An integrative framework for understanding the origin and evolution of avian migration

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In a recent article in the *Journal of Avian Biology*’s “Forum” section, entitled, “Towards a framework for understanding the evolution of migration,” R. M. Zink (2002) has stimulated discussion about necessary future directions to take in approaching this subject. Zink’s article addresses the pertinence, or lack thereof, of studies other than phylogenetics to the understanding of migrant evolution and origin. He states, “A phylogenetic tree is required to make inferences about the evolutionary history of migration.” (emphasis added). His initiative is timely and potentially promising, and we herein subject the theme to further consideration based on data concerning migration biology. Before doing so, we need to clarify an apparent confusion over the term *origin*. In the sense in which it is used by migration theorists, Zink included, the word “origin” clearly has two meanings, i.e., 1) the (first) appearance of migration in evolutionary history, and 2) appearance of migration in a particular lineage of migrants. The first meaning involves “deep history.” We consider it now largely consensus that “original” migration in the first sense occurred early in organismic development, which is why it is found in such disparate groups as insects, fish, reptiles, mammals, and most orders of birds (Baker 1978), and that there is extensive evidence to indicate that most, if not all, birds possess the basic mechanistic repertoire required for migration (Dingle 1996, Berthold 1999, Prum 2002, Helbig 2003, Rappole 2003, Rappole and Jones 2003). Thus, “origin” in the second sense often refers to relatively recent events in a given lineage.

Clarification of the different meanings of the term “origin” is important since Zink’s (2002) discomfort with ecological approaches to understanding the origin and evolution of avian migration appears to rest in part on a fundamental misunderstanding of the two senses in which the term “origin” is used. For instance, he criticizes the discussion of evolution of migration in Rappole (1995), as an inadequate and flawed attempt to address the origin of migration in the first sense. However, the stated purpose of Rappole’s discussion was to address the origin of migration in the second sense; specifically to present arguments for reconstructing the evolution of migration in birds that breed in temperate North America and migrate to the Neotropics.

Understanding the evolution of migratory behavior in given lineages of birds entails reference “to its modification and maintenance,” as Zink (2002) suggests in his example of fox sparrows *Passerella iliaca*. We take this view as a common starting point for explorations into the evolutionary course of migratory behavior, and suggest that cooperative efforts by ornithologists from different fields are not only valuable, but necessary to understand the evolution of complex behaviors such as migration (Alerstam and Hedenström 1998). The framework Zink (2002) suggests involves phylogenetic analyses that consider the various components of migratory behavior separately. There is no doubt that migration, or the “migratory syndrome” (Dingle 1996), consists of multiple components that merit individual consideration. We suggest, however, that there are problems with Zink’s approach. Firstly, extensive evidence indicates that migratory traits are parts of an...
integrated system (Dingle 1996, Pulido and Berthold 1998, 2003), and separating a set of such traits can bias analyses (Hennig 1950). Thus, it is doubtful whether analysis of the individual components of migratory behavior separately can produce meaningful results. Secondly, the value of mapping migratory traits on phylogenetic trees depends on the degree of direct genetic control over migratory behavior. There is now ample evidence that complex behaviors in general, and migratory behaviors in particular, are frequently phenotypically plastic: i.e., their genetic architecture allows for the expression of different behaviors depending on conditions of the environment, including internal state variables (Baker 1978, West-Eberhard 1989, Schlichting and Pigliucci 1998). Differences in migratory behavior observed in captivity and the field may therefore indicate differences in condition-sensitive expression of migratory behavior.

Zink (2002) recommends three component traits of the migratory syndrome for closer phylogenetic analysis: hyperphagia, navigation, and Zugunruhe. Zugunruhe refers to the restlessness that migratory birds display in captivity during migration periods (Gwinner 1975, Berthold 2001). Hyperphagia is a contributing factor to migratory fat deposition, and is closely coupled to Zugunruhe, at least during the post-breeding period (Ramenský 1990, Dingle 1996, Berthold 2001). Broad comparisons of orientation behavior are currently, as Zink concedes, unrealistic subjects for phylogenetic study. The importance of endogenous contributions to migratory behavior has been well-documented (e.g., Naumann 1897–1905, Groebbels 1928, Rowan 1929, Gwinner 1968, 1975, Berthold 2001). Yet, captivity data cannot be understood properly without reference to field studies. Environmental and state factors influence orientation behavior in the field, and experiments on caged birds can introduce bias (e.g., Nievergelt et al. 1999, Sandberg 2003).

