

African penguins (*Spheniscus demersus*) can detect dimethyl sulphide, a prey-related odour

Gregory B. Cunningham^{1,*}, Venessa Strauss² and Peter G. Ryan¹

¹Percy FitzPatrick Institute DST/NRF Centre of Excellence, University of Cape Town, Rondebosch 7701, South Africa and

²Southern African Foundation for the Conservation of Coastal Birds, PO Box 11116, Bloubaerg 7443, South Africa

*Author for correspondence at present address:

Department of Biology, St John Fisher College, 3690 East Avenue, Rochester, New York, NY 14618, USA (e-mail: gcunningham@sjfc.edu)

Accepted 15 July 2008

SUMMARY

Although it is well established that certain procellariiform seabirds use odour cues to find prey, it is not clear whether penguins use olfactory cues to forage. It is commonly assumed that penguins lack a sense of smell, yet they are closely related to procellariiforms and forage on similar types of prey in similar areas to many procellariiforms. Such regions are characterized by having high levels of dimethyl sulphide (DMS) a scented compound that many marine animals use to locate foraging grounds. If penguins can smell, DMS may be a biologically relevant scented compound that they may be sensitive to in nature. To test this hypothesis, we investigated whether adult African penguins (*Spheniscus demersus*) could detect DMS using two separate experiments. We tested wild penguins on Robben Island, South Africa, by deploying μ molar DMS solutions in the colonies, and found that birds slowed down their walking speeds. We also tested captive penguins in a Y-maze. In both cases, our data convincingly demonstrate that African penguins have a functioning sense of smell and are attracted to DMS. The implication of this work is that the detection of changes in the odour landscape (DMS) may assist penguins in identifying productive areas of the ocean for foraging. At-sea studies are needed to investigate this issue further.

Key words: olfaction, African penguin, *Spheniscus demersus*, dimethyl sulphide, foraging behaviour.

INTRODUCTION

Penguins (Sphenisciformes) and procellariiforms (albatrosses and petrels) are phylogenetically closely related (Ksepka et al., 2006; Hackett et al., 2008) and share many common traits with respect to their foraging behaviour. For example, species within these two broad groups tend to forage on similar types of prey, such as krill, fish and squid, and exploit similar ocean habitats (for reviews, see Warham, 1990; Williams, 1995). Furthermore, both penguins and procellariiforms must search for relatively small and ephemeral productive locations where prey aggregate (reviewed in Weimerskirch, 2007). Finally, members of both orders tend to nest in large colonies and are central place foragers during the breeding season (Stephens and Krebs, 1986; Williams, 1995). Despite these many similarities, it is typically assumed that these birds use different sensory modalities to locate prey. Procellariiforms have large olfactory bulbs (Bang and Cobb, 1968), suggesting that they hunt by smell. Numerous studies have confirmed this, as procellariiforms are attracted to a variety of prey-related odours at sea such as fishy smelling compounds (Nevitt et al., 2004) and the scent of krill (Nevitt, 1999b). By contrast, it is typically thought that penguins are primarily visual hunters (Wilson et al., 1993; Wilson and Wilson, 1995; Ryan et al., 2007), and the potential use of olfactory cues by penguins for foraging has largely been ignored (but see Culik et al., 2000; Culik, 2001).

A first step in determining whether penguins use odours to hunt is to demonstrate whether or not penguins have a functioning sense of smell. Dimethyl sulphide (DMS) is a scented compound produced by phytoplankton that is elevated when they are grazed upon by zooplankton (Dacey and Wakeham, 1986; Wolfe and Steinke, 1996), and is associated with seamounts and shelf breaks (Berresheim et

al., 1989; Daly and DiTullio, 1996; McTaggart and Burton, 1992) where seabirds tend to forage (reviewed by Nevitt, 2000). Nevitt et al. (Nevitt et al., 1995) demonstrated that DMS serves as a foraging cue (see also Van Buskirk and Nevitt, 2008). Since many petrels forage on zooplankton, high levels of DMS may be a reliable indicator of the birds' prey (reviewed by Nevitt, 2000). Other studies on marine animals such as the harbour seal (*Phoca vitulina*) and the predatory copepod (*Temora longicornis*) suggest that this odour is used by a wide variety of marine predators to locate prey in the ocean (see Kowalesky et al., 2006; Steinke et al., 2006). Testing the responses of birds to odours at sea is difficult (Nevitt, 1999a) (reviewed by Nevitt, 2008) but techniques have been developed for testing animals in colonies or experimental laboratories in field settings.

