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PERSPECTIVES

ECOLOGY:
Bird Navigation--Computing Orthodromes

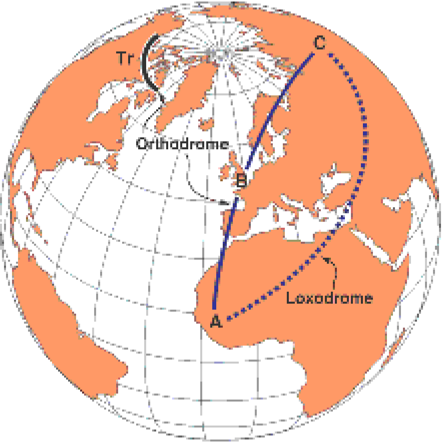
Rudiger Wehner[*]

Studies of bird navigation usually follow two gold standard approaches: the relocation and release of thousands of pigeons and the tracking of their return, and the hand raising of hundreds of songbirds and the testing of their navigation capabilities in orientation cages. The data obtained from such endeavors are exciting, but the conclusions drawn are varied, often controversial, and always hypothetical, because little is known about how the avian brain computes navigational information. A favorite hypothesis is that birds primarily use a magnetic compass, or even a magnetic map of the Earth (1), to navigate, but so far magnetoreceptive sensory neurons have not been found in the brains of any bird species. Numerous laboratory experiments show that migratory birds use multiple sources of directional information based on magnetic, stellar, solar, and other environmental cues (2). Such experiments further suggest that birds must have ways to calibrate their celestial and magnetic compasses against each other (3), but how this is achieved as they fly vast distances on their annual journey is not known. There is good evidence that young birds are equipped with endogenous migratory programs, which tell them roughly how many days and/or nights that they must fly, and in what direction (4). Computational models suggest that such clock-and-compass strategies might explain the accurate "geographical knowledge" carried by avian migrants, which has been revealed by recovery of ringed birds (5, 6).

Two experimental approaches could help to sort out exactly how birds navigate. The first is to record the trajectories of migrating birds with radar tracking or satellite-based telemetry. The second, complementary strategy is to look for particular combinations of real-world geographical cues in selected areas of the Earth and to relate the directional choices of migrating birds to these cues. As reported on page 300 of this issue, Alerstam and his crew have successfully combined both of these approaches.

These investigators tracked the trajectories of migrating Arctic shorebirds with a radar mounted on a Canadian coast guard icebreaker vessel (7). They provide clear evidence that migrating New World shorebirds, such as plovers and sandpipers, fly along the Earth's great-circle routes (orthodromes) and use their sun compass for orientation. Arctic shorebirds migrate from their breeding sites in the far northern latitudes, across the mythical Northwest Passage, to the eastern United States; they then fly down the east coast of North America to their winter quarters in South America. By tracking shorebirds migrating close to the magnetic North Pole, the authors knew that the birds could not be using either magnetic or stellar cues for orientation, and inferred that they must be steering with their sun compass along orthodrome routes.

The favored routes of Old World shorebirds such as the Siberian wader also follow great-circle courses. After departing their winter quarters in West Africa in the spring, Siberian waders fly in a 4300-km nonstop journey along the East Atlantic Flyway to their next staging site (the Dutch Wadden Sea), and then continue to their breeding grounds in Northern Siberia (see the figure). They follow a great-circle route--this trajectory, although navigationally demanding, conserves energy because it is the shortest distance to the final destination (8). Birds migrating along orthodromes must continuously change their compass course because their route intersects successive longitudes. An alternative approach would be to travel on a constant compass course (rhumbline or loxodrome), which is easier to navigate but results in longer flight distances. Orthodrome and loxodrome routes differ the most dramatically for east-west movements at polar latitudes. Thus, Alerstam and his co-workers deliberately chose to do their radar-tracking studies of shorebirds in the Arctic circle.



Around the world in 80 days. Each spring, millions of Old World shorebirds leave their winter quarters in West Africa (A) and migrate along the East Atlantic Flyway nonstop to their next staging site in Europe (B). They then continue to their Siberian breeding areas (C), flying along a great-cirlce toute (orthodrome, solid line) (8). New World Arctic shorebirds migrate east along the path Tr, from their main breeding sites in Northwestern Canada and Alaska. They then fly south along the shore of the eastern United States to their winter quarters in South America. They navigate with a sun compass, keeping their internal clock out of phase with local time. This ensures that they fly along the orthodrome routes of the Arctic (7).

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But how do these Arctic migrants accomplish the demanding task of computing great-circle courses? It seems they apply an intelligent trick. Mathematicians have worked out that if one uses a time-compensated sun compass without resetting one's internal clock while traveling across different time zones (longitudes), the resulting curved route would look like an orthodrome (9). Apparently, it is not only mathematicians who realized that navigating by the sun with the internal clock kept out of phase with local time automatically results in a flight route that is roughly parallel to an orthodrome. Laboratory studies on birds have shown that, with exposure to a new (time-shifted) 24-hour day/night regime, it takes 3 to 6 days for them to recalibrate their sun compass. But, we also know from field tracking studies that Arctic shorebirds take long east-west nonstop flights during which they may cross different time zones within a relatively short period (often 1 or 2 days). Such nonstop flights would cause their internal clock to become out of phase with local time as they would not have the requisite 3 to 6 days for recalibration.

Steering a sun-compass course with an out-of-phase internal clock provides the approximate direction of an orthodrome route and saves the bother of having to solve complex mathematical equations (9). The higher the geographical latitude, the better this short-cut strategy works. But in the real (windy) atmosphere, there is much more that migrating birds must be doing. If there is wind, say, from the left of the great-circle course, the bird's direction must deviate somewhat to the right from the desired track direction (that is, the direction relative to the ground). And this is indeed what the bird does. Let us return to the Siberian waders migrating from West Africa to Europe (see the figure). They encounter favorable tailwinds (which are necessary to keep the flight energy costs reasonable) only at altitudes greater than 3 km; at these altitudes they fly by adjusting their headings so as to allow themselves to be wind-drifted in the proper track direction (8). If, instead, they headed directly for their destination--that is, if flight angles and track angles coincided--they would be wind-drifted straight northeastward into the Sahara desert. Alerstam's Arctic shorebirds also take into account the local wind conditions. On their orthodrome route they align their heading direction more or less with their track direction.

Depending on large-scale synoptic weather patterns, the shortest route might not always be energetically-speaking the most economic route. If this is the case, the migratory program of birds is indeed likely to include segments of different loxodrome routes or other detours (4, 10). Whatever the navigational algorithms used by bird migrants, they are likely to involve simplifications and approximations that will be valid only in particular geographical areas. Natural selection has shaped a bird's navigational toolkit--its compasses and odometers--in specific ways, tailored to particular navigational needs. Future research must focus on these needs and take a closer look at the exact trajectories that migrating birds follow on their journeys. The era of the grand unified hypothesis of bird navigation--for example, steering only by the stars as Captain Cook did--is certainly past. Bird migrants, like ancient mariners, combine all sorts of regionally specific geographical cues to ensure on-time arrival at their destination.

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The author is in the Department of Zoology, University of Zürich, Zürich CH-8057, Switzerland. E-mail: rwehner@zool.unizh.ch