S19-3 Bird ringing as a means for studying the evolution of avian migration — potentials, limits and prospects

Wolfgang FIEDLER[1], Francisco PULIDO[2]

Max Planck Research Centre for Ornithology, Vogelwarte, Schlossallee 2, D-78315 Radolfzell, Germany; [1] fiedler@vowa.ornithol.mpg.de; [2] pulido@vowa.ornithol.mpg.de

Abstract Bird ringing is the most widespread and longest established approach for studying avian migration patterns. It has been pivotal to the investigation of the evolution of migration by providing information on migration routes and their variation in space and time. Most hypotheses on the evolutionary history of migratory behavior, and constraints on evolutionary change, hinge upon precise descriptions of population-specific migration patterns. Long-term data sets collected in trapping and ringing programs have helped us to identify recent changes in avian migration in response to environmental changes. While trapping programs have limitations in identifying the causes of these changes, population studies with individually marked birds are essential for understanding selection processes and for identifying the ecological interactions underlying the changes. Future research into the evolution of avian migration will greatly benefit from combining ringing results with those from other techniques (e.g., stable isotope marking, genetic marking and satellite tracking).

Key words Climate change, Genetic markers, Migration flyway, Population studies, Stable isotopes

1 Introduction

Bird ringing has been unquestionably the most important method for those disciplines that require the identification of individuals in the field, as in population biology and behavioral ecology, or which study bird movements, as in migration and dispersal. The management of recovery data by national ringing centers facilitates the collection of large, long-term data sets that may encompass large geographic areas, complementing data obtained by local population studies. This information, across different scales, is essential for understanding the dynamics of populations at different levels and for developing and testing new ecological and evolutionary concepts, such as metapopulation theory.

Although a number of new telemetric and molecular techniques have recently been introduced to track individual birds and the movements of populations (e.g., Webster et al., 2002), bird ringing is still the simplest and most cost-effective approach for collect large samples over extensive geographic areas. Moreover, banding and capturing techniques can easily be learned and are non-invasive, which renders them suitable for studying individuals over a longer period of time. Its most important shortcomings, however, are low recovery probabilities, particularly in small passerines, and the lack of randomization of recoveries in space and time. The high dependence of recovery rates on capture and re-sighting probabilities limits the inferences that can be derived in population studies.

Accordingly, we discuss the potentials and limits of bird ringing for studying the evolution of migration and evaluate its importance for future research.

2 Identification of migration patterns

The central contributions of bird ringing to the study of migration have come from the identification of migration routes and location of wintering areas. Yet, although many national and international atlases summarize detailed information on species-specific migration routes and winter distributions, much of the data is based on a very low number of recoveries, and the spatial and temporal resolution of recovery analyses are few, if attempted at all. A precise spatiotemporal picture of bird movements, however, is a prerequisite for identifying population-specific migration patterns and migratory connectivity (cf. Webster et al., 2002). Atlases with finer resolution are now being published or are under way (e.g., Wernham et al., 2002).

In addition to providing basic information on migration routes and wintering areas, ringing studies with a large number of recoveries, such as those for the European white stork (Fiedler, 2001), can help to detect changes in time and intra-specific variation in migration patterns. Detailed analyses of large-scale recovery data may identify distinct population-specific flyways or wintering areas. This may be the basis for drawing inferences on historical and current environmental factors, such as geographic or climatic "barriers", that favor or constrain the evolution of migration patterns and cause the isolation of populations. Analyses of ringing recoveries of European robins (*Erithacus rubecula*), for instance, reveal that populations apparently wintering in different regions of southern Europe use different migra-

tion flyways and differ in migration phenology. Remisiewicz (2001) hypothesized that this migration system "probably reflects the pattern of re-colonization of Europe after the glacial period from the primary refuges". Even so, the inferred migration pattern may not reflect actual migration differences but inter-site variation in ringing and recovery effort instead.