In the present study, we tested whether African penguins (*Spheniscus demersus* L.) responded to artificial sources of DMS. African penguins are currently listed as a 'vulnerable' species (Birdlife International, 2004), breeding exclusively on the coast and coastal islands of Namibia and South Africa (Shannon and Crawford, 1999). They feed primarily on anchovies (*Engraulis capensis*) and sardines (*Sardinops sagax*), and competition for food with the commercial purse seine fishery is one of the key factors driving current population decreases (Crawford and Dyer, 1995; Crawford et al., 2001; Crawford et al., 2006). In the present study, we examined whether wild African penguins could detect DMS by deploying this scent in the penguin colony (Clark and Shah, 1992; Nevitt and Haberman, 2003). We confirmed attraction to DMS using a Y-maze, a technique that has previously been used in olfactory studies with birds (e.g. Bonadonna et al., 2003).

MATERIALS AND METHODS

Testing responses of wild birds to odours deployed along walking routes

From 22 to 24 June 2006 (two observations/day), wild African penguins were tested for their responses to DMS on Robben Island, South Africa (33.807 deg.S, 18.366 deg.E), a site where more than 6000 pairs of African penguins breed (Wolfaardt et al., 2001). Most breeding birds at this time of year are rearing chicks (Cooper, 1980), when adults head to sea daily to provision their young (Petersen et al., 2006). Penguins breed in burrows or under the cover of introduced *Acacia cyclops* trees, 10–200 m from the shore, and commute along paths between their nests and the sea. We took advantage of these well-utilized routes to investigate whether birds could detect and would respond to DMS released in the colonies.

We deployed DMS (1 μ molar dissolved in 25 ml distilled water) or a control (25 ml distilled water) in Petri dishes along three separate penguin walkways. These sites were separated by approximately 500 m. The concentration of DMS used in the present study is similar to what has been used in preliminary tests of procellariiform responses to DMS in the past (Cunningham et al., 2003). Flags were placed 1.5 m from the Petri dish in each direction along the walkway. We recorded the time interval that randomly selected penguins spent within the 3 m span between the two flags. Observations were conducted from approximately 30 m from the walkway using 10 \times 50 binoculars in the morning following sunrise (07.30–09.00 h), when most penguins head to sea, and in the evening prior to sunset (16.30–18.00 h), when they return to the island to provision young (Wilson, 1985a; Petersen et al., 2006). Wind direction was offshore on all three days. Thus, as penguins exited the colony, they walked downwind whereas when they approached the colony from the sea they walked upwind. Since penguins were either walking from the nest to the beach or returning from the sea back to their nests, each individual only walked once through the 3 m span during each observation period. Thus, no penguin was counted more than once on any given day. Observations were collected in a blind fashion such that the observer did not know the identity of the solution that was deployed along the walkway. We used an unpaired *t*-test (Zar, 1996) to test whether birds spent significantly different amounts of time in the presence of DMS compared with the presence of the control. Using the same test, we also compared whether there was a significant difference in the time spent between the flags for birds in the morning compared with the evening.

Testing responses of captive birds to odours in a Y-maze

Thirty-one captive adult African penguins of unknown age and sex were tested for their attraction to DMS at the Southern African Foundation for the Conservation of Coastal Birds (SANCCOB) facility at Rietvlei, Cape Town, South Africa. Each year, this facility receives hundreds to thousands of injured or oiled birds. Birds are cleaned, treated, fed for a period of four to five weeks (Parsons and Underhill, 2005) and then released into the wild. Prior to their release, we tested birds in a Y-maze in an outdoor pen at the facility.

The three arms of the Y-maze, each measuring 90 cm length and 53 cm in diameter, were made of opaque plastic. The Y-junction was made of opaque fibreglass. A CPU fan (model # 8850N; EBMPapst, Cape Town, South Africa) was mounted at the end of each of the odour-choice arms to generate a controlled airflow through the Y-maze (6171 min^{-1}). In each odour-choice arm, a Petri dish was placed directly in front of the fan in a compartment separated from the maze by chicken wire. The Petri dish contained either the odour (1 μ molar DMS in 25 ml of distilled water) or a

control (25 ml of distilled water). The location of the experimental and control dishes was varied throughout the trials. The Y-maze was completely cleaned with 75% methanol between trials.

