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On the behaviour and ecology of the Black-tailed Godwit

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General discussion

Mo A. Verhoeven, A.H. Jelle Loonstra

We believe this dissertation is special and exciting in multiple ways. We were in the unique position of being able to perform a number of descriptive, comparative and experimental studies on one of the most iconic meadow birds: the Black-tailed Godwit (hereafter “godwit”). These studies changed our understanding of the godwit as a parent, chick, fledgling, and especially as a long-distance migrant. And so did the variation in migration we observed among Dutch godwits, Polish godwits and other migratory bird species. All of these observations form the basis for exciting (new) hypotheses and predictions about the causes and consequences of the observed variation, which are set forth in chapters of this dissertation.

Also notable is that although science, academic life and most of the world is becoming more individualistic, this dissertation is the product of a truly enjoyable and fruitful collaboration between two authors who have worked together to get a better understand of avian migration. We argue (based on a sample size of one) that working individually, we would never have been able to gain the depth and breadth of knowledge that we attained together. Two pairs of hands not only perform more practical work than a single pair, but they complement and motivate each other in such a way that they create a virtual third pair of hands. As the owners of these hands, and the people who have benefited most directly from this collaboration, we therefore want to stress the importance of true scientific collaboration and discussion. We believe that only through such collaboration and discussion can scientists maximize their potential for producing new insights.

In this thesis we made progress to finding limits among adults, understanding these limits through ontogeny, and finally understanding ontogeny through an experiment. Despite these advancements in knowledge, our understanding of the causes or “sources” of

the observed variation in these behaviours is still incomplete. After five years of work and discussion, we could make a long list of hypotheses on the possible “sources” of the observed variation. However, we would rather test some of these hypothesis than list them. As the saying goes: “A hypothesis can be interesting, but that is not what a hypothesis is for”. Therefore, we present our thoughts on how to study these causes or “sources” by collaboratively answering hypotheses.

LESSONS LEARNED

By demonstrating that there is variation in the traits of individuals, populations and species, one shows that the environment is either permitting or favouring a range of phenotypic variation. We can have long circular discussions about whether the environment permits or favours a range of phenotypic variation:

“Why do we observe a range of behaviour? *Because that range is not selected against.*

Why is that range not selected against? *Because it has no costs.*

Why is there a range then? *Either because it has benefits or is not selected against.* So is it permitted or favoured? *Could be both.*”

The bottom line is that the environment both generates (i.e. developmental plasticity) and limits phenotypic variation (i.e. selection). We will therefore continue by saying that phenotypic variation is *conditional* on the current environment. Why is this important? For one, it means that when a consistent migratory behaviour is observed, it is conditional on the environment. Thus, different environments may also lead to differences in the migratory phenotype (Chernetsov *et al.* 2004, Meyburg *et al.* 2017). For example, the migratory route of hand-raised Dutch godwits is *conditional* on whether

they are released in The Netherlands or Poland (Chapter 15).

However, there is also evidence that the observed phenotypic variation is not only *conditional* on the current environment. For example, experiments have shown that certain genetically constructed traits such as photo-refractoriness also set limits to phenotypic variation (Gwinner 1996, Berthold 1996). Compelling empirical evidence for these limits comes from barn swallows (*Hirundo rustica*) which have shown the plasticity to breed both in the northern and the southern hemisphere (Winkler *et al.* 2017). However, despite this plasticity they appear to be limited to breeding only north of the tropic of Cancer and south of the tropic of Capricorn. Furthermore, the annual cycle events of barn swallows breeding in the northern and the southern hemisphere differ by exactly six months, i.e. they are mirror images (Winkler *et al.* 2017). Given our knowledge on the photoperiodic control in other birds, breeding only outside of the tropics and an exact shift of the annual cycle, may not be a coincidence, but in all likelihood the current limits set by photoperiodic control (Gwinner 1996, Berthold 1996). We will call these types of limits, which are likely a result of previous and current environments, the *organismal* limits to current phenotypic variation.

Because an observed migratory behaviour is the result of the current conditional and organismal limits, figuring out why a certain range of behaviours is observed in a particular context requires knowing both the conditional and organismal limits. In our example, we used a range of behaviours to illustrate that a current range of behaviours could have conditional and organismal causes. However, also when a behaviours change (in contrast to a fixed range), such as the earlier timing of migration later in life, that change could have conditional and organismal causes. Also, note the similarities between the idea of current phenotypic variation being organismal and conditional, to the ideas of (i) nature and nurture, (ii) genotype and phenotype and (iii) individual and environmental quality.