The question of whether different populations use different wintering areas and reach them by different flyways has concerned migration researchers ever since the very beginning (e.g., Palmén, 1876). The study of migration connectivity is now receiving increased attention as new techniques for its study become available and its importance for the conservation of migratory species becomes recognized (Webster et al., 2002). Genetic markers, in particular, help to identify the breeding populations of birds captured on migration or wintering grounds. This approach is particularly valuable because a knowledge of genetic population structure is essential for understanding the processes leading to inter-population differences in migration. Wennerberg (2001), for example, located the origin of migrating and wintering dunlins (*Calidris alpina*) by tracing geographic variation in the distribution of mtDNA haplotypes. She showed that different dunlin populations migrate in parallel, western populations to wintering areas in the west and eastern populations to those further east, where migration distances increase from west to east. Ringing recoveries and morphometric data supported her results.

However, the utility of genetic markers for identifying the origin of individuals is often limited because of the meager and overlapping genetic variation usually found within and among avian populations. The advent of recently developed highly polymorphic genetic markers (e.g. microsatellites, AFLPs) has improved resolution. Yet the "genetic homogeneity" of avian species is a consequence of the high mobility of most birds, resulting in strong gene flow among populations or of their recent origin. Consequently, genetic differences in neutral genetic markers are normally only found among populations that have been isolated for significant periods.

Thus, genetic studies can often assign birds only to large, well-separated breeding populations and areas (Clegg et al., 2002). Bensch et al. (1999), for example, studied genetic differentiation in a hybrid zone between two subspecies of the willow warbler (*Phylloscopus trochilus*) in central Sweden. This hybrid zone coincides with a migratory divide previously identified by ringing-recovery analyses. They found clear morphological and behavioral differences among populations on both sides of the divide, but no genetic differentiation at neutral loci (mtDNA and microsatellites, cf. Bensch et al. 2002), suggesting either recent evolution of the extrinsic differences and/or strong selection on these characters in the presence of gene flow. Stable isotope ratios in primary feathers, moreover, differ between the populations on either side of the divide, indicating in turn that each willow warbler subspecies winters

in different areas in Africa, a result reflected in the distribution of ringing recoveries (Chamberlain et al., 2000).

As do genetic markers, stable isotopes can thus help to delineate the breeding and wintering areas of unmarked birds, and unravel previously unknown migration patterns (cf. Hobson, 2002). However, the validity of data obtained by this technique has still to be assessed against other methods, such as ringing, because a number of variables (e. g., age-composition, among-year variation, altitudinal variation) can confound results (Graves et al., 2002).

3 Constraints on evolutionary change

Migration routes are commonly considered to be adaptive, to represent optimal solutions to prevailing environmental conditions (Pulido, this symposium). Yet analyses of ringing recoveries suggest that some migration routes may not be optimal. Some populations do not migrate to the closest suitable wintering area; and other populations migrate on unexpectedly long routes that resemble detours. So it is assumed that these populations use historical migration routes and destinations because they have not evolved optimal flyways. Sutherland (1998) found 43 examples of bird populations that had recently changed migration routes; and 14 currently migrate on apparently suboptimal routes. Potentially constrained evolution of migration was found exclusively in species in which parental care is short, i.e. small passerines for which we know that migration patterns are genetically controlled (Berthold, 2001). In species in which parental care is extended, i.e. those with culturally transmitted migratory behavior, changes were frequent and no evidence of suboptimal migration routes was found. This result seems to indicate that changes in migration direction are more frequent and faster in species with culturally transmitted migration patterns. However, we cannot yet exclude the possibility that this result is an artifact of biased representation of taxa.

Although some migration routes seem to be maladaptive, and constraints to evolutionary change appear to be the best explanation for them, ringing studies alone cannot exclude adaptive explanations for these patterns. Here, again, other methods can help to corroborate hypotheses founded on the results of ringing studies. Swainson's thrush (*Catharus ustulatus*), for example, is separated in coastal and continental populations which differ in migration route and wintering area. Birds breeding in Alaska undertake a long westward flight before turning south, whereas those of the coastal population on the other side of a migratory divide fly immediately southwards.

