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Flyway evolution is too fast to be explained by the Modern Synthesis: proposals for an 'extended' evolutionary research agenda

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Abstract In this paper I argue that to fully grasp the generation and maintenance of variation in the migratory phenotypes of (shore-)birds we need to expand our scientific search-image and include developmental processes and non-genetic pathways of inheritance in the explanatory frameworks. Traditionally, studies of micro-evolution of migratory phenotypes were restricted to comparative studies on migratory versus non-migratory taxa, and artificial selection and heritability experiments on quantitative behavioural traits related to migration. Such studies had a focus on the genetic axis of inheritance and were restricted to songbirds. In avian groups such as the shorebird families Scolopacidae and Charadriidae all but a few island species are migrants, which precludes comparative studies at the species level. Just as other taxa, shorebirds have geographically separate breeding populations (either or not recognized as subspecies on the basis of morphological differences) which differentiate with respect to the length, general direction and timing of migration, including the use of fuelling at staging sites and the timing of moult. However, their breeding systems preclude artificial selection and heritability experiments on quantitative traits. This would seem to limit the prospects of evolutionary analysis until one realizes that the speed of evolutionary innovation in shorebird migratory life-histories may be so fast as to necessitate other avenues of explanation and investigation. According to our best current estimates based on mitochondrial gene sequence variation, in red knots *Calidris canutus* considerable phenotypic variation has evolved since the Last Glacial Maximum ca. 20,000 years ago, to the extent that six subspecies are currently recognized. This would be too short a time for the origin of the qualitatively and quantitatively distinct and non-overlapping traits to be explained by

random point mutations followed by natural selection, although we cannot dismiss the possibility of previously unexpressed (standing) genetic variation followed by selection. I argue that to understand the flyway evolution of such shorebirds in the ‘extended’ evolutionary framework, we need to give due attention to developmental versatility and broad-sense epigenetic evolutionary mechanisms. This means that experimental studies at the phenotypic level are now necessary. This could involve a combination of observational studies in our rapidly changing world, common garden experiments, and even experiments involving global scale displacements of particular migratory phenotypes at different phases of development. I provide suggestions on how such experiments could be carried out.

Keywords *Calidris canutus* · Common garden experiment · Epigenetics · Evolution · Extended synthesis · Last Glacial Maximum · Migration · Red Knot · Shorebirds

Introduction

Most of what has been written about the evolution of bird migration (Alerstam et al. 2003) had a strong focus on the (micro-)evolution of migration traits in songbirds (e.g. Berthold and Querner 1981; Berthold 1995; Able and Belthoff 1998) and comparative studies between migrant and non-migrant taxa (e.g. Zink 2002, Helbig 2003; Outlaw et al 2003; Rappole et al. 2003; Salewski and Bruderer 2007). The portfolio included studies of artificial selection and heritability experiments on quantitative behavioural traits related to migration such as the duration and timing of migratory restlessness (e.g. van Noordwijk et al. 2006; Pulido 2007; Pulido and Berthold 2010). As impressive and as valuable all these studies are, I have found myself frustrated to apply the supposedly unifying but passerine-biased frameworks to the thinking about flyway evolution in the group of birds that I am most familiar with, the shorebirds, and especially the family of sandpipers Scolopacidae (Piersma et al. 1996) and the plover family Charadriidae (Piersma & Wiersma 1996).

Here is why. All but a few (island) species of shorebirds are migrants which precludes comparative studies on closely-related migratory and non-migratory species. As other taxa, shorebirds do have geographically separate breeding populations (either or not recognized as subspecies on the basis of morphological differences; Engelmoer and Roselaar 1998) which differentiate with respect to the length, general direction and timing of migration, including the use of fuelling at staging sites and the timing of moult. However, the peculiarities of their breeding systems preclude studies of inheritance of quantitative traits such as migratory restlessness. Importantly, the traits on the basis of which subspecies are distinguished are distinct and do not overlap, i.e. they seem to show evolutionary *novelty* rather than the gradual variation that natural selection can work on (van Noordwijk et al. 2006).

