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A new pressure sensory mechanism for prey detection in birds: the use of principles of seabed dynamics?

Theunis Piersma[1,2*], Renée van Aelst[1,3], Karin Kurk[1,4], Herman Berkhoudt[4] and Leo R. M. Maas[5]

[1]*Department of Marine Ecology, Netherlands Institute for Sea Research (NIOZ), PO Box 59, 1790 AB Den Burg, Texel, The Netherlands*
[2]*Centre for Ecological and Evolutionary Studies (CEES), University of Groningen, PO Box 14, 9750 AA Haren, The Netherlands*
[3]*Department of Animal Sciences, University of Illinois, 1207 West Gregory Drive, Urbana, IL 61801, USA*
[4]*Institute of Evolutionary and Ecological Sciences (IEEW), Leiden University, PO Box 9516, 2300 RA Leiden, The Netherlands*
[5]*Department of Physical Oceanography, Netherlands Institute for Sea Research (NIOZ), PO Box 59, 1790 AB Den Burg, Texel, The Netherlands*

We demonstrate a novel mechanism for prey detection in birds. Red knots (*Calidris canutus*), sandpipers that occur worldwide in coastal intertidal areas, are able to detect their favourite hard-shelled prey even when buried in sand beyond the reach of their bills. In operant conditioning experiments designed to find out whether the birds could tell buckets containing only wet sand from buckets containing hard objects in wet sand, we show that they detect the presence not only of deeply buried live bivalves but also of stones. The latter finding virtually excludes, under experimental conditions, prey-detection mechanisms based on vision, acoustics, smell, taste, vibrational signals emitted by prey, temperature gradients and electromagnetic fields. A failure to discriminate between food and non-food trays with dry sand indicates that pore water is involved. Based on the presence of large arrays of Herbst corpuscles (sensory organs that can measure the acceleration due to changes in pressure), the specifics of foraging technique and the characteristics of sediments on which red knots feed, we deduce that the sensory mechanism involves the perception of pressure gradients that are formed when bills probe in soft sediments in which inanimate objects block pore water flow. To our knowledge, this mechanism has not been described before. It is argued that repeated probing in soft, wet sediments allows red knots to induce a residual pressure build-up of sufficient strength to detect the pressure disturbance caused by a nearby object. The cyclic process of shaking loosely packed sand grains followed by gravitational settling into a closer packing, leads, owing to insufficient drainage of the sediment, to a locally increased pressure disturbance that is 'pumped up' at each shake.

Keywords: sensory ecology; operant conditioning; foraging; mechanoreceptor; hydrodynamics

1. INTRODUCTION

Invertebrates living out of sight, buried in soil or soft sediments, still run the risk of detection and capture by above-ground predators. Terrestrial birds like thrushes use auditory cues to detect the subsurface presence of worms (Montgomerie & Weatherhead 1997). On intertidal flats, probe-feeding shorebirds such as oystercatchers detect buried bivalves by direct touch (Hulscher 1982). Sandpipers of the genus *Calidris* probe in the sand and detect actively moving invertebrates by their vibrations (Gerritsen & Meijboom 1986). Among the sandpipers, the red knot, *Calidris canutus*, is a special case (Piersma *et al.* 1996). Although red knots do eat moving invertebrates on their high arctic tundra breeding grounds, they only take surface-living arthropods detected visually. Red knots spend the rest of the year in coastal areas, where they feed almost uniquely on molluscs and hard-shelled crustaceans (Piersma & Davidson 1992; Piersma 1994). Prey may be pulled loose from exposed parts of the rocky intertidal zones (Summers & Smith 1981; González *et al.* 1996), but most red knots forage on intertidal flats by probing in soft sediments (Zwarts & Blomert 1992; Piersma *et al.* 1993*a*). Prey items are ingested whole, crushed in their heavy and strong gizzard, and the shell fragments are excreted in compact faecal pellets (Dekinga & Piersma 1993; Piersma *et al.* 1993*b*).

By their nature, most mollusc prey are not highly mobile and are unlikely to emit vibrational signals. As red knots have been found to detect bivalves buried at a depth of 3 cm between seven and eight times more often than predicted by 'random search' and 'direct touch' models, these birds must possess additional sensory capacities (Piersma *et al.* 1995). We conducted operant conditioning experiments and studied the morphology of the sensory organs in the bill tip to examine the hypothesis

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*Author for correspondence (`theunis@nioz.nl`).

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that red knots are able to detect hard-shelled prey buried in soft sediments without touching them. On the basis of these findings we deduce the nature of the detection mechanism and present a novel physical model based on principles of seabed dynamics.

