

Arie J. van Noordwijk · Francisco Pulido
Barbara Helm · Timothy Coppack · Julia Delingat
Hugh Dingle · Anders Hedenström · Henk van der Jeugd
Chiara Marchetti · Anna Nilsson · Javier Pérez-Tris

A framework for the study of genetic variation in migratory behaviour

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Abstract Evolutionary change results from selection acting on genetic variation. For migration to be successful, many different aspects of an animal's physiology and behaviour need to function in a co-coordinated way. Changes in one migratory trait are therefore likely to be accompanied by changes in other migratory and life-history traits. At present, we have some knowledge of the pressures that operate at the various stages of migration, but we know very little about the extent of genetic variation in various aspects of the migratory syndrome. As a consequence, our ability to predict which species is capable of what kind of evolutionary change, and at which rate, is limited. Here, we review how our evolutionary understanding of migration may benefit from taking a quantitative-genetic approach and present a framework for studying the causes of phenotypic variation. We review past research, that has mainly studied single migratory traits in captive birds, and discuss how this work could be extended to study genetic variation in the wild and to account for genetic correlations and correlated selection. In the future, reaction-norm approaches may become very important, as they allow the study of genetic and environmental effects on

phenotypic expression within a single framework, as well as of their interactions. We advocate making more use of repeated measurements on single individuals to study the causes of among-individual variation in the wild, as they are easier to obtain than data on relatives and can provide valuable information for identifying and selecting traits. This approach will be particularly informative if it involves systematic testing of individuals under different environmental conditions. We propose extending this research agenda by using optimality models to predict levels of variation and covariation among traits and constraints. This may help us to select traits in which we might expect genetic variation, and to identify the most informative environmental axes. We also recommend an expansion of the passerine model, as this model does not apply to birds, like geese, where cultural transmission of spatio-temporal information is an important determinant of migration patterns and their variation.

Keywords Individual variation · Migration · Migratory syndrome · Migratory traits · Quantitative genetics

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A. J. van Noordwijk (✉) · F. Pulido · C. Marchetti
Netherlands Institute of Ecology,
Boterhoeksestraat 48,
6666 Heteren, The Netherlands
E-mail: a.vannoordwijk@nioo.knaw.nl
Tel.: +31-26-4791258
Fax: +31-26-4723227
E-mail: f.pulido@nioo.knaw.nl

B. Helm
Max Planck Institute for Ornithology,
Von-der-Tann-Street 7,
82346 Andechs, Germany

T. Coppack · J. Delingat
Institute of Avian Research, "Vogelwarte Helgoland",
An der Vogelwarte 21, 26386 Wilhelmshaven,
Germany

H. Dingle
Department of Entomology, UC Davis, One Shields Avenue,
Davis, CA 95616-8584, USA

H. Dingle
School of Integrative Biology, University of Queensland,
4067 Brisbane, Australia

A. Hedenström
Department of Theoretical Ecology, Lund University,
Ecology Building, 22362 Lund, Sweden

H. van der Jeugd
SOVON Dutch Centre for Field Ornithology,
Rijksstraatweg 178, 6573 Beek-Ubbergen,
The Netherlands

A. Nilsson · J. Pérez-Tris
Department of Animal Ecology, Lund University,
Ecology Building, 22362 Lund, Sweden

Introduction

We know very little about the extent of genetic variation in nearly all aspects of bird migration, yet such knowledge is essential for predicting to what extent and how fast birds could adapt to environmental changes, such as those caused by climate change (Pulido and Berthold 2004). Even without environmental threats, migration would deserve more genetic study. Bird migration is a prime example of a process that can only be understood through its ultimate fitness consequences. This is because successful migration requires an anticipation of changing seasons. Whereas one can conceive how selection should favour individuals that successfully anticipate seasonally changing conditions (e.g. Lack 1968), it is difficult to understand migration from its immediate consequences. Just the fact that migration requires substantial amounts of energy implies that preparation for migration must start when local conditions (still) permit such an accumulation of energy reserves. We therefore need an evolutionary approach, of which the documentation of the extent of genetic variation is an essential part. Studying genetic variation presupposes that variation is present, and in particular, variation among individuals within populations.

Almost by definition, migration is related to heterogeneity of important environmental conditions in time and space. Thus, the classical first approximation, where we subdivide the phenotypic variation into a genetic and an environmental component, can be used only in model systems where traits are measured under strictly controlled conditions. In nature, migration occurs over a considerable time interval, involving several substages, and at multiple locations, and thus a necessary first step for studying migration is simplification. In particular, we need to reduce our study to a limited number of phenotypic traits at a time. The choice of suitable traits is by no means trivial. In principle, any aspect that can be expressed as a number could be defined as a trait. However, good trait definitions should take into account how the phenotype is being formed, because the processes involved give us important information. Changes in wing length within one season are due to feather abrasion, but re-measuring after a moult includes all the genetic and environmental components in feather growth. Having reduced our bird to one trait value, we can use the concept of reaction norms to study phenotypic variation of a series of genotypes over a range of environmental conditions (e.g. van Noordwijk 1989; Postma and van Noordwijk 2005; Rappole and Helm 2006). Each genotype is represented as a line that specifies the phenotype over a range of values on an environmental axis. Again, the choice of the most informative trait and environmental axis is by no means trivial. For example, variation in the amount of fat that birds carry during migration is unlikely to depend on genetic variation. Instead, the rate at which fat is deposited may well depend on physiological efficiency,

which is in turn dependent on genetic variation in the enzymes involved. The major environmental variables involved might be prey density or ambient temperature or prey quality.

