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Field Studies of Bird Migration — A Brief Overview and Some Unanswered Questions

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The mysteries of migration may take decades to solve, but anyone in the field can turn up valuable clues. Here, a leading professional migration researcher who is also an active birder points out the possibilities

ON A crisp early morning in late August we were hiking the trail between Rustler and Barfoot Parks, high in the Chiricahua Mountains of southeastern Arizona. This is an area of the country in which migration is thought to be sparse and inconspicuous, at least by those of us who have come up through the "eastern establishment." The Chiricahuas comprise a large area of heavy forest and cannot be considered a migrant trap. Yet on this short hike we encountered several large mixed species flocks with many migrants. Hermit Warblers *Dendroica occidentalis* predominated, followed by Townsend's *D. townsendi*, Black-throated Gray *D. nigrescens*, Orange-crowned *Vermivora celata*, and Wilson's Warblers *Wilsonia pusilla*, plus numbers of several species that breed in the immediate vicinity. The number, variety and behavior of the birds was in every way comparable to what one might see in the East during a good fall migration wave. I was struck by how little we know about the basic natural history of bird migration even on this relatively well-studied continent.

In this article I hope to give an overview of the state of knowledge and recent work in a few areas of migration study. While outlining some of what we know, I also want to spotlight areas in which our knowledge is inadequate, especially those aspects that are amenable to investigation by field birders. I believe that amateurs (I imply nothing by this term except that the person does not earn a living from ornithology) can make significant contributions to our understanding of migration. True, many aspects of migration study require sophisticated, expensive equipment, elaborate procedures, maintenance of experimental birds, and investment of time that are beyond the capabilities of the non-professional. On the other hand, many skilled field observers possess an intimate knowledge of avian natural history far exceeding that of many products of today's Ph.D. programs. Ironically, the avian biologists emerging from our graduate schools are often completely untrained in classical ornithology. In addition, the young professional interested in bird migration cannot often justify to his peers (or to the granting agencies on which he depends) pursuing the kinds of descriptive studies for which the amateur is best suited. Yet we still need those basic data. Thus there exists considerable potential for productive complementarity.

The migration patterns we observe today are the products of gradual evolutionary change over geological time. The major steps of this process are easy to reconstruct. Take, for example, an individual bird that disperses and by chance comes upon an area with an unexploited flush of resources, where it breeds. If the dispersal behavior of that bird is under genetic control and if it is able to produce more viable offspring than its sedentary conspecifics, the type of dispersal it exhibited will increase in the population. The beginnings of migration would have evolved. There is every reason to believe that this process is occurring constantly and in both directions, i.e., sedentary forms evolving migratory behavior and vice versa; but accounting for the details has remained difficult.

Field Methods

There are several ways in which field data on migration can be obtained: 1) direct observation as in hawk watching, counting sea birds on passage, migrants on the ground, etc.; 2) banding; 3) observation of nocturnal migration by moon-watching or portable ceilometers; 4) flight call counts of nocturnal migrants; 5) surveillance radars (Airport Surveillance Radar, ASR, and Weather Surveillance Radar, WSR) maintained by government agencies. All of these techniques could be employed in migration study in most areas of the country. Some additional comment is in order with regard to some of these methods.

Millions of birds have been banded by the army of volunteer banders that serve the Bird Banding Laboratory of the U.S. Fish and Wildlife Service. Many kinds of information about birds (survival rates, life expectancies, details of migration routes, settlement patterns of young birds, etc.) can be obtained in no other way. Ironically, most of the kinds of questions that the banding program was conceived to answer have proven intractable in passerine birds. The basic problem is that recovery rates for small non-game birds are incredibly low, making it almost impossible to get at the life history phenomena listed above. Often the most valuable information is in the hands of the bander himself, and all too few make use of the data they have gathered. However, banding has answered and can continue to answer many basic questions about migration, some of which are pointed out below.

Because most species and individual birds migrate under cover of darkness, means of observing their behavior has been a major impediment. However, with nothing more than a 20x spotting scope and a reasonable incidence of clear skies during spring and fall, one can quantitatively observe nocturnal migration by moonwatching. Traffic rates of migration and the flight directions of birds can be determined quite precisely using the methods outlined by Lowery (1951) and Nisbet (1959, 1961). For many areas of the country these basic aspects of nocturnal migration remain undescribed.

