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de Fouw, Jimmy

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# Structurally complex seagrass obstructs the sixth sense of a specialized avian molluscivore

Jimmy de Fouw, Tjisse van der Heide, Thomas Oudman,  
Leo R. M. Maas, Theunis Piersma and Jan A. van Gils

## ABSTRACT

Predators have evolved many different ways to detect hidden prey by advanced sensory organs. However, in some environmental contexts sensory information may be obscured. The relation between sensory organs, obstruction, and searching efficiency remains little explored. In this study we experimentally examined the ways in which a sensory system ('remote detection'), which enables red knots *Calidris canutus* to detect hard objects buried in wet soft sediments, is obstructed by plants. At an important coastal nonbreeding site of this species, the Banc d'Arguin (Mauritania, West Africa), most of the intertidal foraging area is covered by seagrass. The structurally complex networks of belowground roots and rhizomes and aboveground seagrass may obstruct information on the presence of buried bivalves and thus affect searching efficiency. Under aviary conditions we offered red knots buried bivalves in either bare soft sediments or in seagrass patches and measured prey encounter rates. In seagrass, red knots detected prey by direct touch rather than remotely, the latter which we confirmed they do in bare sediment. Physical modelling of the pressure field build-up around a probing bill showed that within a layer of seagrass rhizomes, permeability is reduced to the extent that the pressure field no longer reveals the presence of an object. In bare sediment, where searching efficiency is constant, red knot intake rate levelled off with increasing prey density (described by a so-called type II functional response). In the seagrass beds, however, prey density increases with seagrass density and simultaneously decreases searching efficiency, which will at some point lead to a decrease in intake rate when prey densities increase (i.e. a type IV functional response). Clearly, prey detection mechanisms dictate that the combined effects of prey density and habitat complexity should be taken into account when predicting forager distributions and habitat preference.

## INTRODUCTION

Insights into the morphology and functionality of sensory organs in animals have contributed to our basic understanding of habitat selection and foraging distribution of animals searching for prey (Miller and Surlykke 2001, Sleep and Brigham 2003, Cunningham et al. 2010, Piersma 2012). Predators have evolved multiple ways to detect their prey other than by sight. For example, bats detect their prey in the dark by ultrasonic signalling (Schnitzler and Kalko 2001), owls use high acoustic sensitivity to detect their prey by sound in the dark (Martin 1986) and cetacean species often use echolocation to detect their prey in the water column (Madsen et al. 2004, Au et al. 2007). Using their sensitive bill tip, shorebirds (Scolopacidae) have evolved a variety of ways to detect prey buried out of sight in soft sediments, including smell, taste, detection of prey vibrations, direct touch and even ‘remote detection’ (Hulscher 1982, Gerritsen and Meiboom 1986, Piersma et al. 1998, Nebel et al. 2005).

In some environmental contexts, sensory information may be obscured. For example, vegetation cover on the water surface obstructs echolocation-based prey detection in insectivorous bats (Boonman et al. 1998), and underwater seagrass meadows may serve as an acoustic refuge for fish from the echolocation sounding by dolphins (Wilson et al. 2013). Yet, the relation between sensory organs, obstruction, and searching efficiency remains rather little explored (Piersma 2011). In this study we experimentally examined whether seagrasses can obstruct prey detection by red knots *Calidris canutus*. Red knots are highly specialized molluscivorous birds that usually forage on bivalves buried in the soft sediments of intertidal mudflats (Piersma 2007, Piersma 2012). Red knots have a sensory organ in the tip of the bill to detect hard-shelled prey buried in soft wet sediments without direct contact (Piersma et al. 1998). As is the case for other shorebirds, the tip of the bill contains numerous tiny pits with clusters of Herbst corpuscles, which in red knots enable the detection of self-induced pressure differences during repeated probing in wet soft sediments. Using this form of ‘remote prey detection’, red knots detect buried prey faster and more efficiently than if they had to rely on direct touch (Piersma et al. 1995, Piersma et al. 1998). A similar mode of prey detection has been described for kiwis (Apterygidae) and ibises (Threskiornithinae) (Cunningham et al. 2007, Cunningham et al. 2009, Cunningham et al. 2010).

This model of prey detection is applicable to red knots foraging on hard-shelled prey in bare soft sediments (Piersma et al. 1995, van Gils et al. 2006). However, at Banc d’Arguin (Mauritania, West Africa), the subspecies *C. c. canutus* mostly encounters and uses seagrass habitats (Altenburg et al. 1982, van Gils et al. 2015). These habitats consist of structurally complex networks of belowground roots, rhizomes and aboveground leaves (Larkum et al. 2006). We hypothesize that searching efficiency, i.e. the standardized rate at which foragers encounter their prey (Holling 1959), will be negatively influenced by these structures, because the remote detection system requires unobstructed passage of water between the sediment particles (Piersma et al. 1998). To test this idea, we measured searching efficiency in red knots by offering them buried prey either in bare sedi-

ment or in seagrass-covered sediment. Here, the bare sediment treatment served as a control to verify whether red knots were able to find prey remotely (Piersma et al. 1998). Additionally, we developed a model to show the obstructing effect of seagrass rhizomes on the pressure field build-up by the probing bill. We will briefly discuss the implications of this effect on the predicted relationship between prey density and intake rate (i.e. the functional response).