Penguins were randomly chosen from the available birds at SANCCOB. These birds had been brought to the facility because they had been oiled in the wild and were housed in an outdoor facility in large groups (>20 birds). Penguins were individually tested in the Y-maze between 12.00 and 15.00 h (local time), 1.5 to 4.5 h after being fed at 10.30 h. Birds were placed, one at a time, inside an acclimating compartment at the base of the maze for five minutes. The compartment was separated from the rest of the Y-maze by a trap door. Once the trap door was opened, the bird was able to proceed into the Y-maze. To assess the choice made by the bird, we listened to the sound and felt the vibrations of it walking in the Y-maze. A bird was considered to have made a choice when it travelled halfway up an odour-choice arm and remained there for at least one minute (from Bonadonna et al., 2006). The researcher who decided whether a penguin had made a choice was blind to the experimental conditions of each trial. A Binomial test was used to test whether the number of birds choosing the control arm was significantly different from the number of birds choosing the arm scented with DMS. We also recorded the time between the trap door opening and when a bird chose an arm; however, so few penguins chose the control arm (see Results) that we were unable to conduct statistical analyses on these data.

RESULTS

Responses of wild penguins

In the morning observation periods, we collected data on 141 penguins for the DMS deployments and 110 birds for the control exposure. In the evening we observed 84 and 152 birds for the DMS and control deployments, respectively. The response to DMS depended upon the time of day. Penguins presented with DMS in the morning when heading downwind and out to sea spent the same amount of time in the 3 m span as those penguins presented with the control Petri dishes (unpaired *t*-test; $t=0.90$, d.f.=249, $P=0.37$; Fig. 1A). In the presence of DMS, penguins tested in the evening, when walking upwind and returning from their foraging trips walked significantly slower when compared with control birds ($t=2.98$, d.f.=234, $P=0.003$; Fig. 1B). When we pooled the data according to the time of day, we found that penguins spent a significantly longer amount of time between the flags during the evening as compared with the morning observations ($t=8.59$, d.f.=485, $P<0.0001$; data not shown).

Responses in the Y-maze

Seventeen of the 31 penguins tested in the Y-maze responded, with 14 choosing the arm containing DMS and three choosing the control arm (Binomial test; $P=0.005$; Fig. 2). Penguins that chose the DMS arm made their choices in 527 ± 50 s (means \pm s.e.m.) whereas birds choosing the control arm took 707 ± 73 s (means \pm s.e.m.).

DISCUSSION

We investigated how wild African penguins responded to μ molar deployments of DMS, a food-related odour that other seabirds use to locate productive areas of the ocean where prey is likely to be found (reviewed by Nevitt, 2008). Although the concentration of DMS used in our study is higher than seabirds are likely to encounter at sea (see Nevitt, 2000; Nevitt and Bonadonna, 2005b), our results are, nonetheless, an important first step demonstrating that penguins can smell and may use olfactory cues while foraging. We found that wild penguins were able to detect DMS deployments in their

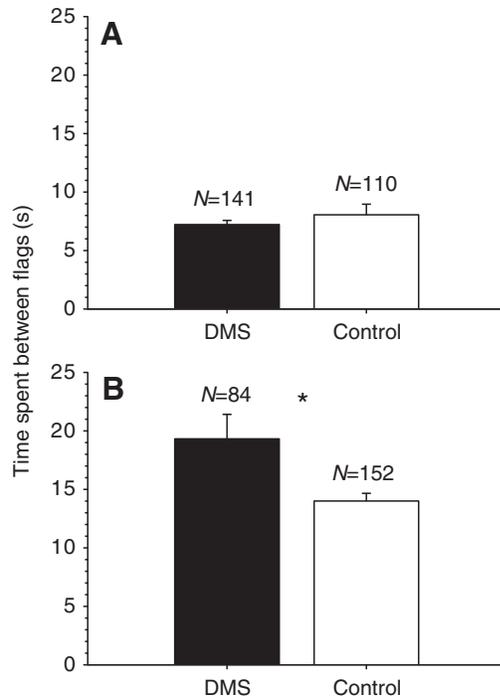


Fig. 1. The mean time (\pm s.e.m.) spent by African penguins in a 3 m span where either DMS or a control was deployed during the (A) morning or (B) evening presentations. In the morning, when birds were walking downwind, there were no significant differences, but penguins spent significantly longer in the presence of DMS in the evening when walking upwind (unpaired *t*-test, **P*=0.003).

