	0	0	0	8	6	39	53	81	139	252	578	
<i>Field Sparrow (Spizella pusilla)</i>														
Adult	0	0	0	0	0	0	0	0	0	2	4	0	6	2.9
Immature	0	0	0	0	0	0	0	0	11	23	143	25	202	
<i>White-throated Sparrow (Zonotrichia albicollis)</i>														
Adult	0	0	0	0	0	0	0	1	5	11	12	1	30	5.0
Immature	0	0	0	0	0	12	10	127	93	154	92	87	575	
<i>Swamp Sparrow (Melospiza georgiana)</i>														
Adult	0	0	0	0	0	0	0	0	4	5	12	5	26	6.8
Immature	1	0	0	0	0	0	3	11	43	102	159	36	355	

¹ Periods include, and extend from, the date given up to the date of the beginning of the next period.

TABLE 2
NUMBERS OF SOME PASSERINES AT ISLAND BEACH, NEW JERSEY, AUTUMN, 1963
(SAMPLES OF 25 TO 99 INDIVIDUALS)

Group	Period ¹											Totals	Per cent adult	
	August					September				October				
	2	10	17	24	31	7	14	21	28	5	12 19-26			
	House Wren (<i>Troglodytes aedon</i>)													
Immature	1	2	0	0	1	6	4	9	5	1	1	0	30	0.0
	Solitary Vireo (<i>Vireo solitarius</i>)													
Adult	0	0	0	0	0	0	0	1	1	1	1	0	4	12.9
Immature	0	0	0	0	0	0	0	8	12	5	0	2	27	
	Philadelphia Vireo (<i>V. philadelphicus</i>)													
Adult	0	0	0	0	0	0	1	0	1	0	0	0	2	6.7
Immature	0	0	0	0	4	6	10	6	2	0	0	0	28	
	Tennessee Warbler (<i>Vermivora peregrina</i>)													
Adult	0	0	0	2	3	4	0	2	6	0	1	0	18	30.5
Immature	0	0	0	4	2	2	1	8	17	1	6	0	41	
	Nashville Warbler (<i>V. ruficapilla</i>)													
Immature	0	0	1	1	3	11	3	11	9	3	7	1	50	0.0
	Parula Warbler (<i>Parula americana</i>)													
Adult	0	0	0	0	0	1	2	6	2	0	0	0	11	26.8
Immature	0	0	0	0	0	3	9	9	3	3	3	0	30	
	Yellow Warbler (<i>Dendroica petechia</i>)													
Adult	2	1	2	0	2	1	1	1	0	0	0	0	10	14.9
Immature	9	3	2	10	14	6	5	7	1	0	0	0	57	
	Black-throated Green Warbler (<i>D. virens</i>)													
Adult	0	0	0	0	0	0	0	1	0	0	0	0	1	2.2
Immature	0	0	0	1	2	3	6	14	11	2	5	0	44	
	Chestnut-sided Warbler (<i>D. pensylvanica</i>)													
Adult	0	0	0	0	0	1	0	2	0	0	0	0	3	9.1
Immature	0	0	2	7	10	5	3	1	2	0	0	0	30	
	Bay-breasted Warbler (<i>D. castanea</i>)													
Adult	0	0	0	0	1	0	0	3	4	1	1	0	10	20.0
Immature	0	0	0	2	9	3	3	11	9	2	1	0	40	
	Connecticut Warbler (<i>Oporornis agilis</i>)													
Adult	0	0	0	0	0	1	0	0	1	0	0	0	2	2.6
Immature	0	0	0	0	1	21	18	19	14	0	1	0	74	
	Mourning Warbler (<i>O. philadelphia</i>)													
Immature	0	0	0	3	18	14	1	0	1	0	0	0	37	0.0
	Wilson's Warbler (<i>Wilsonia pusilla</i>)													
Immature	0	0	0	5	11	21	6	8	6	1	1	0	59	0.0
	Purple Finch (<i>Carpodacus purpureus</i>)													
Adult	0	0	0	0	0	0	0	1	0	0	2	1	4	13.8
Immature	0	0	1	0	0	1	5	10	0	2	6	0	25	
	Savannah Sparrow (<i>Passerculus sandwichensis</i>)													
Adult	0	0	0	0	0	0	0	2	1	0	2	0	5	7.1
Immature	0	0	0	0	0	6	7	29	8	5	9	1	65	
	Chipping Sparrow (<i>Spizella passerina</i>)													
Adult	0	0	0	0	0	0	0	0	1	1	0	0	2	2.5
Immature	0	0	0	1	2	4	1	3	13	12	38	5	79	
	White-crowned Sparrow (<i>Zonotrichia leucophrys</i>)													
Adult	0	0	0	0	0	0	0	0	0	0	3	0	3	4.4
Immature	0	0	0	0	0	0	0	2	8	24	26	5	65	
	Lincoln's Sparrow (<i>Melospiza lincolni</i>)													
Adult	0	0	0	0	0	0	0	1	0	1	0	0	2	5.1
Immature	0	0	0	0	0	2	3	12	11	4	5	0	37	