In some places frequent cloud cover renders moon watching impractical. For less than \$25 one can assemble a portable ceilometer, a 100W bulb with a parabolic reflector that produces a narrow beam of light pointed vertically into the sky. The observer lies on the ground and looks up the light beam with a 20x scope. Birds as high as 2,000 ft. are readily seen as they pass through the beam. As with moon-watching, the traffic rate of migration and flight directions of birds can be determined (for methods

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see Gauthreaux, 1969, 1980; and Able and Gauthreaux, 1975). Ceilometers can be operated off standard car batteries and are thus highly portable, enabling observations to be made in remote areas with little advance preparation. With both moon watching and ceilometer observation it is possible to discriminate types of birds (e.g., passerines vs. waterfowl or shorebirds) and occasionally even species (a Great Blue Heron Ardea herodias passing in silhouette across the moon is unmistakable).

Most of us have marvelled at the "seeps," "chips," and whistles emanating from the night sky during migration. On some nights the number of calls is amazing. The well-trained ear can identify species groups and many species by their characteristic nocturnal calls. Unfortunately, many of the calls heard at night are rarely used during the day and it is difficult to associate a given call note with the species that makes it. Especially around dawn, however, many migrants emit the nocturnal flight calls, allowing a careful observer to associate call and caller. To the same end, one might also observe migrants at night around TV towers, lighthouses or floodlighted tall buildings.

There is at least one large-scale migration study based almost entirely on flight call data (Ball, 1952), but the technique has major limitations. The number of calls heard in a given time interval is a poor indicator of the number of birds passing over. Among other things, calling rate may vary with time of night, species composition (e.g., thrushes seem especially vocal), weather conditions, etc. Our ability to hear the calls will surely be a function of how high birds are flying, among other factors. Thus, one can learn something about the composition of the migrant swarm by listening to flight calls, but it is important to be aware of the possible biases (see Graber, 1968, for an evaluation). The most intriguing question about flight calls relates to their function. Despite some speculation (Hamilton, 1962; Griffin and Buchler, 1978), it is fair to say that we have no clear answer to the question, why do nocturnal migrants call as frequently as they do?

At most airports and many National Weather Service offices around the country ASR-4 and WSR-57 surveillance radars are in use that are ideally suited for the study of bird migration. How they can be used to reveal the spatial patterns, quantity and direction of migration has recently been summarized by Gauthreaux (1980). With proper advance arrangements, many of these radars could probably be used by interested persons to study migration in various regions.

Routes and Timing

Certainly for passerines, and probably for other species as well, the old idea of discrete flyways is invalid and obscures the complexity that characterizes migratory route patterns. Whereas a few species have rather proscribed routes of passage, migration in general takes place on a broad front. For only a few regions of orth America, however, do we have sufficient data from radar or visual observations to delineate the relative magnitudes of migration in various directions across the seasons.

For a few species we know from banding data that adults and immatures migrate at somewhat different times during autumn (e.g., Murray, 1966; Hussell *et al.*, 1967; Clench, 1969; Johnson, 1973; Leberman and Clench, 1973). The picture for many other species could certainly be worked out from existing banding data and would be worth knowing. With careful field observation, such data could also be obtained for some groups without handling the birds. In most shorebirds, the adults, especially the adult males, depart the breeding ground earlier than the young of the year. The age classes of many of these species are easily separable in the field (see the excellent guide by Prater *et al.*, 1977) and large amounts of data could be obtained by direct observation. Similar aging and sexing of many species would probably be readily accomplished under field conditions once adequate study of plumage variation had been made.

Geographic variation within species also provides an opportunity to learn interesting things about migration routes and timing. The carefully trained eye can often discriminate with reasonable accuracy the subspecies of even difficult groups by direct observation. For example, Jehl (1963) studied the timing of fall migration among the races of Short-billed Dowitcher *Limnodromus griseus* in New Jersey entirely by careful observation. Because birds need not be captured for this kind of study, large amounts of data can sometimes be accumulated rapidly and with minimal effort. Methods for identifying the sex, age, or geographic origin of individual birds are often discussed in the pages of *Continental Birdlife* and *British Birds*, but more analyses are needed.

