Anim. Behav., 1982, 30, 49–53

WIND DRIFT, COMPENSATION, AND THE USE OF LANDMARKS BY NOCTURNAL BIRD MIGRANTS

BY VERNER P. BINGMAN, KENNETH P. ABLE & PAUL KERLINGER

Department of Biological Sciences, State University of New York at Albany, Albany, New York, USA

Abstract. In this paper we describe fall nocturnal migration at three localities in eastern New York, one adjacent to the Hudson River, the other two 30 km to the west in a topographically more uniform area. Migrants at both study areas moved southwest in winds not out of the west and were, therefore, seemingly unaffected by the river. In west winds, however, birds away from the river moved south-southeast whereas those in the vicinity of the river flew a track west of south paralleling the river. In addition, a relative increase in the number of migrants along the river compared to away was observed in west winds as birds presumably became concentrated near the river. We conclude that on most autumn nights migrants passing through this area have a preferred track direction toward the southwest and in strong winds from the west and northwest they are drifted. Upon reaching the vicinity of the Hudson River, some birds alter their headings yielding a track direction that closely parallels the river resulting in at least a partial compensation for wind drift. No alternative hypothesis is consistent with all the data.

During the past two decades a great deal of effort has been devoted to the question of whether nocturnal migrants are drifted in flight by lateral wind components. As large quantities of surveillance radar data accumulated, it became commonplace to observe substantial changes in the average migration direction from night to night. These shifts in flight direction were usually correlated with shifts in the lateral wind force impinging on the birds and it seemed reasonable to propose that the birds were being displaced or drifted by crosswinds (Lack 1962, 1963; Eastwood 1967; and others). It was soon pointed out, however, that an alternative interpretation explained most of the data equally well. Rather than a manifestation of drift, the night-to-night variability in flight direction might simply reflect the fact that different species or populations of migrants with different goals select different wind directions under which to initiate migration (Evans 1966; Nisbet & Drury 1967). In fact, a continuum of possibilities exists such that a migrant might fly with a fixed heading and be displaced laterally over the ground by crosswinds, alter its heading under different wind conditions so as to compensate for the drifting effects of wind and fly on a fixed track, or strike some middle ground by compensating partially for drift. Radar and visual observation data provide circumstantial evidence that under certain conditions migrants do all of these things (Alerstam 1976; Able, in press). Without knowing the migratory goal of a given bird, however, these studies cannot unequivocally distinguish between drift and compensation.

A bird attempting to compensate for wind drift requires some means of perceiving lateral displacement from a preferred direction. This could be accomplished by monitoring fixed visual reference markers on the ground relative to its heading. Observations sufficiently detailed to document migrant response to landmarks interpretable as corrective changes for wind drift have not been published. In this paper we explore fall nocturnal migration at three localities in eastern New York, one adjacent to the Hudson River, the other two located 30 km west of the river in a topographically more uniform area. We hypothesized that migrants could utilize the Hudson River as a topographical reference by which to perceive wind drift from a preferred track and correct at least partially for these effects. The results point to great complexity in the flight behaviour of nocturnal migrants.

Methods

Nocturnal migration was observed at two locations during autumn 1978 and three locations during autumn 1979 (Fig. 1) to test the possible effects of the Hudson River on the flight orientation of passerine migrants. Berne (Albany County, New York; elevation 495 m), monitored both years, and Rensselaerville (Albany County, New York; elevation 558 m), monitored during 1979 only, were both located on the