## METHODS

### Birds

The experiment was conducted in January 2011 at the research station of the Parc National du Banc d'Arguin, Mauritania, West Africa (19°53'N, 16°17'W). Six red knots were caught with mist nets on a nearby shoreline high-tide roost and colour-ringed for individual identification. All birds were successfully released after the experiments. Average bill length was 35.1 mm (range 33.6–37.0 mm) and body mass just after catching was 129 g (range 118–144 g). Birds were kept as a group in a small aviary (2.0 × 0.6 and × 0.4 m high) with sand on the floor, freshwater *ad libitum*, and with local natural day-light cycles and temperatures (varying between 18 and 24°C). Every morning, the birds were weighed and their health status assessed. Birds were fed commercial trout feed (Trouvit; Skretting, Stavanger, Norway) and live bivalves that were collected locally on a daily basis. To keep birds motivated to feed during the trials, daily portions were adjusted to keep body mass just above 100 g (e.g. Oudman et al. 2014, van Gils and Ahmedou Salem 2015).

### Experimental design

Feeding trials were conducted in the housing cage, in which a feeding patch (10 cm depth and 15 cm radius) was created with either bare sediment or seagrass (Figure 6.1C-E). *Loripes lucinalis* (8.5–10.5 mm length), the most common bivalve in our study area (Honkoop et al. 2008), was used as prey. Per patch, either 20 or 40 prey items were offered (283 and 566 ind. m<sup>-2</sup>). All prey were buried at a fixed depth at either 1, 2 or 3 cm. For practical reasons all trials of each combination were offered in the same patch in which prey items were replaced after each trial. All density and depth combinations were offered twice to each bird (although never on the same day). Densities and depth of bivalve prey were well within the range reported for the field (Piersma et al. 1993, van der Geest et al. 2011, van Gils et al. 2013, Ahmedou Salem et al. 2014, van Gils et al. 2015). Patches were filled with sand (mean medium grain size ± SE (n = 6): 248.0 ± 2.7 µm) collected at the nearby intertidal beach (19°53.026'N, 16°17.573'W). Penetrability of the seawater-saturated sand was kept constant by adding seawater till 2 mm of water remained on top of the surface.

Seagrass was collected on a tidal flat (19°53.051'N, 16°17.367'W) 500 m east of the field station. Seagrass densities were within the range reported from the field (range:

2,200–13,000 shoots  $\text{m}^{-2}$ ) (van Lent et al. 1991, Vermaat et al. 1993). A 15-cm high sharpened PVC ring (15 cm radius) was pushed gently into the seagrass (mean shoot density  $\pm$  SE ( $n = 5$ ):  $8,842 \pm 700 \text{ m}^{-2}$ ). The ring with the seagrass bed was taken out. Metal pins were pushed in horizontally from the side of the ring through the seagrass rhizome mat forming a  $2.5 \times 2.5$  cm mesh holding the seagrass mat intact. Next, the sediment was carefully sieved out, a time-consuming process that was needed to remove all prey living in the seagrass in order to be able to offer precise experimental prey densities. Eventually, a ‘clean’ intact seagrass mat (rhizomes, roots and leaves) remained in the ring, which was then placed in a 15-cm radius, 10-cm high container, thereafter filled with wet sand, after removing the metal pins. Next, a plastic rod with a scale was used to insert prey in their natural position into the sediment at the aimed depth, at random spatial positions. The hole was filled and the sand was smoothed (Piersma et al. 1995, Piersma et al. 1998).

After a trial ended, the remaining prey items were counted. We never noticed prey movements or any other signs of their presence (i.e. the bivalves showing a siphon or extending a foot). Each trial was conducted with one individual bird at a time, with each bird being involved in at least one trial per day. Within each combination offered on a given day, the order of the birds in the trials was randomly chosen by rolling a dice. The five remaining birds were held in a separated part of the cage such that they were in vocal and visual contact with the experimental bird. A trial stopped after six prey items were encountered or after 15 minutes.

### Searching efficiency and touch model

A digital video camera (CANON Powershot G9) recorded each trial. Timing of prey encounters and ingestions were scored digitally with Etholog (Ottoni 2000), and the recordings were played back in slow motion to confirm that we had not missed a prey encounter. In a randomly-searching forager, the interval between two prey encounters, search time ( $T_s$ ), is inversely related to the product of searching efficiency ( $a$ ) and current prey density ( $D$ ; initial prey density minus the number of prey removed (van Gils et al. 2003)):

$$\frac{1}{T_s} = aD \quad (1)$$

which can be rewritten as:

$$\log(T_s) = -\log(a) - \log(D) \quad (2)$$

In this relationship, a slope of -1 indicates random search, while the intercept,  $-\log(a)$ , reflects the negative of searching efficiency (Piersma et al. 1995, van Gils and Piersma 2004). A searching efficiency that does not vary with prey density, together with a handling time that is constant across prey densities, leads to Holling’s type II functional response (Holling 1959). In this well-known equation, the intake rate of a forager

increases as a function of prey density, initially at a rate given by searching efficiency until it levels off due to the handling time constraint. Hence, when red knots use remote prey detection the functional response has a steeper slope than in comparison with direct touch (Piersma et al. 1995).

