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VISIBLE MORNING FLIGHT OF NEOTROPICAL LANDBIRD MIGRANTS AT CAPE MAY, NEW JERSEY

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ABSTRACT.—We studied the autumn morning flight of Neotropical migrants for two years at Cape May, New Jersey. A majority (86%) of the 24,378 identified Neotropical migrants were warblers, while thrushes (0.01%) rarely made morning flights. A disproportionately large number of migrants was seen on the day of and the day following cold fronts. Only 23% of all Neotropical migrants flew on days not associated with cold fronts, and nearly 12% flew in rain. Morning flights of Neotropical migrants commenced in late July, and 72% passed before 15 September. All migrants flew north. At Cape May, 87% of visible morning flight occurred within 2 h after sunrise. We examine several hypotheses advanced to explain morning flight and reverse migration, and conclude that the morning flight of Neotropical landbird migrants at Cape May probably consists of a combination of birds returning to land from the ocean, birds compensating for lateral drift incurred during the previous night's migration, and birds seeking habitat in which to rest and forage. Topography may dictate the direction of morning flight. We suggest that researchers in North America commence studies of autumn passerine migration in late July and that researchers studying habitat selection by migrant passerines wait 2 to 3 h after sunrise before conducting surveys to avoid sampling birds undertaking morning flight. *Received 18 March 1991, accepted 13 January 1992.*

THE MORNING FLIGHT of nocturnally migrating songbirds occurs in several locations in North America (Gauthreaux 1978, Bingman 1980, Hall and Bell 1981) and Europe (Alerstam 1978, Lindstrom and Alerstam 1986). In the autumn of 1988 and 1989, we studied the morning flight of Neotropical migrant songbirds at Cape May Point, New Jersey (38°56′N, 74°58′W). We sought to determine which species undertook morning flight, study their flight behavior, and describe the seasonal and diel timing of their morning flight. In addition, we examined the influence of weather frontal systems on the number of birds observed flying. In 1988, we conducted a daily transect survey through representative vegetation types to compare the species composition of birds remaining in the habitat to that of birds migrating out. This comparison allowed us to determine which of the Neotropical migrants undertook morning flight and which did not. With our data, we examine seven of the hypotheses Richardson (1982) listed to explain northbound migration in the fall, as well as Bingman's (1980) onward-migration hypothesis for diurnal passerine migration.

The fact that so many species and such large numbers of migrants participate in morning flight strongly suggests that this behavior is an integral part of migration. Our study examines the function of morning flight. In addition, morning flight has important implications for researchers studying both seasonal timing of passerine migration and use of stopover habitat by passerine migrants.

METHODS

From 25 July 1988 to 5 October 1988 and from 25 July 1989 to 5 October 1989, a team of observers conducted daily watches from the top of a dredge-spoil containment dike at the Higbee Beach Wildlife Management Area (WMA) in Cape May, New Jersey (Fig. 1). The dike is level with the 10-m high forest canopy and affords an unimpeded view in all directions. We began counts at sunrise, and recorded observations in 0.5-h intervals starting at sunrise (time of sunrise taken from *New York Times* daily weather maps). We made observations each day for a minimum of 2 h after sunrise, and longer if the flight was still underway (i.e. >1 migrant per 5 min). The number of observers sampling the flight varied from one to five. On most days, we employed three observers, one of whom recorded data exclusively. We increased the number of observers when the magnitude of the flight increased; this had an unknown effect on the percentage of birds identified and the number of species seen on a given day, but facilitated a more thorough

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sampling of larger flights, which would have overwhelmed a smaller number of observers. We identified birds in flight by structure, size, flight characteristics, plumage, and call note. We do not include in this study data from the many birds we did not identify. All observers used 7×42 Zeiss Dialyt binoculars except one, who used 10×40 Zeiss Dialyt binoculars.

For each day, we recorded wind speed, wind direction, and temperature. Early in the study, we found no variation in the direction the birds flew when leaving Higbee Beach WMA, so we stopped recording the flight direction of migrants.

We conducted daily transects in 1988 at the conclusion of morning flight to determine the species composition of birds that did not fly out of Higbee Beach WMA. The 3.5-km transect sampled six habitat types representative of major vegetation types in Cape May: *Phragmites* marsh; deciduous forest; forest/field edge; dune forest; dune scrub; and old farm field. Observers used "pishing" noises and screech-owl calls to attract birds.

We focused on Neotropical migrants because of the pressing need for information on preserving and managing these diminishing species, and because we are preparing to study these migrants' use of habitat. We excluded Eastern Kingbirds (*Tyrannus tyrannus*), Bobolinks (*Dolichonyx oryzivorus*), and Dickcissels (*Spiza americana*) from the study because their meandering track and high altitude during morning flight made it impossible to assess their numbers accurately. Several species are notable for the difficulty of identification in flight; therefore, we pooled them for the flight count: *Empidonax* flycatchers, recorded as *Empidonax* spp.; Bay-breasted Warblers (*Dendroica castanea*) and Blackpoll Warblers (*D. striata*), recorded as "Baypoll" warblers; Northern Waterthrushes (*Seiurus noveboracensis*) and Louisiana Waterthrushes (*S. motacilla*) recorded as Waterthrush spp. (although observers believed the vast majority to be Northern Waterthrushes); and Connecticut Warblers (*Oporornis agilis*) and Mourning Warblers (*O. philadelphia*), recorded as *Oporornis* spp.