THE DAUNTING TASK AHEAD

We believe it is necessary to find and develop an ecological understanding of the extent to which migration (and indeed other) behaviours are conditional and organismal in order to understand the causes or “sources” of the variation currently observed. This might seem straightforward, were it not that the

observed variation is necessarily the result of repeated interactions between what is conditional and what is organismal. As such this is an incredibly complex and daunting task! At the same time, it is a fantastic journey without an end.

For now, we divide this complex study on the limits of observed or “current” phenotypic variation in migratory behaviour into four parts. (1) Seasonal migration is a ‘syndrome’ (an amalgam of many different traits, Piersma *et al.* 2005), and therefore we need to know which traits contribute to an individual’s observed migratory routine. We also need to (2) experimentally reveal the limits of these component traits, i.e. their full ‘reaction norms’. We furthermore need to know (3) how and when trade-offs among these component traits may limit the potential for phenotypic variation. The difficulty will be that even when we know the conditional and organismal limits, we do not know to what extent the observed trade-offs are conditional or organismal. Again, these reflect the more general challenges in identifying to what extent a behaviour or observation is the result of (i) nature and nurture, (ii) genotype and environment and (iii) individual and environmental quality. We therefore think we should (4) attempt transcriptomic and genomic approaches to understand the genetic basis that may underlie these component traits and the level of genetic diversity existing for these traits across populations (Merlin & Liedvogel 2019). If there is a genetic basis or “construct” for these traits, we could learn how their reaction norms work in terms of transcriptomics (our point 2, Horton *et al.* 2019). This might allow us to more fully understand to what extent the migratory behaviour we observe is organismal and conditional.

WHERE TO START?

It likely makes most sense to start with points (1) and (2) knowing which component traits (e.g. pre-migratory fattening rates, absolute potential fuel loads, etc.) contribute to an observed migratory routine and revealing the limits of these component traits. However, in the case of migratory behaviour, we are far removed from an understanding that approximates that of a well-studied subject like the timing of breeding. Consider the complex studies already performed to study the timing of breeding, such as (i) advance and delay, (ii) cross-fostering and (iii) endocrinological experiments (Verhulst & Nilsson 2008). Making headway like this for migratory behaviour is a daunting task in and of itself.

We think that one of the properties of migration that we must learn about first is, knowing when migratory routines are formed. As a result, we believe there is a need for life-long tracking studies, combined with studying the relevant circumstances that might contribute to observed differences that are present from birth and those that arise through life. This follows from our work in **Chapters 14 and 15**, which compares the range of variation in timing and routes between adult and juvenile godwits. Clearly, the observed spatiotemporal organization of migration among juveniles is different from adults. To eventually approach the

adult pattern, the tracked juveniles will have to change their migration beyond the two annual cycles we so far could study them (see discussion in **Chapter 14**). In fact, our preliminary analysis in Figure 16.1 shows that at least during the first two migration there is a change. Thus, the development of their migratory timing was still ongoing when we were obliged to round off our PhD projects. In the case of convergence we predict that individuals will advance the timing of their migrations the most between their first and second migration, which would be similar to black kites (*Milvus migrans*) (Sergio *et al.* 2014).

