

Towards a framework for understanding the evolution of avian migration

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Bird migration has fascinated humans for millennia. Consequently many scientific studies have investigated in detail the physiology and ecology of migration. A large number of authors also have explored the evolution of migration. A typical conclusion is that “migration” evolved in a tropical, sedentary avian ancestor. There is, in fact, no evidence to support this assertion because these past analyses have not distinguished the historical and ecological components of migration. Part of the problem with past hypotheses about the evolution of migration has been a misunderstanding of the actual question itself. Understanding the evolution of a phenotypic trait, such as migratory behavior, requires some effort to determine if it is a character, amenable to analysis using comparative methods, or an attribute, essentially a manifestation of several independent components. Attributes are overly broad summaries of an organism’s phenotype, and require dissection into characters for proper historical analysis. Subsequently, to understand the evolution of a character, one must identify at least three aspects, namely its origin, its maintenance, and its modification (Brooks and McLennan 1991). This requires an explicitly phylogenetic context, because the question is historical in its nature.

Most studies of avian migration have used “migration” as a character, which is likely incorrect, and furthermore, confused the origin of migration with its modification and maintenance. Hence, our understanding of the evolution of avian migration is incomplete. In this paper, I present a framework for understanding migration in evolutionary terms by integrating information on the genetics of migration with a macroevolutionary view provided by comparative systematics.

Current theory on the evolution of avian migration

It is relevant to review some current theory before exploring historical analysis of migration. Rappole

(1995) clearly articulated his view that migration evolved in a tropical sedentary bird. This was echoed by Berthold (1999), who extended the idea to a tropical bird at the time of the origin of birds themselves (which recognizes the deep history implicit in this question).

Rappole’s hypothesis has two components. First, he recalls Malthus’ observation that populations produce more offspring than can survive in a given area. Hence, there is a pool of individuals, at least some of which might be genetically predisposed to be colonists. If these reach an area in which reproduction results in increased fitness relative to breeding in the ancestral area, and they can successfully return if conditions in the new area deteriorate, then a migratory population could evolve. Hence, Rappole’s (1995) idea involves population pressure forcing exploration and exploitation of seasonally abundant resources away from a tropical ancestral home, followed by a return to the tropics upon seasonal decline of these resources. Berthold (1999) believes that a partially migratory population is an intermediate step.

To support his view, Rappole (1995) noted that the putative relatives of many north temperate migrants are sedentary tropical birds. For example, Rappole reviews gnatcatchers in the genus *Polioptila*, in which the blue-gray gnatcatcher *P. caerulea* migrates to northern North America, whereas the other species are tropical and sedentary. This suggests to Rappole that the tropics are the ancestral home of gnatcatchers, “sedentary” is the ancestral condition, and that only the blue-gray gnatcatcher has been able to escape its evolutionary heritage and exploit the insect-rich north temperate zone via evolution of migration.

Such a scenario does not frame the question in a testable phylogenetic framework. Biogeographers (e.g., Voelker 1999) have mostly discounted the notion that the center of diversity reveals the center of origin of lineages (if it did, one would think that *Drosophila* evolved in Hawaii). A phylogenetic tree is required to make inferences about the evolutionary history of mi-

gration. It might be appropriate to map both the wintering and breeding areas on a phylogenetic hypothesis, assuming that the non-breeding range represents the site of the taxons origin (Joseph et al. 1999; but see Chesser and Zink 1994). Molecular comparisons (Zink and Blackwell 1998) show that the blue-gray gnatcatcher is well differentiated from its congeners, suggesting that migratory habits existed early in the lineage's history. It is possible that during the last few rounds of glaciation, other migratory gnatcatcher species went extinct, and that migration was once more common (e.g., ancestral) in the genus. Without a phylogenetic hypothesis to ascertain the ancestral condition, there is no evidence that gnatcatchers provide a model for the ancestral condition being tropical and sedentary. In contrast, Burns (1998) showed that a clade of tanagers all exhibited migratory behavior, which suggests that the common ancestor was migratory, and by referencing the phylogeny, one could infer the ancestral area. Minimally, comparative studies using phylogenetic hypotheses provide the proper historical context for posing questions about evolutionary changes in migratory behavior.

Placing the questions in proper historical context

A central question concerns the origin, *per se*, of avian migration. The present tropical-sedentary theory is motivated by the fact that the north temperate regions currently receive large numbers of seasonal migrants from the tropics. However, we do not know if this situation reflects conditions present at the inception of migration, or is instead another in a large series of modifications of migratory behavior that have been occurring throughout avian evolutionary history. Understanding the evolutionary origin of avian migration requires a broad phylogenetic context, not only within birds, but also across vertebrates.

