

University of Groningen

Sex-specific foraging

Duijns, Sjoerd

IMPORTANT NOTE: You are advised to consult the publisher's version (publisher's PDF) if you wish to cite from it. Please check the document version below.

Document Version

Publisher's PDF, also known as Version of record

Publication date:

2014

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

Citation for published version (APA):

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

Copyright

Other than for strictly personal use, it is not permitted to download or to forward/distribute the text or part of it without the consent of the author(s) and/or copyright holder(s), unless the work is under an open content license (like Creative Commons).

The publication may also be distributed here under the terms of Article 25fa of the Dutch Copyright Act, indicated by the "Taverne" license. More information can be found on the University of Groningen website: <https://www.rug.nl/library/open-access/self-archiving-pure/taverne-amendment>.

Take-down policy

If you believe that this document breaches copyright please contact us providing details, and we will remove access to the work immediately and investigate your claim.

Downloaded from the University of Groningen/UMCG research database (Pure): <http://www.rug.nl/research/portal>. For technical reasons the number of authors shown on this cover page is limited to 10 maximum.

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 leveling 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; Zwarts & Wanink 1984). However, deeper burial may also result in a lowering of food intake which in turn reduces body condition (de Goeij & Luttikhuisen 1998; Zwarts & Wanink 1993). In the Baltic tellin *Macoma balthica*, a preferred prey of shorebirds, burrowing deeper reduces predation risk (Edelaar *et al.* 2005; Zwarts & 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 extent 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 ± 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 ($P < 0.001$).

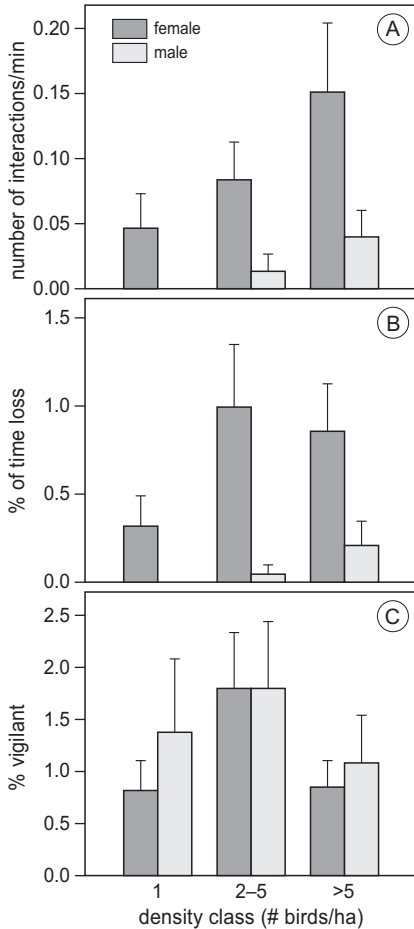


Figure 6.1. Mean number of agonistic interactions of bar-tailed godwits separated in (A) female and male (B) the consequent percentage of time loss caused through this, and (C) the percentage of time spent vigilant.

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.

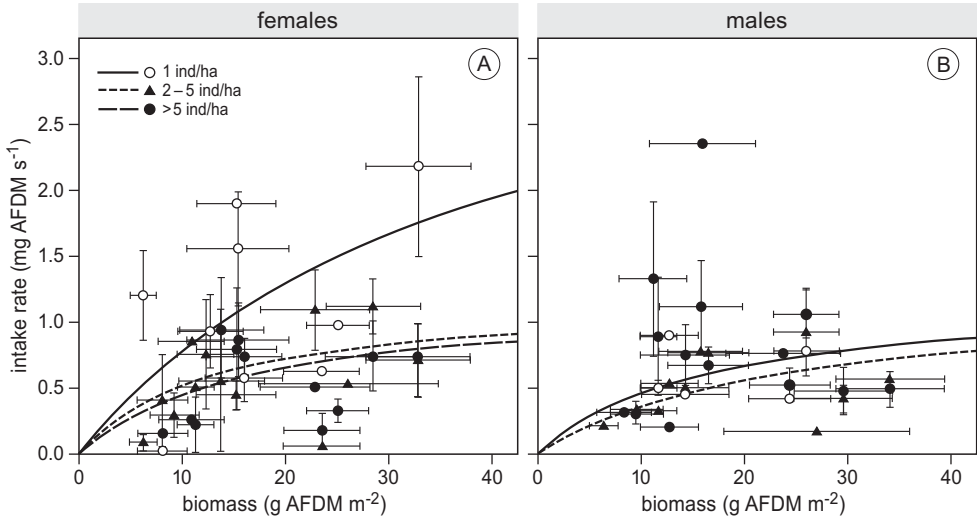


Figure 6.2. The relation between the mean (\pm SE) intake rate (mg AFDM s^{-1}) for female and male bar-tailed godwits and the mean (\pm SE) biomass (g AFDM m^{-2}) available. Different symbols represent different competitor densities. Plotted lines represent type II functional responses fitted to the 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.