¹ Periods include, and extend from, the date given up to the date of the beginning of the next period.

TABLE 3
NUMBERS OF SOME PASSERINES AT ISLAND BEACH, NEW JERSEY, AUTUMN, 1963

Group	Period ¹												Totals	Per cent adult
	August					September				October				
	2	10	17	24	31	7	14	21	28	5	12	19-26		
White-breasted Nuthatch (<i>Sitta carolinensis</i>)														
Adult ♂	0	0	0	0	0	0	0	1	0	1	0	0	2	6.1
Adult ♀	0	0	0	0	0	0	0	1	0	0	0	0	1	
Immature ♂	0	0	0	0	0	0	0	1	2	7	3	0	13	
Immature ♀	0	0	0	0	0	1	3	7	5	10	6	1	33	
Red-breasted Nuthatch (<i>S. canadensis</i>)														
Adult ♂	0	0	0	0	0	4	6	24	20	6	18	15	93	28.6
Adult ♀	0	0	0	1	3	5	7	27	20	11	17	6	97	
Immature ♂	0	0	0	4	1	16	11	54	48	22	59	16	231	
Immature ♀	0	0	0	2	3	19	16	81	27	36	39	21	244	
Black-and-white Warbler (<i>Mniotilta varia</i>)														
Adult ♂	0	0	0	0	13	3	5	2	2	0	0	0	25	17.2
Adult ♀	0	0	0	0	12	0	3	2	0	0	0	0	17	
Immature ♂	2	0	1	14	38	16	16	12	3	0	0	0	102	
Immature ♀	1	2	1	20	30	15	10	19	2	1	0	0	101	
Cape May Warbler (<i>Dendroica tigrinum</i>)														
Adult ♂	0	0	0	0	1	1	1	2	0	0	1	0	6	6.5
Adult ♀	0	0	0	0	1	1	3	2	0	0	0	0	7	
Immature ♂	0	0	0	1	4	8	12	52	19	0	2	1	99	
Immature ♀	0	0	0	0	5	12	13	32	19	2	3	0	86	
Immature, ?	0	0	0	0	1	0	1	0	1	0	0	0	3	
Black-throated Blue Warbler (<i>D. caerulescens</i>)														
Adult ♂	0	0	0	0	0	1	1	1	2	0	0	0	5	5.8
Adult ♀	0	0	0	0	2	0	2	1	1	1	0	0	7	
Immature ♂	0	0	0	1	11	29	15	20	15	5	1	0	97	
Immature ♀	0	0	0	1	9	30	16	21	16	2	1	1	97	
Immature, ?	0	0	0	0	0	1	0	0	0	0	0	0	1	
Prairie Warbler (<i>D. discolor</i>)														
Adult ♂	0	0	0	0	0	2	2	2	2	0	0	0	8	20.6
Adult ♀	0	0	0	0	2	0	1	2	0	0	0	0	5	
Immature ♂	0	0	2	4	5	7	5	2	1	0	0	0	26	
Immature ♀	0	1	0	0	7	5	6	2	1	0	0	0	22	
Immature, ?	0	0	0	0	0	1	0	0	0	0	0	0	2	
Scarlet Tanager (<i>Piranga olivacea</i>)														
Adult ♂	0	0	0	0	0	0	0	1	1	0	0	0	2	6.3
Adult ♀	0	0	0	0	0	0	1	0	0	0	0	0	1	
Immature ♂	0	0	0	1	0	1	5	17	2	0	0	0	26	
Immature ♀	0	0	0	0	1	3	3	8	3	0	0	0	18	
Immature, ?	0	0	0	0	0	1	0	0	0	0	0	0	1	
Rose-breasted Grosbeak (<i>Phoebastria ludovicianus</i>)														
Adult ♂	0	0	0	0	0	0	0	4	1	0	0	0	5	13.2 (♂♂ only)
Adult ♀	0	0	0	0	0	0	0	1	0	0	0	0	1	
Unaged, ♀	0	0	0	1	1	2	3	16	4	1	0	0	28	
Immature ♂	0	0	0	1	2	2	6	20	2	0	0	0	33	

¹ Periods include, and extend from, the date given up to the date of the beginning of the next period.

chats occurred at the beginning and one at the end of the chat's migratory period.