RESULTS

Although we observed birds flying north from the tree line to the east of the observation point, the greatest concentration of migrants moved northwest along the tree line in front of the observation point before flying north. These birds often passed the observers at or below eye level, at distances of 5 to 20 m. After leaving the trees individually or in small groups, the birds typically faced the wind while they gained altitude, and then proceeded north over the Cape May Canal (Intra-coastal Waterway) at 50 to 150 m altitude. In agreement with the observations of Bingman (1980), as individual migrants left the tree cover and were gaining altitude, they often joined other birds in flight. The flocking birds often were of different species. Birds at 50+ m altitude occasionally pursued other individuals down into the forest canopy in what appeared to be aggressive chases. Although this behavior was not quantified, observers judged that Northern Waterthrushes and Red-eyed Vireos (*Vireo olivaceus*) initiated this behavior more often than other species. On days with large flights, migrants left the forest canopy and gained altitude before reaching the observers. Many of these birds were too distant to identify.

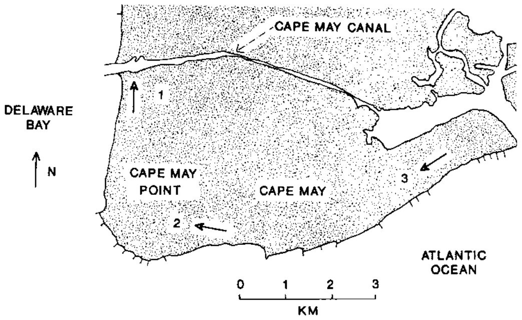

Fig. 1. Direction of morning flight at three sites in Cape May, New Jersey. Direction of flight estimated by ground observers. Site 1, dredge spoil "dike" at Higbee Beach Wildlife Management Area; site 2, Cape May Point State Park; and site 3, Sewell Point/Pittsburgh Avenue tract.

In 1988 and 1989, we counted 63,981 birds of all species as they undertook morning flight from Higbee Beach WMA and headed north. Of this number, we identified 24,378 (38%) as Neotropical migrant species; all other birds either were not identified or not Neotropical migrants. We counted an additional 3,819 Neotropical migrants during the 1988 field transects.

The majority of Neotropical migrants (78%) flew when wind speeds were light to moderate (6–19 km/h). Migrants initiated morning flight in a wide range of temperature conditions, from a minimum of 5°C to a maximum of 26°C. Migrants also flew under a variety of wind directions (Fig. 2), although the greatest numbers flew on mornings with winds from approximately 350° to 100° (NNW to E winds). Interestingly, inclement weather did not preclude morning flight; 11.7% of the Neotropical migrants we observed flew in drizzle or rain.

Researchers often view cold fronts as proxi-

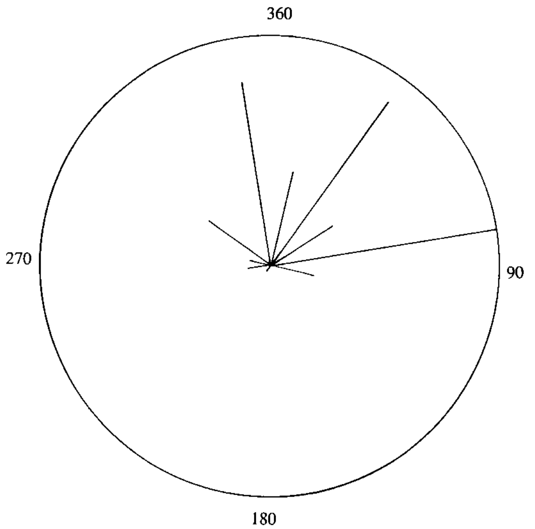

Fig. 2. Percentage of Neotropical migrants flying out of Higbee Beach WMA, Cape May, New Jersey, with each wind direction (compass divided into 15 equal sectors; radius = 23.7%; 386 birds [1.6%] flew under still conditions). Vectors represent percentage of birds observed when wind blew from direction of a given sector.

mate causes of migratory flights in autumn. To determine the effect of cold fronts on the number of Neotropical migrants observed in morning flight, we summed flight counts for five categories of days: (1) days one day before cold fronts; (2) days of cold fronts; (3) days one day after cold fronts; (4) days two days after cold fronts; and (5) all other days (Fig. 3; cold fronts illustrated in daily *New York Times* weather maps; cold-front days defined as days when a cold front passed through Cape May during the period from 12 h before to 12 h after the start of a given count). Figure 3 illustrates that cold fronts were associated with greater numbers of Neotropical migrants observed. The number of birds counted more than two days after a cold front or more than one day before a cold front accounted for less than 23% of the total seen. Wilcoxon paired-sample tests revealed that the numbers of birds seen on days of cold fronts were not significantly greater than those seen one day after a cold front ($P > 0.10$). This test also revealed that there were significantly fewer birds on the day before a cold front than on the day of a cold front ($P < 0.01$), and that there were significantly fewer birds on the second day after a cold front than on the day after a cold front. We excluded from our analysis days that we could place in more than one category. Anecdotal accounts from the same study site at Higbee Beach WMA report infrequent flights of up to about 600 warblers on spring mornings following cold fronts.