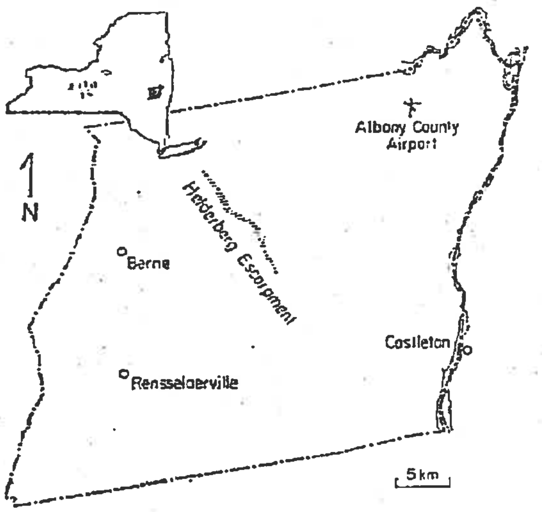

Fig. 1. Location of lookouts. The outline of New York State is shown at upper left. The blackened area, which is shown expanded, is Albany County. The Hudson River forms the easterly boundary of the County.

Helderberg Plateau approximately 30 km west of the Hudson River. No differences existed in the mean nightly direction of migration between these lookouts (Watson U^2 test, Batschelet 1965), so they were pooled in the analysis. Castleton-on-Hudson (Rensselaer County, New York; elevation 10 m) is located on the east shore of the Hudson River and was monitored both years.

Two 100-W portable ceilometers were used to observe migrants as described by Gauthreaux (1969) and Able & Gauthreaux (1975). Twenty-power binoculars were used on most nights at both stations during 1978, while during 1979 20 × binoculars were used at Berne and Rensselaerville and 10 × binoculars were used at Castleton-on-Hudson. Moonwatching (Lowery 1951) with 20 × binoculars or spotting scope was also employed to observe nocturnal migration near the time of the full moon. Observations took place within the first two hours after sunset and lasted for 30 min or until at least 20 birds were recorded. Partial overlap in the timing of observations at the different lookouts occurred regularly, with observations rarely separated by more than 30 min.

Circular statistics as described by Batschelet (1965) were used to analyse the data. All mean vectors mentioned in the text were significant ($P < 0.001$) by the Rayleigh test. The Watson U^2 test was used in all evaluations of differences

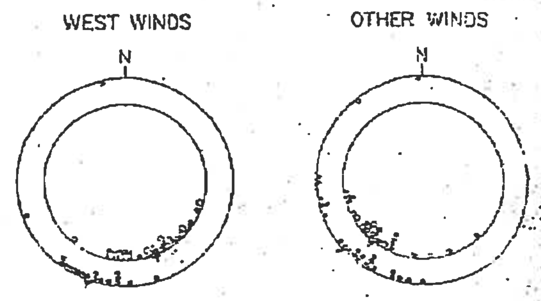

Fig. 2. Nightly mean directions at the two study areas in 'west' and 'other' winds. Points on the outer circles were from Castleton-on-Hudson; on the inner circle closed points were from Berne and open points were from Rensselaerville. Triangle refers to the mean nightly direction for each distribution.

between distributions of directions. Winds-aloft soundings at 1800 EST were obtained from the National Weather Service located at the Albany County Airport (Fig. 1). Because of the differences in elevation, winds recorded at about 300 m were used for the Castleton-on-Hudson study site while the winds recorded at 600 m were used for Berne and Rensselaerville.

Results

Under calm wind conditions, the average direction of nocturnal passerine migration in the region of Albany, New York, is toward the southwest (resultant vector of mean directions on 14 nights over four seasons with wind speed ≤ 2.5 metres per second, 238°, $r = 0.85$). Even pooling all data under light and moderate winds (≤ 8 metres per second) the resultant direction is southwestward (resultant vector of mean directions on 36 nights = 217°, $r = 0.74$). Winds from the northwest are the only ones that are both frequent enough and strong enough to be an important potential source of drift in this area. Strong southeast winds are rare and usually accompanied by rain. Therefore, we divided the migration data into two sets based on the direction of winds aloft: (1) 'west' winds, from 250 to 335° at speed of greater than or equal to 5 metres per second at both 300 m and 600 m altitude; (2) 'other' winds, comprising all other wind velocities. Figure 2 shows that under 'other' winds the flight direction of the migrants at all sites was toward southwest (Berne-Rensselaerville resultant of mean track directions = 220°, $r = 0.89$; Castleton-on-Hudson resultant of mean track directions = 229°, $r = 0.81$) and no differences existed between the sites (see Table I). In 'west' winds, however, the mean direction at Berne–Rensselaerville was toward the SSE (resultant of mean track directions = 159°, $r = 0.89$) and significantly different from the resultant of 201°, $r = 0.87$ observed at Castleton-on-Hudson ($P < 0.001$; Fig. 2). It should also be noted that in 'west' winds, the flight direction at Castleton-on-Hudson closely paralleled the orientation of the Hudson River (195°), a direction significantly different from the 229° mean at this site under 'other' winds ($P < 0.01$). The raw data are available upon request.

