

Sex-specific foraging

The distributional ecology of a polychaete-eating shorebird

Sjoerd Duijns



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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.

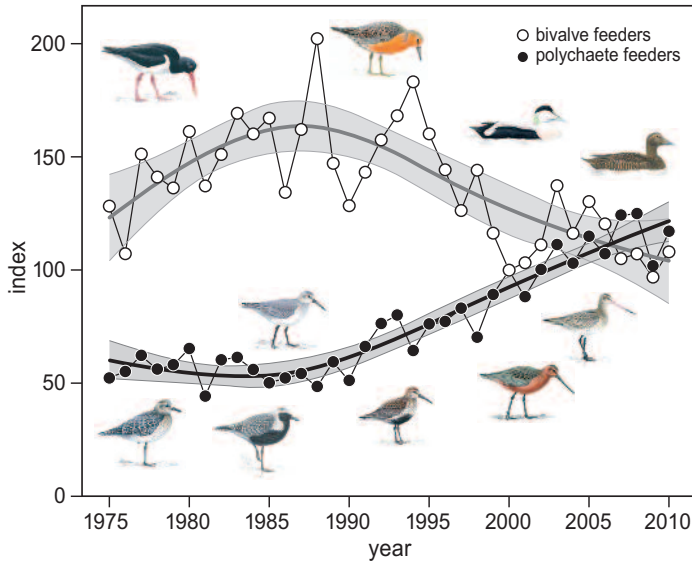


Figure 1.1. Development in the annual numbers (index) of bivalve and polychaete feeding waterbirds in the Dutch Wadden Sea in 1975 – 2010. Data SOVON.

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 experimentally 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.



2

Revisiting the proposed leap-frog migration of bar-tailed godwits along the East-Atlantic Flyway

Sjoerd Duijns, Joop Jukema, Bernard Spaans,
Peter van Horssen & Theunis Piersma

Abstract

Two populations of bar-tailed godwits *Limosa lapponica* occur along the East-Atlantic Flyway. The European population *L. l. lapponica* is supposed to breed in northern Scandinavia and has been suggested to only winter in Europe. The Afro-Siberian population *L. l. taymyrensis* is supposed to breed in Northern Siberia and is thought to winter exclusively in West Africa. An analysis of 946 metal ring recoveries accumulated by EURING (with data going back to 1935), in combination with an analysis of over 13,000 resightings of almost 4000 individuals marked with colour-rings in 2001–2010, enabled us to examine whether there is evidence for overlap of the populations in summer and winter. Nearly all marked individuals behaved according to the previously suggested leap-frog migration pattern. On the basis of the present sample, only 0.8% of (colour) ringed birds that were recovered and/or resighted on the wintering grounds in Europe or West-Africa made a change between the two supposed wintering areas. This is far less than was previously estimated on the basis of biometric data. The distinct migratory behaviour of the two populations makes them near-completely separated in summer and winter. The bar-tailed godwit along the East-Atlantic Flyway thus exhibits a clear leap-frog migration, in which the Siberian breeders winter south of the European breeders.

Introduction

Shorebirds provide excellent opportunities to study migration strategies. They occur in open landscapes and often rely on relatively few wetlands (Piersma 2007) where they can be captured, marked and resighted with relative ease (Piersma & Spaans 2004; Spaans *et al.* 2011). Not surprisingly then, shorebirds have their ‘connectivity’ well resolved (van de Kam *et al.* 2004; Delany *et al.* 2009).

In many migrating birds, populations breeding in northerly areas migrate to wintering areas south of populations from more southerly breeding ranges (Newton 2008). This so-called leap-frog migration occurs in several species of shorebirds (Salomonson 1955; Alerstam & Högstedt 1980; Alerstam 1990) and is thought to occur in bar-tailed godwits *Limosa lapponica* wintering in Europe and West-Africa (Drent & Piersma 1990; Scheiffarth 2001b). The European population breeds and winters in Europe (breeding from Scandinavia to the Kanin peninsula and resides around the North Sea and Irish Sea in winter), and the Afro-Siberian population breeds in north-central Siberia (from Yamal peninsula in the west to the delta of Anabar river in the east) and winters along the west coast of Africa, with large concentrations on the Banc d’Arguin, Mauritania, and in Guinea-Bissau (Scott & Scheiffarth 2009).

The characterization of the leap-frog migration pattern (Drent & Piersma 1990) was based on Prokosch (1988), who found morphological differences in time and space suggestive of subspecific differentiation. Engelmoer & Roselaar (1998) proposed that the two bar-tailed godwit populations should be recognized as distinct subspecies. They named the birds with smaller body dimensions breeding in north-central Siberia *taymyrensis* and proposed to retain the larger-bodied European population as the nominate subspecies *lapponica*. When reviewing Engelmoer & Roselaar (1998), Tomkovich & Serra (1999) argued about some of their subspecies assignments, but not about the distinction between *lapponica* and *taymyrensis*. In later studies the two populations appeared to be not only morphologically, but also ecologically distinct (Scheiffarth *et al.* 2002; Duijns *et al.* 2009).

Based on morphological measurements of birds captured in the Wadden Sea, and discrimination functions based on museum specimens from the breeding grounds, Engelmoer (2008) estimated that about 20% of the bar-tailed godwits wintering in the Wadden Sea belong to the Afro-Siberian population. This implies that of the 120,000 birds wintering in the Wadden Sea (the European population; Scott & Scheiffarth 2009), no fewer than 24,000 individuals represent Afro-Siberian birds that were supposed to all winter in West-Africa. If so, this would mean that the leap-frog migration pattern is partial at best.

In this paper we aim to reconsider all available evidence using historical ringing, recovery and colour-ring resighting information of bar-tailed godwits along the East Atlantic Flyway. Based on seasonal itineraries (Fig. 2.1), we derived three criteria to assign

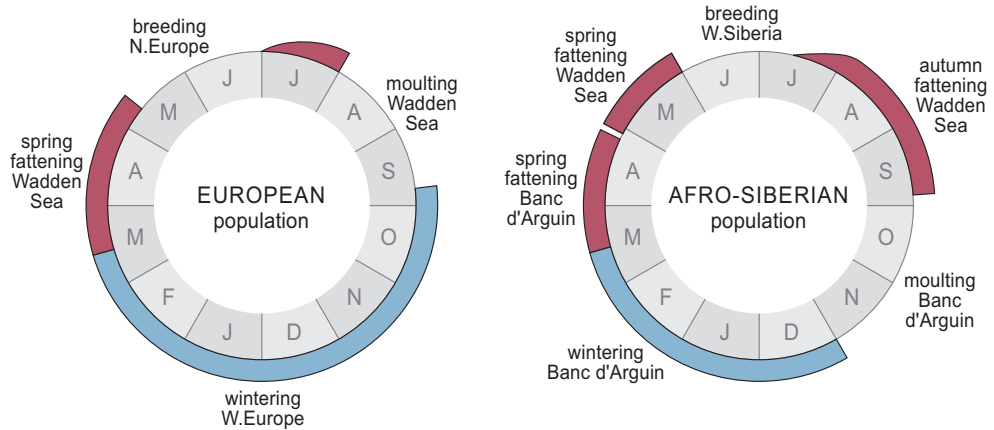


Figure 2.1. The seasonal itinerary of the two populations of bar-tailed godwits (European and Afro-Siberian) indicating the sequence of phases experienced by the two populations in the course of the year (from Drent & Piersma 1990).

individuals to either population at capture and ringing: (1) individuals (re)captured and/or resighted between November and March in Europe belong to the European breeding population, (2) individuals captured and/or resighted in West-Africa belong to the Siberian breeding population, and (3) individuals captured in the Wadden Sea during autumn in active primary moult are also expected to belong to the European population, as wing-moulting individuals tend to winter in Europe (Atkinson 1996). We use then the recoveries and resighting data to establish whether the suggested leap-frog migration pattern of the two subspecies holds up.

Methods

Bar-tailed godwits were captured at various sites in the Dutch and German Wadden Sea and on the Banc d'Arguin, Mauritania, West-Africa. Birds were processed immediately after capture, length of bill (exposed culmen, from tip of bill to base of feathers), wing (flattened and straightened; Prater *et al.* 1977) and tarsus being measured on most individuals using standard methods. The primary moult score was given according to Newton (1966); old: 0; growing: 1–4; new: 5. A bird that had completed moult of all 10 primaries had a primary moult score (PMS) of 50.

Each bar-tailed godwit was marked individually with four colour-rings (blue, red, white and yellow), combined with one yellow or red flag, and a metal ring. There were two colour-rings on the left and two on the right tarsus, and the metal ring was placed on one of the tibiae, but was not part of the code. The flag was the marker of the scheme and was

placed on the tarsus or on one of eight different positions. In this way it was possible to individually mark 2,048 combinations per flag colour. The colour-ring combination could easily be observed in the field by telescope.

Unfortunately, mistakes were sometimes made as the rings are subjected to colour deterioration through time, especially yellow and white (Burton 2000; Ward 2000). One should keep this in mind in the case of exceptional life-histories based on single ring-reading occasions. From spring 2001 to the end of 2010 a total of 3,996 individuals were colour-ringed and 13,326 individual resightings from 2,373 individual birds (59% of birds marked) were received from 311 different locations. The majority of the colour-ringed birds were caught in the Wadden Sea (91%), followed by Mauritania in West-Africa (7%). The colour-ring resightings show the same geographic bias, as most of the birds were resighted in the Wadden Sea (87%) followed by West-Africa (11%). A similar pattern is observed for the metal rings. Most birds were captured in Western Europe (85%; i.e. United Kingdom, the Netherlands, and Germany), and recovered in Western Europe (85%; Appendix 1).

From the EURING database 946 recoveries of metal rings were obtained, with the earliest recovery dating from 1935 and the latest from 2010. A preliminary analysis showed no spatial or temporal difference between earlier (<1980) and later records, so all recoveries were used. In total 790 catching or recovery locations were identified. From only 35% of the individuals, relevant biometric (age and sex) information was available. To avoid reducing the sample size, all individuals were therefore included in the analysis.

Capture and resighting data were used to create a map with a resolution of 0.25 degrees (Fig. 2.2). Resighting colour-ringed individuals is highly dependent on volunteers, and therefore the data were skewed towards locations where volunteers were active. To reduce the effect of identification errors, only individuals that were resighted twice in their wintering areas (i.e. West-Africa or Western Europe) were included in the analysis ($n = 1,399$). Most bar-tailed godwits were caught and/or resighted during spring migration in the Dutch Wadden Sea in May when both populations occur in the Wadden Sea (Drent & Piersma 1990; Duijns *et al.* 2009), and therefore 790 (56%) of the colour-ringed birds could not be assigned to any population. Furthermore, only adult birds were included in the analysis as juvenile bar-tailed godwits may migrate differently than adults (NIOZ, unpubl. data) and they are known to be scarce at Western European staging sites in spring (Prokosch 1988). This age-differential migration, (i.e. different geographical wintering distributions of juvenile and adult birds) is not uncommon (Cristol *et al.* 1999; Lok *et al.* 2011).

To test for differences in morphological variables between the two populations, we performed an ANOVA with population and sex as fixed factors and date of catch as a covariate. Basic assumptions of parametric tests were examined by testing for normality with a Kolmogorov-Smirnov test, and the application of the Levene's test for equality variances.

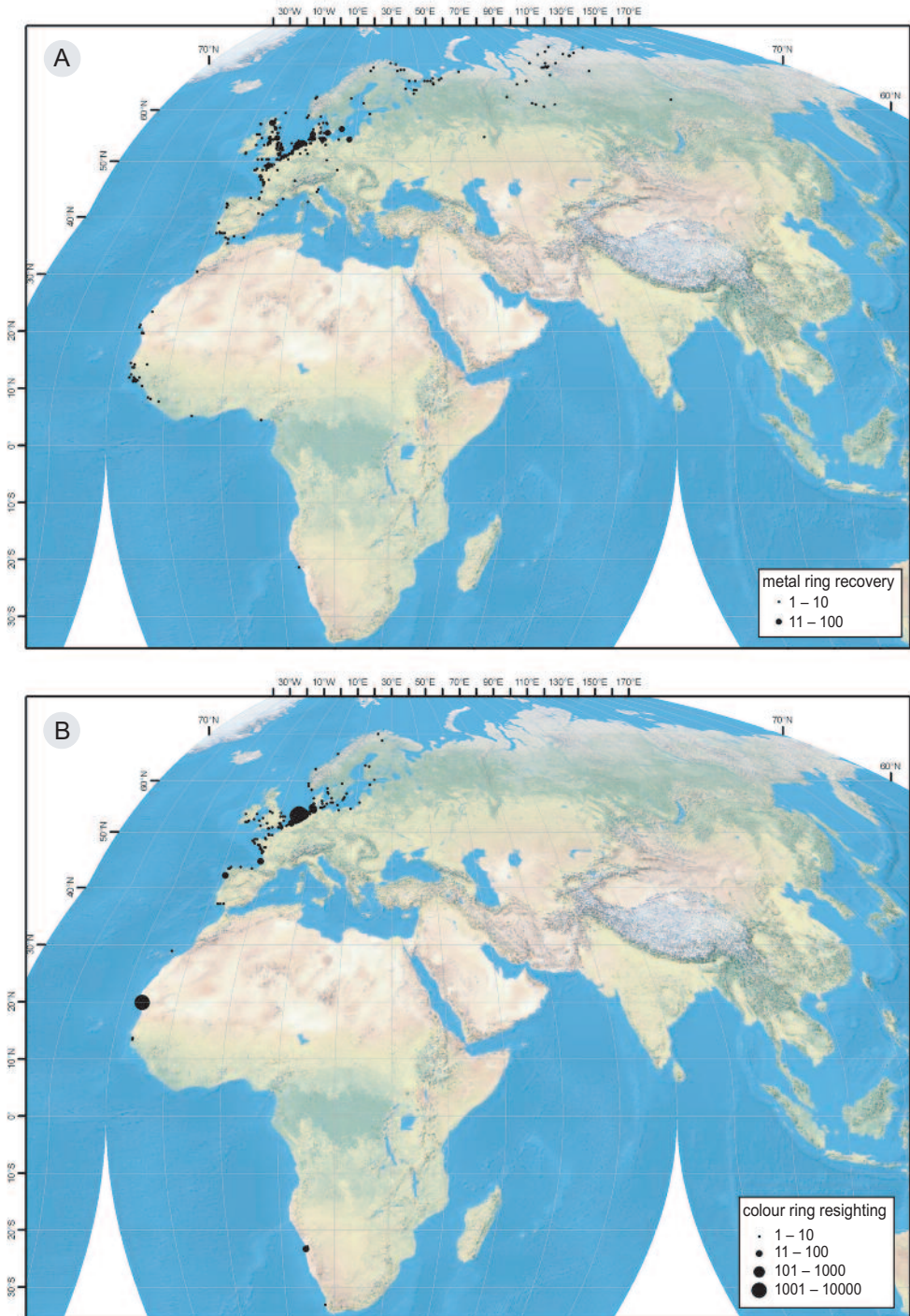


Figure 2.2. Recoveries and resightings of bar-tailed godwits along the East Atlantic Flyway. (A) Metal ring recoveries ($n = 946$) are from 1935–2010 and (B) colour-ring resightings ($n = 13,326$) from 2001–2010.

Results

Despite a large overlap in morphological variables (Figure 2.3), bill and wing length (but not tarsus) confirmed that birds of the European population are larger-bodied than birds assigned to the Afro-Siberian population (ANOVA: $F_{1,381} = 39.21$, $P < 0.001$, $F_{1,278} = 15.8$, $P < 0.001$ and $F_{1,372} = 0.5$, $P = 0.481$, respectively).

Of the assigned individuals, 224 (16%) colour-ringed birds wintered in Western Europe, or were in active primary moult in autumn; 385 (28%) wintered in West-Africa. Of the 946 metal ring recoveries, 291 (31%) individuals wintered in Europe and 68 (7%) individuals wintered in West-Africa. Most of the marked individuals that were recovered or resighted behaved as predicted on the basis of the previously inferred leap-frog migration pattern (Table 2.1). As predicted, the two colour-ringed individuals that were observed in the breeding range in Northern Scandinavia were resighted in Europe in winter, and the 27 metal-ringed individuals assigned to the European population were recovered in Northern Scandinavia (Fig. 2.4A). Of the metal-ringed birds, 23 African-winterers were recovered in the Northern Siberian breeding range (Fig. 2.4B), thus confirming the links between wintering areas and breeding grounds. Of the 992 assigned birds (i.e. European or Afro-Siberian), only eight (0.8%) individuals did not follow the predictions. This included four colour-ringed birds and four metal-ringed birds (Appendix 2).

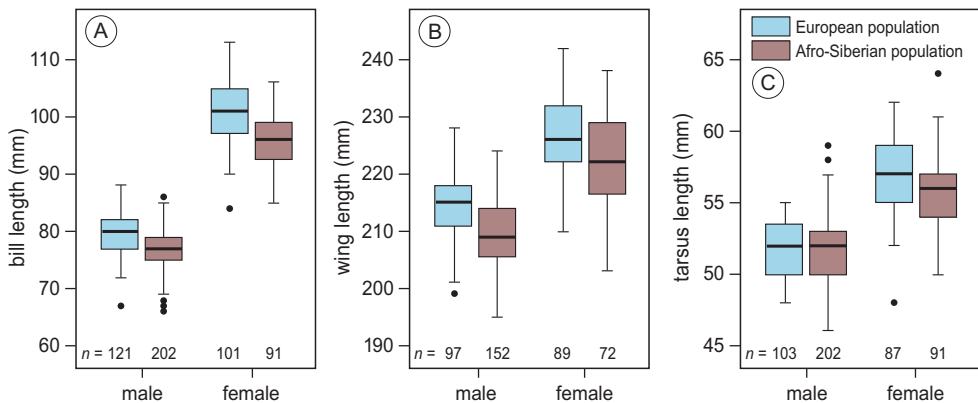


Figure 2.3. Morphological characteristics of bar-tailed godwits, by sex and population. The box-and-whisker plots show median (line in box), interquartile range (box), range (bars), and outliers (small dots) of: (A) bill length, (B) wing length and (C) tarsus length.

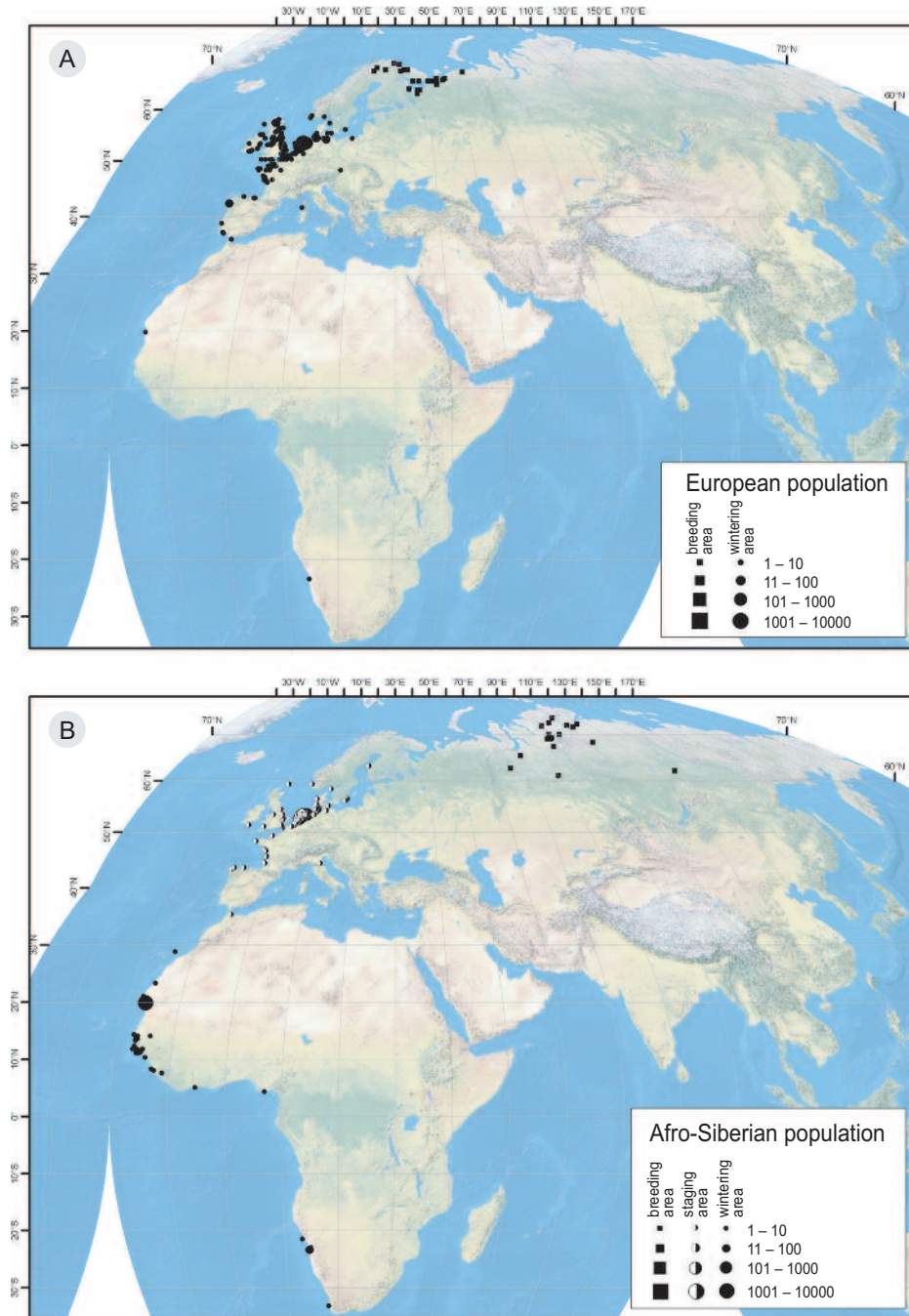


Figure 2.4. Wintering, staging, and breeding sites for bar-tailed godwits. (A) Recoveries of the European population with the main wintering sites in the Dutch and German Wadden Sea, the NW of Spain and the SE of the United Kingdom. (B) Recoveries of the Afro-Siberian population, with ‘hot spots’ in the Dutch and German Wadden Sea and the Banc d’Arguin in Mauritania.

Table 2.1. Assignment criteria of ringed and colour-marked bar-tailed godwits to the two populations and the verifications testing the leap-frog migration hypothesis based on resighting and recovery locations: the eight exceptions are listed in Appendix 2. The sample sizes refer to the total number of individuals, either colour-ringed or with only a metal ring. Individuals may feature in different categories (e.g. an individual was caught and resighted), and therefore the totals differ from the sum of the separate assignment criteria.

locality	European population	<i>n</i>	<i>n</i> total	Afro-Siberian population	<i>n</i>	<i>n</i> total
Assignment criteria						
Wintering area	Captured in Europe between November and March	55	224	Captured in Africa	200	385
Wintering area	Resighted in Europe between November and March	94		Resighted in Africa	309	
Staging period July - Sep	Active primary moult when caught during autumn migration in Wadden Sea	132		Non-moulting when caught in Wadden Sea between July and October	250	
Verifications in different seasons and locations						
Breeding area	Recovered in Northern Scandinavia and White Sea area	29		Recovered in North Central Siberia	23	
Wintering area	Subsequent field observations of moulting individuals in Wadden Sea between November and March	83		Subsequent field observations of non-moulting individuals in Africa	19	

Discussion

Due to the low density of breeding birds and the very low ring-reading efforts on the breeding grounds, we received only two resightings in the breeding areas. Yet, the recoveries from the Scandinavian and north-central Siberian areas support a leap-frog migration system, with little evidence for overlap of the breeding populations in winter. The leap-frog migration hypothesis is further supported by the observation that of 1009 birds caught in May and resighted more than once, only 3.8% were resighted in Europe during winter (NIOZ, unpubl. data). Similarly, Wilson *et al.* (2007) found “low levels” of exchange for two other populations of bar-tailed godwit (*menzbieri* and *baueri*) with a comparable migration system. The eight exceptions (Appendix 2) were in fact all quite peculiar in terms of age (at the time of capture less than 2 years old), recovery dates (i.e. mid-April and mid-May when such individuals should still be in Europe), or ring colour (white and yellow may have been confused). Even if correct, these individuals switching wintering areas represent a small proportion of the population, and this suggests that the estimate by Engelmoer (2008) of 20% of the wintering population in the Wadden Sea as north-central Siberian-breeding (Afro-Siberian), is an overestimate. Our results thus

suggest almost complete separation of the wintering and breeding grounds of the two populations of bar-tailed godwits along the East-Atlantic Flyway, and confirm that the two populations represent as clear an example of a leap-frog migration system as Drent & Piersma (1990) suggested it to be.

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Appendix 1. Total number of ringed bar-tailed godwits resighted and recovered per country.

Country	Colour rings				Metal rings			
	Caught		Resightings		Caught		Recovered	
	<i>n</i>	%	<i>n</i>	%	<i>n</i>	%	<i>n</i>	%
Russia					1	0.11	57	6.03
Norway			6	0.05	8	0.85	3	0.32
Finland			6	0.05	1	0.11		
Sweden			18	0.14	22	2.33	9	0.95
Estonia			1	0.01			1	0.11
Latvia			1	0.01				
Denmark			17	0.13	22	2.33	43	4.55
United Kingdom			44	0.33	334	35.31	242	25.58
Ireland			19	0.14	5	0.53	1	0.11
Poland			3	0.02	24	2.54	18	1.90
Germany	48	1.20	96	0.72	99	10.47	73	7.72
The Netherlands	3653	91.42	11577	86.88	374	39.53	356	37.63
Belgium			2	0.02	2	0.21	1	0.11
France			51	0.38	17	1.80	91	9.62
Switzerland					1	0.11		
Czech Republic					2	0.21		
Italy					9	0.95	6	0.63
Spain			42	0.32	7	0.74	14	1.48
Portugal			3	0.02	5	0.53	2	0.21
Morocco							3	0.32
Mauritania	295	7.38	1420	10.66	4	0.42	2	0.21
Senegal			3	0.02	1	0.11		
Gambia			1	0.01				
Guinea Bissau					8	0.85	18	1.90
Sierra Leone							3	0.32
Ghana								
Ivory Coast							1	0.11
Nigeria							1	0.11
Namibia			14	0.11			1	0.11
South Africa			2	0.02				
Total	3996	100	13326	100	946	100	946	100

Appendix 2. (Colour-) ringed individual bar-tailed godwits that were unfaithful to their wintering area, or that were reported in Europe in winter where they were expected to be in West-Africa at the time of resighting. If a bird was resighted twice on the same day, this means that the individual was observed by at least two independent observers.

Ind. Code	AC ^a	Sex	PMS	Age	Catching location	Date	Latitude	Longitude	Resighting location	Date	Latitude	Longitude	Caveat
DN44314	CD	F	-	juvenile	UK	5-11-1983	56°10'N	3°03'W	Russia	15-4-1988	55°59'N	92°54'E	Age at catching and questionable recovery date
DS86344	CD	F	-	juvenile	UK	3-1-1977	55°15'N	1°30'W	Russia	20-5-1979	62°13'N	70°38'E	Age at catching and questionable recovery date
DR99482	CD	M	-	full grown	UK	12-3-1983	53°31'N	4°09'E	Guinea-Bissau	6-8-1993	11°20'N	16°00'W	Age at catching and questionable recovery date
1098920	CD	-	-	>2nd year	The Netherlands	17-3-1972	53°16'N	5°00'E	Russia	13-5-1972	62°13'N	70°38'E	Age at catching and questionable recovery date
Y2RYBW	CD	M	0	adult	The Netherlands	31-3-2003	53°15'N	5°16'E	The Netherlands	5-5-2003	53°00'N	04°46'E	White and yellow in the colour-ring combination
									The Netherlands	23-3-2004	53°15'N	05°15'E	
									Mauritania	12-12-2004	19°54'N	16°19'W	
									The Netherlands	30-1-2006	53°09'N	04°54'E	
									Mauritania	18-12-2009	19°54'N	16°19'W	
									Mauritania	18-12-2009	19°54'N	16°19'W	
Y5WYRR	PMS	F	29	≥ 2nd year	The Netherlands	30-9-2003	53°28'N	6°15'E	Mauritania	20-12-2006	19°54'N	16°19'W	Age at catching and white and yellow in the colour-ring combination
									Mauritania	12-12-2009	19°52'N	16°17'W	
Y5WYWY	PMS	F	36	≥ 2nd year	The Netherlands	30-9-2003	53°29'N	6°15'E	Mauritania	25-12-2006	19°53'N	16°19'W	Age at catching and white and yellow in the colour-ring combination
									Mauritania	25-12-2006	19°53'N	16°19'W	
Y3YYRR	PMS	M	49	> 2nd year	The Netherlands	9-9-2002	53°29'N	6°15'E	Mauritania	28-3-2006	53°09'N	04°54'E	Age at catching and white and yellow in the colour-ring combination
									The Netherlands	28-3-2006	53°09'N	04°54'E	
									The Netherlands	7-5-2006	53°22'N	05°20'E	
									The Netherlands	8-5-2006	53°22'N	05°20'E	
									The Netherlands	9-5-2006	53°22'N	05°20'E	
									The Netherlands	6-1-2008	53°08'N	04°55'E	
									Namibia	23-1-2009	23°22'S	14°30'E	
									Namibia	24-1-2009	23°22'S	14°30'E	
									Namibia	24-1-2009	23°22'S	14°30'E	

^a Assignment criterion: CD = Catching location and date, PMS = Primary moult score.



3

Sex-specific winter distribution in a sexually dimorphic shorebird is explained by resource partitioning

Sjoerd Duijns, Jan A. van Gils, Bernard Spaans, Job ten Horn, Maarten Brugge & Theunis Piersma

Abstract

Sexual size dimorphism (SSD) implies correlated differences in energetic requirements and feeding opportunities, such that sexes will face different trade-offs in habitat selection. In seasonal migrants, this could result in a differential spatial distribution across the wintering range. To identify the ecological causes of sexual spatial segregation, we studied a sexually dimorphic shorebird, the bar-tailed godwit *Limosa lapponica*, in which females have a larger body and a longer bill than males. With respect to the trade-offs that these migratory shorebirds experience in their choice of wintering area, northern, and colder wintering sites have the benefit of being closer to the Arctic breeding grounds. According to Bergmann's rule, the larger females should incur lower energetic costs per unit of body mass over males, helping them to winter in the cold. However, as the sexes have rather different bill lengths, differences in sex-specific wintering sites could also be due to the vertical distribution of their buried prey, that is, resource partitioning. Here, in a comparison between six main intertidal wintering areas across the entire winter range of the *lapponica* subspecies in northwest Europe, we show that the percentage of females between sites was not correlated with the cost of wintering, but was positively correlated with the biomass in the bottom layer and negatively with the biomass in the top layer. We conclude that resource partitioning, rather than relative expenditure advantages, best explains the differential spatial distribution of males and female bar-tailed godwits across northwest Europe.

Introduction

Migratory animals need to acquire appropriate resources at multiple locations throughout their annual cycle (Alerstam & Lindström 1990; Newton 2008). Where populations occur over a large non-breeding range, sites within that range may show different food regimes, weather conditions, levels of competition and predation danger. Therefore, such migrants have to trade the costs (i.e. maintenance- and migration costs) against the benefits (i.e. quality) of their alternative wintering sites (e.g. Drent & Piersma 1990; Castro *et al.* 1992; Alves *et al.* 2013a).

When ecological opportunities differ between classes of animals, such as sex, age or subspecies, these classes may be expected to show different distributions (Cristol *et al.* 1999; Ruckstuhl 2007; Alves *et al.* 2010). Sexual size dimorphism (SSD) could result in males and females facing different trade-offs affecting migratory strategy and winter-site selection (Alves *et al.* 2013a), where the dominant sex may outcompete the other sex (e.g. Cristol *et al.* 1999; Blanckenhorn 2005). Indeed, segregation between the sexes during the non-breeding season has been documented for some migratory birds at different spatial scales (e.g. Ketterson & Nolan 1976; Myers 1981; Mathot *et al.* 2007; Nebel *et al.* 2013).

When individuals differ in body size, they will not only differ in energetic requirements but also in the use of a given resource. Such resource partitioning can lead to spatial segregation (Schoener 1974). In many bird species, bill size is a strong predictor of foraging niche (Selander 1966) and differences in bill structure and size will be associated with differences in feeding technique and diet (Rubega 1996; Durell 2000). Thus, sexual differences in bill morphology might lead to sex differences in diets related to prey size or prey burying depth (Mathot *et al.* 2007; Alves *et al.* 2013b; Duijns & Piersma 2014).

In this study we examine wintering site selection for a long-distance migrating sexually dimorphic shorebird, the bar-tailed godwit *Limosa lapponica lapponica*. This subspecies breeds in northern Scandinavia and winters almost exclusively in Europe (Duijns *et al.* 2012). Sexual dimorphism is most pronounced in body size and bill length, with females being 20% larger and having 25% longer bills than males (e.g. Piersma & Jukema 1990; Duijns *et al.* 2012). Within the wintering range of this population, spatial segregation between the sexes has been observed. The smaller males occur in climatically mild areas such as the United Kingdom (Atkinson 1996; Summers *et al.* 2013), whereas most females are found in the northern and colder parts of the European Wadden Sea (Smith 1975; Prokosch 1988; Scheiffarth 2001b). It has been hypothesised that the high living costs at sites closer to the breeding areas may be energetically more advantageous for the larger sex (Smith 1975; Scheiffarth 2001b). One of the best-known ecological generalizations with respect to large-scale distributions of species is Bergmann's rule (1847). This rule states that within a genus of endothermic vertebrates, the larger variants will be

found in cooler environments as they have lower surface to volume ratios and will proportionally radiate less heat per unit body mass.

Alternatively, for shorebirds that feed in soft substrates, shorter-billed birds may rely more heavily on shallowly buried prey from the sediment surface compared to longer-billed birds, which are able to probe more deeply into the sediment to extract more deeply buried prey (e.g. van de Kam *et al.* 2004; Mathot *et al.* 2007). Benthic organisms are distributed throughout intertidal sediment with the larger and more profitable prey (e.g. Alves *et al.* 2013b; Duijns & Piersma 2014) found deeper and the smaller prey occurring closer to the surface (Reading & McGrorty 1978; Zwarts & Wanink 1991). Indeed, bar-tailed godwit diet composition differs between the sexes, where the shorter-billed males frequently feed on the smaller and shallowly buried prey, and the longer-billed females predominantly feed on the larger and more deeply buried prey (Scheiffarth 2001a; Duijns & Piersma 2014). This would suggest that the shorter-billed males should spend the non-breeding season at sites with a high density of food items available at or near the surface, whereas the longer-billed females should winter in areas with a high density of deeper buried prey. To address the mechanisms underlying this sex-specific spatial pattern, we have quantified the occurrence of these shorebirds and benthic prey availability at six important non-breeding sites across the wintering range in Western Europe (Fig. 3.1).

Methods

Study sites

Field work was carried out at six nonbreeding sites. The initial choice for the sites was based on the top ten highest mean January counts from 1995-2005, as obtained from the Wetlands International midwinter count database. In only six areas numbers seemed high enough and logistics were favourable. The sites were located throughout Western Europe, spanning 1,200 km and 14° of longitude and 11° of latitude. Although we visited the sites in as brief a period as possible, measurements could not be made simultaneously. However, individual shorebirds that have selected a wintering site are known to be site-faithful (e.g. Burton 2000; Leyrer *et al.* 2006) and benthic prey availability was shown to be relatively constant during the winter months (Zwarts & Wanink 1993). The German Sylt-Rømø Wadden Sea area (55°01'N, 8°26'E) was visited in mid-October 2010, the Dutch Delta area (51°40'N, 04°07'E) in late October 2010, the Wash in the UK (52°56'N, 00°19'E) in early November 2010, Dublin bay in Ireland (53°19'N, 06°11'W) in late November 2010, the Western Wadden Sea island Griend (53°14'N, 05°15'E) in early February 2011 and Ré island (46°15'N, 01°29'W) in France in late December 2013. See Table 3.1 for more details on the study sites.