With this general framework in mind, we will discuss several interrelated topics. We start by discussing the migratory syndrome and how to identify suitable traits for further study. Repeated measurements on single individuals are often easier to obtain than data on relatives and can thus be helpful for identifying and selecting traits for further study, since consistent variation among individuals is expected if genetic variation is important, although such individual consistency may have other than genetic causes. Next, we discuss two major groups of techniques for the study of genetic variation with particular focus on their application to bird migration. By including information from related animals, genetic contributions can be estimated. This has so far been mostly done by comparison of siblings taken from the field, by breeding experiments, and by observation of individually marked animals (reviewed in: Merilä and Sheldon 2001; Pulido and Berthold 2003). Reaction-norm approaches help us understand how migratory decisions are influenced by the environment. These approaches involve systematic testing of migratory traits under different environmental conditions. Although reaction norms are not often used outside a genetic context, they provide a valuable tool to study the relevant eco-physiological processes which in turn gives us important information on how to choose our traits (e.g. van Noordwijk 1989; Postma and van Noordwijk 2005).

In an outlook section, we suggest steps to extend our understanding of the genetics and evolution of avian migration. We discuss optimality models and the contribution they could make. One merit could be in identifying underlying processes and constraints and thereby traits in which we might expect variation, as well as environmental axes that may be most informative. In addition, optimality models can place results from studies of individual traits in a larger context, e.g. annual cycles, and thereby identify possible consequences of migratory decisions. We also recommend an expansion of the passerine model. Suggestive empirical data come from groups of birds where cultural transmission of information plays an important role, such as in goose migration, whereas passerines often migrate independently. The need to consider social context to understand the genetic regulation of bird migration is corroborated by results from studies of bird personalities as an example of strong links between very different kinds of behaviour (e.g. exploratory or foraging behaviour). Avian social systems and bird personalities are not in contrast to genetic determination of migration, as has been suggested, but are themselves partly genetically determined (Drent et al. 2003; van Oers et al. 2005). Apart from the fact that it is essential to translate our results on isolated traits back to whole organisms, social interactions and avian personalities may well interfere with our measurements of individual traits. After all, our standardised measuring

devices will be experienced as mildly stressful conditions, and personality types differ in their reactions to stress and thus to the experimental set-up.

Even though everyone realises the importance of evolutionary explanations for migration and all its aspects, discussion of genetic and individual variation have been almost absent from the ornithological literature. We hope that the framework we describe shows that most aspects of studying individual variation and genetics can be incorporated into bird migration research. Although complicated because of a large number of potential variables, genetic aspects can be studied and should be studied if we want to understand how migration can evolve.

Defining the migratory syndrome and decomposing it into traits

A major difficulty we encounter in analysing individual variation in migration strategies is their complexity. Hence, they need to be decomposed into discrete traits for which the different components of phenotypic variation can be estimated. Ideally, these traits should be easily measurable, allow estimation of repeatability, and be transportable between different taxa. Perhaps a first step with which to better approach this problem is structuring the migratory syndrome into two, largely interconnected, sets of components, which can be referred to as the “narrow-sense” and the “broad-sense” migratory syndromes:

Narrow-sense migratory syndrome

Migration as a behaviour defines a syndrome in its own right, formed by phenotypically correlated traits such as hyperphagia, food choice, organ plasticity, fat deposition, migratory restlessness, timing of departure, behavioural decision rules, orientation ability, arrival time, etc. (Dingle 1996; Piersma et al. 2005). Some of these traits show a large amount of genetic additive variation (Pulido and Berthold 2003), so they are prone to evolve rapidly. For example, new migratory distances and directions have evolved in European blackcaps (*Sylvia atricapilla*) and eastern North American house finches (*Carpodacus mexicanus*) in just a few generations (Berthold et al. 1992; Able and Belthoff 1998). However, genetic correlations between migratory traits (e.g. between migration timing and amount of migratory activity) may strongly modify the adaptability of migratory behaviour under changing environmental conditions (Pulido et al. 1996; Pulido and Berthold 1998). Moreover, phenotypic plasticity (e.g. of the timing of reproduction in response to changing migration distance) may override genetic changes (Coppack et al. 2003; Helm and Gwinner 2005). Separating genetic and environmental components of phenotypic variation in migratory traits is therefore decisive for understanding their potential for rapid adaptive change.

Traditionally, the traits defining ongoing migration have been measured through behavioural observations, for instance onset of migratory activity, fat deposition during first autumn migration or gonadal maturation (Berthold 2001). A major caveat, however, is that many of these traits cannot be measured more than once, so their repeatability cannot be determined. In other cases, it is difficult to decide how to measure the relevant trait, for example when a bird starts accumulating fat. One possibility for exploring the repeatability of “single-event” traits, such as the age of initiation of the first autumn migration, is to study the focal trait in genetically related individuals (e.g. in the offspring of an individual) under different conditions (e.g. different clutches, different years; see Pulido et al. 2001). The use of alternative measures for migratory traits (e.g. physiological changes traceable from metabolites in the bloodstream) could help to solve problems of measurement accuracy and interpretation in the future.

Another possible but barely explored problem when interpreting variation in migration-related traits is homoplasy, i.e. similarity through common descent. Although migration is probably an ancestral character of all birds (Berthold 1999), the mechanisms through which birds accomplish migratory tasks (orientation, fat accumulation, etc.) might have evolved independently in different taxa. This would make it difficult to generalise from the findings on the genetics of migration in one species to other groups. Comparative studies addressing this particular problem are required to place particular traits of the migratory syndrome into correct evolutionary context (Rappole et al. 2003; Helbig 2003; Zink 2003; Pérez-Tris et al. 2004; Piersma et al. 2005).

