Insight of scent: experimental evidence of olfactory capabilities in the wandering albatross (*Diomedea exulans*)

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SUMMARY

Wandering albatrosses routinely forage over thousands of kilometres of open ocean, but the sensory mechanisms used in the food search itself have not been completely elucidated. Recent telemetry studies show that some spatial behaviours of the species are consistent with the 'multimodal foraging strategy' hypothesis which proposes that birds use a combination of olfactory and visual cues while foraging at sea. The 'multimodal foraging strategy' hypothesis, however, still suffers from a lack of experimental evidence, particularly regarding the olfactory capabilities of wandering albatrosses. As an initial step to test the hypothesis, we carried out behavioural experiments exploring the sensory capabilities of adult wandering albatrosses at a breeding colony. Three two-choice tests were designed to investigate the birds' response to olfactory and visual stimuli, individually or in combination. Perception of the different stimuli was assessed by comparing the amount of exploration directed towards an 'experimental' display or a 'control' display. Our results indicate that birds were able to perceive the three types of stimulus presented: olfactory, visual and combined. Moreover, olfactory and visual cues were found to have additional effects on the exploratory behaviours of males. This simple experimental demonstration of reasonable olfactory capabilities in the wandering albatross supports the 'multimodal foraging strategy' and is consistent with recent hypotheses of the evolutionary history of procellariiforms.

Key words: *Diomedea exulans*, behaviour, multimodal, olfaction, vision, signal-detection theory.

INTRODUCTION

Procellariiform seabirds (albatrosses, petrels, shearwaters) are unusual among other avian orders in that most of these so-called 'tube-nose' birds have a well-developed olfactory neuroanatomy (Bang, 1966) and good associated capabilities. Procellariiforms use, or have been suggested to use, their sense of smell in various behaviours including foraging (Hutchison and Wenzel, 1980), homing (Bonadonna et al., 2001), ocean navigation (Nevitt and Bonadonna, 2005) and even some social aspects such as individual recognition and mate choice (Bonadonna and Nevitt, 2004; Hagelin and Jones, 2007; Mardon and Bonadonna, 2009). Following Grubb's pioneering experiments (Grubb, 1972), most of the early work investigated sensitivity to food-related scents by exposing wild seabirds to odorous stimuli such as cod liver oil-soaked sponges (Jouventin and Robin, 1983; Lequette et al., 1989), scented oil slicks (Hutchison and Wenzel, 1980; Nevitt et al., 1995; Nevitt, 1999; Nevitt et al., 2004) or aerosol plumes (Nevitt et al., 1995). These experiments provided an extensive list of procellariiform species for which olfactory foraging was supported, including storm petrels (*Oceanites oceanicus*, *Oceanodroma leucorhoa*), petrels (*Pagodroma nivea*, *Macronectes giganteus*, *Daption capense*, *Procellaria aequinoctialis*), shearwaters (*Puffinus gravis*, *P. creatopus*, *P. griseus*, *P. puffinus*, *P. tenuirostris*), fulmars (*Fulmarus glacialis*, *F. glacialoides*), albatrosses (*Diomedea nigripes*, *D. chrysostoma*, *D. melanophris*, *Phoebetria palpebrata*) and prions (*Pachyptila* sp.).

The wandering albatross (*Diomedea exulans*, Diomedeidae, Linnaeus 1758) is the largest of the procellariiform seabirds and has the largest wingspan of any living bird. Its foraging activity usually takes it over thousands of kilometres of open ocean, where it feeds on a variety of squids that are captured or found dead at the surface (Cherel and Weimerskirch, 1999). Yet, the sensory mechanisms used in this foraging search are still not completely understood. Early experiments on the response of albatrosses to olfactory foraging cues did not provide conclusive results. For instance, black-footed (Hutchison and Wenzel, 1980) and light-mantled sooty albatrosses (Lequette et al., 1989) are regularly attracted to food-related odours. In contrast, wandering, grey-headed and black-browed albatrosses do not appear to be attracted to either cod liver oil or dimethyl sulphide (DMS)-scented oil (Lequette et al., 1989; Nevitt et al., 1995), though black-browed albatrosses significantly respond to pyrazine- and herring-scented stimuli (Nevitt et al., 2004). Such intricacy probably explains why albatrosses are commonly thought to hunt visually (Prince and Morgan, 1990; Warham, 1990; Nevitt et al., 1995).

