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

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Summary

1. 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.

2. 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'.

3. 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*.

4. 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 30–70 times), compared with measurements from controlled experimental conditions.

5. In agreement with the assumptions of Holling's disc equation, under controlled experimental settings both the instantaneous area of discovery and the 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.

6. 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.

Key-words: digestive constraint, distribution, energetics, foraging, Holling's disc equation, intake rate, interference, *Limosa lapponica*, prey detection, shorebird

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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, Stillman & Norris 2008). These measurements can be fitted to Holling's disc equations (e.g. Gill, Sutherland & Norris 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, Alonso & Alonso 1995; van der Meer & Ens 1997; van Gils & Piersma 2004).

In Sutherland & 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-maximizing models are transformed into 'fitness-maximizing 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, Kopp & Tollrian 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, Boyce & Merrill 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.* 2005a). 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):

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

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. 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 the handling time and the instantaneous area of discovery to be constant across different prey densities.

Materials and methods

STUDY SYSTEM

Bar-tailed godwits are sexually dimorphic shorebirds wintering in intertidal areas; females are 20% heavier with 25% longer

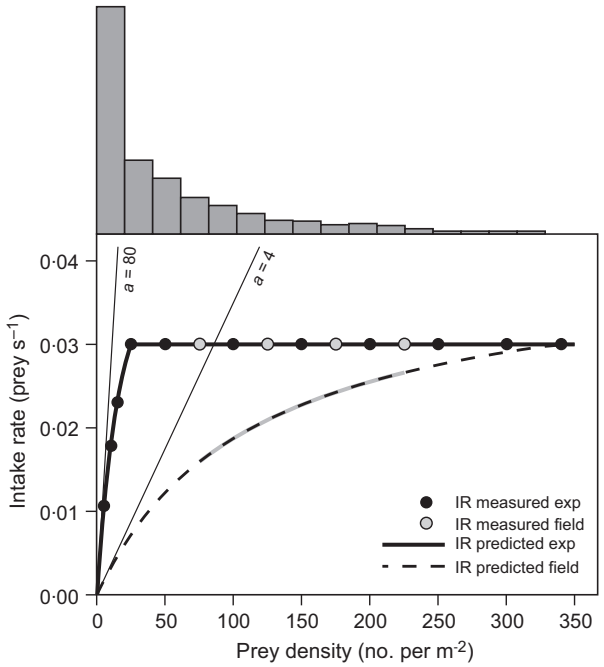

Fig. 1. Conceptual graph of intake rate as a function of prey density following Holling's disc equation for foragers digestively constrained at 0·03 prey s^{-1}. The solid black dots represent intake rate (IR) measurements at experimentally offered prey densites, the solid black line represents the prediction based on experimental measurements of instanaeous area of discovery (a), handling time and digestion time. The solid grey dots represent IR measurements at prey densites 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 cm^2 s^{-1} under the experimental setting to 4 cm^2 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.

bills than males (Cramp & Simmons 1983; Duijns *et al.* 2012). During the non-breeding season males feed mainly on small prey items and females predominantly forage on lugworms (Scheiffarth 2001; Duijns & Piersma 2014). Additionally, spatial segregation between the sexes has been observed (Smith & Evans 1973; Both, Edelaar & Renema 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) positioned 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^{-1}). 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× 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 ± 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, five benthic cores of 0·0177 m^2 were taken at *c.* 25 m from each corner and one 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 *c.* 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 EXPERIMENTS

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^{-1}), 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. 2). These adjacent aviaries served as roosting areas and always contained a fresh water tray. For general habituation and training purposes (*c.* 4 weeks), all birds were kept in the experimental area with access to the smaller adjoining aviaries. Within the aviaries, the light was kept synchronized 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 2 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).

