

## University of Groningen

### Sex-specific foraging

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*Document Version*

Publisher's PDF, also known as Version of record

*Publication date:*

2014

[Link to publication in University of Groningen/UMCG research database](#)

*Citation for published version (APA):*

Duijns, S. (2014). *Sex-specific foraging: The distributional ecology of a polychaete-eating shorebird*. [Thesis fully internal (DIV), University of Groningen]. [S.n.].

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# 1

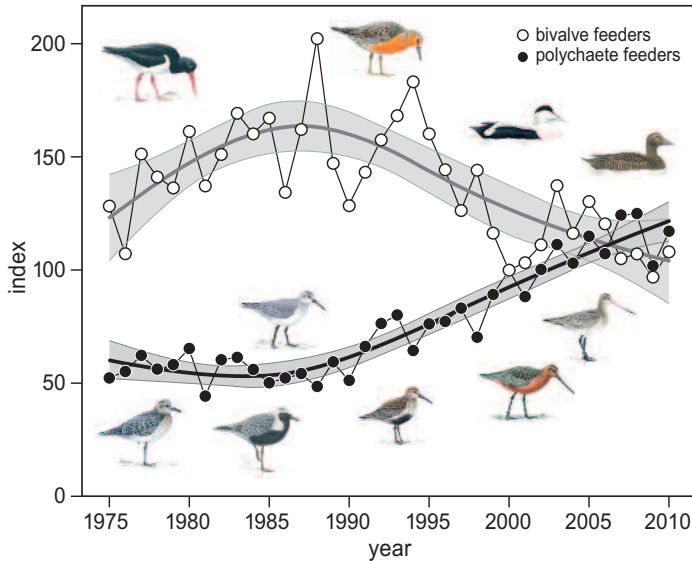
## General introduction

This thesis was inspired by the realization that comparisons have power. Differences between species, sexes or age classes for example, can be seen as the basis in understanding biology and ecology (e.g. Wilson 1992; Piersma 2007). One of the most important wintering and staging site for shorebirds, the Dutch Wadden Sea, has seen a considerable change in the composition of waterbirds during the last two decades. Bivalve predators as red knot *Calidris canutus*, oystercatcher *Haematopus ostralegus* and common eider *Somateria mollissima* have declined in numbers, whereas polychaete predators such as bar-tailed godwit *Limosa lapponica*, dunlin *Calidris alpina* and grey plover *Pluvialis squatarola* have increased in numbers (van Roomen *et al.* 2005; Ens *et al.* 2009; Fig 1.1). This dietary comparison between these two distinct groups suggests that something in the environment has changed.

By using the 15-yr-long benthic survey throughout the western Dutch Wadden Sea carried out by our research group, a resource landscape could be derived. By analysing this resource landscape, it became apparent that shellfish stocks suffered from cockle dredging, while polychaete stocks remained constant and was even suggested to increase (Piersma *et al.* 2001; van Gils *et al.* 2006; Kraan *et al.* 2009a). The decline of the red knot, (a bivalve feeder) in 1996 and 2005, could be attributed to the decline in food abundance (Kraan *et al.* 2009b). Changes in resources are therefore likely to be responsible for the observed numerical changes in the Dutch Wadden Sea feeding guilds. It is still unclear, however, whether the increase of worm-eating birds is in fact driven by a possible increase of food abundance. To be able to answer this question, it is imperative to know their diet, and consequently the resource landscape, and how these polychaete feeders utilize this area.

### **Foraging**

Animals spend most of their available time searching for food, underlining the importance of foraging to an animal's life. In the 1960's MacArthur and Pianka (1966) developed a theory allowing researchers to predict the 'optimal or most economical' choices an individual should make while foraging. For example which prey to feed on and how long to feed in a patch. This theory is nowadays known as optimal foraging theory (Stephens & Krebs 1986). As the name 'most economical' already indicates, it was inspired by economics and is still widely used in ecology (e.g. Houston & McNamara 1999; Hengeveld *et al.* 2009; Yang *et al.* 2013; Houston & McNamara 2014). As animals continuously face choices on where to feed, select a mate or avoid being eaten themselves, these choices have consequences on the long and the short term. When individuals are rewarded by their behaviour (in terms of fitness) and as behaviour appears to have a genetic basis (Plomin *et al.* 1994), natural selection would select for individuals that make optimal choices. Although optimal foraging theory has also been criticized as these models are considered too simple (e.g. Pierce & Ollason 1987; Ginzburg & Jensen 2004; May 2004), intuitively they may still be useful as null hypothesis testing, and work presented in this thesis adopted some of these ideas.



**Figure 1.1.** Development in the annual numbers (index) of bivalve and polychaete feeding waterbirds in the Dutch Wadden Sea in 1975 – 2010. Data SOVON.

Predicting and understanding the rate of prey consumption by individual predators as a function of predator and/or prey densities has been conceptualised in functional response models, with Holling (1959) being the path-breaker here. Despite the simplicity of these functional response models (and maybe especially *because* of their simplicity), they are still widely used and has proven to be extremely helpful in understanding and predicting foragers' distributions (e.g. Piersma *et al.* 1995; Abrams & Ginzburg 2000; Jeschke *et al.* 2002; van Gils *et al.* 2004; van Gils & Piersma 2004; Fryxell *et al.* 2007). Therefore, a large part of this thesis also used this functional response model to be able to understand and predict the occurrence of a sexual dimorphic migratory shorebird.