New elements from telemetric studies (Weimerskirch et al., 2005; Phalan et al., 2007) have recently improved our understanding of wandering albatrosses' behaviours. For instance, foraging activity is greater during daylight, when they feed mainly on large, isolated squids using active flight search (Phalan et al., 2007). At night, however, they feed on small, aggregated and bioluminescent squid by switching to a 'sit-and-wait' strategy at the water surface, probably because of the limited visual cues available for an active search (Phalan et al., 2007). Using the same GPS data, Nevitt and colleagues (Nevitt et al., 2008) showed that some spatial behaviours of foraging wandering albatrosses are consistent with the

'multimodal (vision and olfaction) foraging strategy' hypothesis (VanBuskirk and Nevitt, 2008). This hypothesis proposes that birds use more than a single mechanism of sensory detection when foraging, taking advantage of olfactory cues for initial detection and localisation of potential prey, whereas vision would be predominant during prey capture. The 'multimodal foraging strategy' hypothesis, however, still suffers from a lack of experimental evidence, particularly regarding the olfactory capabilities of wandering albatrosses, probably due to the difficulty of carrying out controlled experiments on large marine predators.

The purpose of our study was to provide an initial test of the 'multimodal foraging strategy' hypothesis by exploring the sensitivity of wandering albatrosses to relevant types of stimuli. Therefore, we investigated the birds' behavioural response to olfactory and visual cues. To do so, three similar experiments were carried out on incubating adults (at the colony), in which birds were offered the choice between an experimental/stimulus display and a control/empty display. Displays were designed so that they could provide (i) olfactory stimuli alone in the first experiment (olfaction test), (ii) visual stimuli alone in the second experiment (vision test), and (iii) both olfactory and visual stimuli in the third experiment (combined test). We assumed that a bird perceived and responded to a stimulus (olfactory, visual or both) if the experimental display elicited more exploration behaviours than the control display.

MATERIALS AND METHODS
Study site and animals
We studied wandering albatrosses in January 2009 at Cape Ratmanoff (49°14′S, 70°34′E) on the west coast of Kerguelen Island, a French sub-Antarctic territory in the Southern Indian Ocean. A total of 32 breeding pairs (N=64 birds), forming a loose colony around the area, were monitored daily for foraging and incubating shifts. Birds were sexed using reliable morphological secondary sexual traits such as plumage patterns, beak morphology and size (Weimerskirch et al., 1989).

Experimental procedure
Three behavioural experiments were designed to test the sensory capabilities of adult wandering albatrosses, focusing on vision and olfaction. In each experiment, birds were offered a choice between two sample displays: an experimental display containing chunks of tuna and a control display left empty. A roughly similar quantity (about 25 g) of freshly opened, unflavoured, canned tuna ('Thon au naturel' Albacore®) was used as the experimental stimulus for all tests. Canned tuna was not chosen in order to simulate an artificial foraging situation but simply to provide a shapeless, unfamiliar yet naturally intense stimulus. All displays were similarly made of a 50 ml transparent centrifuge tube (with a conical bottom) taped to a metal peg, used to secure them to the ground during tests. We used three different sets of experimental displays, each one being adapted to one of the three experiments performed (Fig. 1). In experiment 1, the 'olfaction test', we tested the effect of olfactory stimuli alone by covering the whole surface of the centrifuge tubes with black opaque masking tape while leaving the top of the tubes open. Care was taken that the depth of the tubes made it impossible for the bird to see the tuna at the bottom. In experiment 2, the 'vision test', we tested the effect of visual stimuli alone by sealing the top of the tubes with Parafilm® while leaving the surface of the tubes uncovered and therefore transparent. In experiment 3, the 'combined test', we tested the combined effects of olfactory and visual stimuli by leaving the surface and top of the tubes uncovered. Note that the design of the displays ensured that the intensity of a given stimulus (olfactory or visual) was similar in the isolated and combined tests. Indeed, the visual stimulus was as readily accessible in the vision test as it was in the combined test (transparent tubes). Similarly, the olfactory stimulus was equivalent in the olfaction and the combined tests as diffusion of volatile chemicals was unconstrained in both cases.