Broad-sense migratory syndrome

Migration as a part of birds' life styles requires adaptations other than the ones described above (but note that it is difficult to draw a clear frontier between both sets of traits). Migratory and sedentary birds face different environmental influences through their lives. First, migration involves selection favouring morphological adaptations for long-distance flight. Migrants usually have longer and more pointed wings, shorter tails and a smaller body size than their resident conspecifics (Leisler and Winkler 2003). Migrants also expose themselves to different habitat types, predators or parasites, which may promote variation in life-history strategies (increased fecundity but lower survival in seasonal environments), behaviour (flocking, secretiveness during fat deposition, etc.) or immune responsiveness (Alerstam et al. 2003). Furthermore, the need to complete two migratory journeys each year affects the organisation of the annual cycle (e.g. timing of gonadal maturation, moult pattern and speed; Gwinner 1996).

So far, variation in these traits has primarily been identified as differences between populations (e.g. Dierschke and Delingat 2001) or from differences

between closely related taxa with different migratory habits. But, as these taxa not only differ in migratory behaviour but also in the environment they experience, a large portion of phenotypic variance may be due to individual adjustment (= phenotypic plasticity) in response to environmental variation. This problem has been addressed by experimental approaches, for instance manipulation of environment and common-garden experiments, as elaborated below. The relative importance of genetic and environmental factors differs among study traits. For instance, it is very likely that migration-related morphological differentiation is due to genetic variation. Heritability of morphological traits such as wing length is high and evolution can be very fast, as shown by the incipient increase in wing aspect ratio of eastern North American populations of house finches since they acquired migratory behaviour some decades ago (Egbert and Belthoff 2003). Predictions on the causes of variation in other traits of the “broad-sense migratory” syndrome (e.g. the timing of annual cycles, onset of breeding) are probably less reliable as these traits are more liable to environmental influence. We currently know little about genetic correlations of these traits with other components of the migratory syndrome (but see Coppack et al. 2001; Pulido and Coppack 2004), and to what extent they are influenced by other mechanisms causing phenotypic correlations. For example, hormonal releases involved in physiological switches governing migratory disposition might affect morphological traits or reproductive status. Future studies should try to disentangle the relative contribution of additive genetic variation, genetic correlations and epistatic effects to phenotypic variation in migration traits. Some of these questions have been successfully explored in research, mostly targeted at the simplified passerine model, with the tools of quantitative genetics (see Pulido and Berthold 2003, and below).

Individual variation, repeated measurements

If there is genetic variation for a particular trait, there must be variation among individuals. Hence, measuring the extent of individual variation is a logical start for any genetic investigation.

In series of repeated measurements, it is possible to compare the variation in measurements made on the same individual with the variance among different individuals. Moreover, in a number of cases, subdividing the data into different groups can give interesting insights. For example, by calculating repeatabilities of pairs, females with different partners and males with different partners, it was shown that in great tits (*Parus major*) and blue tits (*P. caeruleus*) clutch size and lay date are characteristics of the female independent of their mates, but hatching failure of the eggs depends on the specific combination of males and females (Kempnaers et al. 1996; van Noordwijk et al. 1981a, b). In the sparrowhawk (*Accipiter nisus*), however, laying date is affected

more strongly by the male than by the female, as shown by the fact that the repeatability of males with different partners is higher than the repeatability of females with different partners (Newton and Marquiss 1984). There is ample scope for comparing repeatabilities, for instance within and among seasons (see, e.g., Pulido et al. 2001). This, however, has hitherto hardly been done for migratory traits (Pulido and Berthold 2003).

Typical migratory traits for which repeated measurements from the field might be available are arrival and departure dates on wintering or breeding grounds, fattening rates at stopover sites, and orientation measurements of birds caught during migration. In the case of orientation measurements, it is unlikely that the same (wild caught) individuals will be retrapped in different seasons, but a typical application might be to study orientation at different times of the night or as a function of different conditions and/or presence of different orientation cues (e.g. Sandberg 2003). Many traits, like, for example, the beginning and duration of migratory activity, fat deposition and food choice, might be easier to measure in caged birds in a controlled environment. Comparison of repeatabilities of the same group of individuals under different sets of conditions has substantial opportunities for the study of causal aspects of the variation that have not yet been exploited. For example, in repeated measurements of wing length on the same day, the only cause of within-individual variation is measurement error. Measurements taken half a year apart, but not including a moult, will include feather abrasion, and measurements taken before and after a moult will include the environmental component in re-growing the feathers. Whereas the first two will not be related to heritability of wing length, the third repeatability might be closer to heritability, although feather growth and wing-length are known to change with age and the timing of moult in some species (e.g. Jenni and Winkler 1994; Hall and Fransson 2000; Pérez-Tris and Tellería 2001). It is therefore essential to have some idea of the potential causes of variation and to consider which of these are included in the within- and among-individual components.

In dealing with variation among individuals, there are three important causes for variation. Apart from the genetic component (V_g), there are two different environmental components: one component that is constant for each individual but varies among individuals (V_{eg}), and another that affects the variation within and among individuals in the same way (V_{es}). Each of these components is interesting and should be studied, because they have different implications. In measuring the constancy of individuals, V_{eg} cannot be separated from V_g and thus the repeatability is only equal to the heritability if there are no permanent environmental differences among individuals. The repeatability is defined as $(V_g + V_{eg})/V_p$, where V_p is the phenotypic variance, given by the sum of the variance components $V_g + V_{eg} + V_{es}$. The variance components can be derived from a simple ANOVA where the variance is split

into within- and among-individual variance. However, care should be taken to use the variance components and not the mean squares, since the relation between mean square and variance component depends on the average number of measurements per individual.

