

HISTORICAL PERSPECTIVES BIRD MIGRATION: METHODOLOGIES AND MAJOR RESEARCH TRAJECTORIES (1945-1995)¹

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As a new graduate student at Louisiana State University in the early 1960s, I was greatly impressed by a paper published by Niko Tinbergen (1963). In that paper he pointed out that the first phase in the study of animal behavior is that of observation and description. Once this phase is completed, if it is ever really completed, the scientist can then proceed to ask questions that Tinbergen grouped into four categories: immediate causation, development, evolutionary history, and function. These categories have proven very useful to me in "classifying" the types of bird migration studies that have been conducted through time, and I use them to organize my review of important research trajectories in the study of bird migration over the past fifty years.

Tinbergen (1963) cautioned that observation and description should be the foundation for the formulation of hypotheses, but this has not always been the case. Unfortunately many young investigators today have the impression that descriptive studies are a waste of effort and money. They have been told that hypothesis testing is where the action is, and if you are not testing hypotheses, your interests and efforts are surely misguided or at the very least outmoded. Nothing could be farther from the truth, and Lorenz (1973) said it best when he referred to the trend as the "fashionable fallacy of dispensing with description." There can be no debate about the importance of testing hypotheses, but this phase of scientific endeavor should be predicated on strong underpinnings of observation, description, and discovery. Hypotheses should not be based on unfounded assumptions. The historical perspective that follows first reviews the important role of methodology in the "observation and description" phase of migration as studied in the field and in the laboratory. It then briefly addresses what I consider the major trends in migration research relative to Tinbergen's four classes of questions in the last half century. Because of space limitations, the citations that are included are representative and are not intended to be exhaustive.

CLASSICAL METHODS USED IN THE OBSERVATION AND DESCRIPTION OF BIRD MIGRATION

During the past fifty years studies of bird migration based on observation and description have greatly out-

numbered all other types, undoubtedly because of the ease of conducting such studies. Most of these studies have used straightforward methods to gather data on migratory birds: 1) observations of visible migration in progress, 2) observations of migrant birds at stop-over areas, 3) the capture and banding of migrants, and 4) the gathering of dead and injured migrant birds after collision with man-made structures.

The vast majority of the studies of the visible migration of birds have used field observations with binoculars and telescopes to monitor the low-altitude passage of birds at a particular location (Thomson 1953). Several long-term studies have been conducted at observatories in Europe (Edelstam 1972, Ulfstrand et al. 1974), however similar work has not been undertaken to any great extent on the western side of the Atlantic. The only studies in North America that resemble those of visible migration in Europe are at sites where migrating raptors pass in large numbers (Heintzelman 1975). The usefulness of the data gathered during studies of the visible migration of birds cannot be disputed, but one must be cautious when interpreting these data because of possible hidden biases and inherent limitations of the methods. For example, birds may be passing over the same observation point several times, and an unknown amount of migration might be "invisible" to the observer because the birds are flying too high or too far away to be seen with binoculars (Alerstam 1978, Kerlinger 1989).

Studies of visible migration have contributed considerable data on the seasonal and daily temporal patterns of migration for many different species, and it has been argued that these data may be important in monitoring population sizes of the various species (but see Svensson 1978). Many of the studies of visible migration have spanned decades and have generated sizable data sets. Because of the difficulty of publishing compilations of essentially "raw data," I suspect that many data sets are archived in bird observatory libraries or associated institutes throughout the world, and the data are used mostly in local and regional publications on bird migration.

The observations and censusing of migrant birds at stopover areas has also been an important part of migration studies in the field. Systematic observations of the behavior of birds at migration stopover areas have produced important findings on feeding behavior during migration (Ferns 1975), territoriality while enroute (Rappole and Warner 1976), and bird-habitat associations during migration (Parnell 1969, Hutto 1985a, Moore et al. 1990) to mention a few. Additional data

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on the seasonal timing of migration in different species at different locations along the migratory route have been gathered by censusing migrants at stopover areas (Saunders 1959, Weydenmeyer 1973, Pinkowski and Bajorek 1976, Clark et al. 1993). Unfortunately the methods of censusing stopover migrants, including limited area searches, transects, and point counts, have not been used in a systematic way and the rigor of the censuses have varied greatly from study to study making comparisons of data sets difficult or impossible. Attempts to correct these problems are underway (Husell 1981, McCracken et al. 1993, and Ralph et al. 1993) as the importance and necessity of monitoring bird populations during their migratory journey increases. The study of migration in the field has been improved greatly when systematic observations and counts have been combined with banding operations.

