The Journal of Experimental Biology 206, 1615-1620

doi:10.1242/jeb.00286

A comparison of the olfactory abilities of three species of procellariiform chicks

Gregory B. Cunningham[1,*], Richard W. Van Buskirk[1], Francesco Bonadonna[2], Henri Weimerskirch[2] and Gabrielle A. Nevitt[1]

[1]*Center for Animal Behavior and the Department of Neurobiology, Physiology and Behaviour, University of California, One Shields Avenue, Davis, California, 95616, USA* and [2]*Centre d'Etudes Biologiques de Chizé, Centre National de la Recherche Scientifique, F-79360 Villiers en Bois, France*

*Author for correspondence (e-mail: gbcunningham@ucdavis.edu)

Accepted 10 February 2003

Summary

Most studies investigating olfactory sensitivities in procellariiform seabirds have concentrated on adults, but little attention has been paid to how olfactory behaviours develop. We took a first step towards understanding the ontogeny of these behaviours by testing the olfactory abilities of the blue petrel *Halobaena caerulea*, the thin-billed prion *Pachyptila belcheri*, and the common diving petrel *Pelecanoides urinatrix*. We scored the responsiveness of chicks in a sleep-like state to puffs of odours presented near their nostrils. We tested reactions to dimethyl sulphide (DMS, a prey-related odourant) and phenyl ethyl alcohol (PEA, a novel odourant); distilled water was used as a control. Scores for blue petrel chicks were significantly greater for DMS and PEA than for control presentations, while scores for thin-billed prions were significantly greater only for PEA. Common diving petrels did not respond significantly to either odourant. These results are consistent with what is known of adult olfactory behaviours. A negative correlation between the mass of blue petrel chicks and their mean responsiveness to odours indicates that older or recently fed birds are less responsive to these stimuli.

Key words: olfaction, procellariiform, *Halobaena caerulea*, *Pachyptila belcheri*, *Pelecanoides urinatrix*, Kerguelen island, dimethyl sulphide, foraging, sleep-like state.

Introduction

Many species of procellariiform seabirds forage over the open ocean using their sense of smell (reviewed by Roper, 1999; Warham, 1996). While olfactory foraging behaviour in adult procellariiforms has been a topic of great interest (Hutchison and Wenzel, 1980; Nevitt, 1999, 2000; Nevitt et al., 1995), almost no information is available on the ontogeny of these behaviours. Given that procellariiform chicks conduct initial foraging trips without aid or instruction from their parents, many questions arise as to how individuals develop these behaviours. For example, are species that forage by smell particularly attuned to odours as chicks?

A major impediment to investigating such questions is the difficulty of using laboratory protocols at remote locations where petrels tend to nest. Field applications of two-choice Y-maze experiments, for example, have been used with European storm-petrel *Hydrobates pelagicus* chicks to test responses to nest-specific odours. Results suggest that these storm-petrel chicks can smell, and that they use nest odours to identify their home burrow (Minguez, 1997). However, many birds failed to make a choice under test conditions, resulting in low sample sizes and reduced statistical power. In addition, though Y-mazes can be used to test homing behaviour, it is not clear how well they can be applied to test the development of foraging behaviour. While physiological techniques have been used in the field to measure the sensitivity of adult birds to prey-related odours, these physically invasive methods are stressful to birds and difficult to perform successfully (Clark and Shah, 1992). Because of the manipulations involved, such methods are not easily applied to chicks without high mortality.

Porter et al. (1999) have introduced a new technique (referred to here as the 'Porter method') that simplifies the study of chick olfactory abilities. These authors found that chicken *Gallus domesticus* chicks could be induced to 'sleep' in the hand. Once asleep, chicks responded to olfactory stimuli in predictable ways (head shakes, beak claps and peeping). We saw in the Porter method a field-ready means of assaying behavioural responses to odourants, and used it to investigate the olfactory sensitivities of three procellariiform seabirds: the blue petrel *Halobaena caerulea*, the thin-billed prion *Pachyptila belcheri*, and the common diving petrel *Pelecanoides urinatrix*. At-sea studies have demonstrated that blue petrels and thin-billed prions are attracted to and associate with prey-related odours (Nevitt, 2000; Nevitt et al., 1995). In contrast, common diving petrels exhibit none of these behaviours (reviewed in Nevitt, 2000) and presumably have a poor sense of smell (Wenzel, 1986). Our goal was thus to

determine how chicks of these species respond to novel and prey-related olfactory stimuli using this relatively non-invasive method.

