# On the behaviour and ecology of the Black-tailed Godwit

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# 1 General introduction

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When an ornithologist wanders through one of the few polders in The Netherlands still populated by meadow birds, his or her heart will beat faster with all the exciting observations to be made. On a winter's day, in the absence of geese and other birds, these polders can be boring and cold – but life flows back as the days lengthen. Tumbling Lapwings, displaying Black-tailed Godwits, whistling Common Redshanks, drumming Common Snipes and sometimes even fighting Ruffs can be seen. This diversity of fascinating meadow birds inspires an unlimited number of questions. Focusing only on the Black-tailed Godwit, as we do in this thesis, might therefore seem narrow in scope. However, in concentrating on the "King of the Meadows," we have been able to draw from and build on a long history of Black-tailed Godwit research in The Netherlands (Haverschmidt 1963, Mulder 1972, Beintema 1991, Kruk 1993, Groen 1993, Schekkerman 2008, Roodbergen 2010, Schroeder 2010, Lourenço 2010, Trimbos 2013, Kentie 2015).

Enabled by recent technological advances, our goal was to begin understanding the observed differences in the annual routines of Black-tailed Godwits (hereafter "godwits"), by focusing primarily on differences in their migratory routines. These differences include, for example, why godwits winter both north and south of the Sahara and why certain godwits leave the breeding grounds in May while others leave in July (Hooijmeijer *et al.* 2013). In order to make inferences about traits of interest, most ecological studies leverage observations made across different contexts – such as between species, populations, or individuals (Trierweiler *et al.* 2014, Lok *et al.* 2015, Oudman *et al.* 2019). However, it is inherently impossible to make such comparisons without first having an understanding of the natural variation in those traits of interest. We therefore start this thesis by describing the natural variation in the migratory routines of adult Black-tailed Godwits breeding in southwest Fryslân, The Netherlands. In **Chapter 2**, we focus primarily on the temporal organization of their migration, by describing the between- and within-individual differences in timing. We go on to describe the between- and within-individual variation in migratory routes, stopover site use and non-breeding destinations in **Chapter 3**. As part of a comparative exercise to understand the causes of the observed variation in migratory behavior among Dutch-breeding godwits, we describe the spatial-temporal variation in migration of a Polish-breeding population in **Chapter 4**, and discuss why adult Black-tailed Godwits of these two populations might differ in their migratory habits. On the theme of describing variation in godwit behaviour, we describe how much variation there exists in their mating strategies in **Chapter 5**. And in **Chapter 6**, we show how we used geolocators to improve our understanding of clutch initiation date and renesting behavior. Finally, we describe the variation in egg-size in **Chapter 7**.

Without describing the ins and outs, the descriptive part of our thesis shows that godwits consistently differ from one another in a number of traits. However, we were not able to satisfactorily identify why these individual differences exist, nor why we observed the range of variation that we did. Especially in the literature on bird migration, we found that a lack of understanding on observed variation is common: there are many excellent descriptions of individual differences in routines, but there is still very little understanding of the mechanistic processes underlying the observed individual differences (e.g. Hooijmeijer *et al.* 2013, Hill *et al.* 2019, Phipps *et al.* 2019). At this stage, researchers often start looking at the fitness consequences of migratory routines to better understand the observed variation in migration (Sillett & Holmes 2002, Strandberg *et al.* 2010, Klaassen *et al.* 2014, Lok *et al.* 2015, Ward *et al.* 2018, Reneerkens *et al.* 2019). The idea behind this approach is that routines are shaped by natural selection, so identifying fitness consequences will provide a broader understanding of the shaping factors of these routines. We too compared differences in reproduction and survival across contexts to accomplish this. In **Chapter 8**, we therefore use satellite transmitters to determine the daily survival of adult female godwits and discuss our findings by making a species-specific comparison to some closely related migratory species. In **Chapter 9** we hone in on a particular life-stage and try to understand why we observe an increased mortality rate when godwits cross the Sahara during northward migration. Then, in **Chapter 10**, we compare how the different sexes and natal habitat types impact the survival of godwit chicks and study whether the sex-biased survival rates among different life-stages result in a biased adult sex-ratio.

All of these survival comparisons across contexts did provide us with better ideas about the ecological factors that shape routines and set the limits for a range of behaviours. However, they failed to deliver a satisfactory understanding of the mechanistic processes underlying the observed individual differences – which is another pattern found in the literature (Lok *et al.* 2011, 2013, Reneerkens *et al.* 2019). But there are exceptions: a few papers that were published just before we began our PhD research do manage to identify some of these underlying mechanistic processes more clearly than the rest of the literature. These were the papers by Mueller *et al.* (2013) *"Social learning of migratory performance"*, Gill *et al.* (2014) *"Why is timing of bird migration advancing when individuals are not?"*, and Sergio *et al.* (2014) *"Individual improvements and selective mortality shape lifelong migratory performance"*. The common denominator of these studies is that they followed juveniles throughout their lives, starting from an early age. These studies, combined with our supervisor's long-held ideas about how individual differences develop over time (Piersma 2011, Piersma & van Gils 2011) – voiced most recently in: *"An ontogenetic approach to individual differences"* (Senner *et al.* 2015) – made us more and more convinced that part of the answer might lie within the development of individual godwits. We therefore discuss in **Chapter 11** whether an observed change in spring staging site use among godwits could be the result of an age-specific behavioral change and that this change in staging site use can be generated without the need for microevolution. To learn more about developmental effects on migratory behavior and to form hypotheses, we examine and discuss the interpretations of Albert Perdeck's post-war displacement experiments with adult and juvenile Starlings in **Chapter 12**.

Our results from **Chapter 11** and our literature review in **Chapter 12** illustrate that certain consistent individual differences can arise through developmental plasticity. In **Chapter 13** we therefore evaluate the plasticity of growth in juvenile godwits. Our results and conclusions in **Chapter 11** and **12** also made us realize that in order to draw conclusions about the mechanistic processes underlying individual differences, it is necessary to perform experiments with truly naïve juveniles. We therefore decided to follow juvenile godwits from birth to adulthood (described in **Chapter 14**) and we also hand-raised juveniles in captivity to manipulate their spatiotemporal context during their first migration (shown in **Chapter 15**).

In summary, our thesis starts with describing the current variation of a number of among Black-tailed Godwits, with a focus on migration. We 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 variation in these behaviours is far from complete. In **Chapter 16** we therefore synthesize our findings and discuss our vision of the way forward by proposing further experimental work that would bring us a little closer toward understanding variation in migration….