In 1900 the Danish ornithologist H. Chr. C. Mortensen pioneered the scientific use of bird-banding to study bird migration on a large geographical scale (Jespersen and Tåning 1950). Since then banding has grown greatly in scientific value as millions of birds are banded at well-known observatories and netting stations throughout the world. The European Union for Bird Ringing (EURING) has been organized in an effort to standardize methods and coordinate banding activities at the 30 or so banding stations in Europe. In North America, the Canadian Wildlife Service and the United States Fish and Wildlife Service's Bird Banding Laboratory have developed a two-volume manual to assist authorized banders in following firm protocols. A handbook devoted to statistical inference from band recovery data has been developed by Brownie et al. (1977), and some attempts to standardize mist net captures for the quantification of migration have been explored by Ralph (1976).

The banding of nestlings can provide data on linkages between breeding and nonbreeding areas—information that is critically important for the management of many Neotropical migrant species with populations that are in a state of decline. Despite the very low recoveries of banded birds, particularly for those passerines banded as nestlings, the only way we know the linkage between breeding and wintering areas for a specific population of a species is through the “recovery” of birds banded as breeders or nestlings. Perhaps the capture and banding of post-fledglings in a study area such as is done in the MAPS program of DeSante (1992) will enhance the likelihood that more birds will be recovered after completing their autumn migration. The value of banding programs that delimit the endpoints of a migratory journey cannot be overstated. Without such efforts the information contained in McClure's (1974) volume on the migrations of Asiatic birds would not have been available.

The capture and banding of birds at migration stopover areas has been one of the most popular methods of studying migration (Bergstrom and Drury 1956). One of the best organized efforts in North America included several different stations along the Atlantic coast and was known as Operation Recovery (Baird et al. 1958, 1959). The initiative produced, among other findings, valuable information on the complexities of the migration schedules of males and females and adults and young during fall migration (Murray 1966). Other

studies of birds captured during migration have revealed that the geographical pattern of migration in several species of warblers is different for adults and immatures during autumn migration. In these studies (Ralph 1971, 1978), adults were found to be distributed inland and away from the coast while immatures were more abundant on and close to the coast.

It has long been known that considerable mortality can occur at lighthouses during nighttime migration (Brewster 1886, Bonhote 1903), and that such mortality is a source of important information on species composition, timing, energetics, and other aspects of nocturnal migration (Goodpasture 1963, Taylor 1972, Odum et al. 1961). In the last fifty years additional sources of mortality have appeared: tall buildings and broadcast towers, airport ceilometers, and illuminated monuments. In many cases bright light is the critical factor associated with the mortality. As buildings in large cities increased in height, lighted windows on the upper floors posed a hazard to birds migrating at night (Pough 1948). With the advent of television, tall broadcast towers with anticollision warning lights and supporting guylines were erected in the United States—some reaching heights of 2,500+ ft (762 m). These structures have been known to cause tremendous mortality, particularly in the fall when cold fronts stimulated large migrations and weather conditions deteriorated (Tordoff and Mengel 1956, Stoddard 1962, Crawford 1974). In the 1950s fixed vertical light beams of nearly one million candle power were installed at airports to measure the heights of cloud ceilings. During migration when the ceiling was low and it was misty, large numbers of birds collided in mid air as they were attracted to the bright beam, and some possibly blinded by the beam flew directly into the ground (Johnston and Haines 1957). Tall monuments illuminated by powerful spotlights have also attracted migrating birds at night and occasionally cause mortality (Overing 1936). Weir (1977) has provided a comprehensive, annotated summary of bird collisions with man-made objects, and most of the references relate to migration mortality.