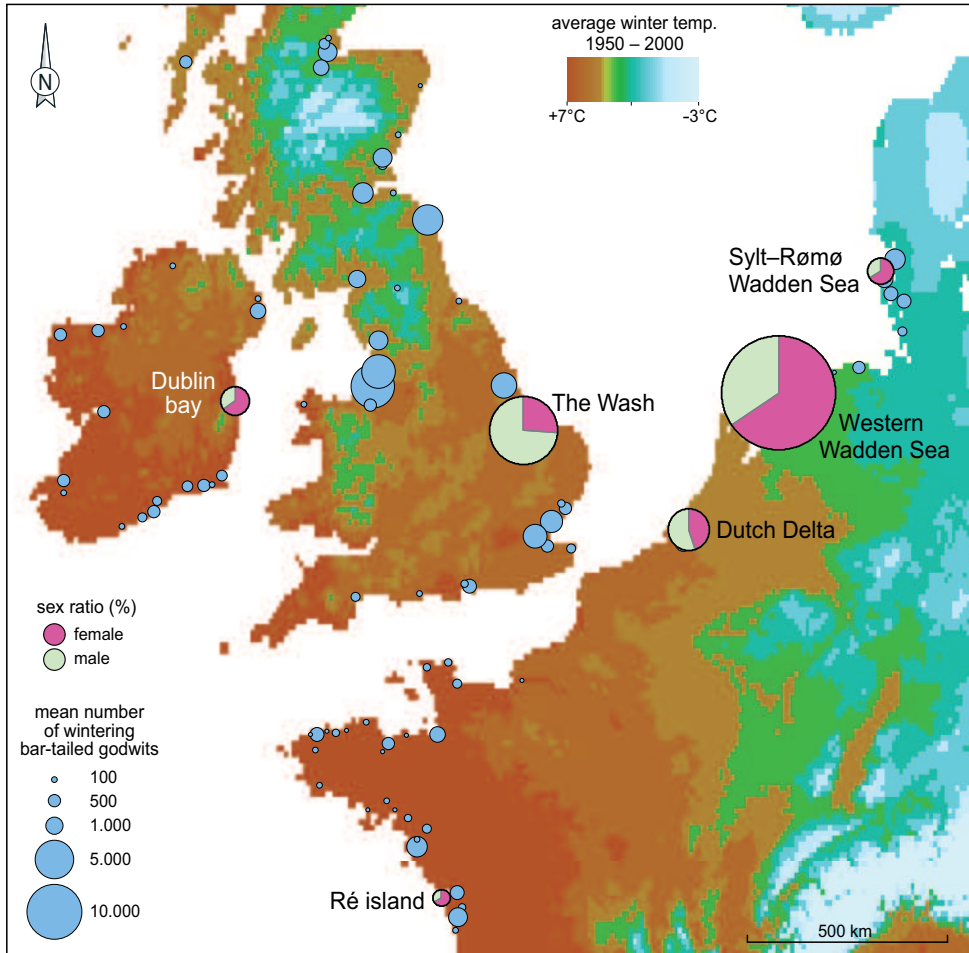


Figure 3.1. Map of North-western Europe, encompassing all wintering sites of bar-tailed godwits. Location of the study sites, with the mean January numbers of bar-tailed godwits (1995 – 2005) counted at high tide roosts, based on the Wetlands International midwinter count database. Mean winter temperature data (1950–2000), of high spatial resolution were derived from satellite images through interpolation of climate data (Hijmans *et al.* 2005). There is a clear gradient in temperature from Sylt-Rømø Wadden Sea to the Dutch Western Wadden Sea, to the UK and Ireland and southern wintering areas in France.

Sex-ratio counts

At each study site multiple sex-ratio counts were made. On average, a count covered 117 ± 108.4 SD individuals ($n = 61$) and sex ratios are expressed as % females. Since bar-tailed godwits show such a strong sexual dimorphism, the sex of each bird could easily be distinguished in the field on the basis of overall body size dimensions (see Zwartz *et al.* 1990; Scheiffarth 2001b), and all birds were observed in full winter (basic) plumage. Each flock was scanned by initiating a count with a randomly chosen individual and then by moving

away either always left or right from the first bird. This ensured that the same individual was not counted twice. We also noted the abdominal profile score per sex (ranging from 1 – lean – to 5 – abdomen bulging), to estimate body condition (Wiersma & Piersma 1995; Duijns *et al.* 2009), as individuals wintering at more northerly (and thus colder) sites are expected to increase energy stores (*sensu* Lindström & Piersma 1993) to survive days that food may not be accessible at all (e.g. the freezing over of mudflats in the Wadden Sea; see Zwarts *et al.* 1996). New counts were made when flocks arrived or departed. We validated our visual estimates of sex by assigning marked individuals of known sex in the field, based on morphological measurements (Prater *et al.* 1977) at different distances (20 – 150 m) and locations, prior to this study. That we correctly could assign 354 marked individuals of 364 sightings (97.3 %), suggests that our observational sex assignments were robust.

Benthic food availability

At locations where we observed (> 30 min) foraging flocks of bar-tailed godwits, 10 randomly located benthic samples were taken. Each sample consisted of a core of 0.0177 m² to a depth of 30 cm, which was sieved through a 1 mm mesh. Note that some prey items such as the lugworm *Arenicola marina*, a preferred prey for female bar-tailed godwits, can live up to depths of 30 cm. In order to split prey availability into shallow and deep prey we sieved the top 4 cm separately from the rest of the sample. The reason for separating prey availability in top and bottom in this manner was threefold. (1) From previous work on this species (Duijns & Piersma 2014), it was found that males were more successful in finding prey items after pecking, whereas females are most successful in finding prey items after probing (Table 3.2). Pecks include all behaviours that involve contact of the bill to the sediment surface (i.e. approx. 3 - 4 cm), and probes included all behaviours

Table 3.1. Main characteristics of the study sites, including distance to the breeding grounds, benthic biomass (distinguished in ash-free dry mass of top and bottom layer and percentage of AFDM in the bottom layer) and mean winter temperature.

Location	Distance (km) to breeding grounds	Biomass top layer (0 - 4 cm) g AFDM m ⁻² ± sd	Biomass bottom layer (5 - 30 cm) g AFDM m ⁻² ± sd	Percentage of AFDM ± sd in the bottom layer	Mean winter temperature (°C)
Sylt-Rømø Wadden Sea	1,940	1.73 ± 0.94	14.85 ± 13.40	80.09 ± 24.07	0
Western Wadden Sea	2,196	1.42 ± 1.35	8.06 ± 5.32	89.02 ± 9.65	2
The Wash	2,357	1.58 ± 1.31	2.22 ± 1.94	64.99 ± 16.98	4
Dutch Delta	2,388	1.11 ± 0.67	7.82 ± 6.58	75.28 ± 25.61	3
Dublin bay	2,502	0.47 ± 0.65	7.35 ± 2.96	93.25 ± 10.13	5
Ré island	3,093	0.39 ± 0.26	1.75 ± 2.26	80.79 ± 22.33	7

Table 3.2. Percentage of successful pecks and probes for male and female bar-tailed godwits observed in the Dutch Wadden Sea (Duijns & Piersma 2014).

	% successful pecks	<i>n</i>	% successful probes	<i>n</i>
Males	67	425	33	120
Females	13	42	87	124

involving insertion at least 1/3 of the bill into the sediment. (2) Separating the top 4 cm from the bottom part of the core has been the standard approach in the last two decades within our research group (Piersma *et al.* 2001; van Gils *et al.* 2006; Kraan *et al.* 2009b), enabling us to compare the benthic food abundances between different areas. (3) As this species' diet comprises mostly polychaetes (Duijns *et al.* 2013), which are mobile and can move through the sediment (Duijns & Piersma 2014), separating the benthic sample in more layers would result in many prey to break, making it impossible to distinguish in which layer they would predominantly occur.

All prey items were counted per species and stored in a 4% formaldehyde saline solution for later analyses. To determine the ash-free dry mass (AFDM; g), prey items were dried to constant mass in a ventilated oven at 55–60°C, after which dry mass was determined. The dried flesh of all species was incinerated at 560°C for 5h. The remaining ash-mass was then subtracted from the dry mass to determine the AFDM (Table 3.1).

Maintenance energy requirements

The maintenance energy requirements (M_{maint}) were calculated as basal metabolic rate (BMR; W) plus extra costs for thermoregulation (i.e. standardized heat loss, H_{sm} ; W) at environmental temperatures:

$$M_{\text{maint}} = \text{BMR} + H_{\text{sm}} \quad (\text{eqn 1})$$

where BMR per sex was calculated using the equation for shorebirds wintering in temperate Europe (Kersten & Piersma 1987):

$$\text{BMR} = 5.06 \times \text{BM} (\text{kg})^{0.729} \quad (\text{eqn 2})$$

in which body mass (BM; kg) was taken as the mean of winter catches at 0.270 and 0.323 kg for males and females respectively (NIOZ, unpubl. data). The standardized heat loss (H_{sm}) was calculated using Wiersma and Piersma's (1994) equation:

$$H_{\text{sm}} = (K_{\text{es}} + K_{\text{u}} u^{\text{exp}}) \times (T_{\text{b}} - T_{\text{a}}) - K_{\text{r}} R_{\text{g}} \quad (\text{eqn 3})$$

where K_{es} represents the thermal conductance of a live bird ($W\ ^\circ C^{-1}$), which was sex specific (0.0914 for males and 0.1111 for females; see Scheiffarth *et al.* 2002); The coefficients K_u and K_r , as well as the exponent for wind speed (exp), were based on the iterative regression procedure from Scheiffarth *et al.* 2002; u denotes the average winter wind speed ($m\cdot s^{-1}$), as obtained from the European Climate Assessment & Dataset project (www.eca.knmi.nl); T_b represents body temperature ($^\circ C$), which was assumed to be equal for both sexes (i.e. $41\ ^\circ C$); T_a represents the mean winter temperature ($^\circ C$; October to March), as derived from weather stations (Hijmans *et al.* 2005) based long-term averages (1950 – 2000) and R_g represents the mean winter global radiation ($W\ m^{-2}$) as obtained from SoDa (www.soda-is.com).

Migration costs

Flight distances (km) between wintering sites and a fixed site in the breeding grounds in Norway ($70^\circ 16'N$, $24^\circ 05'E$; Aarvak & Oien 2009), were measured using the distance tool in Google Earth ver. 7.1.2 (<http://www.google.com/earth/>) and multiplied by 2. This web-based software measures distances in great circle lines (or orthodrome lines), which are the shortest routes between two points on the globe (Alves *et al.* 2012). The migration costs (C_{flight} ; kJ) per sex were calculated using the following equation:

$$C_{flight} = \left(\frac{D}{S}\right) * C_{sex} \quad (\text{eqn 4})$$

where the distance (D ; km) is divided between the average flight speed (S) of 75 km/h and a sex-specific empirical flight cost (C_{sex}) of 67 and 55 kJ/h for females and males respectively (Piersma & Jukema 1990).

Statistical analyses

The frequency of occurrence of male and female bar-tailed godwits per area were analysed with linear mixed models (LMMs), where the response variable proportion of sex per observation session was logit transformed (Warton & Hui 2011), the explanatory variable was study site and observation session was the random effect. Differences in top and bottom layer biomass were analysed with a general linear model (GLM), and a Tukey's test was used to detect differences between sites. A Pearson correlation coefficient (r) was used to determine the relationship between the available biomass in the top and bottom layers and to determine the correlation between costs and benefits (i.e. food availability separated in top and bottom layer) and the % females per area. All analysis were performed using R, version 3.1.0 (R Development Core Team 2014) and the package lme4 (Bates *et al.* 2013) was used to fit linear mixed models.

Results

Large-scale sexual segregation

The sexes were differentially distributed over the six different sites across North-western Europe (LMM: $X^2 = 57.81$, $df = 5$, $P < 0.001$; Fig. 3.2). The Wash and the Dutch Delta area were different from the other four sites (Tukey's test: $P < 0.05$). Relatively more males were found in The Wash, while in Dublin bay, Sylt-Rømø Wadden Sea, Ré island and the Western Wadden Sea, a higher proportion of females was present (Fig. 3.2).

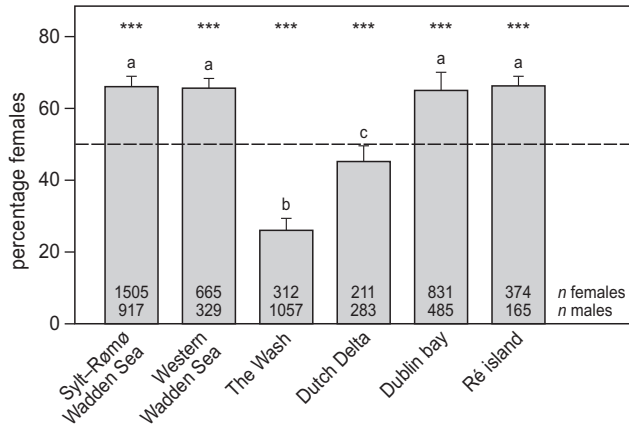


Figure 3.2. Geographical variation of the mean percentage (95% CI) of female bar-tailed godwits. The dashed line indicates a balanced sex ratio. Letters refer to the differences between the different sites and asterisks above the figure refer to significantly biased sex ratios within areas (all $P < 0.001$). Sample sizes of total number of birds counted per sex are given inside the bars.

Resource abundance

Study sites differed in prey biomass (i.e. g AFDM/m²) in the top (ANOVA: $F_{5,52} = 3.725$, $P = 0.006$; Fig. 3.3A) and in the bottom layer ($F_{5,54} = 4.998$, $P < 0.001$; Fig. 3.3B). However, due to high variation within sites, the difference was only due to the relatively high food abundance in the Sylt-Rømø Wadden Sea area, both for top as well as for bottom layer (Tukey's test: $P < 0.05$).

Maintenance and migration costs

The maintenance costs decreased in a linear fashion with increasing distance from the breeding grounds ($F_{1,10} = 39.75$, $R^2 = 0.79$, $P < 0.001$), with no difference between the sexes. Additionally, the cost of migration, at about 3% of the maintenance costs, turned out to be small and not affecting the overall picture. Hence, costs of wintering including the cost of migration also decreased linearly with increasing distance from the breeding

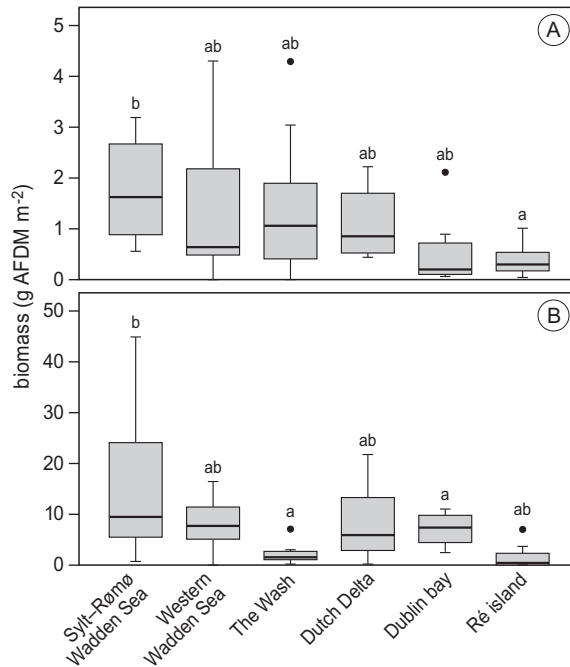


Figure 3.3. Biomass of (A) top 0 - 4 cm and (B) bottom 5 - 30 cm layer, as expressed in Ash Free Dry Mass (g AFDM m⁻²). The letters denote significance levels (Tukey's test), where the top layer of the Sylt-Rømø Wadden Sea area is different from Ré island and the bottom layer from the Sylt-Rømø Wadden Sea area is different from Dublin bay and the Wash.

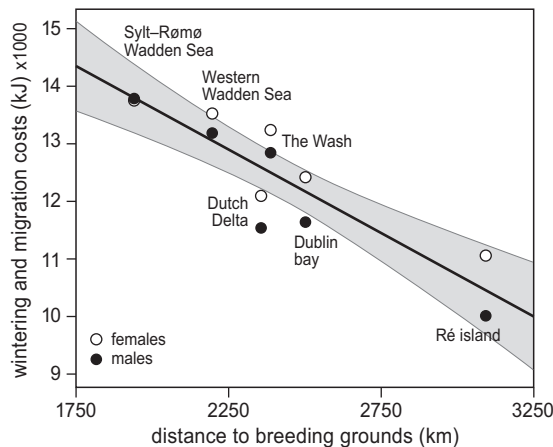


Figure 3.4. Relation between the costs of wintering (including the migration costs) in relation to the distance to their breeding grounds (the grey area represent the 95% CI level) for male and female bar-tailed godwits. There is a negative relation between the cost and the distance to the breeding grounds for both sexes ($P < 0.001$). Note that the difference in costs between females and males increases with increasing distance. This is consistent with Bergmann's rule as the thermoregulatory benefits of wintering further south increase fastest for the smallest sex (losing more heat per unit body mass).

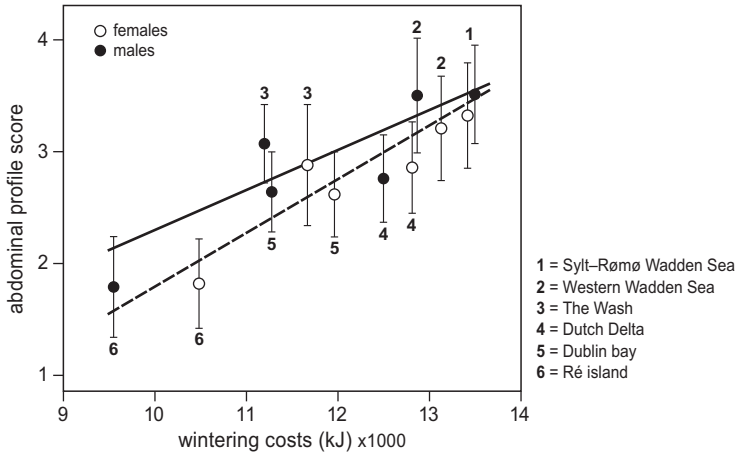


Figure 3.5. Mean abdominal profile score increases with increasing wintering costs, with significant differences between the sexes ($P = 0.006$; dashed line represents the males and the solid line the females) and a significant interaction term ($P = 0.016$).

grounds ($F_{1,10} = 48.03$, $P < 0.001$, $R^2 = 0.83$; Fig. 3.4). The abdominal profile scores suggest that male and female bar-tailed godwits did indeed adjust body mass to the costs of wintering (Fig. 3.5), with the males opting for a higher relative level of energy stores than females ($F_{3,585} = 105$, $P = 0.006$, $R^2 = 0.35$), with a significant interaction between sex and the cost of wintering ($P = 0.016$).

Resource partitioning vs maintenance and migration costs

The percentage of females wintering at a given site was not correlated with wintering costs ($r = 0.22$, $df = 4$, $P = 0.67$; Fig. 3.6A). Despite the fact that the biomass (g AFDM m^{-2}) in the top and bottom layer were positively correlated ($r = 0.50$, $n = 60$, $P < 0.001$), the percentage of females was only positively correlated with the biomass in the bottom layer ($r = 0.38$, $df = 59$, $P = 0.002$; Fig. 3.6B) and negatively with the biomass in the top layer ($r = -0.29$, $df = 59$, $P = 0.002$; Fig. 3.6C). There was a strong positive correlation between the percentage females and the percentage of AFDM in the bottom layer ($r = 0.88$, $df = 4$, $P = 0.02$; Fig. 3.6D). These patterns are consistent with the resource partitioning hypothesis.

Discussion

In this study we show evidence for resource partitioning between the sexes of a migratory shorebird with respect to their differential winter distribution at a large scale. At the level of sites separated by at least 200 km, we observed an unequal distribution of the sexes

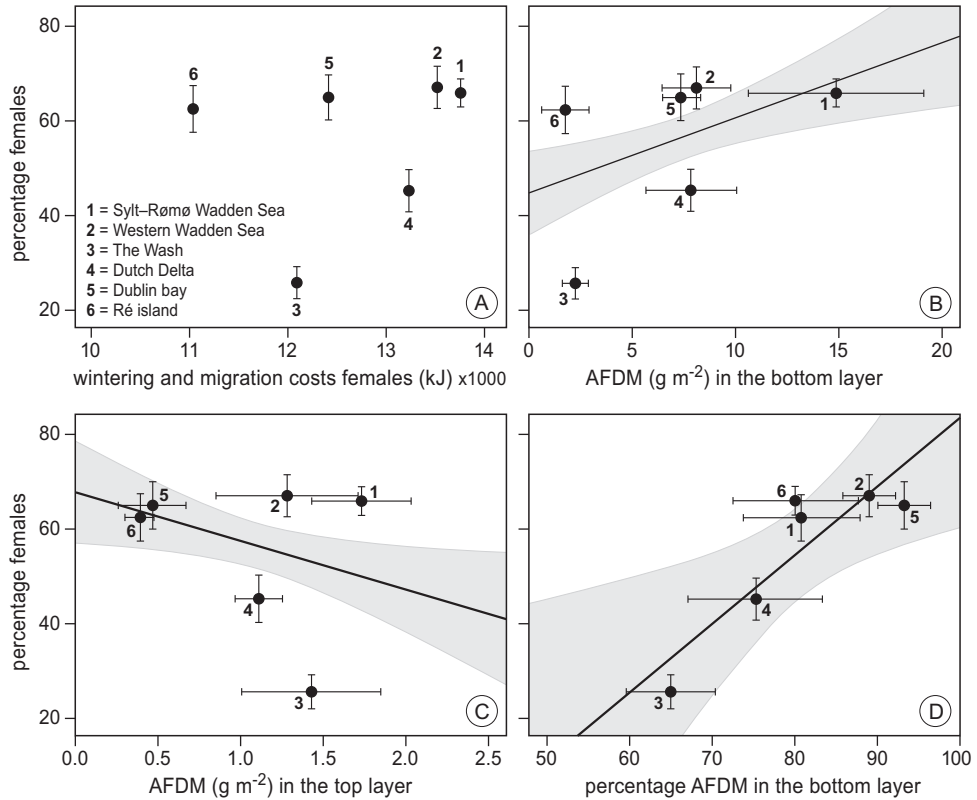


Figure 3.6. (A) Cost of wintering at different wintering site does not correlate with the percentage of females. (B) The (absolute) food abundance in the bottom layer (5 – 30 cm) is positively correlated with the percentage of females (the grey area represent the 95% CI level), (C) The (absolute) food abundance in the top layer (0 – 4 cm) is negatively correlated with the percentage of females. (D) The percentage of AFDM in the bottom layer is positively correlated with the percentage of females.

and could link this to the availability and vertical distribution of their benthic prey. Any relatively lower costs for the larger sex wintering closer to the breeding areas (according to Bergmann's rule) would surely be overridden by the fact that at the northerly sites food availability for the larger sex was much higher than for the smaller sex. Therefore, the present study suggests that at this scale the birds go where the food is most available to them. This was previously found in a species bar-tailed godwits share the general habitat with, but eating molluscs rather than polychaetes, the red knot *Calidris canutus* (e.g. van Gils *et al.* 2004; Quaintenne *et al.* 2011; Piersma 2012).

The uneven distribution between the sexes found in this study corresponded with data collected in a similar fashion at the Sylt-Rømø Wadden Sea area (Scheiffarth 2001b), Ré Island (P. Bocher, pers. obs) and in previous years at the Dutch Wadden Sea (S. Duijns pers. obs). Also at the Wash, where birds were caught by cannon nets, were the sex ratios

consistent with our study (Atkinson 1996). The results of this study therefore reveal a temporally consistent pattern.

Our results provide an interesting contrast with data on sex-related differences in coastal habitat use in a congener, the Icelandic black-tailed godwits *Limosa limosa islandica* (Alves *et al.* 2013b). Here, over the entire winter range during the non-breeding season, no evidence of large-scale sex differential distribution was found, when compared to seasonal population estimates of sex ratios. The sexes differed in their selection of prey types and sizes, leading to small-scale sexual segregation within, rather than between estuaries. In bar-tailed godwits such small-scale segregation between male and females also exists, and was documented for coastal Guinea-Bissau (Zwarts 1988), in the UK (Smith & Evans 1973; Summers *et al.* 2013), the western Wadden Sea (Both *et al.* 2003), and in France (P. Bocher, pers. obs). That females seemed more abundant than males at the sampled sites is unlikely due to a biased overall sex ratio, since unbalanced wild bird populations tend to be male-skewed rather than female-skewed (Donald 2007).

These results however, do not mean there are no expenditure-related costs of wintering close to the breeding grounds. That male and female bar-tailed godwits adjust their body mass with the males opting for a relatively higher level of energy stores than females suggests that they may need a larger safety margin because they would face a greater risk of being without food than females (e.g. MacLeod *et al.* 2006; 2007). Due to their larger surface to volume ratios, males will also have more variable energy expenditures between days. If we interpret the levels of stores as indication of higher costs carried due to risk aversion, or buffering against lower quality habitat (MacLeod *et al.* 2008), males might thus be in less favourable habitats. Their greater nutrient stores would enable them to survive periods of unpredictable food resources (Rogers 1987).

Wintering closer to the breeding grounds could facilitate the timing of migration, as residing closer to breeding area, local weather systems may promote an advantageous migratory flight strategy (Piersma *et al.* 1994). However, escape performance in birds generally is reduced by extra body mass, as it leads to a decrease in take-off speed and manoeuvrability (e.g. Dietz *et al.* 2007). As both sexes, based on their abdominal scores (Fig. 3.5), have a larger anti-starvation safety margin at colder sites, it could make both sexes more susceptible for predation there. Note that we never witnessed any attacks by aerial predators.

In conclusion, the resource partitioning hypothesis best explained the distribution between the sexes, where the larger females may have a subtle benefit of wintering close to the breeding area, as their relatively smaller stores suggest a lower risk of starvation relative to males.

Acknowledgements

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4

Foraging site selection of two subspecies of bar-tailed godwit *Limosa lapponica*: time minimizers accept greater predation danger than energy minimizers

Sjoerd Duijns, Jacintha G.B. van Dijk, Bernard Spaans, Joop Jukema, Willem F. de Boer & Theunis Piersma

Abstract

Different spatial distributions of food abundance and predators may urge birds to make a trade-off between food intake and danger. Such a trade-off might be solved in different ways in migrant birds that either follow a time-minimizing or energy-minimizing strategy; these strategies have been assigned to two subspecies of bar-tailed godwits *Limosa lapponica* that use the European Wadden Sea during northward migration. At the study area on Terschelling, we recorded feeding site selection, time budgets and intake rates (prey/min) in the period that both *lapponica* (energy minimizer) and *taymyrensis* (time minimizer) subspecies were present (late April till the end of May 2007). Prey availability (number of prey/m²) was negatively correlated to the distance from cover. Based on resightings of colour-ringed bar-tailed godwits, *taymyrensis* was foraging closer to cover, and for a higher proportion of time than *lapponica* (67% vs. 33%). During the high tide period *taymyrensis* was also foraging on inland coastal meadows. Moreover, *taymyrensis* was more vigilant than *lapponica*, whereas *lapponica* showed more resting and preening behaviour. *Lapponica* had a higher instantaneous intake rate, but *taymyrensis* had a higher overall intake rate and the birds were more successful in taking larger prey items than *lapponica*. Supposedly, due to the increased foraging time and additional foraging on the inland meadows, the time-minimizing *taymyrensis* achieved a higher fuel deposition rate than *lapponica*. *Taymyrensis* shifted towards food-rich areas, apparently accepting higher predation risks, whereas energy-minimizing *lapponica* avoided predation danger by foraging further from cover.

Introduction

A successful migration strategy results from optimizing at least three selective factors: time, energy and predation (Alerstam & Lindström 1990). Birds may minimize the time for migration, i.e. flight as well as fuelling time (maximize speed of migration), minimize the total energy cost of migration (energy cost of transport), or minimize predation risk during migration. Depending on the migration and energetic status, individuals may opt for different solutions to balance these selective factors. Theoretical studies of migration usually incorporated the dichotomy between time and energy minimization (Lindström & Alerstam 1992; Hedenström 1993; Vrugt *et al.* 2007), and only few studies addressed the issue of predation minimization (e.g. Weber *et al.* 1998; Burns & Ydenberg 2002). Most empirical studies that have focused on predation minimization during migration are concerned with passerines (e.g. Lindström 1990; Fransson & Weber 1997; Schmaljohann & Dierschke 2005) and to a lesser extent with shorebirds, such as western sandpiper *Calidris mauri* (Ydenberg *et al.* 2002; Lank *et al.* 2003; Pomeroy 2006; Pomeroy *et al.* 2006; 2008), dunlin *Calidris alpina* (Dierschke 1998) and ruddy turnstone *Arenaria interpres* (Metcalfe & Furness 1984). To explore in which way predation danger modulates decisions of birds on migration, we investigated foraging behaviour of two subspecies of bar-tailed godwit *Limosa lapponica* that are known to exhibit contrasting migration schedules.

The bar-tailed godwit is a long-distance migrant of which two subspecies occur along the East-Atlantic Flyway (Engelmoer & Roselaar 1998; Engelmoer 2008). These two subspecies follow a leap-frog migration, with the European Wadden Sea as staging and stopover site (Drent & Piersma 1990). The subspecies *taymyrensis* (600 000 birds; Wetlands International 2006) visits the Wadden Sea twice a year during one month to replenish stores needed for migration between breeding areas in northern Siberia and wintering sites in West Africa (Smit & Piersma 1989; Engelmoer 2008). *Taymyrensis* follows a time-minimizing migration strategy (Scheiffarth *et al.* 2002): it faces a tight time schedule before leaving to the breeding grounds, and devotes as much time as possible for fuel deposition, while minimizing other energy consuming activities. By increasing foraging time, the time at the stopover site is minimized, and consequently time spent on migration is minimized. *Lapponica* (120 000 birds; Blew & Südbeck 2005; Wetlands International 2006), on the other hand, stays in the Wadden Sea for the entire winter before leaving to less distant breeding grounds in northern Scandinavia and the White Sea area (Cramp & Simmons 1983; Prokosch 1988; Engelmoer 2008). *Lapponica* follows an energy-minimizing migration strategy (Scheiffarth *et al.* 2002), as the subspecies builds up the required spring reserves over a long period before leaving to the breeding grounds. These birds do not have to forage the entire available time, which enables them to spend more energy and time on activities as moulting and predation avoidance.

Aerial predators of wader species, such as falcons, often make use of vegetation, hills, dikes and other structures to cover their approach when hunting close to the salt marsh (Bijlsma 1990; Cresswell & Whitfield 1994). Several studies have confirmed that the hunting success of aerial predators is higher on salt marshes than on open mudflats without any cover, suggesting that predation risk declines with distance from cover (Cresswell 1994; Ydenberg *et al.* 2002; Whitfield 2003; Dekker & Ydenberg 2004; van den Hout *et al.* 2008). To study the role of predation minimization on the stopover ecology of the two bar-tailed godwit subspecies, we focused on the importance of distance from cover. We recorded feeding site selection, time budgets and intake rates in the period that both subspecies are present in the Wadden Sea during northward migration from late April to the end of May.

Methods

Study area

Data were collected on the tidal flats and on inland coastal meadows of the Dutch Wadden Sea island Terschelling (53°24'N, 05°21'E; Fig. 4.1). Bar-tailed godwits are known to primarily forage on tidal flats (Cramp & Simmons 1983), although in spring they also use inland coastal meadows for feeding (Piersma *et al.* 1993; van de Kam *et al.* 2004).

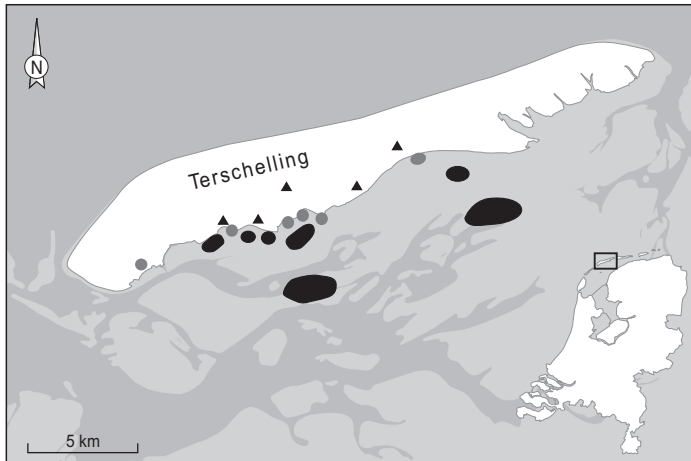


Figure 4.1. The island Terschelling located in the Dutch Wadden Sea. The black circles indicate sites of benthic sampling and main foraging areas of bar-tailed godwits. The intermediate grey circles indicate the most important high tide roosts. The small inland triangles represent the main feeding sites of the meadows.

Population identification

In 2000 the Royal Netherlands Institute for Sea Research (NIOZ) on Texel, in association with various ringing groups, started a colour-ringing program on the bar-tailed godwit. Based on the catching and/or previous resighting dates of colour-ringed individuals, they can be assigned to either the subspecies *lapponica* or *taymyrensis*. Birds caught and/or resighted between October and March in the Wadden Sea were assigned to the subspecies *lapponica*, and individuals caught and/or resighted in West Africa to the subspecies *taymyrensis*. In the Dutch Wadden Sea area, many birds were caught with 'wilsternets' (Jukema *et al.* 2001) on inland coastal meadows in May, or were resighted only in May. It is estimated that only a small fraction (6.7%) of the birds caught in May are *lapponica* (NIOZ, unpubl. data). We therefore assume that all birds caught and/or resighted only in May are *taymyrensis*. Up to March 2007, a total of 2,173 bar-tailed godwits were colour-ringed, of which 15% were *lapponica* and 85% *taymyrensis*.

Since only a small fraction of the birds observed were colour-ringed, we tested the degree to which the two subspecies mixed while foraging. If they would not mix, the presence of colour-ringed individuals in a flock could indicate to which subspecies the flock belonged. In all flocks observed on inland coastal meadows and on tidal flats during low tide (3 hours before and after low water) that contained multiple colour-ringed individuals ($n = 32$), it never occurred that an assigned colour-ringed *lapponica* was foraging together with an assigned *taymyrensis* (Fisher's exact test: $P < 0.001$). Therefore, we assumed that flocks could be assigned to a subspecies on the basis of the identity of single individuals in the flock. In total we resighted 371 different colour-ringed bar-tailed godwits, of which 69 were *lapponica* and 302 *taymyrensis*.

Observations and benthos sampling

Behaviour of bar-tailed godwits was recorded during daylight on tidal flats, high water roosts and inland coastal meadows. Within each flock, 2-min focal animal observations were conducted (Martin & Bateson 1993) of randomly chosen birds with 20–60 × zoom spotting scopes. Five different categories were distinguished: foraging, resting, preening, vigilance and flight. Vigilant behaviour was scored when the bird had raised the head from the head-down foraging position to at least a horizontal position ('head-up vigilance'; Metcalfe 1984). Flight behaviour was scored when a focal bird flew in the air. Bar-tailed godwits are highly dimorphic in bill- and body size, which can affect their foraging behaviour (Smith & Evans 1973; Cramp & Simmons 1983; Glutz von Blotzheim *et al.* 1985), therefore the sex of each focal bird was recorded. Sex was determined by body size, coloration and bill length (Both *et al.* 2003). Abdominal profiles (ranging from 1 – lean – to 5 – abdomen bulging – were scored to estimate the body condition of the birds (Wiersma & Piersma 1995). Every 30 min the number of individuals was estimated, and the contours of the flock were plotted on Google Earth maps.

Prey items were scored to determine the intake rate. Bar-tailed godwits in the Wadden Sea mudflats mainly feed on lugworm *Arenicola marina*, ragworm *Nereis diversicolor*, catworm *Nephtys hombergii* and bristleworm *Scoloplos armiger* (Scheiffarth 2001a). When foraging on inland coastal meadows, bar-tailed godwits mainly feed on crane fly larvae *Tipula paludosa* (Piersma *et al.* 1993; van de Kam *et al.* 2004). The prey items were scored in four classes: (1) small polychaetes (all items up to half the bill length; i.e. smaller than 5 cm), (2) large polychaetes (all items exceeding half the bill length; i.e. larger than 5 cm), (3) lugworms, and (4) crane fly larvae.

To assess food availability of the tidal areas, soil samples were taken on spots where foraging flocks had been observed. Per foraging area, 10 random samples with a depth of 15 cm (equal to ± 1.5 times the bill length) were taken with a standard PVC tube (1/56 m²) in a randomly placed square of 100 × 100 m. The samples were sieved over a 1-mm mesh sieve and the four main polychaetes species were identified and measured by a ruler to the nearest 0.5 mm. Per sample, we calculated the abundance of prey/m². As our sampling sessions on inland coastal meadows failed, we took crane fly densities from a similar grassland polder on another Dutch Wadden Sea island, Schiermonnikoog (Tinbergen 1981).