Migration is widespread across the animal kingdom; even some plants are considered migratory. Thus, one needs to determine if "migration" *per se* is homologous. The answer is, probably not. That is, the genetic programs responsible for physiological preparation and orientation have probably not been inherited from a common ancestor in those forms that migrate. Instead, migration seems to have evolved independently in diverse lineages, such as birds, mammals, squid and butterflies, as a solution to exploiting geographically and seasonally abundant resources, or conversely avoiding the deterioration of such.

The primary question about the evolutionary origin of migration in birds concerns where in avian history migration first occurred. In particular, is migration an ancestral trait in birds? The answer rests in knowing

whether the physiological machinery was present in the common ancestor of birds. This requires knowing the sister group to birds, which was likely a small bipedal theropod dinosaur (Wagner and Gauthier 1999, Prum 2002), as well as successive sister groups, and mapping the occurrence of "migratory physiology" on the avian tree. It is not possible at this time to reconstruct the paleoenvironments in which birds and their successive sister taxa evolved, let alone whether they were migratory, with enough precision to ascertain the ancestral state of migration in birds. Given the widespread occurrence of migration in birds and other vertebrates, it is reasonable to conclude that migration existed early in avian history if not in the common ancestor of birds (as opposed to multiple origins). Migration was surely present long before the current set of lineages became established in world's currently tropical regions. Thus, discussions (e.g., Rappole 1995) about the "evolution" of migration from a sedentary tropical ancestor refer actually to its modification and maintenance, not its origin, which is currently unclear.

Components of migration: Finding the characters in the system

Leaving behind the currently unanswerable question about the origin of avian migration, we can ask how evolutionary studies should proceed. The previous sections treated both "migration" and "sedentary" as though they were characters. Although this can have heuristic value, migration potentially consists of components that independently are amenable to evolutionary character mapping (Brooks and McLennan 1991, Martins 1996). Migrant songbirds enter predictable periods of restlessness (Zugunruhe) and hyperphagia ("eating to excess"). Hyperphagia prepares the fat layer needed to fuel a migratory journey; possibly, it is an ancestral feature that prepared individuals for the onset of seasonal food shortages, or molt. Annual onset and offset of migratory restlessness, the period during the circadian and circannual cycle in which birds engage in migratory flight, is genetically determined. Arrival date at breeding sites is heritable (Møller 2001). Navigation, whether by sun, polarized light, stars or magnetic field, or some combination (Able 1998), is also under genetic control. Thus, "migration" is shorthand for the genetic machinery underlying migratory physiology and orientation and consists of several linked adaptive systems. That is, migration, as it has been treated in most literature, is an attribute rather than a character.

These adaptive systems can be altered rapidly (Berthold 1999). Matings in captivity between conspecific individuals from migratory and nonmigratory populations yield a mixed population, with for example, intermediate migratory direction and length of Zugun-

ruhe. From a polymorphic captive population, migratory and nonmigratory populations can be produced by selective matings in three to six generations. However, whether sedentary individuals lack the genetic programs for migration, or whether they are dormant, is unknown from such experiments. It would seem likely that they are suppressed rather than eliminated. Thus, there are several components in species that are migratory (or sedentary), and considering all migratory species as equivalent (i.e. mapping migratory as all-or-none) masks the interesting evolutionary phenomena.

The evidence for rapid changes in migratory physiology and orientation in nature is well known. A migrating flock of fieldfares *Turdus pilaris* blown off course ended up in Greenland and “became” sedentary (Gill 1995). That is, the entire migratory program was suppressed; likely it could be reconstituted just as quickly. On a deeper time scale, one has only to consider the extent of the Laurentide Ice Sheet, extending south to 40° N 18,000 years before present in North America, to realize that the migratory populations of many species currently living north of 40° N have developed or redeveloped migratory populations and routes since deglaciation. Modification of species’ migratory behavior occurred well after their origin, because many north temperate migratory passerines are at least one million years old (Klicka and Zink 1997). In fact, many glacial advances and retreats have occurred during the Pleistocene, suggesting numerous modifications to the migratory program over recent evolutionary history. Thus, when asking evolutionary questions about migration in extant species, the issue concerns the maintenance and modification of the components of migration, not their origins.

Evolutionary analysis of migration requires knowing the phylogenetic distribution of Zugunruhe, hyperphagia, and the various compass systems. Recent experimental studies reveal the potential independence of these components of migration (Berthold 1999). Blackcaps *Sylvia atricapilla* developed a novel migratory route and distance, from Germany to the United Kingdom, beginning in the 1960s. Breeding experiments showed the genetic basis and heritability of the new migratory path. However, there was considerably more modification of the direction of orientation than, presumably, of the other components. Thus, the analyses of evolutionary modifications in migration require dissection of the components.