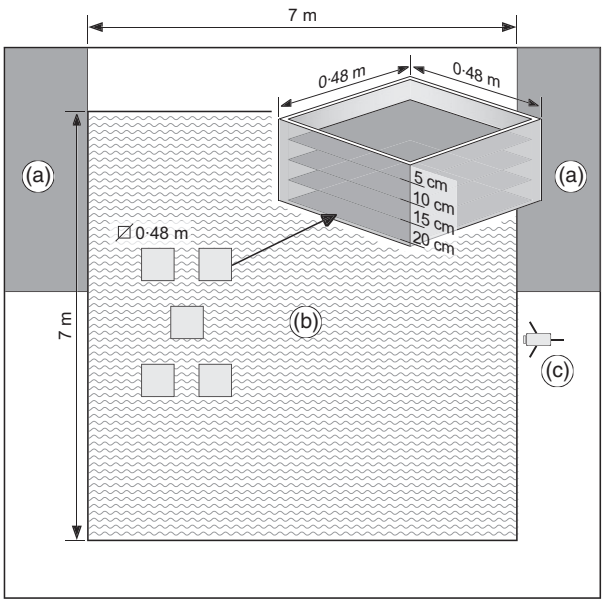

Fig. 2. The experimental set-up: (a) aviary/high-tide roost; (b) experimental area (covered with water during the experiment), with the experimental patches, of which only one was accessible during an experimental trial; (c) observation hide. The inset diagram at the upper right patch shows a feeding 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 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 ± 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 × 0·48 m (0·23 m^2) in dimension and was filled with sediment collected from the Wadden Sea (median grain size 269·5 μm; 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 *c.* 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. 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 min 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. 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 characterized by probing of the sediment in search of prey, either while moving or standing still. (2) *Handling time* was characterized 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 s 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 (s) of all observed birds, the mean food abundance per plot (no. m^{-2}) and intake rates (prey s^{-1}), the instantaneous area of discovery (cm^2 s^{-1}) was estimated by the nonlinear 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 $\log_{10}$-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:

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

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 m^{-2} and used mean (female) bird densities per plot; this relation was tested with a nonlinear 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 eight trials, just two prey were found and in two 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, Prates & Lachos 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 three 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:

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

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

where T_s is search time (s) and T_h is handling time (s) for bird i and prey j, a is the instantaneous area of discovery ($cm^2\ s^{-1}$), b is the random slope of bird identity, βn 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_s), 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 ($F_{1,55} = 0{\cdot}75$, $R^2 = 0{\cdot}013$, $P = 0{\cdot}39$; Fig. 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, $\chi^2 = 84{\cdot}9$, $P < 0{\cdot}001$; Fig. 3b). In this log–log correlation, the slope was $-0{\cdot}93$ ($\pm 0{\cdot}09$ 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, $\chi^2 = 8{\cdot}4$, $P = 0{\cdot}003$; Fig. 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).

HANDLING TIME

Handling time was independent of prey density in both the field study ($F_{1,55} = 1{\cdot}97$, $R^2 = 0{\cdot}03$, $P = 0{\cdot}17$; Fig. 5a) and the experiment (GLMM, $\chi^2 = 2{\cdot}6$, $P = 0{\cdot}10$; Fig. 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, $\chi^2 = 0{\cdot}5$, $P = 0{\cdot}46$). Prey length had a significantly positive effect on handling time in the experimental setting (GLMM, $\chi^2 = 165{\cdot}9$, $P < 0{\cdot}001$), as well as in the field study ($F_{1,55} = 19{\cdot}84$, $R^2 = 0{\cdot}27$, $P < 0{\cdot}001$). Observed prey handling times did not differ from the field study and the experiment ($t = 0{\cdot}09$, d.f. = 31·4, $P = 0{\cdot}93$; Fig. 6a). However, when handling time was ignored or is unknown, Holling's disc equation overestimates handling time greatly (Fig. 6a). Additionally, when the asymptote was set to the digestive constraint, handling time was overestimated even more (Fig. 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 ± SE = 0·7 ± 0·1; Fig. 6b). In the experiments, a was found to be much higher. Calculations using equation 4 yielded values of $a = 52{\cdot}4\ cm^2\ s^{-1}$ for a prey depth of 5 cm, $a = 41{\cdot}3\ cm^2\ s^{-1}$ for depth 10 cm, $a = 32{\cdot}6\ cm^2\ s^{-1}$ for depth 15 cm and $a = 25{\cdot}7\ cm^2\ s^{-1}$ for depth 20 cm (bias-corrected back-transformed; Sprugel 1983; Fig. 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.

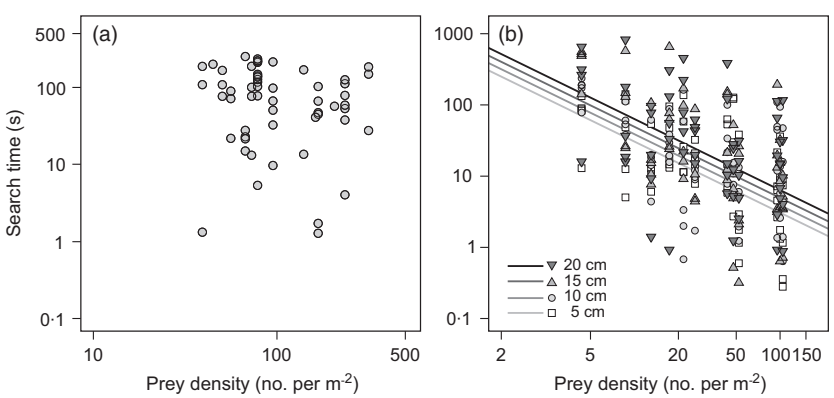

Fig. 3. (a) In the field-based study, Holling's first assumption was not upheld as there was no effect of prey density on search time ($P = 0{\cdot}39$). (b) However, in the experimental setting, Holling's first assumption was met with search times being inversely related to prey density. The four lines represent the four different burial depths (symbols shown in legend), which, as predicted, had an effect on searching time, that is more deeply buried prey resulted in longer search times per prey. Note the log–log scales in both plots.