Cover

To assess the distance from cover per subspecies, the location of each colour-ringed individual on the tidal flat and the inland coastal meadows was mapped. The distance (m) from each foraging location to cover (e.g. dike, tree, and scrub) was measured from the centre of the flock. In this way the distance of each foraging colour-ringed individual from cover could be determined.

Data analysis

For the analysis we merged observations into so-called 'sessions', with a mean for both sexes. Each session ended when the observed flock flew up, the flock size changed or the session exceeded one hour. Over all tidal hours, we performed 1,569 observations (692 low tide hours; i.e. 3 hours before and after low water) which we pooled per sex into 445 sessions (195 low tide hours), resulting in a mean number of 3.5 observations (3.5 low tide hours) per session. In the meadows we conducted 192 observations which were also pooled per sex into 49 sessions, resulting in 3.9 observations per session. Analyses are based on the sessions, with mean values for males and females to correct for sex in the model, hence sample sizes refer to sessions and not to individual birds. In all models sex is included as fixed factor to allow for morphological and behavioural differences between the sexes. Tidal and weather (i.e. temperature, wind speed, wind direction) data were obtained from Rijkswaterstaat Rijksinstituut voor Kust en Zee and the Royal Netherlands Meteorological Institute (KNMI), and were used as covariates whenever they were significant in the model.

Taymyrensis shows fast increases in body mass when staging in the Wadden Sea in May, whereas *lapponica* increases with a rather slow rate (Prokosch 1988; Drent & Piersma 1990). To determine the fattening rate of the two subspecies, mean abdominal profiles (\pm SE) per session of all tidal hours during the fattening period of both subspecies were used. A general linear model (GLM) was performed, with date as covariate, to assess differences between the two subspecies.

To assess differences in intake rate between the two subspecies, we calculated the instantaneous intake rate (prey/min) as the number of prey items taken when foraging. Only sessions of low tide hours were used in the calculation. The overall intake rate (prey/min) is defined as the number of prey items taken during entire focal observation periods (2 min) and further includes all tidal hours, including the inland coastal meadows. Besides the overall intake rate, we calculated the intake rate for each of the four prey items (i.e. small polychaetes, large polychaetes, lugworm, crane fly larvae), which were all log-transformed. For the instantaneous and overall intake rate calculations, a GLM was performed with sex as an additional fixed factor. Data were log-transformed to satisfy the assumption of normality (Zar 1996). Time budgets of both subspecies were determined by the percentage of time spent per activity within the 2-min observations.

Effects of cover (as proxy for predation danger) on foraging behaviour were tested by correlation analysis. The mean time (s) per session spent on each behavioural category was converted into percentages and arcsin-transformed. Only data of the low tidal hours have been used, as during high tide birds are much limited in where to forage. Moreover, we examined whether intake rate and prey availability were correlated with distance to cover. Analyses were performed with Pearson correlation (r) or Spearman's Rho (r_s). Graphical data of these correlations were pooled into 250-m points. Meadows are shown in graphs, but are excluded from correlation analyses. We performed GLM's to test for differences in behavioural activity between the two subspecies, with sex as additional fixed factor, by pooling data from all tidal hours. The behavioural category flight did not satisfy the assumption of normality, and therefore the non-parametric Mann-Whitney U test was used. Differences in foraging mean distance (\pm SE) from cover between the two subspecies were analysed with a Student's t -test, in which data of low tide hours and meadows were used.

Basic assumptions of parametric tests were examined by testing for normality, residual analysis, and the application of the Levene's test for equality variances. The reported mean values and SE are back-transformed without corrections. All analyses were performed using SPSS version 15.0.

Results

Seasonal occurrence

From March until mid-April 2007, only colour-ringed *lapponica* individuals were seen. An influx of colour-ringed *taymyrensis* began on 22 April (Fig. 4.2). From the beginning of May, *lapponica* started to leave the study area and gradually decreased in numbers in May. *Taymyrensis* did not leave the study area until the end of May.

Fuelling patterns

Taymyrensis were on average slimmer than *lapponica* individuals (GLM: $F_{70,650} = 5.30$, $P < 0.001$). However, in *taymyrensis* the daily increase of abdominal profile was almost 10 times faster than in *lapponica* (Fig. 4.3).

Correlations with distance to cover

Resting and preening increased with distance from cover, whereas time spent foraging and prey availability decreased with distance (Fig. 4.4). Vigilance, intake rate and time spent flying were not correlated with distance from cover. *Lapponica* foraged at a mean distance of 397 ± 67 m from cover, and *taymyrensis* at a mean distance of 85 ± 21 m from the nearest cover (t-test, $t_{21} = 4.26$, $P < 0.001$). In particular *taymyrensis* on inland coastal meadows were foraging close to cover.

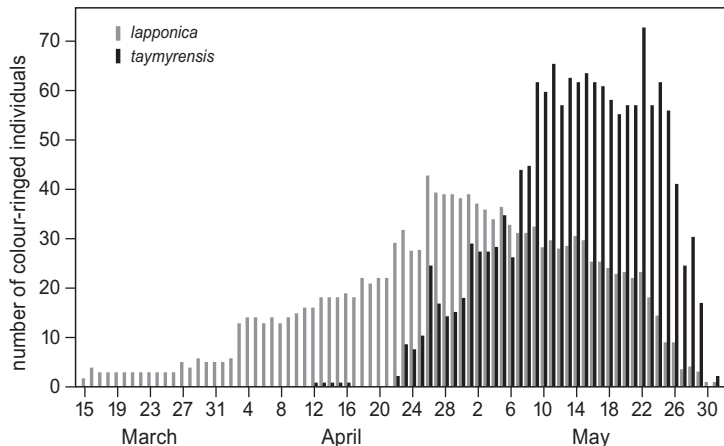


Figure 4.2. Daily number of resighted colour-ringed *lapponica* and *taymyrensis* bar-tailed godwits on Terschelling, spring 2007.

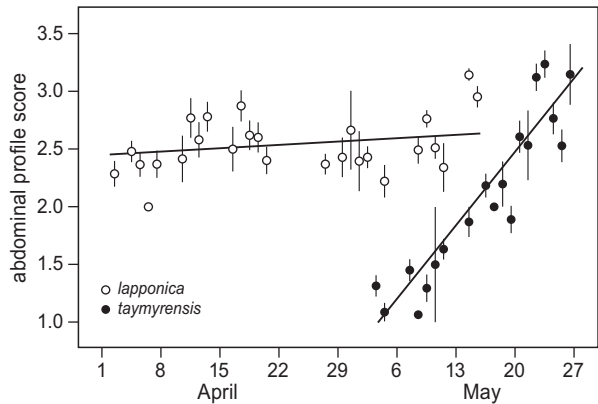


Figure 4.3. Abdominal profile score (mean \pm SE) of two bar-tailed godwit subspecies throughout spring 2007. Regression coefficients are 0.004 AP-units/d for *lapponica* ($F_{1,434} = 7.14$, $R^2 = 0.016$, $P = 0.008$) and 0.043 AP-units/d for *taymyrensis* ($F_{1,283} = 136.13$, $R^2 = 0.325$, $P < 0.001$).

Foraging behaviour

Taymyrensis spent more time foraging than *lapponica* (Table 4.1), as the subspecies was still foraging during high tide when *lapponica* was roosting (Fig. 4.5). *Lapponica* spent more time resting and preening, whereas *taymyrensis* was more vigilant. There was no difference in time spent flying between the subspecies.

During low tide, *lapponica* had a higher instantaneous intake rate (3.5 prey/min) than *taymyrensis* (2.8 prey/min; GLM: $F_{1,188} = 4.27$, $P = 0.040$). However, the overall intake rate showed an opposite trend (1.1 and 1.3 prey/min, respectively; $F_{1,431} = 6.56$, $P = 0.011$). *Taymyrensis* ingested large polychaetes at a higher rate than *lapponica*, whereas intake rates of small polychaetes and lugworms did not differ between the subspecies (Table 4.2). No comparison was made for cranefly larvae, as only *taymyrensis* was foraging on inland coastal meadows. For *taymyrensis*, intake rates on tidal flats and meadows were similar (1.2 prey/min; $F_{1,277} = 0.97$, $P = 0.326$).

Table 4.1. Time budgets of two subspecies of *Limosa lapponica*, based on 2-min observation periods. Mean values and SE are back-transformed without corrections.

Behavioural category	<i>Lapponica</i> $n = 166$		<i>Taymyrensis</i> $n = 285$		Test	P
	Mean	Upper/lower SE	Mean	Upper/lower SE		
Foraging	33.12	5.22/4.92	66.82	4.46/4.52	$F_{1,439} = 20.47$	< 0.001
Rest	34.69	5.12/4.89	14.77	2.40/2.22	$F_{1,437} = 8.68$	0.003
Preen	5.27	1.18/1.06	1.84	0.37/0.34	$F_{1,442} = 15.80$	< 0.001
Vigilant	2.21	0.33/0.31	3.42	0.50/0.47	$F_{1,440} = 16.93$	< 0.001
Flight	5.00	0.93/0.93	3.70	0.58/0.58	$U = 22072.50$	0.151

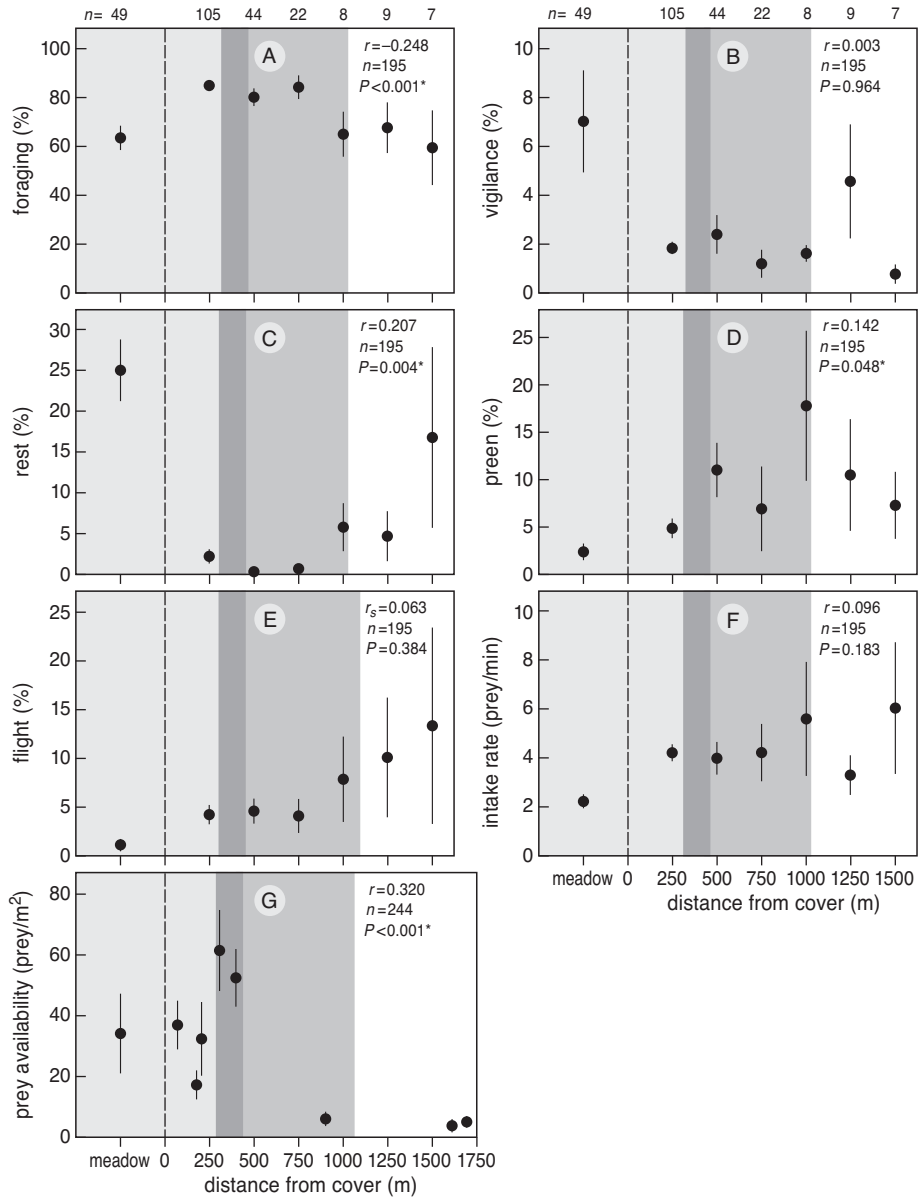


Figure 4.4. Bar-tailed godwit time budgets (%; A–E) and intake rate (prey/min; F), and prey availability (prey/m²; G) in relation to distance from cover (pooled into 250 m classes). The dotted line represents cover. The light grey area represents 95% CI of all resighted colour-ringed *taymyrensis* individuals, the dark grey area represents 95% CI of all resighted colour-ringed *lapponica* individuals, and the darkest grey area is the overlap. Correlations are shown in each graph (meadows excluded from analysis). Sample sizes refer to number of sessions. * indicates $P < 0.05$.

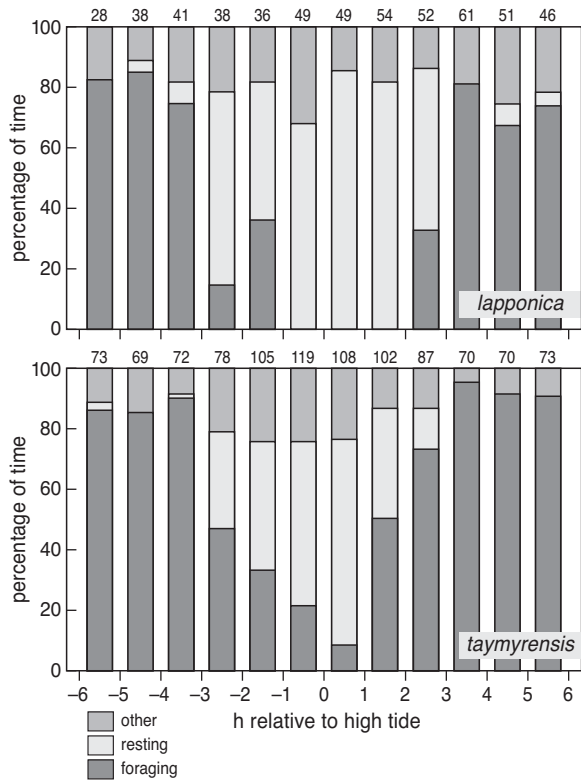


Figure 4.5. Activity pattern of two bar-tailed godwit subspecies in relation to tidal stage. The category 'other' includes preening, vigilance and flight. Sample sizes (total number of birds recorded) are given for each hour.

Table 4.2. Overall intake rate (prey/min) by prey class taken by two subspecies of bar-tailed godwit. Mean values and SE are back-transformed without corrections.

Prey items	<i>Lapponica</i> n = 160		<i>Taymyrensis</i> n = 236		Test	P
	Mean	Upper/lower SE	Mean	Upper/lower SE		
Small polychaetes	1.05	0.14/0.13	1.22	0.011/0.01	$F_{1,393} = 1.035$	0.310
Large polychaetes	0.07	0.01/0.01	0.13	0.01/0.01	$F_{1,393} = 9.486$	0.002
Lugworm	0.02	0.00/0.00	0.01	0.00/0.00	$F_{1,393} = 0.863$	0.354

Discussion

By using resightings of colour-ringed individuals, we confirmed the established patterns of *lapponica* and *taymyrensis* presence in the Wadden Sea (Prokosch 1988; Piersma & Jukema 1990; Scheiffarth *et al.* 2002; Engelmoer 2008). *Lapponica* was present during winter till mid-May and *taymyrensis* from late April to late May. The idea that 20% of the wintering bar-tailed godwit population in the Wadden Sea consists of *taymyrensis*, as suggested by Engelmoer (2008) on the basis of biometry, was not supported by our resightings.

Body stores of *taymyrensis* arriving in the Wadden Sea at the end of April were close to depletion. Throughout their stay of only one month they were able to prepare for the next leg of the migration route of more than 3000 km. The apparently high daily food intake was achieved by (1) foraging a large proportion of time per day, which they achieved by feeding during high and low tide close to the cover on mudflats, (2) feeding on inland coastal meadows and (3) selecting sites where they found large prey species. Thus, our results confirm that *taymyrensis* follows a time minimizing strategy (Scheiffarth *et al.* 2002).

Taymyrensis foraged close to cover in areas with a higher prey density. By foraging close to cover, birds are more vulnerable to surprise attacks by raptors (e.g. Cresswell & Whitfield 1994; van den Hout *et al.* 2008), and apparently *taymyrensis* accepted a higher predation danger in favour of better feeding opportunities. The trade-off between food and danger has inspired many investigators (e.g. Milinski & Heller 1978; Sih 1980; Brown & Kotler 2004). Dark-eyed juncos *Junco hyemalis* which had been deprived of food opted for a riskier habitat to enhance their feeding rates (Lima 1988). In a study of western sandpipers, heavy birds predominated at safe stopover sites, while leaner birds used sites where predation danger was greater (Pomeroy 2006). Our observations of bar-tailed godwits add well to these findings: initially heavier bar-tailed godwits foraged further from cover, and leaner birds closer to cover. Thus, the benefit of better feeding opportunities outweighed the risk of selecting more dangerous areas. *Taymyrensis* were foraging at extreme low distances from cover when foraging on inland coastal meadows during high tide, as foraging on meadows necessarily entails foraging closer to cover (e.g. creeks, trees or buildings).

A study on ruffs *Philomachus pugnax* showed that birds foraging on meadows avoided fields that were located near trees and buildings (Verkuil & de Goeij 2003). We suspect that especially individuals that face difficulties in reaching their departure fuel load in time, would supplementary forage in the meadows. Caldow *et al.* (1999) showed that oystercatchers *Haematopus ostralegus* tend to feed in meadows to supplement their low-tide intake on the tidal flats. Piersma & Jukema (1993) found that bar-tailed godwits at a coastal site were 40 g heavier than those feeding on an inland meadow. In line of this

finding, we found the mean abdominal profile score (corrected for date) of 1.8 in meadows compared to 2.2 on tidal flats (GLM: $F_{1,279} = 10.424$, $P = 0.001$).

We suggest that bar-tailed godwits traded distance to cover against food abundance. By increasing foraging time and by facing a higher predation risk, the time-minimizing *taymyrensis* ensured the accumulation of a sufficient fuel load, within a short stopover period, whereas the energy-minimizing *lapponica* minimized predation by foraging in the safer areas. It is expected that these strategies influence survival rates, and we predict higher mortality rates due to a higher predation risk for the *taymyrensis* subspecies during the migration seasons.

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5

Bar-tailed godwits *Limosa l. lapponica* eat polychaete worms wherever they winter in Europe

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Abstract

Across the European wintering range bar-tailed godwits *Limosa lapponica lapponica* selected polychaete worms and especially ragworms *Hediste diversicolor*, with differences between areas due to variations in prey availability. To determine the diet of bar-tailed godwits across their wintering range in Europe by the analysis of droppings, collected at five important wintering sites. Diet was estimated by the identification of undigested prey remains in droppings. We provide the rationale for quantifying the contributions of jawed and non-jawed polychaetes. We identified 18 different prey species in the diet of wintering bar-tailed godwits. The ragworm was the most common prey item and the only one actively selected. Ragworms, on average, contributed 79% to the diet in terms of biomass, followed by king ragworm *Alitta virens* (with 17% biomass) and lugworms *Arenicola marina* (with 2%). Polychaetes such as *Alitta succinea* and *Scoloplos armiger* were also regularly found in the diet. Bivalves, snails and crustaceans contributed less than 1% to the diet. This study highlights and confirms the importance of polychaete worms in the diet of European-wintering bar-tailed godwits.

Introduction

Classical foraging theory predicts that animals select their food rationally, i.e. in such ways that maximum fitness gains are achieved (Stephens & Krebs 1986). Such 'optimal' foraging decisions vary with ecological context, and their rationale underlies relationships between population level processes and changes in food quality and abundance (e.g. Goss-Custard 1977; van Gils *et al.* 2006; Piersma 2012). However, any understanding of the relevant food-predator relationships starts off with solid descriptions of diet (e.g. Dekinga & Piersma 1993; Moreira 1994a; Quaintenne *et al.* 2010). Diets can be reconstructed in direct and indirect ways. Direct methods are: (1) examining the digestive tracts of the birds, (2) taking regurgitation samples, or (3) the lavage method (Verkuil 1996). All these methods have limitations, as the birds have to be caught and sometimes euthanized (e.g. Barrett *et al.* 2007). Direct visual observations of foraging birds often yield large amounts of unidentified prey (e.g. Scheiffarth 2001a), so the alternative is to study the diet based on indirect methods, such as pellet- and dropping analysis (e.g. Alerstam *et al.* 1992; Sanchez *et al.* 2005). Hard parts from prey, such as jaws and chaetae of worms, or hinges of bivalves are indigestible and often remain in birds droppings, which can be used to reconstruct the diet. The advantages of these methods are that they are non-invasive and simple to perform (e.g. Alerstam *et al.* 1992; Dekinga & Piersma 1993).

Here we provide a study of the diet of a shorebird species that forages on prey that are difficult to assess: small fragile polychaete worms and similar invertebrates. Shorebirds are gregarious and occur in vast and open landscapes outside the breeding season and have been the focus of a large body of feeding ecological work (e.g. Zwarts & Wanink 1991; van de Kam *et al.* 2004; Piersma & van Gils 2011; Piersma 2012).

Although the molluscivore shorebirds in the Wadden Sea have recently shown steady declines, the wintering population of bar-tailed godwits *Limosa lapponica lapponica* has seen an increase (Ens *et al.* 2009). During the non-breeding season in the German Wadden Sea the diet (i.e. prey items) consisted of 99% polychaetes (Scheiffarth 2001a), whereas in Spain the diet (i.e. prey items) consisted of 83% polychaetes (Perez-Hurtado *et al.* 1997). Extending these studies, we here examine the diet of the *lapponica* subspecies throughout most of its coastal wintering range in northwest Europe (Scott & Scheiffarth 2009). Our diet assessments were based on the analysis of droppings collected on intertidal foraging areas.

Methods

Study sites

Droppings were collected in intertidal foraging sites at five important wintering areas

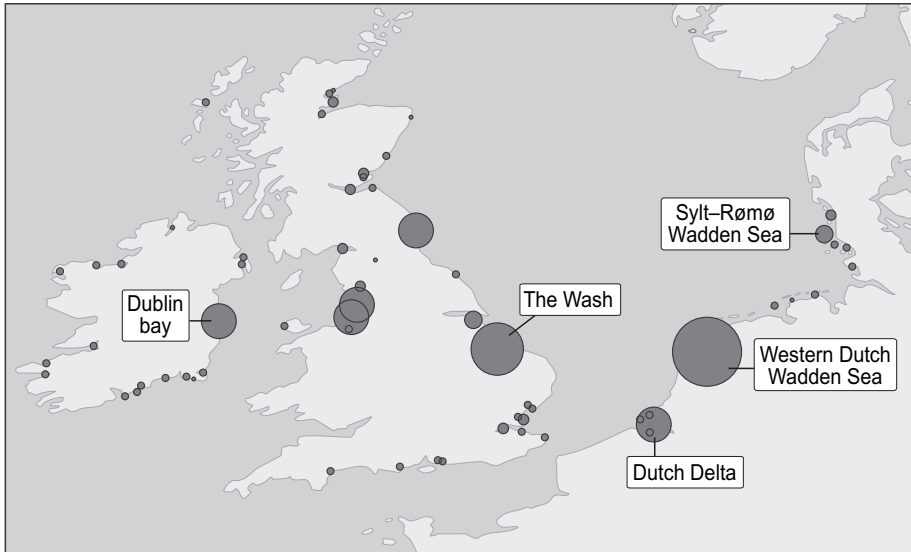


Figure 5.1. Location of the study sites, with the mean January numbers of bar-tailed godwits (1995 – 2005) counted at high tide roosts, based on the Wetlands International midwinter count database. The surface of the dots reflects to the mean winter abundances of bar-tailed godwits. As a gauge, the Western Dutch Wadden Sea had the highest average number with almost 40.000 individuals, followed by the Wash with an average of 14.000 individuals.

during the non-breeding season 2010-2011 (Fig. 5.1). In order to minimize seasonal and year-to-year variations in prey abundance, availability and quality (Zwarts & Wanink 1993), as well as in the preferences of birds, because of changes in state (e.g. Piersma 2012), we carried out all fieldwork in the briefest possible time period within a single winter season. The German Wadden Sea island of Sylt (55°01'N, 8°26'E) was visited mid October 2010, the Dutch Delta area (51°40'N, 04°07'E) late October 2010, the Wash in the UK (52°56'N, 00°19'E) early November 2010, and Dublin bay in Ireland (53°19'N, 06°11'W) was visited late November 2010. Finally the Dutch Wadden Sea island of Griend (53°14'N, 05°15'E) was visited early February 2011.

Benthic sampling

At locations where we had been observing foraging flocks of bar-tailed godwits for over 30 min, 10 random benthic samples (1 / 56 m²) were taken to a depth of 25–30 cm and sieved through a 1 mm mesh. As the duration of food processing would be ca. 25 min (Scheiffarth 2001a; pers. obs.), waiting at least 30 min before assigning a spot as the one to sample for benthos, ensured that we collected droppings and food abundance data based on ingestions on that location. All potential prey items were counted per species and stored in 4% formaldehyde saline solution for later analyses in the laboratory, where size

classes (lengths) were measured to the nearest mm. To determine the AFDM (g) and shell mass of prey, the fleshy parts were removed from the shell and both shell and flesh were dried to constant mass in a ventilated oven at 55–60°C. Dry mass of both shell and flesh were determined. The dried flesh of all species was incinerated at 560°C for 5 h, after which the remaining ash-mass was subtracted from the dry mass to determine the AFDM.

Dropping analyses

Fifty individual droppings were collected at each site (except in the Sylt-Rømø Wadden Sea area where we collected 40 droppings). At each site we observed the birds at the high tide roost and followed them with the retreating tide. This ensured that we collected fresh droppings and only from specific foraging areas where we observed the birds. We even photographed each individual dropping before collection, so that later we could examine them for possible identification mistakes. This never seemed necessary.

Collectively, droppings were stored frozen at -18°C. Before the analysis, the samples were thawed for at least 60 min and cleaned by using an ultrasonic cleaner (Branson 5510) and consequently sieved over an 80-µm mesh sieve. The samples were initially sorted by using a 40x magnification stereo microscope (Olympus SZ51). All unique parts of prey remains that were visible in the droppings (i.e. hinges and jaws) were taken out and identified to species level whenever possible (Table 5.1). Following this, a 10% sub-sample was taken and re-sorted for polychaete chaetae only. All chaetae were identified whenever possible and counted. Identification referred to the NIOZ reference collections and literature (e.g. Hartmann-Schröder 1971).

Estimating the number of prey items

Bar-tailed godwits were never seen regurgitating pellets, nor were pellets found at feeding or roosting sites, and we therefore considered the prey remains in the droppings to provide a complete and unbiased picture of the diet (see Dekinga & Piersma 1993). The occurrence of the different prey items could be calculated from the number of hinges, claw, body whorl, jaws, chaetae, and paleae (Table 5.1). The number of bivalves was calculated as the number of hinges divided by two. Worms of the Nereididae family have paired jaws (Bakken *et al.* 2009), but instead of calculating the number of individuals by dividing the number of jaws by two, we estimated the number of Nereididae by matching left and right jaws, based on the number and position of the teeth on each jaw, considering the maximum size difference of 5% between the right and left jaws of the ragworm *Hediste diversicolor* (Lourenço 2007) and the variation in the teeth of its jaw (Hefferan 1900). The number of bloodworms *Glycera alba* per sample was calculated by dividing the number of jaws by four, since *G. alba* has four jaws (Hartmann-Schröder 1971). The number of individuals of different Nereididae species (common clam worm *Alitta succinea*,

king ragworm *Alitta virens*, clam worm *Eunereis longissima* and *H. diversicolor*) could also be calculated from number of chaetae found in the droppings. The mean number of chaetae per setiger of *H. diversicolor* is 28.2 (Moreira 1995) and the mean setiger per individual is 105 (Chambers & Garwood 1992), resulting in a mean number of 2,961 chaetae per individual. No references for the number of chaetae of *A. succinea*, *A. virens* and *E. longissima* was found, therefore it was assumed they would have similar numbers of chaetae per setiger as *H. diversicolor* since they belong to the same subfamily. *A. succinea* has 160 segments and *A. virens* 200 segments (Hartmann-Schröder 1971) resulting in 4,512 and 5,640 chaetae per species respectively. The number of occurrence per prey was based on the maximum number of predicted individuals, based on either jaws or chaetae.

For the non-jawed polychaetes, the occurrence of prey in the droppings could only be calculated from number of chaetae, which were identified and counted for 7 polychaeta species. *Phyllodoce mucosa* has a mean number of 76.5 setiger and each setiger bears six pairs of chaetae (Tzetlin 1998), resulting in 918 chaetae per individual. For the lugworm

Table 5.1. Remains of different prey items found in the droppings used for identification and how to calculate these into the number of individual prey.

Group	Species	Remains counted	Calculate occurrence of prey
Bivalves	<i>Cerastoderma edule</i>	hinges	hinges / 2
	<i>Macoma balthica</i>	hinges	hinges / 2
	<i>Angulus tenuis</i>	hinges	hinges / 2
Crustaceans	<i>Crangon crangon</i>	claw	claw
	unidentified crab species	carapace	carapace
Snails	<i>Peringia ulvae</i>	terminal/body whorl	body whorl
Polychaetes	<i>Alitta succinea</i>	jaws and chaetae	paired jaws or unpaired jaws or chaetae / 4,512
	<i>Alitta virens</i>	jaws and chaetae	paired jaws or unpaired jaws or chaetae / 5,640
	<i>Arenicola marina</i>	chaetae	chaetae / 1,138
	<i>Eunereis longissima</i>	jaws	paired jaws or unpaired jaws
	<i>Glycera alba</i>	jaws	jaws / 4
	<i>Hediste diversicolor</i>	jaws and chaetae	paired jaws or unpaired jaws or chaetae / 2,961
	<i>Lanice conchilega</i>	chaetae	chaetae / 802
	<i>Phyllodoce mucosa</i>	chaetae	chaetae / 918
	<i>Sabellaria spinulosa</i>	paleae	paleae / 102
	<i>Scoloplos armiger</i>	chaetae	chaetae / 1,698
	Unidentified species	jaws	jaws / 2
	Unidentified species	aciculae	NA

Arenicola marina and sand mason worm *Lanice conchilega* no literature values were found. As these two species may contribute a large proportion of the diet of bar-tailed godwits (Scheiffarth 2001a), 25 adult *A. marina* and 25 adult *L. conchilega* were collected in the Dutch Wadden Sea and dissected. All chaetae were counted and averaged per individual. This resulted in 1,138 and 802 chaetae per species respectively. The equation provided by Scheiffarth (2001a) was used to calculate the number of chaetae of *Scoloplos armiger* from its thoracic hooks, resulting in 1,698 chaetae per individual. No information was available concerning the number of paleae of the Ross' worm *Sabellaria spinulosa* and therefore, we assumed the number of paleae to follow a similar species, the honeycomb worm *Sabellaria alveolata* with 50 inner paleae, 24 middle paleae, and 28 outer paleae (Ebling 1945), consequently summed as 102 paleae per individual.

The remains of three other prey were found in the droppings (unidentified crabs *Carcinus* spp, the blue mussel *Mytilus edulis*, and sea urchin *Echinocardium cordatum*), but were so rare that we could conveniently exclude them from further analysis. In fact, the spines of *E. cordatum* may have been collected inadvertently when droppings were collected (Ruiters 1992).

Estimating prey sizes

Prey sizes can be estimated from indigestible parts if these correlate with the size of the individual prey eaten (e.g. Zwarts & Esselink 1989). Shell length of bivalves was calculated from hinge (and hinge + top) height (Dekinga & Piersma 1993). Jaw length was measured in two ways: (1) from the tip of the proximal tooth to the distal end of the jaw, and (2) from the jaw base to the distal end of the jaw. Method 1 was only used ($R^2 = 0.31$), when method 2 ($R^2 = 0.45$; Table 5.2) could not be used, due to a broken base or tip. When jaws were paired, the mean of the jaw length was used and when no jaws were present, all

Table 5.2. Relationships between measurable parts in droppings and prey size.

Group	Species	<i>n</i>	Parts measured	Regression	R^2	<i>P</i>
Bivalves	<i>Cerastoderma edule</i>	36	hinge	$Y = 23.1x + 1.0$	0.75	< 0.001
		36	hinge + top	$Y = 8.1x + 0.6$	0.93	< 0.001
	<i>Macoma balthica</i>	67	hinge	$Y = 17.2x + 1.6$	0.91	< 0.001
		67	hinge + top	$Y = 13.0x + 0.7$	0.96	< 0.001
	<i>Tellina tenuis</i>	103	hinge	$Y = 21.7x + 3.3$	0.58	< 0.001
		103	hinge + top	$Y = 20.7x + 0.8$	0.75	< 0.001
Polychaetes	<i>Arenicola marina</i>	72	chaetae	$Y = 25.9x - 1.3$	0.79	< 0.001
	<i>Hediste diversicolor</i>	58	short jaw	$Y = 7.0x + 4.6$	0.31	< 0.001
		58	total jaw	$Y = 5.0x + 1.0$	0.45	< 0.001

chaetae in the droppings were counted and from a subsample the length was measured from the tip to the base of the chaetae. The benthic samples collected per area were used as references, with additional references that were collected in the Dutch Wadden Sea. All chaetae and jaws were measured to the nearest 0.1 mm, under an inverted microscope (Zeiss Axiovert 200), equipped with digital camera and imaging processing software.

Prey selection and prey-size selection

Prey selection was determined by means of the Jacobs (s)electivity index (Jacobs 1974):

$$J = (r - p) / (r + p - 2rp) \quad (\text{eqn 1})$$

where r is the fraction of a prey item in the diet and p is the fraction of a prey item in the habitat. The index J ranges from +1 (complete preference) to -1 (complete avoidance), and the value of 0 indicates that the particular habitat's component was used in proportion to its availability in the study area.

From dietary items to biomass composition

To estimate the energy content of the different prey, the biomass was calculated by using the regression equations (Table 5.3). Whenever no measurements could be taken of an indigestible part of the prey species, the mean AFDM per species was taken from the NIOZ gridded sampling effort (Synoptic Intertidal Benthic Survey, SIBES), which encompasses the entire intertidal Dutch Wadden Sea, consisting out of more than 4,500 benthos samples (Compton *et al.* 2013). The AFDM equations and mean AFDM used in calculating biomass per prey species are listed in Table 5.3.

The total biomass of prey consumed by bar-tailed godwits per area was calculated as the sum of biomass per species occurring in the droppings. The proportions of prey biomass per area were calculated to determine the importance of prey in diet of bar-tailed godwits.

Results

In total we identified 18 different prey species in the diet of wintering bar-tailed godwits, at the five study sites (Table 5.4). *Hediste diversicolor* was the most common prey in the diet at four wintering sites: the Dutch Wadden Sea area, Sylt-Rømø Wadden Sea area, the Wash, and the Dutch Delta area, where it represented 80, 41, 91 and 74% of the total number of prey, respectively. In Dublin bay, *H. diversicolor* was the second-most common prey, with bloodworms *Glycera alba* (38%) being the most frequent prey found. Even though they were present in smaller proportions, other polychaetes such as *Alitta succinea*, *Arenicola marina*, and *Scoloplos armiger* were also regularly found in the droppings.

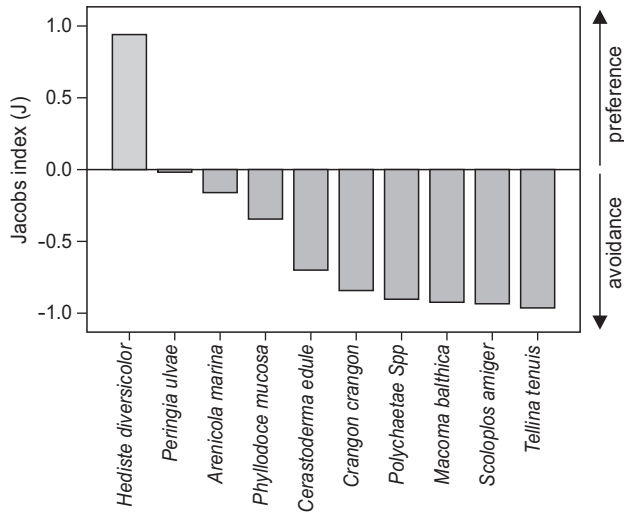


Figure 5.2. Bar-tailed godwits prey preferences determined with Jacobs' index (J) calculated from five wintering sites at different prey densities. When the index is positive, the prey species is preferred.