To test to what extent red knots remotely detect buried prey, we compared the experimentally observed searching efficiency with the calculated searching efficiency based on a direct touch model (see for details Hulscher 1982, Zwarts and Blomert 1992, Piersma et al. 1995). We predicted a strong relation with prey depth for the observed searching efficiencies in seagrass, following the touch-model (Piersma et al. 1995). The touch-model was determined with the touch area of the prey (surface projection of prey area), enlarged by the surface area of the bill tip multiplied by the probe rate at each depth (1-cm classes) (Appendix A6) (Zwarts and Blomert 1992). Probe rates were scored during five time intervals (ca.10 s) for a selection of trials (all six birds equally distributed over the two habitat-treatments and three prey depths,  $n = 36$ ), by slowing down digital video recordings (1/8th of the recording speed). Probe depth was measured five times in each interval by freezing the digital video image at a probe's maximum depth and using an individual's bill length as a reference.

### Statistics

Average search- and handling times (each denoted by  $Y_i$ ) were calculated for every trial, with individual bird as random effect ( $bird_i$ ):

$$\log(Y_i) = \alpha + \beta_1 \text{prey depth}_i + \beta_2 \log(\text{prey density}_i) + \text{habitat}_i + \text{bird}_i + \varepsilon_i$$

where  $\varepsilon_i \sim N(0, \sigma^2)$ .

Search and handling times were log-transformed to meet model assumptions (when Holling's type II functional response holds then the predicted values for  $\beta_2$  are  $-1$  and  $0$  for search time and handling time, respectively). We used a one-sample t-test for difference between observed- and the estimated (touch-model) searching efficiency. All statistical analyses were done in R (package *nlme* for mixed-effect models) (R Development Core Team 2014).

### The physical model

We developed a physical model to get mechanistic insight into how seagrass may obstruct the remote detection of red knots (for mathematical descriptions see Box 6.1). Observations and experiments by Piersma et al. (1998) showed that knots are able to remotely sense the presence of shells in wet bare sediment, and that their sensory capacity fails in dry but also in very liquid mud. However, a belowground seagrass mat, consisting of a network of roots and rhizomes, reduces the sediment layer's permeability. This may reduce the effective porosity of the soil and obstructs the pressure field build-up by the probing bill of red knots. We will consider first the response to a shell in a mud layer

without rhizomes mat, qualitatively discussed in Piersma et al. (1998). Second, the response to a shell buried in the lower layer containing the rhizomes mat.

The probing of the bill will produce pressure variations in wet sediment (pore-size 180  $\mu\text{m}$ ). Red knots rapidly probe in the sediment over a depth of about 0.5 to 1 cm, usually in series of five to 10 probes at a rate of about 6–9 Hz (Piersma et al. 1998). The property of the medium at hand determines in what way it responds to pressure variations. In dry sediments it can either be supported by normal stresses (pressure) in the rigid sediment structure, or be released instantaneously when it surpasses a certain threshold. In fluids, on the other hand, the pressure cannot be built up, as it will immediately respond by means of flows and of waves on the water surface that will quickly remove the added energy towards infinity (see Box 6.1). In wet sediment, however, there is enough water in the pores to produce a flow through it driven by pressure differences. But as the pores are tiny channels whose sides exert a drag on the flow along them, this local increase in pressure needs time to relax and can be maintained for a while, which is the property employed by the birds.

The classical description of flow through wet sediment is one in which the pressure gradient is balanced by friction, proportional to the flow velocity. Because of the complexity of the sand skeleton this is necessarily an empirical relation, known as Darcy's law (e.g. Sleath 1984). Since the fluid is nearly incompressible, this implies the pressure field is governed by a Poisson equation (Lamb 1932) (see for details Box 6.1).

The knot's sense of remote prey detection involves repetitive, shallow probing, followed by a single deep probe in another direction, apparently used to build up of residual pressure near the bill tip. Very likely, compaction is of dominating influence. This refers to the continuous increase in residual pore pressure, owing to the 'shaking' of the muddy sand by the probing action of the bill, which may lead to a (local) compaction of sediment due to a rearrangement of sand grains in closer packing and an associated increase in pore pressure. This process plays a dominant role in liquefaction and the formation of quick sand (Sleath 1984). For red knots, the important aspects of this are that also the residual (i.e. time-averaged) pressure pattern is affected by the presence of a shell and that this pattern becomes increasingly 'visible' due to its increase at each successive cycle of the probing motion. Together with the directionality offered by the set of pressure sensors (Herbst corpuscles), present over the whole circumference of the bill, this should offer the knot the ability to sense both prey direction and distance (for details see Box 6.1).

For red knots, when foraging in seagrass, however, the permeability of the lower rhizomes layer will be less than that of the upper mud layer. This is due to the decrease in the effective porosity of the sediment. We will assume that the rhizome root structure is so small that we can represent its presence in the form of a reduced effective permeability which will affect the radial pressure distribution discussed above. For simplicity, we assume the permeability to be constant within the rhizome layer. Hence the pressure will again be inversely proportional to radial distance, but with reduced 'transmitted' amplitude. In fact, the semi-permeable interface between the mud and rhizome layers acts as a partial mirror. This will result in an augmented pressure field in the upper sediment layer.



### Ethical note

All possible efforts were made to minimize physical and mental impact on the experimental animals. Each bird was weighed and visually inspected for general condition daily. All experimental animals were released in the wild in healthy condition after the experiment with an average body mass of 147 g (range 136–160 g) after two days of *ad libitum* food. The experiment was performed under full permission by the authorities of the PNBA. No animal experimentation ethics guidelines exist in Mauritania but the experiments were performed in accordance with Dutch animal experimentation guidelines. The NIOZ Royal Netherlands Institute for Sea Research has been licensed by the Dutch Ministry of Health to perform animal experiments under licence number 80200.