2. METHODS

(a) *Birds*

This study is based on trials with four different individual red knots, not an unusual number of replicates in behavioural studies of this kind (e.g. Rechten *et al.* 1983; Montgomerie & Weatherhead 1997). The birds were captured with mistnets in the Wadden Sea in October 1995, and kept in a cage measuring 245 cm x 70 cm, with height varying from 45 cm at one end to 65 cm at the other. Exposed to a constant 15.5:8.5 h L/D cycle and an air temperature of about 17 °C, they were fed specified rations of commercial trout food pellets and live bivalves. The body masses of the experimental birds were kept constant within the 100–120 g range. The experiments reported here took place from September 1996 to March 1997.

(b) *Operant conditioning experiments*

Operant conditioning experiments (Mackintosh 1983) are ideally suited to test whether birds are able to tell the difference between objects (visible or otherwise), without getting into the trouble of immediate food rewards when studying prey-detection mechanisms. Our experiments were designed to see whether red knots could tell buckets with only wet sand from buckets containing objects buried in wet sand. We trained birds according to the operant (or instrumental) conditioning technique, using food pellets as a positive reinforcer (Dickinson 1981; Mackintosh 1983), to differentiate between sand-filled buckets (9.5 cm deep and 15 cm in diameter) containing no prey and buckets containing either 15 buried individuals of the tellinid bivalve *Macoma balthica* (17.0–17.9 mm long) or 15 stones similar in size (16.0–19.0 mm measured across their longest axis) and shape (slightly elongated and laterally flattened) to *Macoma*. The stones originated from foreign river deposits and had never been in contact with Wadden Sea water or sand.

Buckets were prepared in the hour before the experimental sessions (thus, there was time for sand and inserted objects to equilibrate with respect to temperature, etc.). A scaled tube was inserted into the sand to create a small hole in which the hard object was placed. Then the remaining hole was filled and the sand was smoothed. The depths given here measure the distance between the upper rim of the bivalve or stone and the surface of the sediment. To eliminate possible effects of our burying actions, 'empty' buckets received similar treatment, except that no objects were placed in the holes before they were refilled with sand. We kept the penetrability of the sand constant over all experiments using a penetrability gauge (a scaled stainless steel pen dropped from a standard height) for a single reference measure, and either sand or fresh seawater (except for the experiment with dry sand) was added to reach that reference state. The buried *Macoma* were alive, but we believe that they did not signal anything but their presence, e.g. by making movements. We never encountered *Macoma* that had moved or clearly opened their valves and extended their siphon after the maximum 2 h between implantation and the completion of a session.

To demonstrate that the birds could discriminate between buckets either containing, or not containing, hard objects, after a 15 s period during which they were required to probe (usually no deeper than 0.5 cm) for a minimum of 3 s, the birds were trained to go to the right-hand feeder for a reward (a few food pellets) when the bucket contained objects, and to the left-hand feeder when the bucket contained only sand. Throughout an experiment the observer remained silent and out of view (behind a one-way screen) to avoid 'Clever Hans' effects.

Birds were tested singly. The three birds not participating in the trial waited in an adjacent cage but were still in visual and vocal contact with the focal individual; the test buckets were out of sight. A sequence of two lights and one pair of lights was used to steer the bird through the experiment. A light was switched on above the 'waiting compartment' to indicate the start of a trial. As this light was switched off, another light, automatically switched on above the bucket, indicated that the bird should come towards it and probe in the sand. At the termination of the 15 s probing period, lights above each of the two feeders were switched on for the bird to choose one. With the light above the waiting compartment turned on again, the birds returned there. In relative darkness the bucket was replaced in preparation of the next trial without the bird being disturbed or even able to see the observer's hand. Each session consisted of eight successive trials lasting 1–2 min, each of the latter consisting of presentations of a bucket randomly chosen from a series of three positive and three negative but otherwise identical buckets (two buckets were thus offered twice within a session, the sandy surface being smoothed before the second presentation). There were between one and four sessions per day.

During the training periods, to aid detection for the birds, *Macoma* were placed in a horizontal position to give a large area for detection, rather than the vertical position found in nature. The birds easily learned this task (see table 1) and the only further training (14 sessions with *Macoma*) was after a four-week break in experiment 3. There were 39 sessions before, and 32 sessions after the break. During the actual experiments the birds were only rewarded after a correct choice. Note that in operant conditioning experiments it is impossible to randomize experimental tasks. The technique relies on the fact that birds learn a simple reward rule. As we did not vary the order of tasks between individuals, we checked for changes in response patterns over time by repeating one task (with *Macoma* buried flat at 3.5 cm depth) three times in the course of this study.

As we were interested only in whether or not the four birds learned to discriminate between buckets with and without buried objects, and as we had no prior knowledge about the number of trials necessary to reach significant discrimination, and to mimimize the time needed per task, sequential statistics based upon proportions from a binomial distribution (Krebs 1994) were used to determine when for all four birds the results of the successive sessions demonstrated a statistically significant preference for the proper (rewarded) feeders.