Table 5.3. Overview of equations and mean AFDM (g) used in calculating prey biomass.

Group	Species	Parts measured	Regression of log AFDM (Y)	R^2	n	Mean AFDM (g)	P
Bivalves	<i>Cerastoderma edule</i>	hinge	$Y = 4.3x - 3.8$	0.72	36	-	<0.001
		hinge + top	$Y = 1.5x - 3.9$	0.88	36	-	<0.001
	<i>Macoma balthica</i>	hinge	$Y = 2.8x - 3.7$	0.85	67	-	<0.001
		hinge + top	$Y = 2.1x - 3.8$	0.87	67	-	<0.001
	<i>Angulus tenuis</i>	hinge	$Y = 2.1x - 2.9$	0.47	103	-	<0.001
		hinge + top	$Y = 1.9x - 3.1$	0.55	103	-	<0.001
Crustaceans	<i>Crangon crangon</i>	*	-	-	539	0.011	-
Snails	<i>Peringia ulvae</i>	*	-	-	1,453	0.001	-
Polychaetes	<i>Alitta succinea</i>	*	-	-	907	0.016	-
	<i>Alitta virens</i>	*	-	-	164	0.183	-
	<i>Arenicola marina</i>	chaetae	$Y = 0.8x - 3.3$	0.93	72	-	<0.001
	<i>Eunereis longissima</i>	*	-	-	284	0.022	-
	<i>Glycera alba</i>	*	-	-	23	0.007	-
	<i>Hediste diversicolor</i>	shorter jaw	$Y = 1.3x - 2.7$	0.34	86	-	<0.001
		total jaw	$Y = 1.1x - 3.8$	0.78	86	-	<0.001
	<i>Lanice conchilega</i>	*	-	-	2,690	0.022	-
	<i>Phyllodoce mucosa</i>	*	-	-	873	0.001	-
	<i>Sabellaria spinulosa</i> **	*	-	-	21,332	0.002	-
	<i>Scoloplos armiger</i>	*	-	-	6,357	0.004	-
	Unidentified jaws ***	*	-	-	1,974	0.005	-

* Based on dataset from Compton *et al.* 2013.

** AFDM was calculated as an average AFDM of various similar species

*** AFDM of unidentified jawed-polychaetes was calculated as an average AFDM of various similar species

Compared with the relative abundance, *Hediste diversicolor* was the only prey actively selected by bar-tailed godwits (Fig. 5.2). The composition of the diet indicates a negative selection for other polychaetes and bivalves such as the thin tellin *Angulus tenuis* and the Baltic tellin *Macoma balthica* (Fig. 5.2). However, when categorizing the diet into four groups (i.e. bivalves, crustaceans, snails and polychaetes), the Jacobs' selectivity index indicates a positive selection for polychaetes. Small snails were positively selected in the Dutch Delta area and in the Sylt-Rømø Wadden Sea area.

Table 5.4. Diet composition of bar-tailed godwits in the five wintering areas, based on frequency of occurrence.

Group	Species	Dublin bay %	The Wash %	Dutch Delta %	Western Dutch Wadden Sea %	Sylt-Rømø Wadden Sea area %	Total %
Bivalves	<i>Cerastoderma edule</i>	12.5	0.4	0	0	3.1	1.3
	<i>Macoma balthica</i>	7.5	0	1.0	0	0	0.6
	<i>Angulus tenuis</i>	10	0	0	0	0	0.5
Crustaceans	<i>Crangon crangon</i>	0	0	0	1.8	0	0.1
Snails	<i>Peringia ulvae</i>	0	0.2	2.6	0	39.6	6.5
Polychaetes	<i>Alitta succinea</i>	2.5	1.1	0.5	1.8	0.8	1.0
	<i>Phyllodoce mucosa</i>	2.5	0.4	2.6	0	0.8	1.0
	<i>Arenicola marina</i>	2.5	0.4	8.8	14.5	3.1	3.6
	<i>Eunereis longissima</i>	0	0.7	0	0	0	0.3
	<i>Glycera alba</i>	37.5	0.4	1.6	0	0	2.3
	<i>Hediste diversicolor</i>	17.5	90.8	73.7	80.0	40.5	75.7
	<i>Lanice conchilega</i>	2.5	0.2	0.5	0	0.8	0.5
	<i>Alitta virens</i>	0	1.9	7.2	0	10.6	4.2
	<i>Sabellaria spinulosa</i>	0	1.9	0	0	0	1.0
	<i>Scoloplos armiger</i>	2.5	0.7	1.6	1.8	0.8	1.0
	unidentified	2.5	0.9	0	0	0	0.6
Other bivalves	<i>Mytilus edulis</i> * (shell fragments)	-	-	-	++	+++	p
Crustaceans	crabs* (carapace fragments)	+	+	++	+	+++	p
Echinoidea	<i>Echinocardium cordatum</i> * (spines)	++	+++	-	+	-	p
Polychaetes	Aciculae & chaeta* (unidentified)	+	++	+++	+	+	p

*excluded from analysis (+ = <10%, ++ = between 10-50%, and +++ = >50% in relative frequencies, p=present)

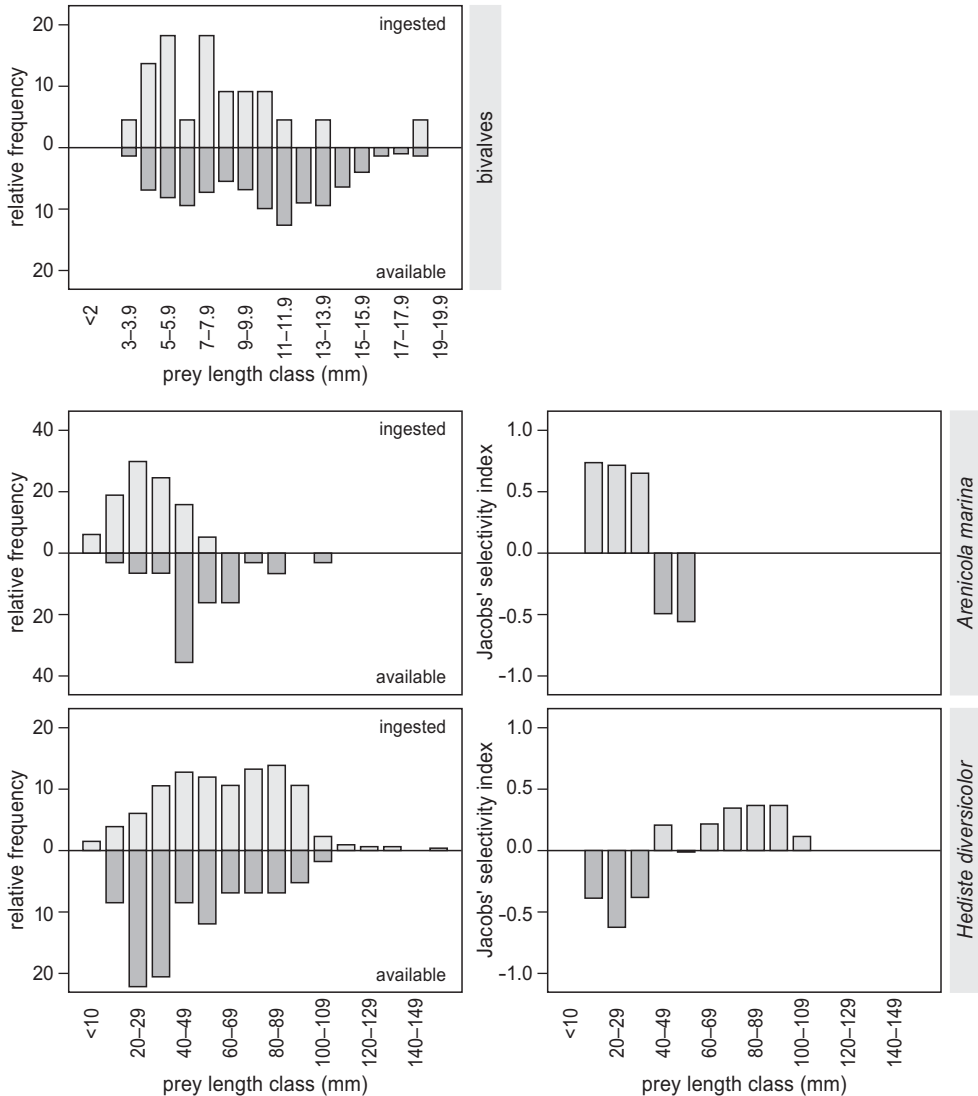


Figure 5.3. The relative size distributions of three bivalve species (*Macoma balthica*, *Cerastoderma edule* and *Angulus tenuis*), the polychaete *Arenicola marina* and *Hediste diversicolor* ingested by bar-tailed godwits at the five study areas (upward histograms), in comparison with the size distributions of those prey species present on the feeding sites (downward histograms) are shown in the left panels. The right panels represent the prey preferences of *A. marina* and *H. diversicolor*, as determined with Jacobs' index (J) based on the five wintering sites. The index shows a positive value, whenever the prey species is preferred and when it is a negative value, there's a negative selection for this prey species.

H. diversicolor was not only the most preferred prey item, but it was also the most important prey item in terms of biomass (AFDM content; i.e. 79%). Next were *A. virens* and *A. marina*, with 17 and 2% of the biomass respectively, as the most important

species, while the other prey combined only contributed 2% of energy intake. Although other prey items were taken regularly, 99.6% of the diet's biomass consisted out of polychaetes and remained the most preferred and important prey. In Dublin bay, a relative high proportion of biomass consisted out of bivalves (i.e. the thin tellin), although they were not preferred (Fig. 5.2).

We aggregated the size distribution of all bivalve species of all areas, both in the droppings and in the sediment, due to low sample size of bivalve prey occurring in the droppings ($n = 19$). The available size distribution for bivalves varied between 3 to 19 mm of shell length ($n = 222$), however, only the smaller bivalves were consumed (mean size \pm SE 8.2 ± 0.8 mm; range 4 - 11 mm; Fig. 5.3). Based on Jacobs' selectivity index, we compared the size of the lugworm and ragworm between the sediment and their diet. Bar-tailed godwits showed positive selection of ragworm with length between 40 to 110 mm, while they positively selected lugworms shorter than 40 mm. The mean lengths of the ragworms and lugworms eaten by bar-tailed godwits were 62.5 ± 1.1 mm and 29.4 ± 0.7 mm, respectively (Fig. 5.3).

Discussion

With at least 18 prey species contributing to the diet of bar-tailed godwits across the European wintering range, the diet showed high diversity compared with the recorded diets of molluscivores such as red knots (e.g. Dekinga & Piersma 1993; Moreira 1994b; Piersma *et al.* 1994) and European oystercatchers (e.g. Goss-Custard *et al.* 1977a; Durell *et al.* 1993). Confirming previous studies (e.g. Goss-Custard *et al.* 1977b; Perez-Hurtado *et al.* 1997; Scheiffarth 2001a), bar-tailed godwits selected polychaetes. Not surprisingly, the diet varied between wintering sites. In Dublin bay for example, the bivalve *Abra tenuis* occurred frequently in their diet, which would be explained by these bivalves being the most abundant benthic species in the core samples. The preference for snails in two areas (i.e. the Dutch Delta area and the Sylt-Rømø Wadden Sea area), is likely caused by benthic sampling design. Mudsails *Peringia ulvae* have a very patchy occurrence (e.g. Bocher *et al.* 2007), and thus easily missed in 10 benthic cores. As they only contributed a small fraction of the total consumed biomass, this issue seems a minor one.

There was a positive selection for the smaller *Arenicola marina* (< 4 cm) which is perhaps surprising. This might be due to their burying depth. Benthic prey are buried deeper in winter than in summer, as is also the case for *A. marina* (Zwarts & Wanink 1993), and is also related to the length of the individual. *A. marina* exceeding 4 cm in length, are buried 17 cm and deeper (Zwarts & Wanink 1993), mostly out of the bill length of (female) bar-tailed godwits (i.e. mean bill length females 9.9 cm; Prater *et al.* 1977), whereas the smaller individuals are closer to the surface. Additionally, bar-tailed godwits rely on cast

formation by lugworms to detect them, and at ambient temperatures below 3°C, casts are not produced (Smith 1975). Therefore, the low ambient temperatures may explain a shift to *H. diversicolor*.

The preference for the larger *H. diversicolor* can be expected for birds wintering in temperate climates because these polychaetes, even in winter, never really bury much beyond the length of the bill (Esselink & Zwarts 1989). The largest, and most profitable individual ragworms (13 cm; Zwarts & Esselink), have a maximum burying depth of approximately 16 cm in winter, which will put them out of reach even for females. That *H. diversicolor* is such an important prey species throughout their wintering range concurs with their widespread distribution, e.g. occurring in 30% of all sampled locations ($n > 4,257$) in the entire Dutch Wadden Sea (Compton *et al.* 2013). Furthermore, of all polychaetes, ragworms contributed the third highest biomass contribution across the Wadden Sea in three years (Compton *et al.* 2013).

This study brings together information about the bar-tailed godwit's diet in different wintering areas across Europe. The scale of the comparison, at least with respect to shore-bird studies (but see Quaintenne *et al.* 2010; Alves *et al.* 2013b), is quite novel. Although some variation in diet composition was found, it is apparent that across the wintering range bar-tailed godwits rely on polychaete worms.

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6

Interference competition in a sexually dimorphic shorebird: prey behaviour explains intraspecific competition

Sjoerd Duijns & Theunis Piersma

Abstract

When males and females come in distinct sizes and shapes they often forage at different sites, selecting different prey. In the sexually dimorphic bar-tailed godwit *Limosa lapponica*, females generally forage along the tideline, whereas the smaller (and subordinate) males generally forage across dry mudflats. On this basis we predict that interference competition would occur within, rather than between, the sexes. We tested whether density-dependent aspects of foraging behaviour are indeed sex-specific and additionally examined the roles of sex-specific prey types. With increasing conspecific densities, intake rates levelled off in females, but not in males. At increasing densities, both sexes engaged in more agonistic interactions, but females more than males. Consequently, females lost more foraging time than males. However, time lost to interactions could not explain the density-dependent decrease in their intake rate. As lugworms *Arenicola marina* contributed 71% to the energy intake of females and 18% in males, we experimentally tested whether the burying behaviour of lugworms explained the sex-difference in interference. Both in the field and in the laboratory, lugworms responded to probes. In experimentally probed plots in the field, lugworms produced fewer casts per unit time, indicating a decrease in near-surface presence. In laboratory settings, increased experimental probing intensity resulted in deeper burying by lugworms. We therefore argue that prey depression is responsible for most of the reduction in intake rates of females foraging at high conspecific densities. The search for undisturbed shallow-living lugworms would explain why female bar-tailed godwits tend to forage along the moving tideline.

Introduction

According to the ‘ideal free distribution’ (IFD; Fretwell & Lucas 1970), individuals should distribute themselves such that everyone achieves equal fitness. However, when individuals differ in competitive ability, individuals with the highest competitive ability would occupy the best patches, leading to despotic types of distributions (Houston & McNamara 1988; Parker & Sutherland 1986). Intake rate and foraging distribution models must therefore combine prey density and interference effects. This is formalized in the so-called ‘generalized functional response models’ (van der Meer & Ens 1997), which are used to evaluate and predict spatial foraging distributions (e.g. Bautista *et al.* 1995; Ruxton 1995; van Gils & Piersma 2004).

High quality food patches usually attract high densities of foragers, and this may lead to declines in individual intake rates (Hake & Ekman 1988). If the declines are caused by depletion of available prey, the process is called exploitative or scramble competition (Krebs 1978). When it is caused by behavioural interactions such as aggression (Kotrschal *et al.* 1993), kleptoparasitism (Brockmann & Barnard 1979), foraging site replacement (Bautista *et al.* 1998), or by creating a barrier to a resource (Shealer & Burger 1993), it is referred to as interference or contest competition (Miller 1967). Interference competition may not always be obvious, as some animals subtly avoid each other without directly interacting, i.e. ‘cryptic interference’ (e.g. Bijleveld *et al.* 2012; Gauvin & Giraldeau 2004; Gyimesi *et al.* 2010; van Dijk *et al.* 2012). For predators foraging on mobile prey, the levelling off of intake rate may also be a result of prey depression, which can result from a number of different processes and do not require actual harvesting of any prey items by the predator (Charnov *et al.* 1976). Prey depression –prey becoming temporarily unavailable– can occur when prey respond to the presence of predators, for instance by retreating down a burrow (Backwell *et al.* 1998; Ens *et al.* 1993; Stillman *et al.* 2000). The deeper the prey is buried, the smaller the chance of them being depredated (Myers *et al.* 1980; Zwartz & Wanink 1984). However, deeper burial may also result in a lowering of food intake which in turn reduces body condition (de Goeij & Luttikhuisen 1998; Zwartz & Wanink 1993). In the Baltic tellin *Macoma balthica*, a preferred prey of shorebirds, burrowing deeper reduces predation risk (Edelaar *et al.* 2005; Zwartz & Blomert 1992), but also reduces food intake (de Goeij & Luttikhuisen 1998). Therefore, the selection of burying depth is an essential and integrated part of the life-strategy of organisms (Santamaria & Rodriguez-Girones 2002; van Gils *et al.* 2009).

Here we aim to document the presence of interference in a sexually dimorphic gregarious forager, the bar-tailed godwit *Limosa lapponica*, and decipher the behavioural mechanisms causing it. Females are about 20% heavier and have 25% longer bills than males (Cramp & Simmons 1983; Duijns *et al.* 2012). Bar-tailed godwits feed especially on polychaete worms (Duijns *et al.* 2013). In the field they show little aggression during foraging,

but when it occurs, it is mainly between females (Both *et al.* 2003). Habitat use differs between the sexes, both at large spatial scales (Atkinson 1996; Scheiffarth 2001b), and at small scales (Both *et al.* 2003; Smith & Evans 1973; Zwarts 1988). Sex-related diet preferences have been observed (Scheiffarth 2001a): females forage on the larger and deeper buried prey, whereas males mainly forage on smaller shallower living species. The lugworm *Arenicola marina*, an important prey species for the bar-tailed godwit (e.g. Scheiffarth 2001a; Smith 1975), can comprise up to 80% of the female diet. It lives in burrows and has a number of modes of behaviour. For much of the time they remain deep in their U-shaped burrow, ingesting sand. At regular intervals they move their tails to the surface to produce the well-known sand castings (Wells 1966). At such moments, lugworms are best available to probing predators.

During spring staging, a period during which bar-tailed godwits almost double in body mass (Piersma & Jukema 1990), these long-distance migrants forage at maximum rates (Duijns *et al.* 2009; Scheiffarth *et al.* 2002). Given that the sexes differ in small-scale habitat use and diet (e.g. Atkinson 1996; Scheiffarth 2001b; Smith & Evans 1973), we hypothesized that intra-sexual competition, rather than intraspecific competition, would drive interference competition, and that sex-specific prey behaviour to be the explanatory mechanism. In addition to our field observations on the birds, we conducted two experiments: (1) a prey depression field-experiment, and (2) an indoor prey depression experiment, in both of which we mimicked foraging behaviour of shorebirds to study the activity of lugworms in relation to predation pressure.

Methods

Field observations

In May 2011 field observations ($n = 144$) on 15 different days were made on the mudflats of the Wadden Sea near Texel ($53^{\circ}05'N$, $4^{\circ}48'E$). Eighteen plots (100 x 100 m) on the intertidal mudflats were marked at every corner with PVC poles (1.5 m long), inserted 0.5 m in the sediment. PVC poles did not seem to disturb the foraging of the birds. As soon as the tide started to retreat (still approx. 30 cm of water standing), a single observer (SD) placed himself 30 – 125 m away from a plot and awaited the arrival of the birds. One focal bird was randomly selected for a five-minute observation and behaviour and sex was recorded on a digital voice recorder (Sony ICD-P620; focal animal sampling, continuous recording).

We used the following ethogram: search, vigilance, preen, rest, interactions with conspecifics or with other bird species. When a bird was foraging solitary in a plot (i.e. 1 ind/ha), interactions with other bird species were also recorded, but this only occurred on three occasions and only in females. Interactions were recorded as kleptoparasitism and

time lost in aggressive interactions are generally assumed to cause interference competition (Smallegange & van der Meer 2009; Stillman *et al.* 1997). We avoided repeated observations of individuals by consistently moving at least 3 birds away from the focal bird.

All ingested species and their estimated sizes were recorded and ingested prey converted into biomass (AFDM), based on the length-biomass relation per species. To verify whether we estimated prey sizes correctly in the field, estimations of bill lengths of colour-ringed individuals at distances of 20 – 200 m were made. These birds had known bill lengths, which enabled us to validate our visual estimates. That estimated bill lengths were highly correlated with measured bill length (Pearson correlation coefficient = 0.87, $df = 28$, $P < 0.001$), suggested that our observational prey size estimations were robust. Small items (< 2 cm) could not be identified and therefore the mean AFDM of all small prey items encountered in the benthos samples were used. These small prey items were later analysed in the lab and predominantly comprised small crustaceans such as *Urothoe poseidonis*, *Corophium volutator* and small worms as *Pygospio elegans* and *Eteone* species and to a lesser extend the snail *Hydrobia ulvae*. All ingested prey were converted into biomass (AFDM), based on the length-biomass relation per species (for more details see: Duijns *et al.* 2013).

The recorded trials were analysed with Observer 5.0 (Noldus, 2003) at normal speed and this resulted in: foraging time (s), other behaviour (s) and number, type and length of prey items ingested, enabling us to calculate instantaneous intake rate (mg AFDM s⁻¹), handling time (s) and profitability (mg AFDM s⁻¹) per prey item.

Prey density

We sampled prey density in all plots prior to the arrival of the birds from their wintering grounds in West Africa (early May) and immediately after the birds left (early June; Drent & Piersma 1990; Duijns *et al.* 2012), to correct for any depletion effects. Five samples were taken per plot at approximately 25 m from each corner and 1 sample in the centre of each plot. As we sampled each plot twice, food densities based on the results of both sampling events were based on the total of 10 benthic samples. Each benthic sample consisted of a sediment core (diameter, 15 cm), taken to a depth of approx. 30 cm and sieved through a 1-mm mesh. All relevant prey items were counted per species and stored in 4% formaldehyde saline solution for later analyses in the laboratory, where size classes (lengths) were measured to the nearest mm. AFDM (g) of prey was determined by drying the prey items to a constant mass in a ventilated oven at 55–60°C, after which dry mass was measured (± 0.1 mg). The dried flesh of all species was incinerated at 560°C for 5 h, after which the remaining ash-mass was subtracted from the dry mass to determine the AFDM.

Prey depression field-experiment

To study the lugworms' activity in relation to predation pressure, we deployed 2 plots (1 x 1 m), an experimental and a control plot in close proximity of each other (~1 m distance) at the Mokbaai, a small intertidal mudflat area on the island of Texel, The Netherlands. The experiment started during the outgoing tide (still 30 cm of standing water), approx. 20 min before the tidal flats became exposed. At 10-min intervals over a total observation period of 3 h we mimicked foraging behaviour of shorebirds (50 probes with a 5 mm diameter metal pole) to a maximum depth of 10 cm in the experimental plot and did nothing in the control plot. We counted the number of new casts produced every 10 min and repeated this procedure for two days.

Indoor prey depression experiment

Adult lugworms were collected in April 2013 in the Mokbaai. Different densities (2, 4, and 6 lugworms) were placed in transparent plastic aquariums (50 x 40 cm high with a thickness of 1.4 cm) directly after collection. The 4 aquariums were placed adjacent to each other, in 2 groups of 2, meaning that 2 density treatments were done simultaneously. As soon as the lugworms were released in the aquarium, they dug themselves in. The lugworms that did not dig themselves in ($n = 5$), were removed and released. A substrate of glass pearls (grain size 200-300 μm ; coinciding with the natural grain sizes of sediments they naturally live in, e.g. Compton *et al.* 2013), ensured that we could see the lugworms, which were fed with approx. 0.10 ml of commercial shellfish feed (Instant Algae; Shellfish diet 1800, USA), which was deposited on the substrate before each trial. That this shellfish diet was used, was suggested by the finding that in additional trials the lugworms lived longer with this food than without (unpubl. obs.). The aquariums were kept in a dark climate chamber with continuously running seawater. Water and room temperature was kept constant at 15°C. After acclimatising them for at least one h, the experimental treatment started.

Before and immediately after each trial, the length and depth of each lugworm was measured and marked with non-permanent markers on the aquarium windows. At each trial one aquarium was randomly selected as the experimental one and the adjacent consequently as a control. We used 3 intensity treatments where we manually probed in the sediment (i.e. 5, 10 or 30 times), up to a maximum depth of 10 cm (coinciding with the mean bill length of a female bar-tailed godwit; Duijns *et al.* 2012). We placed a light source behind the aquaria, but this was only turned on when measuring the initial depth during the probing treatment and the depth measurement after the treatment. Each treatment (density and probing intensity) was repeated 8 times and new lugworms were used for every trial. After each experimental day, all lugworms were released in close proximity of the capture site.

Data analysis

Comparisons between the sexes for number of interactions per unit time, time loss due to interactions, and vigilance were made with a Poisson-distributed generalized linear mixed model (GLMM) with observed density (no of birds/ha) as main effect, sex as factor and food availability as a random factor. Since all interaction terms were non-significant (all $P > 0.1$) in these three models, the interactions were therefore excluded from the final analysis. For graphical purposes we grouped the density in three classes; i.e. 1 ind/ha, 2-5 ind/ha and > 5 ind/ha. As bar-tailed godwits often follow the tideline (e.g. Both *et al.* 2003), we initially separated the analysis in individuals foraging with the tideline and individuals on dry mudflat, but no differences were detected. To make sure that we measured direct effects, rather than the effects of previously passed flocks, we discarded observations of individuals in the low density situation (< 3 ind/ha; $n = 8$) that were performed within 30 min after which a large flock had foraged in the plot.

By using the mean observed handling times, mean food abundance (g AFDM m^{-2}) and (instantaneous) intake rates (mg AFDM s^{-1}), the searching efficiency ($cm^2 s^{-1}$) could be estimated by using the non-linear least-square fitting function (nls) of the software package R (R Development Core Team 2013). As males consume much more small prey items within the same time than females, sample sizes on handling time differ markedly between the sexes (Table 6.1). By using the density dependent intake rate and searching efficiency we fitted the relationship between the intake rate and the density of food as type II functional responses (Holling 1959) for the different forager densities.

We used a two-sample *t*-test to test for differences in number of casts/h between the experimental and control plot in the field experiment. Linear mixed models (LMMs) were used to determine differences between probing treatments in the indoor prey depression experiments. These two LMMs were very similar as we measured the depth and length of

Table 6.1. Mean handling time and average searching efficiency of bar-tailed godwits.

Density class (# birds/ha)	Sex	<i>n</i>	Handling time (s)	Searching efficiency ($cm^2 s^{-1}$)	<i>P</i> value
1	M	7	0.56 ± 0.05	0.75 ± 0.2	< 0.05
2-5		15		0.52 ± 0.1	< 0.001
> 5		35		0.79 ± 0.2	< 0.001
1	F	18	0.84 ± 0.2	0.97 ± 0.6	0.09
2-5		34		0.91 ± 0.3	< 0.05
> 5		27		0.71 ± 0.2	< 0.05

Handling times were measured in the field ($n = 2,394$ for males and $n = 953$ for females), and searching efficiency was estimated from fitting the Holling's disc equation (Holling 1959). The *P* values refer to whether the fitted functional response type II function is significant. Values are given \pm SE.

all prey after each experimental trial. Therefore depth (first model) and length (second model) were the explanatory variables, density (i.e. 2, 4, or 6 lugworms per aquarium) and initial depth (first model) and length (second model) as factors and lugworm ID as a random factor. All analyses were conducted using R 3.0.1 and the package lme4 (Bates *et al.* 2013) was used to fit (G)LMMs, and the package multcomp (Hothorn *et al.* 2008) was used to perform Tukey post hoc tests.

Results

Field observations

Females suffered from higher levels of agonistic interactions than males (GLMM: $X^2 = 18.52$, $P < 0.001$; Fig. 6.1A), and a positive effect of forager density was observed (GLMM: $X^2 = 6.21$, $P = 0.012$; Fig. 6.1A). Females initiated interactions more frequently than males (chi-square test: $X^2 = 6.74$, $P = 0.03$, $n = 25$) and when interactions occurred, females won these interactions more often than males (chi-square test: $X^2 = 9.19$, $P = 0.026$, $n = 28$). With no intra-specific competitors around, females still suffered from interference from other species such as black-headed gulls; the males did not experience this. The higher degree of interactions consequently led to a decrease in available foraging time for both sexes, with the greatest decrease for females (GLMM: $X^2 = 73.25$, $P < 0.001$; Fig. 6.1B). A positive effect of forager density for both sexes was observed (GLMM: $X^2 = 4.29$, $P = 0.038$; Fig. 6.1B). As expected (e.g. Beauchamp 1998; Sansom *et al.* 2008), vigilance was negatively correlated with density (GLMM: $X^2 = 6.26$, $P = 0.014$; Fig. 6.1C), but no difference between the sexes was observed (GLMM: $X^2 = 0.13$, $P = 0.72$; Fig. 6.1C).

The intake rate of bar-tailed godwits was a function of available biomass (Fig. 6.2; Table 6.1), and followed a type II functional response (Holling 1959). Only females foraging at the lowest densities of ca. 1 bird/ha did not suffer from interference (Fig. 6.2A), whereas males did not appear to suffer from interference at any density (Fig. 6.2B).

As expected, diets differed between the sexes. Females obtained most energy by foraging on lugworms (71.4% of ingested AFDM). Males obtained most food by foraging on smaller prey (71.8% of the energy intake and only 17.8% from lugworms; Table 6.2). Note that the profitability (AFDM s^{-1} handling) of lugworms, relative to the other prey types, is also the highest (Fig. 6.3). There was no difference in prey profitability between the sexes (Tukey's test: all comparisons $P < 0.05$), except for small prey items and shore crabs ($P < 0.001$).

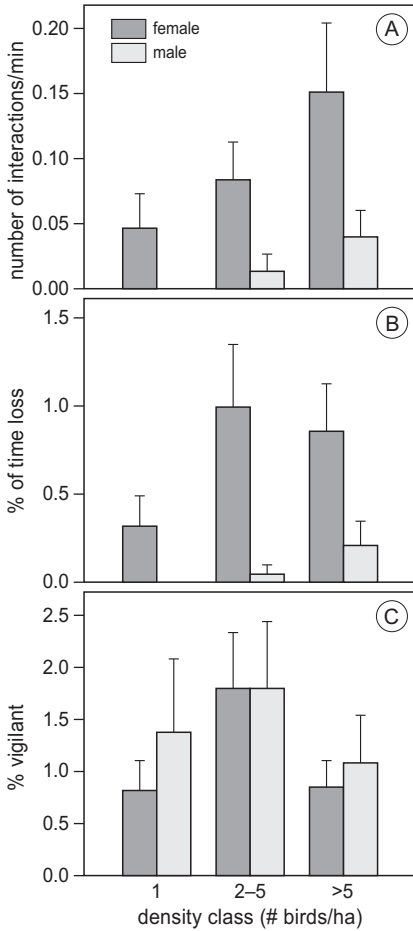


Figure 6.1. Mean number of agonistic interactions of bar-tailed godwits separated in (A) female and male (B) the consequent percentage of time loss caused through this, and (C) the percentage of time spent vigilant.

Table 6.2. Diet composition of both sexes of bar-tailed godwits.

Prey	% of occurrence		% of AFDM	
	Male	Female	Male	Female
Lugworm <i>Arenicola marina</i>	0.5 (32)	7.9 (210)	17.8	71.4
Shore crab <i>Carcinus meanas</i>	0 (0)	0.2 (4)	0	0.2
Common shrimp <i>Crangon crangon</i>	0.2 (12)	0.2 (5)	0.5	0.1
Ragworm <i>Nereis spec.</i>	0.8 (45)	2.8 (74)	3.5	5.5
Bristleworm <i>Scoloplos armiger</i>	3 (181)	3.3 (88)	6.4	2.4
Small prey (< 2 cm)	95.5 (5,693)	85.6 (2,261)	71.8	20.4

Data based on visual observations and presented in percentage of occurrence (sample sizes in brackets) and percentage of AFDM in the diet.

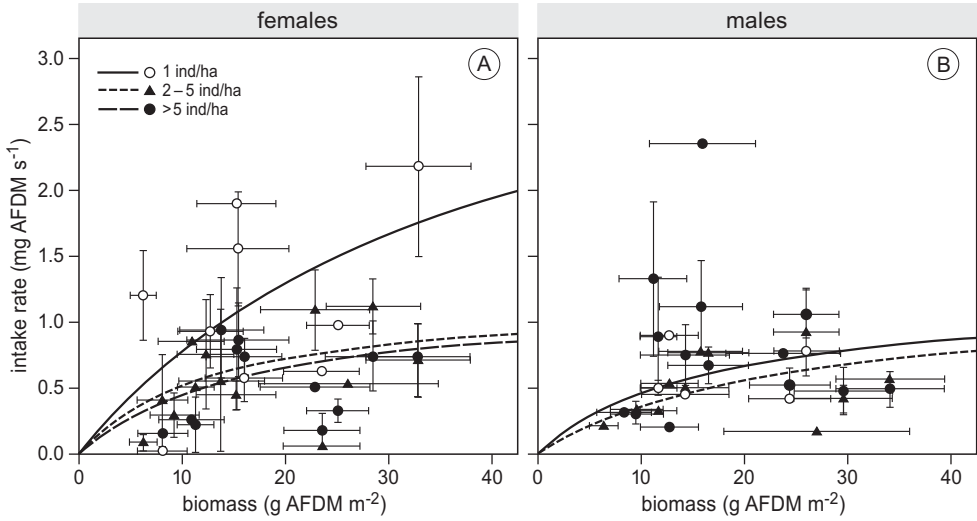


Figure 6.2. The relation between the mean (\pm SE) intake rate (mg AFDM s^{-1}) for female and male bar-tailed godwits and the mean (\pm SE) biomass (g AFDM m^{-2}) available. Different symbols represent different competitor densities. Plotted lines represent type II functional responses fitted to the data using the Holling's (1959) disc equation, see Table 6.1 for parameters. For the females (A), a clear effect of increased competitor density is visible, whereas this effect is absent for males (B). Note that the lower density functional response line for males follows exactly the functional response at the highest densities and is thus not visible.

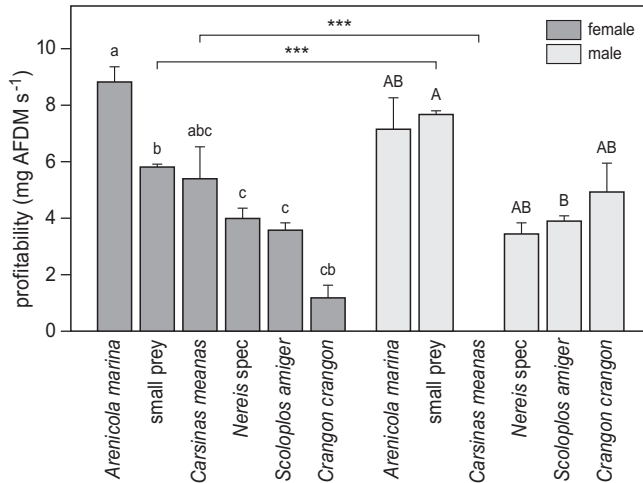


Figure 6.3. Profitability per prey species of bar-tailed godwits, separated per sex. The lower case letters in the graph represent the differences ($P < 0.05$) between prey species for the females and the capital letters represent differences in prey profitability for the males. The asterisks refer to the significant differences ($P < 0.001$) between the sexes within species.