A question of basic importance involves the routes taken by individual birds on subsequent migratory journeys. Do birds navigate with precision sufficient to allow them to repeat the route in detail, stopping at the same lay-over points enroute? Certainly many large water birds do so, but what of passerine nocturnal migrants? Are there cases in which banded songbirds have been captured in transit at the same place in different years? Only one certain case comes to mind (Goodpasture, 1979), but others may exist and I would be glad to hear of them. If such route retracing does not regularly occur, it suggests that navigation during much of the migration trip may be imprecise or lacking altogether. Perhaps birds use relatively simple compass orientation during most of the journey, true navigation occurring only when the goal is approached. If, on the other hand, it can be shown that passage migrants retrace routes in detail on subsequent migrations, quite different mechanisms of navigation might be implicated.

Weather Influences

Short-term weather events have major effects on bird migration. Most importantly, ambient weather, especially wind direction and trends of temperature change, has a major impact on the quantity of migration from night to night (Richardson, 1978, provides a comprehensive review). Migration traffic rates may vary by three orders of magnitude from night to night, and a significant proportion of this variability can be explained by weather. The correlation between nocturnal migration and weather variables is often difficult to detect by observing grounded migrants. Frequently the conditions that produce large concentrations of migrants on the ground (stalled fronts, fog, drizzle, etc.) are in fact quite unfavorable conditions for large migrations aloft. The various means described for observing nocturnal migration directly should all yield good results, however.

Banders could provide useful information regarding weather influences on layover times of passage migrants. On the average, it appears that songbirds stay at stopover points for 3-4 days in inland areas, but published data are few. Recapture records from inland localities are the most desirable because they are likelier to be free of biases than samples from coastal areas. Possible correlations between layover times and ambient weather, fat levels, age, and species should be sought.

As flying animals, birds are naturally affected by wind in major ways. Wind direction and speed are among the primary determinants of the probability that a bird will take off on a given night during migration. Depending on the direction of flight,

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wind can obviously facilitate or impede a bird's progress over the ground. For passerine birds which have generally low air speeds, a tail wind can often result in a ground speed of twice the air speed. In the case of long over water flights this fact may frequently mean the difference between success and death. It is not surprising that birds pay particular attention to this most important variable in their environment.

Wind Drift

Large migrations almost invariably occur with a following wind component, but often not a precise tail wind. This raises a difficult problem. A bird heading due south and flying in a wind from the west will move along a southeast course over the ground, i.e., it will be drifted by the lateral wind component. Field birders have long been aware of migratory drift — it is often relevant to the arrival of vagrants during migration — and most would accept it as dogma. Yet in the technical literature over the past two decades it has been a subject of great controversy. The crux of the problem is this: in the simple example used above, the usual assumption is that the bird wants to go south, i.e., that is the direction toward its migratory goal. By moving southeastward over the ground, it takes an indirect route to the goal, suffering lateral displacements that must be compensated for on subsequent flights. However, that the heading of the bird is really directed toward the goal is almost always an assumption in field studies. The second school of thought says that the bird's goal is really toward southeast, and having analyzed the wind situation, the bird alters its heading such that its path over the ground is toward the goal, i.e., it compensates for the drift. Why, then, should we see large differences in the direction of migration from night to night that are almost invariably correlated with wind direction? On the one hand it could be wind drift, but on the other it could be that birds with goals in certain directions selectively fly only on nights with the most favorable winds — if our bird wanted to go southeast it would wait for a night when the wind had an eastward component.

A little thought will convince you that without knowing the goal of a given bird, it is impossible to resolve this dilemma directly. Numerous less direct tests of the



hypotheses have been made and the overview seems to be that some birds are drifted by wind and others correct for drift. One has only to stand on Block Island, Rhode Island, following the passage of an autumn cold front, watching hundreds of nocturnal migrants beating their way northward back to the mainland, to perceive the reality of wind drift. Another clear-cut demonstration of drift will be described below. On the other hand, there is support for the wind selection-compensation hypothesis as well. Most recently, Crawford (1980) analyzed the composition of TV tower kills from northern Florida. He found that kills on nights with winds from the northwest contained significantly more individuals of species that are known to be Antillean migrants, whereas in northeast winds the samples contained predominantly trans-Gulf migrants.