Using differences in mtDNA haplotypes, Ruegg and Smith (2001) showed that the Alaskan population is closer genetically to the continental group and was established after a recent range expansion. Its apparent detour on migration most probably reflects its colonization route, constraining evolution of a more direct migration route. Nevertheless, although genetic studies can help to reconstruct colonization histories, they cannot show if or by what

factors evolutionary change has been constrained. There may be different explanations for evolutionary stasis, for which the lack of genetic variation is just one possibility (Merilä et al., 2001). The study of such causes requires long-term population monitoring to assess selection regimes, genetic variation, and the interaction of genotype and environment (Pulido and Berthold, 2003; Pulido, this symposium).

4   Recent changes in migration patterns

Many recent studies have demonstrated that migratory behavior is highly flexible, and may respond rapidly to environmental change, natural and man-made (Burton, 1995; Moss, 1998; Sutherland, 1998; Berthold, 1998; Fiedler, 2003). Migratory responses can be grouped into four main categories: (1) change in migration distance, (2) change in route, (3) change in migrant frequency, and (4) change in timing (Fiedler, 2003). The first evidence for such changes came from field observations: winter counts, visual observations of migration, first arrival counts. To address questions on evolutionary mechanisms, however, it is necessary to investigate changes within discrete populations which, in most cases, requires individual marking.

Trapping data from willow warblers on autumn migration in southwestern Germany show a recent trend towards an increase in the number of birds migrating late in the season, while the population mean has remained unaltered (Fiedler, 2003). In this study, standardized trapping and individual marking have revealed a complex change in pattern over time. Though this change may be interpreted as evidence for relaxed selection during late passage, alternative explanations cannot be excluded. It could, for example, result from an increase of individuals from late-migrating populations, in which case it would mirror changes in the admixture of populations on passage rather than timing shifts within the populations themselves. Other techniques, as for instance stable isotope analyses, could help to identify the origin of late birds and resolve the competing explanations.

In partially migratory populations, local and regional changes in the frequency of migrants may be difficult to detect because of the year-round presence of residents. Here individual marking is a prerequisite for elucidating patterns of change. In his analysis of greenfinch (*Carduelis chloris*) ringing recoveries in two areas in England, Main (1996) found an increase in mean winter recoveries from 33% to 53% and from 17% to 29 % for distances over 20 km, respectively. This trend was correlated with an increase in population density and may have resulted either from an increase in the frequency of migrants or from an increase in migration distance, or both. Although both traits are tightly correlated and so difficult to separate (Pulido et al., 1996), it is important for evolutionary biology to be able tease out and distinguish between these alternative demographic scenarios. This, in principle, is possible from analysis of large, representative, long-term data sets of ringing

recoveries. Hitherto, few such studies have attempted to investigate the mechanisms leading to changes in the numbers of overwintering birds (Dhondt, 1983; Adriaensen et al., 1993; Able and Belthoff, 1998).

As it is, examples for all four types of change in migratory behavior have been found in the wild (Fiedler, 2003); and the question now arises whether some migratory traits may change more easily than others. Ringing studies can only provide circumstantial evidence for intra-trait variation in evolutionary rates. Any hypotheses arising from it need to be verified by quantitative genetic studies (Pulido and Berthold, 2003).

5   Population studies on natural selection in the wild

In his study on stonechats (*Saxicola rubetra*) wintering in Belgium, Dhondt (1983) was probably the first to use fluctuations of numbers observed in winter to obtain circumstantial evidence for the genetic basis of migratoriness and residency. He showed that the number of wintering birds varied among years, and that wintering stonechats were recruited from the local breeding population. He tested three potential explanations for this: (1) stonechat numbers could be determined directly by the environmental conditions at the time of departure from the breeding grounds, (2) the population could be polyphenetic for migratory status, and (3) the number of wintering stonechats could vary as a consequence of fluctuations in numbers of breeding birds and of breeding success. Dhondt (1983) found no correlation between the number of wintering stonechats and the number of breeders or autumn temperatures of the area and year, rejecting hypotheses 3 and 1, respectively. He did, however, find a correlation between the number of resident birds and mean temperature in the previous winter, indicating that "differential survival of overwintering and migratory individuals took place and that individuals differ in their tendency to migrate".