We assumed that an above 60% correct choice ($H_1=0.6$) proves an ability to discriminate. This is quite a low threshold level (see Templeton 1998). However, red knots are a species for which good feeding grounds are notoriously variable and patchy (Zwarts *et al.* 1992; Piersma 1994). Even when fully informed, red knots may have the natural inclination to make strategic 'mistakes' in order to check out whether alternative reward rules have come into fashion. We tried to reject the null hypothesis of 50% correct choice ($H_0=0.5$), i.e. no discrimination. Given that the type-I and type-II error levels are set to 5% ($\alpha=\beta=0.05$), that $H_0=0.5$, and that $H_1=0.6$ (see Krebs 1994), we calculated an uncertainty zone which the cumulative positive scores had to exceed.

Table 1. *Results of discrimination experiments using an operant conditioning approach*

(Except for the experiments with stones, prey on offer in the wet or dry sand were always *Macoma balthica* in a vertical or horizontal (flat) position. We present the number of trials at which the bird had left the statistical uncertainty zone for a correct preference; n.s. = not significant indicates that even after 328 trials the bird showed no evidence of a preference (see figure 1*c*).)

successive experiments	prey condition	condition of sand	N_{sessions}	N_{trials}	N_{trials} before significance			
					bird 1	bird 2	bird 3	bird 4
training	flat, 3.5 cm deep	wet	27	216	112	104	112	120
exp. 1	vertical, 3.5 cm deep	wet	51	408	376	56	296	176
exp. 2	vertical, 5 cm deep	wet	41	328	224	312	288	256
exp. 3	stones, 5 cm deep	wet	71	568	528	520	408	168
exp. 4	flat, 3.5 cm deep	wet	28	224	216	168	216	184
exp. 5	vertical, 5 cm deep	dry	41	328	n.s.	n.s.	n.s.	n.s.
exp. 6	flat, 3.5 cm deep	wet	28	224	208	168	168	208

(c) *Light microscopy*

Bills of two adult red knots (which were perfused under complete anaesthesia with 4% formalin via the left ventricle) were embedded in epoxy resin and metacrylate plastic (Epon C without accelerator; Historesin, Reichert Jung) and sectioned, without prior decalcification, on a Jung Polycut E sliding microtome at 10 µm in coronal and sagittal planes. Epon cross-sections were stained for routine histology (Mallory, counterstained with Hematoxilin (Anker *et al.* 1974)). Sagittal sections embedded in Historesin were stained with a specific silver-staining technique (Sevier & Munger 1965) to show corpuscular nerve endings.

(d) *Scanning electron microscopy*

To show the presence of sensory pits on the bill, scanning electron micrographs were made of dorsal surfaces of additional bill tips of which the keratin and underlying dermis had been removed by gentle maceration. The samples were rinsed in a series of graded alcohols to acetone mixtures, and air-dried. After drying, they were sputter-coated with gold using a BAL-TEC SCD 005. Preparations were photographed in a JEOL JSM-5300 scanning electron microscope.

3. RESULTS

During the training phase of the operant conditioning experiments, the discrimination task between prey and non-prey buckets was relatively easy, as *Macoma* were buried horizontally at shallow depths. The birds learned quickly, and within 120 trials their preference for feeders indicating buckets with prey had reached significance (table 1). When *Macoma* were buried in their natural vertical position at 3.5 cm, three of the four birds took somewhat longer to achieve significant preference. In the subsequent experiment where *Macoma*, buried at 5 cm depth, were definitely out of reach of the 3.2–3.5 cm bills (note that their tongue cannot be extended beyond their bill), two birds needed fewer and two needed more trials than during the previous experiment to statistically demonstrate that they were able to distinguish buckets with and without prey (table 1 and figure 1*a*). Note that once the threshold level was crossed, scores did not fall back into the uncertainty zone, and that, at this point, the null hypothesis that birds are not able to discriminate had long been rejected.

In the critical experiment where *Macoma*-sized stones were buried at 5 cm, all birds had reached significant discrimination after about 500 trials. Although an examination of individual differences is beyond the scope of this paper, it is striking that three of the four birds took longer to gain a significant preference than during the first two experiments with live *Macoma* (table 1 and figure 1*b*). This might be due to a decrease in motivation with time, a more difficult task (a weaker signal?), the presence of a novel object (Roitblat 1987), or an increase in the birds' strategic sampling of the alternative. To test the motivation hypothesis, we continued with an experiment repeating the 'easy' condition of the training sessions. In support of this hypothesis the birds required a similar number of trials to reach significance as they did in the 'more difficult' experiments 2 and 3, but took longer than during the training sessions (table 1). To ascertain the role of interstitial water in the perception of buried objects, we then offered them *Macoma* buried vertically in a dry substrate at a depth of 5 cm. Even after 328 trials, equal to the number to reach significance in a similar experiment with wet sand (experiment 2), the birds remained on the 50% line (table 1 and figure 1*c*). A final experiment (experiment 6) was made to check for a long-term decline in motivation. As the number of trials needed to reach significance was not much different from experiment 4 in any of the birds (table 1), there is no evidence for further loss of motivation.