Questions of wind drift and compensation cannot be readily addressed by ordinary field observation, except in special circumstances. It would, however, be of interest to have detailed data on the flight directions of passerine migrants re wind direction from many more areas of the continent. At present, adequate samples exist only for maritime Canada, New England and the southeastern states.

Orientation and Navigation

What information birds use to guide their flights on these immense journeys has intrigued scientist and layman alike for decades. Indeed, questions about orientation and navigation occupy much of the time and effort of ornithologists engaged in professional studies of migration. Only a very brief synopsis of what we know can be given here, but a factual summary of the subject appeared in the August, 1979, issue of *National Geographic* and more technical reviews are Keeton (1979) and Able (1980).

Orientation refers to the ability to determine compass directions. We now know that at least some kinds of birds possess the ability to derive directional information from the sun, star patterns, and the earth's magnetic field. Wind direction may also be used in orientation, but because it varies over time does not give absolute compass directions. In the southeastern United States there is a very strong tendency for birds to head downwind, no matter which way the wind is blowing. Flights in seasonally inappropriate directions are frequent, even when stars and other compass cues are readily available to the birds. The more general case, as we have found in upstate New York, seems to be that the visual cues (sun and stars) take precedence over wind direction when they are available. If solid overcast prevents a view of the afternoon sun and the stars, however, songbirds orient downwind even if that results in flight in a seasonally wrong direction.

Whereas magnetic influences have been demonstrated in migrants tested in orientation cages, such effects have been elusive in the free-flying situation. That is perhaps not surprising because a free-flying bird has access to much more information than the birds used in experiments to test magnetic orientation. Nonetheless, it would be worthwhile to make some observations on migrants around magnetic anomalies, i.e., in areas where the earth's magnetic field is distorted by large deposits of iron. Such places are really quite numerous, although not well mapped in many areas. Unfortunately, oil companies, which do much of the mapping, are not generous with the information. The effects of such an anomaly, if any, might be manifest only among birds that initiated migration within the distorted field, not those that are simply passing over the area. Likewise, any effects might be discernible only when other orientation information is lacking, e.g., under heavily overcast conditions. Portable ceilometers are ideally suited for this kind of investigation.

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Dogma in this field has been that night migrants pay little attention to landmarks. This was based on the fact that, unlike many diurnal migrants, nocturnal flights often passed across coastlines with no sign of turning or responding to the potential "leading line." There is recent evidence, however, that night migrants do respond to landmarks in rather subtle ways. In eastern New York, the predominant direction of fall migration is southwest in calm or light winds. When strong west or northwest winds blow, migrants track southeastward in areas away from the conspicuous north-south Hudson River. Near the river, however, birds apparently turn because there, on the same nights, they fly southward, parallel to the river. This difference in orientation near and away from the river occurs only in strong winds lateral to the general flow of migration. We believe it is a clear demonstration of both wind drift over upland areas and compensation using landmarks at night when appropriate features on the ground are available. Similar behavior might be observable in many other areas, but it is important to remember that response to landmarks at night may occur only under certain conditions.

If birds migrating at night are sometimes drifted off course by winds, when do they perform corrections? We don't really know, but most of us have seen diurnal movements of birds usually thought to be strictly nocturnal migrants, especially in early morning hours. Gauthreaux (1978) has recently studied this phenomenon in inland South Carolina and hypothesized that the birds were compensating for wind drift accrued during previous nights' flights. Most morning flights were toward the northwest. In eastern New York, Bingman (1980) observed similar movements of loose groups of night migrants, usually accompanied by much vocalization. However, the migrants moved predominantly in the same directions as nighttime flights, i.e., no compensation was apparent. What is clear is that morning flights by nocturnal migrants are of frequent occurrence in most areas of the continent and they deserve careful attention. Important information can be obtained with nothing but binoculars and a compass. What species are involved? Are they a random sampling of the grounded migrants in the woods? Are adult birds over-represented in the fall flights (adult males of many species are identifiable even in flight), perhaps exercising navigational skills absent in young of the year? In South Carolina, Gauthreaux believes that they are.