Wandering albatrosses have historically been relatively unexposed to human or predatory disturbances on their colony sites and do not show a strong response to slow ground-level approaches. For each trial, an incubating bird was therefore approached by slowly crawling to the nest. The two sample displays (experimental and control) were placed on the turf surrounding a nest, within 30 cm of each side of the bird's head. The experimenter then crawled back and the bird's response to the displays was recorded from 15 m away by a focal animal sampling observation of 10 min. For each trial, we recorded three complementary variables: the direction of the initial peck, the number of pecks on each display and the total time spent exploring each display. In our experiments, we defined a 'peck' event as a head movement from the normal incubating position towards one of the displays resulting in at least one contact between the bird's bill and the display. We considered a peck event to be finished when the bird returned to its normal incubating position. The durations of all peck events were recorded using a stopwatch and summed to obtain the total exploring time over a trial. Sample containers were removed immediately after the end of each trial.

To reduce disturbance of the animals and obtain independent data between treatments, each individual participated in only one of the three experiments. Overall, 21 birds (9 females and 12 males) were tested in the olfaction test, 18 birds (9 females and 9 males) in the vision test, and 21 birds (8 females and 13 males) in the combined test. The position of the two different displays (control and experimental) was randomised between trials with respect to the bird's side (left or right) to avoid lateralisation effects. The order of the trials, with regard to the type of experiment, was also randomised to reduced possible environmental effects. Finally, trials were carried out only under low-wind conditions (Beaufort wind force scale <3) to reduce possible wind effects on odour dispersion. The variable nature of the direction faced by incubating birds, together with the randomisation of the position of the two displays, should have further reduced possible wind-induced bias.

Animal ethics
All aspects of the study were performed according to guidelines established by the IPEV (Institut Polaire Français Paul-Emile Victor) and the CNRS for the Ethical Treatment of Animals and complied with current French regulations. Several factors indicate that the
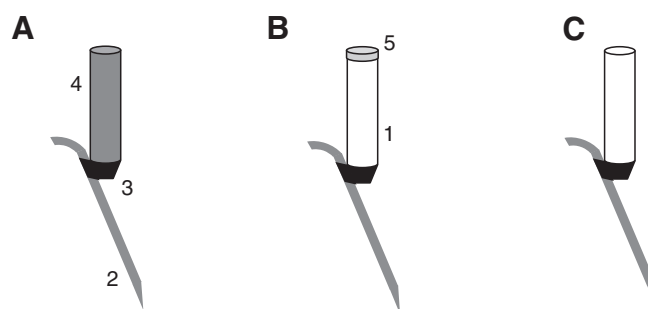

Fig. 1. Schematic layout of the different types of sample display used in the experiments: (A) Olfaction test, (B) vision test, (C) combined test. Key: 1, transparent plastic vial; 2, metal peg; 3, attaching tape; 4, opaque masking tape; 5, Parafilm® seal.

experiment is unlikely to have caused any major disturbance to the birds. No bird was handled and each was approached only once as mentioned above. Moreover, none of the tested individuals deserted the nest or moved away from the experimenter, and all resumed resting activity on the nest during or soon after the trial. Disturbance was therefore much less than in most current monitoring and telemetry studies, which have been reported to have no effect on albatross survival and breeding success (Weimerskirch et al., 2007).

