



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



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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 predicted 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.

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According to the 'ideal free distribution' (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, Alonso, & Alonso, 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, Hemetsberger, & Dittami, 1993), kleptoparasitism (Brockmann & Barnard, 1979), foraging site replacement (Bautista, Alonso, & Alonso, 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 ('cryptic interference', e.g. Bijleveld, Folmer, & Piersma, 2012; Gauvin & Giraldeau, 2004; Gyimesi, Stillman, & Nolet, 2010; van Dijk, Duijns, Gyimesi, de Boer, & Nolet, 2012). For predators foraging on mobile prey, the levelling off of intake rate may also be caused by prey depression, which can result from a number of different processes and does not require actual harvesting of any prey items by the predator (Charnov, Orians, & Hyatt, 1976). Prey depression, that is, prey becoming temporarily unavailable, can occur when prey respond to the presence of predators, for instance by retreating down a burrow (Backwell, O'Hara, & Christy, 1998; Ens, Klaassen, & Zwartz, 1993; Stillman, Goss-Custard, & Alexander, 2000). The deeper the prey

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is buried, the smaller the chance of them being caught (Myers, Williams, & Pitelka, 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, Piersma, & Postma, 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 aimed 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, Jukema, Spaans, van Horsen, & Piersma, 2012). Bar-tailed godwits feed especially on polychaete worms (Duijns, Hidayati, & Piersma, 2013). In the field they show little aggression during foraging, but when it occurs, it is mainly between females (Both, Edelaar, & Renema, 2003). Habitat use differs between the sexes, both at large spatial scales (Atkinson, 1996; Scheiffarth, 2001a) and at small scales (Both et al., 2003; Smith & Evans, 1973; Zwarts, 1988). Sex-related diet preferences have been observed (Scheiffarth, 2001b): 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, 2001b; Smith, 1975), can comprise up to 80% of the females' diet. It lives in burrows and has a number of modes of behaviour. For much of the time lugworms remain deep in their U-shaped burrows, 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 most 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, Wahls, Ketzenberg, & Exo, 2002). Given that the sexes differ in small-scale habitat use and diet (e.g. Atkinson, 1996; Scheiffarth, 2001a; Smith & Evans, 1973), we hypothesized that intrasexual competition, rather than intraspecific competition, would drive interference competition, and that sex-specific prey behaviour would 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 the island of Texel, The Netherlands ($53^{\circ}05'N$, $4^{\circ}48'E$). Eighteen plots (100×100 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 approximately 30 cm of water standing), a single observer (S.D.) placed himself 30–125 m away from a plot and awaited the arrival of the birds. One focal bird was randomly selected for a 5 min observation and behaviour and sex were recorded on a digital voice recorder (Sony ICD-P620; focal animal sampling, continuous recording).

We used the following ethogram: searching, vigilance, preen, rest, interactions with conspecifics or with other bird species. When a bird was foraging by itself in a plot (i.e. 1 individual/ha), interactions with other bird species were also recorded, but this only occurred on three occasions and only in females. Interactions were recorded because kleptoparasitism and time lost in aggressive interactions are generally assumed to cause interference competition (Smallegange & van der Meer, 2009; Stillman, Goss-Custard, & Caldow, 1997). We avoided repeated observations of individuals by consistently moving at least three 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, we estimated bill lengths of colour-ringed individuals at distances of 20–200 m. These birds had known bill lengths, which enabled us to validate our visual estimates. That estimated bill lengths were highly correlated with measured bill lengths (Pearson correlation: $r_{28} = 0.87$, $P < 0.001$) 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 was used. These small prey items were later analysed in the laboratory and predominantly comprised small crustaceans such as *Urothoe poseidonis*, *Corophium volutator* and small worms such as *Pygospio elegans* and *Eteone* species and to a lesser extent the snail *Peringia 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 Information Technology Inc., Wageningen, The Netherlands) 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), handling time (s) and profitability (mg AFDM/s) 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 one 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 approximately 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 two plots (1×1 m), an experimental and a control plot in close proximity to each other (ca. 1 m distance) at the Mokbaai, a small intertidal mudflat area on Texel. The experiment started during the outgoing tide (still 30 cm of standing water), approximately 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 new casts produced every 10 min and repeated this procedure for 2 days.