SIGNIFICANT METHODOLOGICAL DEVELOPMENTS

FIELD STUDIES

Methodology is critically important to the success of any study of migration whether it be descriptive or experimental, in the field, or in the laboratory. Two important areas of development have had a major impact on the methodology of migration studies over the last half century—technological advancements and the introduction of statistical procedures that assist in the design of studies and data analysis. The first has enabled new discoveries to be made and the second has guided the development of study design and analysis protocols that have produced statistically sound studies.

Although not exactly a technological development, the advent of moon-watching, or using the disc of the moon as a background for observing the silhouettes of migrating birds flying in the night sky, marked the beginning of a new research trajectory in field studies of migration that enabled the quantitative study of “visible” nocturnal migration (Lowery 1951; Lowery

and Newman 1955; Nisbet 1959, 1963). Because of the requirements of a nearly full moon and clear skies, there was a need for another less restrictive technique for studying nocturnal migration. That technique proved to be radar. The discovery that birds could be detected on surveillance radars came early in the 1940s (McKay 1945, Brooks 1945, Lack and Varley 1945, Buss 1946). The pioneering work of Ernst Sutter (1957*a*, 1957*b*) demonstrated that surveillance radar could readily detect small migrating birds in the atmosphere. Radar could "see" birds flying above or even in clouds layers, and on the radar screen only rain obscured the echoes from migrating birds. Interest in radar studies increased greatly, and by the late 50s and early 1960s many studies were underway to discover the patterns of daytime and nighttime bird migration in different regions of North America (Nisbet 1963, Drury and Nisbet 1964) and Europe (Lack 1959, 1960, 1962, 1963*a*, 1963*b*). Much of the information from early radar studies through the mid-1960s has been summarized by Eastwood (1967). By the late 1960s and early 1970s radar studies were numerous. Much of what we know about the large scale temporal and spatial patterns of bird migration has resulted from radar studies.

A major shortcoming of many of the surveillance radar studies was that they were based solely on radar information and lacked simultaneous information on visible migration. By combining moon-watching and radar surveillance it was not only possible to quantify radar displays of nocturnal migration, but also to determine the types of birds responsible for the radar echoes (Gauthreaux 1970). Because of the need to make direct visual observations of nocturnal migration during radar studies when no moon was visible, a portable ceilometer was used to monitor migration overhead (Gauthreaux 1969, Able and Gauthreaux 1975). Although the older, very high intensity fixed-beam ceilometers attracted migrants and caused mortality in cloudy, misty weather; the smaller, portable units did not seem to affect migrating birds in most weather conditions. The portable ceilometer technique was greatly improved with the use of an image intensifier instead of binoculars or a telescope (Gauthreaux 1985). The recent use of forward looking infrared (FLIR) thermal imaging devices for migration studies at night holds great promise (Winkelman 1992, Liechti et al. 1995). The range of detection is better than that of moon watching or the ceilometer technique, and unlike the ceilometer technique, the FLIR technique does not require a light beam to illuminate the birds, because the FLIR sensors detect the heat of the birds as they pass overhead.

The use of call notes from migrating birds to determine the types and numbers of birds passing overhead has received limited attention. One of the first systematic studies to use flight call counting was that of Ball (1952) who studied fall migration at Gaspé Peninsula. Tape recorders with sensitive microphones have been used to record the flight calls of nocturnal migrants in Illinois (Graber and Cochran 1959), and Dorka (1966) used calls of nocturnal migrants to delimit migration patterns at the Col de Breilot pass in the Alps on the border of Switzerland and France. Recent studies have used voice activated circuitry to record calls from mi-

grating birds (Dierschke 1989) and computer analysis to identify and classify call notes recorded with a very sensitive hearing aid microphone and a tympanic membrane-like collector (Evans 1994, pers. comm.). The shortcomings of the acoustical method of studying nocturnal bird migration are serious. Some species of nocturnal migrants apparently do not vocalize in flight, and it is well known that the rate of calling increases as cloud cover increases (Ogden 1960, Graber 1968). These problems make truly quantitative studies of nocturnal migration unlikely using this method alone.