## RESULTS

### Searching efficiency and Holling's type II functional response

Search time decreased with increasing prey density with an estimated slope  $-0.947$  (95% confidence interval: lower  $-1.172$ ; upper  $-0.722$ ) which did not differ from  $-1$  (i.e. random search), showing that searching efficiency was independent of prey density (Table 6.1). Likewise, handling time was independent of prey density (Table 6.1). Thus, both assumptions of Holling's type II equation were met. Searching efficiency differed significantly between bare sediment and seagrass and decreased with depth (Table 6.1) in both habitat treatments, with the decrease being stronger in seagrass than in bare sediment (significant interaction between depth and habitat treatments: Table 6.1, Figure 6.1A). Handling time increased significantly with prey depth in both habitat treatments and was higher in the seagrass ( $1.01 \pm 0.05$  s; mean  $\pm$  SE) than in the bare patches ( $0.82 \pm 0.05$  s) (Table 6.1, Figure 6.1B).

### Touch-model

There was a significant effect of depth on the probe rate (Table 6.2), but no an effect of habitat treatment (bare sediment versus seagrass) or of prey density (Table 6.2). In bare sediment, there was a significant difference between the predicted searching efficiency based on the touch model and the observations (Figure 6.1A; at 1 cm:  $\text{difference}_{\text{obs-pred}} = -1.58 \text{ cm}^2 \text{ s}^{-1}$ ,  $t_{23} = -2.98$ ,  $P < 0.01$ ; at 2 cm:  $4.30 \text{ cm}^2 \text{ s}^{-1}$ ,  $t_{24} = 5.98$ ,  $P < 0.001$ ; at 3 cm:  $3.52 \text{ cm}^2 \text{ s}^{-1}$ ,  $t_{23} = 11.22$ ,  $P < 0.001$ ). In seagrass, however, the predicted searching efficiency based on a touch-model did not differ from the observations when prey were buried at greater depths (Figure 6.1A; at 1 cm:  $\text{difference}_{\text{obs-pred}} = -3.78 \text{ cm}^2 \text{ s}^{-1}$ ,  $t_{23} = -5.31$ ,  $P < 0.001$ ; at 2 cm:  $-0.16 \text{ cm}^2 \text{ s}^{-1}$ ;  $t_{22} = -1.53$ ,  $P = 0.14$ ; at 3 cm:  $0.11 \text{ cm}^2 \text{ s}^{-1}$ ,  $t_{24} = -0.84$ ,  $P = 0.41$ ) (observed estimates: bias-corrected back-transformed; Sprugel 1983). This implies that red knots were unable to use remote detection when foraging in seagrass.

**Table 6.1** Mixed-effect model of the log-transformed search time, searching efficiency and handling time. Models include fixed effects prey depth (continuous), prey density (continuous), habitat (categorical; seagrass or bare sediment) and individual bird as random effect.

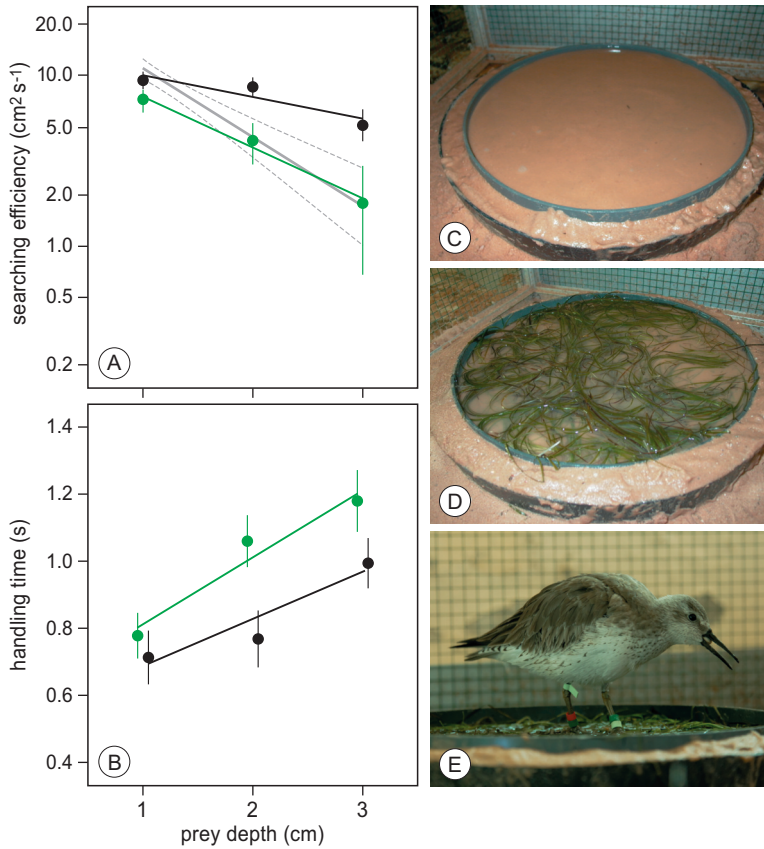
| Search time (s)         | Estimate                     | SE    | <i>t</i> | <i>P</i> |
|-------------------------|------------------------------|-------|----------|----------|
| <b>Fixed effects</b>    |                              |       |          |          |
| Intercept               | -0.983                       | 0.172 | -5.725   | <0.0001  |
| prey depth (1, 2, 3 cm) | 0.135                        | 0.030 | 4.535    | <0.0001  |
| habitat (seagrass)      | -0.024                       | 0.091 | -0.261   | 0.773    |
| prey density            | -0.945                       | 0.114 | -8.320   | <0.0001  |
| habitat × prey depth    | 0.170                        | 0.042 | 4.053    | <0.001   |
| <b>Random effects</b>   |                              |       |          |          |
| Individual bird         | 1.20 × 10 <sup>-5</sup> (sd) |       |          |          |
| Residual                | 0.202 (sd)                   |       |          |          |