All of these impossibilities may actually turn out to be a blessing in disguise as it forces us to think about evolutionary mechanisms of flyway evolution other than those involving genes and the genetic inheritance pathway only. This is especially relevant as in shorebirds extant trait variation seem to have evolved over very short time spells relative to the evolutionary timescales necessary for new point mutations and subsequent natural selection to live out their creativity (Barrett and Schluter 2008). For example, studies of neutral markers in the mitochondrial genome of Red Knots *Calidris canutus* have indicated that the outspoken global flyway pattern that we observe today (Fig. 1) may be of recent, post-Pleistocene, origin (Buehler and Baker 2005; Buehler *et al*. 2006). The discontinuous

circumpolar breeding range of red knots incorporates breeding areas of at least six populations that are morphologically sufficiently distinct to count as subspecies (Tomkovich 1992, 2001), but which appear to have diversified recently from a small founder population that survived the Last Glacial Maximum at approximately 20,000 years ago. The subspecies are certainly distinct when it comes to their migratory trajectories and the seasonal timing of their movements (Piersma et al. 2005; Buehler & Piersma 2008; Piersma 2007). For the classic evolutionary mechanisms of random point mutations and gene selection mechanisms to explain the divergence of qualitatively and quantitatively distinct and non-overlapping traits, populations and time since divergence simply have been too small (Haldane 1957; Nunney 2003).

In this brief contribution I aim to propose that to understand the flyway evolution of such shorebirds we need an 'extended' evolutionary framework with a mindset that is prepared to consider the many creative possibilities of individual development (Turner 2007; Badyaev 2011a,b) and broad-sense epigenetic evolutionary mechanisms (Jablonka and Lamb 2006). In addition to further genomic work to establish timelines of divergence in different clades of long-distance migrants, I will argue that we need intensive observational studies in our rapidly changing world and experimental studies at the phenotypic level.

Microevolution of contrasting seasonally changing phenotypes

Red Knots and other long-distance migrating shorebirds show amazing seasonal variation in phenotype. For example, body mass is doubled before take-off on flights of 5,000 km or more, and halved during the continuous flight which may take up to 10 days (Battley et al. 2000; Gill et al. 2009). These changes involve great modifications in fat stores, but also include modifications to most organs (other than the kidneys, the lungs and the brain; Piersma et al. 1999; Battley and Piersma 2004; Piersma and van Gils 2011). On top of all these seasonal variations, shorebirds also adjust phenotypes to unpredictable environmental changes in food type, climatic conditions and disease pressure (Vézina et al. 2007, 2010; Buehler et al. 2008a,b).

If some of today's flyways indeed were established within the past 1000 years (as in the split between the Red Knot subspecies *rufa* and *islandica*; Buehler et al. 2006), then it follows that it is possible for very drastic changes in phenotype (body size, plumage characters, annual cycle characteristics) to occur within 100 generations (Fig. 2). The

subspecies *rufa* and *islandica* are both relatively large-bodied (Tomkovich 1992), but despite its name, *rufa* is the palest subspecies, whereas *islandica* is among the darkest (Buehler and Piersma 2008). *Rufa* has the longest seasonal migration, commuting between the sub-Antarctic during the nonbreeding season and the Canadian High Arctic during the breeding season (see Fig. 1), whereas the *islandica* which breeds nearby has the shortest migration of all the subspecies. The two subspecies differ with respect to departure directions, the timing of fuelling, flight and moult episodes, seasonal disease pressures (Buehler et al. 2009b) and diet — especially during northward migration (Piersma et al. 2005).

Interestingly, and arguing for a hard-wired programming of annual cycles, the seasonal phenotypic changes shown outdoors are maintained by Red Knots and Great Knots *Calidris tenuirostris* kept in photoperiodic- and temperature-constant indoor environments (Piersma 2002; Reneerkens et al. 2007; Piersma et al. 2008). When adult birds of the contrasting subspecies *islandica* and *rufa* are brought into similar conditions in captivity, they show very distinct annual cycles (Fig. 3). Birds of the *islandica* subspecies typically show a single mass peak in spring and carry their alternate plumage relatively briefly (see also Piersma 2002; Reneerkens et al. 2007), whereas *rufa* knots in captivity show two mass peaks and carry the alternate plumage much longer. If the divergence of the flyways of *rufa* and *islandica* knots really represent historic rather than prehistoric phenomena, this raises the compelling question as to how shorebirds could adjust migration-related traits so quickly.