The ability of red knots to identify buckets in which stones were buried at 5 cm depth excludes many of the possible perception mechanisms suggested in the literature on this topic (Hulscher 1982; Gerritsen *et al.* 1983; Gerritsen & Meijboom 1986; Piersma *et al.* 1995): vision, acoustics, smell, taste and the detection of vibrational signals emitted by prey. Indeed, when red knots are offered sandy sediments with a mix of living bivalves and similarly sized stones, birds will not only bring bivalves to the surface but also some of the stones (T. Piersma *et al.*, unpublished data). Assuming that the stones share the temperature and electromagnetic characteristics of the surrounding sand, perception mechanisms based on

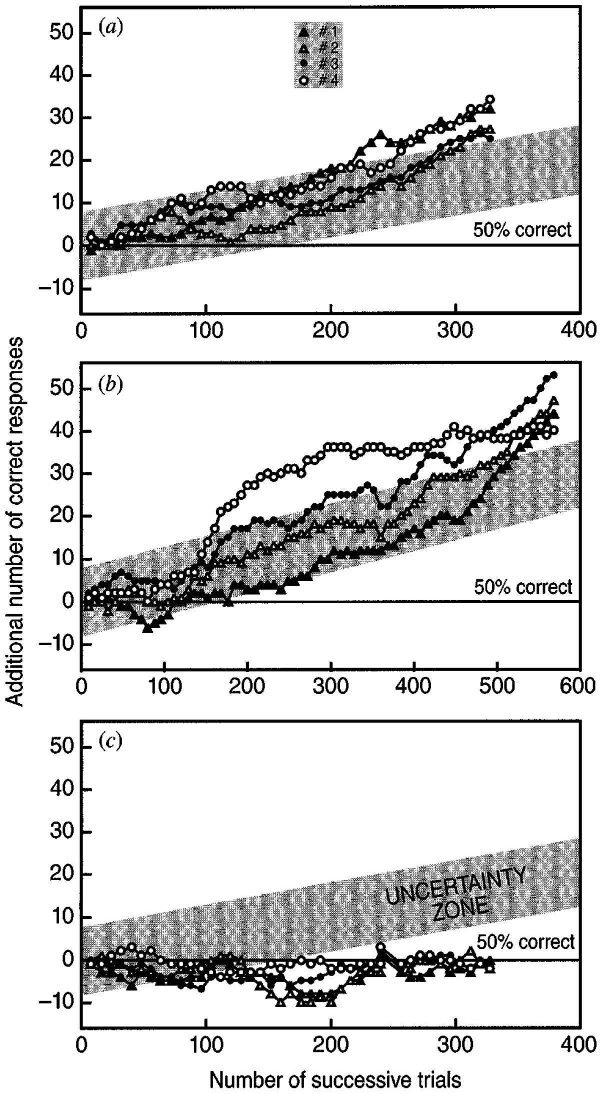

Figure 1. Cumulative curves for the number of correct responses additional to the prediction of 50% correct made by the null hypothesis of 'not being able to make a distinction' for the four trained red knots in successive trials (data points given for each session). (*a*) In half of the test buckets, 15 *Macoma* were buried in a vertical position at 5 cm depth (experiment 2); (*b*) 15 stones were buried at 5 cm depth (experiment 3); and (*c*) 15 *Macoma* were vertically buried at 5 cm depth in dry sand (experiment 5). The shaded areas represent the zones of statistical uncertainty; points above the uncertainty zone indicate a significant deviation from the alternative hypothesis, H_1.

the detection of temperature gradients or electromagnetic fields also seem unlikely. Our experiments cannot exclude a possible acoustic mechanism based on a type of 'sonar' system where pressure waves are generated by the rapidly probing bill (*ca.* 10 Hz (Piersma *et al.* 1995)), with prey detection being based on reflections received from hard surfaces. However, such an acoustic mechanism would not work on theoretical grounds. The wavelength of a 10 Hz vibration would be over 100 m (Dusenbery 1992) and would make detection of objects of a few centimetres impossible. What remains is a mechanism based on the perception of a pressure build-up in the direction of a solid object as the bill penetrates the sediment (Piersma *et al.* 1995). Such a mechanism would require advanced pressure gauges in the bill tip.