colony. Penguins departing the colony in the morning to forage appeared to ignore the DMS presentations, while birds returning to their nests at dusk slowed down in response to the DMS deployments. The direction that penguins were travelling relative to the wind may explain the differences in behaviour that we observed between morning and evening. In the morning, penguins would have been walking with the wind and, hence, would not be likely to detect the DMS until they were at or past the source of the odour. The beach, however, was located downwind of the source of our DMS deployments. Therefore, penguins returning during the evening would be travelling into the wind and could likely detect the presence of DMS prior to arriving at the 3 m span surrounding the DMS source, thus modifying their behaviour. Penguins also appear to be more likely to respond to the odour when in less of a rush, since the pooled data support the observation that penguins returning from the sea walked slower overall than penguins departing the colony in the morning. We also confirmed these results by testing captive birds in a Y-maze; birds preferred the arm of the maze that was scented with DMS. The high number of penguins making no choice in the Y-maze that we observed may be due to the fact that we were working with a stressed captive population that had recently been oiled, which may have compromised their sense of smell (see Solangi and Overstreet, 1982) or their willingness to respond. Both results suggest that African penguins can detect and orient towards this food-related odour.

Foraging penguins typically commute to predictable regions where productivity tends to be high but where their prey are patchily distributed (Williams, 1995), and thus there is an advantage to having a way to detect prey aggregations from a distance. While *en route* to a foraging zone, penguins swim faster and dive to shallower depths

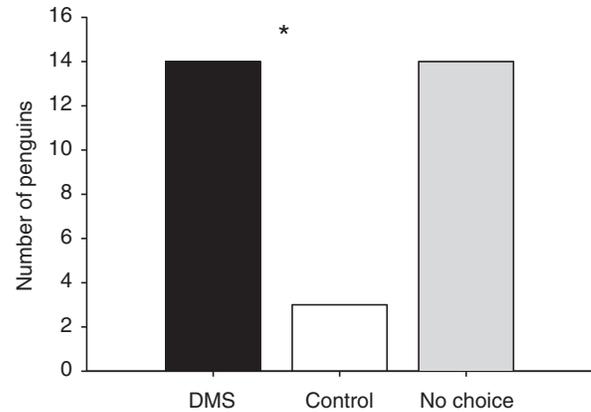


Fig. 2. The number of African penguins that chose the arm of the Y-maze containing DMS or control solutions and those that did not choose either arm (no choice). When analyzing only the birds that made a choice, DMS was significantly preferred over the control (Binomial test, **P*<0.001).

than they do when they are actively foraging (e.g. Wilson et al., 2005; Petersen et al., 2006). Once a productive area is located, a penguin initiates deeper dives to search for prey. The results of the present study suggest that African penguins can detect DMS, and this ability may assist them in foraging. Like procellariiforms (Silverman et al., 2004), penguins might use a multi-modal search strategy to locate prey. On a coarse scale, the presence of high levels of DMS at the water surface may be used to identify foraging areas where fish are located (e.g. Nevitt, 2000; Nevitt and Bonadonna, 2005a) (see also Culik et al., 2000), since dimethylsulphoniopropionate (DMSP), a precursor to DMS (Simo, 2004), has also been shown to serve as a foraging cue to fish across a wide phylogenetic range (Nakajima et al., 1989; Nakajima et al., 1990; DeBose et al., 2008). Even within historically productive areas, aggregations of foraging prey are likely to be patchily distributed, and changes in airborne odours may alert penguins that foraging in a particular area is more or less likely to be successful. Anchovies and sardines, the main prey of African penguins, primarily feed on zooplankton and large phytoplankton (James, 1987; van der Lingen, 2002), both of which have been implicated in the release of DMS (Dacey and Wakeham, 1986; Daly and DiTullio, 1996; Wolfe and Steinke, 1996) (reviewed by Nevitt, 2000; Nevitt, 2008). On a finer scale, visual cues are probably used by penguins to locate their prey. For example, in African penguins, dive depth is limited by ambient light levels (Wilson et al., 1993) with little foraging at night (Wilson and Wilson, 1995; Ryan et al., 2007). Whether smell could be used underwater to help find prey, as is the case in certain mammals (see Catania, 2006), is an intriguing question worthy of further investigation.

