COMMENTARY

Priorities in Bird Migration Studies[1]

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A few years ago when I first saw the title "Migration in the doldrums" in the table of contents of British Birds (68: 202, May 1975), I naively thought that the contribution by D. I. M. Wallace would consider bird migration in the equatorial ocean regions noted for dead calms and light fluctuating winds—a topic of considerable interest to me. I soon realized that my definition of doldrums was the second given in the dictionary. The viewpoint that Wallace wished to convey to the readers of the journal was that, since the 1950's, the interest in studies of bird migration in Britain had waned and dulled, and he accused ornithologists of "failing to honour a long heritage of migration science." Although Wallace's views were a bit overstated (see W. R. P. Bourne 1976, British Birds 69: 511), I nevertheless found it easy to empathize with him, and it appears that many American ornithologists had a similar conviction. A demonstration of this comes in the form of a recommendation from the Workshop on a National Plan for Ornithology (J. R. King and W. J. Bock 1978, Final Report, p. 34) that calls for the A.O.U. and the National Science Foundation to collaborate in the development of a nationwide investigation of avian migration itineraries in North America. The workshop pointed out that "in view of the prominence of migration in avian life styles, it is ironic to note that the routes, rates, and calendars of migration are known for only a handful of species aside from waterfowl. No modern syntheses of information on North American migration systems exist, yet such information is essential not only to the resolution of questions about the dynamics of migration, but also to an assessment of the hazards encountered by rare and endangered species and analysis of the role of birds as disease vectors and biological monitors of habitat quality."

It is obvious that studies of bird migration during the 1960's and 1970's have increasingly emphasized questions related to the mechanisms and development (proximal causation) of migration, while questions related to the evolution and function (ultimate causation) of migration have been largely ignored by ornithologists. In the first five volumes of *Avian Biology* no paper on migration systems and pathways was included. In volume five (1975) three migration papers were included, but these emphasized the control and metabolic physiology of migration (P. Berthold), the orientation and navigation of migrants (S. Emlen), and circadian and circannual rhythms in birds (E. Gwinner). These three excellent reviews contain important information on the mechanisms and to some extent the development of selected aspects of bird migration, but they devote precious little attention to the evolution and function of bird migration. Since these reviews were published in *Avian Biology,* studies of bird migration have shifted even farther toward investigations of orientation and navigation mechanisms. Recent articles in Smithsonian (June 1979), Mosaic (May–June 1979), and National Geographic (August 1979) have explored the "mysteries" of bird migration, but all of the articles have shown an overwhelming concentration on the orientation and navigation aspects of bird migration. I must

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admit this area of migration study is attractive and fascinating, but I thoroughly acknowledge that such a strong bias in a field can be unhealthy in a scientific sense. I shall attempt to explain what I mean by this last statement.

Various bird migration systems have evolved in response to particular temporal and spatial changes in the environment, and most of the aspects of these migration systems (e.g. orientation, energetics, timing) have been shaped by evolutionary selective pressures associated with the particular changes in time and space. Each bird migration system encompasses a set of aspects that collectively permit an individual bird to insert the maximum number of its genes into the next generation. The investigation of any aspect of a particular bird migration system must proceed along four basic lines simultaneously if real advances in our understanding are to be achieved. The lines of investigation include: 1) immediate causation, 2) ontogeny, 3) function, and 4) evolution. When too much emphasis is placed on one line of investigation at the expense of the others, serious problems can arise. For instance, the ontogeny of migratory behavior has received relatively little attention by ornithologists, and this is also somewhat true of the orientation aspect of migration. Most ornithologists are aware of the numerous studies of migratory orientation in caged nocturnal migrants, and these studies have produced considerable information on the mechanisms of orientation. However, nearly all the researchers who have done experiments of this type have found that horizon glows from the lights of nearby and distant cities seriously disrupt the experiments, because the birds often orient their activity to the bright areas on the horizon. Only recently has some understanding of this phenomenon been achieved through a study of the nocturnal migratory orientation of caged sparrows of different ages in spring (J. N. Williams and S. A. Gauthreaux, Jr., in preparation). In brief, the study found that adult White-crowned Sparrows (*Zonotrichia leucophrys*) oriented northward in the cages, but the immatures directed their activity toward a distinct horizon glow to the east-southeast. Thus the *age* of the birds being tested can make a profound difference in the results of an orientation experiment. Without knowledge about ontogenetic effects like the one just given, studies on the immediate causation of migratory orientation would eventually flounder. Those who are interested in pursuing studies of selected aspects of bird migration should be aware of the pitfalls of a myopic approach to their research, and they should strive to follow different lines of investigation (e.g. ontogeny, function, and evolution). Moreover, we should endeavor to study bird migration from several different biological viewpoints.