A comparative study of 17 shorebird species (Bolze 1969) indicated that, particularly in red knots, high numbers of Herbst corpuscles are found in lacunae or 'sensory pits': cups or holes in the bony tip of the premaxilla and mandible. Based on much more detailed descriptive material (figure 2), we can confirm the existence of lacunae with Herbst corpuscles and, in addition, quantify their densities. Between 2 and 4 mm away from the bill tip the cups vary in width from 112 to 200 μm, and are up to 300 μm long if measured along the axis of the bill (figure 2*b*). We counted 140 cups in the exterior bony surface of the upper, and 145 cups in the lower bill tip. Each cup contains two parallel rows of up to 25 Herbst corpuscles (figure 2*c*,*d*) placed around a central core of axons (figure 2*d*). The Herbst corpuscles are 35–52 μm in width and 74–88 μm in length. The cross-section 2–4 mm from the tip has the largest density of sensory pits and Herbst corpuscles. The sensory pits are asymmetrical over a transverse plane (figure 2*b*). At the tip of the bill, 'stacks' of Herbst corpuscles are nested in very deep holes that are focused forward (figure 2*d*). Further away from the bill tip, clusters of Herbst corpuscles sit in cups that are also focused forward (figure 2*c*), rather than sideways as in the symmetrical cups of shorebird species that are sensitive to invertebrate-induced vibrations (Goglia 1964; Gerritsen & Meijboom 1986).

Herbst corpuscles are fast-adapting sensors that detect the accelerating components of pressure build-ups (Gottschaldt 1985). As red knots usually probe with a slightly open bill, any receptors inside the bill may also be of interest. In the rostral palate we found very small (10–15 μm) corpuscular nerve endings reminiscent of Merkel or Grandry corpuscles. These sensory organs were not detected by the earlier students of shorebird bills. Under the keratin spines on the palate are complexes of large sensory cells of the Grandry type (axonal disks sandwiched between the cells). Grandry corpuscles of geese and ducks are rapidly habituating velocity detectors; Merkel corpuscles are claimed to be pressure receptors (Gottschaldt 1985).

4. DISCUSSION

Red knots thus possess large numbers of sensors of which the threshold sensitivities and response times are presently unknown, but which in principle could detect the build-up of pressure differences. By which principle would such sensors, mounted on a bill repeatedly probing (10 Hz) to a depth of 0.5 cm, enable the detection of the remotely buried (⩾3 cm) hard objects with a diameter of about 1 cm, given (i) the characteristics of the hydrodynamic and sedimentary environment (wet, muddy sand with 180 μm median grain size); (ii) the finding that detection fails in dry sand (table 1); and (iii) that red knots were also unable to find live bivalves during feeding trials on miniaturized mudflats with liquid mud (T. Piersma *et al.*, unpublished data; cf. Piersma *et al.* 1995)?

In any sediment the probing bill will act as a source of pressure perturbations that drop off in inverse proportion