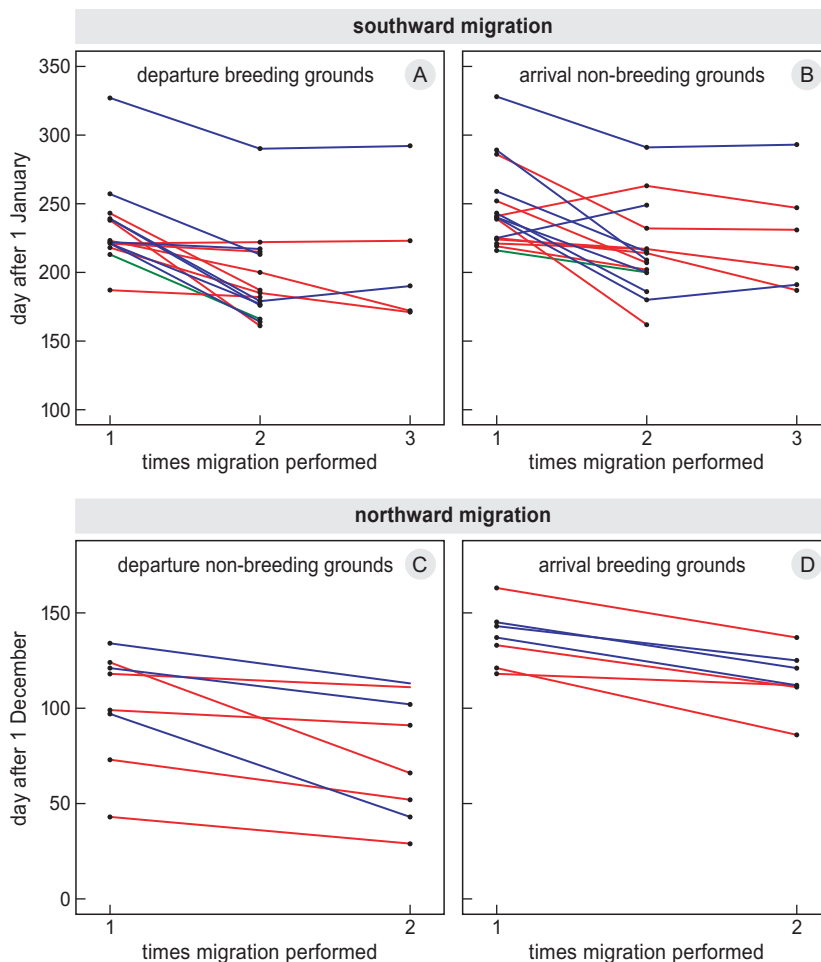


Figure 16.1. Individual change in the timing of migration between consecutive north- and southward migrations of young free-living or hand-raised godwits that were tracked from fledging in 2016 and 2017. The x-axis is the number of migrations performed, while the y-axis is the timing of events during these consecutive migrations: (A) departure from the breeding grounds during southward migration, (B) arrival at the non-breeding grounds during southward migration, (C) departure from the non-breeding grounds during northward migration and (D) arrival at the breeding grounds during northward migration. Each line corresponds to a single individual and separate colors refer to the different origin of juveniles: blue = hand-raised juveniles released in The Netherlands (see for all information: **Chapter 15**); green = hand-raised juvenile released in Poland (see for all information: **Chapter 15**); red = wild juveniles born in The Netherlands (see for all information: **Chapter 14**).

This will raise new questions: why do we observe these advancements, why this amount of difference in advancement between years of experience and, also why some individuals advance their timing at faster rates than others. And if this is the rate of advancement, how do we explain that some individual godwits cross the Sahara during northward migration as early as October, while others wait till March (**Chapter 2**)? In the case of timing of migration, we think these differences could be related to the success of that migration: was a northward migration successful in terms of arriving at the breeding grounds? Did it result in obtaining a partner? Laying a clutch? Hatching chicks? But many more relevant circumstances might exist.

A comparison of lifelong tracking among species will also be worthwhile – perhaps especially so among species that show different lengths of developmental plasticity. For instance, short-lived passerines are often hypothesized to be less plastic in developing migratory routines (Berthold *et al.* 1992, Cresswell 2014), partly because lab studies showed they possess innate programmes for these routines (Berthold 1996, Gwinner 1996, Pulido *et al.* 2001). Other species are known to exhibit more plasticity to develop a migratory routine, but adopt a consistent routine at some point in life (Lok *et al.* 2011, Gill *et al.* 2014, **Chapters 2, 11**). Lastly, some species are known to make adjustments to their migratory routines throughout life (Mueller *et al.* 2013, Sergio *et al.* 2014, Teitelbaum *et al.* 2016, Tombre *et al.* 2019). Comparisons among species with these apparent differences might show, for instance, whether the development of migratory routines is related to general life histories that are already better understood in comparison to migration, such as longevity and senescence. In that case, these better developed generalities might enable us to ask more accurate questions and thus perform better experiments to make inroads into what extent these differences among species are conditional or organismal.