| Searching efficiency (cm <sup>2</sup> s <sup>-1</sup> ) | Estimate   | SE    | <i>t</i> | <i>P</i> |
|---|------------|-------|----------|----------|
| <b>Fixed effects</b>                                    |            |       |          |          |
| Intercept   | 1.111      | 0.065 | 16.961   | <0.0001  |
| prey depth (1, 2, 3 cm)                                 | -0.135     | 0.030 | -4.517   | <0.0001  |
| habitat (seagrass)                                      | 0.026      | 0.091 | 0.290    | 0.773    |
| habitat × prey depth                                    | -0.172     | 0.042 | -4.061   | <0.001   |
| <b>Random effects</b>                                   |            |       |          |          |
| Individual bird   | 0.015 (sd) |       |          |          |
| Residual  | 0.209 (sd) |       |          |          |

| Handling time (s)       | Estimate   | SE    | <i>t</i> | <i>P</i> |
|-------------------------|------------|-------|----------|----------|
| <b>Fixed effects</b>    |            |       |          |          |
| Intercept               | -0.351     | 0.065 | -5.388   | <0.0001  |
| prey depth (1, 2, 3 cm) | 0.095      | 0.016 | 5.872    | <0.0001  |
| habitat (seagrass)      | 0.097      | 0.049 | 1.984    | <0.05    |
| prey density            | -0.001     | 0.001 | -1.373   | 0.172    |
| habitat × prey depth    | 0.001      | 0.022 | 0.011    | 0.992    |
| <b>Random effects</b>   |            |       |          |          |
| Individual bird         | 0.135 (sd) |       |          |          |
| Residual                | 0.111 (sd) |       |          |          |



**Figure 6.1** (A) Searching efficiency as a function of prey depth of knots foraging on prey in bare (black) and seagrass (green) habitat. The grey lines indicate the touch-model with confidence interval (95%). (B) Prey handling time as a function of prey depth of knots foraging on prey in bare (black) and seagrass (green) habitat. (C) Bare patch, (D) seagrass patch, (E) knot swallowing a prey during an experimental trial on a seagrass patch.

### The physical model

The physical model shows that the pressure patterns produced by the probing knot's bill, located at the interface between air and sediment, and the flow through the pores, driven by pressure differences, is influenced by the presence of a spherical shell deeper in the sediment (Figure 6.2A). The imposed pressure gradient is displayed by a spherically symmetric radial decay decreasing from high pressure to low pressure. The isobars are obstructed in the vicinity of the shell (Figure 6.2A). The pressure pattern induced by the presence of the shell is defined by subtracting the response of the initial pulse with the spherical shell in place and without the shell in place. It is this difference that we argue is sensed and informs the knot about the presence of a prey, at some radial distance and direction (Figure 6.2B). When the spherical shell is situated within an infinite rhizomes

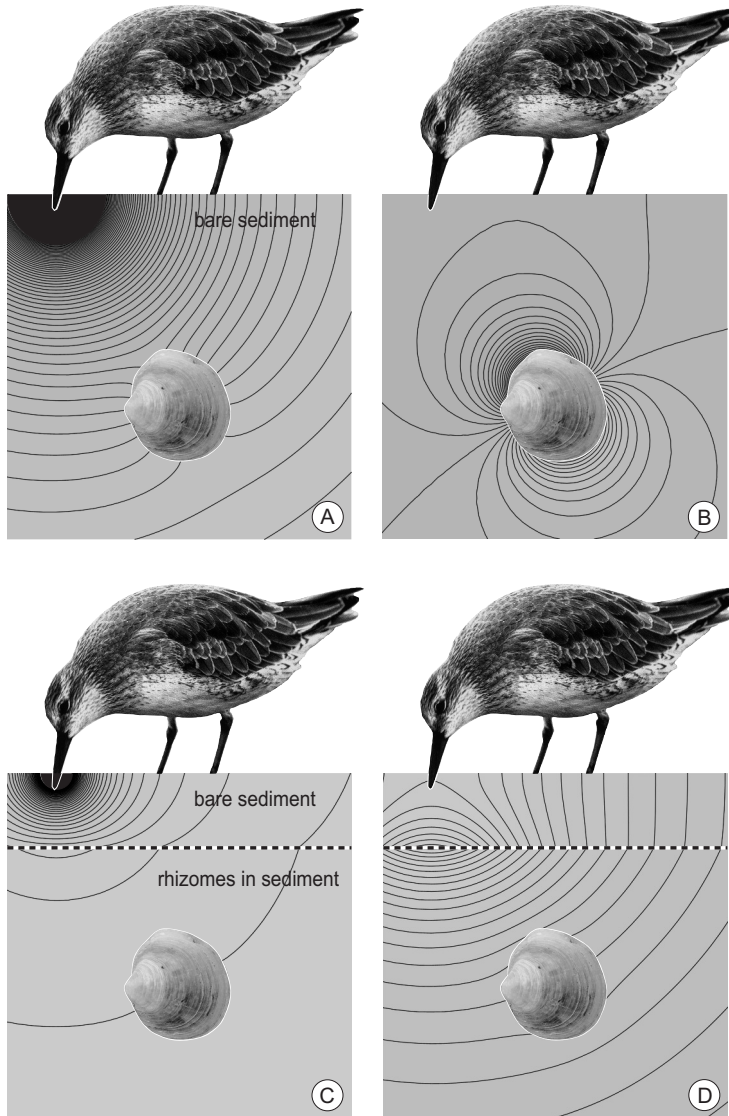
layer, which reduces the permeability, the rhizomes layer changes the apparent strength of the source at the origin. The change in the pressure field at the interface between wet sediment and rhizomes layer is clearly visible in a changing isobar inclination (Figure 6.2C). When we again subtract the response pulse with the spherical shell in place and without the shell in place, it shows that the pressure field no longer reveals the presence of the shell. The pressure difference is very nearly symmetric at the bill tip, at the origin, and no longer offers any clues on the direction (nor distance) at which the prey can be found (Figure 6.2D).