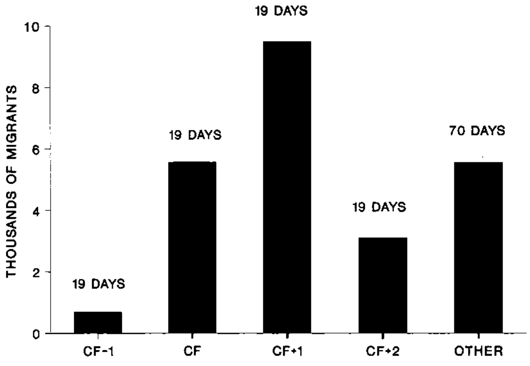

Fig. 3. Comparison of total number of Neotropical migrants counted flying on days defined as one day before a cold front (CF−1), day of a cold front (CF), day after a cold front (CF+1), two days after a cold front (CF+2), and all other days (OTHER).

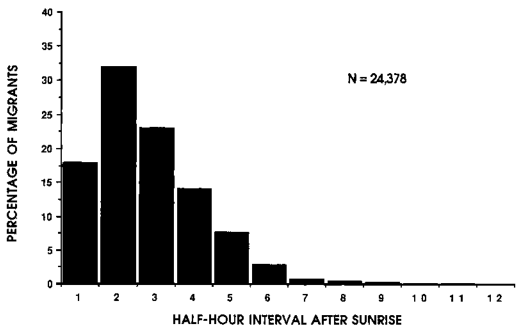

Fig. 4. Percentage of Neotropical migrants flying out of Higbee Beach WMA, Cape May, New Jersey, in each half-hour interval after sunrise.

In a few instances, flights continued until 6h after sunrise, but the vast majority (87%) of migrants flew in the first 2 h after sunrise, with the overall peak in the second half-hour interval (Fig. 4). The count for 19 of the 60 species considered in this study peaked in the third or later half-hour interval after sunrise. Notable are: Blue-gray Gnatcatchers (*Polioptila caerulea*; $n = 499$), which peaked in the third half-hour interval, but showed an extended flight period; Nashville Warblers (*Vermivora ruficapilla*; $n = 92$), which peaked in the fourth half-hour interval; and Tennessee Warblers (*V. peregrina*; $n = 372$), which peaked in the fifth half-hour interval. We cannot explain the atypical behavior of these three species.

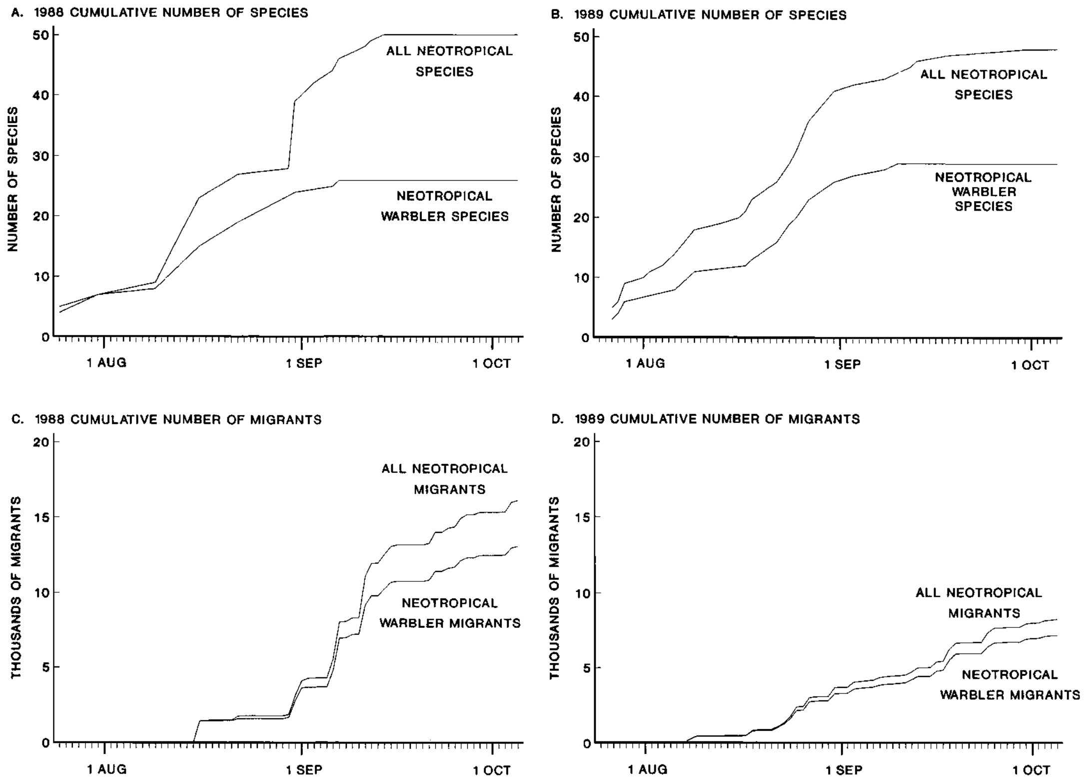

Fig. 5. Cumulative number of species and cumulative number of individuals from 1988 and 1989 flight counts. Graphs compare: (A) cumulative number of all Neotropical species observed undertaking morning flight with cumulative number of Neotropical warbler species observed undertaking morning flight in 1988; (B) same comparison for 1989; (C) cumulative number of individual Neotropical migrants and cumulative number of individual Neotropical warblers undertaking morning flight in 1988; and (D) same comparison for 1989.

