

S19-2 Phylogenetic approaches to the evolution of migration

Leo JOSEPH¹, Thomas WILKE², Deryn ALPERS³

1. Dept. of Ornithology, The Academy of Natural Sciences, 1900 Benjamin Franklin Parkway, Philadelphia, PA 19103-1195, USA; leo.joseph@csiro.au

2. Dept. of Microbiology and Tropical Medicine, George Washington University Medical Center, Ross Hall, Room 731, 2300 Eye Street, NW Washington, DC 20037, USA

3. Dept. of Veterinary Biology, Murdoch University, Perth, WA 6150, Australia

Abstract The evolution of migration has long been the domain of evolutionary ecology. Work has focused on how natural selection drives the gain and loss of migration. We review applications of phylogenetic approaches to the question. By examining the deeper evolutionary history of migratory species and their populations rather than just their present-day ecology, such approaches, which can include historical biogeography and phylogeography, complement ecology. For example, breeding distributions appear to have been commonly displaced during the evolution of migration; component species of a migration system need not have evolved migration at the same time nor by the same processes nor in response to the same environmental pressures. The tools of historical biogeography, phylogeny and population genetics allow one to tease apart such spatiotemporal heterogeneity that may underlie the evolution of any migration system.

Key words Biogeography, *Charadrius*, *Myiarchus swainsoni*, mtDNA, Phylogeography

1 Introduction

The evolution of bird migration across and between continents has long been a major focus of study (Pulido et al., 1996; Alerstam and Hedenström, 1998). Excluding mechanisms of navigation, we note that central concerns have been how and why natural selection drives the evolution of migratory populations from non-migratory ones and vice versa (e.g., Cox, 1985; Gauthreaux, 1982; Pulido et al., 1996). The evolution of migration has thus fallen squarely within evolutionary ecology, the guiding paradigm of which is natural selection (e.g., Cockburn, 1991). How might we address questions such as whether unrelated species in a migration system, which obviously evolved migration independently, did so at the same or different times or in response to one or more environmental stimuli?

Another set of questions that evolutionary ecology has addressed but which we argue may be seen from other, complimentary, standpoints concern the so-called “ancestral home” of migrants. Seeing the problem of the ancestral home as a problem in historical biogeography, one can try to determine where long-distance migrants originally evolved and how their present-day disjunct breeding and non-breeding distributions developed. That is, did they evolve in their present-day breeding grounds with displacement of their non-breeding range or vice versa?

This paper reviews some cases in which these and other issues have been addressed with the methodologies of phylogeny and historical biogeography. Also illustrated are uses of phylogeography, i.e., the bridge between sys-

tematics and population genetics (Avice, 2000) in studying the evolution of migration. Our aims are twofold. First, we will show that these essentially historical approaches compliment and expand on the shorter term ecological approaches that have dominated the study of evolution of migration until now. In particular, we show that reconstruction of distributional shifts that have occurred during the evolution of migration is a strength of using phylogenetic, biogeographic and phylogeographic approaches. Secondly, we will show that phylogenetic approaches can bring a temporal dimension to understanding the evolution of migration. The ecology of why migration evolves is excluded from our scope although we submit that the results of phylogenetic approaches can inform ecological questions.

We stress several caveats, however. First, migration can evolve rapidly (Berthold et al., 1992) and mapping migratory status on the branches of a phylogeny should be done with caution, if at all (Klein and Brown, 1994; Joseph et al., 1999). Secondly, migratory status is likely not a single character with two character states, present or absent (Pulido et al., 1996; Zink, 2002). As Zink (2002) notes, the term “migration” is shorthand for the genetic machinery underlying migratory physiology and orientation and so comprises several different adaptive systems. We further suggest that where migration has evolved once within a clade (e.g., tanagers *Piranga* spp. — Burns, 1998; eye-ringed vireos *Vireo* spp. — Cicero and Johnson, 1998), there has also been one evolutionary shift due to homologous genetic, navigational and physiological character state changes in the ancestor of the migratory species. Where migration gains

and losses are more complex (e.g., pipits *Anthus* spp — Voelker, 1999), with possibly multiple origins, non-homologous shifts in one or more of these characters may lead to evolution of different migratory species. It is thus important to carefully set the scope of questions asked when using phylogenetic approaches to the evolution of migration.

