



Commentary

From spoonbill to Spoon-billed Sandpiper: the perceptual dimensions to the niche

THEUNIS PIERSMA^{1,2}

¹*Animal Ecology Group, Centre for Ecological and Evolutionary Studies, University of Groningen, PO Box 11103, 9700 CC Groningen, The Netherlands*

²*Department of Marine Ecology, Royal Netherlands Institute for Sea Research (NIOZ), PO Box 59, 1790 AB Den Burg, Texel, The Netherlands*

According to Begon *et al.* (2006), a niche is not a place but an idea. A niche is a summary of an animal's tolerances and requirements. This determines where an animal would do best and where it likes to be; in other words, how an animal would select its habitat. Habitat selection is usually represented graphically in terms of prey selection, food intake rates and predator avoidance (Piersma 2011), but when this is done for particular animal species, their morphological, physiological, behavioural and sensory design features are mostly taken for granted (e.g. Wiens 1989, Morrison *et al.* 1990, Goss-Custard *et al.* 2006).

How helpful even a limited understanding of, in this case, prey detection mechanisms could be for predictive models of habitat selection and foraging distributions became clear early on in our work on Red Knots *Calidris canutus*. The precise arrangement of pressure sensors in the bill tip and their wiring to and in the brain explained the considerable capacity of Red Knots to detect hard objects such as bivalves and snails in wet soft sediments (Piersma *et al.* 1998). However, these sensory insights then also helped us to understand the rather low giving-up densities of available prey at some sites (Piersma *et al.* 1993), the near-absence of soft-bodied prey such as polychaete worms in their diets (Piersma 1991), and the foraging distributions of Red Knots over intertidal mudflats at a variety of spatial and temporal scales (Piersma *et al.* 1995, van Gils *et al.* 2006b, Quaintenne *et al.* 2011). Thus, if a little understanding of even a single 'design' feature helped so much to make sense of this species' ecology, imagine what an understanding of multiple design features would do (van Gils *et al.* 2006a).

This takes me back to a symposium that I once attended at Leiden University. I was there to tell the story of the specialized bill-tip organ of Red Knots and how this helped us understand their food and habitat choices. The audience consisted of functional morphologists in the tradition of Leiden's van der Klaauw (1948) and see, for example, Gerritsen & Sevenster 1985, Zweers *et al.* 1995, van der Leeuw *et al.* 2003). Apart from the widespread whisperings during the conference dinner about functional morphology rapidly becoming a dying trade, the composition of the nationalities around the table struck me as odd. Whereas the behavioural, ecological and ornithological meetings that I was used to were usually dominated by scientists from English-speaking countries, none of those were there; the audience was German, Dutch, Austrian and French only. Here were the scientists who could tell one bone, one set of muscles or one sensory organ from another and know how to study their morphology and functionality, and there we were, apparently losing these remarkable, if somewhat inward-looking, specialists.

Still, as witnessed by a steady trickle of new bird-related publications (e.g. Guillemain *et al.* 2002, Cunningham *et al.* 2010a, 2010b, Demery *et al.* 2011), the trade that merges insights from morphology, sensory physiology and ecology is alive and well. In this issue of *Ibis*, Martin and Portugal (2011) describe the visual fields of four ecologically distinct but phylogenetically related wading birds from one family, two ibises and two spoonbills, and interpret their findings in the context of the foraging ecology of these threskiornithids. They were in for a surprise when finding that even such tactile foragers with long bills have fields of vision that enables them to look binocularly at freshly captured prey. Clearly, careful scrutiny of captured prey, during handling between the tips of their mandibles before ingestion, is important enough for these spoonbills and ibises to give up the possibility of complete celestial coverage by having highly placed eyes. The ingestion of Three-spined Sticklebacks *Gasterosteus aculeatus* in full self-defence must be something like eating barbed wire. It involves the disarmament of the spines by careful head-up positioning of the fish before swallowing, and I can see why spoonbills need to use binocular visual input to do this efficiently. That spoonbills and ibises are large bodied, and thus have less to fear from avian predators than have smaller tactile-feeders such as ducks, may explain why the large wading birds have given up complete celestial vision, whereas the ducks have not (Martin 1986b, 2007, Guillemain *et al.* 2002, Martin *et al.* 2007a).