Further, 11 species were represented by 50 to 99 individuals (Tables 2 and 3). The percentage of adults ranged from 0.0 to 30.5. In two species, the Nashville and Wilson's warblers, no adults were seen. Adults of Tennessee, Yellow, Bay-breasted, and Prairie warblers appeared throughout most of the season. One adult Connecticut Warbler occurred

at the beginning and the other at the end of the migratory period. Adults of Savannah, Chipping, and White-crowned sparrows were scarce, but they occurred during the weeks when many immatures of their species occurred. Adult male Rose-breasted Grosbeaks occurred toward the end of the migratory period, when most of the immature males occurred. Females were not aged.

Finally, 11 species were represented by 25 to 49 individuals (Tables 2 and 3). The percentage of adults ranged from 0.0 to 26.8. Adults of the Solitary Vireo and the Parula Warbler occurred throughout the migratory period of the species. Adults of the White-breasted Nuthatch, Philadelphia Vireo, Black-throated Green Warbler, Chestnut-sided Warbler, Scarlet Tanager, Purple Finch, and Lincoln's Sparrow were few, but for the most part they occurred during the middle of the migration of immatures of their species. No adults of the House Wren or Mourning Warbler were seen.

Sex was determined in eight species (Table 3). Males and females occurred in approximately equal numbers, with two exceptions. In the White-breasted Nuthatch 72 per cent of the immatures were female, and in the Scarlet Tanager 59 per cent of the immatures were male. Regardless of age, the times of occurrence of males coincided with the times of occurrence of females.

DISCUSSION

Considering only the timing of migration of adults and immatures, several migration patterns can be imagined: (a) *non-overlapping asynchronous*, in which all of the adults precede all of the immatures, or vice versa; (b) *overlapping asynchronous*, in which the times of migration of adults and immatures overlap, but the ratio of adults to immatures shifts; and (c) *synchronous*, in which the times of migration of adults and immatures coincide. Similar patterns can be described for differences in migration routes of adults and immatures and for differences in times and routes of males and females. In the following discussion the above terms refer only to differences in times of migration.

Differential migration in time.—If adequate sampling occurs throughout the period of migration, differences in time of migration between age classes can be determined. In none of the 44 species is there any indication of a non-overlapping asynchronous pattern, while there is evidence for a synchronous pattern in 26 species. The Red-eyed Vireo is the only species that clearly shows an overlapping asynchronous pattern, while in the remaining 17 species there are too few adults to permit distinguishing a synchronous pattern from an overlapping asynchronous pattern.

The decreasing ratio of adults to immatures during the season in the Red-eyed Vireo at Island Beach is interesting; a similar decrease has been

reported from Kansas (Tordoff and Mengel, 1956) and from Tennessee (Goodpasture, 1963). It should be pointed out that adult and immature Red-eyed Vireos begin migrating at the same time and that the migration period of adults almost spans that of immatures, although the adult peak is earlier than the immature peak.

Significance of synchronous migration.—The demonstration that adults and immatures travel at the same time in many species and the absence of evidence indicating a non-overlapping asynchronous migration pattern in any species may be of significance in the study of the orientation of long-distance migrants. Investigators of orientation of migratory birds (see reviews by Matthews, 1955, and Kramer, 1961) have placed emphasis, in their discussions, on those species in which adults and immatures are thought to travel separately in the autumn. They have hypothesized that young birds inherit a "directional tendency," which enables them to reach the normal winter quarters of the species. This widely-accepted hypothesis seems to have become a generalization that includes species in which even "differential migration" has not been demonstrated. Because the orientation of so few migratory species has been studied in the laboratory or the field, it is too early to generalize about the orientation of migratory birds. Premature generalization may deter investigation of potential orientational cues that may be used by migrants.