**Table 6.2** Mixed-effect model of probe rate, with fixed effects prey depth (continuous), prey density (continuous), habitat (categorical; seagrass or bare sediment) and individual bird as random effect.

| Probe rate ( $s^{-1}$ ) | Estimate   | SE    | <i>t</i> | <i>P</i> |
|-------------------------|------------|-------|----------|----------|
| <b>Fixed effects</b>    |            |       |          |          |
| Intercept               | 15.277     | 1.401 | 10.882   | <0.0001  |
| prey depth (1, 2, 3 cm) | -4.977     | 0.397 | -12.548  | <0.0001  |
| habitat (seagrass)      | 1.562      | 0.916 | 1.705    | 0.1      |
| prey density            | -0.032     | 0.049 | -0.654   | 0.512    |
| <b>Random effects</b>   |            |       |          |          |
| Individual bird         | 1.062 (sd) |       |          |          |
| Residual                | 1.946 (sd) |       |          |          |

## DISCUSSION

Searching efficiency of red knots foraging in seagrass was much lower than when foraging in bare sediment, especially for prey buried at greater depths, and was better explained by the touch model than by remote detection (Figure 6.1A). The present estimates of searching efficiency on bare sediment were similar to previous estimates ( $5.8 - 26.2 \text{ cm}^2 \text{ s}^{-1}$ ) (Piersma et al. 1995, van Gils and Piersma 2004). Nevertheless, we found a small negative effect of depth in bare sediment, an effect not found by Piersma et al. (1995). However, as searching efficiencies in bare sediment were higher than predicted by the touch model, and were quantitatively in line with previous estimates, we conclude that red knots used remote prey detection in bare sediment at all depths (Figure 6.1A). Our finding of the low searching efficiencies (even lower than in the direct touch model) at the shallower prey depths (Figure 6.1A) is probably the result of invisible prey rejections below ground. Searching efficiency is derived from number of prey encountered, so that when prey are detected but rejected below ground without being noticed by the observer, searching efficiency will be underestimated (Wanink and Zwarts 1985, Piersma et al. 1995, van Gils et al. 2015). This bias is likely to become more systematic at high



**Figure 6.2** (A) The pressure field build-up by the bill of the knot in bare wet sediment of a hypothetical mudflat. The imposed pressure gradient is displayed by a spherically symmetric radial decay decreasing from high pressure (densely packed isobars near bill tip) to low pressure (wider spaced isobars to right). (B) The isobars are obstructed in the vicinity of the shell, and the disturbance pressure field (shown here) is sensed and informs the knot about the presence of a prey, in the form of radial distance and direction. (C) When the spherical shell is situated within an infinite rhizome layer (below the interface between bare wet sediment and infinitely deep rhizome layer, dashed line), which reduces the permeability, the rhizome layer changes the apparent strength of the source at the origin. The change in the pressure field at the interface between wet sediment and rhizomes= layer is visualized by a changing isobar inclination. (D) Here, the pressure difference is nearly symmetric at the bill tip, at the origin, and no longer offers any clues on the direction (or distance) at which the prey can be found (for details see Box 6.1).

prey densities or at shallow depths when prey are more easily found (Wanink and Zwarts 1985; T. Piersma, personal observation).