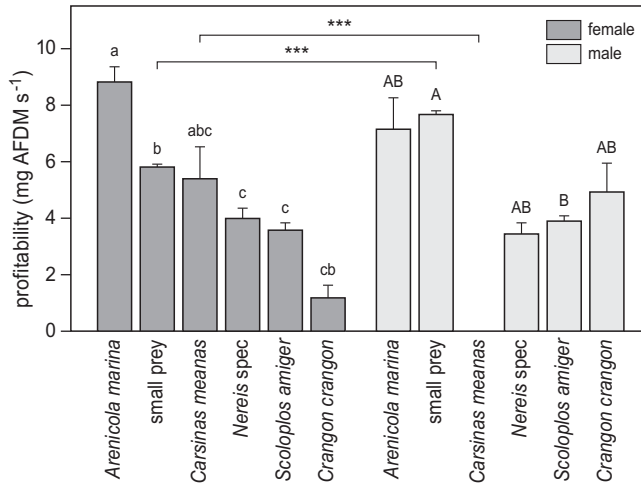


Figure 6.3. Profitability per prey species of bar-tailed godwits, separated per sex. The lower case letters in the graph represent the differences ($P < 0.05$) between prey species for the females and the capital letters represent differences in prey profitability for the males. The asterisks refer to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

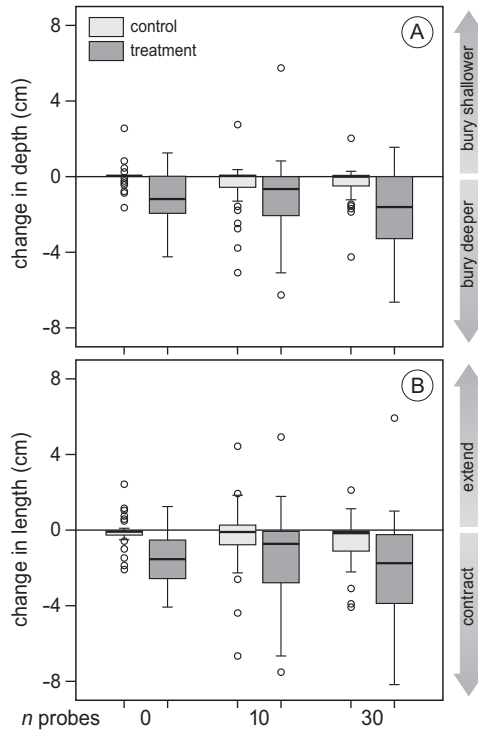


Figure 6.4. Mean depth (A) and mean length (B) difference between the different probing intensities (light grey bars) and control plots (dark grey bars). Increased probing intensities lead to a deeper burial (A) and also lead to smaller lugworms (B), by contracting their muscles. Box plot shows median (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 (Losey & 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. Zwartz & 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. Zwartz & 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.

Acknowledgements

We thank Johan van Heerwaarden for constructing the experimental aquaria and the following students of the RUG-NIOZ Marine Biology and Oceanography course for their help with the experiments: Hannah van Noort, Cleo Offers, Julian Robertson, Karsten Roelfsema, Malenthe Teunis, Lisa Detzkeit and Vera Rullens. We thank Eric Menkveld, Loran Tinga and Eckard Boot from Vereniging Natuurmonumenten for permission to work at the mudflats around the island of Texel. Bram Fey, Hein de Vries, Anne Dekinga, Bernhard Spaans, Piet van den Hout, Emma Alves, Andreas den Boer, Rutger Steever, Aron te Winkel and Job ten Horn are acknowledged for help in the field. Jan A. van Gils and two anonymous reviewers gave important feedback on the manuscript. The study was supported by operational funds from NIOZ and by Metawad (WF 209925), a project awarded by Wadendfonds to TP.