Radiotelemetry and tracking radar studies in the 1960s greatly enhanced our understanding of the flight behavior of individual migrating birds, and allowed them to be tracked over large geographical areas. Prior to the mid 1960s, radio transmitters were so large and heavy that only large birds could carry them. The first use of radiotelemetry in studies of the migration of small birds began in the mid 1960s when William Cochran developed transmitters small enough to be carried by thrushes (Graber 1965, Cochran et al. 1967, Cochran 1972, Cochran and Kjos 1985, Cochran 1987). The technique is still relatively expensive and involves tracking vehicles (planes and trucks), tracking equipment (expensive receivers and analysis equipment), and a great deal of work and patience. It is little wonder that the technique has not been used more frequently. A major breakthrough in circumventing the limitations of traditional radiotelemetry surfaced in the mid 1980s—the use of satellites to track birds with radio transmitters (Fuller et al. 1984, Strikwerda et al. 1985). The use of satellite tracking corrected some of the limitations associated with the ground tracking of radio-tagged birds in migration, but introduced others such as the requirement of a heavier transmitter, the availability of satellite platforms for tracking, the precision of location data, and time interval between samples. Most of the recent work has involved large birds such as waterfowl, eagles, storks, and large seabirds (Nowak and Berthold 1987, Jouventin and Weimerskirch 1990, Berthold et al. 1992, Nicholls et al. 1994). At present the transmitter powerpacks are too heavy for small passerines to carry, but with miniaturization it may eventually be possible to have transmitters that can not only track a small bird on a long-distance migration, but monitor physiological (e.g., body temperature, heart rate) and environmental (e.g., atmospheric temperature, barometric pressure) variables in the process.

Unlike surveillance radars, tracking radars are designed to detect, lock on, and follow a single target in the atmosphere (Eastwood and Rider 1966). The systematic use of tracking radars to study bird migration began in Switzerland in the late 1960s (Gehring 1967, Bruderer 1971, Steidinger 1972), and in these studies many different free-flying birds were tracked for short periods (two minutes) of time. A similar study was also underway in 1969 at Wallops Island, Virginia and at Bermuda (Williams et al. 1972) and in eastern New York state (Able 1977). The narrow pencil beams of tracking radars make precise measurements of altitude, speed, and direction possible. The first study to use tracking radar to follow known individuals released aloft at night were those of Emlen and Demong (1978) and Demong and Emlen (1978). These studies exam-

ined the orientation of experimentally manipulated free-flying migrants after being released from a box that had been carried aloft by a weather balloon.

The aforementioned studies and many others have contributed greatly to our knowledge of bird migration in the field. They have played an important role in the description and quantification of daytime and nighttime patterns of migration at vastly different spatial and temporal scales. We now have a much better understanding of the geographical patterns of migration in relation to landforms and climatic patterns at one end of the spatial spectrum and the flight and foraging strategies of individual migrants at the other end of that spectrum. Likewise we know a great deal about the seasonal timing of migration for most species and whether they migrate at night, or during the day, or both. These field studies have provided the necessary substrate for further investigations of migration in the laboratory, but how has migration been studied in the laboratory?

LABORATORY STUDIES

The discovery that migratory birds show restlessness (*Zugunruhe*) during periods when they would normally be migrating in the field (Naumann 1795–1817) has had a tremendous impact on the study of “bird migration” in the laboratory (see also Wagner 1930, Helms 1963). Modern activity registration cages have taken advantage of technological developments. No longer is one limited to using perches connected to microswitches that are connected to an event recorder. Now instead of the traditional microswitches, activity cages can be equipped with photodiodes, acoustical and pressure switches, and the data can be recorded and analyzed by a personal computer. Because perch registrations may not record accurately the amount of restlessness shown by some caged migrants, closed-circuit television with infra-red lighting has been used to record the wing whirring type of *Zugunruhe* (Berthold and Querner 1988). Even inexpensive, “low tech” paper funnels with ink pad bases (Emlen and Emlen 1966) have been used to measure the amount *Zugunruhe*. These methods have been critically important to our understanding of the control mechanisms of migratory behavior, including, daily and seasonal rhythms, orientation, and duration.