Materials and methods

The study was conducted at Mayes Island (49°28′S, 69°57′E) from 12 December 2000 to 15 January 2001 (for blue petrels and thin-billed prions) and from 16 January to 27 February 2002 (for common diving petrels). Mayes Island is a subantarctic island located within a protected gulf on the eastern side of the Kerguelen Archipelago. The location of the archipelago on a submarine plateau just south of the Antarctic Convergence provides birds with extensive nearby foraging opportunities in highly productive waters. During the austral summer, the Kerguelen Archipelago harbours large colonies of 23 species of procellariiform seabirds. Breeding populations of thin-billed prions and common diving petrels, for example, have each been estimated to approach one million pairs (Weimerskirch et al., 1989).

The laboratory where the experiments were performed was a well ventilated, 4 m×6 m cabin equipped with a propane space heater. All odourants were tested at room temperature, which ranged from 16–19°C for experiments conducted on blue petrel and thin-billed prion chicks, and 17–23°C for experiments conducted on common diving petrels.

We tested 46 blue petrels *Halobaena caerulea* (Gmelin), 13 thin-billed prions *Pachyptila belcheri* (Matthews) and 55 common diving petrels *Pelecanoides urinatrix* (Gmelin) over the two field seasons. Blue petrel and thin-billed prion chicks were tested during daylight hours between 17:00–19:00 h (local time), when adults were absent from the burrow. Common diving petrel chicks were tested between 15:00–17:00 h. Prior to testing, chicks were removed from the burrow and transported to the laboratory. Chicks were transported and tested one at a time. The length of time that a chick was kept outside of its burrow ranged from 10–20 min, depending upon the distance from the burrow to the laboratory and how quickly the chick ‘slept’. Each chick was weighed immediately prior to being returned to its burrow.

The Porter method

For each test, a chick was held on its back in one hand, with its head tilted slightly downward. A 40 W light bulb was positioned approximately 3 cm from the body to warm the bird and put it into an apparent ‘sleep’ state (Porter et al., 1999). The light bulb was positioned posteriorly so that the body of the bird cast a shadow over the head (Fig. 1). Chicks were considered to be ‘asleep’ when the eyes were closed, the head became droopy, and the legs and wings relaxed.

A team of two people performed experiments. One person held the light bulb while the other held the chick, delivered odourants and scored the data. For some diving petrels, a hand cupped over the chick was used in place of the light bulb to warm the bird and induce the sleep-like state. Chicks were held in position for 1 min to acclimate them to the experimental setup.

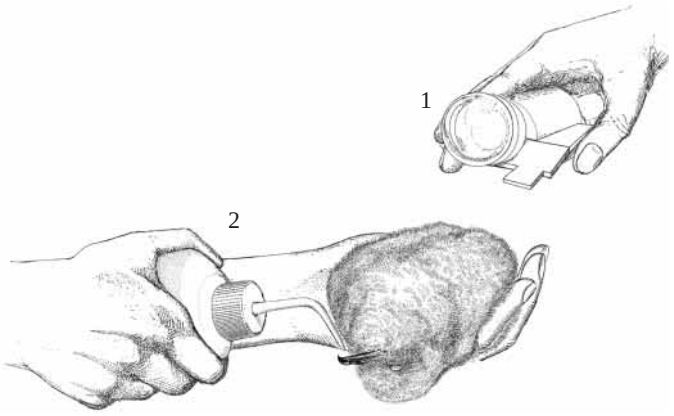

Fig. 1. Experimental set-up showing odour presentation to a sleeping Blue petrel chick. Note the position of the light bulb (1) and squeeze bottle (2). We use the term ‘sleeping’ following the convention of Porter et al. (1999); it may be that birds were not technically sleeping.

Following acclimatization, we waited for the bird to sleep, and then waited 1 min before initiating a test. If the bird awoke during the experiment, we waited until it went back to sleep, and then allowed it to sleep for 1 min before proceeding with the next stimulus. If the bird did not fall asleep within 10 min, we aborted the experiment and returned the bird to its burrow.