Such trade-offs are paramount in the designs of all animals, and it is tribute to Graham Martin that he has built up such an extraordinary portfolio of comparative studies at the interface between morphology, sensory physiology and ecology (e.g. Martin 1994, 2009, 2011, Martin & Katzir 1995, Martin & Coetsee 2004, Martin

*Email: theunis.piersma@nioz.nl

et al. 2007b, 2008). Starting off with studies explaining aspects of the ecology of owls with reference to their capacity to see in the dark (Martin 1984, 1986a, 1990), he went on to examine a wide variety of birds using his self-constructed avian ophthalmoscope (Martin 2007). Time and again Martin and his associates have found that, beyond the grand design features of clades of birds, the details of the perceptual systems reflect the finer details of birds' ecologies rather than shared ancestry. More often than not, studies of fields of vision hint at key ecological features that ecologists had failed to notice. For example, Eurasian Golden Plovers *Pluvialis apricaria* are known as night foragers (Gillings *et al.* 2005, Gillings & Sutherland 2007), and indeed they have very large eyes (and probably sharp ears as well, Lange 1968) to help them locate earthworms (Lumbricidae) close to and on the surface of arable fields and meadows. In fact, the eyes are so big that this has necessitated special supraorbital bones to better anchor the eyes in the eye-sockets (Martin & Piersma 2009). However, the presence of this extra bone, the eye-brow of plovers, then leads to a wide blind area above the head: the plovers cannot detect dangers coming from above and behind. This realization suddenly explained why European Golden Plovers are often so immensely cryptic in their behaviour. They are true masters of disappearance even in daytime and even in open landscapes. They do this by sitting tight on the ground (this would make them hard to locate and unavailable for Peregrines *Falco peregrinus* which do not capture prey on the ground), or by circling in flocks high in the air on warm days with thermals (again taking them out of the reach of raptors).

A remarkable avian radiation is that of the sandpipers, the Calidrinae (family Scolopacidae), ranging in size from the puny 20-g Least Sandpiper *Calidris minutilla* to the relatively mighty 200-g Great Knot *Calidris tenuirostris* (Piersma *et al.* 1996). Within this subfamily, the Great Knot (together with the much shorter-billed and rocky shore-foraging Surf-bird *Aphriza virgata*) belongs to the sister clade of Red Knots (A.J. Baker unpubl. data). When one watches Great and Red Knots foraging together in mixed flocks on mudflats in northwest Australia, doing the same sort of things and taking the same sorts of prey, one would assume that they share the same sensory tools. But closer examination shows that they do not. With respect to the bill-tip organ that makes Red Knots so special (Piersma *et al.* 1998), with far fewer and not-forwardly-directed sensory pits in the tips of the upper and lower mandible, Great Knots and Surf-birds are actually very similar, and quite distinct from Red Knots (H. Berkhoudt & T. Piersma unpubl. data). This tallies with behavioural observations on captive Great Knots, which do not appear to have the urge to spend 10–20% of the day probing soft sediments to locate prey that are never there, as is the wont of cap-

tive Red Knots (T. Piersma unpubl. data). I am quite convinced that neither Great Knots nor Surf-birds possess the remote prey detection system of Red Knots. However, they may not be as 'blind' to vibrations made by burrowing worms and shrimp as Red Knots are, a sensory modality that appears to be the specialization of Sanderling *Calidris alba* (Gerritsen & Meijboom 1986).

Then there exists the fantastic morphological spoon-bill-like bill specialization of the critically endangered Spoon-billed Sandpiper *Calidris/Eurynorhynchus pygmaeus* (Piersma 1986, Taldenkov & Gerasimov 2006), but by and large sandpiper bills are rather uniform in shape and size. I suggest that the evolutionary radiation of sandpipers to large extent is a radiation of the bill-tip organ. Comparative studies of that organ, in combination with other sensory modalities such as taste (Gerritsen *et al.* 1983) and vision, as explored by Martin and Portugal in this issue of *Ibis*, could generate considerable and unexpected insights into the ecology and distribution of this group of birds. In fact, I believe that future studies in avian biology that deal with daily activity rhythms, foraging distributions, habitat selection and indeed the niche will always profit from taking the perceptual characteristics of the focal species seriously into account.