Indoor Prey Depression Experiment

Adult lugworms were collected in April 2013 in the Mokbaai. Different densities (two, four and six lugworms) were placed in transparent plastic aquaria (50 × 40 cm high with a thickness of 1.4 cm) directly after collection. The four aquaria were placed adjacent to each other, in two groups of two, meaning that two density treatments were done simultaneously. As soon as the lugworms were released in the aquarium, most 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 approximately 0.10 ml of commercial shellfish feed (Instant Algae; Shellfish diet 1800, Reed Mariculture Inc., Campbell, CA 95008, U.S.A.), which was deposited on the substrate before each trial. We used this shellfish diet because, in additional trials, the lugworms lived longer with this food than without (S. Duijns, personal observation). The aquaria were kept in a dark climate chamber with continuously running sea water. Water and room temperature were kept constant at 15 °C. After the lugworms had been acclimatized for at least 1 h, the experimental treatment started.

Before and immediately after each trial, the length and depth of each lugworm was measured and marked with nonpermanent markers on the aquarium windows. At each trial one aquarium was randomly selected as the experimental one and the adjacent one was used as a control. We used three intensity treatments in which 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 carried out eight times and new lugworms were used for every trial. After each experimental day, all lugworms were released close to the capture site.

Data Analyses

Comparisons between the sexes for vigilance, number of interactions per unit time and time lost because of interactions were made with a Poisson-distributed generalized linear mixed model with observed density (number of birds/ha) as the main effect, sex as a factor and food availability as a random factor. Since all interaction terms were nonsignificant (all $P > 0.1$) in these three models, the interactions were excluded from the final analysis. For graphical purposes we grouped the density into three classes: 1 individual/ha, 2–5 individuals/ha and >5 individuals/ha. As bar-tailed godwits often follow the tideline (e.g. Both et al., 2003), we initially separated the analysis into 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 individuals/ha; $N = 8$) that were made within 30 min after a large flock had foraged in the plot.

By using the mean observed handling times, mean food abundance (g AFDM/m²) and (instantaneous) intake rates (mg AFDM/s),

the searching efficiency (cm²/s) could be estimated by using the nonlinear least-square fitting function (nls) of the software package R (R Development Core Team, 2013). As males consume many more small prey items per unit time than females, sample sizes for handling time differ markedly between the sexes (Table 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 plots 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 all prey after each experimental trial. Therefore depth (first model) and length (second model) were the explanatory variables, density (i.e. two, four or six lugworms per aquarium) and initial depth (first model) and length (second model) were factors and lugworm ID was a random factor. All analyses were conducted using R 3.0.1 and the package lme4 (Bates, Maechler, Bolker, & Walker, 2013) was used to fit (G)LMMs, and the package multcomp (Hothorn, Bretz, & Westfall, 2008) was used to perform Tukey post hoc tests.

RESULTS

Field Observations

Females suffered from higher levels of agonistic interactions than males (GLMM: $\chi^2 = 18.52$, $P < 0.001$; Fig. 1a), and a positive effect of forager density was observed (GLMM: $\chi^2 = 6.21$, $P = 0.012$; Fig. 1a). Females initiated interactions more frequently than males ($\chi^2_5 = 6.74$, $N = 25$, $P = 0.03$) and when interactions occurred, females won these interactions more often than males ($\chi^2_5 = 9.19$, $N = 28$, $P = 0.026$). With no intraspecific competitors around, females still suffered from interference from other species such as black-headed gulls, *Chroicocephalus ridibundus*; 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: $\chi^2 = 73.25$, $P < 0.001$; Fig. 1b). A positive effect of forager density for both sexes was observed (GLMM: $\chi^2 = 4.29$, $P = 0.038$; Fig. 1b). As expected (e.g. Beauchamp, 1998; Sansom, Cresswell, Minderman, & Lind, 2008), vigilance was negatively correlated with density (GLMM: $\chi^2 = 6.26$, $P = 0.014$; Fig. 1c), but no difference between the sexes was observed (GLMM: $\chi^2 = 0.13$, $P = 0.72$; Fig. 1c).

The intake rate of bar-tailed godwits was a function of available biomass (Fig. 2, Table 1), and followed a type II functional response

Table 1
Mean handling time and average searching efficiency of bar-tailed godwits

Density class (no. of birds/ha)	N	Handling time (s)	Searching efficiency (cm ² /s)	P
Males				
1	7		0.75±0.2	<0.05
2–5	15	0.56±0.05	0.52±0.1	<0.001
>5	35		0.79±0.2	<0.001
Females				
1	18		0.97±0.6	0.09
2–5	34	0.84±0.2	0.91±0.3	<0.05
>5	27		0.71±0.2	<0.05

Handling times were measured in the field ($N = 2394$ for males and $N = 953$ for females), and searching efficiency was estimated from fitting the Holling's (1959) disc equation. The P values refer to whether the fitted functional response type II function is significant. Values are given ± SE.

