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Evidence for Redetermination of Migratory Direction Following Wind Displacement

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Nocturnal passerine migrants are capable of *selecting* a direction with reference to a variety of environmental cues (Emlen 1975, Able 1980b, Able and Cherry 1986, Moore 1987). How well they *maintain* that direction is difficult to evaluate. Although free-ranging migrants are seldom observed to be disoriented, flight in seemingly inappropriate directions is not an uncommon observation (Griffin 1973; Richardson 1978; Able 1980a, 1982; Alerstam 1979, 1981). Besides the problem of maintaining a predetermined heading, orientation errors occur, especially among young, inexperienced migrants (Herbert 1970, Ralph 1978, McLaren 1981, Gauthreaux 1982, DeSante 1983, Moore 1984).

For small passerines, displacement by wind is a real possibility. Whether migrants correct for displacement or the extent to which they correct is difficult to determine (Evans 1968; Alerstam 1979, 1981; Richardson 1982; Bingman et al. 1982). Migrants may "correct" while aloft (Myres 1964, Richardson 1978, Cochran and Kjos 1985), or they may redetermine directions soon after landing or before their next departure (Evans 1968, Gauthreaux 1978). If migrants select a direction at the time of takeoff, the next morning would be a convenient time to reorient if displaced during a night's flight (Vleugel 1954, Lowery and Newman 1955, Moore 1987).

During a study of migrants after they migrated across the Gulf of Mexico, natural variation in wind conditions over five days provided an opportunity to investigate the orientation of migrants in response to presumed wind displacement. South-southwesterly winds (3–4 m/s) prevailed on 14 and 15 April 1985, but they shifted to moderately strong easterly winds (7–8 m/s) by 17 April after the passage of a weak front. Winds returned to southerly by midafternoon on 17 April. The pattern of change in prevailing winds as migrants arrived over the northern Gulf Coast represents a natural analog of a pre-test/post-test experimental design for the treatment effect (wind change). Most trans-Gulf migrants arrived on 17 April between 1000 and 1200 CST after experiencing easterly winds over the northern Gulf of Mexico. If they drifted from their preferred heading, which is likely when migrating over water (Lack 1959, Alerstam and Pettersson 1976), migrants might compensate for the displacement and reorient their activity the night of their arrival or the following morning. Differences in orientation should exist among migrants sampled during the 5-day period if they redetermine direction in response to wind conditions experienced during migration.

I conducted cage-orientation experiments with migrating warblers (Parulinae) that had stopped over at an isolated woodland (29°45′N, 93°33′W) along the northern coast of the Gulf of Mexico following trans-Gulf migration (see Moore 1986, Moore and Kerlinger 1987). Birds were captured in mist nets on the day of arrival, held overnight, and placed in funnel-shaped orientation cages (Emlen and Emlen 1966) the next morning near the beginning of civil twilight. Activity was recorded for 90 min; then I released the birds.

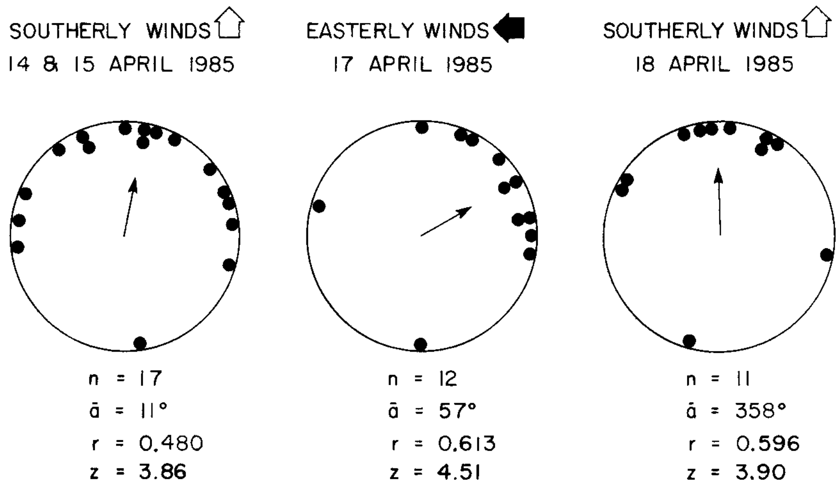

Fig. 1. Orientation behavior of migratory wood-warblers in relation to wind conditions experienced during trans-Gulf migration. Each black dot represents the mean heading of an individual and each distribution is based on a different sample of migrants. The arrow within the circle gives the mean direction for the sample, and its length is proportional to the concentration of mean headings (r). All three distributions are significantly different from uniform according to a Rayleigh's Test ($P < 0.05$). North is to the top of the figure.

Analysis of the orientation records followed procedures described earlier (Moore 1986).