Repeated measurements allow us to calculate repeatabilities, but one can also calculate the correlation between first and second measurements on the same individuals. The difference between these two is that the repeatability is based on the total phenotypic variance including all repeated measurements whereas in the estimation of correlations the two sets of measurements are treated independently. Thus, if there are systematic differences between first and second measurements, the correlation between first and second measurements of each individual will be higher than the repeatability, because in a correlation the systematic difference is taken out of the analysis, whereas it remains part of the within-individual variance in the repeatability. It should be emphasised that repeatability is a tool, and calculating it is not an aim in itself. Comparing different repeatabilities, or repeatabilities with correlations, can however yield very useful information on the structure of the environmental variation.

The genetic study of individual variation

There have been two different approaches in the investigation of genetic variation in migratory traits (reviewed in Pulido and Berthold 2003). The first approach, i.e. quantitative genetics, is concerned with the evolvability of migratory traits, i.e. their heritability. The amount of additive genetic variation present in a population—the main determinant of the strength of the response to selection—is estimated by statistical techniques. Trait expression in relatives is used to estimate the relative contribution of different sources of variation to phenotypic variance. This approach thereby minimises and/or accounts for genetic variation. The second set of studies addresses environmental effects. These studies have been interested in whether phenotypic differences among individuals living in different environments have a genetic origin, or whether they are due to differences among environments. This has been done by common-garden and reciprocal transplant experiments. The principle of these experiments is to identify the causes of phenotypic variation by minimising or accounting for environmental variance. Reaction-norm approaches combine exploring genetic and environmental effects, and therefore target interactions between genes and environment.

Quantitative genetics

The main aim of any quantitative-genetic study is to predict the response to selection of a particular trait in a population. To achieve this goal, we need to quantify additive genetic variation present in a population. This is

done by partitioning phenotypic variation into genetic and non-genetic components of variance. Practically, this can be done by measuring a well-defined trait in a set of related individuals, i.e. individuals sharing genes. The resemblance in the measured trait between related individuals compared to unrelated or more distantly related individuals allows us to estimate the proportion of the phenotypic variance explained by genetic differences, i.e. the heritability.

The heritability (h^2) is the central parameter for predicting selection response (Δz), which is the product of the heritability and the strength of selection, i.e. the selection differential (s): $\Delta z = h^2 \times s$ (= breeder's equation).

To date, there are some 20 published heritability estimates for migratory traits in birds (see Pulido and Berthold 2003; F. Pulido, unpublished data). Although these studies are limited to few species and traits, they show that: (1) most migratory traits have moderate to high heritabilities; (2) heritability estimates derived from different sets of relatives (e.g. parents–offspring versus full sibs), or by different methods (i.e. parent–offspring regression versus artificial selection experiments) give equivalent results; and (3) heritability estimates obtained from populations in the wild or in the laboratory are very similar. In populations where pedigrees are known, the estimation of genetic components can be improved upon by simultaneous consideration of phenotypes of all relatives and among-year environmental effects by using so-called animal models (Kruuk 2004). The main advantage of this new methodology lies in smaller standard errors for the same sample sizes.

Difficulties with the estimation of heritabilities in the wild in general, and of migratory traits in particular, are: (1) that environmental perturbation may be so large that it may be very difficult, or impossible, to reliably estimate genetic variance components (requiring very large sample sizes); (2) that relatives often not only share genes but live in the same environment and therefore resemblances could be due to similarity of environmental influences; (3) that it is difficult to follow large sets of relatives over the period of interest (i.e. when the trait is expressed); and (4) that the traits of interest may not be measurable in the wild (e.g. speed of migration).

Difficulty (1) is not severe because the response to selection is determined by the ratio of genetic variation over phenotypic variation. If environmental variation is much larger than genetic variation, we may not be able to accurately measure genetic variation, but we will also know that most likely responses to selection in the wild will be small. Problem (2) can be overcome by using sets of relatives that are unlikely to share environmental conditions (e.g. grandparents–grandchildren, half-siblings, cousins), or by experimentally cross-fostering parts of the brood. If we take account of the environmental conditions in our analyses we can test for genotype-by-environment correlations, that is the

non-random distribution of genotypes over environments (see below). Generally, experiments under controlled environmental conditions can avoid some of these problems. Comparing heritability estimates obtained from the resemblances between full siblings with those obtained from parent–offspring covariation may give us a first indication of whether significant common-environment effects are to be expected. First results in captive blackcaps indicate that common-environment effects in migratory traits may be small (Pulido 2000; Pulido and Berthold 2003).

Problems (3) and (4) limit the sets of traits that can potentially be measured in wild populations. Actually, the only migratory traits in passerines which have been measured repeatedly in the field are the timing of migration (i.e. arrival and departure on breeding or wintering areas), and migration status (i.e. whether a bird is a migrant or a winter resident). These are the only traits for which we currently have heritability estimates in the wild (see Pulido and Berthold 2003). Other traits like migratory orientation or fattening rate could, in principle, also be measured in the wild by using related individual birds at stopover sites, if it was possible to identify the sites where the majority of birds from one population could be captured. However, at present this is only possible for larger, long-lived bird species, which can be followed over several years (waders, geese, etc.).

In the laboratory, other migration-related traits (e.g. incidence, timing and amount of *zugunruhe*, i.e. nightly migratory activity, mass gain, moult patterns) can be easily and reliably measured and have been successfully used for estimating heritabilities. These experimental approaches using captive birds have the advantage that environmental conditions can be controlled or randomised, thereby minimising common-environment effects. Moreover, results can be cross-validated by conducting artificial selection or cross-breeding experiments (see Pulido et al. 1996, 2001). However, even though laboratory measurements seem to hold the greatest potential for new insights into the evolutionary genetics of migratory traits, they are not without problems. As with all laboratory studies, we need to test whether results obtained in the laboratory are valid under natural conditions. There are a number of observations that indicate that the level of genetic variation and covariation is similar between natural and the artificial environments (see Pulido 2000; Pulido and Berthold 2003). Yet, it is not clear how *zugunruhe* translates to migratory activity in the wild and how environmental factors may modify the endogenous program expressed under laboratory conditions. Recent results in resident blackcaps and stonechats (*Saxicola torquatus*), which show migratory activity in cages but not in the wild, indicate that the interaction between environmental cues and endogenous programs may be complex and requires more in-depth investigation (Gwinner 1990; Dingle 1996; Rappole et al. 2003).

