INLAND MORNING FLIGHT BEHAVIOR OF NOCTURNAL PASSERINE MIGRANTS IN EASTERN NEW YORK

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ABSTRACT.—The morning movement by nocturnal passerine migrants over inland areas is poorly understood. Gauthreaux (1978) suggested that morning flight involves a correction for displacement by wind accrued during nocturnal migration. If so, morning flight should: (1) involve a change in flight direction from that at night, i.e. a reorientation, and (2) be directed upwind. Gauthreaux's observations in South Carolina agreed with these predictions, but morning migrants that I observed in eastern New York flew northeast during spring and southwest during autumn— the same directions flown at night. In general, the direction of morning flight was independent of wind direction, with birds flying relatively fixed northeast-southwest tracks. Unlike migrants in South Carolina, morning migrants in New York did not correct for displacement accrued at night; I interpret their behavior as continued migration. Associated with morning flight, however, were increased variability in the direction of vanishing bearings compared with that observed at night and a tendency for some birds to be affected by local topographic features. These results suggest that other factors besides continued migration affect the directional behavior of morning migrants. *Received 3 August 1979, accepted 10 January 1980.*

PASSERINE species normally considered obligate nocturnal migrants are often observed moving during daylight hours. Research on the diurnal movements of nocturnal passerine migrants has focused on the coastward flight of birds at sea. Such flights may be a continuation of the previous night's migration with no change in direction, as in the case of the spring trans-Gulf migration (Gauthreaux 1971). Diurnal coastward movements may also involve a change in flight track from the previous night, as in the case of so-called dawn reorientation (Baird and Nisbet 1960, Myres 1964, Murray 1976, Able 1977, Richardson 1978a). Morning flight with reorientation presumably occurs when migrants, which typically fly overland, are over water at dawn. The reoriented movement at dawn usually results in birds reaching the coast.

Inland morning movement by nocturnal migrants has received little attention aside from scattered anecdotal reports (Bagg 1950, Lack and Lack 1953). Basing his hypothesis upon data from western South Carolina, Gauthreaux (1978) suggested that inland morning flight functions to correct for wind displacement from a preferred heading during a previous nocturnal migration. In this study, I investigated the morning flight behavior of nocturnal passerine migrants in eastern New York to assess the generality of Gauthreaux's hypothesis.

METHODS

During spring and autumn 1978, observations of nocturnal migrants flying in the morning were conducted at three sites within 50 km of Albany, New York:

(1) Wilson M. Powell Bird Sanctuary, Old Chatham, Columbia County, New York—a 1.0-ha grassy meadow bordered to the east, south, and west by mixed hardwood forest and to the north by farmland and hedgerows. The local topography lacked any notable feature that might have affected the directionality of morning migrants. Observations at this site took place on 15 mornings in spring and 15 in autumn.

(2) Berne, Albany County, New York—0.5 ha of open, early successional vegetation bordered on the south and east by mixed hardwood forest and to the north and west by farmland with scattered deciduous
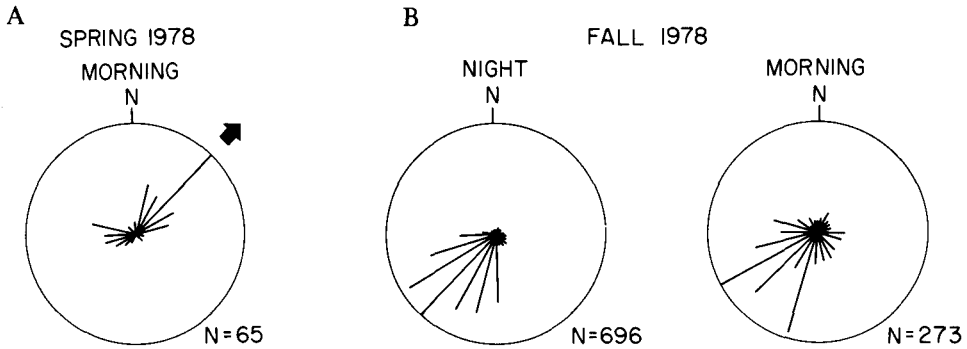
Fig. 1. **A.** Directionality of morning flight during spring 1978. North is at the top of the diagram, and the radius is equal to the greatest number of vanishing bearings in any 15° sector. N at the lower right of diagram is the total number of vanishing bearings recorded. Arrow indicates the predominant direction of nocturnal migration. **B.** Directionality of morning flight and nocturnal migration during autumn 1978.

woods. Although the study site was located on an east-west oriented ridge, birds observed here were never seen to alter their flight behavior upon approaching or crossing the ridge. Observations at this location occurred on six mornings in spring and one in autumn.