Beyond hard-coding: soft coding and the extended synthesis

Over the last 100 years biology has strongly focused on the two-stage evolutionary process of mutational changes to the genome with downstream consequences for the phenotype on which natural selection operates. This is a relatively slow process, and the finding that rapid phenotypic change commonly occurs in a wide variety of organisms, has lead to explanations invoking selection for previously unexpressed (hidden or ‘standing’) genetic variation (Barrett and Schluter 2008; Le Rouzic and Carlborg 2008). Whilst I cannot dismiss this possibility, I also like to be open to explanations that go beyond the hard-coding of phenotypic traits.

Increasingly, evolutionary biologists appreciate that inheritance pathways other than the transmission of genes play a role in evolution (Jablonka and Lamb 2006; Pigliucci and

Müller 2010). Interestingly, these ‘soft-coded’ inheritance pathways (Fig. 4) would imply considerable interaction and even trans-generational feedbacks between the environment and the phenotype, and this could speed up the ways in which organisms adapt to rapid environmental change (West-Eberhard 2003; Jablonka and Lamb 2006; Turner 2007; Laland et al. 2008; Piersma and van Gils 2011).

The revolution in molecular biology has spawned an enormous research effort to refine the molecular basis of evolutionary change (Bromham 2008). Yet, despite the availability of a wealth of advanced quantitative and molecular genetic techniques and innovative statistical tools (Ellegren and Sheldon 2008; Rice et al. 2011), an understanding of the ways in which genetic change underpin phenotypic change (i.e. the translation from genotype to phenotype) is a long way off (Sheldon 2010). The gene-up approach to the microevolution of bird migration is now yielding the first successes (e.g. Karell et al. 2011; Mueller et al. 2011), but is still far removed from understanding the evolution and maintenance of trait variation. Apart from notable exceptions to do with rare diseases, the detection of DNA variations that explain the phenotype has been frustratingly complex (Dowell et al. 2010). One of the reasons is that non-genetic factors play such an important role in the expression of genotypes (Jablonka and Lamb 2006; Turner 2007). Biology could be enriched by the acknowledgement that non-genetic factors such as developmental processes (expressed as phenotypic plasticity) and learning can affect the generation and maintenance of variation and rapid change of phenotypes (Fig. 5). The explanatory Darwinian ingredients of the Modern Synthesis (Mayr 1963, 1982) no longer suffice (Both 2010; Pigliucci and Müller 2010).

There are various ‘soft-coded’ ways in which the actual translation into phenotypes of the genetic code in DNA may be blocked or facilitated (Fig. 4). In the cellular epigenetic scenario, the presence or absence of methyl, acetyl or phosphate groups to the DNA or histones can transiently or permanently modify gene expression by altering the local chromatin structure (Johannes et al. 2008; Law and Jacobsen 2009). These cellular epigenetic changes can be induced by environmental and/or genetic factors, and can remain relatively stable over several generations (Teixeira et al. 2009; Reinders et al. 2009). Phenotype can also be changed by mechanisms other than (epi)genome variation (Fig. 4). For example, the physiology of a bird embryo can also be affected by variable levels of maternal hormones, immune factors, etc.; *developmental* inheritance). Also, young birds can learn the migration route from more experienced birds (*behavioural* inheritance).

Research opportunities in the anthropocene

We live in the Anthropocene (Steffen et al. 2007, Kolbert 2011), an era of loss and of opportunity. Our time is one of strong declines in biodiversity (Pereira et al. 2010), yet it is also a time when we can learn from the rapid ongoing changes if we care to look. 'Looking carefully' at global scales is now made possible by the close connections (through internet and cheap airfares) of focussed observers worldwide (e.g. Rahkimberdiev et al. 2011), the availability of capture-recapture datasets spanning several generations of birds (van der Jeugd et al. , and by the possibility to examine survival and dispersal using an amazing array of remote sensing and tracking tools (Robinson et al. 2010). Even for small organisms that travel the world such as Red Knots, the tools are now available to track their survival and movements across the globe with considerable spatial and temporal precision.