Cohesion among traits

Selection rarely acts on single traits but rather on suites of integrated traits that compose the phenotype. Thus, for predicting evolutionary response of migration, we need to consider selection on the whole suite of traits of the migratory syndrome. For example, selection for shorter migration distance may be correlated with selection for earlier arrival at the breeding grounds, for shorter, more rounded wings, for decreased rate of fat accumulation, for earlier egg-laying, longer developmental time of chicks, etc. In such multi-trait evolution, the selection response of a single trait is determined by the selection intensity on that trait and its heritability (direct selection response as determined by the breeder's equation), plus the product of the genetic correlation of the trait with other traits and the intensity of selection on these other traits (correlated selection response). Therefore, for predicting the selection response of each single character, we need to know the sign and amount of genetic covariation among traits.

As with the heritability, genetic correlations may be obtained by estimating covariation of traits in groups of related individuals. The approaches and caveats are the same, although sampling errors of genetic correlations are usually much larger requiring large sample sizes to obtain reasonably accurate estimates (Klein et al. 1973; Roff 1997). If environmental covariation is small, phenotypic correlations, particularly estimated from family means, can give us a good indication of genetic correlations, with a much smaller sampling error. This has been established for many morphological traits (Roff 1996), and seems also to hold for migratory traits in the blackcap (Pulido and Berthold 1998; Pulido 2000). Lacking accurate genetic estimates of correlations for migratory traits, phenotypic correlations may therefore be useful as a first approach to build predictive models of multitrait evolution. We will need to test the usefulness of this approach in other species and other traits.

Common-garden experiments

The main approach to distinguish the genetic and environmental origin of phenotypic differences involves common-garden experiments. In common-garden experiments, we transfer individuals that differ in phenotype and in the environmental conditions they experienced in the wild into a common controlled environment. If phenotypic differences persist under these identical conditions, they are likely to be caused by genetic differences. If phenotypic differences disappear, we may well assume that they originated from differences in the environment, or from differences in the response to the environment, which in turn could be due to genetic differences.

Common-garden experiments are probably the most straightforward method for studying the genetic basis of

differences in migration. Taking advantage of the extensive within- and among-species variation in migration patterns, a number of studies has shown that differences in migratory behaviour are genetic (e.g. Gwinner 1969; Berthold and Querner 1981; Widmer 1999; Derégnaucourt et al. 2005; Helm et al. 2005). The main environmental factors that were controlled for in these studies have been day length and food. Even though many studies have attempted to reduce the environmental influence of the area of origin to a minimum by transferring eggs or chicks, it is not possible to exclude all early environmental or any maternal effects by this approach. However, lasting environmental effects can be reduced or eliminated by breeding birds for at least one generation in a controlled environment. This approach is a powerful way to separate genetic and environmental effects of phenotypic differences between populations. However, if differences are found, further breeding may be required to exclude confounding environmental effects. Moreover, the environment should be carefully chosen, or more than one environment should be used (see below). Controlled environments should mimic natural conditions in the wild to allow drawing inferences for free-living populations, as we cannot assume that interactions between genotypes and the environment are absent (see Lambrechts et al. 1999). Common-garden experiments can be fruitfully combined with quantitative genetics approaches. Accounting for pedigree may yield a good data basis for estimating heritabilities for many migratory and other life-history traits and assessing the correlation between them in only one generation.

Because of the relatively little amount of time and facilities they require, common-garden experiments may become the basic tool and initial step in future studies on the genetics of migration. A straightforward, extended research program could be: (1) sample individuals from clearly divergent migratory populations, e.g. migratory and non-migratory birds, short- and long-distance migrants, or early and late migrating birds, and keep them in a controlled environment; (2) if you find differences, breed within populations to eliminate maternal and early environmental effects; (3) if differences persist, cross F1-offspring and create F2 generation; and (4) use F2 generation to produce backcrosses and reciprocal backcrosses. This may allow the separation of additive genetic, dominance and maternal effects (e.g. van Oers et al. 2004).

The study of reaction norms

One potential cause of population differences in migratory traits could be different responses to environmental cues. This is best tested in experimental set-ups which investigate phenotypic plasticity of traits under different environmental conditions. If populations differ in phenotypic plasticity, their response to the environment is likely to have a genetic basis. Responses to the

environment can be described by a reaction norm (i.e. the range of phenotypes expressed by a single genotype as a function of a specified environmental variable). This approach can be extended to populations by calculating mean population responses to the environmental variable (van Noordwijk 1989; Rappole and Helm 2006). The most basic approach for studying reaction norms is a reciprocal transplant experiment. This approach is similar to common-garden experiments, but instead of keeping the environment constant, the study populations are exposed to one another's naturally experienced environmental conditions. Reciprocal transplants have been conducted in the wild by swapping eggs among bird species with different migratory behaviours (Välikangas 1933; Putzig 1938; Harris 1969). Generally, reciprocal transplant is the method of choice for studying the genetic basis of phenotypic differences whenever there is no possibility of studying the expression of a trait in a controlled environment (aviaries, cages), or when the environmental variables causing differences in migratory behaviour have not yet been identified, or when the environment as a whole is of interest (see, e.g., James 1983; Alatalo and Gustafsson 1988). This is a useful first approach to identify potential environmental influences on the expression of a trait that has been widely used for investigating the mechanisms of migratory orientation in a variety of large migratory species like storks, crows and geese (see Schüz 1950; Chernetsov et al. 2004). In laboratory-based studies, cross-over designs employ the rationale of reciprocal transplants: closely related taxa are compared under their own and the other population's simulated environmental conditions (e.g. Berthold and Querner 1992; Helm and Gwinner 1999, 2001).