In the last half century researchers have devoted considerable attention to the energy required for migration. Several methodological innovations have been responsible. The use of wind tunnels has allowed investigations of flight physiology in migratory birds in a controlled, laboratory environment (Tucker 1968, Torre-Bueno and Larochelle 1978, Nachtigall 1990). Prior to the use of wind tunnels the techniques used to measure flight metabolism were indirect and many of the aspects of the bird's flight were assumed (Butler and Woakes 1990). These problems have been overcome with the use of wind tunnels, and it is possible to measure directly power input and respiratory and cardiovascular variables in birds flying for several hours. Long flights in excess of a day, however, are not yet possible.

Because lipids are the primary fuel for long-distance flights, the quantification of lipid levels in migrants has been of great interest. Although somewhat crude meth-

ods have been developed for assessments of lipid levels in the field (Helms and Drury 1960, but see Kremzntz and Pendleton 1992), the extraction of lipids from cells and tissues with nonpolar solvents is still the most reliable method (Folch et al. 1957, Odum et al. 1961, Dobush et al. 1985). Unfortunately this technique requires the destruction of the bird. Within the last decade new technology has enabled the estimation of lean and lipid mass using a nondestructive method of measuring total body electrical conductivity (TOBEC). Walsberg (1988) has evaluated this technique for measuring fat stores in small birds and mammals in the field and in the laboratory and emphasized that calibration is necessary for different species using traditional means of lipid extraction. Once the relationships among TOBEC, lipid mass, and lean mass are known using traditional fat extraction methodologies, the TOBEC can be used with no further destructive sampling. Although this method holds great promise, high error rates have been noted in predicting lipid mass in migrating birds (Skagen et al. 1993, Lyons and Haig 1995; Spengler et al. 1995), and additional concerns about the effects of dehydration on TOBEC measurements of the body composition of migrating birds have been noted by Roby (1991). Considerable advancement in our knowledge of the biochemistry of fat storage and metabolism has been achieved in the last two decades (Ramenofsky 1990, Mostafa et al. 1994), and this is reflected in studies that not only measure the total lipid content in the fat, muscle, liver, and plasma of birds, but also the protein, total lipid, and triglycerides (the most abundant form of plasma lipids) in blood samples collected in heparinized tubes (Cantos et al. 1994). For a review summarizing the temporal control of migration and migratory fattening in long-distance migrants and the known nutritional adaptations that allow them to cope with the enormous migratory energy storage requirements see Bairlein and Gwinner (1994).

Classical metabolic studies in birds required exact measurements of the net difference between the energy in food consumed and the energy in excreta (Helms 1968). Because the mode and intensity of activity in caged birds and free-living birds may be very different, extreme care must be taken when extrapolating the findings of studies of caged birds to birds in the field. The measurement of CO_2 production by doubly-labeled water ($\text{DLW}-^3\text{H}_2^{18}\text{O}$) and subsequent analysis of isotopes in the blood is potentially the most accurate technique available for measuring the average metabolic rate of free-living animals (Nagy 1980). Recently it has been shown that heart rate is as good a predictor of the mean metabolic rate of free-ranging birds as doubly labeled water or time-energy budgets combined with either DLW or respirometry (Bevan et al. 1994). The use of the heart rate technique for the detailed measurement of daily energy budgets of birds over much longer periods than was previously possible holds great promise.

Since William Rowan's classic experiments on the relation of photoperiod to bird migration (Rowan 1929, 1930, 1932), the role of hormones in controlling migratory behavior has been a research topic of great interest (Farner 1955). The early procedures used to study hormones and behavior involved: 1) removal of the gland thought to be the source of the hormone, 2)

observation of the effects of removal, 3) replacement of the hormone by reimplantation of the gland or injection of homogenate or purified extract of the gland, and 4) observations to see if the replacement therapy worked. Through technological advancement, replacement procedures have improved as new recombinant DNA methods can be used to make highly purified hormones, thus eliminating the possibility that impurities are responsible for the effects. Hormonal titers were originally measured by bioassay (e.g., Meier and Farner 1964), but the development of the radioimmunoassay (RIA) eliminated much of the tediousness of the older methods and greatly increased the precision of the measurements (Gwinner et al. 1993). An additional technique of measuring hormone titers include enzyme immunoassay (EIA)—similar to RIA but not requiring radioactive tags. At present 10–15 different hormones can be measured quantitatively from a small quantity of blood (about 0.2 ml in passerines) taken from the veins in the wing (Berthold 1993: 28).