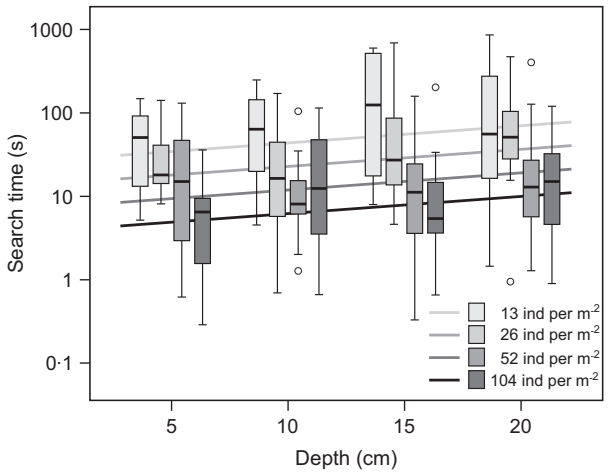

Fig. 4. In the experiment, search time not only increased with decreasing prey density (see also Fig. 3b), it also increased with increasing prey depth. Box plots indicate the median, and the 25th and 75th percentiles; whiskers indicate the 5th and 95th percentiles. Note that the *y*-axis is plotted on a log scale.

FIELD VS. 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 ± SE) was 0·0067 ± 0·00005 prey s^{-1} (GLMM, $\chi^2 = 10{\cdot}215$, $P < 0{\cdot}001$), 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. 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 ($I > 0$; $F_{3,14} = 46{\cdot}91$, $R^2 = 0{\cdot}89$, $P < 0{\cdot}001$; Fig. 7b). The field-based functional response predicted that, below a prey density of 100 prey m^{-2}, 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 m^{-2}, 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 ($F_{1,236} = 7{\cdot}19$, $R^2 = 0{\cdot}03$, $P = 0{\cdot}008$; Fig. 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, Stillman & Norris 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 30–70 times higher in the experiment than when estimated on the basis of field data (Fig. 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 discovery 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

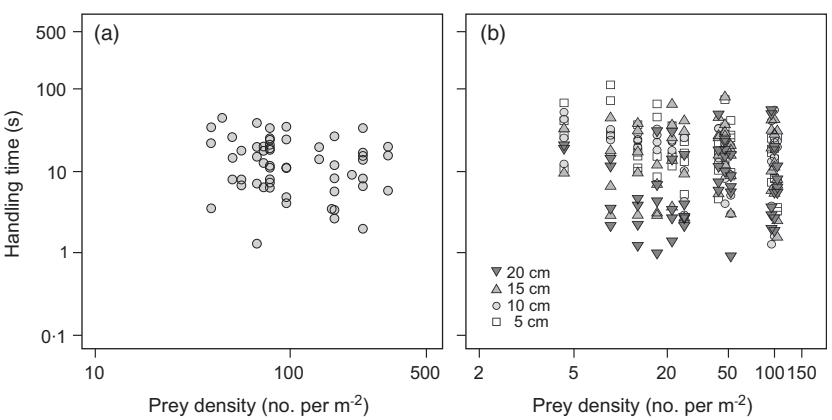

Fig. 5. Prey handling times did not vary with prey density in the field (a), nor in the experiment (b), where the different symbols represent different prey depths (shown in legend). Therefore, the second assumption of the Holling's disc equation was upheld by both approaches. Note the log–log scales.

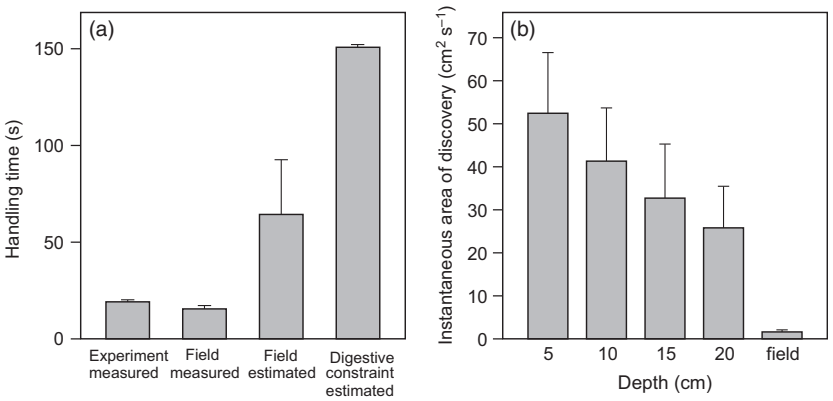

Fig. 6. (a) Mean (±SE) handling times, measured separately in the experiment, in the field estimated from fitting Holling's disc equation to the field data (short protocols), and estimated from long-term intake rate (long protocols; i.e. by neglecting existence of digestive constraint). (b) Mean instantaneous area of discovery (±SE) estimated in the experiment for different depths and by fitting Holling's disc equation to the field data (short protocols).