Zugunruhe, at first consideration, appears to be a trait amenable to phylogenetic analyses. A key assumption in its study is that it can be related directly to migration of free-living conspecifics (Berthold et al. 1972, Berthold 1973). However, the relationship is not always straightforward. Identification of Zugunruhe can be difficult because captive birds show various types of nocturnal restlessness (e.g., Berthold 1988). For instance, resident blackcaps Sylvia atricapilla from the Cape Verde Islands display nocturnal activity, but unlike long-distance migratory Blackcaps from Sweden, do not reduce nocturnal melatonin peaks (Fusani and Gwinner 2001). Presumably, a reduction of nightly melatonin levels during the migratory season enhances nocturnal flights of migrants. Therefore, the difference between the populations suggests that although both show nocturnal restlessness, it might represent migratory disposition in only one population. Further evidence regarding the complex relationship that exists between Zugunruhe and actual migration comes from comparative studies of white-crowned sparrows Zonotrichia leucophrys (Mewaldt et al. 1968). Resident populations showed Zugunruhe patterns similar to those of migrant populations, with only slightly reduced amplitudes. This finding suggests that birds of both populations were genotypically migrants, differing in migratory behavior in the field but almost identical in captivity, whose migratory behavior is triggered or suppressed by additional factors, as has been suggested for several other migratory species (e.g., Lack 1943, Kalela 1954, Schwabl and Silverin 1990, Helm 2003). The complex relationship between endogenous and environmental factors is illustrated by seasonal variation in the control of migratory behavior, e.g., in dark-eyed Juncos Junco hyemalis in which a period of obligatory migratory behavior is followed by a period during which Zugunruhe is sensitive to social and feeding conditions (Terrill 1990). These findings caution against use of Zugunruhe as a character for phylogenetic mapping, or at least against straightforward interpretation of results. Further evidence confirms the importance of phenotypic plasticity in the control of migratory behavior. In many species the expression of migratory behavior is context-sensitive. Studies of heritability indicate that the degree of genetic control over migratory behavior differs among species, populations, and even years (e.g., Potti 1998, Pulido et al. 2001, Partecke 2003, Pulido and Berthold 2003). Several factors, such as dominance and condition of a bird can affect the expression of migratory behavior (Gauthreaux 1982, Ketterson and Nolan 1983, Terrill 1990). For instance, migrant populations are often segregated into sex or age classes that migrate differentially (Gauthreaux 1982, Ketterson and Nolan 1983, Winker and Rappole 1992, Cristol et al. 1999). In addition, the same individual can exhibit both migratory and sedentary behaviors at different times in its life, as reported in field and captivity studies for song sparrows Melospiza melodia and other species (Nice 1937, Fretwell 1972, Schwabl and Silverin 1990). Environmental and genetic impacts on behavior are not mutually exclusive because genes play a central role in defining the potential range of organismic responses to environmental cues (e.g., Schmalhausen 1949, Van Noordwijk 1989, West-Eberhard 1989, Stearns 1992, Schlichting and Pigliucci 1998, Merilä and Sheldon 2001). In migration theory, thresholds and reaction norms (Baker 1978, Ketterson and Nolan 1983, Pulido et al. 1996, Berthold 2001) relate migratory behavior to internal and external cues.

It is obvious that migration has numerous important genetic components and that a study of phylogenies can improve our understanding of the behavior. What is not obvious, to us at least, is why a “detailed phylogenetic tree” should be “required,” as suggested by Zink (2002). In fact, despite Zink’s presentation, we fail to see how a phylogenetic tree alone can solve the question of the origin of migration. The crux of Zink’s critique of “past analyses” of the origin and evolution of migration is that these analyses fail to, “frame the question in a testable phylogenetic framework.” (Zink 2002). Of course, this claim is true, because a “testable phylogenetic framework” requires genetic change, meaning presumably that the first migratory individual in a sedentary population is genetically different from other individuals in the population. If, however, genetic
change is not necessarily required in order for migration to occur, then search for such changes in closely-related populations of migrant and sedentary groups of the same species may not provide evidence relevant to origins of the migration phenomenon.