REFERENCES

- Begon, M., Townshend, C.R. & Harper, J.L. 2006. *Ecology: from Individuals to Ecosystems*. Oxford: Blackwell Publishing.
- Cunningham, S.J., Alley, M.R., Castro, I., Potter, M.A. & Pyne, M.J. 2010a. Bill morphology of ibises suggests a remote-tactile sensory system for prey detection. *Auk* **127**: 308–316.
- Cunningham, S.J., Castro, I., Jensen, T. & Potter, M.A. 2010b. Remote touch prey-detection by Madagascar Crested Ibises *Lophotibis cristata urschi*. *J. Avian Biol.* **41**: 350–353.
- Demery, Z.P., Chappell, J. & Martin, G.R. 2011. Vision, touch and object manipulation in Senegal Parrots *Poicephalus senegalus*. *Proc. R. Soc.* **278**. doi: 10.1098/rspb.2011.0374.
- 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. & Sevenster, J.G. 1985. Foraging behaviour and bill anatomy in sandpipers. *Fortschr. Zool.* **30**: 237–240.
- 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.
- Gillings, S. & Sutherland, W.J. 2007. Comparative diurnal and nocturnal diet and foraging in Eurasian Golden Plovers *Pluvialis apricaria* and Northern Lapwings *Vanellus vanellus* wintering on arable farmland. *Ardea* **95**: 243–257.