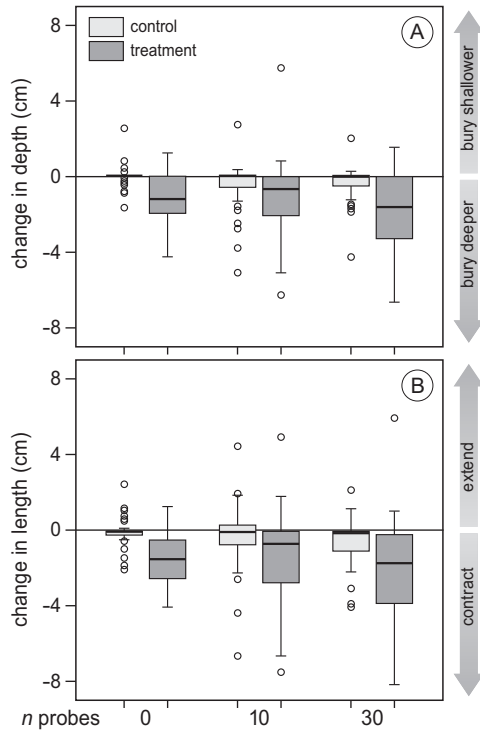


Figure 6.4. Mean depth (A) and mean length (B) difference between the different probing intensities (light grey bars) and control plots (dark grey bars). Increased probing intensities lead to a deeper burial (A) and also lead to smaller lugworms (B), by contracting their muscles. Box plot shows median (line in box), interquartile range (box), 10th and 90th percentile (bars) and outliers (dots; data points outside the 10th and 90th percentiles).

Prey depression experiments

In the field, lugworms decreased their activity when experimentally disturbed by probing 'bills'. The mean number of casts/h \pm SE decreased from 6.4 ± 0.3 in the control plot to 2.8 ± 0.3 in the experimental plot (t -test: $t = 8.68$, $df = 96.1$, $P < 0.001$). A decrease in defecation rates suggested that lugworms spent less time near the sediment surface.

In the aquaria, the lugworms responded directly when disturbed and were found deeper in the sediment than the animals in the control aquarium (LMM: $X^2 = 43.75$, $P < 0.001$). There was also a difference in probing intensity (Tukey's test: $P < 0.001$, $P = 0.006$ and $P = 0.002$ for 5, 10 or 30 times manually probing respectively; Fig 6.4A). There was no effect of lugworm density ($P = 0.53$), but there was a positive effect of the initial depth (LMM: $X^2 = 12.72$, $P < 0.001$). The latter indicated that the lugworms' response is greater when initially buried less deeply. When disturbed, lugworms also responded directly by becoming shorter (i.e. contracting their muscles; LMM: $X^2 = 49.43$, $P < 0.001$), and also differed in probing intensity (Tukey's test: $P = 0.001$, $P = 0.04$ and $P < 0.001$ for 5,

10 or 30 times manual probing respectively; Fig 6.4B). There was no effect of density ($P = 0.63$), and a positive effect of initial length (LMM: $X^2 = 4.28$, $P = 0.04$) was detected, implying that the contraction was greater, when the lugworms were larger. The correlation between depth and length of all experimental lugworms after treatment (Pearson correlation coefficient: $r = 0.77$, $n = 286$, $P < 0.001$), suggests that the immediate response of lugworms is to shorten their bodies, rather than to bury deeper in the sediment.

Discussion

Previous studies on bar-tailed godwits reported sex differences in foraging behaviour (e.g. Both *et al.* 2003; Zharikov & Skilleter 2002). Small scale habitat segregation and diet differences were shown, but the studies did not investigate how the sex-differences came about. Lugworms produce casts and this makes them vulnerable to predation either at the tide-edge (when casts are most often produced) or in the course of the low tide (e.g. Vader 1964; Smith 1975). That casts would be most frequently produced at the tideline already suggests an explanation why the lugworm-eating females follow the tide. Our results indicate that there is an additional, and perhaps overriding, reason why they do so: to find undisturbed lugworms within reach of their bill, in order to maximize their intake rate.

We showed that prey behaviour can influence the susceptibility to interference. A levelling off of intake rate only occurred in the class of dominant birds (the females) at the higher densities. Kleptoparasitism and time lost in aggressive interactions are generally assumed to be the mechanisms of interference competition (Stillman *et al.* 1997; Smallegange & van der Meer 2009). Although density-related increases in agonistic behaviour were observed in females as well as males, the $< 1\%$ of foraging time lost cannot explain the 50% reduction in intake rate in females. Nevertheless, despite evidence for prey depression, we cannot dismiss the possibility of cryptic interference, i.e. animals anticipate and try to avoid physical encounters with conspecifics. This subtle avoidance behaviour cannot be observed other than in experiments (Bijleveld *et al.* 2012), but will be important to explain foraging distributions (Gyimesi *et al.* 2010). In addition, it is important to note that in large prey species such as lugworms the asymptote of the functional response is considerably lower than the profitability. This can be explained by the fact that behavioural states other than feeding (e.g. vigilance, preening, digestive breaks) are not included in the Holling's disc equation. Also, the asymptote of the functional response is driven by the majority of small prey items in their diet (86%; Table 6.2), and therefore represents a weighted average of short handling times.

That prey behaviour can suppress the intake rate of foragers was previously shown in several taxa including mammals (Kotler 1992), insects (Loosey & Denno 1998) and shore-

birds (e.g. Goss-Custard 1970; Selman & Goss-Custard 1988; Ens *et al.* 1993; Backwell *et al.* 1998). In all these studies the capture and intake of individual prey was visible, which facilitates the measurement of prey depression. To the best of our knowledge, the present study is the first to show predator avoidance behaviour (i.e. prey depression from the predator point of view) in a buried invisible prey. During the prey depression experiments in the laboratory, the lugworms did appear to respond to the artificial light. Lights were therefore only turned on during the actual measurements. Still, we need to be cautious in translating the depth and length measurements into field situations.

The mean \pm SE observed densities of birds in this study (9.5 ± 1.5 ind/ha) were slightly higher than the estimates of 1.5 – 4.5 ind/ha measured in the Dutch Wadden Sea by other methods and at other times of the year (Folmer *et al.* 2010; van den Hout & Piersma 2013); outside the spring migration period fewer bar-tailed godwits occur in the Dutch Wadden Sea (e.g. Drent & Piersma 1990). In this study densities were measured in 1 hectare plots. As measured in the same study area in the previous year, there was a positive correlation between inter-bird distances and flock size (Pearson correlation coefficient: $r = 0.55$, $n = 29$, $P = 0.001$). Thus at low overall densities, birds foraged closer to each other than at higher densities.

The reason why we did not observe a levelling off in intake rate due to interference competition in males may come about in three ways. (1) Prey depression did not play a role at all because their diet consisted of smaller prey items than females, which live closer to the surface and are not very mobile (Scheiffarth 2001b). (2) Agonistic behaviour (i.e. stealing prey from conspecifics) was not profitable, as their mean \pm SE handling times 0.56 (s) ± 0.05 of their most occurring prey (> 95%) was rather low, whereas the mean time \pm SE lost 4.3 (s) ± 2.2 from agonistic interactions was much higher. Hence, the time required to steal a prey may not outweigh the benefit and the birds are better off finding a new prey item themselves (Ens *et al.* 1990). (3) Small prey items were more abundant mean \pm SE numbers 93.7 ± 2.6 (m⁻²) compared to a lower abundance of larger prey items 58.0 ± 0.8 (m⁻²), and therefore it may not be worth stealing them.

The density of available prey is the major factor determining the intake rate of a predator (Holling 1959). As prey availability usually can only be measured with difficulty (e.g. Zwarts & Esselink 1989), total prey density tends to be measured instead. The implicit assumption is that the proportion of available prey does not differ spatially or temporally (but it does: e.g. Zwarts & Wanink 1993), and ignores that the predators themselves influence the availability of their prey. This study shows the importance of the latter, a mechanism that in this case can explain sex differences in interference competition.

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Field measurements give biased estimates of functional response parameters, but help explain foraging distributions

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Abstract

Mechanistic insights and predictive understanding of the spatial distributions of foragers are typically derived by fitting either field measurements on intake rates and food abundance, or observations from controlled experiments, to functional response models. It has remained unclear, however, whether and why one approach should be favoured above the other, as direct comparative studies are rare. The field measurements required to parameterize either single or multi-species functional response models are relatively easy to obtain, except at sites with low food densities and at places with high food densities, as the former will be avoided and the second will be rare. Also, in foragers facing a digestive bottleneck, intake rates (calculated over total time) will be constant over a wide range of food densities. In addition, interference effects may depress intake rates further. All of this hinders the appropriate estimation of parameters such as the 'instantaneous area of discovery' and the handling time, using a type II functional response model also known as 'Holling's disc equation'. Here we compare field- and controlled experimental measurements of intake rate as a function of food abundance in female bar-tailed godwits *Limosa lapponica* feeding on lugworms *Arenicola marina*. We show that a fit of the type II functional response model to field measurements predicts lower intake rates (about 2.5 times), longer handling times (about 4 times) and lower 'instantaneous areas of discovery' (about 30 to 70 times), compared with measurements from controlled experimental conditions. In agreement with the assumptions of Holling's disc equation, under controlled experimental settings both the instantaneous area of discovery and handling time remained constant with an increase in food density. The field data, however, would lead us to conclude that although handling time remains constant, the instantaneous area of discovery decreased with increasing prey densities. This will result into highly underestimated sensory capacities when using field data. Our results demonstrate that the elucidation of the fundamental mechanisms behind prey detection and prey processing capacities of a species necessitates measurements of functional response functions under the whole range of prey densities on solitary feeding individuals, which is only possible under controlled conditions. Field measurements yield 'consistency tests' of the distributional patterns in a specific ecological context.

Introduction

Functional response relationships are fundamentally important as they enable the explanation and prediction of forager distributions over known resource landscapes (e.g. Sutherland 1996; van Gils *et al.* 2006; Piersma 2012). The functional response is defined as the relationship between a forager's intake rate and the concurrent density of its prey. In general, intake rates will be low when food densities are low, as foragers will spend most of their time searching for prey. When food densities increase, intake rates will also increase, but ultimately level off at a plateau where prey handling times become limiting. This relationship is described by the 'type II functional response model', also known as Holling's disc equation (Holling 1959).

Information on intake rates as a function of prey density can be generated with relative ease by field observations, and can include estimates of searching-, handling- and vigilance time (see e.g., Goss-Custard *et al.* 2006; Gillings *et al.* 2007; Smart *et al.* 2008). These measurements can be fitted to Holling's disc equations (e.g. Gill *et al.* 2001; Lourenço *et al.* 2010; St-Louis & Cote 2012; Duijns & Piersma 2014). If birds distribute themselves 'ideal' and 'free' (Fretwell & Lucas 1970), there will be more birds at higher prey densities. However, in observational field studies, positive effects of high prey densities may be masked by interference effects (van Gils & Piersma 2004). To capture this, 'generalised functional response models', which combine the interactive effects of prey and competitor density, are used to evaluate and predict the spatial distributions of foragers (e.g. Bautista *et al.* 1995; van der Meer & Ens 1997; van Gils & Piersma 2004).

In Sutherland and Anderson's (1993) 'rate-maximising depletion model', foragers are predicted to use lower food density patches only when their expected intake rate is sufficient to maintain a balanced energy budget. Yet animals, even those that are omniscient, sometimes do forage at even lower food density patches, an observation that may be explained when rate-maximising models are transformed into 'fitness-maximising models' that separately consider metabolic costs, predation costs and the availability of different patches (van Gils *et al.* 2004). Nevertheless, most animals avoid areas with very low food densities and they will rarely encounter patches with very high food densities (because food densities are usually negative binomially distributed; Pielou 1977). This narrows the range of food densities over which intake rates can be collected for free-living birds.

Adding insult to injury, it is becoming evident that most foragers are 'digestion-limited' rather than 'handling-limited' (Kersten & Visser 1996; Jeschke *et al.* 2002). When animals face a digestive bottleneck they can spend their time inactive (Zwarts & Dirksen 1990), or if digestion proceeds during competition, they can feed at higher competitor densities without depressing their long-term intake rate (Fortin *et al.* 2004; van Gils & Piersma 2004). Thus, when foragers face a digestive constraint, field measurements of the functional response will show a relatively constant intake rate at different food densities;

hence the asymptote will not be set by the bird's handling time, but by the digestive constraint (van Gils *et al.* 2005b). This is a problem, as measurements on intake rates at low food densities are essential to estimate the 'instantaneous area of discovery' (a), and measurements at high densities would enable estimates of handling limitation. By rewriting Holling's disc equation (Holling 1959), the instantaneous area of discovery (a) is calculated from the estimated intake rate (IR), handling time (T_h) and prey density (N):

$$a = \frac{IR}{(N - (IR * N * T_h))} \quad (\text{eqn 1})$$

Fitting a type II functional response model on field-based data for digestively constrained foragers will therefore greatly underestimate a , as the intake rate calculated over total time is not only limited by a , T_h , and N , but also by the time it takes to digest the food (Fig. 7.1). Since a digestively constrained intake rate remains constant even when N increases, a will be increasingly underestimated with an increase in N .

To arrive at the most general estimates of a and T_h in order to predict forager distributions, Piersma *et al.* (1995) and van Gils *et al.* (2004) emphasized the importance of site-independent quantification of the functional response and advocated that standardized assays of measurements of functional responses should be collected in experimental settings. This approach of extrapolating site-independent (experimental) results assumes that the examined processes and patterns are scale-independent. In contrast, Bergström & Englund (2004), argued that such experiments suffer generality because of issues of spatial scale (see also Cooper & Goldman 1982; Sarnelle 1997; Bergström & Englund 2002).

In this study these contrasting views are examined by using both field-observational data and observations collected in an experimental laboratory setting to examine the functional response in a single sex (females) of a shorebird species (bar-tailed godwit, *Limosa lapponica*), using a single prey type (lugworm, *Arenicola marina*). We use the data to determine the type of functional response and to evaluate the implications and accordance of Holling's disc equation (Holling 1959), which assumes both handling time and the instantaneous area of discovery to be constant across different prey densities.

Methods

Study system

Bar-tailed godwits are sexually dimorphic shorebirds wintering in intertidal areas; females are 20% heavier with 25% longer bills than males (Cramp & Simmons 1983; Duijns *et al.* 2012). During the nonbreeding season males feed mainly on small prey items and females predominantly forage on lugworms (Scheiffarth 2001; Duijns & Piersma

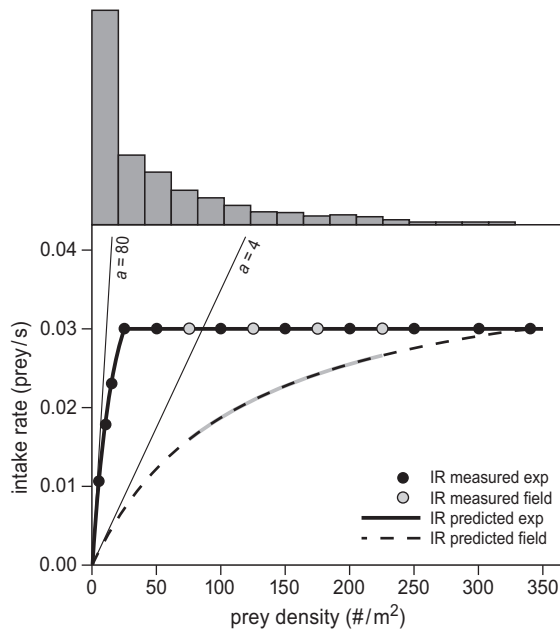


Figure 7.1. Conceptual graph of intake rate as a function of prey density following Holling's disc equation for foragers digestively constrained at 0.03 prey/s. The solid black dots represent intake rate (IR) measurements at experimentally offered prey densities, the solid black line represents the prediction based on experimental measurements of instantaneous area of discovery (a), handling time and digestion time. The solid grey dots represents IR measurements at prey densities observed in the field, and the dashed black line represents Holling's disc equation fitted through these field measurements. The estimated a decreases from 80 $\text{cm}^2 \text{s}^{-1}$ under the experimental setting to 4 $\text{cm}^2 \text{s}^{-1}$ in the field-based approach. Handling time (T_h) is fixed in both conceptual graphs and is set at 18 s (equals the field handling time). The grey bars at the top of the graph denote the frequency distribution of lugworms over the entire Dutch Wadden Sea in 2011 ($n = 1,465$ samples; Compton *et al.* 2013). Clearly, the lowest densities occur most frequently, which emphasizes the importance of intake rate measurements at these low densities.

2014). Additionally, spatial segregation between the sexes has been observed (Smith & Evans 1973; Both *et al.* 2003; Duijns *et al.* 2014b). These sexual differences in habitat and diet result in females foraging on large deeply buried prey, and females also being more vulnerable to behavioural prey depression than males (Duijns & Piersma 2014). This means that when studying the functional response of females, as we will do here, we better include the burying depth of prey as a factor.

Field observations

SHORT INTAKE RATE PROTOCOLS

Field observations were made in May 2011 on the mudflats in the Dutch Wadden Sea, close to the island of Texel, the Netherlands (53° 05' N, 4° 48' E). A total of 18 plots, each measuring 100 by 100 m (1 ha), were marked with PVC poles (1.5 m long) at every corner, inserted 0.5 m in the sediment. Prior to the tidal retreat, a single observer (SD), posi-

tioned himself about 50-100 m from a randomly chosen plot where the animals gradually entered. To minimize interference effects, only solitarily foraging females ($n = 57$) were chosen for focal animal sampling (Duijns & Piersma 2014). Individuals were observed for a 5-min period and behaviour was recorded on a digital voice recorder (Sony ICD-P620; continuous recording). Because during this time of year females are much paler than males (Piersma & Jukema 1993), the sexes could easily be identified.

The following behavioural categories were distinguished: searching, handling, being vigilant, preening and resting. Ingested lugworms were counted and the numbers converted into intake rate (prey/s). Repeated observations of the same individuals were avoided by waiting at least 30 min after a given individual had been observed at a plot. The recorded trials were analysed with Observer 5.0 (Noldus 2003) at normal speed and this resulted in measurements of: foraging time (s), other behaviour (s), handling time (s) and intake rate (prey s^{-1}).

LONG-TERM INTAKE RATE

To determine how the digestive constraint limits the long-term intake rate, we filmed three individuals for longer times (56, 49 and 30 min, respectively) through a 20-60 \times spotting telescope (ATS 80HD, Swarovski Optik, Absan, Austria), using a digital camera (PowerShot S95, Canon Inc., Tokyo, Japan). These solitarily foraging bar-tailed godwits fed on lugworms and regularly took digestive breaks during foraging. Their digestive constraints are given by the slope of the cumulative number of prey in relation to elapsed time (e.g. Zwarts *et al.* 1996; van Gils *et al.* 2003).

BIRD DENSITY AND ACTIVITY PATTERNS

Density measurements and activity scans of bar-tailed godwits were also performed at most plots ($n = 12$) throughout the study period, using a 5-min interval. During each interval, all individuals per sex were counted and the activity (foraging, resting or other), was noted. On average each plot (mean \pm SD) was observed for 9 ± 3.2 h; only female densities were used for the analysis.

PREY DENSITY

The lugworm density was sampled in all plots prior to the arrival of the birds from their wintering grounds in West Africa (early May) and sampled again immediately after the birds' departure (early June; Drent & Piersma 1990; Duijns *et al.* 2009; 2012). At each plot, 5 benthic cores of 0.0177 m^2 were taken at approximately 25 m from each corner and 1 sample from the centre of each plot. This procedure was repeated in early June, resulting in a total of 10 benthic samples per plot. Each benthic sample was taken to a depth of approximately 30 cm and sieved through a 1-mm mesh. Note that lugworms can live as deep as 30 cm in their U-shaped burrow, but regularly move their tails to the surface to

produce the well-known sand castings (Wells 1966). It is then that they are available to probing predators such as bar-tailed godwits. All lugworms were counted and stored in 4% formaldehyde saline solution for subsequent analyses in the laboratory.

Indoor experiment

BIRDS AND HOLDING CONDITIONS

Five adult female bar-tailed godwits were captured with ‘wilsternets’ (Piersma *et al.* 2005) on 15 May 2012 near Oudeschild (53°05’N, 4°85’E) on the Wadden Sea island of Texel. Immediately after capture (< 5 min), the birds were lightly sedated with midazolam (2 mg/kg), to avoid a stress response (Ward *et al.* 2011) and brought into the nearby indoor aviaries at the Royal Netherlands Institute for Sea Research (NIOZ). They were kept there until their release in early July 2012. A metal identification ring was fitted to one of the tibiae together with one or two plastic colour rings on one of the tarsi to allow individual recognition.

The indoor aviaries consisted of one 7 × 7 m wide and 3 m high indoor aviary in which a mudflat system had been created (the experimental area) with two adjacent aviaries of 3.85 × 1.85 × 2.40 m each (Fig. 7.2). These adjacent aviaries served as roosting areas and always contained a fresh water tray. For general habituation and training purposes (~4 weeks), all birds were kept in the experimental area with access to the smaller adjoining aviaries. Within the aviaries, the light was kept synchronised with the natural light regime (adjusted daily for changes in the times of sunset and sunrise). Water temperature was kept constant at 8°C and air temperature constant at 12°C (to prevent any temperature effects on the experiments).

The staple food given to the experimental birds was Trouvit fishmeal pellets (Trouw Nutrition, Putten, the Netherlands), mixed daily with 100 g of commercially available mealworms *Tenebrio molito*. Staple food was offered after each experimental day, but the times at which the staple food was provided were varied between days to avoid that birds in the experiment would simply wait for ‘easy food’ at a known, fixed time and thus not ‘work for food’ during the trials. To ensure that birds were all motivated to participate in the trials, food was withheld from 22:00 h the previous day. All trials were carried out between 09:00 and 17:00 h. To allow using the focal bird of choice, the birds were captured in animal transport cages with the help of a sluice system to reduce the stress of handling. After being caught, the individuals were kept separately in these cages. This also allowed each bird to be weighed daily and for their health status to be monitored. After the experiment, in order to increase body mass before release, the birds were fed *ad libitum* for two days. On 5 July 2012 they were tagged with unique colour-coded ring combinations placed around their legs to allow for individual identification in the field (Spaans *et al.* 2011) and released near the catching site. The experiment was in full compliance with Dutch law regarding animal experiments under permits issued by the DEC-KNAW (NIOZ 12.01).

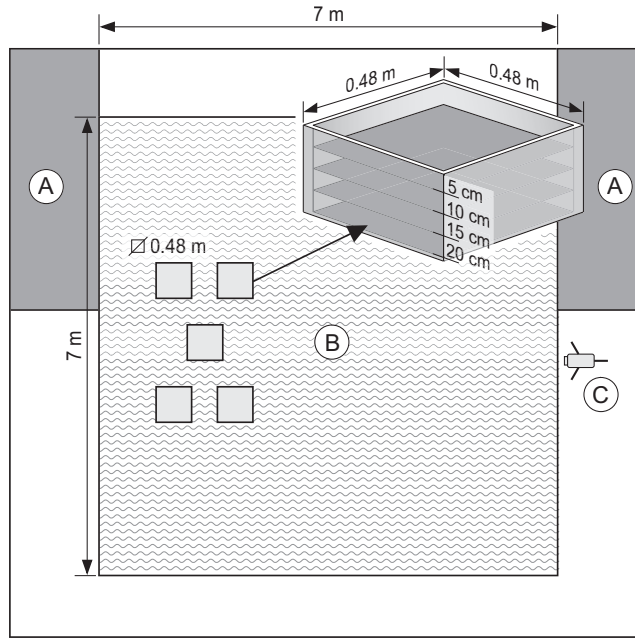


Figure 7.2. The experimental setup: (A) aviary / high-tide roost; (B) experimental area (covered with water during the experiment); (C) observation hide. The inset diagram at the upper right patch shows a feeding patch in greater detail. The grid could be switched between four prey burial depths: 5, 10, 15 and 20 cm.

EXPERIMENTAL PREY ITEMS

The experimental prey, lugworms, were obtained every second day from a commercial supplier (Arenicola BV, Oosterend, the Netherlands). They were stored in a tray containing 300 individuals in fresh seawater and kept at 4°C, which kept them in perfect condition. Only lugworms with a wet mass between 1.7 g and 7.3 g were used as experimental prey items; the cut-off points for mass were based on the normal size distribution found under natural conditions on Texel, which excludes the 5% extremes (4.4 ± 1.4 g, mean \pm SD; $n = 1,923$).

EXPERIMENTAL PROTOCOL

Five trials were carried out per day, with each bird participating in one trial per day. A patch measured 0.48 x 0.48 m (0.23 m²) in dimension and was filled with sediment collected from the Wadden Sea (median grain size 269.5 μ m; comparable to natural grain sizes; e.g. Compton *et al.* 2013). The water level in the experimental area was kept at 30 cm in such a way that the patches were covered with approx. 1 cm of water to facilitate penetrability, mimicking the natural foraging situation. The maximum prey burial depth in the trays was set by placing a grid at different depths (Fig. 7.2). Only one patch was available per trial. The other patches were covered and thus rendered inaccessible.

The experimental treatments consisted of four prey burial depths (5, 10, 15 and 20 cm, respectively) and five prey densities (3, 6, 12, 24 and 96 lugworms per tray). Note that even though the prey at the maximum depth of 20 cm were buried deeper than bill length, the birds could still access the prey by inserting their head and bill in the sediment. Density treatment and order of birds were randomized to control for day and time-of-day effects. The highest density treatment (i.e. 96 worms per tray), resulted in similar searching times compared to the second highest density (i.e. 24 worms per tray). This was most likely to be the result of increased selectivity, as has been found in a similar experimental setting with extremely high densities of prey for oystercatchers *Haematopus ostralegus* (Wanink & Zwarts 1985); this treatment was therefore excluded from further analyses. Consequently, the numbers of treatments per individual used in the analysis decreased from 20 to 16 treatment conditions per bird.

Before each experimental day, the lugworms were counted by hand and weighed (± 0.1 g). Different prey densities were randomly distributed per patch 30 minutes prior to the first trial of the day. As a quality indicator of the used prey items, only lugworms that actively dug themselves into the sediment (< 5 min) were used. The overall length of preparation time (30 min) proved to be sufficient for the lugworms to dig themselves in the sediment and to settle at the maximum available depth, as had been shown by a pilot study. In this pilot study three prey items were simultaneously released to allow them to settle at different prey depths (i.e. 5, 10, 15 and 20 cm). Since lugworms respond to the probing behaviour of foragers (Duijns & Piersma 2014), after the lugworms had been allowed to dig themselves in, the sediment was probed 50 times, the trays were emptied per 5 cm and the whole procedure was repeated twice ($n = 8$). All prey items ($n = 24$) were indeed found at the maximum depth provided. This probing treatment was repeated during the experiment and all traces were erased from the surface to prevent the birds from using visual clues to locate the prey.

Each of the 80 experimental trials lasted until the birds had either taken three prey, spent a maximum of 15 min of foraging (measured with a stopwatch), or spent a total of 1 h in the experimental area. After each trial, remaining lugworms (or parts thereof) were removed from the patch, counted and weighed again.

VIDEO ANALYSIS

All experimental trials were recorded on video cameras (Fig. 7.2). The recordings were analysed using The Observer 5.0, which allowed for measurements with an accuracy of 0.04 s. The following six behaviours were distinguished: (1) *Searching*, (2) *Handling time*, (3) *Handling component*, (4) *Preening*, (5) *Vigilance* and (6) *Resting*. (1) *Searching* was characterised by probing of the sediment in search of prey, either while moving or standing still. (2) *Handling time* was characterised by the touching of the prey with the bill until ingestion. (3) *Handling component* was divided into three subcategories: extraction,

cleaning and consumption of the prey. 'Extraction' was defined as the period from first moment of intense probing (recognition of a prey) up to the moment when the prey item was extracted from the sediment. 'Cleaning' was defined as lasting from the moment of extraction up to the moment of consumption. 'Consumption' was defined as lasting from the moment the prey enters the bill until the moment of swallowing the prey. (4) *Preening* was defined as a number of preens uninterrupted by other behaviour, and considered finished when the bird lifted its head so that the bill was free from the feathers. (5) *Vigilance* was defined as interrupting any other behaviour to watch the surroundings. (6) *Resting* was defined as the bird being at rest with at least one of the eyes being completely closed for more than 1 second or the head tucked into the plumage.

In addition, we kept a tally on the number of prey ingestions, the order in which the prey were found, the part of the prey that was handled (complete prey, body, tail or intestines; body and tail are easily distinguishable through the lack of segmentation in the tail) and the prey length (in cm, measured relative to the bill of the focal bird). The order in which the prey were found was made possible by marking and numbering individual prey with a non-permanent marker on the monitor. Whenever a prey was broken, all parts of the same individual were summed up to total length and treated as one prey ingestion.

Statistical analyses

FIELD MEASUREMENTS

By using the mean observed handling times of all observed birds, the mean food abundance per plot (no./m²) and intake rates (prey/s), the instantaneous area of discovery (cm² s⁻¹) was estimated by the non-linear least-square fitting function (nls) of the software package R (R Development Core Team 2013). Linear models were used to test the assumptions of Holling's disc equation for searching and handling time, which were both log₁₀ transformed. The long-term intake rate observations, which were used to estimate the digestive constraint, were analysed with a linear mixed model using bird ID as a random factor.

Ivlev's electivity index (*I*) was used to express prey density preference (Jacobs 1974). For a given prey density, the index compares its relative fraction of the mean bird density F_{dens} with its relative fraction in the available food density F_{avbl} , as follows:

$$I = (F_{\text{dens}} - F_{\text{avbl}}) / (F_{\text{dens}} + F_{\text{avbl}}) \quad (\text{eqn 2})$$

Thus *I* ranges from -1 to 1, with *I* > 0 indicating a preference and *I* < 0 indicating aversion. We grouped the sampled prey density into classes with a width of 50 prey/m² and used mean (female) bird densities per plot; this relation was tested with a non-linear regression analysis. The analysis of the proportion of birds foraging in relation to food density was logit transformed and analysed with a linear regression (Warton & Hui 2011).

EXPERIMENTAL APPROACH

Holling's disc equation assumes both handling time (T_h) and instantaneous area of discovery (a) to be constant across prey densities (N). The latter implies that the slope of log search time (T_s ; i.e. the search interval between two prey encounters) as a function of log prey density equals -1, as explained here:

$$\text{Encounter rate} = \frac{1}{T_s} = a * N \quad (\text{eqn 3})$$

This equation can be rewritten as:

$$\log(T_s) = -\log(a) - \log(N) \quad (\text{eqn 4})$$

In the experimental setting only the first three prey items were used, which were always ingested whenever they were found. This enabled us to use all handling times. In 70 trials all three prey items were found and consumed; in 8 trials, just two prey were found and in 2 trials, the focal bird only found one prey. These exceptions only occurred in the lowest density treatments. This resulted in 10 (out of 238) incomplete search times due to failure to find the third prey, which makes the last unsuccessful search interval (i.e. finding the third prey) a censored observation. To deal with these 'right-censored data' (Haccou & Meelis 1992), the package *tlmec* (Matos *et al.* 2012) was used to fit mixed-effects models with censored data, with bird identity as a random intercept and depth as a factor. Searching time, density of prey and prey length were \log_{10} transformed to normalize the distribution and searching times were increased by 0.04 s (i.e. minimal length of all recorded behavioural bouts).

In all models a correction for depletion (i.e. initial prey density – prey consumed) was applied, as patches could be 100 % depleted (in the case of a prey density of 3 prey). To test the assumptions of Holling's disc equation, a generalized linear mixed model was used for searching (Model 1) and for handling (Model 2). Bird identity was included as a random effect in both models:

$$\log T_{s, ij} = \alpha + b_i + \beta_1 \times \log N_{ij} + \beta_2 \times D_{ij} + \epsilon_{ij} \quad (\text{Model 1})$$

$$\log T_{h, ij} = b_i + \beta_1 \times \log N_{ij} + \beta_2 \times D_{ij} + \beta_3 \times \log L_{ij} + \beta_4 \times D_{ij} \times \log L_{ij} + \epsilon_{ij} \quad (\text{Model 2})$$

where T_s is search time (s) and T_h is handling time (s) for bird i and prey j , α is the instantaneous area of discovery ($\text{cm}^2 \text{ s}^{-1}$), b is the random slope of bird identity, β_n is the slope of the fixed effect, N is prey density (m^{-2}), D is the prey depth (cm), L is the prey length (cm) and ϵ is the residual. Model selection was based on the Akaike Information Criterion (AIC; Burnham & Anderson 2002), and the model was considered to be substantially better when its value was at least 2 points lower than another model. This explains why

prey length is not included in Model 1 but was included in Model 2. For the dependent search time variable (T), the fixed effects of prey density and prey depth (Model 1) were included. The mixed model for the dependent variable handling time (T_h), included prey density, prey depth, prey length and the interaction between prey depth and prey length as fixed effects (Model 2).

Results

Search time

In the field, search time did not decrease with an increase in prey densities ($F_{1,55} = 0.75$, $R^2 = 0.013$, $P = 0.39$; Fig. 7.3A), and, therefore did not obey the first assumption of Holling's disc equation. In the experimental setting, search time decreased with increasing prey densities (GLMM, $X^2 = 84.9$, $P < 0.001$; Fig. 7.3B). In this log-log correlation, the slope was $-0.93 (\pm 0.09 \text{ SE})$, so the first assumption of Holling's disc equation (a slope of -1) was within the 95% CI of the estimate. Additionally, search time in the experimental setting increased when prey were located at a greater depth (GLMM, $X^2 = 8.4$, $P = 0.003$; Fig. 7.4). This increase was found at all prey densities, consistent with the idea that greater prey burying depths interfere with prey detection (Duijns & Piersma 2014).

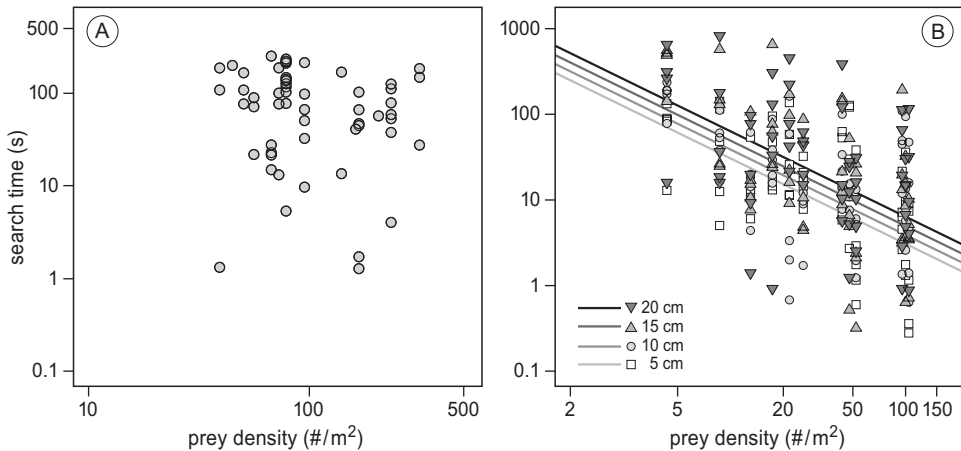


Figure 7.3. (A) In the field-based study, Holling's first assumption was not upheld as there was no effect of prey density on search time ($P = 0.39$). (B) However, in the experimental setting Holling's first assumption was met with search times being inversely related to prey density. The four lines represent the four different burial depths (symbols shown in legend), which, as predicted, had an effect on searching time, i.e. more deeply buried prey resulted in longer search times per prey. Note the log-log scales in both plots.

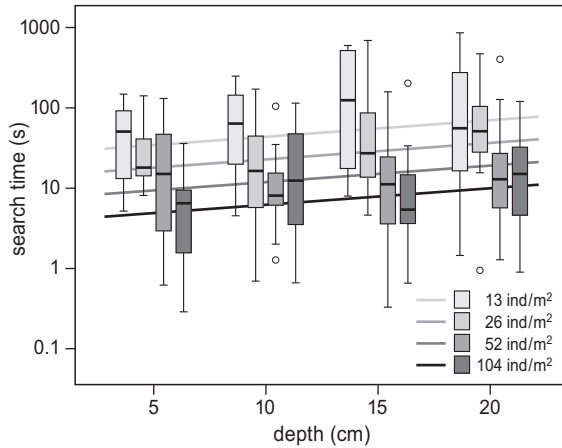


Figure 7.4. In the experiment, search time not only increased with decreasing prey density (see also Fig. 3B), it also increased with increasing prey depth. Box plots indicate the median, and the 25th and 75th percentiles; whiskers indicate the 5th and 95th percentiles. Note that the y-axis is plotted on a log scale.