In the laboratory and in the field, these experiments can also be fruitfully combined with quantitative genetics by exposing related birds to different environmental conditions (split-brood experiments; Helm and Gwinner 1999, 2001; Pulido and Coppack 2004). Thereby, the influence of environmental variation, genetic variation and variation in reaction norms can be explored even with moderate sample sizes. In the wild, reciprocal transplants with split-brood design are also a powerful tool for separating the causes of resemblance between relatives due to sharing of genes and environment (e.g. Wiggins 1989; Gustafsson and Merilä 1994). However, further experiments under controlled conditions or manipulative experiments may be necessary to identify the specific environmental factors that cause phenotypic differentiation.

The ideas underlying reciprocal transplant experiments can be extended into the study of reaction norms, where traits are systematically measured over a range of environmental conditions. Reaction-norm approaches have been successfully applied, for instance in studies of the physiological control mechanisms underlying migratory traits. Among-population differences in the timing and extent of migration have been shown to arise from direct influences of local environmental conditions,

but also to be a consequence of different reaction norms to the environmental cues used to synchronise the annual cycle with seasonal fluctuations in resource availability (Widmer 1999; Gwinner and Helm 2003; Helm et al. 2005).

Being the most predictive source of seasonal information, photoperiodic stimuli play a crucial role in the overall scheduling of the avian annual cycle (Gwinner 1996). Thus, the spatio-temporal change in photoperiod experienced in the course of a year is a key environmental axis to consider when studying reaction norms in migratory birds. Since the first experimental demonstration of a photoperiodic response in a migratory bird in 1925 (Rowan 1925), numerous studies have dealt with the physiological control mechanisms underlying avian breeding and migration cycles (reviewed in: Gwinner 1996; Dawson et al. 2001). The photoperiod can only be a functional zeitgeber if birds have adapted their response thresholds precisely to the local seasonal conditions under which they live. Species which move or are distributed over a vast latitudinal gradient experience a wide range of different photoperiodic conditions, and we may therefore expect intraspecific local differentiation of photoperiodic reaction norms (Gwinner and Helm 2003; Coppack and Pulido 2004; Helm et al. 2005). There is indeed some indication that birds have adapted their response thresholds to these conditions. However, understanding the migratory syndrome requires a more thorough knowledge of reaction norms in different species and of different migratory traits, and of their evolvability.

Establishing population reaction norms can be a starting point from which to address further questions about the eco-physiology and evolvability of migratory traits. Once the influence of an environmental factor is known to partly account for population differences, we should begin exploring the variation in responses within a population. Evolutionary change can only be achieved if there is sufficient genetic variation in the reaction norm on which selection can act.

Research on reaction norms is not easily done, but because of its value we greatly encourage further studies. The first consideration before embarking on new projects is searching for suitable traits. Traits should be consistently measurable, and exploratory studies on ways to precisely quantify a trait are highly recommended. Secondly, we should look for traits that bear a close relationship to measurable environmental factors. In nocturnally migrating songbirds, the onset of migratory activity appears to be more strongly controlled by photoperiodic responses than its termination (Widmer 1999; Pulido 2000), which is fine-tuned by state-dependent responses to multiple non-photoperiodic factors. Thirdly, selecting study populations which differ in migratory behaviour and selecting the environmental testing conditions requires much consideration. Once a good system has been selected, there are various approaches to studying reaction norms. Among the most promising approaches are: (1) split-brood

experiments, in which siblings are studied under different conditions; (2) repeated measures which sequentially test individual birds under different conditions; (3) possibly also cross-fostering experiments of birds in the wild; and (4) comparisons of sibling-resemblance in wild populations under different natural and experimental conditions.

Outlook: extending the simple passerine model of the genetics of migration

The majority of research reviewed above pertains to the study of individual traits in passerine birds, mostly under controlled captivity conditions. However, avian migration is a complex subject as it occurs over a long time-span and, in different environments, it involves various behaviours, and relates to the particular life-style of a species. In the following, we discuss three topics that are normally not included in genetic studies, but that could potentially make important contributions in future research.

Optimality models

The successful migration of a bird must involve the integration of many traits and environmental information. Clues to the manner in which different traits interact, and which constraints and processes may shape migration, can be derived from optimality modelling (Alerstam and Lindström 1990; Holmgren and Hedenström 1995; Houston and McNamara 1999; Kokko 1999). Although nearly all models so far are concerned with the average individual of a species, these models can also be used to explain variation among individuals, either as a consequence of other traits or as a consequence of varying conditions.

The optimality approach aims at defining the optimal landscape for a suite of traits that together make up the migration syndrome. To this end, it assumes a “currency” for calculating the relative “pay-off” of different migration strategies (Alerstam and Lindström 1990; Houston 1998). Various optimality approaches focus on different questions, ranging from evolution of migration to adaptations for the migration process (Alerstam and Lindström 1990; Alerstam et al. 2003; Houston 1998; Weber et al. 1998; Weber 1999). They simply assume that there is ample genetic variation and time so that an optimum will be approached. However, they also point out the likely selection pressures and therefore suggest relevant traits to investigate. When we find a population with a trait value deviating far from an optimum, there are at least three alternative interpretations: (1) there is strong directional selection, (2) there is a constraint that has been overlooked, or (3) the currency does not apply to this system.

