Structurally complex sea grass obstructs the sixth sense of a specialized avian molluscivore

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Predators have evolved many different ways to detect hidden prey by using 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 sea grass. The structurally complex networks of belowground roots and rhizomes and aboveground sea grass 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 sea grass patches and measured prey encounter rates. Red knots detected prey by direct touch in sea grass but remotely in bare sediment. Physical modelling of the pressure field build-up around a probing bill showed that within a layer of sea grass 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 sea grass beds, however, prey density increases with sea grass 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.

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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 (Cunningham et al., 2010; Miller & Surlykke, 2001; Piersma, 2012; Sleep & Brigham, 2003). 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 &

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 (Au, Benoit-Bird, & Kastelein, 2007; Madsen, Kerr, & Payne, 2004). 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' (Gerritsen & Meiboom, 1986; Hulscher, 1982; Nebel, Jackson, & Elner, 2005; Piersma, van Aelst, Kurk, Berkhoudt, & Maas, 1998).

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

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(Boonman, Boonman, Bretschneider, & van de Grind, 1998), and underwater sea grass meadows may serve as an acoustic refuge for fish from echolocation sounding by dolphins (Wilson, Wilson, Greene, & Dunton, 2013). Yet, the relation between sensory organs, obstruction and searching efficiency remains little explored (Piersma, 2011). In this study we experimentally examined whether sea grasses 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, 2012). They 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., 1998; Piersma, van Gils, de Goeij, & van der Meer, 1995). A similar mode of prey detection has been described for kiwis (Apterygidae) and ibises (Threskiornithinae) (Cunningham et al., 2010; Cunningham, Castro, & Alley, 2007; Cunningham, Castro, & Potter, 2009).

This model of prey detection is applicable to red knots foraging on hard-shelled prey in bare soft sediments (van Gils, Spaans, Dekinga, & Piersma, 2006; Piersma et al., 1995). However, at Banc d'Arguin (Mauritania, West Africa), the subspecies *C. c. canutus* mostly encounters and uses sea grass habitats (Altenburg, Engelmoer, Mes, & Piersma, 1982; van Gils et al., 2015). These habitats consist of structurally complex networks of belowground roots and rhizomes and aboveground leaves (Larkum, Orth, & Duarte, 2006). We hypothesized 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 sediment or in sea grass-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 sea grass rhizomes on the pressure field build-up by the probing bill. We 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 m and 0.4 m high) with sand on the floor, freshwater ad libitum, and with local natural daylight 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. van Gils & Ahmedou Salem, 2015; Oudman et al., 2014).

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 sea grass (Fig. 1c–e). *Loripes lucinalis* (8.5–10.5 mm length), the most common bivalve in our study area (Honkoop, Berghuis, Holthuijsen, Lavaleye, & Piersma, 2008), was used as prey. Per patch, either 20 or 40 prey items were offered (283 and 566 individuals/m²). 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 depths of bivalve prey were well within the range reported for the field (Ahmedou Salem, van der Geest, Piersma, Saoud, & van Gils, 2014; van der Geest, van Gils, van der Meer, Olff, & Piersma, 2011; van Gils et al., 2015; van Gils et al., 2013; Piersma, de Goeij, & Tulp, 1993). Patches were filled with sand (mean medium grain size $\pm$ 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 sea water-saturated sand was kept constant by adding sea water until 2 mm of water remained on top of the surface.

Sea grass was collected on a tidal flat (19°53.051′N, 16°17.367′W) 500 m east of the field station. Sea grass densities were within the range reported from the field (range 2200–13 000 shoots/m²; van Lent, Nienhuis, & Verschuure, 1991; Vermaat et al., 1993). A 15 cm high sharpened PVC ring (15 cm radius) was pushed gently into the sea grass (mean shoot density $\pm$ SE ($N = 5$): 8842 ± 700 per m²). The ring with the sea grass bed was taken out. Metal pins were pushed in horizontally from the side of the ring through the sea grass rhizome mat forming a 2.5×2.5 cm mesh holding the sea grass mat intact. Next, the sediment was carefully sieved out, a time-consuming process that was needed to remove all prey living in the sea grass in order to be able to offer precise experimental prey densities. Eventually, a 'clean' intact sea grass 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, 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 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 separate 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 min.

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;