We exposed each sleeping chick to a series of three stimuli: (1) dimethyl sulphide (DMS), a prey-related odourant; (2) phenyl ethyl alcohol (PEA), a novel rosy-scented odourant; and (3) distilled water (a control). Odourants (1 μmol l^{-1}; 100 ml) were prepared from stock solutions and transferred to a Nalgene® squeeze bottle. Bottles were allowed to sit for 30–60 min to equilibrate the headspace. During trials, odourants were presented by positioning the tip approx. 2 cm from the opening of the nostrils. The bottle was then squeezed 15 times in 20 s, producing puffs of odourant-saturated air near the bird’s nostrils. For each species, we varied the order of stimulant presentation and balanced the number of times each combination was used. Responses to odourant presentations were scored categorically on a scale of 0–3 (ranging from no reaction to vocalizations and/or large head movements), based on the methods of Porter et al. (1999). Experiments and scoring were done blind: the person delivering the stimulus and recording the response did not know the identity of the stimulus being delivered.

Statistics

Categorical scores were not normally distributed. We therefore applied nonparametric statistical tests involving rank transformation to compare our treatment effects. Using a Friedman’s test, we first determined whether there was an overall difference among treatment effects. In cases where the overall effect was significant, we used a Wilcoxon signed-rank test to carry out multiple comparisons of the responses to specific odourants and the control. This technique allowed us to identify pairwise differences among control, DMS and PEA treatments.

We also investigated the relationship between chick mass (an indicator of both age and time since last feeding) and behavioural response to treatments. To determine the strength of the relationship, we calculated Spearman's ρ coefficient, a measure of association based on ranked data. We looked at mean behavioural response by averaging each chick's scores for control, DMS and PEA treatments. A significant test statistic indicated a non-zero rank correlation (Zar, 1996).

Results

Experiments were successfully completed on 65% (30/46) of blue petrel chicks attempted, 92% (12/13) of thin-billed prion chicks attempted, and 53% (29/55) of common diving petrel chicks attempted. Once the light bulb was turned on, blue petrel and thin-billed prion chicks fell asleep within a few minutes (blue petrels: $\bar{x}$=3 min, 50±29 s; thin-billed prions: $\bar{x}$=1 min, 31±20 s). Common diving petrel chicks took longer to fall asleep ($\bar{x}$=5 min, 18±20 s).

Blue petrels ranged in mass from 34 to 140 g (mean ± S.E.M.=84.4±5.4 g, *N*=30). This mass range corresponds to an age range of 4–17 days post-hatching, based on age–mass relationships plotted by Jouventin et al. (1985). Similarly, thin-billed prions ranged from 41 to 102 g (mean=70.1±6.0 g, *N*=12), and were approximately 7–15 days old (based on correlations by Strange, 1980). The mean mass range of common diving petrels was 17–119 g (mean=60.7±4.3 g, *N*=29), corresponding to an age range of 3–24 days post-hatching (Jouventin et al., 1985).

Responses to odourants

For both blue petrels and thin-billed prions, mean scores to DMS, PEA and control stimuli were significantly different (Friedman test statistic: blue petrels, 15.31; d.f.=2; *P*=0.00047; thin-billed prions, 6.45; d.f.=2; *P*=0.04). The mean score for blue petrels was significantly higher for both DMS and PEA than for the control stimuli (Fig. 2), suggesting that chicks could smell these odourants (Wilcoxon signed-rank test: $Z_{PEA\neq control}$=3.24; *P*=0.001; $Z_{DMS\neq control}$=2.45; *P*=0.014). Mean scores for PEA and DMS were not significantly different from one another ($Z_{PEA\neq DMS}$=1.17; *P*=0.10).

For thin-billed prions (Fig. 3), the mean score for PEA was higher than for the control ($Z_{PEA\neq control}$=2.23; *P*=0.026). There were no significant differences between mean scores for DMS and PEA, or between mean scores for DMS and control ($Z_{PEA\neq DMS}$=1.61; *P*=0.28; $Z_{DMS\neq control}$=1.08; *P*=0.28). Our sample size for this species was much lower (*N*=12) due to time constraints.