The number of Neotropical species we identified daily, while variable, peaked in late August and mid-September in both 1988 and 1989, with a maximum species count of 37 on 31 August 1988, and 38 on 11 September 1988. In 1989, we tallied a maximum species number of 29 on both 31 August and 13 September. Both the cumulative number of Neotropical species and the cumulative number of individuals of those species showed the most rapid rates of increase at the same time of year (Fig. 5). The largest morning flight we observed during the study occurred on 11 September 1988 and involved 2,745 identified Neotropical migrants from 5,116 birds of all species identified. On 4 October 1988, a flight occurred of over 17,000 migrants, many of them Neotropical, but observers were unable to identify many of these birds to species. A morning flight exceeding 100,000 birds was observed in late October 1988, but the flight consisted almost entirely of non-Neotropical migrant species. We found that 72% of all Neotropical migrants counted during 1988 and 1989 left Cape May before 15 September.

The transect counts we conducted each morning in 1988 after the conclusion of morning flight suggest that thrushes do not undertake morning flight at Cape May. We noted large discrepancies between the 1988 dike and transect counts of warblers, flycatchers, orioles, thrushes, tanagers, and grosbeaks and buntings (Fig. 6). In 1988, when we performed habitat transects, warblers (81% of flight count, 60% of transect) and tanagers (2.5% of flight count, 0.81% of transect) constituted a much larger percentage of birds flying out than they did of the total transect counts. During the transects, however, we counted disproportionately larger numbers of thrushes, flycatchers, orioles, and grosbeaks/buntings, suggesting that these species are not as likely as warblers and tanagers to undertake morning flight. Statistical com-

TABLE 1. Total counts (with first and last dates in parentheses) for Neotropical migrant species during study period.

Species	Transect	Flight	
	1988	1988	1989
Archilochus colubris	14 (22 Aug–29 Sep)	13 (31 Aug–15 Sep)	44 (27 Jul–17 Sep)
Sphyrapicus varius	7 (31 Aug–4 Oct)	12 (14 Sep–5 Oct)	6 (30 Sep–5 Oct)
Contopus borealis	—	2 (12 Sep–14 Sep)	—
C. virens	21 (20 Aug–26 Sep)	98 (16 Aug–4 Oct)	6 (18 Sep–3 Oct)
Empidonax flaviventris	9 (30 Aug–23 Sep)	—	—
E. virescens	—	—	1 (9 Aug)
E. alnorum	1 (7 Sep)	—	—
E. trailii	1 (16 Aug)	—	—
"Traill's flycatchers[a]	14 (16 Aug–25 Sep)	—	—
E. minimus	33 (16 Aug–26 Sep)	—	—
Empidonax spp.	59 (25 Aug–15 Sep)	120 (16 Aug–5 Oct)	31 (18 Aug–24 Sep)
Myiarchus crinitus	39 (16 Aug–30 Sep)	3 (31 Aug–7 Sep)	1 (25 Aug)
Polioptila caerulea	52 (16 Aug–23 Sep)	351 (16 Aug–5 Oct)	148 (29 Jul–5 Oct)
Catharus fuscescens	196 (16 Aug–26 Sep)	15 (31 Aug–22 Sep)	5 (31 Aug–24 Sep)
C. minimus	1 (5 Oct)	—	—
C. ustulatus	26 (7 Sep–4 Oct)	1 (3 Sep)	—
Hylocichla mustelina	1 (26 Sep)	—	—
Dumetella carolinensis	157 (22 Aug–5 Oct)	7 (1 Sep–28 Sep)	—
Vireo solitarius	3 (26 Sep–4 Oct)	4 (11 Sep–5 Oct)	—
V. flavifrons	3 (8 Sep–12 Sep)	2 (6 Sep–11 Sep)	—
V. gilvus	1 (15 Sep)	—	1 (27 Aug)
V. philadelphicus	9 (1 Sep–19 Sep)	17 (31 Aug–26 Sep)	3 (13 Sep–25 Sep)
V. olivaceus	30i (16 Aug–5 Oct)	1,205 (22 Aug–5 Oct)	258 (16 Aug–5 Oct)
Vermivora pinus	93 (16 Aug–19 Sep)	74 (16 Aug–22 Sep)	30 (9 Aug–16 Sep)
V. chrysoptera	10 (16 Aug–11 Sep)	6 (31 Aug–22 Sep)	3 (24 Aug–31 Aug)
V. peregrina	38 (16 Aug–22 Sep)	320 (16 Aug–4 Oct)	52 (27 Aug–5 Oct)
V. ruficapilla	11 (2 Sep–19 Sep)	72 (22 Aug–4 Oct)	20 (10 Sep–3 Oct)
Parula americana	8 (1 Sep–4 Oct)	491 (31 Aug–5 Oct)	429 (22 Aug–4 Oct)
Dendroica petechia	64 (16 Aug–25 Sep)	456 (25 Jul–4 Oct)	606 (27 Jul–30 Sep)
D. pensylvanica	51 (16 Aug–26 Sep)	130 (16 Aug–4 Oct)	21 (31 Aug–24 Sep)
D. magnolia	62 (25 Aug–4 Oct)	369 (31 Aug–5 Oct)	155 (17 Aug–4 Oct)
D. tigrina	34 (16 Aug–22 Sep)	522 (16 Aug–5 Oct)	224 (22 Aug–3 Oct)
D. caerulescens	171 (16 Aug–5 Oct)	1,035 (22 Aug–5 Oct)	441 (24 Aug–5 Oct)
D. virens	19 (30 Aug–23 Sep)	298 (31 Aug–5 Oct)	76 (24 Aug–3 Oct)
D. fusca	41 (16 Aug–13 Sep)	183 (16 Aug–5 Oct)	47 (22 Aug–3 Oct)
D. dominica	—	—	3 (29 Jul–22 Aug)
D. discolor	98 (20 Aug–23 Sep)	82 (31 Jul–5 Oct)	48 (29 Jul–1 Oct)
D. castanea	52 (1 Sep–22 Sep)	—	—
D. striata	34 (10 Sep–5 Oct)	—	—
"Baypoll" Warbler[b]	—	1,025 (22 Aug–5 Oct)	417 (27 Aug–5 Oct)
D. cerulea	—	1 (31 Aug)	1 (31 Aug)
Mniotilta varia	486 (16 Aug–4 Oct)	723 (31 Jul–5 Oct)	502 (2 Aug–1 Oct)
Setophaga ruticilla	576 (16 Aug–5 Oct)	6,419 (25 Jul–5 Oct)	3,430 (6 Aug–3 Oct)
Protonotaria citrea	5 (16 Aug–31 Aug)	11 (31 Jul–31 Aug)	4 (28 Jul–23 Aug)
Helmitheros vermivorus	23 (16 Aug–19 Sep)	12 (6 Aug–7 Sep)	2 (27 Aug–13 Sep)
Seiurus aurocapillus	220 (16 Aug–26 Sep)	260 (25 Jul–4 Oct)	52 (9 Aug–24 Sep)
S. noveboracensis	121 (16 Aug–29 Sep)	—	—
S. motacilla	3 (20 Aug)	—	—
Waterthrush spp.[c]	—	475 (25 Jul–5 Oct)	580 (27 Jul–20 Sep)
Oporornis formosus	5 (16 Aug–20 Aug)	—	—
O. agilis	6 (31 Aug–4 Oct)	22 (6 Sep–4 Oct)	11 (8 Sep–25 Sep)
O. philadelphia	11 (16 Aug–4 Oct)	8 (16 Aug–4 Oct)	2 (3 Sep–16 Sep)
Oporornis spp.[d]	—	18 (11 Sep–4 Oct)	1 (18 Sep)
Wilsonia citrina	2 (16 Aug–31 Aug)	6 (7 Sep–14 Sep)	3 (18 Aug–6 Sep)
W. pusilla	4 (26 Aug–12 Sep)	48 (16 Aug–14 Sep)	12 (31 Aug–30 Sep)
W. canadensis	47 (16 Aug–26 Sep)	36 (9 Aug–3 Oct)	11 (9 Aug–1 Oct)
Icteria virens	16 (16 Aug–15 Sep)	2 (7 Sep)	2 (25 Aug–8 Sep)
Piranga rubra	—	—	—
P. olivacea	31 (1 Sep–27 Sep)	—	—