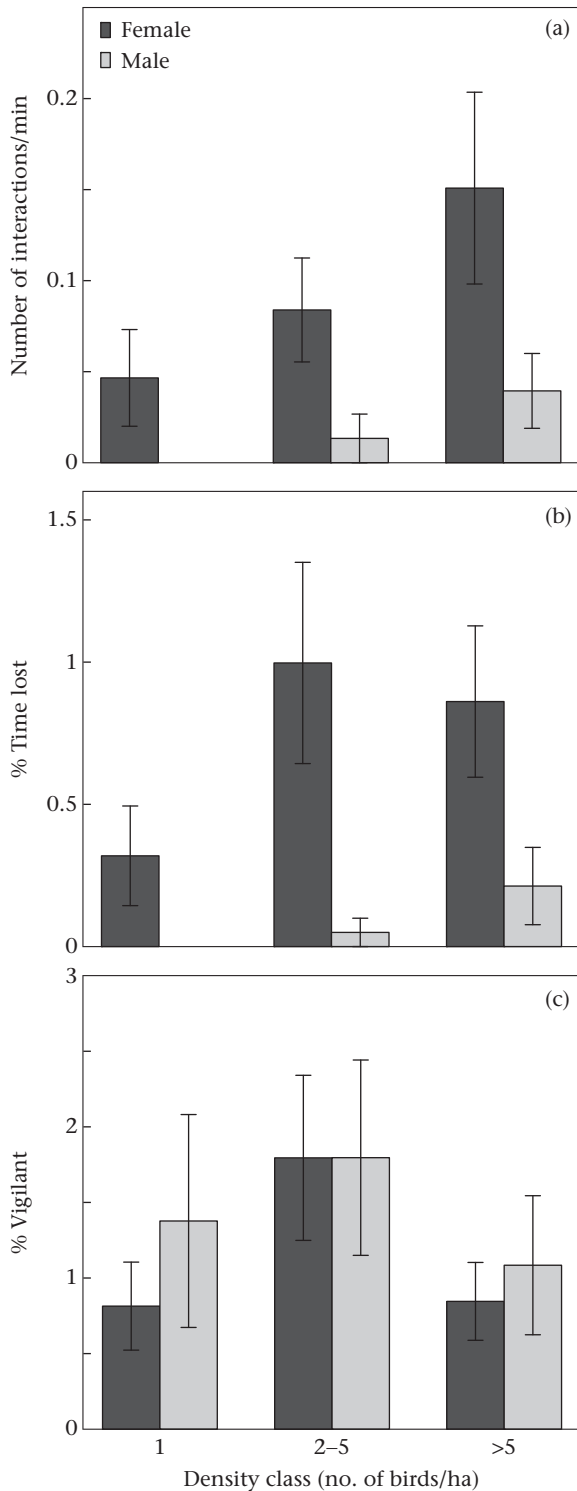


Figure 1. (a) Mean \pm SE number of agonistic interactions of female and male bar-tailed godwits, (b) the percentage of time lost as a result, and (c) the percentage of time spent vigilant.

(Holling, 1959). Only females foraging at the lowest densities of ca. 1 bird/ha did not suffer from interference (Fig. 2a), whereas males did not appear to suffer from interference at any density (Fig. 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 2). Note that the profitability (AFDM/s handling) of lugworms, relative to the other prey types, is also the highest (Fig. 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 (Tukey's test: $P < 0.001$).

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: $t_{96.1} = 8.68$, $P < 0.001$). 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: $\chi^2 = 43.75$, $P < 0.001$). 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 manual probing, respectively; Fig. 4a). There was no effect of lugworm density ($P = 0.53$), but there was a positive effect of the initial depth (LMM: $\chi^2 = 12.72$, $P < 0.001$). The latter indicated that the lugworms' response was greater when initially buried less deeply. When disturbed, lugworms also responded directly by becoming shorter (i.e. contracting their muscles; LMM: $\chi^2 = 49.43$, $P < 0.001$), 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. 4b). There was no effect of density ($P = 0.63$), and a positive effect of initial length (LMM: $\chi^2 = 4.28$, $P = 0.04$) 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: $r_{284} = 0.77$, $P < 0.001$), suggests that the immediate response of lugworms was to shorten their bodies, rather than to bury themselves deeper in the sediment.