Common diving petrels (Fig. 4) did not show a significant difference among mean scores for the three stimuli (Friedman test statistic, 3.00; d.f.=2; *P*=0.22).

Correlations with body mass

We next investigated whether the overall responsiveness to odourants was correlated with body mass. Body mass is an indication of both age and time since last feeding. Fig. 5A–C

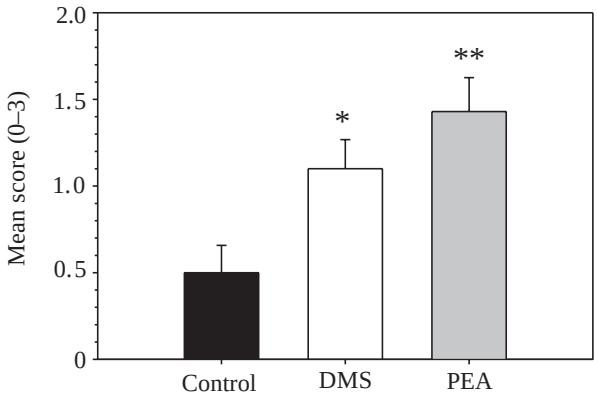

Fig. 2. Mean scores for blue petrel responses to control (black), DMS (dimethyl sulphide; white) and PEA (phenyl ethyl alcohol; gray) odourant presentations. Single and double asterisks indicate significant differences (Wilcoxon signed-rank test, **P*<0.05; ***P*<0.01; *N*=30) between the response to an odourant and the distilled water control.

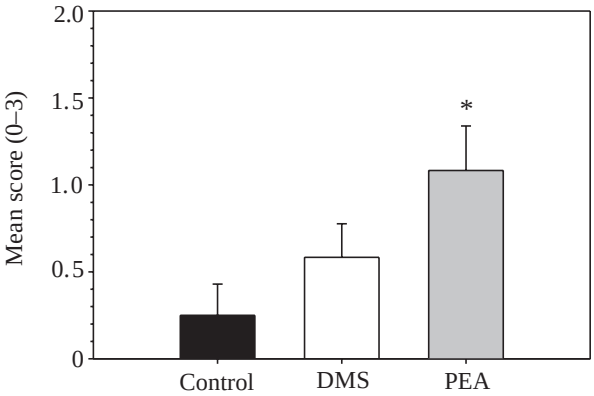

Fig. 3. Mean scores for thin-billed prion responses to control (black), DMS (dimethyl sulphide; white) and PEA (phenyl ethyl alcohol; gray) odourant presentations. Single asterisks indicate significant differences (Wilcoxon signed-rank test, *P*<0.05; *N*=12) between the response to an odourant and the distilled water control.

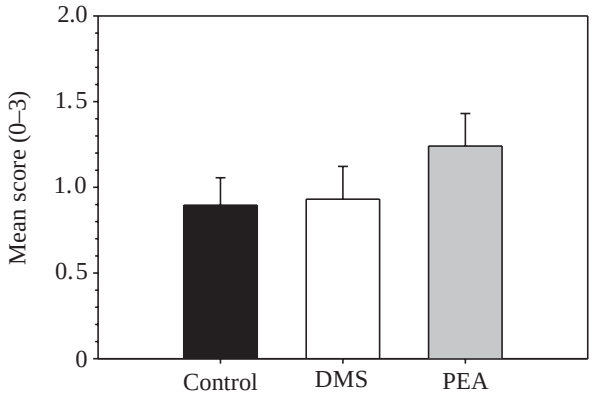

Fig. 4. Mean scores for common diving petrel responses to control (black), DMS (dimethyl sulphide; white) and PEA (phenyl ethyl alcohol; gray) odourant presentations. No significant difference (see text) between the response to an odourant and the distilled water control was found.