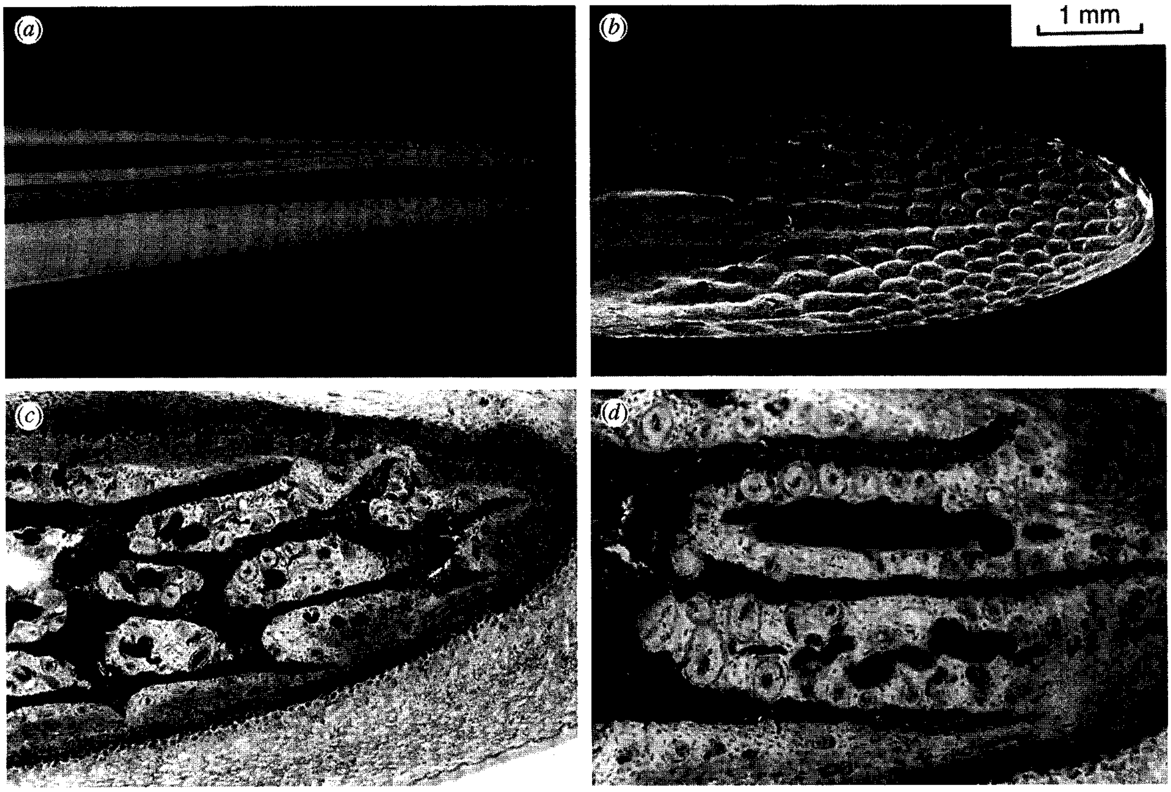

Figure 2. Morphology of the sensory bill tip organ of red knots. (*a*) Photograph of the frontal half of the upper and lower mandibles showing the bare bone. (*b*) Electron microscopy scan of the surface of the bony matrix of the tip of the upper mandible clearly showing the large numbers of sensory pits. (*c*) Parasagittal section through the tip of the lower mandible (magnification × 100) showing elongated clusters of onion-shaped Herbst corpuscles sitting in asymmetric cups in the bony matrix. Note that the small black dots close to the top-edge of the section are Grandry or Merkel corpuscles not embedded in bone, but occurring just outside it under the epidermis, which shows up as a greyish band around the bony matrix. (*d*) Detailed sagittal section through the very tip of the lower mandible, taken slightly closer to the median than in (*c*) (magnification × 200), showing two parallel, rostrally projecting, deep canals in the dark bone. These deep canals replace the more shallow sensory pits that occur further up along the bill and show up in (*b*) and (*c*). Each canal contains a central meandering core of afferent axon filaments surrounded by parallel rows of more than ten Herbst corpuscles.

with distance to the source. Assuming the sand grain skeleton to be rigid, in dry sand the air near the probing bill will not only be easily compressed (so that the pressure drops off so fast that it will not be affected by a remotely buried obstacle), but a locally increased pressure will also easily relax because of the low resistance offered by the sand pores to the air flow. The situation is different in wet sand. As the interstitial water is (nearly) incompressible, the pressure imposed by a probing bill drops off over a larger distance, and as the resistance that the water experiences between sand grains is also higher, the relaxation of a locally increased pressure (the draining) takes more time. When a hard object is present, the flow must go around it and the otherwise spherically symmetric pressure pattern will be disturbed (figure 3*a*). The resulting pattern of pressure differences (figure 3*b*) could be picked up by the pressure sensors in the bill tip. In this context, the fact that the bill of red knots is quite thick, straight, and evenly tapered compared with other *Calidris* species (Paulson 1993), and thus of better value when it comes to induce evenly distributed pressure, may be of significance.

Why do red knots often make more than ten repeated probes at the same spot when such 'imaging' will occur even after a single probe? If we assume that the sand structure, rather than being rigid and immobile, is loosely packed and mobile (owing to a gradual settling of sand grains that takes place on the ebb tide), a pressure increase in the interstitial water, produced by the probing bill, might be able to overcome the force per unit surface area (the 'normal stress') with which a sand grain (owing to its own weight and that of other grains sitting upon it) rests upon sand grains deeper down. When such a 'stress failure' happens, sand particles are lifted and the sand may start to float. When the bill is retreated, this leads, in a gravitational field, to a rearrangement of the settling sand grains, resulting in a denser packing and a local increase in residual pressure within the pore water that is probably much bigger than the pressure disturbance that was produced directly by the probing bill. When draining is not effective during a probing period of about 0.1 s (owing to the high resistance that the pores offer to this flow), repeated probing leads to a successively denser packing and associated pressure build-up. (A similar pressure build-up sometimes occurs in the bottom of a shallow sea, where it may be due to periodic pressure variations associated with wind waves at the sea's surface. Within the sediment this can lead to the formation of