Analysis

For clarity, our data analysis is organised into two sections. The first considers each experiment individually (olfaction, vision and combined tests), exploring whether birds did or did not perceive the stimulus associated with this particular experiment. In the second, the 'signal detection theory' framework is used to compare albatrosses' relative sensitivities to the different types of stimuli.

(A) Intra-experiment analysis

For each experiment, we compared the extent of exploration expressed by the incubating birds towards the two displays using several variables: (i) the direction of the initial peck, (ii) the number of pecks (no. pecks) and (iii) the total exploring time (T_{expl}). We also created a fourth summary variable, the total score, combining the first three variables for each trial. To compute this summary variable, a score out of 3 was calculated for each display; each of the above three variables contributing one point to the total score of the experimental or control display, depending on the direction of disparity. As an illustration, a trial in which the initial peck was directed to the control display, the experimental display received 12 pecks while the control received 5, and the total exploring time was 25 s on the experimental display and 11 s on the control, received a total score of 2 for the experimental display and 1 for the control. No point was attributed, for a given variable, when the two displays received an equal amount of investigation for this variable, a situation hereafter referred to as a 'draw'.

In a first analytical approach, we calculated for each of the four variables the proportion of trials in which the experimental display received more exploration than the control. For instance, out of the 21 olfaction trials, the experimental display received a longer exploring time in 12 instances, the control display received a longer exploring time in 4 instances and the two displays received equal exploring time in 5 instances (draws). The significance of all calculated proportions was then assessed using one-tailed exact binomial tests; that is, we tested the specific hypothesis that the presence of the canned tuna stimulus in the experimental display would increase exploratory behaviours compared with the control display. Note that draw outcomes were not considered in our statistical analyses. Indeed, excluding these while providing their frequency appeared to be the most biologically appropriate and statistically relevant option for several reasons. First, there was no correlation between the occurrence of draws and other variables such as the time of the day, the bird sex or the stimulus involved. Moreover, a large proportion of these draws (43%) were 'zero-draws', i.e. trials in which the bird did not respond at all to the displays. In most of these cases, the bird returned to rest (beak under the wing) straight after deployment of the displays, or did not wake up at all during deployment. Therefore the inclusion of draw outcomes would provide virtually no additional biological information while increasing data noise and the number of statistical tests involved.

In a second approach, we compared, for each experiment, the absolute values of no. pecks and T_{expl} between experimental and control displays. As an acceptable level of normality could not be obtained with these variables, regardless of the transformation applied, we used Wilcoxon rank-sum non-parametric tests. Again, one-tailed tests were chosen to test for the specific hypothesis that the extra stimulus in the experimental display would elicit more exploratory behaviours from the birds.

(B) Inter-experiment analysis

Results from two-choice experiments are generally not well suited for comparison across various treatments as they do not consist of a single variable. Therefore, to allow comparison of the results from our olfaction, vision and combined tests, we used the framework of 'signal detection theory' (Green and Swets, 1966). Signal detection theory was specifically developed by neuropsychologists as a way to analyse sensitivity experiments, in which sensory signals must be distinguished from a noisy background. It provides a method for assessing sensory performance and a framework for analysing this performance. Individuals are considered as decision makers, with four possible outcomes: hit (if signal present and detected), miss (if signal present but undetected), false alarm (if signal absent but detected), and correct rejection (if signal absent and undetected). The probability of the various outcomes can then be calculated from the total number of trials and converted into a z-score using z-tables (for normalised standardised data). In the 'signal detection theory', the sensitivity d' to a signal is defined as 'z (hits)–z (false alarm)'. This framework therefore provided us with a way to quantitatively estimate the birds' sensitivity to the different stimuli. Indeed, in our experiments, exploration of the experimental display could be considered as a 'hit' (signal present and detected) and exploration of the control display as a 'false alarm' (signal absent but detected). This analytical approach has the advantage of accounting for the simple effect of curiosity to new objects around the nest, and for biases associated with the personalities of the tested animals, such as high curiosity or shyness. In the present study, a positive value for sensitivity means that the extra stimulus in this experiment increased detection and/or exploration by the birds compared with the control display.