Studies on how seabirds use DMS to find food have previously focused on procellariiforms that forage over great distances. For example, the blue petrel (*Halobaena caerulea*), which responds to DMS as both a chick and as an adult (Nevitt et al., 1995; Nevitt, 2000; Cunningham et al., 2003; Bonadonna et al., 2006) forages over pelagic waters at distances of >1000 km from their nesting island (Cherel et al., 2002). The ability to smell DMS in these far-flying species is adaptive as it allows these birds to detect aggregations of zooplankton from greater distances than would be possible using visual cues alone. Sensitivity to DMS also allows these birds to exploit a resource prior to the arrival of more aggressive birds that do not respond to DMS (see Van Buskirk and

Nevitt, 2008). Although less is known about the sensory ecology of foraging penguins, hunting by smell is likely in this group for a variety of reasons. Firstly, penguins are the closest relatives to the procellariiforms [see Ksepka et al. (Ksepka et al., 2006) and references therein] and, similar to procellariiform adults, their chicks have a tube-nose (Kinsky, 1960). Thus, it seems logical to predict that penguins also have a functioning sense of smell, particularly in light of recent evidence (Van Buskirk and Nevitt, 2008) that suggests that DMS behavioural sensitivity is ancestral in the procellariiforms. Secondly, although penguins generally forage over shorter distances compared with procellariiform seabirds [17–62 km for African penguins rearing chicks (Petersen et al., 2006)], penguins have a slower commuting speed than flying seabirds [4.8 km h⁻¹ for the African penguin (Wilson, 1985b); 23.1 km h⁻¹ for the white-chinned petrel (*Procellaria aequinoctialis*) (Weimerskirch et al., 1999)], thus making it costly to commute to, and dive in, unproductive areas. Additionally, because penguins are slower, the amount of time spent during transit to and from the foraging grounds is comparable between penguins and procellariiforms, suggesting that these birds may be similar in their foraging strategies. For example, while provisioning chicks, African penguins spend 27–36.6 h away from the nest (Petersen et al., 2006) while a closely related congener, the Magellanic penguin (*Spheniscus magellanicus*), can spend one day to a number of weeks at sea (Wilson et al., 2005). By comparison, while provisioning a chick, the blue petrel and thin-billed prion (*Pachyptila belcheri*) alternate between short and long trips, with a mean of 1.8/7.2 (short/long) and 1.4/6.7 days, respectively (Chaurand and Weimerskirch, 1994; Duriez et al., 2000).

This is the first study to clearly demonstrate, by way of experimentation, that a penguin is able to detect an odour (see also Culik et al., 2000; Culik, 2001). Although the present study does not directly test DMS as a foraging cue, it does implicate the use of odours by penguins while hunting. Future studies at sea in which DMS, or its precursor DMSP, are deployed into the ocean (e.g. Nevitt et al., 1995) need to be conducted to definitively show that penguins, like procellariiforms, are using odours to forage.

We thank the staff at SANCCOB for assistance with handling penguins. The field component of this project would not have been possible without the assistance of Prof. L. G. Underhill and S. Kuyper, Avian Demography Unit, University of Cape Town, who helped with access to Robben Island. We thank Dr D. Bolton (Bristol Zoo, UK), B. Dyer (Marine and Coastal Management, South Africa) and members of the Earthwatch program who collected data on Robben Island, and T. M. Leshoro (Robben Island Museum), whose knowledge of the penguin colony was invaluable. The comments of Dr G. Nevitt, Dr S. Lema, Dr T. Crombach, Dr F. Bonadonna and one anonymous referee greatly improved this manuscript. Finally we thank B. Watkins, M. Honig and Dr R. Wanless for support during the project.