Building on the ongoing demographic studies assembled within a worldwide collaborative research network with a particular emphasis on individually colour-ringing Red Knots and other shorebirds and resighting them (*Global Flyway Network*, see Piersma 2007), comparative analyses can be done of dispersal and survival based on sample sizes of several thousands individually marked Red Knots and multiple resightings of many of these individuals (e.g. Baker et al. 2004; Leyrer et al. 2011). Recent advances in multistate modeling (Lebreton et al. 2009) should enable the estimation of variation in survival rates over several generations within and between flyways and also obtain estimates of dispersal rates. In the case of the best studied Red Knot subspecies *rufa*, *islandica* and *canutus*, this would yield estimates of vital rates and dispersal during periods of habitat decline and restoration (Baker et al. 2004; Kraan et al. 2009) and thus enable us to examine the demographic drivers of micro-evolution.

Phenotypic experimentation

Recent observations suggests that individual Red Knots (*rufa* as well as *islandica*) may sometimes switch flyways. This indicates that individual flexibility of flyway use is higher than what we have assumed so far. An adult Red Knot marked in northern Norway (presumably *islandica*) was resighted a year later in the Mingan Archipelago, in the Gulf of St. Lawrence, Canada. Another bird marked at Mingan (presumably *rufa*) had moved to Iceland two years after marking (Wilson et al. 2010). Given the highly sociable behaviour

of this species, individuals may be tuned by the behaviour of group members (Helm et al. 2006), enabling them to successfully switch between flyways.

I suggest that we could find out about the degrees of flexibility, and the epigenetic mechanisms involved (Fig. 4), by carrying out two types of phenotypic experiments: (1) bring birds together in common environments (common garden experiments) and (2) displacing birds to new conditions (translocation experiments). Building on preliminary results reported in Fig. 3, bringing birds from different flyways under identical environmental conditions would allow us to examine the degree that the seasonally changing phenotypes are (in-)flexible for genetic and non-genetic reasons, or whether the birds can adjust to alternative photoperiodic regimes. If the degree of adjustment is age-dependent, this would additionaly tell us if social learning is involved.

The common garden experiments should be complemented by experiments 'in the wild'. In the 1950s and 1960s Perdeck and collaborators translocated 15,000 Starlings *Sturnus vulgaris* and 1250 Chaffinches *Fringilla coelebs* from The Netherlands to Switzerland and 3500 Starlings to Spain in what is now one of the most classic series of experiments in the study of bird migration (Perdeck 1958, 1967, 1974). We could fit birds with small solar-energized satellite tags and reciprocally translocate them between flyways. To show the scope for testing explicit evolutionary/developmental hypotheses of such phenotypic experimentation, I have worked out a case where young and old *rufa* and *islandica* knots are reciprocally displaced between the staging areas on southward migration (Table 1). We can use the contrast between juveniles and adults to see whether having experienced one or more full migration cycles affects the capacity to adjust flexibly to a new situation and fly with the 'receiving' flocks at the new location, or whether the routines have become fixed with respect to phenotypic change and migration.

Thus, by including young and older birds in the experiment, we can address the role of age-dependent behavioural inheritance, i.e. learning, on the expectation that in their first year, learning phenotypes would still be able to adjust phenotypically to new regimes, whereas older birds might not (Sutherland 1998). Fully flexible individuals will move with their new flocks, and even adjust the timing of fuelling and moult. If this would occur we have to explain an interesting contrast with the results from the preliminary aviary experiments (Fig. 3). Such flexibility would be at variance with the idea that the divergent traits have a rigid genetic background and would emphasize the creative force of two-way interactions between organisms and their environment (Laland et al. 2008).