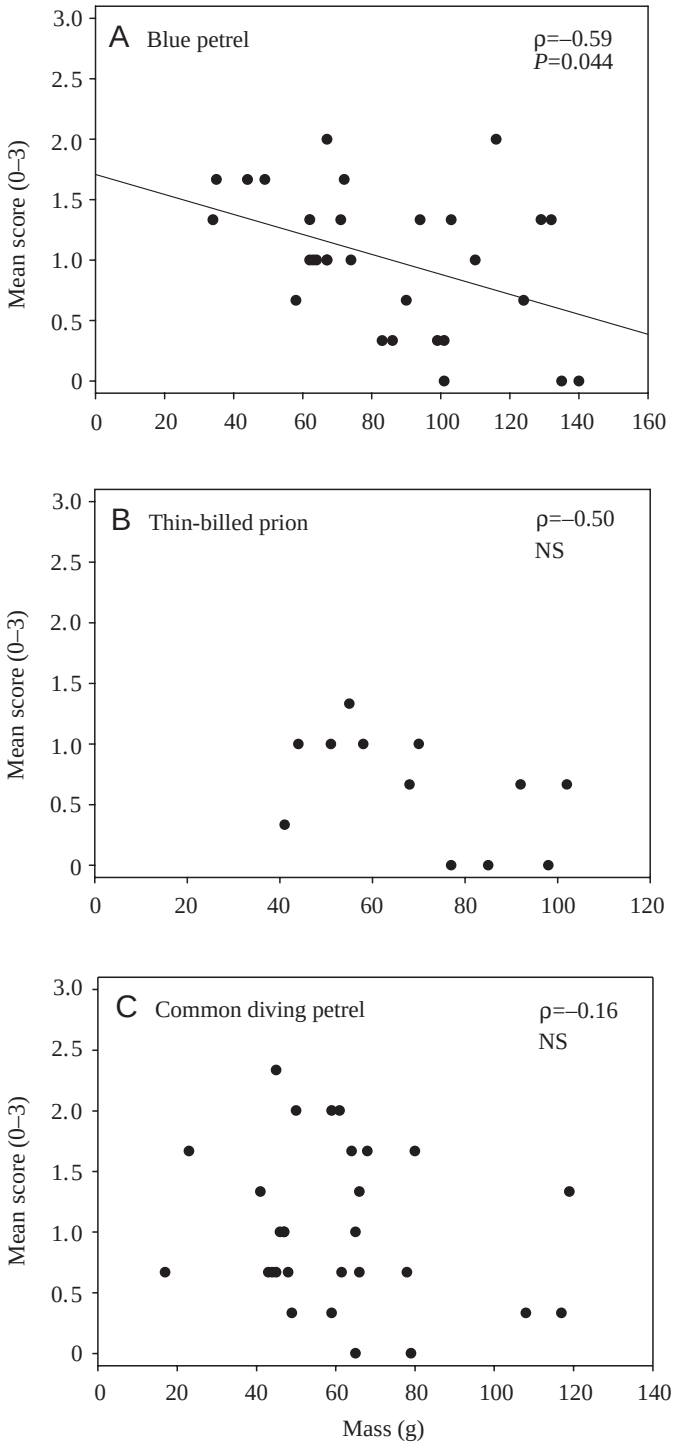

Fig. 5. Scatter plots of mean score (mean of control, DMS and PEA) *versus* chick mass for (A) blue petrels, (B) thin-billed prions and (C) common diving petrels. The trend line for blue petrels highlights a statistically significant Spearman ρ correlation. The sample size for thin-billed prions (12) provides too low a statistical power for detecting an association. Power analysis for the Pearson Product Moment (the parametric equivalent of Spearman's ρ correlation coefficient) indicates that a sample size of 34 is needed for a 90% chance of detecting a ±0.50 correlation coefficient (Cohen, 1988).

shows scatter plots of the mean of each individual's responses to control, DMS and PEA, plotted against its mass. We determined if these variables were related by using the Spearman ρ coefficient to identify non-zero correlations. For blue petrels (Fig. 5A), we found a significant negative correlation between mean response and mass (Spearman ρ=–0.59; P=0.044; N=30). Heavier chicks tended to be less responsive to odourants. Though thin-billed prions (Fig. 5B) showed a similar measure of association (Spearman ρ=–0.50), the correlation was not significant (P=0.096; N=12). In contrast to blue petrels and thin-billed prions, common diving petrels (Fig. 5C) showed a weak and non-significant correlation despite a large sample size (Spearman ρ=–0.16; P=0.40; N=28).