In the context of migration, possible currencies are time, energy and predator minimisation, or a combination of them (Alerstam and Lindström 1990; Houston

1998). By way of example, a time minimising migrant is supposed to maximise U_{migr} , the speed of migration, which integrates flying and fuelling episodes:

$$U_{\text{migr}} = \frac{UP_{\text{dep}}}{P_{\text{dep}} + P_{\text{flight}}} \quad (1)$$

where U is the flight speed, P_{dep} is the energy deposition rate, and P_{flight} is the power required to fly (Hedenström 2003; Jenni and Schaub 2003). U_{migr} increases with fuel deposition rate, a trait which can be subdivided into a further suite of traits: food intake rate, field metabolic rate, search settling time, search settling energy loss, risk proneness with respect to food, physiological adjustment prior to fuelling, and dominance and other behavioural characteristics, including personality traits. Among these factors, we might expect to find genetic variation. Fuel deposition rate also affects departure loads. If there is individual variation in fuel deposition rates we therefore expect variation in optimal departure loads and timing. This variation is calculated by optimality modelling and represents the strategic response of a bird to environmental and physiological variation.

Equation 1 also indicates that migration speed is maximised if the power required to fly is minimised, something that can be understood from flight mechanical theory (Hedenström 2002, 2003). Morphological traits associated with the “migratory syndrome” contribute to power reduction. For instance, the induced power, a component of the total power required to fly, is minimised by a long wing span. The induced power also decreases with body mass, and so the bird should fly with the smallest possible fuel deposits. Hence, in migrants there should be selection for long wings and low body mass.

Optimality models have great potential for integrating behavioural effects over time, for instance throughout the annual cycle. In annual routine models, the optimum scheduling and effort of birds are derived by using dynamic optimisation models (Holmgren and Hedenström 1995; Houston and McNamara 1999). Sequential behavioural decisions, typically on a weekly basis, are calculated to suggest the optimal strategy. These models derive the timing of migration, moult and breeding (timing and effort) from a variety of factors entered into the model. In this approach, there should be ample possibilities for connecting the optimality approach with quantitative-genetics data, for example, from common-garden cage breeding experiments (Roff 1994; Gwinner and Helm 2003).

The importance of cultural transmission

A classical view of bird migration distinguishes between two modes by which birds perform their seasonal movements (e.g. Sutherland 1998; Berthold 2001). In the passerine model, birds primarily navigate unaided by conspecifics, using a suite of cues such as the Earth’s

magnetic field, sun, moon and stars, as well as visible marks in the landscape. In the goose model, the way to the final destination is culturally transmitted from parents to offspring, typically in species with extended parental care, or socially mediated in flocks. The two models have different implications for modes of inheritance. In the passerine model, timing and possibly the course of migration are predominately regulated by endogenous, circannual programs, at least in inexperienced birds (Gwinner 1996; Berthold 2001; Mouritsen 2003). In contrast, the characteristic mass departures and arrivals of flock-living species are predominately socially mediated and hence represent “sociable schedules” (Helm et al. 2006). They result from tracking the behaviour of family or flock members, or from other forms of information exchange (e.g. Danchin et al. 2004; Simons 2004; Couzin et al. 2005).

To treat these models as two separate entities would be naïve. Given the potentially high costs that are associated with navigational errors or a mistimed journey, it is likely that passerines also use a variety of social cues that would enable fine-tuning of their migration. Passerines exhibit a spectrum of social behaviours during migration which ranges from heterospecific attraction or competition to flock-formation (e.g. Rappole and Warner 1976; Forsman et al. 2002; Helm et al. 2006). Likewise, there is evidence that birds associated with the cultural model do possess endogenous programs (e.g. Rees 1987, 1988; Chernetsov et al. 2004). These programs could serve as a back-up strategy for separated individuals and are perhaps overridden by social factors or may have decreased in importance through evolutionary time.

Nevertheless, the relative importance of both models in different species makes it likely that they have been under quite different selection pressures. In species that rely to a large extent on endogenous programs it is likely that selection has acted mainly on these programs or closely related traits. The programs thereby may have been optimised to some degree in the course of evolution. In the goose model, selection acts primarily on socially transmitted behavioural traditions, and the spread of new traditions is potentially fast because of cultural in addition to genetic transmission (Sutherland 1998; Danchin et al. 2004). This does not imply that species associated with the goose model generally respond faster to environmental change. Given that there is strong selection and sufficient additive genetic variation underlying the migratory syndrome, fast evolutionary changes might be expected and have indeed been observed (Berthold et al. 1992; Sutherland 1998; Fiedler 2003; Pulido and Berthold 2003, 2004; Pérez-Tris et al. 2004). The spread of innovative migration patterns in sociable migrants depends on the involved social behaviours. If behavioural traditions result from simple social facilitation or naïve copying, cultural variation might be considerably less than the genetic variation underlying the passerine model. In contrast, if birds learn by experience or by assessing the performance of

conspecifics, favourable adjustments could occur fast (Danchin et al. 2004). There is ample evidence for culturally inherited behaviours leading to maladaptive behaviour, or so-called ecological traps (Kokko and Sutherland 2001), as well as for fast successful adjustments (Sutherland 1998; Danchin et al. 2004).

The impact of social effects on sociable migrants calls for an extension of genetic models of avian migration, but does not render them unimportant. Selection acts on multiple traits, including those responsible for maintaining social systems and for enabling communication in sociable migrants (Adriaensen and Dhondt 1990; Sutherland 1998; Helm et al. 2006). We still know almost nothing about the relative importance of genes, the social environment, and their interaction for avian migration. One definite step forwards towards disentangling the roles of genes and culture on migration routes and timing is the use of cross-fostering experiments. However, such experiments have only rarely been conducted in waterfowl or other long-lived species with extended parental care (but see Välikangas 1933; Schüz 1950; Harris 1969). One way of getting around this problem is to use the widespread occurrence of adoption and intraspecific brood parasitism, for instance in geese (Forslund and Larsson 1995) as natural experiments. Our understanding of socially migrating species can expect major impulses from fast technological developments (Helm et al. 2006). With new analytical tools, for instance those enabling the identification of family members and those improving animal tracking, the genetic ecology of sociable migrants can soon be explored.