Although Dhondt could not test whether the consistency of individual behavior resulted from inheritance, cultural transmission, imprinting or other mechanisms, he concluded, that, considering the rapidity of changes in the program of migrants, a genetic basis for migratory behavior was "plausible". One shortcoming in this work arises out of the categorization of "overwintering" birds. Alleged winter recoveries of local birds were made in October; but a recent analysis of stonechat ringing recoveries found that in all stonechat populations, even those exclusively migratory, some migrants remain in the breeding area until October (B. Helm and W. Fiedler, unpubl.). Nevertheless, Dhont's study is exemplary in showing how individual ringing can help to test competing hypotheses for the causes of change in migratory behavior and in identifying selection processes.

Another study using ringing data to test competing hypotheses involved in the evolution of bird migration was conducted on a recently established and exploding popula-

tion of the house finch (*Carpodacus mexicanus*) in eastern USA (Able and Belthoff, 1998). It investigated whether the increase in migration distance and the proportion of migratory individuals in that population reflected evolutionary change, namely changes in genetic composition or phenotypic plasticity. That actual evolutionary change was the cause is supported by two findings. First, migration distances in newly colonizing populations were consistently larger than those in the overall population at the same time. This result is to be expected if there is heritable genetic variation in the migratory trait, because newly colonizing populations should consist of descendants of colonizers with inherently larger-than-average migratory activity. Were migration distance environmentally induced, migration distances would have been correlated with latitude — which they were not. Secondly, a higher frequency of residents in the most recently-established populations was not found, as would otherwise have been expected if migration status had been facultative and determined by environmental conditions. This study has been the first to reconstruct the evolution of migratory behavior, a result made possible only because of the large number of ringing recoveries available.

In this field, population studies may not only help to identify adaptive changes in migratory behavior and their presumptive causes but also to assess adaptability by reconstructing micro-evolutionary change (cf., Pulido, this symposium) and by providing estimates of phenotypic and genetic variation in migratory traits in the wild (Pulido and Berthold, 2003).

6 Conclusions

Bird ringing has been and still is the prevailing approach to the study of avian migration patterns and their changes in time. Ringing studies have revealed large inter- and intra- population variation in migration routes and phenology. Furthermore, they have demonstrated that migration is a very flexible, complex trait that responds sensitively to environmental change. Many bird populations are currently undergoing active shifts in migration distance, direction, timing and migratory composition. The study of these changes in long- and short-distance migrants may provide evidence for inter-trait and inter-species variation in the rate of change, and for constraints on adaptive evolution. Moreover, studies of ringed populations hold great promise for elucidating the mechanisms underlying these changes.

We believe that the combination of ringing-recovery analyses with recently developed molecular technologies will become the most powerful approach for investigating migration patterns and elucidating the evolutionary mechanisms that maintain and change them. The use of these new technologies, in complement with ringing data, will be especially important in studies of species with low recovery probability, in which ring reading is difficult, and for which recovery probabilities, including recovery notification, are highly variable in space and time. Studies on such species will benefit as well from the application of methods that allow the delineation of the breeding areas of individuals without previous marking. Advanced tracking methods (attached data loggers, satellite tracking) will help too to unravel individual migration journeys and to refine knowledge of actual migration patterns and their dynamics.

References

Able K, Belthoff JR, 1998. Rapid "evolution" of migratory behaviour in the introduced house finch of eastern North America. Proc. R. Soc. Lond. B 265: 2 063–2 071.

Adriaensen F, Ulenaers P, Dhondt AA, 1993. Ringing recoveries and the increase in numbers of European great crested grebes *Podiceps cristatus*. Ardea 81: 59–70.

Bensch S, Andersson T, Åkesson S, 1999. Morphological and molecular variation across a migratory divide in willow warblers, *Phylloscopus trochilus*. Evolution 53: 1 925–1 935.