TABLE 1. Continued.

Species	Transect 1988	Flight 1988	Flight 1989
Tanager spp.[e]	—	406 (16 Aug-5 Oct)	86 (1 Aug-5 Oct)
Pheucticus ludovicianus	15 (29 Aug-4 Oct)	91 (31 Aug-4 Oct)	20 (12 Sep-4 Oct)
Guiraca caerulea	74 (20 Aug-29 Sep)	49 (16 Aug-25 Sep)	93 (13 Aug-27 Sep)
Passerina cyanea	90 (20 Aug-5 Oct)	124 (16 Aug-4 Oct)	65 (4 Aug-5 Oct)
Icterus spurius	3 (16 Aug-5 Sep)	—	—
I. galbula	282 (23 Aug-30 Sep)	—	—
Oriole spp.[f]	—	501 (16 Aug-5 Oct)	291 (27 Jul-3 Oct)
Coccyzus americanus	47 (20 Aug-5 Oct)	5 (30 Aug-12 Sep)	—
C. erythropthalmus	20 (16 Aug-26 Sep)	2 (11 Sep)	1 (31 Aug)
TOTALS	3,821	16,132	8,246

[a] *Empidonax alnorum* + *E. traillii*; [b] *Dendroica castanea* + *D. striata*; [c] *Seiurus noveboracensis* + *S. motacilla*; [d] *Oporornis agilis* + *O. philadelphia*; [e] *Piranga rubra* + *P. olivacea*; [f] *Icterus spurius* + *I. galbula*.

parisons of the proportion of these species groups seen flying out versus those seen during the transect counts revealed significant differences (chi-square; $P < 0.01$) for warblers, orioles, thrushes, grosbeaks/buntings, flycatchers, and tanagers. In contrast, the taxa constituting the morning flight remained remarkably stable from one year to the next (Fig. 6). Vireos and flycatchers are the exceptions; percentage compositions for both taxa fell markedly from 1988 to 1989. We rarely observed cuckoos flying out.