For whatever reasons, some birds seem to get lost and wind up in places where they don't belong. Observers in coastal areas where vagrants concentrate are keenly aware of these birds and thousands of man-hours are spent searching for them. Yet there are many questions about vagrancy to which we still do not have clear answers. The number of vagrants reported, especially from the west coast of the United States, has increased dramatically over the last two decades. Are there really more vagrants these days, or can the increase be explained solely by the larger numbers of birders searching for them and by more sophisticated knowledge of where and how to find them? There are marked year-to-year variations in vagrants in California and a trend toward general increase over the last five or ten years of censuses on Southeast Farallon Island (DeSante, 1973, 1980), but no marked, consistent increase in vagrancy is yet evident.

Many other questions about vagrants arise. How do they get so far off course? Are they evolutionary misfits with faulty orientation mechanisms, doomed to fly in a wrong direction until they become statistics of natural selection? David DeSante, who has studied the phenomenon in California, thinks so. Certainly the vast majority are young birds on their first migration so the effects of both faulty orientation behavior and inexperience may be combined. Of course, it is well known among banders that in fall immature birds of most species are disproportionately abundant in coastal regions. Perhaps vagrancy and this so-called "coastal effect" are mechanistically related. On the other hand, immature birds on islands offshore from New England do make reoriented landward flights, and very recently the same "coastal effect" has been found in the Great Lakes (Dunn and Nol, 1980). These observations cast doubt on the hypothesis that orientation malfunction is solely responsible for the well-documented and striking pattern.

What role does weather, especially wind, play in vagrancy? A recent analysis by Elkins (1979) of the occurrence of North American landbirds in Britain and Ireland showed that a strong association existed between strong west to southwest winds, rapid eastward-moving frontal waves and the arrival of vagrants. A similar appraisal of the California situation is somewhat complicated by the disparate origins of the birds, but as records accumulate some clear patterns might emerge.

Large waterbirds often migrate in flocks, frequently as family groups. This provides the opportunity for information sharing and for young to learn details of the migration route from adults. To what extent might information be shared by other birds that migrate in aggregate? Are flocks better oriented than single individuals? Hawks such as Broad-wings (*Buteo platypterus*) might be amenable to study in this regard. Is it possible that the calls of night migrants have significance for orientation? Unlikely perhaps, but no more far-fetched than other phenomena that have now been documented in this field.

Adult birds return with great precision to previously occupied nesting and wintering sites. We know this from a large amount of banding data. The ability to do so requires something more than compass orientation. A bird must be able to assess its spatial position with reference to its goal (in this case, a precise point) and to calculate the appropriate direction of movement. This is called navigation and is conceptualized as requiring analogs of both a compass and a map. The ability to home to a point on the earth requires some direct experience with that area, although exactly what information is assimilated remains unknown. Young birds on their first migrtion appear to be genetically programmed to fly in a particular direction and for a distance that puts them within the winter range of their population. Once there, they apparently imprint on a specific locality sometime later in the winter (see Ralph and Mewaldt, 1975).

These broad outlines are fairly well established, but for most species the specifics are completely unknown. For instance, young birds return to near their natal site when they breed for the first time. But the details of the settlement patterns of first breeders is not well documented. How close to the territory of their birth do they establish their own claims? Do males settle closer to home than females? See Greenwood (1980) for a review of what is known.

Perhaps the most puzzling question in this whole subject of bird migration is what constitutes the mysterious map that seems necessary for homing navigation? Most recent work has concentrated on homing pigeons because they provide a convenient experimental system. Current attention is focused primarily on the possibilities of a map comprised of magnetic information or one based on olfactory cues. We seem not to be very close to an answer to the question. However, some experiments with homing pigeons released wearing frosted lenses revealed that they homed nearly as well as those wearing clear lenses, an indication that whatever constitutes the map does not involve detailed form vision.

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Other sensory capabilities of birds (documented primarily in pigeons) have recently been discovered: detection of polarized light, vision in the ultraviolet, sensitivity to very small changes in barometric pressure, and ability to hear extremely low frequency sounds (so-called infra-sound). Some of this information which is largely beyond our own sensory world may be used by birds in some aspect of migratory behavior (see Keeton, 1979, Able, 1980 for reviews of these aspects).

It should be obvious that many puzzling questions about bird migration remain and each new discovery raises more. It is the possibility of unraveling some of these knotty problems that keeps many of us plugging away at what often seems a hopeless endeavor. But the task is large and there is ample room for significant contributions by layman and professional alike. My hope is that this short and selective review might stimulate such investigation.



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