The data presented here indicate that the migration of adults generally coincides with the migration period of immatures. Therefore, it is possible that the direction taken in the autumn by young migrants is influenced by the adults, rather than being determined by an inherited "directional tendency." Thus, it seems possible that the cues used in orientation are terrestrial cues. Whether the migration route in the species studied is learned and, if so, whether the learned cues are terrestrial or celestial, remains to be determined.

The adult-immature ratio.—The percentage of adults in samples at Island Beach is low (Tables 1–3), as it is at other coastal localities (Baird and Nisbet, 1960; Drury and Keith, 1962), compared with samples from inland localities. For example, adult Blackpoll Warblers form less than 20 per cent of coastal samples, while adults form over 60 per cent in samples taken 20 miles inland in Massachusetts (Table 4). In contrast to the samples taken along the Atlantic coast, the sample from Bermuda contains over 50 per cent adults (Table 4). If the Bermuda birds are representative of the migrants over the ocean and if the Bermuda birds started their migration from the mainland, then the percentage of adults in the population as it crosses the coast should be high. Therefore, the low percentage of adults captured at coastal stations is not an accurate measure of the actual percentage of adults flying through the area.

TABLE 4
PERCENTAGE OF ADULTS IN SAMPLES OF THE BLACKPOLW WARBLER¹

<i>Location</i>	<i>Sample size</i>	<i>Per cent adult</i>
Massachusetts, inland, 1962	1,832	61
New England, coastal, 1959-61	55	18
New Jersey, coastal, 1962	78	19
New Jersey, coastal, 1963	658	9.6
Bermuda, 1962	136	58

¹ Data for all localities except for New Jersey, coastal, 1963, from Nisbet *et al.* (1963).

There is at least one possible explanation of the low percentage of adults in samples from the coast. The birds that have been seen arriving at Island Beach come in from over the ocean (Murray and Jehl, 1964). Perhaps the immatures stop at Island Beach, the first landfall, while adults more often fly the two or more miles across Barnegat Bay to the mainland. The significance of adult-immature ratios in samples of migratory birds cannot be determined until further evidence is available.

ACKNOWLEDGMENTS

I should like to thank the many persons who have helped me during the course of this study. The participants in the program, who assisted in many ways and enabled me to examine so many birds, are: Bruce Adams, Jim Baird, Walter and Peggy Bigger, Mrs. Blanche Bordner, Miss Dorothy Bordner, Bill Buskirk, Tom Crebbs, Miss Mary Rebecca Cregar, Stanley and Elise Dickerson, Mrs. Edna Donelson, Frank Frazier, Sr., Terry Frazier, Ron French, Bill Gette, Miss Gail Goldbeck, Jim and Hazel Gorman, Jon Greenlaw, Jim Hallett, Paul Hamer, Fran Hornick, Joseph R. Jehl [Sr.], John and Carol Logan, Terry Logue, Miss Ann Margerum, Ray Margerum, Fred Mears, John and Soonja Miller, Bob Miller, Chuck and Chip Neel, William and Margaret Pepper, Jim Richardson, Miss Helen Richardson, Chris and Ruth Rose, Tim Sterrett, Frank Sterrett, Jeff Swinebroad, Jim Tyrrell, Mrs. Mabel Warburton, Miss Charl Warburton, and Don Wilkins. Special thanks go to Mrs. Dickerson and Mrs. Warburton, codirectors of the banding program at Island Beach. Mr. Appel, the Chief of Forests and Parks Section, New Jersey State Department of Conservation and Economic Development, granted me permission to begin operations in August. John B. Verdier, Superintendent of Island Beach State Park, and his staff were most helpful in supporting our program. Joseph R. Jehl, Jr., Harrison B. Tordoff, and Robert W. Storer have read and criticized drafts of this paper. A grant from the Frank M. Chapman Memorial Fund of the American Museum of Natural History enabled me to participate in the program in 1963.

SUMMARY

The age and sex of several thousand passerine birds, captured at Island Beach, New Jersey, were determined and data on the migration of age and sex classes analyzed. The data indicate that in many passerine species

of eastern North America adults and immatures travel at approximately the same time. There is no convincing evidence that immatures travel separately from adults in any of the species studied. Therefore, there is the possibility that the direction taken by immatures on their first migration is influenced by the experienced adults and that the orientational cues used on subsequent migrations are learned during the first flight.

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