After the first week of September in both years of the study, we observed dozens of Sharp-shinned Hawks (*Accipiter striatus*), Cooper's Hawks (*A. cooperii*), and Merlins (*Falco columbarius*) hunting passerines engaged in morning flight. When morning flights occurred during this period, observers noted the pursuit or cap-

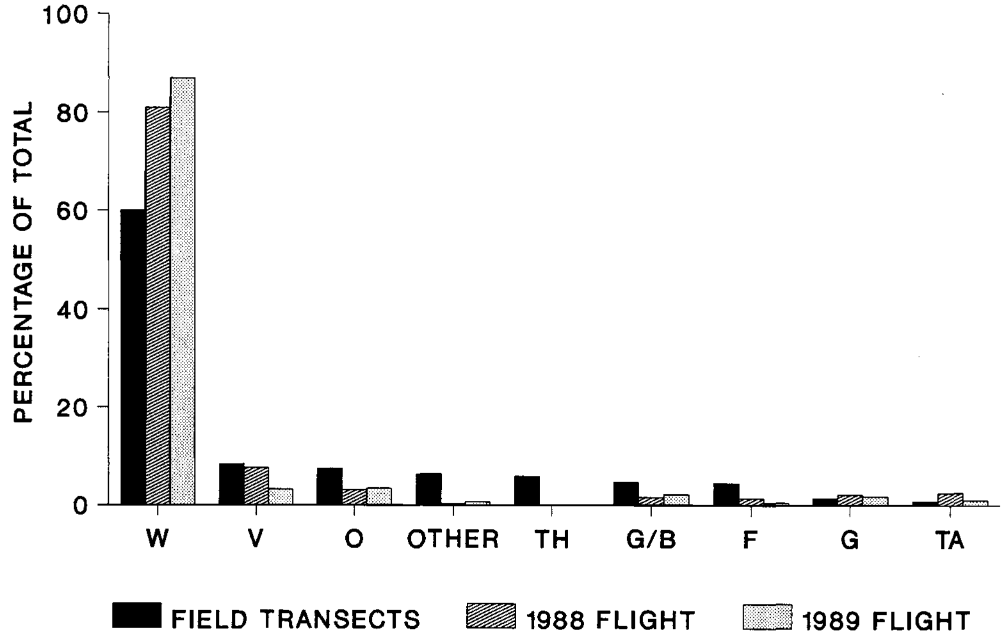

Fig. 6. Comparison of taxa engaged in morning flight with those observed on transects. Percentages represent contribution of each taxon to total of each survey. On the X-axis, W = warblers, V = vireos, O = orioles, TH = thrushes, G/B = grosbeaks and buntings, F = flycatchers, G = gnatcatchers, and TA = tanagers. OTHER refers to other Neotropical species: Ruby-throated Hummingbird (*Archilochus colubris*), Yellow-bellied Sapsucker (*Sphyrapicus varius*), Gray Catbird (*Dumetella carolinensis*), Yellow-billed Cuckoo (*Coccyzus americanus*), and Black-billed Cuckoo (*Coccyzus erythrothalmus*). See Table 1 for complete list.

ture of several passerines every morning. Observers searched for morning flight above the Cape May Canal on at least five days when the flights at the study site were substantial, but did not find significant numbers of migrants. Migrants to the north of the study site either were already too high or too dispersed for us to observe.

DISCUSSION

INFLUENCE OF WEATHER

Although precipitation is thought to severely hamper passerine migration (Richardson 1978), nearly 12% of the total number of Neotropical migrants we identified in this study flew in rain or drizzle. Low-altitude migration in inclement weather may be more common than currently believed. Richardson (1978) also warned that researchers have overemphasized associations between cold fronts and peak migratory flights, mostly because of observer bias. Cold fronts at Cape May appear to make passerine migration far more visible. Radar studies would be necessary, however, to compare the number of birds aloft with the number observed at low altitudes. At Cape May, while the majority of birds seen flew on days associated with the passage of a cold front, 22.7% of observed Neotropical migrants did not. Furthermore, the majority of birds flew when winds were from northerly to easterly directions, although this finding may simply be the result of prevailing wind direction after the passage of a cold front through the area. Most birds flew under conditions of light to moderate wind speeds. Many of the smaller passerines, but especially Blue-gray Gnatcatchers, appear to have some difficulty flying in anything but a light wind.

SPECIES AND AGE COMPOSITION OF MORNING FLIGHT

Why are certain species more likely than others to undertake morning flight? The percentage composition of species at Cape May is reasonably close to the findings of Bingman (1980) and of Hall and Bell (1981). Warblers comprised the majority of Neotropical species (81% in Cape May, 84% in New York, 71% in West Virginia), although neither Bingman (1980) nor Hall and Bell (1981) differentiated between Neotropical and other species. Vireos were represented equally in field and flight counts at Cape May. The most striking discrepancy between our transect counts and our flight counts occurred in the thrushes, which constituted 5.5% of the transect total but less than 0.1% of the flight count. The absence of thrushes in Cape May's morning flight differs markedly from observations from another coastal site (Falsterbo, Sweden; Roos 1974), as well as an inland site (West Virginia; Hall and Bell 1981), suggesting that site-specific factors may greatly influence the species composition of morning flights. Bingman (1980), for example, found that 11% of the visible early morning flight in eastern New York consisted of sparrows, although this finding may also be a result of the later dates of his study. Bingman's study also focused on an earlier diel flight that he felt represented the continuation of prior nocturnal migration. Perhaps the variation in the species composition of morning flight at our site reflects differences among taxa in the ability to compensate for drift (S. A. Gauthreaux, pers. comm.), or differences in foraging technique and habitat use.