Because hormone receptor physiology is a rapidly growing field of endocrinology, the techniques of immunocytochemistry (ICC) and autoradiography hold great promise (Nelson 1995). Wingfield et al. (1990) have provided a summary of the effects of hormones on the hypertrophy of flight muscles and hematocrit in migratory birds and an extensive discussion of the endocrine control of premigratory hyperphagia, fattening, and migratory behavior (*Zugunruhe*). Despite the advances in this field, Wingfield et al. (1990) caution that much of the data is contradictory and confusing, and it is still unclear how hormones influence migratory physiology and behavior.

Methodological breakthroughs in the last decade have already impacted the study of evolution and will likely do so in the future for the study of bird migration. The rapid technological advancements in the area of molecular genetics have generated new research tools in the form of genetic markers that can be used to identify the sex of individuals and the genetic population to which an individual belongs (Avice 1994). For population markers, regions of mitochondrial DNA (mtDNA) can be amplified and sequenced. Total DNA can be extracted from whole blood taken from a wing vein (Sambrook et al. 1989) or purified from tissues such as heart, muscle, liver, or even feathers (Carr and Griffith 1987). Random amplified polymorphic DNA (from a technique that amplifies anonymous portions of nuclear DNA [Williams et al. 1990]), may also serve as genetic markers for populations, or subspecies, or both (Haig et al. 1994).

Some initial findings from the application of this technology are very encouraging. Wenink et al. (1993) have compared sequences of the hypervariable-control-region of mtDNA among populations of Dunlin (*Calidris alpina*), a long-distance migrant, and found global population structuring. The findings suggest that Dunlin populations are highly philopatric and there is little gene flow between populations. In contrast, similar work on Red Knots (*Calidris canutus*), another long-distance migrant, has failed to find significant variability in the genetic markers (low number of haplotypes and very low sequence divergence) of 25 individuals from ten populations from around the world, suggesting that the populations have only recently ex-

panded from a single bottleneck population that survived the rigors of the Pleistocene glaciations (Baker et al. 1994). A similar finding might also be expected if substantial gene flow among populations is the case for the Red Knot. The importance of these findings is that in the future it may be possible to assign birds of certain species encountered in migration or on the wintering grounds to specific populations on the basis of a small blood sample or even feathers.

The desire for genetic markers that can be used to assign individuals to particular geographical breeding populations is of course the same desire that led early students of migration to mark, tag, or band birds: the discovery of associated breeding and nonbreeding locations and the routes followed in moving between the two. Unfortunately the problem of small numbers of recoveries of marked birds has limited this approach. The use of genetic markers should overcome the problem of limited band recoveries and allow the sampling of large numbers of genetically "marked" birds. Once again we have the prospects that a new technological development will contribute a valuable technique to the study of bird migration.

MAJOR RESEARCH TRAJECTORIES IN BIRD MIGRATION

IMMEDIATE CAUSATION

Questions of immediate causation concern the proximate factors that influence behavior of an organism over a relatively short period of time during the life of an individual (Tinbergen 1963). With respect to bird migration, immediate causation concerns the environmental and internal factors that regulate the physiological conditions necessary for migration as well as those factors that cause the immediate release, alteration, or cessation of migratory behavior (Thomson 1951, Farner 1955). Much of the migration literature on this topic from the 1920s through the early 1950s has been summarized by Farner (1955), and much of the progress during the subsequent 20 years has been reviewed by Peter Berthold (1975). Papers presented at symposia in October 1977 (Alerstam et al. 1978), in November 1983 (Rankin 1985: 501–617), and in October 1988 (Gwinner 1990a) addressed in part the research accomplishments in the late 1970s and most of the 1980s. Significant literature in the 1980s has been reviewed by Berthold and Terrill (1991).