Although the methods used sampled birds in the same altitudinal strata at all sites, there were considerable differences in the elevations of the sites themselves. Birds observed at Berne and Rensselaerville, on the Helderberg Plateau, were flying higher with respect to sea level than those along the river and might, on average, have been subjected to stronger winds. Thus the directional differences between the inland and river locations might be in part due to differences in wind velocity. To test this, we assumed an air speed of 10 metres per second (Able 1977) and using the empirically-determined track directions and wind vectors, we calculated nightly mean headings by the triangle of velocities. Using the 600 m Albany winds for the Berne–Rensselaerville data results in a conservative bias because the speeds of these winds should usually be an overestimate because of frictional effects over the higher terrain. Even with this bias, in 'west' winds the mean nightly heading at Castleton-on-Hudson (254°, $r = 0.91$) was significantly west of the mean heading at Berne–Rensselaerville (195°, $r = 0.72$) ($P < 0.001$). Under 'other' winds no difference in headings was observed. These data strongly support the conclusion that the directional differences we observed were not a function of increasing wind speed with altitude, but rather a result of different headings.

We infer from these data that on most autumn nights migrants passing through this area have a preferred track direction toward the southwest. In strong winds from the west or northwest, the birds experience a large side wind component and are drifted. Upon reaching the vicinity of the conspicuously lighted Hudson River, some birds alter their headings to yield a track direction that closely parallels the river, resulting in a significant, if perhaps incomplete, compensation for the wind drift. If these inferences are correct, in 'west' winds birds should become concentrated along the river as individuals flying on southeastward tracks reach its vicinity, turn and move down-river. This prediction provides an independent test of our hypothesis.

To test this prediction, we computed passage rates of migrants for simultaneous observations at Berne and Castleton-on-Hudson (Rensselaerville was excluded because of the small number of observations made there). In 'west' winds, birds passed at Castleton-on-Hudson at an average rate 2.6 times that at Berne (the rate at Castleton exceeded that at Berne on 12 of 15 nights; $P < 0.05$, Sign test; Siegel 1956). In 'other' winds, the average rate of passage at Berne was 1.2 times that at Castleton-on-Hudson (the rate at Castleton exceeded that at Berne on 8 of 18 nights; $P > 0.05$; Sign test). These data thus reveal a marked and consistent concentration of migrants along the river only under the conditions in which the flight direction data predict that it should occur.

Discussion

The conclusion that passerine migrants were drifted from a preferred heading under certain conditions and reoriented in response to the

Table I. Statistical Comparison of Resultants of Nightly Means Within and Between Lookouts in 'West' and 'Other' Winds

		Berne–Rensselaerville		Castleton	
		'West' winds	'Other' winds	'West' winds	'Other' winds
Berne–Rensselaerville	'West' winds	—	$P < 0.001$	$P < 0.001$	$P < 0.001$
	'Other winds	—	—	$P < 0.001$	NS
Castleton	'West' winds			—	$P < 0.01$
	'Other' winds				—

Hudson River rests on two facts. Flight paralleling the Hudson River occurred only with potentially drifting 'west' winds when birds at Berne-Rensselaerville moved on the average east of south. We have tested the independent prediction of a concentration of migrants passing over the river in 'west' winds and obtained results that support the hypothesis. Our case is strengthened by the following facts: (1) we need not assume that the preferred direction of migration remains the same from night to night; (2) our sites are in an inland region and are separated by less than 30 km; (3) we know the track direction of each bird and we can be as certain as any current technique allows that the samples consist entirely of passerines. However, because we have not actually seen a bird change course in the vicinity of the river, the case we have presented is a circumstantial one.