### ***Aim of this study***

To understand the changes in the composition of waterbirds occurring in the Dutch Wadden Sea, it is essential to combine the available resources and knowledge on how these waterbirds utilise this area. Although we are fortunate to be able to contribute and have immediate access to one of the largest benthic sampling efforts in the world (Kraan *et al.* 2009a; Compton *et al.* 2013), we also require detailed information on the foraging behaviour of these waterbird species. Building on the extensive work performed on a bivalve specialist, the red knot, I took up the challenge to study a representative polychaete specialist, the bar-tailed godwit. This species appears to be an ideal study species, as it is a polychaete specialist with similar migration strategies as red knots. Bar-tailed godwits and red knots can therefore be regarded as ideal trophic mirror species.

### ***Study species***

Two populations of bar-tailed godwits occur along the East-Atlantic Flyway (another similarity with red knots). The European population *L. l. lapponica* is suggested to breed and

winter in Europe (breeding from Scandinavia to the Kanin peninsula and reside around the North Sea and Irish Sea in winter). The Afro-Siberian population *L. l. taymyrensis* is suggested to breed in north-central Siberia (from Yamal peninsula in the west to the delta of Anabar river in the east), and winter along the west coast of Africa, with large concentrations on the Banc d'Arguin, Mauritania and in Guinea-Bissau (Drent & Piersma 1990; Engelmoer & Roselaar 1998; Scott & Scheiffarth 2009).

Populations breeding in northerly areas migrating to wintering areas south of populations from more southerly breeding ranges are a well-known phenomenon (Newton 2008). This so-called leap-frog migration occurs in several species of shorebirds (e.g. Salomonsen 1955; Alerstam & Högstedt 1980). For bar-tailed godwits the leap-frog migration system resulted in different spring migration strategies as their requirements and timing differs; the *lapponica* population seems to have adopted an energy minimizing strategy and the *taymyrensis* population a time minimizing strategy (Scheiffarth *et al.* 2002).

### ***Men are from mars, women are from Venus (Gray *et al.* 1993)***

This book by John Gray and co-workers has sold over 50 million copies and spent 121 weeks on the bestseller list. Maybe not surprisingly, as it nicely exemplifies fundamental psychological differences between the sexes, something that has intrigued people for decades. Sexual differences are thus of great interest and a widespread phenomenon throughout the animal kingdom. Numerous studies have exemplified the differences between the sexes in virtually all disciplines, too many to summarize here. Bar-tailed godwits have unusually high intra- and intersexual differences in size and breeding plumage. A referee of one of our manuscripts suggested that male and female bar-tailed godwits could just as well be considered different species. Indeed, their (foraging) behaviour is a clear example of trophic dichotomy. The smaller males mainly peck ( $< 1/3$  of their bill in sediment) in search for small surface prey, whereas the larger females mainly probe ( $> 1/3$  of their bill in sediment), by following the tide line in search for large deeply buried (and more profitable) prey. These foraging differences have resulted in different diets between the sexes (Scheiffarth 2001a).

## **Thesis outline**

Although the two populations of bar-tailed godwits appear to follow a leap-frog migration strategy, it has been suggested that both populations show a considerable overlap in occurrence in their wintering and breeding sites. Based on an analysis of ring recoveries and re-sightings of marked individuals, in **Chapter 2** we demonstrate that nearly all marked individuals behaved according to the suggested leap-frog migration pattern, and only a small fraction (0.8 %) interchanged wintering sites.

Differences between the occurrences of both sexes in the wintering range in North-west Europe have been observed, and these differences were hypothesised to be driven by the relative smaller cost of wintering for females in the northern and colder sites. In **Chapter 3** we studied the occurrence between the sexes of the European population

across their wintering range and could show that males and females distribute themselves according to prey availability (i.e. prey burying depth), rather than choosing a wintering site based on costs.

In **Chapter 4** we studied foraging site selection of the two focal populations during northward migration. Here we could show that the time-minimizing Afro-Siberian population foraged closer to cover where food abundance was higher and foraged for a higher proportion of time than the European population (67% vs. 33%). The energy-minimizing European population avoided predation danger by foraging further from food-rich covers. The Afro-Siberian population apparently accepted a higher predation risk as they need to fuel up for their (longer) migration in a shorter time period than the European population.

To understand the occurrence and recent increase in the number of bar-tailed godwits, we needed to increase our knowledge on their diet. In **Chapter 5** we compared the diet composition of five main wintering sites in North-western Europe based on dropping analysis, where we showed that although the diet differed between sites, their main prey were indeed polychaete worms.

In **Chapter 6** we studied the functional response in the field and discovered interference competition for females only, and could link their reduced intakes as a function of predator density to prey depression. As these larger females mainly forage on mobile deeply buried large prey, their foraging behaviour caused the most profitable prey (lugworms; *Arenicola marina*) to retract and thereby hindering the females in successfully capturing this prey.

Based on the results of the previous chapter, in **Chapter 7** we studied the functional response in more detail in the lab, where we compared our field data with our experimental results. We could show that although field-based functional response parameters provide valuable information on a local scale, they are insufficient in applying them on a larger scale, and the experimental obtained parameters provided a much better understanding of the capabilities of these shorebirds.

In **Chapter 8** we used our experimentally obtained functional response parameters to predict intake rates on a monthly basis using a unique historical dataset on the depth, length and abundance of the most important prey item for the females. We were able to show that in months when prey bury deeper, they would need to diversify their diet with alternative prey, and field data confirmed this. Following this, we could even show that the shorter-billed individuals leave the Dutch Wadden Sea during periods that prey are buried deeper, and only the longer billed individuals remained in the Dutch Wadden Sea during these colder periods.

In **Chapter 9**, we synthesize these results and discuss the implications for understanding the occurrence and distribution of this species, populations and the sexes. Knowledge gaps will be addressed and future directions are outlined in understanding the population dynamics of these shorebirds.