REFERENCES

- Bang, B. G. and Cobb, S. (1968). The size of the olfactory bulb in 108 species of birds. *Auk* **85**, 55–61.
- Berresheim, H., Andreae, M. O., Ayers, G. P. and Gillett, R. W. (1989). Distribution of biogenic sulfur-compounds in the remote southern-hemisphere. In *Biogenic Sulfur in the Environment* (ed. E. J. Saltzman and W. J. Cooper), pp. 352–356. Washington, DC: American Chemical Society.
- BirdLife International (2004). *Threatened Birds of the World* CD ROM. Cambridge: BirdLife International.
- Bonadonna, F., Cunningham, G. B., Jouventin, P., Hesters, F. and Nevitt, G. A. (2003). Evidence for nest-odour recognition in two species of diving petrel. *J. Exp. Biol.* **206**, 3719–3722.
- Bonadonna, F., Caro, S., Jouventin, P. and Nevitt, G. A. (2006). Evidence that blue petrel, *Halobaena caerulea*, fledglings can detect and orient to dimethyl sulfide. *J. Exp. Biol.* **209**, 2165–2169.
- Catania, K. C. (2006). Underwater 'sniffing' by semi-aquatic mammals. *Nature* **444**, 1024–1025.
- Chaurand, T. and Weimerskirch, H. (1994). The regular alternation of short and long foraging trips in the blue petrel *Halobaena caerulea*: a previously undescribed strategy of food provisioning in a pelagic seabird. *J. Anim. Ecol.* **63**, 275–282.
- Cherel, Y., Bocher, P., Trouve, C. and Weimerskirch, H. (2002). Diet and feeding ecology of blue petrels *Halobaena caerulea* at Iles Kerguelen, Southern Indian Ocean. *Mar. Ecol. Prog. Ser.* **228**, 283–299.
- Clark, L. and Shah, P. S. (1992). Information content of prey odour plumes: what do foraging Leach's storm petrels know? In *Chemical Senses in Vertebrates VI* (ed. R. L. Doty and D. Muller-Schwarze), pp. 421–427. New York: Plenum Press.
- Cooper, J. (1980). Breeding biology of the Jackass Penguin with special reference to its conservation. In *Proceedings of the 4th Pan-African Ornithological Congress* (ed. D. N. Johnson), pp. 227–231. Johannesburg: South African Ornithological Society.
- Crawford, R. J. M. and Dyer, B. M. (1995). Responses by four seabirds to a fluctuating availability of Cape anchovy *Engraulis capensis* off South Africa. *Ibis* **137**, 329–339.
- Crawford, R. J. M., David, J. H. M., Shannon, L. J., Kemper, J., Klages, N. T. W., Rioux, J.-P., Underhill, L. G., Ward, V. C., Williams, A. J. and Wolfaardt, A. C. (2001). African penguins as predators and prey – coping (or not) with change. *Afr. J. Mar. Sci.* **23**, 435–477.
- Crawford, R. J. M., Barham, P. J., Underhill, L. G., Shannon, L. J., Coetzee, J. C., Dyer, B. M., Leshoro, T. M. and Upfold, L. (2006). The influence of food availability on breeding success of African penguins *Spheniscus demersus* at Robben Island, South Africa. *Biol. Conserv.* **132**, 119–125.
- Culik, B. (2001). Finding food in the open ocean: foraging strategies in Humboldt penguins. *Zoology (Jena)* **104**, 327–338.
- Culik, B., Hennicke, J. and Martin, T. (2000). Humboldt penguins outmanoeuvring El Niño. *J. Exp. Biol.* **203**, 2311–2322.
- Cunningham, G. B., Van Buskirk, R. W., Bonadonna, F., Weimerskirch, H. and Nevitt, G. A. (2003). A comparison of the olfactory abilities of three species of procellariiform chicks. *J. Exp. Biol.* **206**, 1615–1620.
- Dacey, J. W. H. and Wakeham, S. G. (1986). Oceanic dimethyl sulfide: production during zooplankton grazing on phytoplankton. *Science* **233**, 1314–1316.
- Daly, K. L. and DiTullio, G. R. (1996). Particulate dimethylsulfoniopropionate removal and dimethyl sulfide production by zooplankton in the Southern Ocean. In *Biological and Environmental Chemistry of DMSP and Related Sulfonium Compounds* (ed. R. P. Kiene, P. T. Visscher, M. D. Kellor and G. O. Kirst), pp. 223–238. New York: Plenum Press.
- DeBose, J. L., Lema, S. C. and Nevitt, G. A. (2008). Dimethylsulfoniopropionate as a foraging cue for reef fishes. *Science* **319**, 1356.
- Duriez, O., Weimerskirch, H. and Fritz, H. (2000). Regulation of chick provisioning in the thin-billed prion: an interannual comparison and manipulation of parents. *Can. J. Zool.* **78**, 1275–1283.