An example

The four taxa of the fox sparrow (*Passerella iliaca*; Zink 1994) show that the components of migration are labile in evolutionary time. All of the four taxa are migratory to various degrees (Swarth 1920). Of interest

here is the phylogenetic species *P. unalaschensis*, which breeds coastally in the Pacific Northwest of North America, from Washington to Alaska. In this taxon, the southernmost populations are nearly sedentary, whereas populations to the north migrate to the south in proportion to their distance north of the southernmost populations. That is, the population immediately north of the southernmost population migrates just south of it, whereas the most northerly population migrates the farthest south. This pattern of leapfrog migration has often been discussed, but not in the context of dissecting the migratory components involved. The southern populations likely have become secondarily sedentary, given the widespread occurrence of migration in all four taxa. In the leapfrog populations, what differs is the length of the migratory period, likely involving geographically clinal changes in the duration of Zugunruhe and amount of fat needed (northern birds migrate for a longer period to achieve their wintering sites). Migratory orientation direction would require differing amounts of change, with relatively little change in the southern populations, and progressively more in Aleutian populations, which might need to change from ENE to SE to S along their journey (if overland; see Bell 1997).

Molecular comparisons (Zink and Weckstein, in press) show that these four taxa are all closely related, differing by about 1% in mitochondrial DNA sequence divergence, a time of divergence likely less than 500,000 years (Klicka and Zink 1997). No detectable mtDNA differences occur among populations of *P. unalaschensis*. Hence, in a very short evolutionary period, periods of Zugunruhe and hyperphagia have been evolutionarily modified, and in some populations, suppressed altogether. Other examples of extremes in migratory behavior without significant mtDNA differentiation exist, such as in the North American song sparrow (*Melospiza melodia*; Fry and Zink 1998). An improved understanding of evolutionary modifications in migration obtains from considering the components of migration separately.

Conclusions and future directions

Past studies of the evolution of migration have too often 1) equated the evolution of migration with its origin, when they were actually addressing its maintenance and modification, and 2) not considered migration as a series of physiological and behavioral components. The “origin” of migration involves the innovations that led to the existence and interaction of all the components. There is no reason to believe that these components evolved in the tropics under its current configuration. Rather, migration likely evolved early in avian history, but when during avian evolution is unclear. During avian history, evolutionary change

involved modification to some or all of the components, resulting in the maintenance of a diversity of migratory behaviors, including frequent episodes of it being suppressed (subsequent reappearance is likely a result of removal of suppression of genes controlling the components of migration).

Whether one is interested in the origin, maintenance or modification of migration, a phylogenetic hypothesis is the starting point. Because migratory behavior can change over short time intervals (see Able and Belthoff 1998), mapping "migration" over deep history will run considerable risk, the same risk as mapping third-position transitions over ancient nodes in a phylogenetic tree, or considering the current ranges of species as proxies for their ranges at the time of speciation (Chesser and Zink 1994, Webster and Purvis 2002). Highly labile traits retain phylogenetic information for relatively short times, and hence, it might be that the phylogenetic analysis of migration should be undertaken only for recently isolated taxa. Of course, it is currently unknown whether migration or its components actually contain little phylogenetic information, as was once assumed incorrectly for behavioral traits. For this and other reasons, phylogenetic analyses of migration should attempt to use a framework in which components of migration are separately mapped. Although it is of interest to map the presence and absence of "migration" on a phylogeny, to see which species exploit this strategy, it is then necessary to determine how modifications to the period of Zugunruhe, hyperphagia, and the compass system (which is usually unknown) result in the particular the expression of migratory behavior. Granted, the components are not necessarily completely independent (e.g., one would not expect Zugunruhe without premigratory fattening), but migration *per se* is overly inclusive and masks many interesting evolutionary modifications. For example, two migratory sister species might differ only in the period of Zugunruhe, migratory direction or compass systems, and classifying each as "migratory" is misleading when trying to understand evolutionary modifications.

A future goal is to identify the genes responsible for Zugunruhe, hyperphagia, directional orientation and navigation and to establish their phylogenetic distributions. These genetic systems are, of course, as yet unresolved. It is, therefore, currently unknown whether the components of migration in birds, and therefore avian migration itself, are homologous. One could, in theory, survey species for the existence of genes encoding the components of migration, whether the species was sedentary or not. If the genes for these components were indeed ancestral in birds, then the question of the "evolution" of migratory behavior in extant birds would be a problem of molecular and developmental regulation of these genes. Furthermore, it would establish why and how migratory behavior is so rapidly modulated (and suppressed) in natural populations.

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