(3) Castleton, Rensselaer County, New York—1.0 ha of open, early successional vegetation bordered on all sides by young deciduous woods and early successional vegetation. The north-south oriented Hudson River is located 100 m west of the study site, and the associated north-south ridges delineating the Hudson valley were both visible. The effect of the local topography at this site is examined below. Observations at Castleton occurred on 20 mornings in autumn only.

In the spring, the search for morning migrants generally started 30 min before sunrise and continued for 2 h. Few birds were located before sunrise (Bingman 1978), so autumn observations were not started until sunrise. Nocturnal passerine migrants were assumed to be engaging in "morning flight" if they were flying when seen and either continued to fly until out of sight or landed with a steep descent from an altitude at least 1.5 times the height of the highest trees. Nocturnal migrants were identified to family by size, shape, characteristic flight patterns, and vocalizations. Identification to species was rarely possible. Birds were followed with 7× binoculars until they disappeared from view. The vanishing bearing of a bird flying nearly overhead was immediately recorded with a compass. Visual adjustments in the vanishing bearing of birds not flying overhead were made to correct for errors introduced by parallax. The flight direction of individual birds in a flock could not be assumed to be independent; therefore, a flock of birds was treated as statistically equivalent to a single bird for both spring and autumn data.

Nocturnal migration was monitored on 33 evenings during autumn by portable ceilometer (Gauthreaux 1969). Two 100-W bulbs and 20× binoculars were used. Moonwatching (Lowery 1951) with a 20× spotting scope was used on three additional autumn evenings. All watches took place at Castleton, usually 1.5 h after sunset.

Wind data were obtained from the National Weather Service at the Albany County Airport. Winds aloft were recorded at 0600 and 1800 EST.

RESULTS

A total of 542 nocturnal passerine migrants (112 in spring; 430 in autumn) was observed engaging in morning flight during 1978. Warblers (Parulidae) accounted for 84% of the individuals, while sparrows (Emberizidae) composed 11%. Thrushes (Turdidae), Rose-breasted Grosbeaks (*Pheucticus ludovicianus*), Northern Orioles (*Icterus galbula*), and a Scarlet Tanager (*Piranga olivacea*) accounted for the remaining birds.

Morning flight is a highly social phenomenon. Birds often flocked and regularly

TABLE 1. Directionality of migrants on mornings with five or more vanishing bearings and nights with 10 or more birds.

	Night				Morning		
Date	*n*	Mean flight direction	Length mean vector (*r*)	Date	*n*	Mean flight direction	Length mean vector (*r*)
Nights and mornings in sequence							
26 Aug	52	231°	0.71	27 Aug	15	237°	0.88
27 Aug	41	256°	0.91	28 Aug	9	NS[a]	0.53
31 Aug	14	222°	0.56	1 Sept	5	NS	0.54
1 Sept	37	214°	0.86	2 Sept	7	NS	0.34
2 Sept	15	NS	0.43	3 Sept	21	215°	0.43
4 Sept	21	215°	0.87	5 Sept	7	NS	0.17
5 Sept	11	NS	0.49	6 Sept	14	181°	0.68
7 Sept	25	198°	0.76	8 Sept	6	252°	0.86
12 Sept	29	189°	0.64	13 Sept	6	NS	0.61
16 Sept	28	190°	0.84	17 Sept	13	224°	0.55
19 Sept	30	213°	0.76	20 Sept	13	244°	0.48
22 Sept	32	222°	0.92	23 Sept	10	207°	0.76
23 Sept	24	217°	0.54	24 Sept	16	251°	0.73
28 Sept	39	201°	0.85	29 Sept	5	196°	0.82
29 Sept	13	255°	0.88	+30 Sept[b]	11	NS	0.05
2 Oct	31	229°	0.95	3 Oct	11	229°	0.92
Nights and mornings out of sequence							
28 Aug	15	348°	0.74	14 Sept	12	207°	0.57
29 Aug	28	220°	0.69	16 Sept	8	NS	0.52
3 Sept	22	210°	0.78	21 Sept	11	223°	0.82
9 Sept	21	212°	0.80	22 Sept	8	83°	0.64
25 Sept	43	184°	0.93	28 Sept	8	198°	0.72
7 Oct	33	203°	0.88	2 Oct	5	NS	0.30
				+4 Oct	13	NS	0.13
				7 Oct	11	215°	0.62
Mean length *r* (± SD)	*0.76 ± 0.15[c]				*0.63 ± 0.19		

[a] NS = distribution of vanishing bearings does not deviate from random.
[b] + = bimodal distribution, excluded from analysis.
[c] * = difference significant at *P* = 0.05 level.

uttered call notes similar to those heard at night. Individuals often took flight and joined passing birds, and flying migrants often changed their flight tracks, joining others moving in a different direction.