It is very important that the study of bird migration be integrated with other areas of biology, namely ecology, genetics, and evolution. If one reads the papers by T. R. E. Southwood (1977, J. Anim. Ecol. 46: 337) and L. R. Taylor and R. A. Taylor (1977, Nature 265: 415), one can better appreciate the importance and function of bird migration and migration in general to the fields of community and population ecology. Much more work is needed along these lines. The current behavioral work on navigation mechanisms in homing pigeons has produced several important discoveries, but comparatively little has been said or written about the ecological significance of homing behavior in birds. With proper emphasis on the ecological aspects of homing in birds, other than homing pigeons (increasingly being referred to as the white rat of bird navigation studies), investigators might approach their studies of homing in a different manner. For example, is there anything in the wild comparable to displacement by an automobile? How and when does it occur? In other words, what are the circumstances that necessitate homing in nature? These

questions are nontrivial and certainly need investigation. There are many aspects of bird migration other than orientation and navigation that need work. At present we know very little about the demographic and sexual features of bird migration, the importance of intraspecific and interspecific competition to the timing of migration and the seasonal distribution of the migrants, the relationship between migration and dispersal, the diverse patterns of plumage change among different species of migrants, and the relationship of bird migration to paleoclimatology and to past and current biogeography. These are important topics of investigation that must not be overlooked, for failure to make advancement in these areas will seriously jeopardize advancement in other areas that are currently receiving more than their fair share of attention.

Human Disturbance and Breeding Birds

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There is a growing concern about the effects of scientific investigation on breeding seabirds. For example, Nisbet (1978, Ibis 120: 134) has stated, "human disturbance by biologists is one of the major threats to seabirds," and Nelson (loc. cit.) was of the opinion that "contrary to what most people imply natural production rarely happens in populations that are studied by humans." Unfortunately, there are few studies in the literature to support or discount such pessimism.

The study by Ellison and Cleary of breeding Double-crested Cormorants (*Phalacrocorax auritus*) in the Gulf of St. Lawrence (1978, Auk 95: 510) is one of the very few attempts to see if the methods used in studying nesting success may themselves influence success. They found that "frequent visits caused nest abandonment, gull predation, and discouraged late-nesting birds from settling in disturbed experimental colonies." At one of their two study colonies, however, they found no significant differences in clutch or brood size between disturbed and undisturbed areas. In only one of four comparisons did they find a greater percentage of empty nests in the disturbed area. Even this finding may be questioned, as empty nests disappeared in a few days, the material being taken by neighbors. Because late nesters tended to settle in control plots, there may have been a greater demand for nesting material and, therefore, less chance that an empty nest would be present when Ellison and Cleary made their counts.

At their second colony, the activities of the investigators caused extensive desertions, which were attributed to inexperienced birds and to the proximity of a large gull colony. The only nests studied were those with eggs laid in late June or July. Palmer (1962, Handbook of North American birds, New Haven, Yale, p. 335) notes that nesting cormorants in Quebec generally have eggs present in May and early June. How representative of the species would a colony be if its breeding individuals were inexperienced, nesting late in the season, and "in sites not recently utilized by cormorants"?

The study of Ellison and Cleary is important, because it shows that observers had some effect on the nestings they studied. The type and extent of this effect are unresolved, but these are less important than the problem they raise for anyone undertaking similar studies.

I see two methodological difficulties of such studies of reproductive success and investigator disturbance. First, if one measures success using frequent visits to disturbed sites and less frequent visits to a control, there is the chance that, between visits to the control, nests may disappear altogether, and eggs or young that die may decay, wash away, or be scavenged. The less frequent the visits, the less evidence of mortality there may be and the higher the apparent productivity. Ellison and Cleary avoided this by using similar 1-day censuses for both experimental and control areas, but other studies have not (e.g. Gillett et al. 1975, Condor 77: 492; Robert and Ralph 1975, Condor 77: 495).

Second, there exists a paradox (or an "uncertainty principle"; Lenington 1979, Auk 96: 190) such that, if one disturbs birds while measuring their nesting success and if such disturbance lowers success, then the more "accurate" (=frequent) the measurement, the less real the productivity being measured. There

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