Our analysis does assume that on a given night the birds we observed were sampled from a single population of migrants with the same average preferred flight track. If this assumption is not met, our results are open to alternative explanations. Traffic rates of birds were consistently higher along the river under 'west' winds. Because of this, it is possible that birds moving southeast might have been passing at similar rates over the two areas but their influence on the mean flight direction at the river was overwhelmed by an increased proportion of south-southwestward moving birds. In analysing this possibility it is important to note that some birds observed at Castleton-on-Hudson were flying toward southeast on 'west' wind nights: a nightly average of 21% (range = 6–65%) of the migrants seen there had track directions between 0 and 179° under 'west' winds, compared with an average of 13% (range = 0–41%) under 'other' winds. At Berne, 68% of the individuals observed in 'west' winds had tracks between 0 and 179° (range = 21–100%). We must then ask whether the rate of passage of birds with an eastward track component was lower at the river than would be predicted based on the rate of passage of such birds at Berne. Comparison of 'west' wind nights with data from both Berne and Castleton-on-Hudson showed that although a remnant of the southeast flight component persisted at the river, it was significantly reduced (mean passage rate at Berne 48 birds/h, at Castleton 22 birds/h; $P < 0.005$, t-test for paired observations). If turning by birds in the vicinity of the river is responsible for the pattern we observed, most individuals reoriented.

A more complicated alternative has been suggested by Alerstam (personal communication). It combines differential wind selectivity by species or populations with different preferred tracks (so-called pseudodrift) with altitude selection. The hypothesis is that under strong winds birds with preferred headings downwind will fly higher to take advantage of the usually stronger winds at higher altitudes. Individuals with other preferred directions should remain on the ground or fly at low altitudes where wind speeds are generally lower and drift or wind opposition thereby reduced. In our case, under 'west' winds birds with southeast preferences should selectively fly at higher altitudes and might thereby pass out of range of our sampling strata at the river site. Birds with more westward preferred tracks might fly at lower altitudes and thus be over represented in the river valley sample.

Several lines of evidence argue against this hypothesis. (1) On five 'west' wind nights wind speeds did not differ appreciably ($\leq$ 1 metre per second) at 300 and 600 m and in one case (4 September 1978) winds were stronger at the lower altitude. Nonetheless, large and consistent differences in flight direction between the river and upland areas existed on these nights as we would have predicted. The wind selection hypothesis predicts no difference. (2) If wind selectivity actually functions as Alerstam (1976) and others propose, birds with southwestward preferences should not even be flying on nights with very strong west or northwest winds. Winds from the northeast (tailwinds for this population) are frequent in this area and the birds could easily remain on the ground awaiting those conditions. (3) Under northeast winds the wind selectivity hypothesis predicts that birds with southwestward preferences should fly higher and be over-represented in the Berne–Rensselaerville samples whereas those with southeastward preferences should be relatively more numerous in the river samples. Our data show no clear trends in these directions. (4) Birds passing southeastward over Berne–Rensselaerville in 'west' winds almost certainly initiated migration in an upland area with similar elevations. If it is advantageous for them to fly at higher altitudes, why do they not do so over the Berne–Rensselaerville sites? (5) If birds with southwest preferences do fly at low altitudes under 'west' winds, compensating for wind drift, why do so few pass over Berne-Rensselaerville? One would have to propose that they somehow avoid flying over the modest elevations of this upland area, presumably by using landmarks.