Morning migrants were usually observed 15–50 m above the ground and flew either a linear or zig-zag flight track. Migrants in zig-zag flight regularly changed their headings by as much as 90° during the course of an observation. These heading changes, however, cancelled each other, as birds generally moved in one primary direction [see Bingman (1978) for details on the behavioral correlates of morning flight].

Spring directionality.—The distribution of vanishing bearings for morning migrants during spring was significantly oriented ($P < 0.001$, Rayleigh Test; Batschelet 1972), with most birds moving northeast (Fig. 1A). This was also the direction of nocturnal migration observed in this area (Able 1974b, unpubl. data). In addition to the northeastward movement, a smaller westerly movement also occurred. The bimodal distribution of vanishing bearings in Fig. 1A precluded any calculation of mean direction and derived statistics for morning migrants during spring. The majority of morning migrants in spring, however, moved in a direction similar to predominating directions at night.
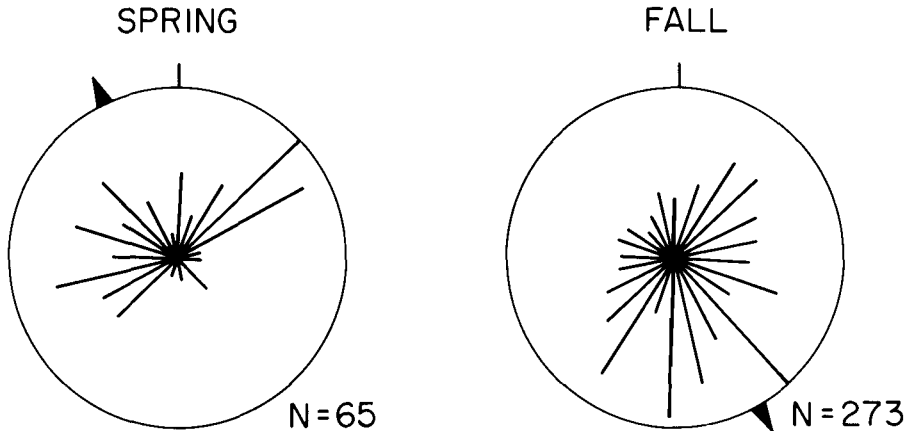
SPRING

FALL

N = 65

N = 273

Fig. 2. Directionality of morning flight with respect to wind. Downwind is at the top of the diagram. Mean direction is indicated by triangle on the circumference of each circle. See Fig. 1 for an explanation of the remainder of the diagram.

Autumn directionality.—The mean direction of morning flight was 222° (length of mean vector $(r) = 0.43; P < 0.001$, Rayleigh Test); the mean direction of nocturnal migration was 218° (length of mean vector $(r) = 0.71; P < 0.001$, Rayleigh Test) (Fig. 1B). The two mean directions do not differ statistically ($0.25 < P < 0.5$, F-test; Batschelet 1972).

Although the mean directions were virtually identical for morning and night movements, Fig. 1B depicts an increase in the dispersion of vanishing bearings for morning movements over that observed at night. Table 1 records the directional data for individual mornings with five or more vanishing bearings and nights with 10 or more birds. The distributions of mean vector lengths (r) are significantly
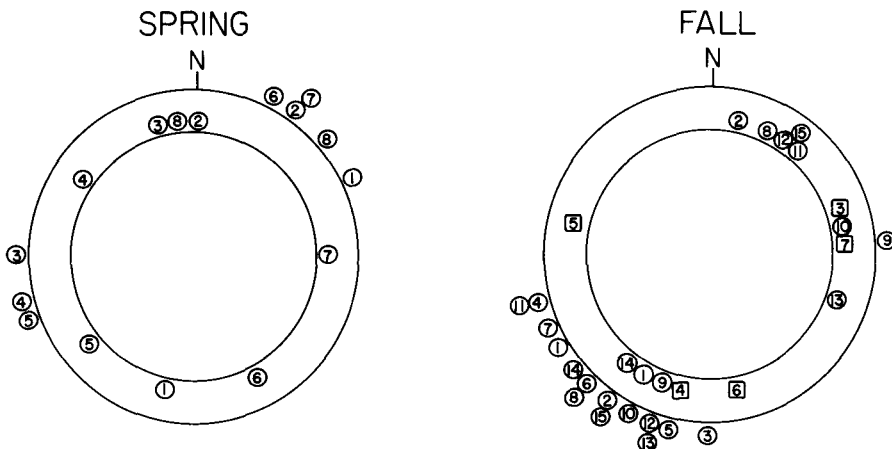
SPRING
N