Handling time

Handling time was independent of prey density in both the field study ($F_{1,55} = 1.97$, $R^2 = 0.03$, $P = 0.17$; Fig. 7.5A) and in the experiment (GLMM, $X^2 = 2.6$, $P = 0.10$; Fig. 7.5B), so that in both approaches the second assumption of Holling's disc equation was met. Furthermore, handling time was also independent of depth in the experiment (GLMM, $X^2 = 0.5$, $P = 0.46$). Prey length had a significantly positive effect on handling time in the experimental setting (GLMM, $X^2 = 165.9$, $P < 0.001$), as well as in the field study ($F_{1,55} = 19.84$, $R^2 = 0.27$, $P < 0.001$). Observed prey handling times did not differ from the field study and the experiment ($t = 0.09$, $df = 31.4$, $P = 0.93$; Fig. 7.6A). However, when handling time was ignored or is unknown, Holling's disc equation overestimates handling time greatly (Fig. 7.6A). Additionally, when the asymptote was set to the digestive constraint, handling time was overestimated even more (Fig. 7.6A).

Instantaneous area of discovery

As predicted, the estimate of the instantaneous area of discovery (a) on the basis of field measurements was rather low (mean \pm SE = 0.7 ± 0.1 ; Fig. 7.6B). In the experiments, a was found to be much higher. Calculations using equation 4, yielded values of $a = 52.4 \text{ cm}^2 \text{ s}^{-1}$ for a prey depth of 5 cm, $a = 41.3 \text{ cm}^2 \text{ s}^{-1}$ for depth 10 cm, $a = 32.6 \text{ cm}^2 \text{ s}^{-1}$ for depth 15 cm and $a = 25.7 \text{ cm}^2 \text{ s}^{-1}$ for depth 20 cm (bias-corrected back transformed; Sprugel 1983; Fig. 7.6B). Thus, the instantaneous area of discovery decreased with prey depth, implying that bar-tailed godwits were able to search less surface area per second for prey when prey burying depth increased.

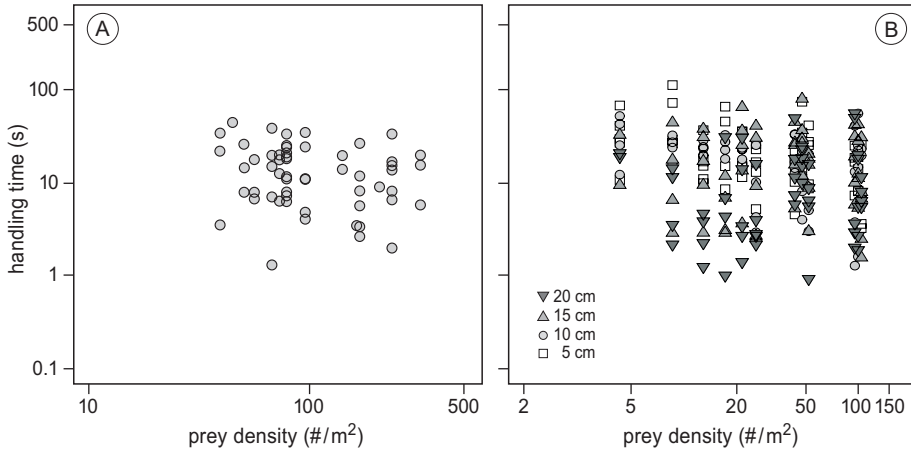


Figure 7.5. Prey handling times did not vary with prey density in the field (A), nor in the experiment (B), where the different symbols represent different prey depths (shown in legend). Therefore, the second assumption of the Holling's disc equation was upheld by both approaches. Note the log-log scales.

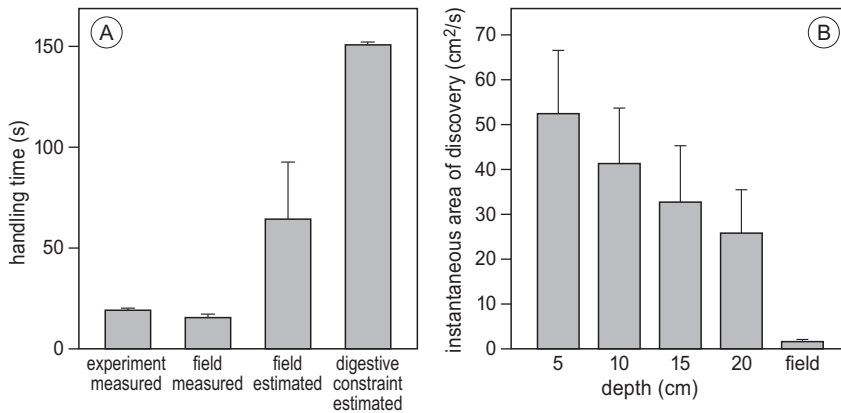


Figure 7.6. (A) Mean (\pm SE) handling times, measured separately in the experiment, in the field, estimated from fitting Holling's disc equation to the field data (short protocols), and estimated from long-term intake rate (long protocols; i.e. by neglecting existence of digestive constraint). (B) Mean instantaneous area of discovery (\pm SE), estimated in the experiment for different depths and by fitting Holling's disc equation to the field data (short protocols).

Field versus experimental approaches

In the field, bar-tailed godwits regularly took foraging breaks. The estimated slope of the cumulative number of prey per elapsed time (mean \pm SE) was 0.0067 ± 0.00005 prey/s (GLMM, $X^2 = 10,215$, $P < 0.001$), indicative of a digestive constraint. In the experimental setting, given that only the first three prey items were used in the analysis, and that no digestive breaks were taken, the levelling off was due to the handling limitation (Fig 7.7A). This ensured that the experiments provided the short-term intake rate. As a consequence, the instantaneous area of discovery estimate based on field measurements was considerably lower than for the experimental setting, and led to a serious underestimation of the possible intake rates at low food densities.

Ivlev's electivity index (I) shows that bar-tailed godwits avoid low density food patches ($I < 0$) and preferred patches with higher prey densities ($I > 0$; $F_{3,14} = 46.91$, $R^2 = 0.89$, $P < 0.001$; Fig. 7.7B). The field-based functional response predicted that, below a prey density of 100 prey/m², intake rates drop under the digestive constraint so that birds would be better off avoiding these areas. With a preference for prey densities ranging between 140 and 240 prey/m², solitarily foraging bar-tailed godwits did seem to avoid these areas. This suggests that when birds encounter low food densities (e.g. due to forced movement away from the best areas by the tidal regime), they need to forage longer (which they also can, as they face no digestive constraint and thus need not take digestive breaks). Our results indicate that, when foraging on low food density patches, bar-tailed godwits indeed foraged for a larger proportion of their time ($F_{1,236} = 7.19$, $R^2 = 0.03$, $P = 0.008$; Fig. 7.7C).

Discussion

In this study we show that female bar-tailed godwits obeyed both assumptions of the type II functional response (Holling's disc equation), but only when the measurements were obtained in a controlled experimental setting, rather than in the field (c.f. Caldow & Furness 2001; Smart *et al.* 2008). In fact, our results based on the cumulative intake measured in the field clearly demonstrated that the levelling off of intake rate was caused by a digestive constraint rather than by handling time. Without taking this digestive constraint into account, the field-estimated instantaneous area of discovery (a) was seriously underestimated. Depending on the burial depth of prey, the estimated a was a factor 30 to 70 times higher in the experiment than when estimated on the basis of field data (Fig 7.6B). This large contrast between field and experimental estimates generates several questions. Why should sensory acuity be so high? Why should digestive capacity provide the limiting factor? As a preliminary answer we suggest that to ensure that these foragers can find enough prey in situations of low density, the instantaneous area of dis-

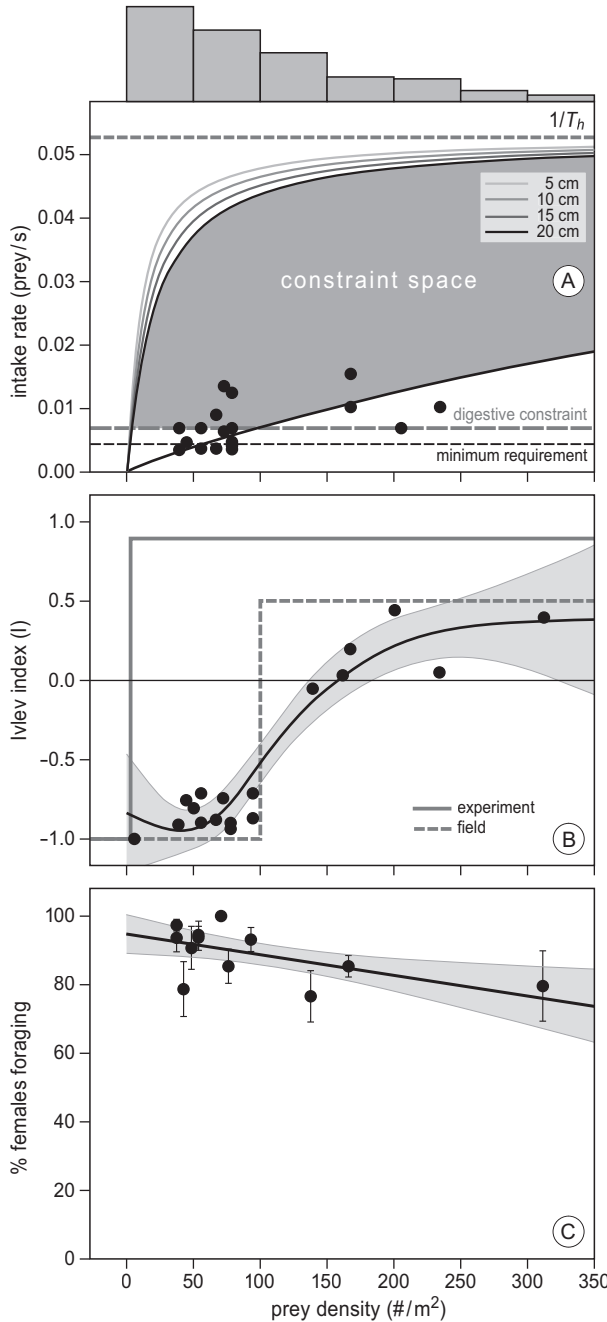


Figure 7.7. (right) (A) The intake rate (prey/s) of solitary bar-tailed godwits feeding on lugworms in the field, with the experimentally obtained functional responses for the four different prey burial depths shown as different greyscale lines. Field estimates were found to be around the level of the digestive constraint (estimated in long protocols). As expected, the field-estimated instantaneous area of discovery is much lower than in the experiment (i.e., 34 to 70 fold). The high intake rates measured in the experiments cannot be sustained in the field due to several constraints (as indicated by the grey 'constraint space'). (B) In the field, female bar-tailed godwits showed a preference for high prey densities (Ivlev electivity index > 0), despite similar intake rates in lower prey density patches. Defining a minimally required intake rate as the digestive constraint, bar-tailed godwits should prefer almost all food densities (> 3 prey/m²), based on the experimentally obtained functional response (solid grey line). However, using the field-based functional response, the birds should avoid such low prey densities (dotted grey line), which is what is found ($R^2 = 0.89$, $P < 0.001$). The grey area indicate the 95% confidence intervals of the non-linear regression. (C) The percentage of actively foraging females (\pm SE) related negatively to prey density ($P = 0.008$), and the grey area indicate the 95% confidence intervals of the linear regression. The frequency distribution of lugworm densities in the study plots is shown on top of panel (A).

covery requires an even larger ‘safety factor’ (Diamond 1998), than does digestive capacity (Piersma & van Gils 2011; McWilliams & Karasov 2014). Additionally, when foragers feed at high prey densities, they are likely to become more selective (Stephens & Krebs 1986). When prey density increases, optimal foraging theory predicts an increase in selectivity, by rejecting low profitable prey (Charnov 1976), and adding higher quality prey to their diet (van Gils *et al.* 2005b).

To meet their minimum energy requirements, the functional response model fitted by field data predicted that bar-tailed godwits need a minimum prey density of 63 prey/m². Based on the experimental observations, the minimum prey density would be 3 prey/m² only (Fig. 7.7A). A benthic sampling effort across the entire intertidal Dutch Wadden Sea, using a combination of sample points taken at 500 m intervals and additional random sample points (Bijleveld *et al.* 2012; Compton *et al.* 2013), enables an evaluation of the implications. Of the 1,465 sampled points where lugworms were present, these birds would be able to meet their daily requirements at only 17% of these points, based on the field-based approach. The results from the experiment, however, predict that birds would be able to meet their daily requirements at 30% of these sampled points, indicating that the birds can survive across a greater range of food situations than what they themselves select or prefer (note that Ivlev electivity index indicated that bar-tailed godwits would avoid these lower food density patches, Fig. 7.7B). The field-based functional response model thus allows predictions on forager’s distributions, but only for the specific ecological context in which the data were collected. Processes such as digestion (e.g. Jeschke *et al.* 2002; van Gils & Piersma 2004), social behaviour (Bijleveld *et al.* 2012), interference and predator avoidance behaviour (e.g. Cresswell & Whitfield 1994; Ydenberg *et al.* 2002; van den Hout *et al.* 2008), constrain these foragers (Fig. 7.7A), and will result into highly underestimated sensory capacities.

Sampling prey abundance in the field does not have the same precision as the measurement of prey densities in experimental settings due to a high variation in the samples. This inaccuracy may result in a bias when testing the assumptions of Holling’s disc equation. The lugworm densities obtained by our field sampling indicated much variation between plots, with the coefficient of variation showing a fivefold range (CV; 69 – 316 %). However, the analysis of search- and handling time in relation to prey density did not show any trends. It is therefore unlikely that the imprecision of prey sampling strategy influenced the conclusions of this study. Nevertheless, the inaccuracy in sampling prey densities should be kept in mind when performing field-based studies.

For species such as bar-tailed godwits foraging on relatively large prey, handling times are relatively long and can be accurately estimated both under field and experimental settings. However, when handling time is unknown, Holling’s disc equation overestimates handling time for digestively constrained foragers in the wild (Fig. 7.6A) Wanink & Zwarts (1985) have already shown that in many field-based studies across a range of taxa,

observed handling times were considerably shorter than the calculated handling time that sets the plateau of an observed functional response. Thus, the assumption of Holling's disc equation is often violated in field studies, but this is seldom acknowledged.

One problem with observing animals in their natural context is that the 'state' of an individual is not known. Although it is possible to predict changes in energetic demand during the annual cycle (e.g. maximum energy intake rates when fuelling for migration; Scheiffarth *et al.* 2002; Duijns *et al.* 2009), it is impossible to remotely assess their actual gut content or digestive organ size. Thus, the length of field observations and the 'random' choice of the focal bird needs to be considered. Choosing only actively foraging animals will risk ignoring the digestive constraint, and thus overestimate the intake rate. Observing relatively short periods of foraging behaviour will have the same effect. Additionally, body size may influence the likelihood of a digestive constraint. On the one hand, while food processing rates for larger and smaller species do not differ (per unit gut length), retention times are longer in larger species as a result of longer digestive tracts (Bruinzeel *et al.* 1998). This suggests that smaller species face larger digestive constraints as their food would be more poorly assimilated. On the other hand, larger species generally forage on lower-quality food than smaller species (Gordon & Illius 1996). The fact that high quality food is usually less abundant than low quality food, and easier to digest, suggests that smaller species might be more search- than digestively constrained, while the larger species would be more likely to be affected by digestive constraints. Clearly, the fact that the effects of body size on the existence of digestive constraints appear to be multiplicative and counteractive (Steuer *et al.* 2014), will make it difficult to generalize across species.

Several studies advocate the use of simple behavioural parameters collected in the field (e.g. Stillman *et al.* 2006; Smart *et al.* 2008), or even suggest that only external characteristics, such as bird and prey sizes, can be used to predict the asymptote (Goss-Custard *et al.* 2006). Our results, in contrast, show that although field measurements may yield a consistency test of the distributional patterns in a specific ecological context (e.g. Gill *et al.* 2001; Lourenço *et al.* 2010), they cannot be mechanistically interpreted and are therefore not generally applicable. The implications of our findings are that, wherever possible, field measurements of the functional response should be independently quantified in an experimental setting, in order to inclusively determine whether and at which level the digestive constraint is operating (preferably this is also determined experimentally; van Gils *et al.* 2003a). When field measurements are the only option, these measurements should preferably be taken at the onset of the foraging bout, when the individual is not yet digestively constrained. However, even then extreme caution should be taken in the generalization of the results.

Acknowledgements

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Phenotype-limited distributions: short-billed birds move away during times that prey bury deeply

Sjoerd Duijns, Jan A. van Gils, Jennifer Smart & Theunis Piersma

Abstract

In our seasonal world animals face a variety of environmental conditions in the course of the year. To cope with such seasonality, animals may be phenotypically flexible, but some phenotypic traits are fixed. If fixed phenotypic traits are functionally linked to resource use, then animals should redistribute in response to seasonally changing resources, leading to a so-called 'phenotype-limited' distribution. Here we examine this possibility for a probe-feeding shorebird, the bar-tailed godwit (*Limosa lapponica*; a long-billed and sexually dimorphic shorebird), that has to reach its cryptic prey with their bill of a fixed length. The main prey of female bar-tailed godwits are lugworms (*Arenicola marina*), which are buried deeper in winter than in summer. By analysing sightings of individually marked females, we found that in winter only longer-billed individuals remained in the Dutch Wadden Sea, while the shorter-billed individuals moved away to estuaries such as the Wash, where prey live closer to the surface. Although longer-billed individuals have the widest range of options in winter and could therefore be selected for, counterselection may occur during the breeding season on the tundra, where their surface living prey may be captured more easily with shorter bills. Phenotype-limited distributions could be a widespread phenomenon and when associated with assortative migration and mating, it may act as a precursor of phenotypic evolution.

Introduction

Most organisms on Earth live in seasonal environments with respect to climate and food (Fretwell 1972). The ability of individuals to reversibly change phenotype in response to a change in environmental conditions is called phenotypic flexibility (Piersma & Lindström 1997; Piersma & van Gils 2011). Animals making adjustments in digestive organ size to cope with different prey types or prey quality represent a well-known example of (often seasonally structured) phenotypic flexibility (e.g. van Gils *et al.* 2003a; McWilliams and Karasov 2014; Zaldúa and Naya 2014). However, some aspects of the phenotype are essentially inflexible. Traits such as bill length in birds that show determined growth, are hardly flexible (Hulscher 1985; Lok *et al.* 2014). Bill morphology is a strong predictor of foraging niche (e.g. Selander 1966; Schoener 1974; Durell 2000, Abzhanov *et al.* 2004; Nebel *et al.* 2005; Temeles *et al.* 2010; Gonzalez-Terrazas *et al.* 2012), and may lead to phenotype-related differences in diet (Mathot *et al.* 2007, Alves *et al.* 2013b). In addition, animals can show behavioural responses to environmental change. They can increase foraging time (e.g. Abrams 1984; Bergman *et al.* 2001), select alternative prey (Oudman *et al.* 2014; Peers *et al.* 2014), or move to sites where food is more favourable (e.g. Alerstam 1990; van der Graaf *et al.* 2006; Duriez *et al.* 2009).

Intra-population variation in dietary optima, and temporal and spatial variation in the abundance or availability of different prey is known for many species of fish, amphibians, insects, mammals and birds (Smith & Skulason 1996). Body size, dominance, prior residency or food availability appear to be responsible for individual differences in migratory tendencies within populations (Chapman *et al.* 2011). Food availability is relatively easy to quantify in intertidal areas, and non-breeding shorebirds provide a good system for correlating distribution of animals with their food resources (e.g. Goss-Custard *et al.* 1977b; Mathot *et al.* 2007; Piersma & van Gils 2011). Non-breeding shorebirds in temperate zones mostly feed on benthic prey that tends to bury deeper in winter than in summer (e.g. Zwarts & Wanink 1989; Zwarts & Wanink 1993). The latter being a response to changes in day length rather than changes in seawater temperature, at least in the case of polychaetes (Zwarts & Wanink 1993). With seasonally changing fractions of benthic prey burying beyond the bill lengths of most shorebird species (e.g. Cadée 1976; Esselink & Zwarts 1989), the part of the population for which too many prey have become inaccessible should move elsewhere. This could lead to 'phenotype-limited' forager distributions, a term that was first used to predict spatial distributions of individuals differing in dominance (Parker & Sutherland 1986).

Here we explore phenotype-limited distributions in female bar-tailed godwits (*Limosa lapponica*). Females have 25% longer bills than males and mainly feed on deep burying lugworms (a polychaete worm, *Arenicola marina*), while the shorter-billed males mainly forage on shallow buried prey (Scheiffarth 2001a; Duijns & Piersma 2014). In addition,

there is considerable variation in bill length within the sexes (Prokosch 1988; Piersma & Jukema 1990; Duijns *et al.* 2012). Among the available benthic prey items, seasonal variation in burying depth is largest in lugworms (Zwarts & Wanink 1993), so the potential for a phenotype-limited distribution should be most pronounced in female godwits. Although the larger sex (females) should incur lower energetic costs per unit body mass, the differential distribution between the sexes is best explained by sex-specific prey availability (Duijns *et al.* 2014b). This pattern could extend to individuals within a sex, such that those with shorter bills would be predicted (Scheiffarth 2003) to (i) move to more favourable wintering sites (i.e. areas with prey buried less deeply) and/or (ii) switch to prey items that are buried less deeply to sustain their minimum intake requirement.

Females with longer bills would be able to reach a larger fraction of the available biomass compared to shorter-billed individuals. This idea is shown in Fig. 8.1. We explored the possibility of phenotype-limited distribution by analysing the monthly distribution in bill lengths using long-term datasets of measured and marked non-breeding females in the Dutch Wadden Sea and in the Wash, UK. To estimate how intake rates depend on prey burying depth, and to predict the observed seasonal changes in diet composition (Scheiffarth 2001a), we used generally applicable functional response parameters (Duijns *et al.* 2014a).

Methods

Study species

Along the East-Atlantic Flyway two subspecies of bar-tailed godwits occur (Engelmoer & Roselaar 1998). The subspecies *L. l. taymyrensis* mainly winters in West Africa, breeds in northern Siberia and uses the Wadden Sea area twice a year as a refuelling site. The *L. l. lapponica* subspecies winters in North-western Europe and breeds in northern Scandinavia (Drent & Piersma 1990; Duijns *et al.* 2012). To explore the possibility of a phenotype-limited distribution, we first distinguished between the subspecies, as the *taymyrensis* subspecies has on average a shorter bill length than the nominate *lapponica* subspecies (Engelmoer & Roselaar 1998; Duijns *et al.* 2012). Although a considerable proportion of bar-tailed godwits cannot be assigned to either subspecies using morphometrics, they may occur together in the Dutch Wadden Sea during six months of the year (April-October; Duijns *et al.* 2012). During this period they would encounter similar environmental conditions in the Dutch Wadden Sea and therefore we included females with known bill lengths from known and unknown sub-specific identity in the analyses.

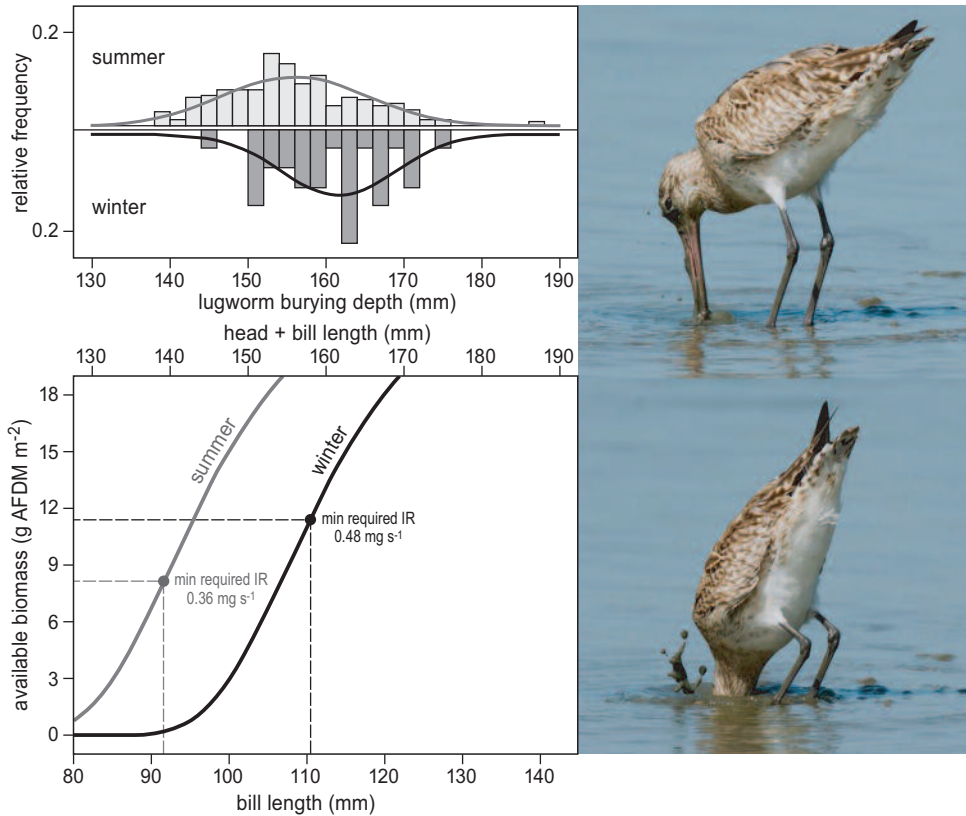


Figure 8.1. Conceptual model of available lugworm biomass in relation to bill length of female bar-tailed godwits in the Dutch Wadden Sea. Upper panel shows the distribution of individual lugworm burying depths, measured in 1981/1982 (corrected for accessibility; i.e. 4 cm subtracted), and separated for summer (Apr – Sep) and winter (Oct – Mar). From this, available biomass in relation to bill length can be deduced (lower panel). In summer, available biomass increases steeply as a function of bill length (due to the shallower burying depth), while minimum required intake rate ($0.36 \text{ mg AFDM s}^{-1}$) is relatively low. Therefore almost all individuals ($> 92 \text{ mm}$ bill) are able to reach their minimum requirement foraging only on lugworms. In winter, available biomass only increases at longer bills and, furthermore, minimum requirement is relatively high (due to higher maintenance costs; Scheiffarth *et al.* 2002). Shorter-billed females cannot acquire their minimum requirement and are predicted to leave this wintering site or shift their diet towards more accessible prey. Minimum requirements were calculated as follows:

$$\text{Minimum requirement} = \frac{\text{DEE}_{\text{season}}}{E} / T_f,$$

where E is a lugworm's energy content ($22 \text{ kJ g}^{-1} \text{ AFDM}$; Zwarts & Wanink 1993), the required daily energy expenditure DEE per season was set at $2.4 \times \text{BMR}$ in winter and $1.8 \times \text{BMR}$ in summer (Scheiffarth *et al.* 2002), daily foraging time T_f was assumed to be 12 h for both seasons (i.e. 50%; Scheiffarth *et al.* 2002), assuming an assimilation efficiency of 80% (Scheiffarth *et al.* 2002). The photos on the right exemplify the ability of female bar-tailed godwits to reach depths beyond the bill length. Original photos by Dave Montreuil.

Sightings of marked individuals

Birds were caught with 'wilsternets' (Jukema *et al.* 2001) or mist nets at various locations throughout the Dutch Wadden Sea area. Before release, length of bill (exposed culmen, from tip of bill to base of feathers), wing (flattened and straightened), tarsus and mass were measured using standard methods (Prater *et al.* 1977). Captures ($n = 2,433$) and sightings of marked individual females in the Dutch Wadden Sea ($n = 4,069$) were analysed over the period from capture up to May 2014 to assess bill length distributions per month. The 4,069 sightings were based on 1,541 individuals, of which 864 individuals were sighted multiple times (i.e. different months and/or years). They were all included in the analysis, as the analyses with and without multiple sightings showed no change, while the repeated presence of an individual is considered indicative of a preference to reside at a site. Full details on number of birds caught and sighted per month and year are given in Table 8.1. To compare bill length distributions with another major non-breeding site, biometric data was obtained from the Wash Wader Ringing Group in the UK. Here, bar-tailed godwits have been caught on the Wash with both cannon-nets and mist-nets (Atkinson 1996). The data on 1,693 female bar-tailed godwits used were collected in 1994–2011.

Although seasonal differences in bill length distributions have been reported in several bird species, differential bill wear was held responsible for this variation (e.g. Davis 1954; Morton & Morton 1987; Matthysen 1989). For shorebirds it is known that the rhamphotheca, the horny covering of a bird's bill, constantly grows at the base of the bill.

Table 8.1. Overview of numbers of female bar-tailed godwits caught and sighted in the Dutch Wadden Sea, by year and month.

year	no. caught	no. sightings	month	no. caught	no. sightings
2001	94	8	Jan	0	9
2002	99	10	Feb	9	28
2003	287	162	Mar	18	122
2004	149	146	Apr	117	237
2005	126	206	May	2057	2504
2006	180	276	Jun	0	38
2007	133	379	Jul	39	190
2008	79	172	Aug	90	641
2009	211	360	Sep	60	234
2010	262	425	Oct	38	42
2011	332	658	Nov	5	10
2012	257	588	Dec	0	14
2013	224	486			
2014	0	193			

Despite this growth, the bill wears and within individual variation appears to be negligible (< 1 mm; Hulscher 1985). Indeed, recaptures (> 1 year interval) of marked bar-tailed godwits show no evidence of intra-individual variation in bill length ($F_{1,12} = 936.5$, $R^2 = 0.99$, $P < 0.001$; slope = 0.95 s.e. 0.03 and intercept = 4.5 s.e. 2.6).

Prey availability

The burying depth, density and length of lugworms was measured each month in the eastern part of the Dutch Wadden Sea along the mainland coast of the province of Friesland ($53^{\circ}25'$ N, $6^{\circ}04'$ E) during two consecutive years (1980/1981; Zwarts & Wanink 1993); the principal investigator (L. Zwarts) ensured that the original raw data became available for later analysis. Burying depth was measured as the distance between the surface and the deepest point of their U-shaped burrow (Zwarts & Wanink 1993). As lugworms will be captured as their tail resides in one of their vertical shafts, while their body is in the bottom of the U-shaped burrow (Smith 1975), all depths were decreased by 4 cm (i.e. half of the mean length of lugworms; $n = 205$), to represent availability.

Although the lugworm data were collected long before most of the data on bar-tailed godwits, this unlikely to influence our results, as although the mean sea water temperature increase over the last 3 decades is about 1.2°C , the current sea water temperatures are similar to the early 1980's (van Aken 2008); note also that the variation between seasons is much larger than the long-term temperature change of 1.2°C .

Predicting intake rates

To examine whether the predicted energy intake rate (*PEIR*) was related to lugworm burying depth, we averaged monthly prey burying depths ($n = 205$) and predicted intake rates throughout the year based on functional response parameters (Duijns *et al.* 2014a). Note that variation of bill lengths of the birds used in the experiment (Duijns *et al.* 2014a) was rather small (95.5 mm, 95% CI (91.33; 99.7), $n = 5$), and no effects of bill length were detected. For these reasons, *PEIR* should fairly represent population averages. By using the slope and intercept of a linear model of the searching efficiency on prey burying depth (Duijns *et al.* 2014a), we here estimated depth i specific searching efficiency a_i . Searching efficiency was independent of prey length and density (Duijns *et al.* 2014a). Handling time (T_h) was independent of prey burying depth and constant for prey density, but not for prey length. We therefore here used the intercept and slope from a linear model of handling time against prey length to estimate handling time per prey. The month-specific predicted energy intake rate (*PEIR_m*) was calculated using the following equation:

$$PEIR_m = \sum_{ij} \frac{(a_i N_{ijm} e_j)}{(1 + a_i N_{ijm} T_{hj})} \quad (\text{eqn 1})$$

For depth i , prey length j and month m , where N is the mean density ($\# \text{ m}^{-2}$) as measured by Zwartz & Wanink (1993), and e the ash free dry mass (i.e. energetic value, mg AFDM) per individual prey using the length-AFDM relation (e.g. Duijns *et al.* 2013; Duijns & Piersma 2014). Next, we evaluated the mean monthly energetic contribution of lugworms to the year-round diet based on field observations ($n = 76$; Scheiffarth 2001a, Duijns *et al.* 2009; Duijns & Piersma 2014) and dropping analyses ($n = 250$; Duijns *et al.* 2013).

Statistical analyses

Monthly lugworm burying depth and monthly bill length distributions (with and without subspecies differentiation), were explored using linear and quadratic models. In the linear (Null) model, prey burying depth or bill length did not depend on month. The alternative (quadratic) model was evaluated using model selection methods and ranked using Akaike Information Criterion (AIC), and the model was considered to be substantially better when the AIC value was at least 2 points lower when compared the other model (Burnham & Anderson 2002). To assess the proportion of available prey in relation to bill length, the empirical cumulative distribution function (ECDF; Forbes *et al.* 2011), was plotted for females captured or sighted in summer (Apr–Sep) and winter (Oct–Mar). All analyses were conducted using R 3.0.1 (R Development Core Team 2014).

Results

Burying depth of lugworms varied predictably throughout the year (Fig. 8.2A). Lugworms bury deepest during winter ($F_{2,202} = 5.03$, $R^2 = 0.05$, $P = 0.007$). The bill length distribution of both subspecies showed comparable seasonal trends ($F_{3,1087} = 28.06$, $R^2 = 0.07$, $P < 0.001$; Fig. 8.2B). The bill length of the *lapponica* subspecies showed a decrease in length from January towards spring and summer, whereas from August onwards bill length increased again. As expected, bill lengths of *taymyrensis* females were shorter than of *lapponica* ($P < 0.001$), though this subspecies showed the same pattern the 7 months they were sighted in the Dutch Wadden Sea (Fig. 8.2B). Not surprisingly then, the bill length distribution of all sighted individuals with known bill lengths showed a strong seasonal trend ($F_{2,6105} = 95.45$, $R^2 = 0.03$, $P < 0.001$; Fig. 8.2C). That shorter-billed females may have moved from the Dutch Wadden Sea towards the Wash was indicated by the inverse relationship of monthly bill length distributions in the course of the nonbreeding season ($F_{2,1690} = 11.81$, $R^2 = 0.013$, $P < 0.001$ Fig. 8.2D). The disappearance of the shorter-billed females from the Dutch Wadden Sea was also indicated by the negative relationship between the mean bill lengths of the Wash and the Dutch Wadden Sea ($F_{1,7} = 6.47$, $R^2 = 0.48$, $P = 0.03$; Fig. 8.3).

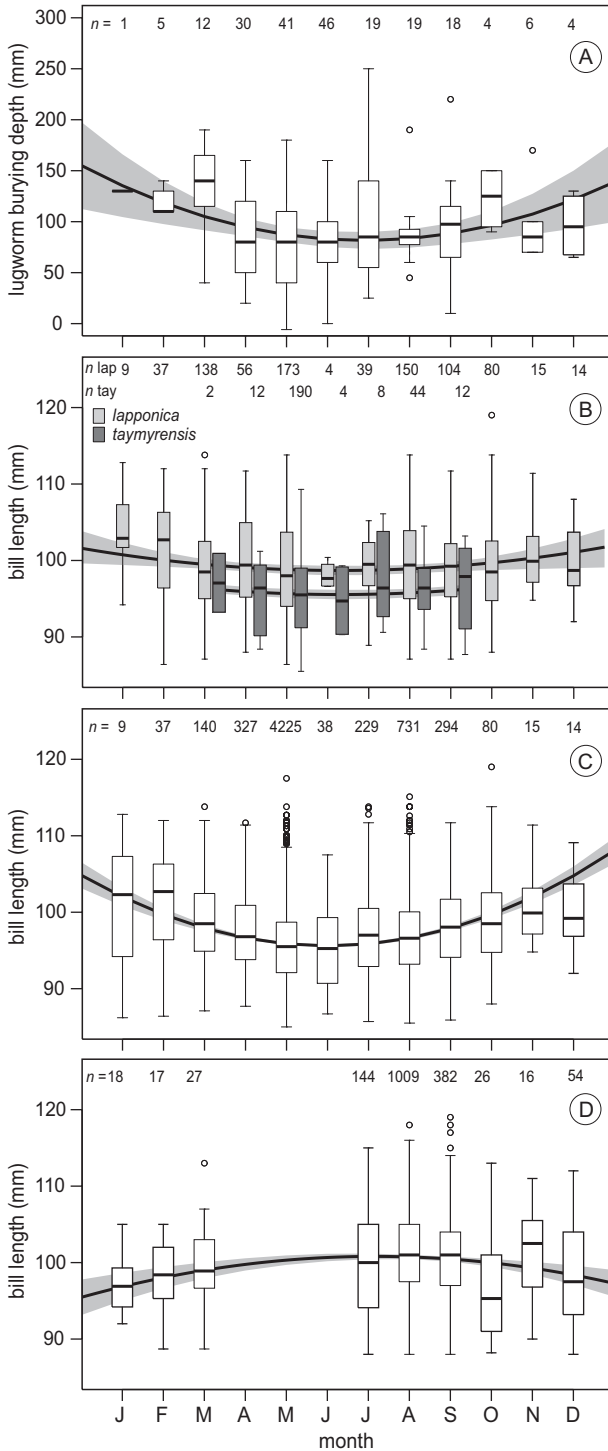


Figure 8.2. By month, (A) lugworm burying depth in the Dutch Wadden Sea, (B) bill length distributions of female bar-tailed godwits in the Dutch Wadden Sea, separated for both subspecies, (C) as B but now subspecies pooled, and (D) bill length distributions for female bar-tailed godwits in the Wash, subspecies pooled. Curved lines represent model outputs and grey areas represent 95% confidence intervals. Box plots show median (line in box), interquartile range (box), 10th and 90th percentiles (bars) and outliers (dots). Sample sizes are shown in all plots.