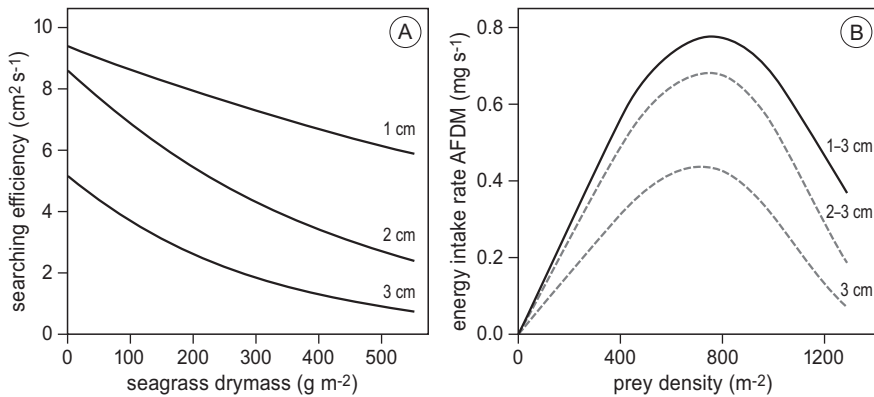
Handling time increased with prey depth and was higher in seagrass, an effect which was also found by Piersma et al. (1995). In addition, handling time increased more strongly with depth in seagrass which may well be caused by the difficulty for red knots of pulling a prey out of a dense network of rhizomes. The average handling time was  $0.92 \pm 0.04$  s, which is close to a mean handling time of 0.7 s measured in the field (van Gils et al. 2015).

Why do red knots lose their ability to remotely detect hard-shelled prey when foraging in seagrass? The outcome of the physical model shows that when the spherical shell is situated within a layer of rhizomes, the permeability of this substrate is reduced; the pressure field is changed at the interface between the sediment and the rhizomes (Figure 6.2C). This overwhelms the much weaker pressure difference due to the reflection by the shell and obscures the directional prey information. Therefore, red knots can no longer rely on their remote detection to encounter the hard-shelled prey 'hidden' by the rhizome layer. It also falsely suggests the presence of a prey item at a certain distance right below the bill tip. This indicates that, relative to the vertical, the angular spread of successful deep probes of knots feeding over a rhizome mat should be significantly less than that over a mud layer without a rhizome mat, a hypothesis that deserves testing in future work (see a detailed discussion on the sensitivity of the pressure gradient to the permeability in Box 6.1). All of the pressure differences, of course, also depend on the actual change in permeability due to the rhizomes mat, on the location of that layer and on its depth (here assumed to be of infinite extent). But the dramatic change in the pressure difference that we see because of the rhizome layer (compare Figure 6.2B and 2D) will not depend too much on these details.

### **Implications for predictions on intake rates and habitat use**

Insights into nonvisual sensory systems may give tantalizing opportunities to actually predict habitat selection rules and even foraging distributions (van Gils et al. 2006, Cunningham et al. 2010, Piersma 2011, Piersma 2012). In this study, the remote detection ability of red knots was obstructed by seagrass resulting in decreased searching efficiencies, an important parameter to predict intake rates with a functional response. The functional response is a commonly accepted function to predict spatial distributions and habitat use of foragers (Stephens and Krebs 1986, Piersma et al. 1995, van Gils et al. 2015). However, in bare sediment, where searching efficiency is a constant, red knots obey the assumptions of Holling's type II functional response, implying that intake rate in relation to prey density levels off at high prey densities (this study, Holling 1959, Piersma et al. 1995). Based on our experimental- and physical model results we will argue below that in seagrass beds the relation between intake rate and prey density will be dome-shaped (so called type IV functional response; Holling 1961, Jeschke and Tollrian 2007), implying that above a certain prey density, the intake rate goes down with increasing prey density.

It is known that seagrass has a positive effect on prey density and abundance (Orth et al. 1984, Honkoop et al. 2008, van Gils et al. 2015). In Banc d'Arguin, seagrass and lucinid bivalve densities are tightly linked due to their mutualistic relationship (van der Heide et al. 2012). While at first sight the increase in prey density would be an advantage for knots, 'simultaneously' increasing seagrass density leads to decreasing searching efficiency (Figure 6.3A). Hence, with an increasing seagrass biomass, the searching efficiency decreases faster than the increase in prey densities, so that the functional response will become dome-shaped, and this goes for all depth distributions (Figure 6.3B) (see mathematical details in Appendix A6).



**Figure 6.3** (A) Observed searching efficiency versus seagrass density based on experimental results at different prey depths. (B) The predicted functional responses by red knots, cumulative across all prey depths within the experiments (1–3 cm), and cumulative across the two deepest layers (2–3 cm) and for the deepest layer (3 cm). Depth-specific prey density fractions from the field were adapted from Piersma et al. (1993). The horizontal line boxplot shows the median value, the bottom and top of the box show the 25th and 75th percentiles (middle 50% of the data), respectively, whiskers show 1.5 times the interquartile range of the data.

Thus, on the Banc d'Arguin, red knots encounter high searching efficiencies at low prey densities in little or no seagrass, and low searching efficiencies with high prey densities in dense seagrass beds. This shows that in seagrass habitats knots may maximize intake rates by feeding on intermediate prey densities and moderately dense seagrass beds (which is indeed what has been found by van Gils et al. 2015). In other words, in this case the functional response may not be a simple function of prey density but also of seagrass density. Note that in herbivores a type IV response is commonly observed, often because digestive quality decreases with increasing biomass (Fryxell 1991, Heuermann et al. 2011). However, in predator-prey interactions a type IV functional response has not received much attention. Only a handful of recent studies have shown that density-dependent defences, and nutritional quality of the prey, lead to a decline in intake rate at high prey densities (Vucic-Pestic et al. 2010, Bressendorff and Toft 2011, Liznarova and

Pekar 2013, Bijleveld et al. 2016), again suggesting that in many foraging contexts animals should aggregate at intermediate prey densities.