FALL
N

Fig. 3. Individual mean morning flight directions when significant ($P < 0.05$; Rayleigh Test) (outer circle), versus direction *toward* which the wind was blowing (inner circle). Numbers refer to a given morning. Mornings with winds less that 2.2 m/s are depicted with squares. North is at the top of the diagram.

MORNING AT CASTLETON

N

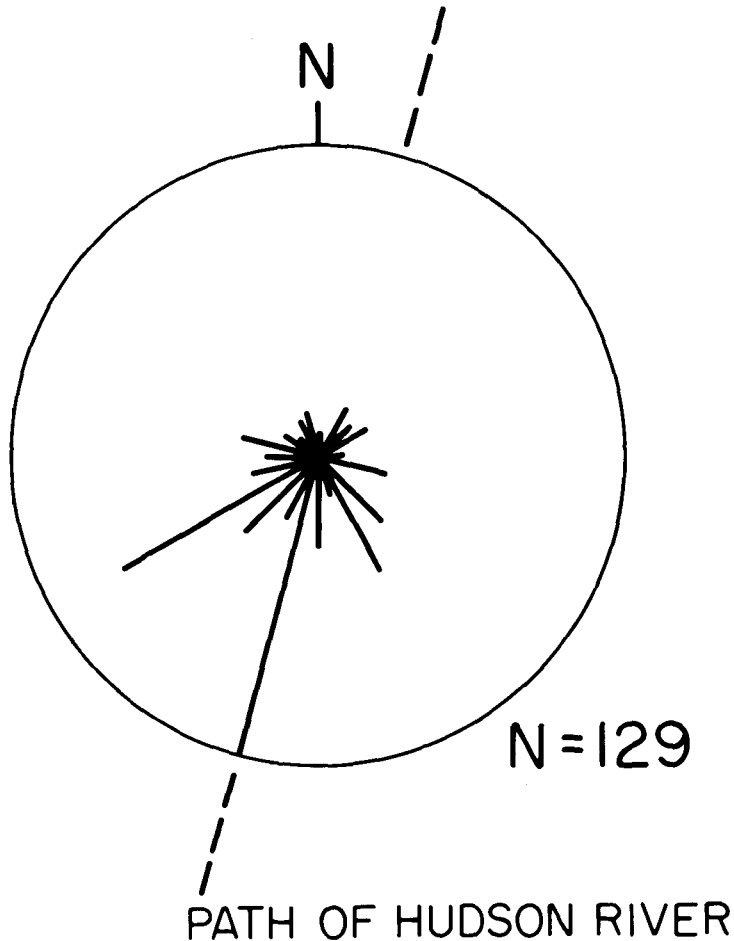N = 129

PATH OF HUDSON RIVER

Fig. 4.   Directionality of morning flight at Castleton during autumn. See Fig. 1 for an explanation of the diagram.

different ($P < 0.05$, Wilcoxon two-sample Test, two tailed; Sokal and Rohlf 1969) between individual morning and nocturnal movements. Thus, dispersion of vanishing bearings was greater during morning movements than during the preceding nights, even though autumn morning and nighttime migrants moved in the same mean direction.