For each experiment, we first calculated the sensitivities d'_1 and d'_2, associated respectively with each of the no. pecks and T_{expl} variables. To do so, we converted the number of pecks on each display (no. pecks) into a probability, simply by dividing by the maximum number of pecks performed on a display, all trials confounded. Similarly, we converted the exploring time on each display (T_{expl}) into a probability, simply by dividing by the total time of the trial (600 s). Finally, in order to create a summary sensitivity variable, the two initial sensitivities d'_1 and d'_2 were scaled and averaged to obtain an overall sensitivity D', comparable across experiments. Note that data from the three experiments were independent as we used different birds in each.

The combined effects of sex and stimulus type ('Experiment') on the sensitivity D' were examined with a global fixed-effects ANOVA model. Based on the outcome of this initial model, we further investigated the experiment effect within each sex separately also using fixed-effects ANOVA models. *Post-hoc* pair-wise comparisons were carried out using standard t-tests.

RESULTS
(A) Intra-experiment analysis

In the olfaction test (21 trials), albatrosses could only discriminate between the two displays based on the odour cues emanating from the vials. Significantly more initial pecks were directed at the experimental display (initial peck: 14 out of 17; 4 trials with no
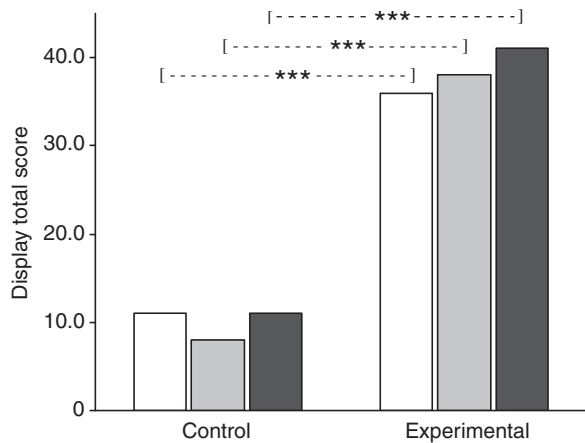
Fig. 2. Total score for each display, control and experimental, for the three experiments. Open bars, olfaction test; grey bars, vision test; black bars, combined test. Asterisks indicate a significant difference between the two displays (***$P<0.001$; one-tailed exact binomial test).

The outcome of the three experiments thus indicates that albatrosses are able to perceive each of the three different types of stimulus presented.

(B) Inter-experiment analysis

The different sensitivities d'_1, d'_2 and D' calculated are presented in Fig. 4. Note that, consistent with the results reported above, sensitivity values are all positive, suggesting that the extra stimuli in the experimental displays all increased detection and/or exploration by the birds compared with the control display.

The fixed-effects ANOVA model investigating the influence of sex and stimulus type on the sensitivity D' (Table 1) shows a significant interaction term. This suggests that the sensitivity varies differently with the type of stimulus, according to the sex of the birds. Thus, we subsequently explored the influence of the stimulus type on the sensitivity D' of wandering albatrosses within each sex separately. The type of stimulus presented did not significantly affect females' sensitivity D' (d.f.=2, sum of squares (SSq) [Type1]=1.3028, F-value=1.1378, $P=0.3387$). In contrast, it significantly affected males' sensitivity D' (d.f.=2, SSq

peck; $P=0.0064$). Moreover, there was a higher proportion of trials in which the experimental display elicited more exploratory behaviours than the control (no. pecks: 10 out of 14, 7 draws, $P=0.0898$; T_{expl}: 12 out of 16, 5 draws, $P=0.0384$; total score: 36 out of 47, 16 draws, $P=0.0002$) (Fig. 2). Comparison of the absolute values of no. pecks and T_{expl} between the two displays (Fig. 3) shows that the olfactory experimental display elicited a higher number of pecks and a longer exploring time than the control display, although these contrasts do not reach significance (no. pecks: Wilcoxon rank-sum test, $Z=0.9831$, $P=0.1628$; T_{expl}: Wilcoxon rank-sum test, $Z=1.5723$, $P=0.0579$).