FLYWAY ENGINEERING – IDENTIFYING POTENTIAL ORGANISMAL LIMITS

To disentangle which traits are contributing to the observed variation in routines and whether the current limits are likely conditional or organismal, we clearly need experiments that manipulate what is currently conditional. We did this in **Chapter 15** and showed that juvenile godwits are able to migrate in another environment after being translocated and/or delayed. These results also already revealed some limits as we

show that later-departing individuals were less likely to complete a migration successfully or cross the Sahara. As is becoming increasingly clear to us, this apparent limit could be both conditional (e.g. not enough food later in the season) and organismal (e.g. photoperiodic termination of migration). Nonetheless, the identification of such limits, now enables us to ask the necessary next questions. For instance, were unsuccessful migrations the result of an inadequate individual fuel-load upon departure from the post-fledging grounds? If so, the causes could still be conditional (e.g. lack of food) and organismal (e.g. photoperiodic termination of fueling) – in which case it is time for the next study!

Nevertheless, to find the current organismal limits, it probably makes most sense to work on traits and/or species that are presumed to be hard-wired, simply because it is more likely (but not necessary) to find an organismal limit. Furthermore, because everything we observe is likely to some degree conditional, it is difficult to find organismal limits within their current environments. An experimental approach whereby individuals are translocated to novel environments which we will call “flyway engineering” (see Piersma 2011 for a first proposal then called ‘phenotypic engineering’) is therefore required.

To illustrate the potential of flyway engineering as a future step, we propose a study on northern wheatears (*Oenanthe oenanthe*; hereafter “wheatear”). We find wheatears interesting because they have breeding populations at opposite ends of the North American Arctic, populations which nevertheless both spend the non-breeding period in sub-Saharan Africa, having arrived there by different migration routes (Figure 16.2). These routes differ in length and direction, but also in the number of geographic areas that require non-stop crossings (Bairlein *et al.* 2012; Figure 16.2). Perhaps as a consequence, wheatears from the eastern Canadian Arctic are heavier on the breeding grounds prior to migration than individuals from Alaska (Maginni & Bairlein *et al.* 2012, Bairlein *et al.* 2012). Interestingly, the observed migratory itineraries among wheatear populations are thought to be the result of breeding range expansion after the Pleistocene, and therefore thought to be under the control of a “well-developed innate migratory program” (Bairlein *et al.* 2012; Figure 16.2).

As might be expected, we would ask whether the variation in migratory routes among wheatear populations is conditional or organismal. To answer this question, we propose a set of experiments with wheatears (though such experiments could of course be applied to other systems as well). First of all, we propose per-