Morning flight with respect to wind.—Plotted in Fig. 2 is the distribution of morning migrant vanishing bearings with respect to wind. The spring data were bimodal, making any statistical interpretation tenuous, with the majority of birds flying with a tailwind. Although few birds flew precisely downwind, the mean vanishing bearing did not deviate significantly from the downwind direction ($P < 0.001$; *V*-test; Batschelet 1972). In contrast to the spring data, the distribution of vanishing bearings for autumn was unimodal, with a mean direction that did not

deviate significantly from one oriented into the wind ($P < 0.001$, V-test). The concentration of activity (h in the V-test) oriented downwind during spring was only 0.292; oriented into the wind during autumn, it was even lower, 0.143. These data suggest that the directional behavior of morning migrants was relatively insensitive to wind direction. Contrasted in Fig. 3 are individual mean morning flight directions, when significant ($P < 0.05$; Rayleigh Test), and wind direction. Although the spring data are too few from which to draw any firm conclusions, migrants flew the predominant northeast direction in both head and tailwinds. The three westward movements recorded, however, were associated with strong winds (> 5 m/s at 300 m altitude) having an easterly component, resulting in tailwind flights. During autumn, migrants flew basically southwest independent of wind direction. The observed tendency of autumn migrants to fly with a headwind results from most migrants flying relatively fixed southwest tracks in prevailing westerly winds. Except for the westward flights during spring, the directional behavior of morning appears independent of wind direction. I consider any interpretation of morning flight as a response oriented into the wind to correct for displacement (Rabøl and Hindsbo 1972) unsupported by my observations.

Topographical effects.—The Castleton observation site was 100 m east of the Hudson River. Morning migrants moving southwestward and reaching the river often changed their behavior. Upon reaching the river, migrants were observed to: (1) land; (2) continue to move but to change their heading to parallel the river; (3) cross over part of the river then return to land or parallel it; or (4) cross the river, seemingly unaffected. The mean direction of morning flight vanishing bearings in autumn at Castleton was 206° ($P < 0.001$, Rayleigh Test) with a modal direction of 195°, a course exactly parallel to the river (Fig. 4). This distribution is significantly different from that observed at the Wilson M. Powell Sanctuary (mean 233°; $P < 0.05$, F-test), where the local topography was observed to have no effect on the behavior of morning migrants. By deflecting many morning migrants, the Hudson River served as a leading line as defined by Mueller and Berger (1967).

DISCUSSION

Morning flight in eastern New York, unlike that in western South Carolina (Gauthreaux 1978), results in birds moving along the same track flown at night. This behavior presumably results in birds coming closer to their ultimate migratory goal, and I interpret these movements as continued migration. Caged nocturnal migrants have also been shown not to change the direction of their activity from night to morning (Wiltschko and Höck 1972).

The directional behavior of night as well as morning migrants differs in the northern and southern United States (Able 1974a, b). Night migrants in the southern United States tend to fly downwind, regardless of wind direction (Able 1974a). Consequently, a bird may be subjected to displacement over large areas when flying in winds other than those oriented along its preferred heading (Gauthreaux 1978). Morning flight may play an important role in keeping these migrants on route to their ultimate goal. In contrast, night migrants in the northern United States usually do not fly downwind when winds are not in the "preferred" direction (Able 1974b). Therefore, northern migrants should not be subjected to similar levels of displacement. The fact that morning migrants in the North continued to fly in similar directions as those observed at night supports the hypothesis that migrants in the

northern United States are subjected to reduced displacement. To compensate for the effects of wind in the northern United States, migrants may change their heading during night flight, maintaining a constant track (Evans 1966). Able (1974b), how- ever, presents data suggesting that nocturnal migrants are at least partially displaced by the wind in eastern New York. If some displacement does occur in the North, correction may be mediated by heading changes on subsequent night flights (as inferred by Evans 1968), as opposed to the corrective morning movements observed in the South.

I conclude that morning flight in eastern New York results in birds continuing toward their ultimate migratory goal. Although morning migrants do not fly into the wind to correct for displacement, strong winds with an easterly component result in birds moving west instead of northeast during spring. These movements are inconsistent with any hypothesis regarding morning flight as continued migration. Strong headwinds may make a northeast flight energetically unfeasible, thus causing the downwind flight. The westward movements during spring may be analogous to "reversed" migrations observed at night (Richardson 1971, 1972, 1978b).

Migrants in eastern New York were observed to show an increase in the dispersion of vanishing bearings during the morning over that recorded at night (Table 1). High altitude, nocturnal migration accompanied by darkness presumably results in broad front migration that is not influenced by local terrain. The differential effect of local terrain (e.g. Hudson River) on the behavior of individual morning migrants undoubtedly contributes to the increased variability in flight directions observed within mornings. Increased variability in the distribution of track directions during the morning was also observed in the Maritime Provinces (Richardson 1978a), but it is unlikely that this increase was a result of topographical influences, as these birds were observed far offshore. I consider the effects of local topography to be at least partly responsible for morning migrants deviating from their nighttime flight track in eastern New York.

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