Having reviewed all these arguments we believe the available evidence supports the validity of the assumption that we have sampled from a single population of migrants. We conclude that the most parsimonious explanation consistent with all the data is that on most autumn nights migrants passing through this area have a preferred track direction toward the southwest. In strong winds from the west and northwest, the birds experience a large side wind component and are drifted. Upon reaching the conspicuously lighted Hudson River, some birds alter their headings to yield a track direction that closely parallels the river. This behaviour results in a significant, if perhaps incomplete, compensation for wind drift. The performance of corrective changes in heading implies that the birds used an in-flight compass that enables them to evaluate their track direction relative to a preferred heading and fixed features on the ground. This response by the birds was a facultative one associated only with potentially drifting winds. Thus, they do not indiscriminately respond to the river as a leading line. Because all of our data were obtained under clear or mostly clear skies, we are in no position to speculate on the cues being used for in-flight reorientation.

James (1955) used moon-watching to look for effects of the Mississippi River on the direction or magnitude of migration. Unfortunately, her primary interest was in whether birds followed the course of the river in detail, changing direction with major bends. They did not and she concluded that the river exerted no major effect on nocturnal migration, at least in passerines. The sample sizes in the study were small and if an influence of the Mississippi River was wind dependent as we have found, her data would not have revealed it. Therefore, it is not clear that any difference in the behaviour of the birds is indicated by these disparities in results. It may be relevant, however, that the shores of the Hudson River are heavily and continuously populated with lights from Albany to New York City, providing a long-distance, virtually linear visual landmark that is a good deal more conspicuous than many rivers in more rural areas.

Experience warns us to expect variation among species and geographic regions. What we have shown is that within the large context of broad front nocturnal migration there is much fine scale complexity in migratory orientation. The behaviour we have observed makes it unlikely that any unitary hypothesis about wind drift/compensation will be viable.

Acknowledgments

This work was supported by NSF grant BNS 76–18524. Part of this work was conducted while the senior author was in residence at the E. N. Huyck Preserve. We thank Sidney Gauthreaux and Thomas Alerstam for their helpful suggestions, Ryland Loos for preparing the figures, Bob Speck for photographs, and Laurie Callahan and Linda Welch for typing the manuscript.

REFERENCES

Able, K. P. 1977. The flight behaviour of individual passerine nocturnal migrants: a tracking radar study. *Anim. Behav.*, 25, 924–935.

Able, K. P. In press. Evidence on migratory orientation from radar and visual observations: North America. *Proc. XVII Intern. Ornithol. Congr.*

Able, K. P. & Gauthreaux, S. A. 1975. Quantification of nocturnal passerine migration with a portable ceilometer. *Condor*, 77, 92–96.

Alerstam, T. 1976. Bird migration in relation to wind and topography. Ph.D. thesis, University of Lund.

Batschelet, E. 1965. Statistical methods for the analysis of problems in animal orientation and certain biological rhythms. Washington, D.C.: AIBS Monograph.

Eastwood, E. 1967. *Radar Ornithology*. London: Methuen.

Evans, P. 1966. Migration and orientation of passerine night migrants in northeast England. *J. Zool. Lond.*, 150, 319–369.

Gauthreaux, S. A. 1969. A portable ceilometer technique for studying low-level nocturnal migration. *Bird-Banding*, 40, 309–320.

James, F. C. 1955. The influence of the Mississippi River on the nocturnal migration of birds. M.S. thesis, Louisana State University.

Lack, D. 1962. Migration across the southern North Sea studied by radar. Part 3. Movements in June and July. *Ibis*, 104, 74–85.

Lack, D. 1963. Migration across the southern North Sea studied by radar. Part 5. Movements in August, winter and spring, and conclusion. *Ibis*, 105, 461–492.

Lowery, G. H. 1951. A quantitative study of the nocturnal migration of birds. *Univ. Kansas Publ., Mus. Nat. Hist.*, 3, 361–472.

Nisbet, I. C. T. & Drury, W. H. 1967. Orientation of spring migrants studied by radar. *Bird-Banding*, 38, 173–186.

Siegel, S. 1956. *Non-Parametric Statistics for the Behavioural Sciences*. New York: McGraw-Hill.

(*Received 7 January 1981; revised 2 April 1981; MS. number:* A2595)