Individuals ($n = 17$) of four species (*Seiurus aurocapillus, S. noveboracensis, Oporornis formosus,* and *Wilsonia citrina*) caught on arrival on 15 April oriented their cage activity to the north (a = 11°) on the morning of 16 April following two days of south-southwesterly winds (Fig. 1). The directional preference of that sample is comparable to the orientation of other individuals of the same species tested in the morning that same migratory season (Moore 1986). I tested a second sample of individuals ($n = 12$) on 18 April after they arrived with easterly winds the day before. Their activity was oriented to the northeast (a = 57°). Northeast orientation would be expected if birds compensated for westerly displacement experienced under prevailing easterly winds. After winds had shifted back to southerly, a third group of arriving birds was caught on 18 April and tested on 19 April; orientation was again northward (Fig. 1). A Watson-Williams multisample F-test failed to distinguish among the three means ($\alpha = 0.05$). I concluded that the three distributions estimate the same population mean ($F = 2.87$, $0.05 < P < 0.10$). Although a more powerful, bivariate test that takes into account within-individual variation might have shown statistical significance (see Batschelet 1981), the Emlen "ink-pad" approach does not permit reliable estimates of individual variability within a test-night. In any case, the pattern of change in orientation in relation to wind conditions leads me to suspect a type II error (e.g. small sample sizes and within-sample variation among individuals contributed significantly to the statistical outcome). It may also be argued that because birds tested on a given day are pooled statistically, the design suffers from pseudoreplication (*sensu* Hurlbert 1984).

The pattern of behavior I found is consistent with the idea that passerines redetermine their migratory direction to compensate for wind displacement experienced while crossing the Gulf of Mexico. This interpretation depends on two assumptions. First, the departure direction of spring migrants following stopover along the northern Gulf coast is northward. Besides being seasonally appropriate for spring migrants in that area (Gauthreaux 1971), two other observations support the assumption. First, the cage activity of migratory warblers tested in another context at the same location was, on average, northward (Moore 1986). Further, during stopover at the same location, foraging migrants move in a northward, seasonally appropriate direction (Moore pers. obs.). Second, I assume that the migrants captured and tested had arrived on the day and under the wind conditions in question. Because trans-Gulf migrants are likely to depart soon after arrival, especially when weather is favorable (see Gauthreaux 1971, Hebrard 1971, Moore and Kerlinger 1987), it is reasonable that most birds at the stopover site arrived the day before their test.

The results of this experiment do not exclude the possibility that birds tested on the morning of 18 April represented a subsample of grounded migrants that were not drifted by easterly winds, but whose preferred migratory direction was actually northeast (e.g. Crawford 1980). The phenomenon of "pseudodrift" is based on the premise that different populations of migrants select following winds relative to their own preferred headings and are aloft with different wind conditions (Evans 1966, Nisbet and Drury 1967, Alerstam 1976). Although it is difficult to refute pseudodrift (Richardson 1982), two observations argue against pseudodrift being the cause of the observed orientation. First, if the migrants that arrived with easterly winds on 17 April had not drifted but preferred a westerly heading, their orientation on 18 April was largely upwind rather than downwind as would be expected if pseudodrift were the explanation. Second, the weather on the days preceding the easterly winds (i.e. south-southwesterly winds) was quite favorable for northeast migration and migrants with a northeast preference should have departed with those following winds.

These results are consistent with redetermined orientation following lateral wind drift (Gauthreaux 1978, Alerstam 1979), and they are reminiscent of the results of an earlier cage experiment with migrants displaced while crossing the North Sea in autumn (Evans 1968). Although no control tests were run with migrants not presumed to be off course and the sample of birds tested at night was small ($n = 13$), most birds oriented their activity to the southeast, which could be interpreted as redetermined migration to compensate for wind displacement. More recently, Rabol (1985) used Emlen funnels to examine the migratory orientation of vagrant passerine migrants ($n = 26$) on the Faeroe Islands. Only two individuals displayed activity that could be interpreted as redetermined migration; most birds oriented their activity in a south-southwesterly direction characteristic of autumn migratory orientation on the European continent and showed no evidence of a compensatory response to their "displaced" location.

Gauthreaux (1978) hypothesized that morning movements at inland localities function to correct for wind drift sustained during nocturnal migration. He regards such flights as redetermined migrations following Lack and Williamson (1959), whereas other early morning movements probably represent onward migration with no change in heading (Bingman 1980). Visual observations of passerine migration in northwestern Germany revealed changes in flight directions from one day to the next when wind conditions promoting drift occurred the previous day (Helbig et al. 1986). Wiltschko and Hock (1972) found that the activity of European Robins (*Erithacus rubecula*) was concentrated in the migratory direction during early morning hours only when the birds showed migratory activity the night before. This led them to speculate that birds might redetermine their migratory direction at that time.

The redetermined orientation apparent in my results should not be confused with "reorientation," which is the term normally applied to birds that change heading while in flight. For example, inflight reorientation by nocturnal migrants over the sea at dawn (Lack 1963a, b; Myres 1964; DeSante 1973; Richardson 1978) may be a fixed compass reaction to being offshore at dawn rather than a response to wind (see also Baird and Nisbet 1960, Murray 1976, Able 1977).

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