DISCUSSION

Previous studies on bar-tailed godwits reported sex differences in foraging behaviour (e.g. Both et al., 2003; Smith & Evans, 1973; 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 during low tide (e.g. Smith, 1975; Vader, 1964). That casts would be most frequently produced at the tideline already suggests an explanation for 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 foragers' 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 (Smallegange & van der Meer, 2009; Stillman et al., 1997). 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, that is, animals anticipate and try to avoid physical encounters with conspecifics. This subtle avoidance behaviour cannot be observed other than in

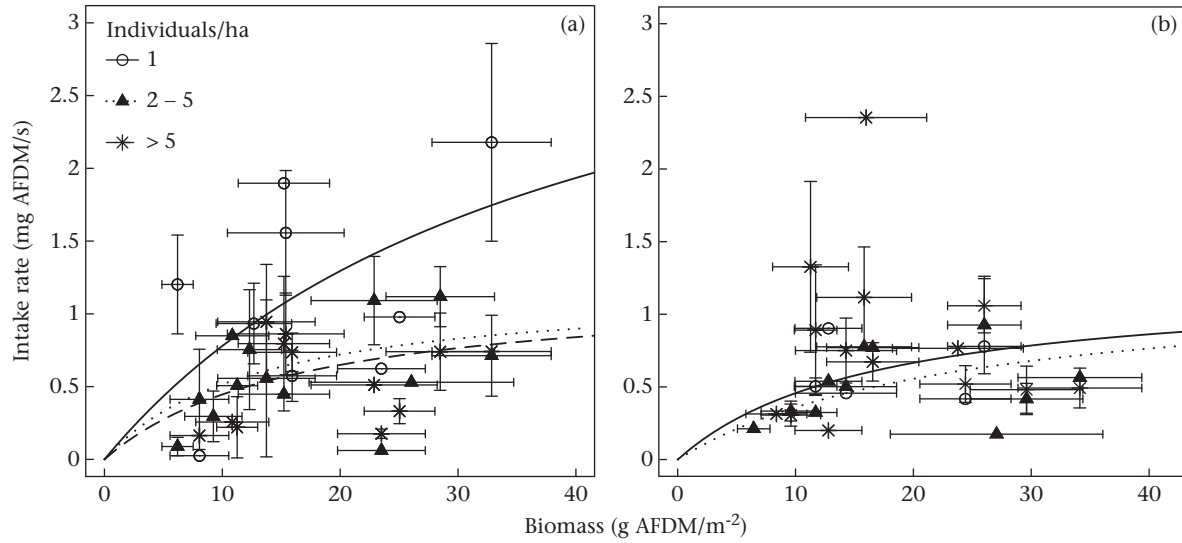


Figure 2. The relation between the mean \pm SE intake rate (mg AFDM/s) for (a) female and (b) male bar-tailed godwits and the mean \pm SE biomass (g AFDM/m²) available. Different symbols represent different competitor densities. Plotted lines represent type II functional responses fitted to the data using the [Holling's \(1959\)](#) disc equation; see [Table 1](#) for parameters. Note that the lower density functional response line for males follows exactly the functional response at the highest densities and is thus not visible.

Table 2
Diet composition of both sexes of bar-tailed godwits

Prey	% Occurrence		% AFDM	
	Male	Female	Male	Female
Lugworm, <i>Arenicola marina</i>	0.5 (32)	7.9 (210)	17.8	71.4
Shore crab, <i>Carcinus maenas</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</i> sp.	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 (5693)	85.6 (2261)	71.8	20.4

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

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 the birds' diet (86%; [Table 2](#)), and therefore represents a weighted average of short handling times.

That prey behaviour can suppress the intake rate of foragers has been shown in several taxa including mammals ([Kotler, 1992](#)), insects ([Loosey & Denno, 1998](#)) and shorebirds (e.g. [Backwell et al., 1998](#); [Ens et al., 1993](#); [Goss-Custard, 1970](#); [Selman & Goss-](#)