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 m^{-2}. Based on the experimental observations, the minimum prey density would be 3 prey m^{-2} only (Fig. 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. 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, Kopp & Tollrian 2002; van Gils & Piersma 2004), social behaviour (Bijleveld, Folmer & Piersma 2012), interference and predator avoidance behaviour (e.g. Cresswell & Whitfield 1994; Ydenberg *et al.* 2002; van den Hout, Spaans & Piersma 2008) constrain these foragers (Fig. 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 under experimental settings. However, when handling time is unknown, Holling's disc equation overestimates handling time for digestively constrained foragers in the wild (Fig. 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 need 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 low-quality food than smaller species (Gordon & Illius 1996). The

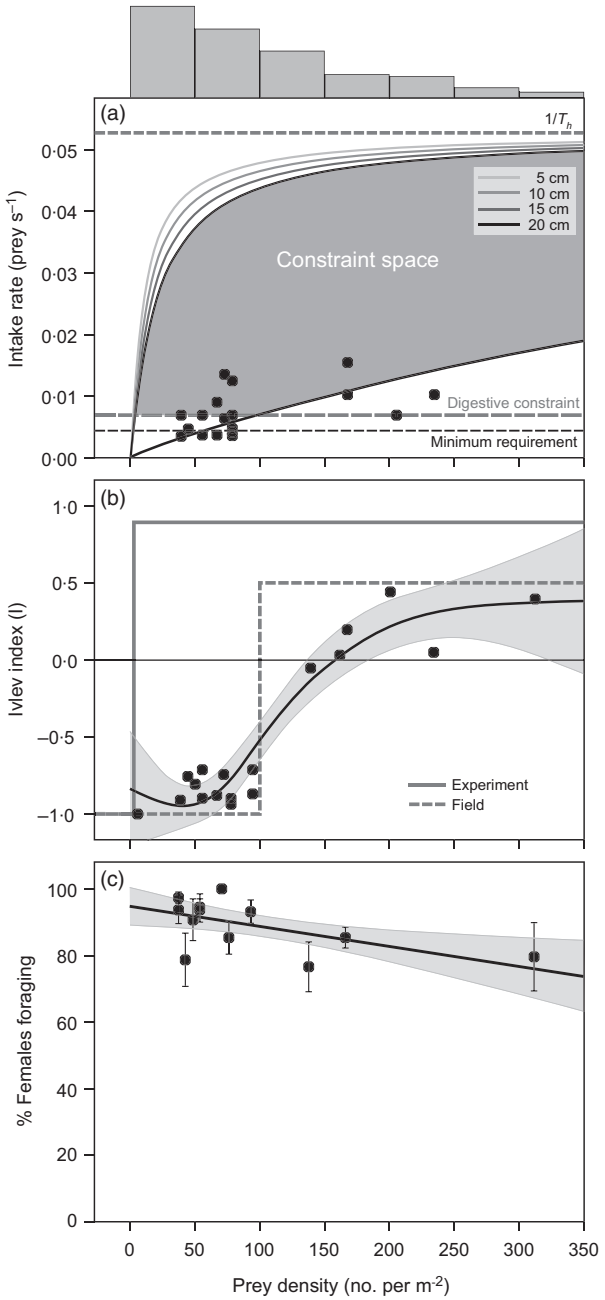

Fig. 7. (a) The intake rate (prey s^{-1}) of solitary bar-tailed godwits feeding on lugworms in the field, with the experimentally obtained functional responses for the four different prey burial depths shown as different greyscale lines. Field estimates were found to be around the level of the digestive 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 m^{-2}), 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 ($R^2 = 0{\cdot}89$, $P < 0{\cdot}001$). The grey area indicate the 95% confidence intervals of the nonlinear regression. (c) The percentage of actively foraging females (±SE) related negatively to prey density ($P = 0{\cdot}008$), 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).

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 & Simmons 2006; Smart, Stillman & Norris 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, Sutherland & Norris 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.* 2003). 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.

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Data accessibility

Data available from the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.nd4g8 (Duijns *et al.* 2014a).

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