Rappole et al. (1983) and others (e.g., Levey and Stiles 1992, Safriel 1995) have argued that no genetic change is required for the origin of migration because migration is a behavior whose genetic components are equivalent to those required for successful dispersal and/or tracking of seasonally variable resources, e.g., subcutaneous fat storage and homing ability, a contention borne out in a number of studies of dispersing sedentary birds (see reviews in Rappole and Warner 1980, Wiltshire 1992, Ramos and Rappole 1994, Rappole and Schuchmann 2003). Thus many individuals of sedentary populations may have the necessary adaptations to undertake migration, and only require a change in the environment to provide the proper context for migration to occur (Rappole and Jones 2003). This argument is based on the idea that no genetic change in reaction norms need take place for an individual to migrate, i.e., that the same reaction norms for such factors as hyperphagia, fat deposition, and homing could provide the basis for both dispersal and migration— with migration simply being an example of dispersal in which the individual is lucky enough to discover and settle in a seasonally-suitable environment for breeding that is populated by similarly-dispersing conspecifics. In this scenario, the change that produces migrants from a “sedentary” population is a change in the environment, potentially an environment located some distance away from the parent population, rather than a genetic change (Rappole and Tipton 1992). Subsequent selection would act rapidly on this population of dispersers, causing genetic change in norms for migration-related factors to improve likelihood of success in their migratory movements. Changes in allele frequencies in key characters would develop between migratory and resident populations, but they would follow development of migration rather than precede it. The argument does not presume a genetic difference between migratory and sedentary individuals in the population at time of origin of these two groups; rather the argument assumes a dramatically different selective environment, and rapid evolutionary divergence in a limited set of specific characters, subsequent to time of origin. In this scenario, it is exposure to novel environmental conditions that activates the “latent selection potential” provided by phenotypical plasticity of migratory behavior (West-Eberhard 1989). Cattle egrets Bubulcus ibis, for example, first arrived in the New World in northern South America during the late 1800’s, where they rapidly colonized much of the Neotropics as a tropical resident species. First records for the North American temperate region were recorded in the early 1950s, but by the 1970s, populations of the species were established as long-distance migrants between northern temperate breeding sites and tropical wintering sites (Telfair 1994). Similarly, in an example provided by Zink (2002), a flock of fieldfares Turdus pilaris, apparently blown off course during migratory flight, landed in Greenland and established a population of sedentary individuals (Salomonsen 1950). Zink has argued that such short-term changes in migrant behavior represent the suppression of gene expression. No doubt, this is possible. But if the genes necessary for migration can be present in individuals of a non-migratory population, then it is clear that genes alone do not determine either presence or absence of the behavior.

There are no data to indicate that genetic change is required either to produce the first migratory individual from an otherwise sedentary population, or the reverse— producing a sedentary individual from a migratory population. Rather, results from genetic experiments (e.g., Pulido and Berthold 2003) have shown that “the impossible, [i.e..] turning residents into migrants” is possible because the genetic machinery for migratory behavior can exist along side resident behavior (West-Eberhard 1989). Selectively breeding individuals with the lowest thresholds for the expression of migratory traits rapidly increases the frequency of migrants (cf. Nice 1937, Salomonsen 1950, Rappole 1995). In fact, actual analyses of genetic differences between sedentary and migratory populations of the same species demonstrate that selection for migration apparently affects relatively few loci, even after several generations during which members of the two populations have pursued different movement patterns (Helbig 1996, 2003).

Phylogenetic approaches have helped significantly to increase our understanding of evolution and migrant relationships (Wenink and Baker 1996, Helbig 2003), and our intent in this response to Zink’s proposal is not to denigrate their value. Yet phylogenetic studies alone are insufficient. We suggest that other types of studies, including physiological and ecological investigations, are not only important but necessary to understand the origin and evolution of migration (cf. Ricklefs 2002, Helbig 2003, Rappole and Jones 2003). We further propose that the optimal procedure is to put forward a theory based on a set of stated assumptions, and then proceed to test the theory by search for information from field observations and/or laboratory experiments that assess the validity of those assumptions. The above examples indicate that by joining forces, rather than adherence to “schools,” we can hope to improve progress toward understanding (cf. Alerstam and Hedenström 1998, Gwinner and Helm 2003).

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References