Internal Factors. During the last fifty years research on the physiological factors that regulate bird migration has focused on the development and maintenance of migratory condition (hyperphagia [Odum 1960]; fat production, storage, and usage [Ramenofsky 1990, Blem 1990]; metabolic changes [Dawson et al. 1983]; nutrition and body composition [Ellis and Jehl 1991, Bairlein and Gwinner 1994, van der Meer and Piersma 1994]; and endocrine, neuroendocrine, and neurotransmitter influences [Wingfield et al. 1990, Gwinner et al. 1993]). One of the most significant discoveries during the last half century is that endogenous biological rhythms may regulate the daily (circadian) and the seasonal (circannual) timing of migratory behavior (McMillan et al. 1970; Gwinner 1968, 1977), and that photoperiod may have an important role in the timing of these cycles (Gwinner 1975, 1990b).

External Factors. Although there has been extensive work on the ecology of migrants on their breeding and wintering grounds (e.g., Keast and Morton 1980, Rappole et al. 1983, Hutto 1985b, Lövei 1989, Hagan and Johnston 1992, Mönkkönen et al. 1992, Finch and Stangel 1993), by comparison much less information has been gathered on environmental factors during the migratory phase. Some investigators have examined the habitat associations of migrants (Parnell 1969, Hutto 1985a, Winker 1995), availability of habitat and habitat suitability at stopover sites (Moore et al. 1990, Moore and Simons 1992), and food and foraging behavior at stopover sites (Ferns 1975, Bairlein 1981, Spina et al. 1985). Weather conditions play an important role in the timing, duration, and successful completion of migratory flights, and a great amount of information on this topic has been gathered in the last half century. David Lack (1960) has summarized most of the early findings up to the late 1950s, and reviews by Elkins (1983) and Richardson (1978, 1990) have synthesized the findings since that time.

DEVELOPMENT AND ONTOGENY OF MIGRATORY BEHAVIOR

Perhaps the greatest accomplishment in bird migration research in the last five decades are those related to the genetic factors involved in the immediate control of bird migration. In the last 15 years the development of methods to breed large numbers of migratory songbirds in captivity has led to a surge in research papers that demonstrate the importance of genetic factors in the control of migratory behavior (Berthold 1990, Berthold 1993, Berthold and Querner 1995). Endogenous circannual rhythms of migratory behavior (Gwinner 1990b) are genetically controlled, and because they determine the onset and termination of migratory periods, genetic control of departure and arrival is highly likely (Berthold and Querner 1995). Likewise, endogenous temporal programs control the duration and direction of migratory behavior and consequently determine the route between breeding and unknown wintering grounds (vector-navigation hypothesis) in naive fall migrants (Berthold and Helbig 1992). The variances in the directions that birds migrate can be attributed to genetic variance (Helbig 1991, 1994). Sex-specific endogenous temporal programs (Terrill and Berthold 1989) have been demonstrated in Blackcaps (*Sylvia atricapilla*), and help explain the well known differences in the spring arrival times of males and females on the breeding grounds. In light of the evidence that both distance and direction can be preprogrammed in fall migrants moving toward their wintering sites for the first time, it is not surprising that the same endogenous program is responsible for the timing of the return to the breeding grounds in spring. The genetics experiments on the heritability of various traits of migratory birds not only relate to the development of migratory behavior but also to evolutionary aspects of migratory behavior in general.

EVOLUTION AND PHYLOGENY OF BIRD MIGRATION

The early notions that bird migration evolved in response to catastrophic events like continental drift (Wolfson 1948), or glacial and interglacial cycles (Cow-

ard 1912) reflect the thinking of the times and are no longer considered viable hypotheses (Gauthreaux 1982). In the mid-1940s, the last vestiges of Lamarkianism appeared in the literature on the evolution of bird migration. Since that time considerable theoretical and empirical research has been devoted to questions about the evolution of bird migration. We now know how the evolutionary process works. Selection operates on genetic variability to produce microevolutionary changes in traits associated with migration. In 1977, Peter Berthold (1978) began two-way selection experiments on partially migratory Blackcaps that demonstrated heritable variation between migratory and non-migratory habits within one generation. Subsequent two-way selection experiments with the same partial migrant (Berthold et al. 1990a), showed that a parent population with 75 percent migrants could "evolve" into either a completely migratory or a completely sedentary population in only three generations. Once the experiments reached the F₆ generation, Berthold et al. (1990b) found that after three generations migratory birds produced almost exclusively migratory offspring, and after four to six generations of selective breeding of non-migratory residents, almost exclusively sedentary offspring were produced. These experiments show an astonishing rate of evolutionary change with heritability estimates ranging from 0.6 to 1.0 (Berthold et al. 1990a).