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[Figures:]

Fig. 1 The worldwide flyways of six morphologically distinct subspecies of Red Knot. Polygons in the Arctic depict breeding ranges; circles depict principal wintering areas with the diameters of circles indicating relative numbers of birds. Arrows depict north- and southward migration routes and use of *en route* sites. Projected above the contemporary distribution of red knots is a 'tree' summarizing the phylo-geographic structure as presently understood (Buehler and Baker 2005). Note that the subspecies *rufa* and *islandica* are impossible to tell apart on the basis of neutral genetic markers yet show very different migratory pathways. Also note that whereas most subspecies have distinct wintering areas, the closely related *piersmai* (mainly tropical northwest Australia) and *rogersi* (mainly New Zealand) show some degree of overlap that may hint at ongoing microevolutionary change.

Fig. 2 Contrasts in the migration and annual cycle characteristics of the two most closely related subspecies of Red Knots (*rufa* and *islandica*), with a suggestion of seven traits that would have to evolve considerable quantitative and qualitative novelty in the presumed descendent subpecies *islandica* within a short spell of time (Buehler et al. 2006). The bars show the typical (average) timing of birds carrying a basic plumage (grey) or the alternate plumage (rusty) and the timing of moult from one plumage type into the other (light rusty). Also indicated are the timings of northward (upward pointing triangles) and southward (downward pointing triangles) flights, generally three each in *rufa* and two each in *islandica*.

Fig. 3. Contrasts in the annual cycle of the most closely related subspecies of Red Knot, *rufa* and *islandica*, as reflected in two flexible and seasonally cyclic traits, body mass and the extent of alternate plumage. Two birds from each subspecies are given. These adult birds lived in small flocks in outdoor aviaries at NIOZ on Texel, The Netherlands, experiencing the local temperature and light regimes.

Fig. 4 In addition to the genetic variation transmitted from generation to generation through the germline, there are four additional 'epigenetic' inheritance pathways. The first of those, 'cellular epigenetic inheritance', transmits acquired information via the gametes. The remaining three are all 'somatic' and include 'developmental inheritance' (e.g. through maternal effects), 'behavioural inheritance' (through niche construction), and

‘symbolic inheritance’. One of the reasons that it took biologists so long to distinguish these layers is that they are thoroughly intertwined. There is also ‘reciprocal causation’, especially between niche and body. Note that ‘symbolic inheritance’ is specific to organisms that read books, watch TV and write grant applications. Of the five possible inheritance pathways of information transfer between generations, two (developmental inheritance and behavioural inheritance) would be especially relevant for the fast evolutionary change of flyways and annual schedules. Developed from Jablonka and Lamb (2005, 2007) and adapted after Piersma & van Gils (2011).

Fig. 5 Schematic representation of the key concepts of Darwinism (centre), the Modern Synthesis (intermediate field) and a more extended synthesis of evolutionary explanations (outer ring) of life forms on earth. This scheme, modified after Pigliucci & Müller (2010), aims to show the near-continuous expansion of evolutionary theory with new and increasingly non-genetic concepts for mechanisms of change. I propose that an understanding of the evolutionary mechanisms of rapid flyway evolution would require research efforts on *phenotypic plasticity* and *learning*.

[Tables:]

Table 1 Predictions to what will happen to birds translocated across the Atlantic from either the *islandica* or *rufa* subspecies of Red Knot, depending on how migration and annual routines are flexibly orchestrated, and whether learning from older birds takes place during early life. For the predictions for 'fixed circannual programmes' we listed the scenario where red knots after displacement know latitude, but not longitude (possibility-1), or know precisely where they are with respect to where they come from (possibility-2).

	islandica moved to Canada		*rufa* moved to Wadden Sea	
	as juvenile	as adult	as juvenile	as adult
Fixed circannual programme-1	Stay in the north (as in Europe)	Stay in the north (as in Europe)	Fly south with *canutus*	Fly south with *canutus*
Fixed circannual programme-2	Return to Europe	Return to Europe	Return to the Americas	Returns to the Americas
Flexible during early ontogeny	Migrate to S. America	Stay north or return to Europe	Stay in Europe or fly south with *canutus*	Fly south with *canutus* or return to America
Fully flexible	Migrate to S. America	Migrate to S. America	Stay in Europe or fly south with *canutus*	Stay in Europe or fly south with *canutus*