Able (1977) and Alerstam (1978) suggested that most of the individuals participating in autumn morning flight are immature. Based on banding data from nearby sites (Gustafson 1986–1987) and observation of birds before they flew, we believe this is also the case at our study site. Future studies would be useful to ascertain which individuals from each species are participating in morning flight; additional banding studies, for example, could determine the age, sex, and weight of these migrants. Such information from several sites could yield important insight into the various factors influencing morning flight.

DIEL TIMING

The diel timing of morning flight at Cape May is comparable to that described by other workers in North America (Gauthreaux 1978, Hall and Bell 1981). As at Cape May (Fig. 4), these studies also report that morning flight commences near dawn, peaks in the first 2 to 3 h after sunrise, and abates by 1000 to 1200. Extrapolating from Figure 4, we predict that a substantial percentage of Neotropical migrants at Cape May begins morning flight before sunrise. An observer conducting a survey during the morning flight period has no means of separating birds that have already selected a stopover site from those that have not. Although migrant birds are most active, audible, and visible during the early morning hours, our findings bring into question the idea that birds at this time have selected stopover habitat. Because the peak of morning flight activity occurs in the second half-hour interval after sunrise (Fig. 4) and more than 87% of visible morning flight occurs within the first 2 h after sunrise, we suggest that researchers studying the habitat choice of songbird migrants commence surveys of migrants at least 2 to 3 h after sunrise.

SEASONAL TIMING

It is apparent from the results of this study that a substantial portion of Neotropical passerine migration occurs quite early in the fall—in fact, in late summer. In the two years of our study, we witnessed morning flights of dozens of individual migrants of several species as early as the last week of July. These flights consisted of Yellow Warblers (*Dendroica petechia*), Prothonotary Warblers (*Protonotaria citrea*), Yellow-throated Warblers (*D. dominica*), Kentucky Warblers (*Oporornis formosus*), and Louisiana Waterthrushes. This early migration may escape detection at inland sites, where migration tends to be diffuse. The Cape May peninsula concentrates migrants and makes migration far more visible. Our findings suggest that traditional views of the seasonal and diel timing of autumn passerine migration should be reexamined.

FUNCTIONAL SIGNIFICANCE OF MORNING FLIGHT

Why do passerines—normally nocturnal migrants—undertake diurnal flight? Nocturnal migrants would be expected to spend daylight hours foraging or resting in preparation for subsequent flight at night. Furthermore, nocturnal migration holds many benefits for passerines, while diurnal passerine migration is unusual in several respects. First, the diurnal atmosphere is less stable than at night because of the presence of thermals and other turbulence. In addition, temperatures are higher during the day, increasing evaporative cooling and, hence, water loss in migrating birds. Finally, during diurnal flight at low altitudes along coastlines, songbirds are exposed to intense predation. Raptor predation is a significant risk at many migrant stopover sites (Lindstrom 1989, Moore et al. 1990), especially coastal sites where migrant raptors are abundant, such as Cape May. We note, however, that the early migration of most Neotropical songbirds occurs before the migration of most bird-eating raptors, so hawk predation probably does not affect the majority of these migrants.

At Cape May, morning flight occurs among more than 60 species of passerine and other migrants. Studies from North America and Europe show that the morning flight of nocturnal migrant songbirds may be ubiquitous; hundreds of nocturnal migrant species worldwide undertake morning flight. Because so many species and such large numbers of migrants are involved, morning flight should be considered an integral part of migration. Richardson (1982) identified 11 hypotheses that attempt to explain reverse migration. We discuss seven of these that are relevant to our study of morning flight. In addition, we examine the onward-migration hypothesis of Bingman (1980).

(1) Late-summer dispersal of juveniles and adults.—Many of the species we observed in Cape May's morning flights breed far to the north of Cape May; only some of the very early migrants may represent dispersed birds. Late-summer dispersal thus fails to explain the presence of most species participating in Cape May's morning flights.

(2) Local flights.—Local flights involve short distances to roosting or feeding areas. Birds engaged in such flights may be seeking out particular habitats. Alerstam (1978) and Lindstrom flight on the coast of southern Sweden occurred when large concentrations of passerine migrants sought less-contested or more-appropriate habitat. Banding data from autumn migration in southern Sweden indicates that underweight, immature birds are disproportionately represented among reoriented migrants (Lindstrom and Alerstam 1986); reorientation, thus, may be an adaptive response by migrants with low fat reserves (Lindstrom and Alerstam 1986). Moore et al. (1990) noted that habitat suitable for rapid accumulation of fat deposits, necessary for long flights, is probably limited. In the resort community of Cape May, development has fragmented once-extensive wooded areas, forcing migrants to take refuge

in the small areas of suitable habitat, to cross the 18 km of Delaware Bay to the southwest, or to seek habitat to the north. A search for more suitable—and less contested—foraging habitat may influence morning flight at Cape May. We call this the habitat hypothesis, and consider it a plausible explanation of a large portion of morning flight at Cape May. The Cape May peninsula's dearth of suitable foraging habitat may, in part, explain the function of morning flight at Cape May.