- Gillings, S., Fuller, R.J. & Sutherland, W.J. 2005. Diurnal studies do not predict nocturnal habitat choice and site selection of European Golden-Plovers (*Pluvialis apricaria*) and Northern Lapwings (*Vanellus vanellus*). *Auk* **122**: 1249–1260.
- van Gils, J.A., Piersma, T., Dekinga, A. & Battley, P.F. 2006a. Modelling phenotypic flexibility: an optimality analysis of gizzard size in Red Knots (*Calidris canutus*). *Ardea* **94**: 409–420.
- van Gils, J.A., Spaans, B., Dekinga, A. & Piersma, T. 2006b. Foraging in a tidally structured environment by Red Knots (*Calidris canutus*): ideal, but not free. *Ecology* **87**: 1189–1202.
- Goss-Custard, J.D. et al. 2006. Intake rates and the functional response in shorebirds (Charadriiformes) eating macro-invertebrates. *Biol. Rev.* **81**: 501–529.
- Guillemain, M., Martin, G.R. & Fritz, H. 2002. Feeding methods, visual fields and vigilance in dabbling ducks (Anatidae). *Funct. Ecol.* **16**: 522–529.
- van der Klaauw, C.J. 1948. Ecological studies and reviews. IV. Ecological morphology. *Bibl. Biotheor.* **4**: 27–111.
- Lange, G. 1968. Über Nahrung, Nahrungsaufnahme und Verdauungstrakt mitteleuropäischer Limikolen. *Beitr. Vogelk.* **13**: 225–334.
- van der Leeuw, A.H.J., Kurk, K., Snelderwaard, P.C., Bout, R.G. & Berkhoudt, H. 2003. Conflicting demands on the trophic system of Anseriform birds and their evolutionary implications. *Anim. Biol.* **53**: 259–301.
- Martin, G.R. 1984. The visual fields of the Tawny Owl, *Strix aluco* L. *Vision Res.* **24**: 1739–1751.
- Martin, G.R. 1986a. Sensory capacities and the nocturnal habit of owls (Strigiformes). *Ibis* **128**: 266–277.
- Martin, G.R. 1986b. Total panoramic vision in the Mallard Duck, *Anas platyrhynchos*. *Vision Res.* **26**: 1303–1305.
- Martin, G.R. 1990. *Birds by Night*. Calton: Poyser.
- Martin, G.R. 1994. Visual fields in Woodcocks *Scolopax rusticola* (Scolopacidae; Charadriiformes). *J. Comp. Physiol. A.* **174**: 787–793.
- Martin, G.R. 2007. Visual fields and their functions in birds. *J. Ornithol.* **148**: 547–562.
- Martin, G.R. 2009. What is binocular vision for? A birds' eye view. *J. Vis.* **9**: 1–19.
- Martin, G.R. 2011. Understanding bird collisions with man-made objects: a sensory ecology approach. *Ibis* **153**: 239–254.
- Martin, G.R. & Coetzee, H.C. 2004. Visual fields in hornbills: precision-grasping and sunshades. *Ibis* **146**: 18–26.
- Martin, G.R. & Katzir, G. 1995. Visual-fields in ostriches. *Nature* **374**: 19–20.
- Martin, G.R. & Piersma, T. 2009. Vision and touch in relation to foraging and predator detection: insightful contrasts between a plover and a sandpiper. *Proc. R. Soc. Lond. B* **276**: 437–445.
- Martin, G.R. & Portugal, S.J. 2011. Differences in foraging ecology determine variation in visual field in ibises and spoonbills (Threskiornithidae). *Ibis* **153**: 662–671.
- Martin, G.R., Jarrett, N. & Williams, M. 2007a. Visual fields in Blue Ducks and Pink-eared Ducks: visual and tactile foraging. *Ibis* **149**: 112–120.
- Martin, G.R., McNeil, R. & Rojas, L.M. 2007b. Vision and the foraging technique of skimmers (Rynchopidae). *Ibis* **149**: 750–759.
- Martin, G.R., White, C.R. & Butler, P.J. 2008. Vision and the foraging technique of Great Cormorants *Phalacrocorax carbo*: pursuit or flush-foraging? *Ibis* **150**: 39–48.
- Morrison, M.L., Ralph, C.J., Verner, J. & Jehl, J.R. Jr (eds) 1990. Avian foraging: theory, methodology, and applications. *Stud. Avian. Biol.* **13**: 1–515.
- Piersma, T. 1986. Feeding method of Spoon-billed Sandpipers on a mudflat in South Korea. *J. Bombay Nat. Hist. Soc.* **83**: 206–208.
- Piersma, T. 1991. Red Knots in New Zealand eat molluscs too: preliminary diet observations at Miranda, Firth of Thames and Farewell Spit, November 1990. *Stilt* **19**: 30–35.
- Piersma, T. 2011. What is habitat quality? Dissecting a research portfolio on shorebirds. In Fuller, R. (ed.) *Birds and Habitat: Relationships in Changing Landscapes*. Cambridge: Cambridge University Press (in press).
- Piersma, T., Hoekstra, R., Dekinga, A., Koolhaas, A., Wolf, P., Battley, P.F. & Wiersma, P. 1993. 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., 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 del Hoyo, J., Elliott, A. & Sargatal, J. (eds) *Handbook of the Birds of the World, Vol. 3. Hoatzin to Auks*: 444–533. Barcelona: Lynx Edicions.
- Piersma, T., van Aelst, R., Kurk, K., Berkhoudt, H. & Maas, L.R.M. 1998. A new pressure sensory mechanism for prey detection in birds: the use of principles of seabed dynamics? *Proc. R. Soc. Lond. B* **265**: 1377–1383.
- Quaintance, G., van Gils, J.A., Bocher, P., Dekinga, A. & Piersma, T. 2011. Scaling up ideals to freedom: are densities of Red Knots across western Europe consistent with ideal free distribution? *Proc. R. Soc.* **278**: 2728–2736.
- Taldenkov, I. & Gerasimov, K.B. 2006. Functional morphology of the Spoon-billed Sandpiper. *J. Ornithol.* **147**: 260.
- Wiens, J.A. 1989. *The Ecology of Bird Communities*. Cambridge: Cambridge University Press.
- Zweers, G., de Jong, F., Berkhoudt, H. & Vanden Berge, J.C. 1995. Filter-feeding in Flamingos (*Phoenicopterus ruber*). *Condor* **97**: 297–324.