Bird personalities

There is rapidly growing evidence that aspects of behaviour such as, e.g., exploring, aggression and learning are interrelated in a very similar way in all vertebrates and non-vertebrates studied (Grootuis and Carere 2005; Sih et al. 2004). In the great tit, extended studies have shown that characters such as fast but superficial exploration, quick formation of behavioural routines, high aggressiveness, quick copying of behaviour of other individuals and long recovery times after a social defeat go together, forming a syndrome which is often referred to as personality. Artificial selection for personality in the great tit has demonstrated a rather high heritability (Drent et al. 2003; van Oers et al. 2004), strong differences in survival interacting with population density and differences in dispersal (Dingemanse et al. 2003). At present, the physiological basis for the coupling of these traits is still unknown. Differences in personality are most clearly visible under conditions of mild stress, and initial pilot studies are showing that similar patterns may be present also in migratory bird species.

There are three general reasons why we should take into account variation in personalities in migration research. Whenever we place birds in standardised

experimental conditions, whether it is a respiration chamber, a cage to measure migratory restlessness or an orientation funnel, part of the consistent variation among individuals may be due to differences between personalities that are also described as pro-active and re-active strategies to cope with stress (Koolhaas et al. 1999; Marchetti and Baldaccini 2003). Thus, personalities may interfere with the possibilities for measuring certain traits under standardised test conditions. It is quite likely that by discarding individuals that do not fly well in a wind-tunnel or that do not orient well in an Emlen-funnel, we systematically under-represent individuals on one end of the personality score axis (Marchetti and Baldaccini 2003). A second issue is that, in nature, personalities also greatly affect social interactions and learning. It is quite likely that these traits have a substantial effect on social and competitive interactions which are known to influence migration (Rappole and Warner 1976; Adriaensen and Dhondt 1990; Helm et al. 2006). In this sense, personality traits are likely to be important parameters in the broad-sense migratory syndrome. Thirdly, first evidence suggests frequency dependent fitness of personality traits. This implies that through selection on personality variation among individuals is maintained (Wilson 1988; Sih et al. 2004).

Conclusion

In the end our abstraction of organisms into separate traits has to be back-translated to whole organisms. What we can observe are phenotypes and variances in trait values. This variance can be split into components due to known variation in environmental conditions, error variation due to uncontrolled or unknown environmental variation, genetic variation in the average phenotype, and genotype–environment interaction, i.e. differences in reaction norms among genotypes. The extent to which results obtained for one trait in one species can be extrapolated and generalised depends very much on how well we understand the underlying biology. In the end, it is whole organisms that survive and reproduce.

Zusammenfassung

Ein Rahmen für die Untersuchung der genetischen Variation des Zugverhaltens

Evolutionärer Wandel ist das Resultat von Selektion auf der Grundlage genetischer Variation. Für einen erfolgreichen Zug müssen viele verschiedene Aspekte der Physiologie und des Verhaltens eines Tieres zusammen koordiniert ablaufen. Änderungen in einem Zugmerkmal werden daher wahrscheinlich von Änderungen in anderen Merkmalen begleitet. Wir haben zum Teil Kenntnis über die Selektionsfaktoren, die auf die

unterschiedlichen Phasen des Zuges wirken, doch wissen wir derzeit nur sehr wenig über das Ausmaß der zugrunde liegenden genetischen Variation. Daher ist es schwer vorherzusagen, welche Vogelarten, wie schnell zu welchen Verhaltensänderungen in der Lage sind. In dem vorliegenden Beitrag erörtern wir, wie sich unser evolutionäres Verständnis vom Zug durch quantitativ genetische Untersuchungen verbessern ließe und stellen Ansätze vor, um die Ursachen phänotypischer Variation zu untersuchen. Wir geben eine Übersicht über die bisherige Forschung, die sich vorwiegend mit einzelnen Zugmerkmalen bei gekäfigten Vögeln befasst hat, und diskutieren, wie dieser Forschungsansatz erweitert werden könnte, um genetische Variation im Freiland sowie genetische Korrelationen und korrelierte Selektionsantworten zu untersuchen. Die Erforschung von Reaktionsnormen könnte dabei künftig sehr wichtig werden, da dieser Ansatz gleichzeitig die Untersuchung genetischer und umweltbedingter Ursachen und deren Interaktion ermöglicht. Wiederholte Messungen an Individuen sind oft einfacher zu gewinnen als Daten von verwandten Individuen und können eine wertvolle Hilfe bei der Auswahl der geeigneten Merkmale sein. Dieser Ansatz ist besonders informativ, wenn Individuen systematisch unter unterschiedlichen Umweltbedingungen getestet werden. Wir regen an, den Forschungsplan durch Optimalitätsmodelle zu erweitern, um das Ausmaß der genetischen Variation und der Co-Variation zwischen Merkmalen und evolutionären Zwängen vorauszusagen. Dieses könnte helfen, Merkmale zu ermitteln, in denen genetische Veränderung zu erwarten ist, und die informativsten Umweltachsen zu identifizieren. Wir empfehlen auch eine Erweiterung des Singvogelmodells, da dieses Modell nicht auf Vögel, wie Gänse, zutrifft, in denen kulturelle Tradierung der räumlich-zeitlichen Information ein wichtiger bestimmender Faktor von Zugmustern und ihrer Variation ist.

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