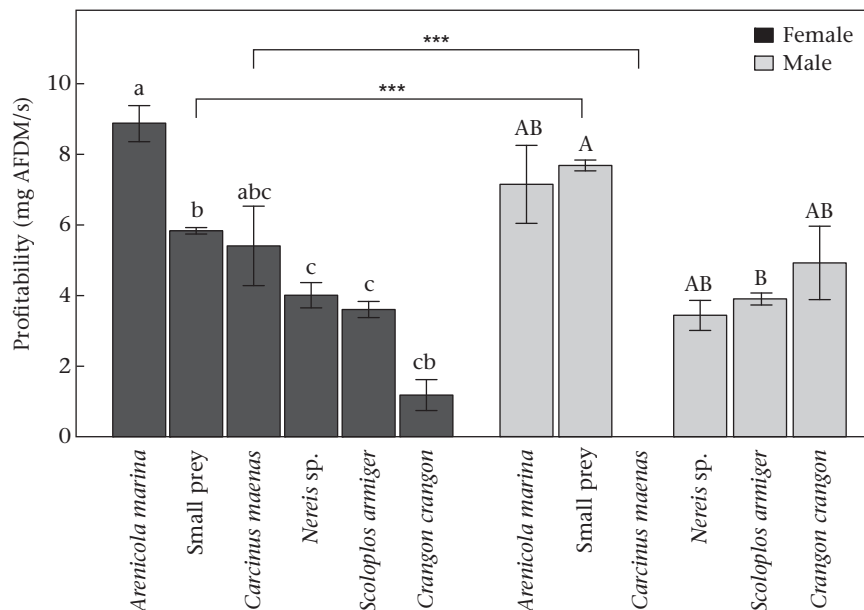


Figure 3. Profitability per prey species of bar-tailed godwits, separated by sex. Lowercase letters represent the differences ($P < 0.05$) between prey species for females and capital letters represent differences in prey profitability for males. Asterisks refer to significant differences ($P < 0.001$) between the sexes within species.

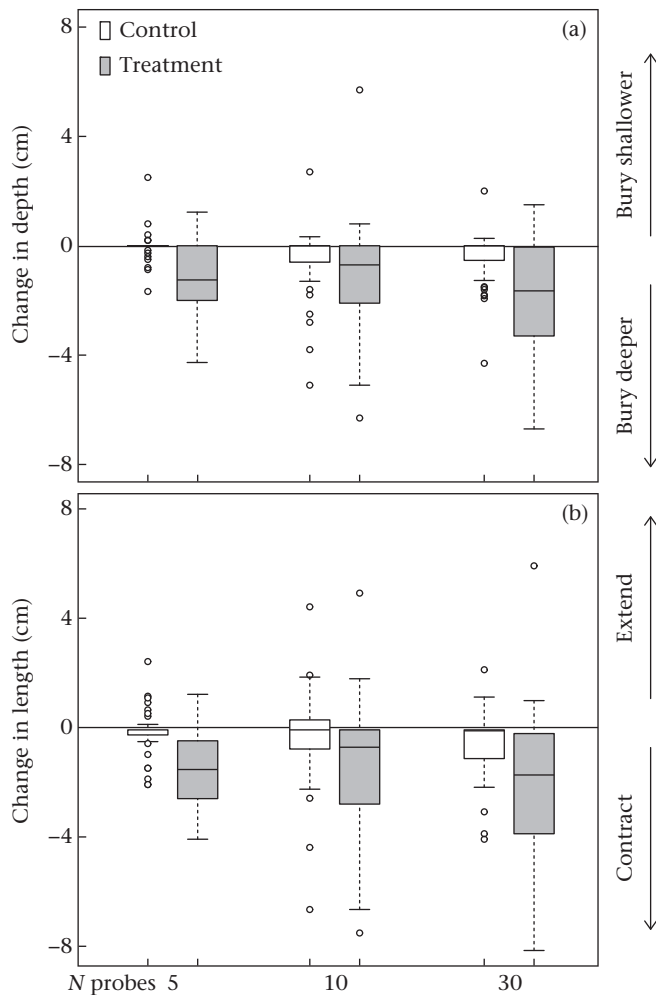


Figure 4. (a) Mean depth and (b) mean length difference between the different probing intensities (grey bars) and control plots (white bars). Box plots show median (line in box), interquartile range (box), 10th and 90th percentiles (bars) and outliers (dots; data points outside the 10th and 90th percentiles).

Custard, 1988). In all these studies the capture and intake of individual prey were 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's 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 individuals/ha) were slightly higher than the estimates of 1.5–4.5 individuals/ha measured in the Dutch Wadden Sea by other methods and at other times of the year (Folmer, Olf, & Piersma, 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 ha plots. As measured in the same study area in the previous year, there was a positive correlation between interbird distances and flock size (Pearson correlation: $r_{27} = 0.55$, $P = 0.001$). Thus at low overall densities, birds foraged closer to each other than at higher densities.

There are three possible reasons why we did not observe a levelling off in intake rate due to interference competition in males.

(1) Prey depression did not play a role at all because their diet consisted of smaller prey items than those taken by 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 the mean \pm SE handling times (0.56 ± 0.05 s) of their most frequent prey (>95%) was rather low, whereas the mean time \pm SE lost (4.3 ± 2.2 s) from agonistic interactions was much higher. Hence, the time required to steal a prey may outweigh the benefit and the birds are better off finding a new prey item themselves (Ens, Esselink, & Zwartz, 1990). (3) Small prey items were more abundant (mean \pm SE = 93.7 ± 2.6 per m^2) than larger prey items (58.0 ± 0.8 per 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 can usually 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 the fact 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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