Bensch S, Åkesson S, Irwin DE, 2002. The use of AFLP to find an informative SNP: genetic differences across a migratory divide in willow warblers. Mol. Ecol. 11: 2 359–2 366.

Berthold P, 1998. Vogelwelt und Klima: gegenwärtige Veränderungen. Naturwiss. Rundsch. 51: 337–346.

Berthold P, 2001. Bird Migration. A General Survey, 2nd ed. Oxford: Oxford University Press.

Burton JF, 1995. Birds and Climate Change. London: Helm.

Chamberlain CP, Bensch S, Feng X, Åkesson S, Andersson T, 2000. Stable isotopes examined across a migratory divide in Scandinavian willow warblers (*Phylloscopus trochilus trochilus* and *Pylloscopus trochilus acredula*) reflect their African winter quarters. Proc. R. Soc. Lond. B 267: 43–48.

Clegg SM, Lovette I, Kimura M, Ruegg K, Milá B, Smith TB, 2002. Molecular genetic approaches to linking breeding and overwintering areas for five Neotropical migrant passerines. Abstracts of the meeting "Birds of Two Worlds": http://natzoo.si.edu/smbc/abstracts.pdf.

Dhondt AA, 1983. Variation in the number of overwintering stonechats possibly caused by natural selection. Ring. Migrat. 4: 155–158.

Fiedler W, 2001. Large-scale ringing recovery analysis of European white storks (*Ciconia ciconia*). Ring 23: 73–79.

Fiedler W, 2003. Recent changes in migratory behaviour of birds: a compilation of field observations and ringing data. In: Berthold P, Gwinner E, Sonnenschein E ed. Avian Migration. Berlin: Springer, 21–38.

Graves GR, Romanek CS, Navarro AR, 2002. Stable isotope signature of philopatry and dispersal in a migratory songbird. Proc. Natl. Acad. Sci. USA 99: 8 096–8 100.

Hobson KA, 2002. Incredible journeys. Science 295: 981–983.

Main IG, 1996. Seasonal movements of British greenfinches *Carduelis chloris*. Bird Study 43: 240–252.

Merilä J, Sheldon BC, Kruuk LEB, 2001. Explaining stasis: micro-evolutionary studies in natural populations. Genetica 112–113: 199–222.

Moss S, 1998. Predictions on the effects of global climate change on Britain's birds. Brit. Birds 91: 307–325.

Palmén JA, 1876. Ueber die Zugstrassen der Vögel. Leipzig: Verlag Wilhelm Engelmann.

Pulido F, Berthold P, 2003. Quantitative genetic analysis of migratory behaviour. In: Berthold P, Gwinner E, Sonnenschein E ed. Avian Migration. Berlin: Springer, 53–77.

Pulido F, Berthold P, van Noordwijk AJ, 1996. Frequency of migrants and migratory activity are genetically correlated in a bird population: evolutionary implications. Proc. Natl. Acad. Sci. USA 93: 14 642–14 647.

Remisiewicz M, 2001. The pattern of winter-quarters of robins (*Erithacus rubecula*) migrating in autumn through the southern Baltic coast. Ring 23: 37–53.

Ruegg KC, Smith TB, 2001. Not as the crow flies: a historical explanation for circuitous migration in Swainson's thrush (*Catharus ustulatus*). Proc. R. Soc. Lond. B 269: 1375–1381.

Sutherland WJ, 1998. Evidence for flexibility and constraint in migration systems. J. Avian Biol. 29: 441–446.

Webster MS, Marra PP, Haig SM, Bensch S, Holmes RT, 2002. Links between worlds: unraveling migratory connectivity. Trends Ecol. Evol. 17: 76–83.

Wennerberg L, 2001. Breeding origin and migration pattern of dunlin (*Calidris alpina*) revealed by mitochondrial DNA analysis. Mol. Ecol. 10: 1 111–1 120.

Wernham C, Toms M, Marchant D, Clark J, Siriwardena G, Baillie S, 2002. The B.T.O. Migration Atlas. Norfolk: British Trust for Ornithology.