In winter a longer bill is needed to access the same proportion of prey available as in summer (Fig. 8.4), which is the likely explanation for the positive correlation between mean monthly burying depth and mean bill length ($F_{1,10} = 15.2$, $R^2 = 0.60$, $P = 0.003$; Fig. 8.5A). There was a clear negative correlation between burying depth of lugworms and predicted intake rate (*PEIR*), suggesting that in winter some bar-tailed godwits would not be able to satisfy their minimum energy requirement by foraging on lugworms only ($F_{1,10} = 12.24$, $R^2 = 0.55$, $P = 0.006$; Fig. 8.5B). Indeed, individuals remaining in the Dutch Wadden Sea in winter included prey other than lugworms in their diet; the energetic contribution (% of AFDM) of lugworms was negatively correlated with lugworm burying depth ($F_{1,8} = 6.97$, $R^2 = 0.40$, $P = 0.03$; Fig. 8.5C).

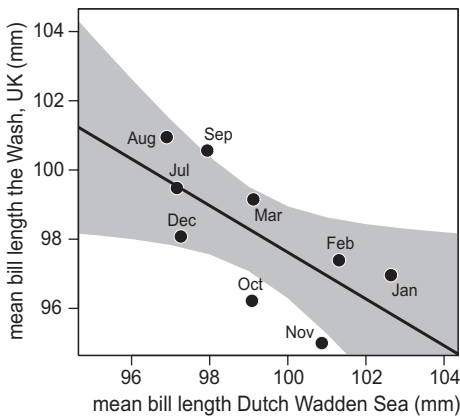


Figure 8.3. Correlation between monthly mean bill length in the Wash and the Dutch Wadden Sea, where the grey shading represents 95% CI level.

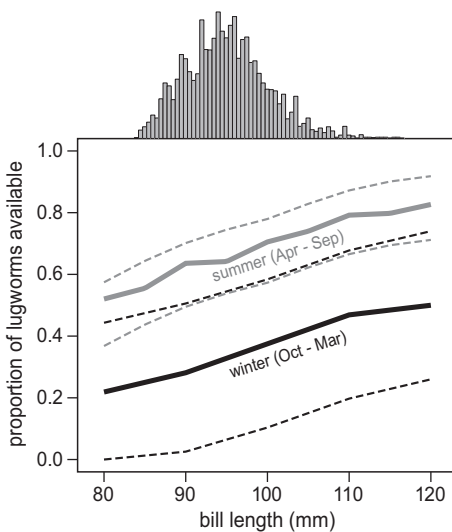


Figure 8.4. Summer and winter pattern of the (numerical) proportion of accessible lugworms in relation to bill length, based on the year-round depth measurements of lugworms. Solid lines represent mean summer (grey) and mean winter (black) lugworm availability (dashed lines represent the 95% CI levels). In either season availability increases with an increase in bill length, though in winter overall availability is much lower. Bars on top of the graph denote the frequency distribution of bill length of female bar-tailed godwits captured in the Wadden Sea ($n = 2,433$).

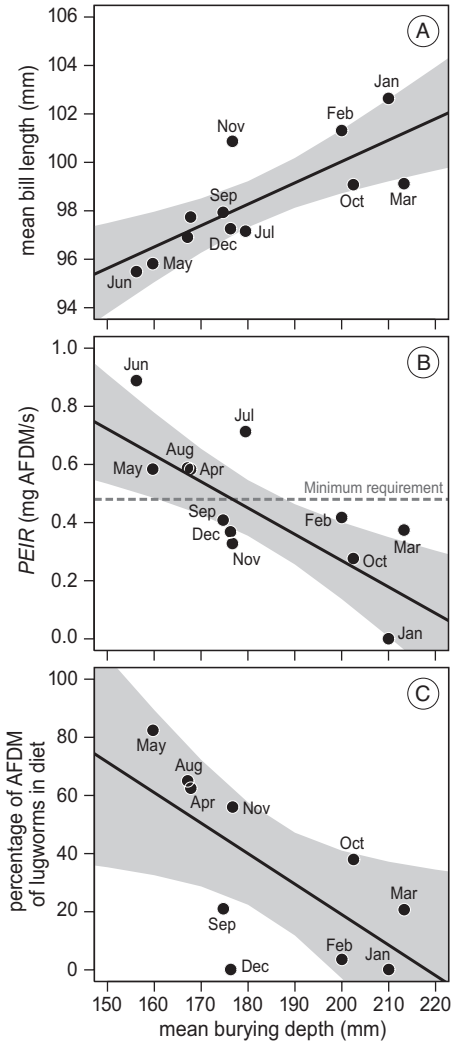


Figure 8.5. Effect of prey burying depth on bill length, intake rate and diet composition of bar-tailed godwits present in the Dutch Wadden Sea. (A) Mean bill lengths of females are larger in winter, when prey are buried deeper (the grey area represent the 95% CI level). (B) Predicted energy intake rates (*PEIR*), based on parameters from the functional response, correlates negatively with mean burying depth. (C) The mean contribution of lugworms to the diet of female bar-tailed godwits (based on AFDM) increases when lugworms are closer to the surface.

Discussion

The vast majority of studies of changing resource landscapes and their use by animals has focused on differences between species or sexes (e.g. Duffy *et al.* 2001; Mathot *et al.* 2007; Griffen & Mosblack 2011; Beaulieu & Sockman 2012). However, the variation between individuals is just as important to understand evolutionary and ecological processes (Bolnick *et al.* 2003; Gunnarsson *et al.* 2012; Piersma 2012). Here we provided an example of seasonally changing phenotype-limited distributions, within one species and even within one sex.

Female bar-tailed godwits redistributed in accordance with the seasonal changes in availability of their dominant prey. In winter, when lugworms are buried more deeply, marked shorter-billed individuals were no longer seen in the Dutch Wadden Sea. One of the areas they moved to is probably the Wash, where during the winter months an increase in numbers has been observed (Holt *et al.* 2012). Indeed, while shorter-billed individuals disappeared from the Wadden Sea during winter, there was a build-up of such individuals in the Wash. This pattern is consistent with the finding that at the Wash, benthic prey are buried less deeply than in the Dutch Wadden Sea (Duijns *et al.* 2014b).

If bill length is such an important determinant of being able to reach deeply burying prey, and if prey bury deeper during northern winters, northerly wintering godwits are expected to have longer bills. That the European wintering subspecies (*lapponica*) have longer bills than the subspecies (*taymyrensis*) wintering in West-Africa (Prokosch 1988; Engelmoer & Roselaar 1998), is consistent with this prediction. Furthermore, if the intake rate benefits accrued by longer-billed individuals result in long-term fitness benefits, there should be directional selection for a longer bill. However, bar-tailed godwits breed on tundra where they feed mainly on surface and shallow-buried arthropods, also available to their shorter-billed self-foraging chicks (Cramp & Simmons 1983; Piersma *et al.* 1996a). It has been suggested that shorter bill sizes may actually be advantageous when feeding on such prey (Jönsson 1987; Jönsson & Alerstam 1990). We propose that there may be balanced selection between longer bills in winter and shorter bills in summer.

After unpredictable extreme conditions such as prolonged drought or cold spells, some phenotypes with particular body size values may die, while other phenotypes survive or even appear to benefit from these events (e.g. Boag & Grant 1981; Clark 2009; van de Pol *et al.* 2010). These examples reflect resident or territorial birds that cannot or will not move, but cases where individuals with certain fixed phenotypic traits move away, is likely to be a general pattern. We may thus find phenotype-limited distributions across many traits across a range of taxa. For example, wing morphology is a non-flexible trait where longer and pointier wings may increase flight efficiency for longer migration distances, while shorter and rounder wings may be beneficial for agility in flight during acrobatic aerial displays, aerial feeding of insects, or take-off performance as an anti-predation adaptation (Rayner 1988; Fernandez & Lank 2007; van den Hout *et al.* 2010). At sites where predation danger has increased (Ydenberg *et al.* 2004), phenotypes with shorter and rounder wings would be expected to cope better with this predation danger and the phenotypes with longer and pointier wings would be predicted to leave such a site. Similarly, variation in neck length could lead to phenotype-limited distributions in swans, giraffes and goats for example, as longer necks would allow for a larger proportion of food availability. Phenotype-limited distributions could be widespread and when associated with assortative migration and mating patterns, they may act as precursors of phenotypic evolution.

Acknowledgements

This study builds on research efforts of many people. First of all we thank our dedicated wilsternetters Joop Jukema, Catharinus Monkel, Jaap Strikwerda, the bird-catchers of VRS-Castricum, VRS-Calidris on Schiermonnikoog and the numerous others that have helped with catching and colour-ringing. We thank our former colleague Bernard Spaans for running the colour ringing programme. We kindly thank Leo Zwarts for his far-sighted efforts to make his impressive data-set available and accessible for future use. Many thanks also to all ring-readers, professional and amateur, and in particular Harry Horn and Jan de Jong, for their continuous efforts to record individually marked bar-tailed godwits at various locations. We also thank the many volunteers of the Wash Wader Ringing Group (WWRG) for their efforts in collecting long-term wader data on the Wash. Jesse Conklin, Phil Battley and an anonymous referee graciously reviewed earlier versions of this manuscript. The study was supported by operational funds from NIOZ. By Metawad (WF 209925), a project awarded by Waddenfonds to T.P., and a VIDI grant (no. 864.09.002) awarded to J.A.v.G. by the Netherlands Organisation for Scientific Research (NWO). We thank Dave Montreuil for making photos available of a female bar-godwit in The Gambia.



9

General discussion

Sexual size dimorphism (SSD) is widespread across the animal kingdom. Its existence is often attributed to sexual selection (Andersson 1994; Fairbairn 1997; Blanckenhorn 2005). When competition for mating opportunities between members of the same sex (typically males) is more intense than between members of the other sex, it could lead to a larger size in the more competitive sex. Indeed, in the animal kingdom males are generally larger than females, although in shorebirds the reverse pattern is quite often observed (Jehl & Murray 1986). When SSD is associated with resource use by inter-sexual competition in different ecological niches, natural, rather than sexual selection may be the driving evolutionary force (Selander 1966; Shine 1989).

In sexual dimorphic shorebirds such as bar-tailed godwits *Limosa lapponica*, females are the larger sex; they are about 20% larger and have about 25% longer bills than males (Prokosch 1988; Piersma & Jukema 1990). This has led to different foraging modes and consequently different diets (Scheiffarth 2001b; Chapter 6), which is consistent with the idea that natural selection drives this remarkable sexual dimorphism. That small-scale differences in habitat use between the sexes have been reported within wintering sites (Smith and Evans 1973; Zwarts 1988; Zharikov & Skilleter 2002; Both *et al.* 2003; Summers *et al.* 2013), as well as between sites (Atkinson 1996; Scheiffarth 2001a), is also consistent with this idea. In this thesis we have shown that the sexes segregate within (Chapter 6) and between sites, due to the resource availability per sex, rather than the costs of wintering at a site (Chapter 3).

Although it was not the aim of this thesis to unravel the evolutionary cause for the remarkable sexual dimorphism in bar-tailed godwits, it is nevertheless worthwhile to mention several proposed hypotheses. (1) The ‘energy storing hypothesis’ suggests that larger females accumulate greater nutrient stores at wintering or refuelling sites to enable earlier egg laying (Jehl & Murray 1986). There is however little evidence that shorebirds carry nutrient stores to the breeding grounds to be used in egg formation (Klaassen *et al.* 2001), with the exception of calcium storage in the skeleton (Piersma *et al.* 1996b) and protein storage in muscle (Vezina *et al.* 2012). (2) The ‘incubation ability hypothesis’ was initially proposed to explain the sexual dimorphism in raptors (Snyder & Wiley 1976), and later for shorebirds (Puttick 1981). This hypothesis suggests that large individuals would incubate more efficiently, as they would cover and warmth the eggs more efficiently than smaller individuals. This hypothesis seems unlikely for bar-tailed godwits, as both sexes incubate the eggs (Hussell 2004). (3) The ‘parental role division hypothesis’ suggests that in species with parental role division and uniparental male care of the chicks, the males would benefit from having a shorter bill, as this would facilitate food acquisition in terrestrial habitats [as they would be the sex escorting the growing chicks] and the larger females would accumulate greater stores for egg laying in coastal sites (Jönsson & Alerstam 1990). (4) The ‘display agility hypothesis’ suggests that small males perform better in acrobatic displays, presumably involved in mate choice, and so females may pre-

fer the more agile males (Peters 1983). (5) The ‘ecological competition hypothesis’ implies that sexes reduce inter-sexual competition by specializing on different ecological niches (Shine 1989). All these hypotheses may have degrees of plausibility for bar-tailed godwits, although they are mutually non-exclusive and most likely a combination of the latter three hypotheses addresses to the evolutionary cause of sexual dimorphism.

From diet to intake rates

The main focus of this thesis was to unravel the remarkable changes in the species composition (i.e. from bivalve-eating waterbirds to polychaete-eating waterbirds) that has been observed in the Dutch Wadden Sea during the last two decades, and the polychaete-eating bar-tailed godwit was chosen as a model species. One of the challenges was to describe the diet composition and acquire (energy) intake rates. A standard method to reconstruct the diet of shorebirds on the basis of droppings was used (Dekinga & Piersma 1993; Scheiffarth 2001b; Onrust *et al.* 2013). Since large dietary differences between the sexes exist (Scheiffarth 2001b; Chapter 4 and 6), the aim was to develop a novel method to distinguish the droppings per sex, where the sex could be determined by DNA extraction from these droppings (Robertson *et al.* 1999). This method could possibly be applied on other sexual dimorphic animals, e.g. to determine sex ratios in time and space non-invasively. However, in our case it did unfortunately not lead to a reliable method, as during a pilot study 60% of the DNA extractions produced negative results (Box 1). It was however possible to reconstruct the diet of a flock, based on multiple droppings (Chapter 5). The diet composition showed a large variation in prey types and the majority of the diet consisted of polychaete worms. Nevertheless, as diet reconstruction on the basis of individual droppings was very time consuming with moderate success in determining the diet per sex (Box 1), we opted for a more ‘old fashioned’ approach to measure (energy) intake rates, namely field observations (focal animal sampling, continuous recording). By incorporating the knowledge of prey items occurring in the diet (Chapter 5) and estimating lengths of prey items, these field observations produced reasonable energy intake rates (mg AFDM/s), as can be expected for a species this size (Kersten & Piersma 1987; Scheiffarth *et al.* 2002).

Functional response

As the change in the composition of waterbirds in the Dutch Wadden Sea could be driven by a change in the benthic species composition and abundance, the type II functional response model (Holling 1959) was parameterized based on field observations in order to predict potential foraging areas for these polychaete feeding shorebirds. This functional response model describes the relation between (energy) intake rate and prey density. In fact, although they cannot be mechanistically interpreted, field measurements yield a consistency test of the distributional patterns in a specific ecological context (e.g. Gill *et*

al. 2001a; Lourenço *et al.* 2010). Site-independent measurements in an experimental setting are necessary to be generally applicable (e.g. Piersma *et al.* 1995; van Gils *et al.* 2004), which is what we also did. We tested for the validity and subsequently parameterized the functional response type II model of female bar-tailed godwits foraging on lugworms by carrying out an experiment in the indoor shorebird facility at the Royal NIOZ (Chapter 7). The results of this experiment indeed showed a large deviation from the field-based study. The minimum prey density (# m²) required by these shorebirds to sustain their minimum daily requirement was about 20 times higher in the field-based study than in the experiment. The main reason for this bias is twofold. (1) Field measurements on low and very high resource densities were absent, as low resource patches will be avoided and high resource patches are rare. In the parameterisation of the functional response model this leads to an underestimation of the instantaneous area of discovery (also called ‘searching efficiency’). (2) Individuals were facing a digestive bottleneck, that intake rates (calculated over total time) were constant over the range of food densities that were selected.

Benthic prey availability and bird numbers

Besides knowledge on predators utilizing the Dutch Wadden Sea, information on the spatial distribution of available benthic prey is required. For that we can turn to a gridded sampling design (Synoptic Intertidal Benthic Surveys, SIBES), which was developed and worked out within our research group at NIOZ (Bijleveld *et al.* 2012; Compton *et al.* 2013). This gridded sampling design encompasses the entire intertidal Dutch Wadden Sea, where a combination of sample points is taken at 500 m intervals and additional random sample points. Besides benthic cores, sediment samples were also taken at each sampling point, as the median grain size is the most important variable in describing differences in benthic species composition (e.g. Kraan *et al.* 2010; Compton *et al.* 2013).

In general, the eastern part of the Dutch Wadden Sea contains a smaller median grain size compared to the western part (Compton *et al.* 2013), which will influence the spatial distribution on benthic species. The Baltic tellin *Macoma balthica*, a small bivalve, shows a preference for muddy areas (Kraan *et al.* 2010), and occurs in relatively high abundances in the eastern part of the Dutch Wadden sea (Compton *et al.* 2013). That shorebirds as red knots *Calidris canutus* feeding on these benthic prey do not always forage in these areas was shown by Spaans and co-workers (2009). Red knots have a tendency to aggregate (mainly in winter) in the western part of the Dutch Wadden Sea. It was suggested that the higher winter temperatures and the smaller migration distance in the west to alternative wintering areas in the UK to be the potential drivers for wintering in the western part of the Dutch Wadden Sea.

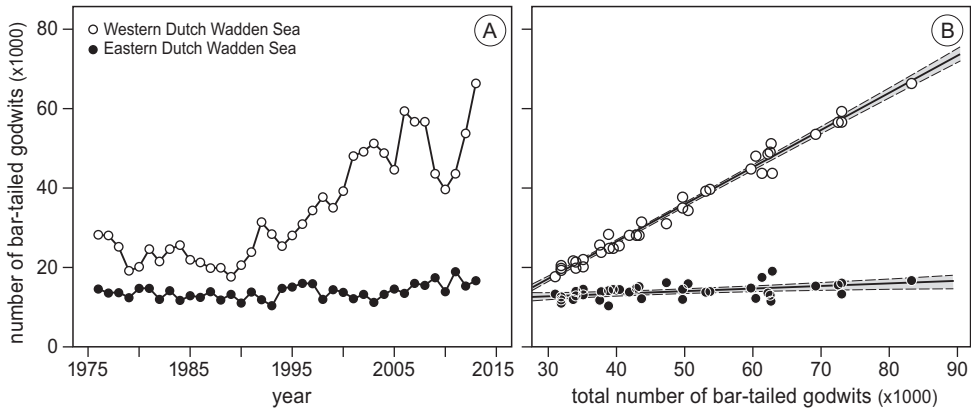


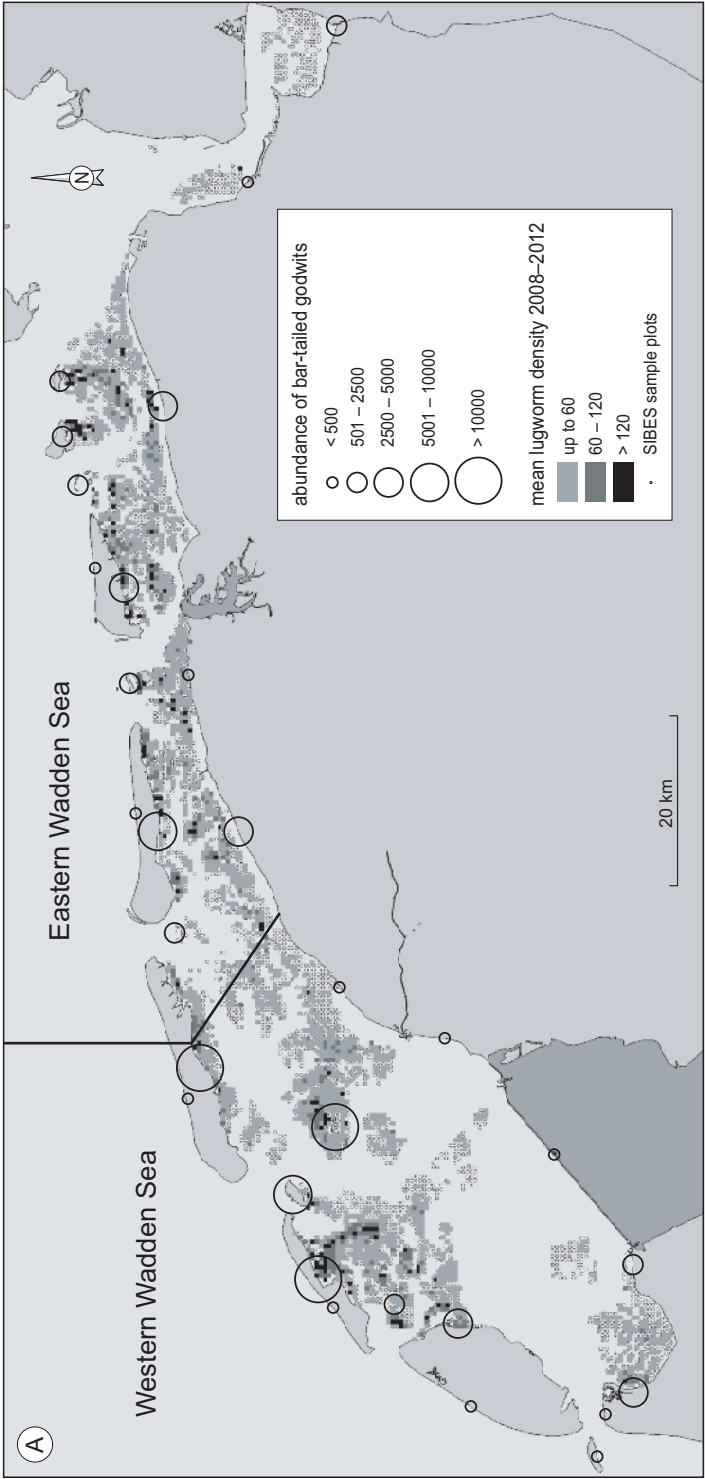
Figure 9.1. (A) Mean yearly abundances of bar-tailed godwits in the western and eastern part of the Dutch Wadden Sea. No clear trends in the eastern Dutch Wadden Sea are apparent, while the abundance in the western part shows a gradual increase from 1990 onwards, although during the last 10 years more variation is apparent. In (B) the relation between the counts of western and eastern part of the Dutch Wadden Sea are plotted against the total number of bar-tailed godwits. The dashed lines represent the 95% CI levels.

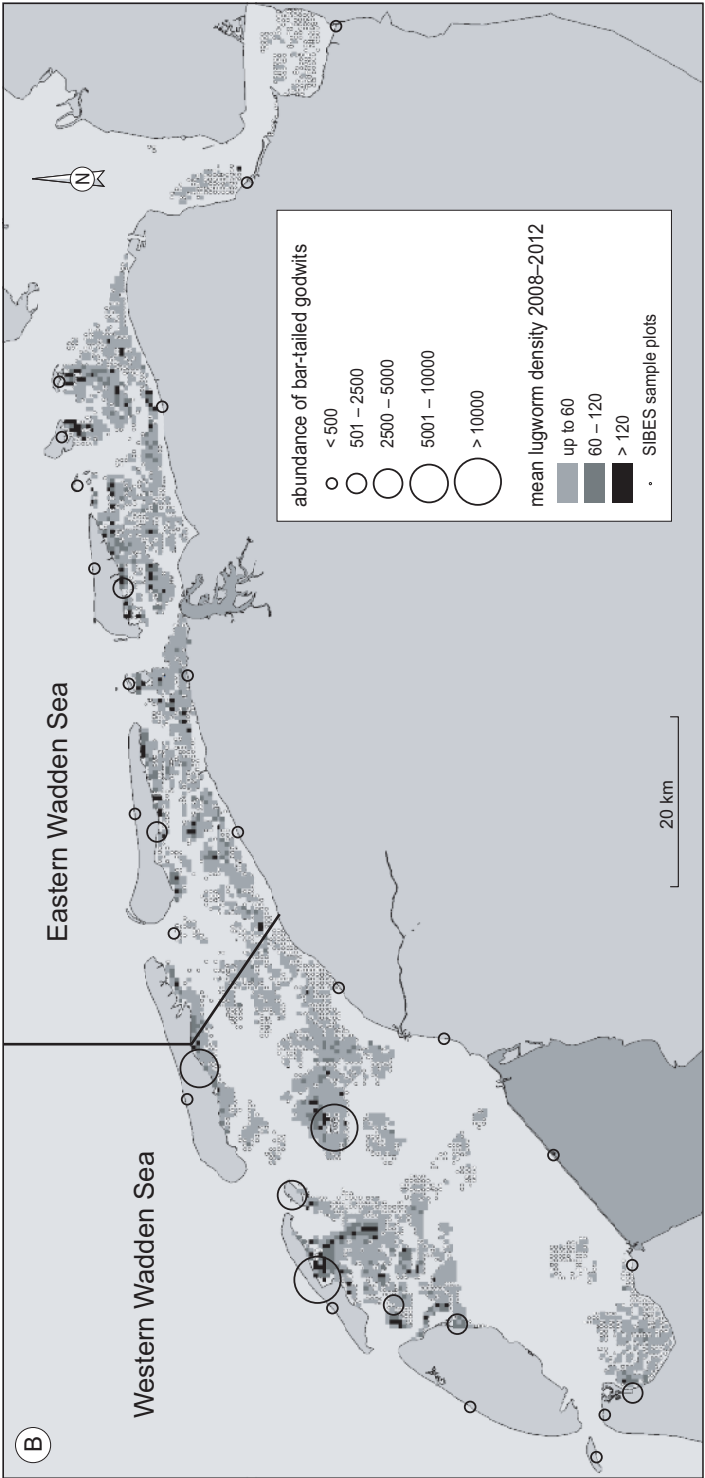
That a difference in the composition of waterbird communities between the eastern and western parts of the Dutch Wadden Sea exists was previously illustrated by Ens and co-workers (2009). Here I elaborate on the distinction between the western and eastern parts of the Dutch Wadden Sea by analysing the high tide roost counts from 1975 – 2013 (Fig. 9.1A). This shows that the overall increase in bar-tailed godwits that is observed in the Dutch Wadden Sea (see also Fig. 1.1 in Chapter 1) is by, and largely due, to a population increase in the western half of the Dutch Wadden Sea, whereas the population in the eastern half has remained fairly stable. Perhaps the food availability has increased more in the west or decreased in the east? Or the increased predation danger has influenced the spatial distribution of these bar-tailed godwits? Below I will speculate as to what may cause this east-west difference.

Buffer effect

If sites vary in quality and the population size in good-quality sites show small fluctuations, while large changes in poorer sites are observed simultaneously is known as the buffer effect (e.g. Kluyver & Tinbergen 1953; Gill *et al.* 2001b; Ntiamoa-Baidu *et al.* 2014). The increase of bar-tailed godwits in the western part of the Dutch Wadden Sea could be an example of this buffer effect. Indeed, the rate of increase in the western part is nearly linear ($F_{1,36} = 2451$, $R^2 = 0.98$, $P < 0.001$; Fig. 9.1B), while the rate of increase in the eastern part, though significant ($F_{1,36} = 10.5$, $R^2 = 0.20$, $P = 0.002$), is almost negligible (Fig. 9.1B). This suggests the eastern part of the Dutch Wadden Sea to represent a good-quality site and the western part a poor-quality site.

Figure 9.2. The mean distribution of lugworm *Arenicola marina* density (no./ m²) as sampled in 2008 – 2012 and mean abundance of bar-tailed godwits (black circles) in (A) summer (Apr – Sep) and (B) winter (Oct – Mar), as counted on high-tide roosts in the same period. In winter, the majority of bar-tailed godwits are roosting in the western part and are only present in low numbers in the eastern part. No clear correlations are apparent between lugworm and bird densities.





There is no evidence that the population of bar-tailed godwits along the East-Atlantic Flyway are increasing (Scott & Scheiffarth 2009; Spaans *et al.* 2011). It therefore seems likely that the habitat quality is deteriorating elsewhere. That at the time of expansion in the western part of the Dutch Wadden Sea a decrease in bar-tailed godwit numbers in Germany was observed (Blew *et al.* 2007), could suggest that the birds in the western part of the Dutch Wadden Sea originated from Germany. Thus, is the western part of the Dutch Wadden Sea a poor-quality site? To address this, I will explore several aspects of what constitutes habitat quality as described by Piersma (2012), and start by examining prey availability at these sites.

Spatial distribution of birds and benthic prey

In the course of the preparation of the research underlying this thesis, the importance of lugworms *Arenicola marina* for female bar-tailed godwits became apparent (Chapters 4 – 8), which justifies the present focus on its spatial distribution in the Dutch Wadden Sea. Lugworms are very widespread across the intertidal mudflats with only few locations of high abundances (Fig. 9.2), yet, annual densities (22.2 ind/m² on average, $sd = 69.1$, $n = 23,618$) varies between years with a factor 3, and this variation in lugworm density is likely to influence the spatial distribution of bar-tailed godwits. On average the mean abundance (ind/m²) of lugworms in the eastern Dutch Wadden Sea (24.9, $sd = 71.9$, $n = 10,875$) is higher than to the western part (19.9, $sd = 66.5$, $n = 12,743$; see Fig. 9.3 for more details). On this basis, the eastern part seems a good-quality site. However, other prey species besides lugworms need to be incorporated in the analysis to evaluate the (food) quality of a site, including the variation in prey densities between years. Additionally, no correlation between the food abundance (lugworms in this case) and average bird numbers roosting in close proximity to their feeding grounds is apparent when looking at Fig. 9.2. This might suggest other factors to be involved, influencing this distribution.

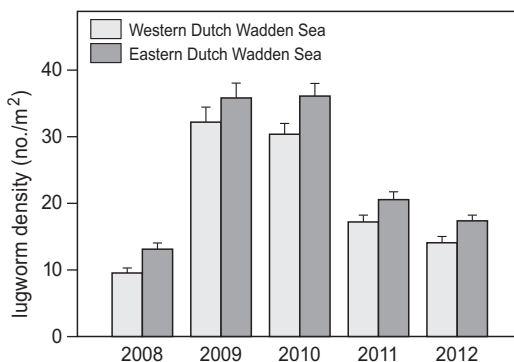


Figure 9.3. Bar graph of mean densities (\pm SE) of lugworms per year and geographic origin (i.e. western and eastern part of the Dutch Wadden Sea). In all sampled years, the mean densities of lugworms are higher in the eastern part.

Predation danger

In chapter 4 the effects of predation danger were proposed as a possible mechanism that influences foraging site selection on a small scale. Clearly, the most obvious way to deal with predation danger is to avoid predators (Cresswell 2008), and perhaps this could also partially explain the difference in bar-tailed godwit densities between the two parts of the Dutch Wadden Sea.

Behavioural adjustments of shorebirds to predation danger are more pronounced and are likely to have a greater impact than direct lethal effects (Cresswell 2008, van den Hout 2009, Cresswell *et al.* 2010). The recovery of peregrine falcons *Falco peregrinus* in British Columbia for example has led to declines in migratory body mass and stopover durations of western sandpipers *Calidris mauri*, illustrating the behavioural adjustments shorebirds are facing (Ydenberg *et al.* 2004). Also in the Dutch Wadden Sea the peregrine falcon has recovered during the last few decades (van den Hout 2009). This recovery started in Scandinavia and Germany (Ratcliffe 1993) and expanded from the east towards the west, possibly shaping the spatial or temporal distribution of bar-tailed godwits. These aerial predators often make use of vegetation, hills, dikes and other structures to cover their approach when hunting close to the salt marsh (Bijlsma 1990; Cresswell & Whitfield 1994). That the hunting success of aerial predators is higher on salt marshes than on open mudflats without any cover, suggests that predation risk declines with distance from cover (Cresswell 1994; Ydenberg *et al.* 2002; Pomeroy 2006; van den Hout *et al.* 2008; 2014).

Large landscape differences exist in the Dutch Wadden Sea area from the west to the east. The available surface area of mudflats differ in size (61,216 ha in the western part and 50,666 ha in the eastern part; Ens *et al.* 2009), but perhaps the most striking difference is the distance to cover, which is about 2 times higher in the western than in the eastern part. As the eastern part the Dutch Wadden Sea is narrower compared to the wider western part, this could provide aerial predators such as peregrine falcons a greater opportunity to hunt. The higher abundance of these predators in the eastern part (Fig. 9.4A), might force these shorebirds more towards the 'safer' and wider western part and suggests the western part a higher-quality site in regards to predation danger.

Interestingly, the different densities of bar-tailed godwits per hectare in the eastern and western part of the Dutch Wadden Sea follow a pattern that is consistent with the buffer effect (Fig. 9.4B). The densities in the eastern part are higher from the moment the high tide counts were initiated (i.e. 1976) and remained fairly stable over time. In the western part the initial densities were lower than the eastern part and gradually increased. From 2000 onwards these densities are within the range of the eastern part, though more variation is observed. That during the migration period (i.e. Apr – Sep) more birds use the Dutch Wadden Sea as a refuelling site, and an increase of bar-tailed godwits in the eastern part is observed (Fig. 9.2A), could suggest the western part to be

used at full capacity as well, resulting in an increase in both areas. That the bird numbers in the west are not increasing much anymore during the last 10 years is supportive of this idea.

Tide-line following

Possibly the timing of the tidal cycle also contributes to the spatial dichotomy, as the tidal cycles differ spatially. In the western part of the Dutch Wadden Sea the cycle is about 2 h 'ahead' compared with the cycle in the eastern part (van Gils *et al.* 2005b; Piersma 2012). Therefore, mudflats in the western part are exposed 2 h earlier than mudflats in the eastern part. For red knots it was shown that these birds gradually move eastwards during low tide, and thereby extend their low tide feeding period with 4 h (van Gils *et al.* 2005b). Given the importance of tide-line following, especially for female bar-tailed godwits that constitute the majority of the wintering population (Chapter 3 and 6), this 'tide extension' might explain why these shorebirds mainly reside in the western part of the Dutch Sea, though more work is needed to confirm this.

Individual variation

In Piersma's review of what constitutes habitat quality (2012), he builds on 25 years of work performed on red knots. One aspect of the red knot studies is the considerable amount of individual variation (e.g. Bolnick *et al.* 2003; Gunnarsson *et al.* 2012). Red knots were not only gape limited (Zwarts & Blomert 1992), but also digestive-rate limited, as they ingest their prey whole and need to crush it in their muscular gizzard that differ in size (van Gils *et al.* 2003a; van Gils *et al.* 2003b; van Gils *et al.* 2005a). Individuals with a smaller gizzard would require different prey (i.e. higher quality), and thus need to search for prey at other sites than the larger gizzard size individuals (e.g. van Gils *et al.* 2005b). The muscular gizzard is a flexible organ that can be increased or decreased in size (e.g. Dekinga *et al.* 2001; van Gils *et al.* 2003a), notably during demanding times such as preparing for migration. In spite of them being flexible, these gizzards however appear to be kept at rather fixed sizes within individuals during winter, as personality drives these physiological adjustments (Bijleveld *et al.* 2014), exemplifying the limitations individuals experience.