In the Wadden Sea, spatial prediction of foraging red knots was better with than without the refinement of the functional response based on remote (Piersma et al. 1995). In seagrass beds, when seagrass-dependent searching efficiency is not taken into account this may lead to an overestimation of intake rates at high prey densities. The notion of a seagrass-dependent searching efficiency offers a quantitative working hypothesis for future research in diet and habitat preference of red knots foraging on seagrass-covered ecosystems.

### **ACKNOWLEDGMENTS**

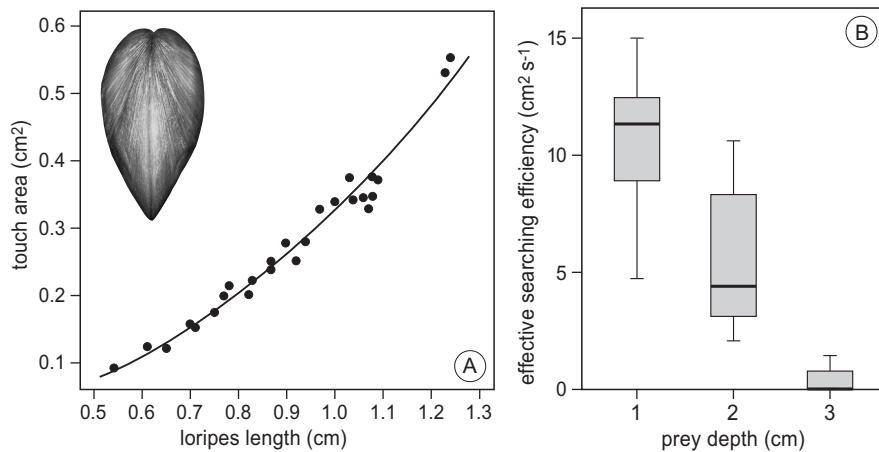
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## APPENDIX A6

**Determination of the effective touch area of the prey**

To calculate the *effective* touch area we need to determine the touch area of the prey, because the probability of prey being touched depends on the surface area of the prey, measured in the horizontal plane (Zwarts and Blomert 1992). The touch area, determined from digital pictures of *Loripes*, is an allometric function of shell length ( $n = 27$ ; see inset of *Loripes* touch area, Figure A6.1A) and was analyzed with a nonlinear model based on least-squares estimates (function nls) (Figure A6.1). Red knots probe with a slightly opened bill, apparently to increase the effective touch area (Zwarts and Blomert 1992, Piersma et al. 1998). Therefore, the touch area is enlarged by the average surface area of the bill tip of the red knot, with:  $t$  (thickness of bill) = 0.3 cm and  $w$  (width of bill) = 0.7 cm (bill parameters taken from: Zwarts and Blomert 1992). The effective touch area is written as:  $wt + 2wr + 2tr + \pi r^2$ , with  $r$  derived from the average touch area from this study based on the allometric function with average prey length of 0.9 cm used in the experiment, see Zwarts and Blomert (1992) for details. Finally, the effective searching efficiency ('touch model') was calculated by multiplying the effective touch area by the effective probe rate at each depth (1-cm classes) (Figure A6.1B).



**Figure A6.1** (A) Touch area as a function of shell length:  $10^a \times L^b$ . ( $a = -0.486 \pm \text{SE } 0.006$ ,  $t = -84.36$ ,  $P < 0.001$ ,  $b = 2.145 \pm 0.083$ ,  $t = 25.88$ ,  $P < 0.001$ ). Average shell length  $L$  in the experiments was 0.9 cm. (B) Estimated searching efficiency based on the touch-model.

**Functional response**

To investigate how searching efficiency affects intake rates (IR) of knots, we integrated the seagrass density dependent searching efficiency into the type II functional response where  $h$  is the constant handling time of the prey (s),  $a$  is the constant searching efficiency ( $\text{m}^2 \text{s}^{-1}$ ) and  $D$  is the prey density ( $\text{no. m}^{-2}$ ):

$$IR = \frac{aD}{1 + aDh}$$

Because searching efficiency is negatively dependent on seagrass density and decreases with prey depth (Figure 6.3A) and prey density increases with seagrass density, we introduced a dynamic searching efficiency  $A(S)$  that is negatively related to seagrass density  $S$ :

$$IR = \frac{A(S)D(S)}{1 + A(S)D(S)h}$$

We described the relation between searching efficiency and prey density by the exponential function  $A(S) = A(S=0) e^{-cS}$ , where the constant  $c$  and  $A(S=0)$  (the searching efficiency on bare sediment) are fitted to the results of this study. Because the detectability of the prey is depth-dependent, all parameters were estimated for all three depth classes separately by a nonlinear model based on least-squares estimates (function *nls* in R, Figure 6.3A) (R Development Core Team 2014). The relationship between prey density and seagrass biomass was recently quantified non-linearly dependent on seagrass ( $D(S) = 256.6 S^{0.24}$ ; chapter 6). We use depth-specific prey density fractions from the field (based on: Piersma et al. 1993) and average energy content of the most common bivalve species, *Loripes* and *Dosinia isocardia*: 7.28 and 2.57 mg AFDM<sub>flesh</sub> (van Gils et al. 2012). The estimated amount of energy gained based on the functional response becomes dome-shaped and the effect becomes stronger with prey depth (Figure 6.3B).