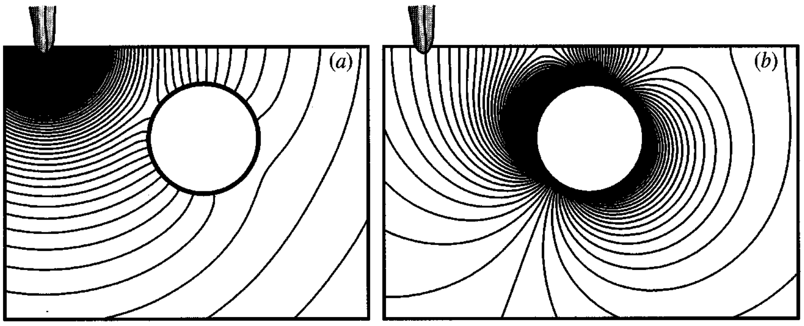

Figure 3. (*a*) Cross-sectional sketch of the pressure pattern produced by a point source (supposed to be an idealized model of the pressure pulse produced by the probing bill), located at the sand–air interface at the top, as influenced by the presence of a (spherical) shell (open circle) buried deeper down in the sand. The pressure pattern is obtained as an (approximate) solution of a Poisson equation (Lamb 1932), which the pressure satisfies as a result of Darcy's law (pressure gradient balanced by frictional drag of pore-water flow, leading to a flow proportional to pressure gradient) and water being nearly incompressible (Sleath 1984). Isobars are required to be perpendicular to the surface of the shell and the mud–air interface, so as to satisfy the impermeability condition at these surfaces. The pressure pattern is dominated by the spherically symmetric radial decay that would occur in the absence of the obstructing shell. This decay is visible as a decrease from high pressure (densely packed isobars) to low pressure (increasingly wider spaced isobars towards the lower right-hand corner). Because of the highly idealized nature of the forcing (as a point source), the pressure increases indefinitely towards that point. For clarity, the intensely crowding isobars close to this source have been omitted (=black). In the vicinity of the shell, the pressure pattern is clearly disturbed by the shell's presence. (*b*) The pressure pattern induced by the presence of a shell. It is defined as the difference between the pressure patterns produced by a point source with (as in (*a*)) and without (not shown) the presence of an obstructing spherical object. The Herbst corpuscles on the bill tip should be able to sense this disturbance as it penetrates to some depth at the source location; the gradient over the bill would enable the bird to find the direction of the prey. The pressure patterns depicted here are on an arbitrary scale. This scale depends on the intensity and time dependence of the source and may, alternatively, be set by the 'rectification mechanism' discussed in the text. The actual magnitude of the pressure disturbance induced by the object, of course, will eventually determine whether the object is detectable or not.

quicksand, resulting in its weakening. This is a recognized potential hazard for the stability of welling platforms (Bjerrum 1973).) A red knot might simply continue probing until the induced pressure perturbation is strong enough to make objects 'visible'. It basically utilizes gravity, in combination with the loosely arranged sand grains, to act as a rectifier and magnifier of the forced oscillatory pressure disturbances that it produces. When the mud is very liquid, as in quick sand, it becomes impossible to produce such a pressure build-up. In such cases, sand grains are already floating in the liquid and this makes gravitational rearrangement ineffective.

There is increasing awareness that studies of mechanism and function should be closely integrated for a complete understanding of behaviour (e.g. Getty & Pulliam 1992; Montgomerie & Weatherhead 1997; Wehner 1997). In the light of our results, the 'old' observation (Prater 1972) that red knots in Morecambe Bay prefer to feed on a sandy substratum with a surface film of moisture, and that they avoid well-drained areas, suddenly makes sense. We believe that, if red knots indeed employ the suggested prey-detection mechanism, the birds' feeding habitats are not only selected on the basis of minimum densities of harvestable mollusc prey, but also in response to the sedimentological conditions (grain size, pore size, fluid content, etc.) that are necessary for the specific imaging mechanism to work.

This study of a prey-detection mechanism of a shorebird species beautifully illustrates how a successful exploitation of a particular resource (buried molluscs) found in a particular habitat (intertidal soft sediments worldwide (Piersma 1994)) has favoured a unique, and hitherto undiscovered, sensory channel.

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REFERENCES

Anker, G. C., Scheers-Dubbeldam, K. & Noorlander, C. 1974 An epoxy resin embedding technique for large objects. *Stain Technol.* **49**, 183–188.

Bjerrum, L. 1973 Geotechnical problems involved in foundations of structures in the North Sea. *Géotechnique* **23**, 319–358.

Bolze, G. 1969 Anordnung und Bau der Herbstchen Körperchen in Limikolen-schnäbeln im Zusammenhang mit der Nahrungsfindung. *Zool. Anz.* **181**, 313–355.

Dekinga, A. & Piersma, T. 1993 Reconstructing diet composition on the basis of faeces in a mollusc-eating wader, the knot *Calidris canutus*. *Bird Study* **40**, 144–156.

Dickinson, A. 1981 Reinforcement. In *The Oxford companion to animal behaviour* (ed. D. McFarland), pp. 471–476. Oxford University Press.

Dusenbery, D. B. 1992 *Sensory ecology: how organisms acquire and respond to information*. New York: Freeman.

Gerritsen, A. F. C. & Meijboom, A. 1986 The role of touch in prey density estimation by *Calidris alba*. *Neth. J. Zool.* **36**, 530–562.