- Hackett, S. J., Kimball, R. T., Reddy, S., Bowie, R. C. K., Braun, E. L., Braun, M. J., Chojnowski, J. L., Cox, W. A., Han, K.-L., Harshman, J. et al. (2008). A phylogenetic study of birds reveals their evolutionary history. *Science* **320**, 1763–1768.
- James, A. G. (1987). Feeding ecology, diet and field-based studies on feeding selectivity of the Cape anchovy *Engraulis capensis* Gilchrist. *Afr. J. Mar. Sci.* **5**, 673–692.
- Kinsky, F. C. (1960). The yearly cycle of the Northern blue penguin (*Eudyptula minor novaehollandiae*) in the Wellington Harbour area. *Rec. Dominion Mus. NZ* **3**, 145–218.
- Kowalewsky, S., Dambach, M., Mauck, B. and Dehnhardt, G. (2006). High olfactory sensitivity for dimethyl sulphide in harbour seals. *Biol. Lett.* **2**, 106–109.
- Ksepka, D. T., Bertelli, S. and Giannini, N. P. (2006). The phylogeny of the living and fossil Sphenisciformes (penguins). *Cladistics* **22**, 412–441.
- McTaggart, A. R. and Burton, H. (1992). Dimethyl sulfide concentrations in the surface waters of the Australasian Antarctic and Sub-Antarctic oceans during an austral summer. *J. Geophys. Res. Oceans* **97**, 14407–14412.
- Nakajima, K., Uchida, A. and Ishida, Y. (1989). A new feeding attractant, dimethyl- β -propiothetin, for freshwater fish. *Nippon Suisan Gakkai Shi* **55**, 689–695.
- Nakajima, K., Uchida, A. and Ishida, Y. (1990). Effect of a feeding attractant, dimethyl- β -propiothetin on growth of marine fish. *Nippon Suisan Gakkai Shi* **56**, 1151–1154.
- Nevitt, G. A. (1999a). Foraging by seabirds on an olfactory landscape. *Am. Sci.* **87**, 46–53.
- Nevitt, G. A. (1999b). Olfactory foraging in Antarctic seabirds: a species-specific attraction to krill odors. *Mar. Ecol. Prog. Ser.* **177**, 235–241.
- Nevitt, G. A. (2000). Olfactory foraging by Antarctic procellariiform seabirds: life at high Reynolds numbers. *Biol. Bull.* **196**, 245–253.
- Nevitt, G. A. (2008). Sensory ecology on the high seas: the odor world of the procellariiform seabirds. *J. Exp. Biol.* **211**, 1706–1713.
- Nevitt, G. A. and Bonadonna, F. (2005a). Seeing the world through the nose of a bird: new developments in the sensory ecology of procellariiform seabirds. *Mar. Ecol. Prog. Ser.* **287**, 292–295.
- Nevitt, G. A. and Bonadonna, F. (2005b). Sensitivity to dimethyl sulphide suggests a mechanism for olfactory navigation by seabirds. *Biol. Lett.* **1**, 303–305.
- Nevitt, G. A. and Haberman, K. (2003). Behavioral attraction of Leach's storm-petrels (*Oceanodroma leucorhoa*) to dimethyl sulfide. *J. Exp. Biol.* **206**, 1497–1501.
- Nevitt, G. A., Veit, R. R. and Kareiva, P. (1995). Dimethyl sulphide as a foraging cue for Antarctic procellariiform seabirds. *Nature* **376**, 680–682.
- Nevitt, G. A., Reid, K. and Trathan, P. (2004). Testing olfactory foraging strategies in an Antarctic seabird assemblage. *J. Exp. Biol.* **207**, 3537–3544.
- Parsons, N. J. and Underhill, L. G. (2005). Oiled and injured African penguins *Spheniscus demersus* and other seabirds admitted for rehabilitation in the Western Cape, South Africa, 2001 and 2002. *Afr. J. Mar. Sci.* **27**, 289–296.
- Petersen, S. L., Ryan, P. G. and Gremillet, D. (2006). Is food availability limiting African penguins *Spheniscus demersus* at Boulders? A comparison of foraging effort at mainland and island colonies. *Ibis* **148**, 14–26.
- Ryan, P. G., Petersen, S. L., Simeone, A. and Gremillet, D. (2007). Diving behaviour of African penguins: do they differ from other *Spheniscus* penguins? *Afr. J. Mar. Sci.* **29**, 153–160.
- Shannon, L. J. and Crawford, R. J. M. (1999). Management of the African penguin *Spheniscus demersus*-insights from modelling. *Mar. Ornithol.* **27**, 119–128.
- Silverman, E. D., Veit, R. R. and Nevitt, G. A. (2004). Nearest neighbors as foraging cues: information transfer in a patchy environment. *Mar. Ecol. Prog. Ser.* **277**, 25–35.