In the vision test (18 trials), albatrosses could only discriminate between the two displays using the visual cues observed through the transparent vials. As in the previous experiment, significantly more initial pecks were directed at the experimental display (initial peck: 14 out of 18; $P=0.0154$). Moreover, there was a higher proportion of trials in which the experimental display elicited more exploratory behaviours than the control (no. pecks: 11 out of 14, 4 draws, $P=0.0287$; T_{expl}: 13 out of 14, 4 draws, $P=0.0009$; total score: 38 out of 46, 8 draws, $P=0.0009$) (Fig. 2). Comparison of the absolute values of no. pecks and T_{expl} between the two displays (Fig. 3) shows that the visual experimental display elicited a significantly higher number of pecks and exploring time than the control display (no. pecks: Wilcoxon rank-sum test, $Z=2.1953$, $P=0.0141$; T_{expl}: Wilcoxon rank-sum test, $Z=1.7484$, $P=0.0402$).

In the last experiment, the combined test (21 trials), albatrosses could use both odour and visual cues from the vials to discriminate between the two displays. In this case again, more initial pecks were directed at the experimental display although this proportion did not reach significance (initial peck: 14 out of 20; 1 trial with no peck; $P=0.0577$). Moreover, there was a higher proportion of trials in which the experimental display elicited more exploratory behaviours than the control (no. pecks: 14 out of 17, 4 draws, $P=0.0064$; T_{expl}: 13 out of 15, 6 draws, $P=0.0037$; total score: 41 out of 52, 11 draws, $P<0.0001$) (Fig. 2). Comparison of the absolute values of no. pecks and T_{expl} between the two displays (Fig. 3) shows that the combined experimental display elicited a significantly higher number of pecks and exploring time than the control display (no. pecks: Wilcoxon rank-sum test, $Z=2.9619$, $P=0.0015$; T_{expl}: Wilcoxon rank-sum test, $Z=2.5025$, $P=0.0062$).
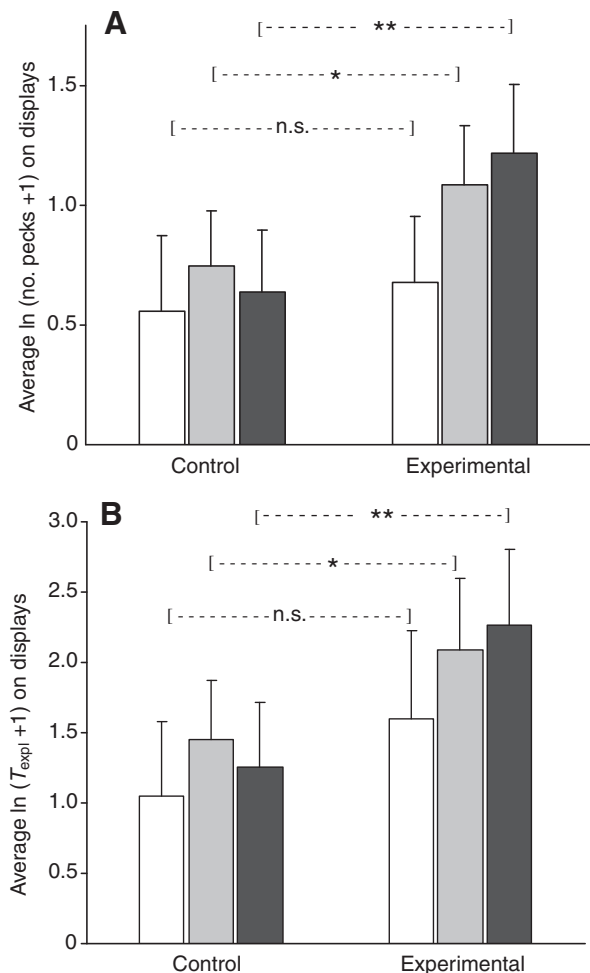