2 Evolution of migration in *Charadrius* plovers and their relatives

A test case for use of phylogeny in exploring the evolution of migration is provided by *Charadrius* plovers and their relatives, e.g., *Oreopholus*, *Vanellus* (Joseph et al., 1999). The procedure followed in this study was to treat breeding and non-breeding ranges of the study species as separate characters to be mapped on to their phylogeny, which was itself derived independently from mitochondrial DNA (mtDNA). The character states for breeding and non-breeding ranges were the different continental regions, e.g., South and North America, as non-breeding and breeding distributions, respectively. These characters were mapped on to a phylogeny derived independently from mitochondrial DNA (mtDNA). Shifts in character states for breeding and non-breeding ranges were first reconstructed using parsimony and then mapped on to the branches of the mtDNA phylogeny. Origins in non-breeding grounds, for example, are expected to be manifest as a change in character state when breeding grounds were mapped on the phylogeny but not non-breeding grounds, and vice versa. Further analytical details of the method are given in Joseph et al. (1999).

Here it is important to stress that in using parsimony to reconstruct a range shift on the branches of a phylogeny, it is arguably more important to determine whether a shift is indicated as having occurred rather than to interpret literally the precise node(s) on the tree where it is reconstructed. This caveat derives from the fact that the behavioral attribute of migration (Zink, 2002) can be gained and lost rapidly (Berthold, 1994).

Limited taxon sampling notwithstanding, analyses suggested that *Charadrius* plovers and their relatives first evolved in the southern hemisphere, arguably in South America. A southern, Gondwanan origin concurs with distributions of genera of obscure intra-family affinity scattered across the Southern Hemisphere (e.g., *Phegornis*, *Oreopholus*, *Anarhynchus*, *Erthrogonyx*). At deeper temporal levels of history, we see evidence for past shifts in breeding range. Later, in the evolution of present-day species, shifts in breeding range are again implied. For example, in *C. vociferus* and *C. semipalmatus*, which currently breed in North America, shifts in breeding range from South to North America appeared on the branches of the phylogeny when the character of breeding distribution was mapped. In *C. alexandrinus*, shifts in both non-breeding and breeding distributions were indicated when the entire range of the species was used in the analysis. This seem-

ingly exceptional case was argued to be informative with respect to the potential of the method.

In sum, phylogenetic and biogeographic approaches to the evolution of migration in plovers and their relatives support and expand on what began to emerge from evolutionary ecology in the 1980s (e.g., papers in Keast and Morton, 1980): that migratory birds generally evolve from ancestors in the present-day non-breeding range through shifts of the breeding range. A corollary is that migratory birds are not “avoiding” winter on their breeding grounds, as much as they have evolved displaced breeding distributions under the influence of natural selection.

3 In which birds is migration most likely to evolve?

Have the same processes driven the evolution of migration in one group of birds in one region as in another? Chesser and Levey (1998) used comparative phylogenetic methodology to address this question. Specifically, Chesser and Levey (1998) tested Levey and Stiles’s (1992) hypothesis that migration will most likely evolve in lineages with at least partially frugivorous or nectarivorous species in “non-buffered” edge, canopy, and open habitats areas rather than those of “buffered” forest interiors. They found that although temperate-tropical migration in all New World passerines does tend to be associated with frugivorous lineages, especially those preferring “non-buffered” edge, canopy and open habitats, this relationship is significant only for habitat. They concluded that although the evolution of migration appears constrained in insectivorous species of forest interiors, release from those constraints has not necessarily led to its evolution. Chesser and Levey (1998) recognized that more detailed phylogenies of Neotropical birds at lower taxonomic levels would be necessary to fully explore their approach. Equally relevant here is that in exploring one more phylogenetic approach to defining the pool of species from which migrants are most likely to evolve, Chesser and Levey (1998) opened up new ways of thinking about the ecological patterns and processes underlying the evolution of migration.

4 Phylogeography and population genetics in the evolution of migration

Several recent studies have employed population genetics and phylogeography to examine the history of migration within species (Bermingham et al., 1992; Buerkle, 1999; Milá et al., 2000; Rugg and Smith, 2001). An excellent model for exploring the use of these approaches is Swainson’s flycatcher, *Myiarchus swainsoni* (Joseph et al., 2003). *M. swainsoni* is the only extensively migratory member of the 11 South American species of *Myiarchus* tyrant-flycatchers (Lanyon, 1978).

Four subspecies are currently recognized under Mayr’s (1942) biological species concept (Lanyon, 1978; Mees, 1985; Haverschmidt and Mees, 1994), two of which

(*M. s. swainsoni*, *M. s. ferocior*) are temperate-tropical migrants within South America and two of which (*M. s. phaeonotus*, *M. s. pelzelni*) are non-migratory, resident taxa in northern and central South America. *M. s. swainsoni* X *M. s. ferocior* morphological intergrades occur in a narrow zone and also are migratory. Lanyon (1978) also recognized zones of morphological intergradation between *M. s. pelzelni* and both *M. s. swainsoni* and *M. s. phaeonotus* to its south and north, respectively. The *M. s. swainsoni* X *M. s. pelzelni* intergrades are migratory.