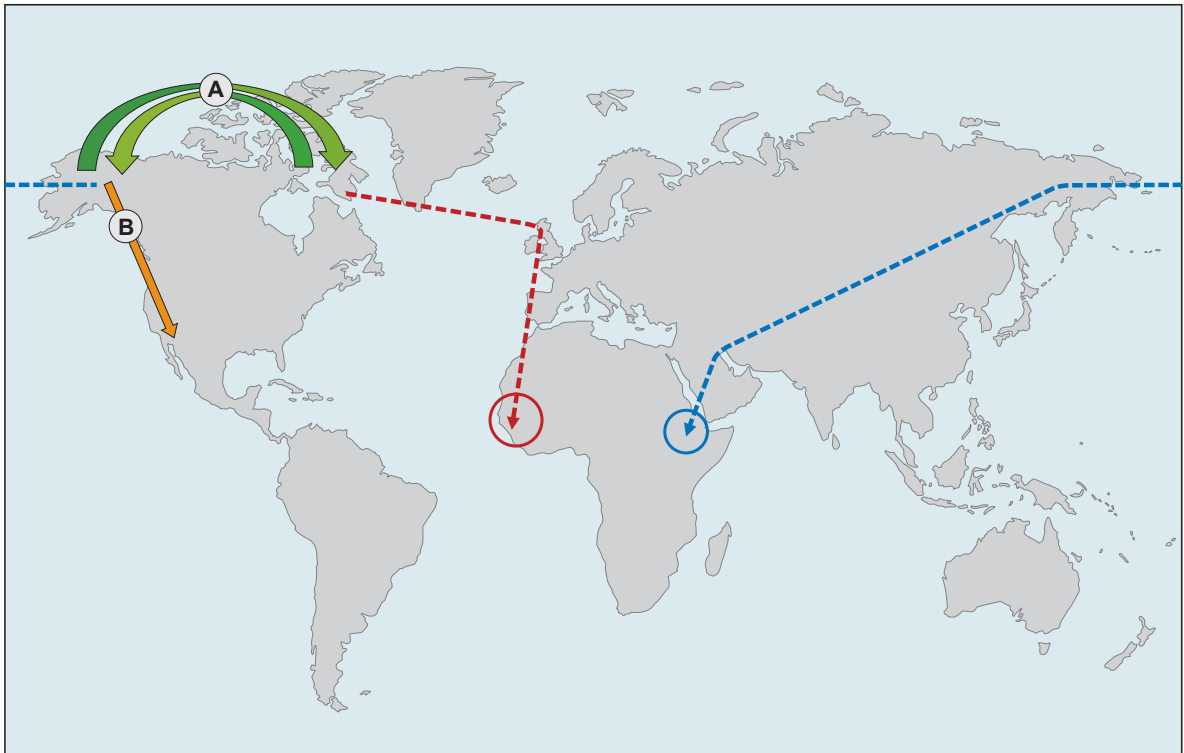


Figure 16.2. Migratory routes (blue dotted line) and wintering grounds (blue open circle) of northern wheatears breeding in Alaska and migratory routes of northern wheatears breeding in the eastern Canadian Arctic (red dotted line) and wintering grounds (red open circle); after Bairlein et al. (2012). (A) The green arrows illustrate proposed first egg-translocation experiment of northern wheatears between eastern Canadian Arctic and Alaska (and *vice versa*). (B) The orange arrow indicates the proposed follow-up experiment wherein northern wheatears are hand-raised in Alaska, then translocated from there to California (U.S.A.).

forming an egg-translocation experiment in which eggs are brought from the breeding grounds in the eastern Canadian Arctic to Alaska and *vice versa* (see: figure 16.2 for visualization). To follow these birds throughout their migratory journey after fledging, all juveniles should be tagged with satellite transmitters. We expect that if organismal limits are of negligible importance, birds will migrate along a migratory route similar to that taken by birds from the area of hatching. If the birds fail to successfully migrate after being translocated, however, we can conclude that there are currently limits of an organismal nature. To illustrate how such an experiment can further our knowledge, we will imagine the hypothetical scenario that juveniles from an Alaskan origin, but not those from a Canadian origin, will encounter problems during the crossing of the Atlantic after leaving Canada (Figure 16.2). Since such a crossing is novel to wheatears from Alaska (Figure 16.2) and given the known difference in weight between Alaskan and Canadian wheatears prior to migration; one could hypothesize that the Alaskan

juveniles did not bring enough fuel for crossing the Atlantic. In that case, we would propose to study the internal control of fueling behavior and the exact causes of death, to see whether these are related and whether or not we should start a study on the genetic regulation of migratory fattening (point 4 of proposed research).

In **Chapter 15** we showed that a migratory route to a certain degree is conditional, so here we will continue under the assumption that all translocated wheatears successfully migrate. In that case, in order to study to what degree their migration routes are conditional, we need an experiment that introduces wheatears to a novel environment (outside their current and historic range). We therefore propose collecting eggs at the Alaskan breeding grounds and subsequently hand-raising these birds in Alaska to ensure that they are imprinted on a breeding ground within their natural range (*sensu* **Chapter 15**). After hand-raising them in Alaska, we propose that these juveniles should be translocated to California, U.S.A. (see Figure 16.2 for

visualization). This is well outside their current and proposed historic range (Brunn 1980). Of course, we should be sensible about releasing them in an environment similar to their natural wintering grounds. As in the first experiment, all birds will be satellite-tagged so that we can have measurements of their movements throughout the year without an observer bias. Because of the imprinting on Alaska, we expect these birds to migrate to Alaska in the following years. However, this is only expected to happen if their routes can be conditional to this degree, i.e. the Californian wheatears do not face any organismal limits.

This experiment explores to what extent the current migratory route of wheatears is the result of conditional or organismal limits. Performing these experiments will ultimately suggest, and hopefully identify, the exact causes for any current organismal limits that are found.

At this point, we have spoken our message. Observed variation can be both conditional and organismal. We hope that it is clear that even our proposed experiments will not fully identify the extent of conditional or organismal effects. However, experiments like flyway engineering will allow researchers first to find current limits and then to ask questions about them! These experiments could even generate further hypotheses about how previous conditional limits might have caused the identified current limits. Of course, testing hypotheses on the current limits is already a complex and daunting task; hypotheses proposed about the past might truly be untestable! As the saying goes: *"A hypothesis can be interesting, but that is not what a hypothesis is for"*. Let's start with finding some testable hypotheses, we'll see where they take us.