Fig. 3. (A) Average number of pecks (no. pecks) and (B) average exploring time (T_{expl}, in s) on each display, control and experimental, for the three experiments. Open bars, olfaction test; grey bars, vision test; black bars, combined test. Error bars correspond to 95% confidence intervals (calculated as $t_{0.95}\times$s.e.m.). Asterisks indicate a significant difference between the two displays (*$P<0.05$; **$P<0.01$; one-tailed Wilcoxon rank-sum non-parametric tests). Note that data were $\ln(x+1)$ transformed for graphic purposes.
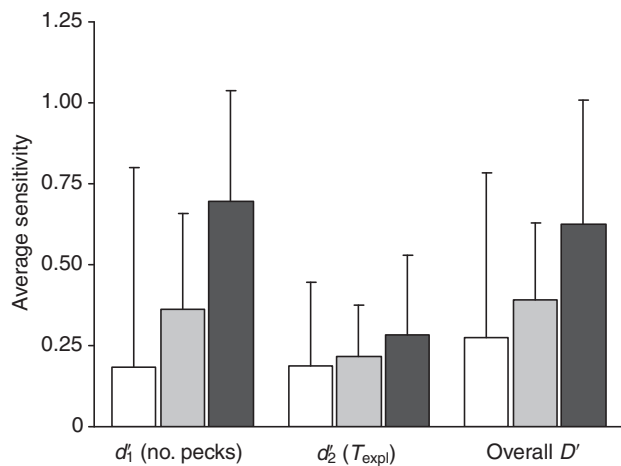
Fig. 4. Average sensitivities d'_1, d'_2 and D' of wandering albatrosses in the three experiments. Open bars, olfaction test; grey bars, vision test; black bars, combined test. Error bars correspond to 95% confidence intervals (calculated as $t_{0.95} \times$ s.e.m.). Note that sensitivity is a dimensionless score.

[Type1]=5.6228, F-value=5.6246, P=0.0091). More specifically, males' sensitivity to the combined stimulus was significantly higher than that to either olfactory (t=–2.9848, d.f.=19, P=0.0076) or visual (t=–2.2226, d.f.=19, P=0.0386) stimuli, while the latter two were not significantly different (t=–1.3036, d.f.=16, P=0.2108).

DISCUSSION

In order to explore the sensitivity of wandering albatrosses to olfactory and visual stimuli, alone and combined, three similar experiments were carried out on incubating adults of both sexes, at the breeding colony. Birds showed a significant response to the experimental displays for the three types of cue presented: olfactory, visual or a combination of the two, indicating that they perceive all types of stimuli. While the finding of visual capabilities comes as no surprise, our simple experimental demonstration of olfactory capabilities in the wandering albatross finds special significance in the number of descriptive investigations and hypotheses that have resulted from the study of albatross behaviour so far (Jouventin and Weimerskirch, 1990; Akesson et al., 2001; Bonadonna et al., 2005; Weimerskirch et al., 2005; Phalan et al., 2007; Nevitt et al., 2008).

Among the procellariiforms, most nocturnal species are burrow nesters and possess an acute sense of smell that they use to locate their nest (Bonadonna and Bretagnolle, 2002). In contrast, diurnal species tend to be ground nesters and probably rely on visual cues to home. Interestingly, the ancestral condition for the whole procellariiform clade was probably nocturnal/burrow nesting with independent adaptations to surface nesting in different subgroups (VanBuskirk and Nevitt, 2008). In addition, the foraging style of these birds has probably evolved in conjunction with nesting behaviours, as attraction to DMS has been found to be associated with burrow-nesting behaviour (VanBuskirk and Nevitt, 2008). The shift that occurred in several independent procellariiform species from nocturnal to diurnal habits, associated with a shift from burrow nesting to ground nesting (Bonadonna and Bretagnolle, 2002), may thus have also decreased the reliance on olfactory cues to locate prey (VanBuskirk and Nevitt, 2008). In these species, visual cues would have become increasingly important while maintaining some olfactory capabilities, thus promoting the emergence of multimodal mechanisms. Such a scenario, supported by our finding of olfactory capabilities in the wandering albatross, could explain why, although all species still exhibit a well-developed olfactory neuroanatomy, the observed responses to food-related scents have remained inconclusive for many species.