Discussion

The results of this study indicate that petrel chicks exhibit behavioural sensitivity to odourants in a species-specific manner. Thin-billed prion and blue petrel chicks responded to test odourants, whereas common diving petrel chicks did not. The responses of blue petrel chicks to both prey-related (DMS) and novel (PEA) odourants suggest that at least some olfactory species are broadly sensitive to scented compounds at a young age (approx. 4–7 days post hatching).

These findings are significant in two ways. First, the results concur with our knowledge of olfactory foraging, suggesting that an early sensitivity to odours is present in species that are likely to use olfactory cues as adults. Second, these findings demonstrate that the simple and efficient Porter method works well in a field setting, allowing for large and statistically powerful sample sizes with minimal impact on the study species.

Sensitivities of chicks reflect olfactory foraging behaviour in adults

Adults of the three study species have different foraging strategies, and vary in their responsiveness to prey-related odourants. Blue petrels and thin-billed prions are burrow-nesting birds that spend a majority of the year foraging over the subantarctic oceans (Prince, 1980; Prince and Copestake, 1990; Ridoux, 1994; Steele and Klages, 1986). These two species tend to forage in large (>1000 individuals) flocks (Prince, 1980; Routh, 1949), feeding on euphausiids, amphipods, myctophids and squid (Chaurand and Weimerskirch, 1994; Harper, 1972, 1987; Prince, 1980; Strange, 1980). Prey capture differs in that blue petrels are able to pinpoint prey items and seize them directly at the ocean's surface (Prince, 1980), whereas thin-billed prions sift small crustacean prey from the ocean's surface using comb-like lamellae on the palate (Harper, 1972). Because the binocular field is diminished in prions (Martin and Prince, 2001), olfactory cues may be particularly critical to them in locating productive areas where prey tend to aggregate (Nevitt, 2000).

Dimethyl sulphide (DMS) is the best understood of the known biogenic foraging cues available to blue petrels and thin-

billed prions. DMS is produced by marine phytoplankton (e.g. *Phaeocystis* sp.) as a byproduct of metabolism, and is associated with primary productivity in the ocean. Levels of DMS are elevated where the probability of finding zooplankton is high (for a review, see Nevitt, 2000), and seabirds likely use elevated DMS levels to identify optimal foraging grounds within an area of high productivity. This ability was first demonstrated in controlled field experiments conducted near South Georgia (Nevitt et al., 1995). Further work demonstrated an association between blue petrels/prions and DMS hot spots under natural foraging conditions (Nevitt, 2000).

Common diving petrels are also subantarctic, burrow-nesting birds, but are not thought to hunt by smell (Wenzel, 1986). While prey of common diving petrels (hyperiid amphipods, copepods and zoea larva of crabs; Bocher et al., 2000) are similar to those of blue petrels and thin-billed prions, foraging behaviours differ dramatically. As their name suggests, diving petrels forage by plunging under water to depths ranging from 7–64 m (Bocher et al., 2000; Chastel, 1994). Unlike blue petrels, prions and other procellariiforms, diving petrels neither recruit to nor track prey-related odourants in experimental trials, and do not associate with DMS hot spots over the ocean (Nevitt, 2000). These observations are supported by anatomical data suggesting that diving petrels have the smallest relative olfactory bulb size among the procellariiforms (Bang and Cobb, 1968). Olfaction has been implicated, however, in nest recognition in diving petrels (F. Bonadonna and G. B. Cunningham, unpublished data) and this is a topic under current investigation.

To summarize, the olfactory responses that we observed in procellariiform chicks are consistent with the adult behavior outlined above. Chicks of both blue petrels and thin-billed prions responded to olfactory stimuli, suggesting that species that use olfaction to forage are responsive to odours as chicks. Common diving petrel chicks, like adults, appear to be unresponsive to odours.