Although the amount of evidence supporting the genetic control of obligate partial migrants continues to grow, the information gained from these experiments does not detail 1) how selection has proceeded, and 2) the ultimate factors responsible for the selection of migratory behavior. This is the domain of theorists and there has been no shortage of theories on the evolution of bird migration (Salomonsen 1955, Alerstam and Enckell 1979, Fretwell 1980, Cox 1985, Lundberg 1988, Levey and Stiles 1992, Holmgren and Lundberg 1993).

The relative contribution of genetics, or environment, or both to changes in various aspects of migration continues to be debated. Berthold (1993) argues that the weight of the data supports genetic control, and that the data in support of an environmental control hypothesis (e.g., the behavioral-constitutional hypothesis *sensu* Miller 1931, also known as the competitive exclusion or behavioral dominance hypothesis of Kalela 1954 and Gauthreaux 1978) is meager. Nonetheless, recent theory suggests that a facultative determination of migratory or sedentary habits may depend on various environmental factors (Holmgren and Lundberg 1993). Variance in migratory behavior has been well documented, but more work in different species will be needed to document the relative contributions of the environment, genes, and their interactions to the variance in the migratory behavior phenotype. It has been and will continue to be difficult to study the environmental control of migratory behavior in a laboratory environment.

FUNCTION

Clearly the function of migratory behavior is to escape from adversity when the annual climatic cycle renders the area temporarily unsuitable for survival (Gauthreaux 1980). Consequently migration contributes to

survival and ultimately to an individual's fitness. Although it is hardly worthwhile to debate the function of migration, considerable interest has been shown in the optimization of the process. With the growth of the fields of evolutionary and behavioral ecology, the interest in conducting cost/benefit analyses of various aspects of migratory behavior has increased (Alerstam and Lindström 1990).

TRANSITION AND FUTURE ISSUES

Overall the amount of descriptive work has greatly outpaced the experimental studies of bird migration. This likely reflects the philosophy of the scientists and the time frame when the work was done. There is still much to do related to the questions of immediate causation, development, evolutionary history, and function of bird migration. Science has matured considerably over the last five decades, and hypothesis testing with carefully designed experiments is the norm. The work that needs to be done will not be easy or inexpensive. Animal welfare regulations have boosted the expense of holding wild birds in captivity, and these regulations have also impacted the work with birds in the field. Tinbergen's four areas of research are still as valid and important today as they were when he proposed them in 1963, but issues related to the health and survival of entire migration systems have emerged since then and are attracting considerable research attention.

Students of migration face two serious issues that have emerged over the last two decades—declines in the populations of migratory birds (Terborgh 1989, Robbins et al. 1989, Marchant et al. 1990, Askins et al. 1990) and the threat of global climatic change (Berthold 1991, Root and Schneider 1995). Both of these topics have important consequences for the conservation of bird migration systems as we know them today. Although many bird species may be showing population declines, the declines of long-distance migratory birds are particularly alarming, because of the difficulties of studying the problem on the breeding and wintering grounds and along the migratory route. The causes of the declines are many and apparently include breeding habitat fragmentation (Wilcove and Robinson 1990, Faaborg et al. 1993), brood parasitism (Robinson et al. 1995), land use practices (Krueper 1993), pesticide use on the wintering grounds, and pollution (Gard et al. 1993). Some or all of the factors are likely to be influential in the different areas that a migrant occupies during its annual cycle. With global climate change, climatic patterns will be altered and the biota will respond accordingly. These events, coupled with the factors recognized as causing population declines, will put entire migration systems at risk. To avoid such devastation we must begin ecological and interdisciplinary research that examines the processes governing how populations, communities, and ecosystems interact with climate change and how climate change may interact with other anthropogenic modifications to the biota (Vitousek 1994).

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