If the various migratory populations in the *M. swainsoni* complex are each other's closest relatives, then the assumption of a single origin of migration is necessary and adequate. More complicated histories of gains and losses of migration must be explored if they are not. A related issue is the history of shifts in breeding and non-breeding ranges that have accompanied the evolution of temperate-tropical migration in the migratory populations of the *M. swainsoni*. Tools of systematics and mtDNA-analysis have been used to address these issues (Joseph et al., submitted). Forty-nine samples from the *M. swainsoni* complex were obtained over a range of about 4 000 km from Guyana in the north to the border between Uruguay and Argentina in the south. They were part of a larger data set of 120 sequences from almost all other species of *Myiarchus* that were sequenced for the overlapping mtDNA genes, *ATPase 8* and *6* (*ATPase 8/6*). The position of *M. swainsoni* in the *Myiarchus* phylogeny reveals deep history; its population genetics and intraspecific phylogeography inform us of more recent history.

mtDNA of migratory nominate *M. s. swainsoni* is not closely related to any other *Myiarchus* sampled, species and subspecies. Residual phylogenetic uncertainty in the broader analysis does not obscure the key point that no single analysis placed all of the migrants as each other's closest relatives. mtDNAs from all other migratory and non-migratory members sampled in the *M. swainsoni* complex were extremely closely related. Thus 44 migratory and non-migratory individuals sampled across some 4 000 km of South America and from populations showing substantial morphological divergence from one another showed zero net mtDNA divergence across South America. As a group, furthermore, they are more closely related to the dusky-capped flycatcher (*M. tuberculifer*) complex than to nominate *swainsoni*. Thus at least two independent origins of migration are implied in the whole *M. swainsoni* complex, one in *M. s. swainsoni* and at least one in *M. s. ferocior* and the *M. s. swainsoni* X *M. s. ferocior* and *M. s. swainsoni* X *M. s. pelzelni* intergrades.

Thirty-one of the 44 migratory and non-migratory individuals had identical *ATPase 8/6* sequences. The other 13, which are equally widely distributed, differed by just one or two base pairs. This finding and the star-shaped statistical parsimony network for the 44 individuals are signatures of a population that has very recently expanded across its geographical range. Support for a recent range

expansion came from highly significant population-genetic statistics (Fu, 1997) and from mismatch analysis (Rogers, 1995), which showed a close fit between observed and expected patterns under a range expansion. A parameter estimated in this latter analysis, τ is the time since the expansion occurred. The range of its estimates (Joseph et al., 2003) places the expansion as having occurred within the last few hundred thousand years at most.

MtDNA of migratory *M. s. swainsoni* is substantially divergent from that of all other migrants and non-migrants in the complex (3.1% net divergence). In birds, this level of divergence is typical of that between well-marked species (e.g., Avise and Walker, 1998). It indicates a deep divergence between nominate *M. s. swainsoni* and other migratory populations in the complex. Conventional calibrations of the rate of sequence evolution in coding regions of mtDNA (Fleischer et al., 1998 and references therein) suggest that migratory *M. s. swainsoni* diverged from sister ancestral populations probably at the beginning of the Pleistocene.

When breeding distributions are mapped on to the phylogeny (*sensu* Joseph et al., 1999), independent shifts to southern South America are seen in the history of migratory *M. s. swainsoni* on one hand and in the migratory populations of the clade of migrants and non-migrants on the other. These shifts almost certainly would have occurred at very different times given the substantial divergence between the two groups of migratory populations and the shallow divergence among the 44 migratory and non-migratory individuals. A more complete analysis (Joseph et al., 2003) finds that paleo-environmental data offer support for these inferences.

5 Conclusions

The tools of historical biogeography, phylogeny and population genetics allow one to tease apart the spatiotemporal diversity in the evolution of migratory systems. A single migration system today need not have evolved in response to one set of environmental factors operating at one time or in one place. At the avian family level in such a system, the conclusion of independent origins of migration may at first seem trivial. If, however, a case can be made that migration evolved among them at different times and places, then the challenging question arises of what and how many ecological processes were involved. The *Myiarchus* example above highlights this challenge for closely related species or populations. Clearly, there is extensive scope for extending the historical approach to the evolution of migrants generally.

The example of *M. swainsoni* also shows how time frames for the evolution of migration in different migratory populations can be set. That finding in turn directs research into the palaeo-environmental processes that may have initially driven different scenarios in the evolution of migration and the range shifts that accompanied them. These scenarios can then be compared with the processes main-

taining present-day migration. Spatiotemporal heterogeneity may underlie the evolution of any migration system, and this finding could serve as a basis for study of the evolution of migration generally.

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