Gerritsen, A. F. C., van Heezik, Y. M. & Swennen, C. 1983 Chemoreception in two further *Calidris* species (*C. maritima* and *C. canutus*), with a comparison of the relative importance of chemoreception during foraging in *Calidris* species. *Neth. J. Zool.* **33**, 485–496.

Getty, T. & Pulliam, H. R. 1993 Search and prey detection by foraging sparrows. *Ecology* **74**, 734–742.

Goglia, G. 1964 L' 'organo tattile apicale' del becco di alcuni volatili. *Acta Med. Romana* **2**, 243–262.

González, P. M., Piersma, T. & Verkuil, Y. 1996 Food, feeding and refuelling of red knots during northward migration at San Antonio Oeste, Rio Negro, Argentina. *J. Field Ornithol.* **67**, 575–591.

Gottschaldt, K.-M. 1985 Structure and function of avian somatosensory receptors. In *Form and function in birds*, vol. 3 (ed. A. S. King & J. McLelland), pp. 375–461. London: Academic Press.

Hulscher, J. B. 1982 The oystercatcher *Haematopus ostralegus* as a predator of the bivalve *Macoma balthica* in the Dutch Wadden Sea. *Ardea* **70**, 89–152.

Krebs, C. J. 1994 *Ecological methodology*. New York: Harper Collins.

Lamb, H. 1932 *Hydrodynamics*, 6th edn. New York: Dover.

Mackintosh, N. J. 1983 *Conditioning and associative learning*. Oxford University Press.

Montgomerie, R. & Weatherhead, P. J. 1997 How robins find worms. *Anim. Behav.* **54**, 143–151.

Paulson, D. 1993 *Shorebirds of the Pacific Northwest*. Seattle: University of Washington Press.

Piersma, T. 1994 *Close to the edge: energetic bottlenecks and the evolution of migratory pathways in knots*. Den Burg: Uitgeverij Het Open Boek.

Piersma, T. & Davidson, N. C. (eds) 1992 The migration of knots. *Wader Study Grp Bull.* **64**(Suppl.), 1–209.

Piersma, T., Hoekstra, R., Dekinga, A., Koolhaas, A., Wolf, P., Battley, P. & Wiersma, P. 1993*a* Scale and intensity of intertidal habitat use by knots *Calidris canutus* in the western Wadden Sea in relation to food, friends and foes. *Neth. J. Sea Res.* **31**, 331–357.

Piersma, T., Koolhaas, A. & Dekinga, A. 1993*b* Interactions between stomach structure and diet choice in shorebirds. *Auk* **110**, 552–564.

Piersma, T., van Gils, J., de Goeij, P. & van der Meer, J. 1995 Holling's functional response model as a tool to link the food-finding mechanism of a probing shorebird with its spatial distribution. *J. Anim. Ecol.* **64**, 493–504.

Piersma, T., van Gils, J. & Wiersma, P. 1996 Family Scolopacidae (sandpipers, snipes and phalaropes). In *Handbook of birds of the world. 3. Hoatzin to auks* (ed. J. del Hoyo, A. Elliott & J. Sargatal), pp. 444–533. Barcelona: Lynx Edicións.

Prater, A. J. 1992 The ecology of Morecambe Bay. III. The food and feeding habits of knot (*Calidris canutus* L.) in Morecambe Bay. *J. Appl. Ecol.* **9**, 179–194.

Rechten, C., Avery, M. & Stevens, A. 1983 Optimal prey selection: why do great tits show partial preferences? *Anim. Behav.* **31**, 576–584.

Roitblat, H. L. 1987 *Introduction to comparative cognition*. New York: Freeman.

Sevier, A. C. & Munger, B. L. 1965 A silver method for paraffin sections of neural tissue. *J. Neuropath. Exp. Neurol.* **24**, 130–135.

Sleath, J. F. A. 1984 *Sea bed mechanics*. New York: Wiley.

Summers, R. W. & Smith, S. M. 1981 The diet of the knot (*Calidris canutus*) on rocky shores of eastern Scotland in winter. *Ardea* **71**, 151–153.

Templeton, J. J. 1998 Learning from others' mistakes: a paradox revisited. *Anim. Behav.* **55**, 79–85.

Wehner, R. 1997 Sensory systems and behaviour. In *Behavioural ecology, an evolutionary approach*, 4th edn (ed. J. R. Krebs & N. B. Davies), pp. 19–41. Oxford: Blackwell Scientific Publications.

Zwarts, L. & Blomert, A.-M. 1992 Why knot *Calidris canutus* take medium-sized *Macoma balthica* when six prey species are available. *Mar. Ecol. Prog. Ser.* **83**, 113–128.

Zwarts, L., Blomert, A.-M. & Wanink, J. H. 1992 Annual and seasonal variation in the food supply harvestable by knot *Calidris canutus* staging in the Wadden Sea in late summer. *Mar. Ecol. Prog. Ser.* **83**, 129–139.

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