(3) Dawn reorientation among landbirds migrating over the sea from a southwest track to a northwest track, to regain land.—It is likely that many of the migrants in Cape May's morning flights arrive in the early morning from offshore (Stone 1937:41-44, 772, 819; pers. observ.). We note, however, that how and why migrant birds reach Cape May may not be related to what they do after they get there. The continuation of reoriented flight after the birds have reached land, therefore, calls for additional explanations. This hypothesis appears to overlap the next.

(4) Overcompensation for wind drift.—This involves redetermining migratory direction to correct for wind drift incurred during the previous night's flight (Gauthreaux 1978, Moore 1990). At other North American locations, fall landbird migrants, arriving from offshore, fly west or northwest in the first few hours after sunrise (Murray 1976, Able 1977; Gauthreaux and Kerlinger, unpubl. data). Gauthreaux (1978) suggested that these flights, and similar flights observed at inland locations, enable birds to return to a "principal axis of migration" after being drifted by wind during the previous night's migration.

An unknown percentage of birds seen in morning flight at Cape May probably flew out over the ocean at night and returned to shore before or after dawn. In addition to explaining some portion of autumn morning flight, this hypothesis also helps to explain reports from the same study site of flights of up to about 600 warblers on spring mornings following cold fronts. Spring or fall migrants crossing the Delaware Bay at night that were drifted out to sea by northwest winds would benefit by reorienting to reach the coast and compensate for wind drift. Redirected migration could explain both why the birds arrive in Cape May (after correcting for offshore drift) and why, in the fall, they orient away from a seasonally appropriate heading. Moreover, the occurrence of greater numbers of migrants after cold fronts is consistent with the drift hypothesis. At Cape May, however, the direction of morning flight remains constant regardless of the wind direction the previous night, indicating that a considerable portion of morning flight at this site may not be redirected migration (sensu Gauthreaux 1978) to compensate for drift. Nevertheless, without information on the direction of nocturnal migration, we cannot reject this hypothesis; nor, unfortunately, is this hypothesis mutually exclusive of the others we discuss. For some species and age classes, redirection may be a reality, especially among weak fliers.

(5) Reverse flights along coastlines.—This refers to the tendency of some diurnal migrants to follow the coast. Nocturnal migrants commonly depart from coastlines; nocturnal migrants undertaking morning flight, however, may be reluctant to cross water, either if they are in search of stopover habitat, or if winds push them farther offshore. Autumn landbird migrants at Cape May, hesitant to cross Delaware Bay during the day, may redirect their flight up the west side of the peninsula. The morning orientation of migrants at three locations in Cape May (Fig. 1) indicates that at least some component of the morning flight consists of birds following the peninsula's shoreline. Other researchers have noted the importance of topography and coastlines on orientation (Bingman 1980, Richardson 1990). Stone's (1937:45, 675, 819, 851) observations also strongly suggest that the direction of morning flight at Cape May depends on topography. We have no evidence, however, that individual migrants follow this pattern. We emphasize that this hypothesis treats only the direction of morning flight, not its function.

(6) Disorientation.—This refers to the idea that disoriented individuals under different wind conditions would fly in different directions. A large proportion of immature migrants at Cape May may be off course and need to reorient regardless of wind (Richardson, pers. comm.); some of Cape May's morning flight might represent the reverse migration of disoriented, maladapted individuals (Richardson 1982). Morning flight at Cape May is consistently to the north. However, some maladapted individuals may orient consistently in inappropriate directions (Richardson 1982). As immature birds appear to constitute the majority of birds in-

volved in morning flight, this hypothesis is plausible. Clear differences exist among species and species groups in the tendency to perform morning flight, however, suggesting that factors other than immature maladaptedness are involved in morning flight. This hypothesis overlaps in part with the next.

(7) Polarity mistakes.—Under this hypothesis, individuals with physiological anomalies might make a polarity mistake and fly in a seasonally inappropriate direction. Flights at Cape May may involve thousands of individuals; it is unlikely that all have suffered from the same condition. Birds in need of rest or food, however, might simply reorient inland, away from the coast (Alerstam 1978; hypothesis 2, above). We are planning banding studies at Cape May to investigate the physiological condition of birds engaged in morning flight.

(8) Onward migration.—This hypothesis indicates that early morning flights may simply be the continuation of the previous night's migration, and the direction of these diurnal flights may be influenced by topography (Bingman 1980). Bingman's (1980) findings support Kerlinger and Moore (1989), who noted that when nocturnal migrants fly during the day they should do so in the early morning, when diurnal atmospheric structure is most favorable. At Cape May, where nocturnal passerine migration is to the southwest (Gauthreaux and Kerlinger, unpubl. data), morning flight to the north does not constitute onward migration, unless the birds involved in morning flight are coming from out at sea and continuing a redirected flight inland, an explanation that overlaps hypotheses (3) and (4) above. Moreover, morning flights at Cape May occur later in the day than the flights reported by Bingman (1980), suggesting a different function.

In summary, we suggest that studies of the habitat use of migrant passerines commence 2 to 3 h after sunrise to minimize the likelihood of counting migrants that have not yet selected stopover habitat. Further, we suggest that researchers begin studies of migrant passerines in North America in the latter part of July. Finally, we conclude that a portion of Cape May's morning flight may be birds regaining land after finding themselves out at sea at dawn. Some of these birds may be compensating for drift incurred during nocturnal migration, and many—regardless of how they arrived at Cape May—are seeking appropriate habitat in which to rest and forage. The direction of morning flight at our study site may be strongly affected by the topography of the Cape May peninsula.

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