In chapter 8 we also investigated individual variation, focusing on bill length and prey burying depth (i.e. availability) and could show that prey accessibility depends on the length of an individual's bill. Simply put, the longer the bill, the larger the proportion of prey that will be accessible, leaving longer-billed individuals with the greater range of options during the colder winter months when prey are buried deepest (Zwarts & Wanink 1993). Indeed, shorter-billed individuals moved away during times that prey are burying more deeply, and longer-billed individuals that stayed in the Dutch Wadden also diversified their diet with other prey to sustain their daily minimum requirements.

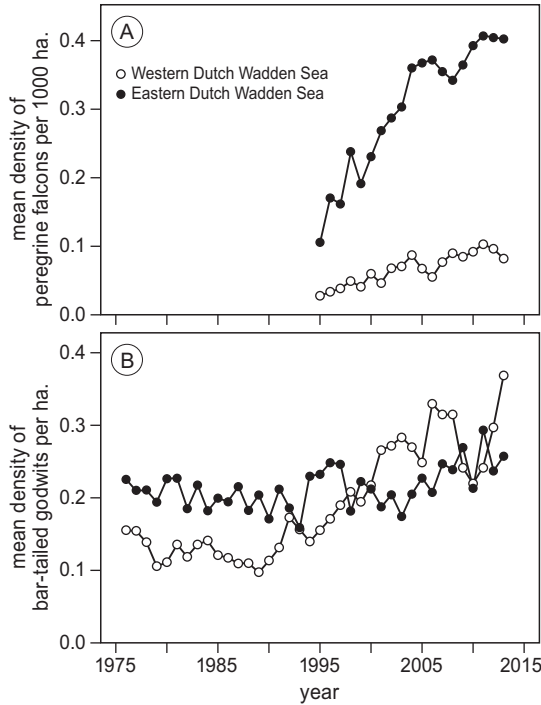


Figure 9.4. Densities (plotted per 1000 hectares of general area) of (A) peregrine falcons and (B) bar-tailed godwits in the Dutch Wadden Sea. The white dots represent the western part and the black dots represent the eastern part.

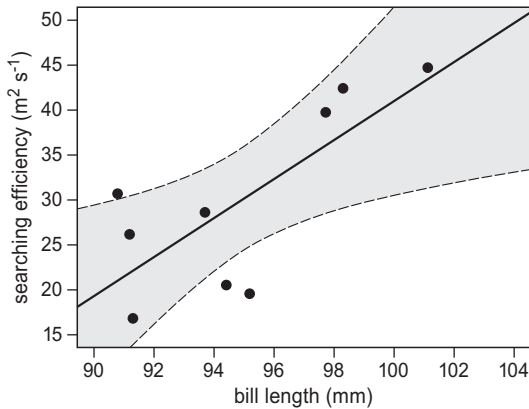


Figure 9.5. Longer billed females have an advantage in reaching the more deeply buried prey in the field, as they experience a higher searching efficiency ($F_{1,7} = 6.95$, $R^2 = 0.50$, $P = 0.03$). The dashed lines represent the 95% CI levels.

If longer-billed individuals experience intake rate benefits that consequently may result in long-term fitness benefits, this poses the question why not all (female) bar-tailed godwits have a longer bill, especially as birds with longer bills were found to have a higher searching efficiency (a ; Fig. 9.5), as can be derived from Holling's disc equation (Holling 1959). However, with a firm focus on the foraging behaviour at non-breeding sites, we ignored an important season, the breeding season. Bar-tailed godwits breed on

the tundra where they feed mainly on surface and shallow-buried arthropods, which are also available to their shorter-billed self-foraging chicks (Cramp & Simmons 1983; Piersma *et al.* 1996a). When feeding on such prey, shorter bill sizes may be advantageous (Jönsson 1987; Jönsson & Alerstam 1990), and there may be a balance between selection for longer bills in winter and for shorter bills in summer.

Concluding remarks

What we have been able to show is that bar-tailed godwits can definitely be counted as polychaete-specialists. However, the root cause of the observed increase of polychaete feeders in the Dutch Wadden Sea as demonstrated by van Roomen *et al.* (2005; Fig. 1), is still inferential at best. For bivalve-eating waterbirds such as the red knot, oystercatcher *Haematopus ostralegus* and common eider *Somateria mollissima*, there is ample evidence that changes in numbers are related to changes in food abundance (e.g. Camphuysen *et al.* 2002; Atkinson *et al.* 2003; van Gils *et al.* 2006; Kraan *et al.* 2009; Laursen & Møller 2014).

Indeed, we have shown that also for a polychaete-eating waterbird food abundances are important (Chapters 4, 6, 7 and 8), but from the initial explorations concerning bird numbers and benthic prey availability (Fig. 9.2), no clear pattern was observed. That the eastern part of the Dutch Wadden Sea appears to be a higher-quality site may seem somewhat surprising, as most bar-tailed godwits are found in the western part. However, this does not automatically imply the western part is a poor-quality site. In the Western part there is less predation danger and a greater opportunity for tide-line following and thereby extending their low tide feeding period (especially in winter when maintenance requirements are higher). This may guide future research to further explore the observed buffer effect. Clearly more work is required to gauge the relevance of the supplementary hypotheses proposed here to explain the differences in trends between the western and eastern Dutch Wadden Sea.

That I could build on an extensive research programme initially set up for the bivalve-eating shorebird, the red knot, has facilitated the work in thesis presented enormously. Understanding the spatial occurrence (or absence) of shorebirds seems rather simplistic at first; if there is no food available, birds will not go there to forage and when there is ample food available, birds are bound to be found there. Clearly, predicting suitable habitat for foragers is more than just measuring food abundances, as was nicely exemplified by Piersma (2012). Many processes that were found for the red knot (i.e. digestive constraint, interference competition, site-independent functional response measurements, individual variation, prey availability, predation danger) could also be verified for, or applied to this 'trophic mirror species', exemplifying the generality of this type of research.

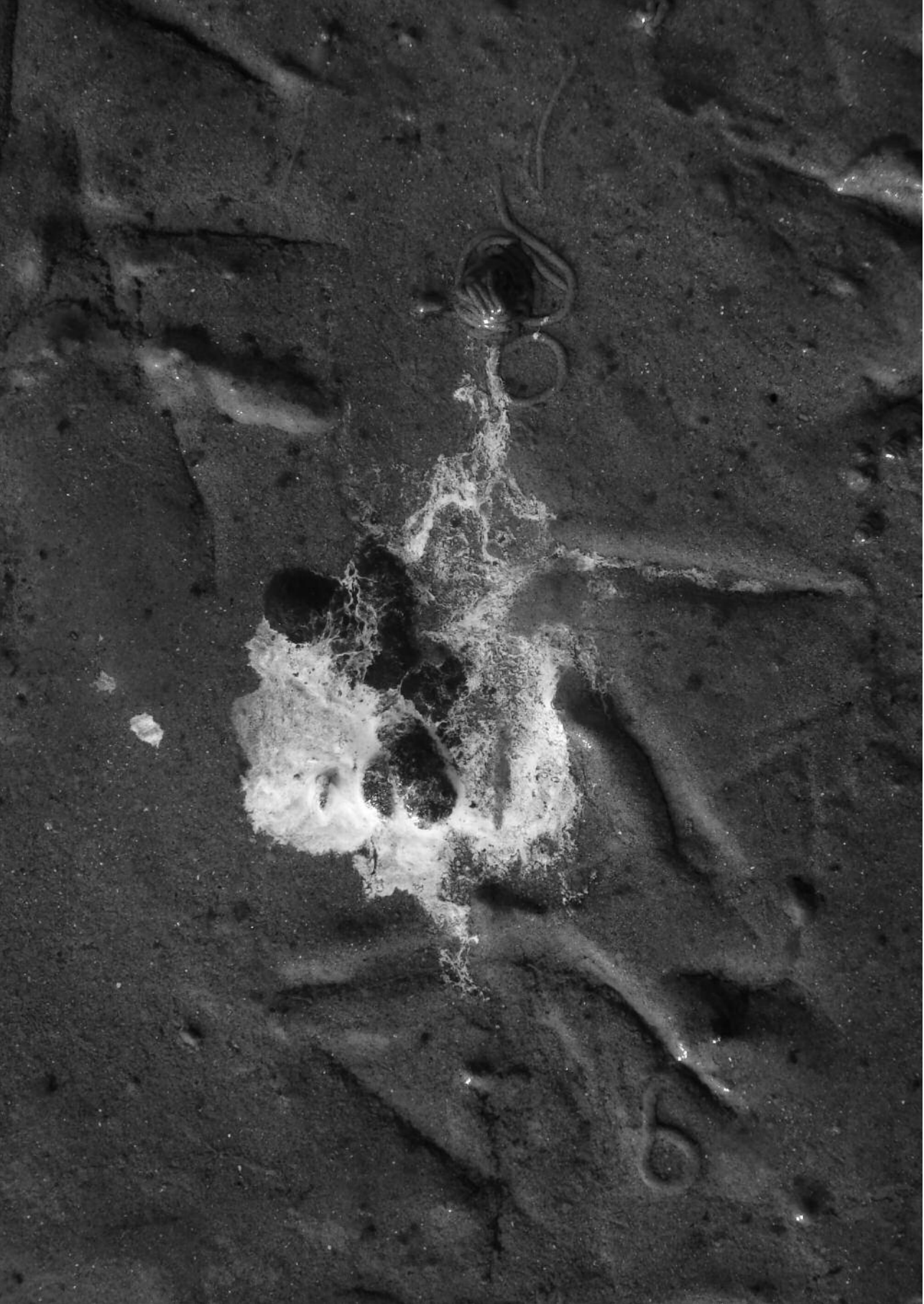
Future directions

One of the challenges we are facing is to identify the causes and consequences of the observed phenotypic variation in the distribution and survival of bar-tailed godwits. Preliminary survival estimates for females of the *lapponica* subspecies are indicative of a negative relationship between survival probability and bill length, coincident with a trend towards smaller bills (unpublished data). That the relationships are absent in males may be explained by males being less dependent on large and deeply buried prey, and by them being the main caregivers to the chicks.

By integrating the knowledge acquired and the supplemental hypotheses outlined in this thesis with the continuous (and previous) effort in sampling the resource landscape (SIBES) and monitoring bird population estimates, the potential drivers for the population increase of polychaete-eating waterbirds in the Dutch Wadden Sea are likely to be identified. Moreover, tracking devices become more and more advanced, enabling us to follow these long distant migrants on different spatial and temporal scales. Given that bar-tailed godwits are relatively easy to catch, easy to observe in the field, large enough to carry long-lasting tracking devices, and even amenable to indoor experiments, makes them a well suited study system for continuing this research.

Acknowledgments

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Box 1

Molecular sexing of bar-tailed godwits *Limosa lapponica* using droppings

Sjoerd Duijns, Pieterella Luttikhuisen,
Anneke Bol & Judith van Bleijswijk

Droppings have proven to be a good, non-invasive source of DNA for molecular ecological studies (e.g. Wasser *et al.* 1997; Robertson *et al.* 1999). Bar-tailed godwits *Limosa lapponica* are sexually dimorphic and sexes are known to forage on different prey (Scheiffarth 2001b; Chapter 6). We therefore opted to first test a method for molecular sexing of bar-tailed godwits by DNA analyses of their droppings, before reconstructing their diet on the basis of microscopical dropping analysis. After comparing different DNA extraction methods we chose FTA® databasing paper (Smith & Burgoyne 2004) to extract DNA from droppings, as this facilitated the collection and storage of samples from the field.

As part of a long-term colour ringing programme, bar-tailed godwits were captured in May 2010 on inland coastal meadows on the Dutch Wadden Sea Island of Texel with wilsternets (Jukema *et al.* 2001). Individual birds were sexed on the basis of coloration and bill length (Prater *et al.* 1977; Piersma & Jukema 1993). Birds with known sex were individually placed in plastic animal transport containers from which droppings were collected ($n = 114$). DNA was isolated from the droppings by swabbing FTA® databasing paper (Smith & Burgoyne 2004) through the fresh droppings and subsequently air drying the paper.

From the dry FTA paper, two small subsamples (2×2 mm) were cut, treated with FTA purification reagent and washed three times with TE Buffer (10 mM Tris-HCl, 0.1 mM EDTA, pH 8.0). After drying at room temperature for one hour the samples were ready for PCR analyses of the chromo-helicase-DNA-binding (CHD) gene (Griffiths *et al.* 1998) which shows sex dependent length polymorphism. This PCR simultaneously amplifies homologous regions on the W and Z chromosomes, allowing assignment of males (ZZ) and females (ZW) in many avian species. PCR reactions were performed in a total volume of 25 μ l buffer containing 0.25 μ l of each primer (M5 and P8; Bantock *et al.* 2008), 2.5 μ l dNTPs, 1 unit of Taq DNA polymerase (BioTherm™ Taq DNA Polymerase) and one subsample (2×2 mm) of the FTA paper. Negative extraction controls were used for all faecal samples and blood samples of bar-tailed godwits with known sex served as positive controls. PCR reactions were performed according to the following program: initial denaturation at 94 °C for 480 s, followed by 45 cycles of 94 °C for 60 s, 54 °C for 30 s, and 72 °C for 30 s, and ending with primer extension at 72 °C for 5 min and 4 °C cooling for 10 min.

Table B.1. Overview of the individuals of which sex was determined on the basis of morphology and DNA analysis

Sex based on morphology	Sex based on DNA analyses		
	Female	Male	Unknown
Female (64)	23	0	41
Male (50)	0	23	27
Total (114)	23	23	68

Sex specific PCR products were separated on 2% agarose gel and stained with ethidium bromide.

The 114 captured birds consisted of 64 females and 50 males based on morphology. DNA based sexing was successful for $n = 46$, i.e. 40%, of the birds, while the remaining 68 individuals did not produce any results (Table B.1). The DNA of all birds was analysed twice. Of the 46 birds that could be molecularly sexed, 21 (46%) gave a positive PCR in both analyses, while 25 (54%) were successfully amplified in only one of the analyses. In all 46 cases, DNA based assay and morphological assay resulted in the assignment of the same sex. Of the 46 successfully assigned individuals, 23 were females (50%) and 23 males (50%). This means that 23 out of 64 females (36%) could be molecularly sexed, and 23 out of 50 males (46%); this difference is not significant (chi-square test, $\chi^2 = 0.79$, $n = 114$, $df = 1$, $P = 0.371$). Although the power of this test with 114 birds is relatively limited, we can nevertheless tentatively conclude that the efficiency of the molecular sexing method does not differ between the sexes for *L. lapponica* droppings.

This pilot study was performed with captured birds, where sex was known and droppings could be collected fast and without contamination of seawater and sediment. Despite the ability of this technique to sex individuals by their droppings, the relatively low success rate in these rather optimal circumstances made us decide not to pursue the optimisation of this technique further. Preliminary tests with droppings collected in the field ($n = 8$), gave all negative results, exemplifying the difficulty of this technique.

Perhaps the diet of these birds might constrain this technique as well. Soft prey, as most polychaetes are, might not produce considerable amounts of intestinal villi in the droppings to be detected. Harder prey such as bivalves and crustaceans might do so and this technique might therefore be more appropriate for species that forage on this type of prey.

Our overall conclusion is therefore that, based on this first test, the method is promising but optimisations (e.g. analysis of larger or more subsamples of the FTA strips and using other species foraging on different prey items), are definitely needed to increase the success rate.

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Summary Samenvatting

Most organisms on Earth live in seasonal environments with respect to climate and food, and these organisms need to cope with these changes. Some individuals stay put in one place, whereas others migrate towards more favorable environments for some time of the year. A group of animals that exemplify this latter phenomenon are migratory shorebirds. The bar-tailed godwit *Limosa lapponica* is an example of a migratory species that follows a leap-frog migration system (i.e. populations breeding in northerly areas migrate to wintering areas south of populations from more southerly breeding ranges). This offers an excellent study system to investigate the constraints and choices acting on different migratory strategies within one species under changing environmental conditions.

Two populations of bar-tailed godwits occur along the East-Atlantic Flyway: the European population *L. l. lapponica*, with a stable population size of 120,000 individuals, breeds and winters in Europe, while the Afro-Siberian population *L. l. taymyrensis*, with an decreasing population size of 600,000 individuals, breeds in north-central Siberia and spends the non-breeding season along the west coast of Africa. Bar-tailed godwits show high intra- and intersexual differences in size and breeding plumage and the sexes could almost be considered different species.

As population trends mirror the quality of a site, population trends need to be evaluated. Although total population estimates of bar-tailed godwits suggests that they still occur in high numbers, analyses of long-term trends are needed. Fortunately, waterbirds have been counted in the Dutch Wadden Sea on a regular basis from 1975 onwards. Analyses of these waterbird numbers clumped according to their diet, showed a vast increase of worm-feeding birds over the last two decades, whereas bivalve-feeding waterbirds declined during the same period. The red knot *Calidris canutus*, a small bivalve-eating migratory shorebird, is one of these species that declined due to a loss of food abundance. The bar-tailed godwit, categorised as a polychaete feeding shorebird, is one of these species that has shown a vast increase in the Dutch Wadden Sea. In this thesis I addressed the mirror question: what caused the increase of bar-tailed godwits in the Dutch Wadden Sea? Could the observed increase be driven by an increase of food abundance, or are there other factors involved? To start with such an ambitious question, it is imperative to know where, when and why bar-tailed godwits occur at sites they occur.

Based on morphology measurements from museum specimens, it was suggested that both bar-tailed godwit populations that occur along the East Atlantic Flyway would show a considerable overlap in occurrence in their wintering and breeding areas. To investigate this, the existing data set of ring recoveries and sightings of colour-ringed birds were analysed (**Chapter 2**). Based on the analysis it was shown that nearly all marked individuals behaved according to the previously suggested leap-frog migration pattern, and that only a small fraction (0.8%) interchanged wintering sites. These exceptions are still doubtful as they could represent incorrect sightings.

Following this result, the next approach was to understand their spatial occurrence on a population-wide scale. As sex-specific winter distribution had been reported within the wintering range in north-western Europe, the European population was studied in more detail. During the non-breeding season in the more northerly and colder sites, relatively more females were present, while in milder climates relatively more males had been observed. On this basis it was hypothesised that these differences could be driven by the relative smaller cost for females wintering in the northern and colder sites, while benefiting from a shorter migration distance to their arctic breeding grounds. By visiting and sampling six important non-breeding sites throughout their wintering range, this hypothesis was rejected. In fact, males and females appeared to distribute themselves according to prey availability (i.e. prey burying depth), rather than choosing a wintering site based on costs (**Chapter 3**).

Given that both populations are spatially distinct in their wintering sites, they were studied when they occur simultaneously in the Dutch Wadden Sea (i.e. during spring migration). The previously assigned time-minimizing strategy for the Afro-Siberian (*taymyrensis*) population was confirmed, as well as the energy-minimizing strategy for the European population (*lapponica*). The Afro-Siberian population foraged closer to cover, thereby accepting a higher predation danger, but encountering a higher food abundance. Additionally, they foraged for a larger proportion of the time than birds belonging to the European population (67% vs. 33%), and were also found foraging on inland coastal meadows. These findings are to be expected from their migration strategy, as they need to fuel up for their (longer) migration in a shorter time period than the European population (**Chapter 4**).

To understand the presence and absence of bar-tailed godwits, more detailed knowledge on their diet was required (**Chapter 5**). This diet composition was generated by the identification of undigested prey remains in droppings. The rationale for quantifying the contributions of jawed and non-jawed polychaetes were also provided. By analysing droppings that were collected at five main wintering sites in north-western Europe, it was shown that despite differences per site, their main prey were indeed polychaete worms. Eighteen different prey species were identified in the diet of wintering bar-tailed godwits, with a high preference for ragworms *Hediste diversicolor*.

With these ingredients (e.g. spatial and temporal occurrence and diet composition), and in order to be able to predict the use of potential foraging areas on the basis of food abundance, the next step was to study the functional response (**Chapter 6, 7 and 8**). The functional response is defined as the relationship between the intake rate of a forager and the density of food and was initially studied in the field. These results revealed interference competition to be present, but only for females. As these larger females mainly forage on mobile and deep burying large prey, their foraging behaviour (probing into the sediment) could induce prey depression (prey becoming temporarily unavailable). Labo-

ratory and field experiments using lugworms *Arenicola marina* showed that they indeed retract themselves, which hinders the females in successfully capturing this prey. Therefore the reduction in intake rate as a function of predator density was mostly due to prey depression.

As field studies limit the parameterization of functional response equations, we designed an experimental set-up, where the functional response could be studied in more detail. These limitations of field studies are that individuals avoid low and high food density areas. The low food density areas are usually avoided, while the high food density areas are scarce. Besides, high food density areas attract many foragers, which will induce interference effects. The experimental set-up confirmed that this species follows a type II functional response, as they obeyed both assumptions of the Holling's disc equation (i.e. handling and searching efficiency was independent of prey density). Bar-tailed godwits apparently are confronted with a digestive constraint, and therefore have an equal intake rate over a range of food densities. In the face of a digestive bottleneck, they either have to take a break or continue foraging on high-quality food. This conclusion could not be drawn from the field observations, since these and other processes, such as interference, social behaviour, predation and selectivity, influence the intake rate.

Considering the importance of prey burying depth on intake rate, we were fortunate to be able to use a historical data set on lugworm burying depths (collected by Leo Zwarts and co-workers), allowing us to predict monthly intake rates for female bar-tailed godwits. The predicted intake rates matched with the birds' observed diet composition in these months (**Chapter 8**). Furthermore, by using sightings of individually marked bar-tailed godwits with known bill lengths, we demonstrate that phenotype-related seasonal redistributions occurred. In midwinter, when lugworms are burying deeper than in summer, only the longest billed individuals remained in the Dutch Wadden Sea. Thus, bar-tailed godwits present in Western Europe constantly redistribute themselves throughout their wintering range according to prey availability, rather than prey abundance. When phenotype-limited distributions are associated with assortative migration and mating patterns, they could act as precursors of phenotypic evolution.

At the end, the main findings of this project are discussed with reference to the initial question. The increase of bar-tailed godwits in the Dutch Wadden Sea appears to be entirely driven by an increase in numbers in the western part. If sites vary in quality and the population size in good-quality sites show small fluctuations, while simultaneously large changes in poorer sites are observed is known as the buffer effect. The increase of bar-tailed godwits in the western part of the Dutch Wadden Sea is consistent with the idea of a buffer effect. This suggests that the eastern part of the Dutch Wadden Sea represents the good-quality area and the western part a poor-quality area. Based on the mean food abundance, the eastern part has indeed on average a higher food abundance, supporting the idea that this is a higher quality site. However, the quality of a site is more

than food abundance alone. The higher predator density in the eastern part of the Dutch Wadden Sea for example, suggests the western part of the Dutch Wadden Sea to be a higher-quality site, as the density of predators is much lower. Given that the latest population estimates for bar-tailed godwits are stable or even declining, suggests the habitat in Western Europe has deteriorated elsewhere and bar-tailed godwits shifted their wintering distribution. Though, without an integrated study on habitat quality a population wide scale, this remains rather speculative.

By integrating the knowledge of this thesis with the continuous (and previous) effort in sampling the resource landscape (SIBES) *and* monitoring of bird populations on a broader scale (i.e. the entire wintering range) and other habitat quality indicators, the potential drivers for the population increase of polychaete-eating waterbirds in the Dutch Wadden Sea will likely be identified. Given that bar-tailed godwits are relatively easy to catch, easy to observe in the field, large enough to carry long-lasting tracking devices, and even amenable to indoor experiments, makes them a well suited study system for a continuation of this research. The observed “phenotype-limited distributions” as described in chapter 8, seems the logical next step to explore the movements and consequences (i.e. survival) of within species variation.

De meeste organismen op aarde leven in seizoensgebonden omgevingen met betrekking tot klimaat en voedsel, waarbij deze organismen moeten omgaan met deze veranderingen. Sommige individuen blijven in één gebied of habitat, terwijl andere juist migreren naar gunstigere plekken. Migrerende steltlopers zijn hier een goed voorbeeld van. De rosse grutto *Limosa lapponica* is zo'n migrerende soort die een 'leap-frog' migratie systeem volgt. Een 'leap-frog' migratie systeem betekent dat de noordelijkst broedende populatie zuidelijker overwintert dan de populatie die minder noordelijk broedt. Dit migratiesysteem leent zich uitermate goed om onderzoek te doen aan de beperkingen en keuzes die deze soort heeft én hoe ze omgaan met veranderende omgevingsomstandigheden.

In de Nederlandse Waddenzee komen twee rosse grutto populaties voor: *lapponica* en *taymyrensis*. De Europese populatie *L. l. lapponica* met een stabiele populatie van 120,000 vogels, overwintert in het waddengebied en broedt in noord Scandinavië. Deze populatie houdt er in het voorjaar een energie minimalisatie strategie op na, wat inhoudt dat ze een periode van 2 tot 3 maanden gebruiken om op te vetten voor hun migratie naar de Scandinavische broedgebieden en niet de hele dag foerageren. De Afro-Siberische populatie *L. l. taymyrensis* daarentegen volgt een tijd minimalisatie strategie, wat inhoudt dat ze een strak schema hebben. Deze populatie overwintert langs de westkust van Afrika en maakt een tussenstop in de Waddenzee, waar ze in 1 maand tijd moeten opvetten om naar hun broedgebieden in Siberië te vliegen. Deze populatie laat een negatieve populatietrend zien, met een geschatte populatie van 600,000 vogels. De seksen van rosse grutto's zijn daarnaast ook erg verschillend, waardoor ze net zo goed als verschillende soorten gezien zouden kunnen worden.

Deze populatieschattingen suggereren dat er veel rosse grutto's in het Waddengebied zijn, maar exacte aantallen zijn onbekend. Hierdoor rijst de vraag of er ook positieve of negatieve trends in populatie aantallen te ontdekken zijn. Gelukkig worden er vanaf 1975 in de Nederlandse Waddenzee watervogels geteld op een regelmatige basis. Uit een analyse van deze watervogels bleek dat er gedurende de laatste twee decennia een behoorlijke toename in worm-etende watervogels heeft plaatsgevonden, terwijl tegelijkertijd schelpdier-etende watervogels aanzienlijk zijn afgenomen. Een voorbeeld van een schelpdier-etende steltloper waarbij een afname is waargenomen is de kanoetstrandloper *Calidris canutus*. Bij deze soort kon de populatie afname worden toegeschreven aan de afname van het beschikbare voedsel. Of een toename van rosse grutto's in de Nederlandse Waddenzee ook mogelijk toegeschreven kon worden aan het voedselaanbod, staat centraal in dit proefschrift. Of zouden er mogelijk andere factoren een rol spelen? Om zo'n vraag te kunnen beantwoorden is het noodzakelijk om te weten waar en wanneer rosse grutto's voorkomen en waarom.

Op basis van biometrie uit museum collecties werd verondersteld dat beide rosse grutto populaties een aanzienlijke mate van overlap zouden vertonen in hun overwinteringsgebieden en broedgebieden (**hoofdstuk 2**). Dit is onderzocht aan de hand van terug-

meldingen. De mate van overlap in overwinteringsgebieden tussen beide populaties (0.8%) was echter veel kleiner dan aanvankelijk op grond van de biometrie van de vogels werd verwacht. We kunnen niet met 100% zekerheid zeggen dat deze vogels inderdaad in beide overwinteringsgebieden geweest zijn, want mogelijk zitten er fouten in het aflezen van kleurringen, onder andere doordat deze aan verkleuringen onderhevig zijn.

Vervolgens wilden we begrijpen hoe de mannelijke en vrouwelijke rosse grutto's hun overwinteringsgebied kiezen (**hoofdstuk 3**). Er waren reeds aanwijzingen dat de seksen zich waarschijnlijk niet gelijk verdeelden in hun overwinteringsgebieden. Relatief meer vrouwen verblijven in de noordelijke overwinteringsgebieden, terwijl in de gematigde gebieden relatief meer mannen worden waargenomen. Er werd verondersteld dat deze verschillen veroorzaakt zouden kunnen worden door de relatieve lagere stookkosten van de grotere vrouwen in deze noordelijke en koudere gebieden, welke ook dicht bij de Arctische broedgebieden liggen. Hiervoor zijn zes belangrijke overwinteringsgebieden in Noordwest-Europa bezocht en het voedsel bemonsterd. Het relatieve voordeel voor de vrouwen bleek echter mee te vallen. Wel konden we aantonen dat de seksen zich verdelen volgens voedselbeschikbaarheid (op basis van prooidiepte).

Gegeven het feit dat beide populaties verschillende overwinteringsgebieden gebruiken, hebben we er voor gekozen om te onderzoeken welke keuzes en gebieden er gebruikt worden wanneer beide populaties tegelijkertijd in de Nederlandse Waddenzee voorkomen, namelijk gedurende de voorjaars trek in mei. De eerder toegewezen migratie strategieën voor beide populaties kon worden bevestigd. De tijd minimaliserende Afro-Siberische populatie zoekt naar voedsel dicht bij de dijk, waar de voedselbeschikbaarheid hoger was, maar ze moeten hiervoor wel een hoger predatierisico accepteren. Ook foerageren Afro-Siberische rosse grutto's langer dan de energie minimaliserende Europese populatie (67% versus 33%) en foerageren ze ook in de nabijgelegen weilanden. Gezien de noodzaak om in een relatief korte tijd het noodzakelijke vertrekgewicht te bereiken, ligt dit in lijn met hun trekstrategie (**hoofdstuk 4**).

Om iets over de aanwezigheid en afwezigheid van een soort te begrijpen, is kennis over het dieet essentieel (**hoofdstuk 5**). Door het analyseren van rosse grutto poepjes, die werden verzameld op vijf belangrijke overwinteringsgebieden in Noordwest-Europa, kon worden bevestigd dat het belangrijkste voedsel inderdaad uit wormen bestond. Prooi-resten als kaakjes en borstels konden geïdentificeerd en geteld worden, zodat ook het relatieve aandeel van de prooiën beschreven kon worden. De zeeduizendpoot *Hediste diversicolor* bleek een belangrijke prooi voor rosse grutto's te zijn.

Met deze ingrediënten (zoals ruimtelijke en temporele verspreiding en de dieetsamenstelling) was de volgende stap om de functionele respons te bestuderen (**hoofdstuk 6, 7 en 8**), om zodoende potentiële foerageergebieden te kunnen voorspellen. De functionele respons is de relatie tussen hoe snel een vogel eet (opnamesnelheid) en de dichtheid van de prooi. De functionele respons hebben we eerst bestudeerd in het veld. Uit deze

gegevens bleek dat er interferentie in het spel was, maar opmerkelijk genoeg werd dit alleen bij de vrouwen gevonden. Tijdens het foerageren hadden de vrouwen dus last van elkaar. De afname in opnamesnelheid als een functie van vogeldichtheid bleek voornamelijk veroorzaakt te worden door het tijdelijk niet beschikbaar zijn van de prooi (prooi depressie). Aangezien de grotere vrouwtjes voornamelijk foerageren op diep ingegraven wadpieren *Arenicola marina*, zorgt hun foeragegedrag (het prikken in de wadbodem) ervoor dat deze wadpieren zich terug trekken. We konden dit aantonen door zowel in het veld als in het lab experimenten met deze prooi uit te voeren. Uit beide experimenten bleek dat wadpieren zich letterlijk terugtrekken, wanneer er in de buurt van hun geprikt wordt. Dit zorgt ervoor dat het voor vrouwtjes rosse grutto's moeilijker wordt om de wadpieren te vinden.

Aangezien het nagenoeg onmogelijk is om in het veld nauwkeurige data te verzamelen welke essentieel zijn om de functionele respons te kunnen voorspellen, is er voor gekozen dit ook experimenteel te onderzoeken. De beperkingen van veldstudies zijn onder meer dat de meeste individuen de lage voedseldichtheden vermijden, terwijl de hoge voedseldichtheden bijna niet voorkomen. Als deze hoge voedseldichtheden al voorkomen, dan zal dit meer individuen aantrekken, wat weer tot interferentie en verhoogde kieskeurigheid kan leiden. De experimentele opzet bevestigde dat rosse grutto's inderdaad een type II functionele respons volgen. Deze conclusie hadden we niet kunnen trekken op basis van de veldgegevens. De vogels in het veld hebben namelijk last van een verteringsbeperking. Als de vogels hun buikje hebben volgegeten en wanneer ze op rijke plekken foerageren, moeten ze even pauzeren of op ander (hoogwaardig voedsel) overgaan om zodoende voldoende energie binnen te krijgen. Naast ander processen zoals predatie, sociaal gedrag en kieskeurigheid zorgt deze verteringsbeperking ervoor dat deze vogels op een scala aan voedseldichtheden een nagenoeg vergelijkbare opname hebben. Veldstudies laten overigens wel een goed beeld zien wat vogels op een bepaalde plek doen, maar ze schieten te kort om algemene voorspellingen te doen.

Gezien het belang van de diepte van een prooi tijdens het foerageren van rosse grutto's, hadden wij het geluk om een dataset te gebruiken (verzameld door Leo Zwarts en collega's), waarbij gedurende 2 jaar de diepte van wadpieren was gemeten. Met behulp van de gegevens uit het experiment konden we de maandelijkse voedselopnames voor de vrouwelijke rosse grutto's voorspellen. Deze voorspellingen bleken goed overeen te komen met wat er in het dieet gevonden werd in diezelfde maanden. Door gebruik te maken van waarnemingen aan individueel gemerkte rosse grutto's met bekende snavellengtes in de Nederlandse Waddenzee, konden we laten zien dat de vogels zich 'aanpassen' aan de voedselbeschikbaarheid in een gebied. In de koude wintermaanden, wanneer wadpieren zich diep ingraven, blijven alleen de vogels met de langste snavel over. Vogels met een kortere snavel kunnen nagenoeg niet meer bij een groot deel van de aanwezige wadpieren en moeten hun dieet aanpassen, of ze moeten zich verplaatsen naar plekken waar het voedsel voor hen nog wel beschikbaar is.

Dit proefschrift eindigt met de belangrijkste bevindingen van het onderzoek, welke besproken worden in een bredere context. De toename van rosse grutto's in de Nederlandse Waddenzee lijkt volledig toegeschreven te kunnen worden aan een populatie-toename in het westelijke deel. Als plaatsen variëren in kwaliteit en de populatiegrootte in gebieden van goede kwaliteit kleine fluctuaties laten zien, terwijl tegelijkertijd grote veranderingen worden waargenomen in gebieden van lagere kwaliteit, dan wordt dit een 'buffer' effect genoemd. De toename van de rosse grutto's in het westelijke deel van de Nederlandse Waddenzee lijkt inderdaad een gevolg te zijn van dit buffer effect. Dit suggereert dat het oostelijke deel van de Nederlandse Waddenzee van goede kwaliteit is, terwijl het habitat in het westelijke deel van mindere kwaliteit is. Gegeven het feit dat Europese populatie nagenoeg stabiel is en de Afro-Siberische populatie zelfs afneemt, veronderstelt dit dat het habitat buiten de Nederlandse Waddenzee is afgenomen in kwaliteit, maar daar is nog te weinig over bekend. Op basis van het voedselaanbod, lijkt het oostelijke deel van de Nederlandse Waddenzee inderdaad een goed habitat, maar er zijn meer factoren die de kwaliteit van een gebied beïnvloedt. De dichtheden van roofvogels bijvoorbeeld is hoger in het oostelijke deel, wat weer suggereert dat het westelijke deel van betere kwaliteit is.

Door de integratie van de kennis vergaard in dit proefschrift, samen met de voortdurende (en de historische) inspanning in de bemonstering van de bentische soorten (SIBES) en de monitoring van vogelpopulaties op een grotere schaal (e.g. het gehele overwinteringsgebied) en andere kwaliteitsindicatoren te meten, zouden we de oorzaak van de populatieontwikkeling van rosse grutto's in het Waddengebied, maar ook daarbuiten beter kunnen begrijpen. Gezien het feit dat rosse grutto's relatief makkelijk te vangen zijn, zich goed laten observeren, groot genoeg zijn om de moderne zenders aan te hangen, en dat ze zelfs inzetbaar zijn voor het doen van (veld en lab) experimenten, maakt ze uitermate geschikt om dit onderzoek voort te zetten. De waargenomen verschillen in aanwezigheid van verschillende snavellengtes door het jaar heen zoals beschreven in hoofdstuk 8, lijkt de volgende logische stap om de verspreiding en consequenties (overleving) van individuen met verschillende snavellengtes in meer detail te volgen.



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List of publications

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