Unexpectedly, the comparison of the relative sensitivities to the different stimuli showed some sex-specific patterns. While females' sensitivity was not affected by the type of cues presented, males' sensitivity to the combined stimuli (visual and olfactory) was significantly greater than sensitivity to each stimulus alone. Interestingly, a sexual dimorphism has been observed in the foraging strategies of many seabirds (González-Solís et al., 2000; Lewis et al., 2002; Phillips et al., 2004), including the wandering albatross (Weimerskirch et al., 1993; Shaffer et al., 2001). It consists typically of the sexual segregation of foraging areas, which has been attributed to size-related differences in flight performance between sexes (Shaffer et al., 2001). However, variations in the foraging behaviours themselves, independent of any size dimorphism, have also been reported but not explained (Lewis et al., 2002). Whether the sex-specific nature of our sensitivity results is somehow related to these considerations is intriguing but further discussion at this stage of the research would be highly speculative. Besides, the difference observed between the two sexes may have simply resulted from a combination of limited sample sizes and some sex-specific personality traits, the males tested being generally less shy and more explorative of the displays than females.

Nevertheless, the higher sensitivity observed in males exposed to the combined cues, when compared with exposure to each cue alone, suggests that olfactory and visual cues may have additional effects on exploratory behaviours, at least in males. If the amount of exploration is directly related to the quantity of stimuli perceived, the combination of visual and olfactory cues would be expected to elicit up to twice as many exploratory behaviours as the single-mode tests, depending on how each modality is integrated. This is consistent with the increase in the combined test response reported here.

Finally, to correctly understand our findings, it is important to identify the limitations of our approach, testing the sensitivity of wandering albatrosses during incubating shifts on land. As discussed in earlier similar studies (Nevitt and Haberman, 2003), we caution that showing a bird's response to a given stimulus at the breeding colony does not prove that such a stimulus is used while foraging at sea. Birds in our study were not placed in a foraging context and,

Table 1. Results of the fixed-effects ANOVA model investigating the influences of sex and stimulus type on the overall sensitivity D'

Source	d.f.	SSq	Mean Sq	F-value	P
Sex	1	0.5267	0.5267	0.9891	0.3249
Stimulus type	2	1.0753	0.5376	1.0097	0.3718
Sex and stimulus type	2	5.8504	2.9252	5.4935	0.0070*
Residuals	49	26.0916	0.5325		

Sum of squares (SSq) reported in the table are Type I sum of squares. Significant effects are indicated by an asterisk.

consistently, none of them exhibited a frantic response to the tuna-filled display nor manifested any intent to feed. This seems to confirm that birds did not consider these experiments as foraging tasks. However, our study does not focus on a bird's attraction to a particular foraging stimulus but rather explores the sensory pathways leading to detection and/or exploration. In this respect, our simple experimental demonstration of olfactory capabilities in the wandering albatross has a general relevance to the ecology of these birds, potentially including foraging at sea (Nevitt et al., 2008), navigation (Nevitt and Bonadonna, 2005) and even social behaviours (Bonadonna and Nevitt, 2004). It may thus be used as a basis for future studies on this species. Despite a bias towards single-modality studies, it is now recognised that detection and attraction behaviours often involve multimodal sensory mechanisms (for details, see Dusenbury, 1992) and our study constitutes one more suggestion that seabirds are no exception.

LIST OF SYMBOLS AND ABBREVIATIONS

d'_1	sensitivity associated with the no. pecks variable
d'_2	sensitivity associated with the T_{expl} variable
D'	overall sensitivity
DMS	dimethyl sulphide
no. pecks	number of pecks on the display
T_{expl}	total exploring time

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