- Simo, R.** (2004). From cells to globe: approaching the dynamics of DMS(P) in the ocean at multiple scales. *Can. J. Fish. Aquat. Sci.* **61**, 673-684.
- Solangi, M. A. and Overstreet, R. M.** (1982). Histopathological changes in two estuarine fishes, *Menidia beryllina* (Cope) and *Trinectes maculatus* (Bloch and Schneider) exposed to crude oil and its water-soluble fraction. *J. Fish Dis.* **5**, 13-35.
- Steinke, M., Stefels, J. and Stadhuis, E.** (2006). Dimethyl sulfide triggers search behavior in copepods. *Limnol. Oceanogr.* **51**, 1925-1930.
- Stephens, D. W. and Krebs, J. R.** (1986). *Monographs in Behavior and Ecology: Foraging Theory*. Princeton, NJ: Princeton University Press.
- Van Buskirk, R. W. and Nevitt, G. A.** (2008). The influence of developmental environment on the evolution of olfactory foraging behaviour in procellariiform seabirds. *J. Evol. Biol.* **21**, 67-76.
- Van der Lingen, C. D.** (2002). Diet of sardine *Sardinops sagax* in the southern Benguela upwelling ecosystem. *Afr. J. Mar. Sci.* **24**, 301-316.
- Warham, J.** (1990). *The Petrels: Their Ecology and Breeding Systems*. London: Academic Press.
- Weimerskirch, H.** (2007). Are seabirds foraging for unpredictable resources? *Deep-Sea Res. Part II Oceanogr. Res. Pap.* **54**, 211-223.
- Weimerskirch, H., Catard, A., Prince, P. A., Cherel, Y. and Croxall, J. P.** (1999). Foraging White-chinned Petrels *Procellaria aequinoctialis* at risk: from the tropics to Antarctica. *Biol. Conserv.* **87**, 273-275.
- Williams, T. D.** (1995). *The Penguins Spheniscidae*. Oxford: Oxford University Press.
- Wilson, R. P.** (1985a). Diurnal foraging patterns of the Jackass Penguin. *Ostrich* **56**, 212-214.
- Wilson, R. P.** (1985b). The Jackass Penguin (*Spheniscus demersus*) as a pelagic predator. *Mar. Ecol. Prog. Ser.* **25**, 219-227.
- Wilson, R. P. and Wilson, M. P. T.** (1995). The foraging behaviour of the African Penguin *Spheniscus demersus*. In *The Penguins* (ed. P. Dann, I. Norman and P. Reilly), pp. 244-265. Chipping Norton: Surrey Beatty.
- Wilson, R. P., Puetz, K., Bost, C. A., Culik, B. M., Bannasch, R., Reins, T. and Adelung, D.** (1993). Diel dive depth in penguins in relation to diel vertical migration of prey: whose dinner by candlelight? *Mar. Ecol. Prog. Ser.* **94**, 101-104.
- Wilson, R. P., Scolaro, J. A., Gremillet, D., Kierspel, M. A. M., Laurenti, S., Upton, J., Gallelli, H., Quintana, F., Freke, E., Muller, G. et al.** (2005). How do Magellanic penguins cope with prey variability in their access to prey? *Ecol. Monogr.* **75**, 379-401.
- Wolfaardt, A. C., Underhill, L. G., Crawford, R. J. M. and Klages, N. T. W.** (2001). Results of the 2001 census of African penguins *Spheniscus demersus* in South Africa: first measures of the impact of the Treasure oil spill on the breeding population. *Trans. R. Soc. S. Afr.* **56**, 45-49.
- Wolfe, G. V. and Steinke, M.** (1996). Grazing-activated production of dimethyl sulfide (DMS) by two clones of *Emiliania huxleyi*. *Limnol. Oceanogr.* **41**, 1151-1160.
- Zar, J. H.** (1996). *Biostatistical Analysis* 3rd Edn. Upper Saddle River, NJ: Prentice Hall.