Assessment of the Porter method

The Porter method has two clear advantages for field applications. First, the method is easy to perform and can yield a large and statistically powerful sample size. In this study we were able to test olfactory responses in 70 out of 114 birds; only 39% did not sleep. In comparison, Y-maze experiments involving odours can be time consuming and difficult to perform under field conditions, particularly when birds are uncooperative, e.g. Leach's storm-petrel *Oceanodroma leucorhoa*, 60% non-choice (Grubb, 1974), common diving petrel, 68% non-choice (F. Bonadonna and G. B. Cunningham, unpublished data). Second, the Porter method is non-lethal and can be performed under field conditions with minimal disturbance to the colony. Past experiments designed to test the olfactory abilities of birds typically are highly invasive and often lethal (Shibuya and Tucker, 1967; Tucker, 1965; Wenzel, 1967). Since many populations of procellariiforms are in decline, non-invasive, low-risk techniques such as the Porter method are needed to conduct experiments with this group.

We investigated the impact of our methods by examining burrows during the week following testing. We did not see an immediate increase in mortality following testing. 3 of 46 (7%) blue petrel, 0 of 13 (0%) thin-billed prion, and 6 of 55 (11%) common diving petrel chicks died within this period. Natural chick mortality rates from hatching to fledging average between 7–33% for blue petrels, 5–41% for thin-billed prions and 12–65% for common diving petrels, depending on the year (H. Weimerskirch, unpublished data). Thus, the levels of mortality we observed fall well within average mortality rates.

The Porter method may be better suited, however, to young or hungry chicks. For blue petrel chicks, we observed a decrease in mean response with increasing mass (Fig. 5A). For common diving petrels, there was no association between mean response and mass (Fig. 5C). Mass fluctuates daily in seabird chicks in relation to feeding state, and also increases steadily with age. We were not able to distinguish between feeding state and age due to missing hatch dates for a number of individuals in this study. Whether this negative association between responsiveness and mass is due to satiation or age is the subject of current research.

Conclusions

Our application of the Porter method yielded robust evidence that at least some species of procellariiforms have well developed olfactory sense even as chicks. The ability of chicks to respond to odours at a young age may be more significant than we have previously suspected for these birds, as we know that olfactory sensitivities are shaped by early experience in many vertebrate species (salmon: Nevitt and Dittman, 1998; rabbits: Semke et al., 1995; chickens: Sneddon, 1998; Turro et al., 1994; ferrets: Vargas and Anderson, 1996). The results presented here are an important first step towards understanding the ontogeny of olfactory behaviour in tube-nosed seabirds.

Special thanks to Dr A. L. A. Middleton. This project was supported by NSF (IBN 0212467 and OPP 9814326) to G.A.N. Logistical support was provided by the French Polar Institute (IPEV Program no. 109). We thank Christopher Burney, Vivien Chartendrault, and Nicolas Delelis for their invaluable assistance in the field. We also thank and credit Maria Pereyra for drawing Fig. 1, and Dr Neil Willits for statistical advice. The comments of Dr Arlene Alvarado, Alexis Blackmer, Dr Tom Hahn, Allison Green, Sean Lema and an anonymous reviewer greatly improved this manuscript.

References

Bang, B. G. and Cobb, S. (1968). The size of the olfactory bulb in 108 species of birds. *Auk* **85**, 55-61.

Bocher, P., Labidoire, B. and Cherel, Y. (2000). Maximum dive depths of common diving petrels (*Pelecanoides urinatrix*) during the annual cycle at Mayes Island, Kerguelen. *J. Zool.* **251**, 517-524.

Chastel, O. (1994). Maximum diving depths of common diving petrels Pelecanoides urinatrix at Kerguelen Islands. *Polar Biol.* **14**, 211-213.

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.

Clark, L. and Shah, P. S. (1992). Information content of odor plumes: what do Leach's storm-petrels know? In *Chemical Signals in Vertebrates* VI (ed. R. L. Doty and D. Muller-Schwarze), pp. 421-427. New York: Plenum Press.

Cohen, J. (1988). *Statistical Power Analysis for the Behavioral Sciences*. Hillsdale, NJ: Lawrence Erlbaum Associates.

Grubb, T. C. (1974). Olfactory navigation to the nesting burrow in Leach's petrel (*Oceanodroma leucorrhoa*). *Anim. Behav.* **22**, 192-202.

Harper, P. C. (1972). The field identification and distribution of the Thin-billed prion (*Pachyptila belcheri*) and the Antarctic Prion (*Pachyptila desolata*). *Notornis* **19**, 140-175.

Harper, P. C. (1987). Feeding behaviour and other notes on 20 species of Procellariiforms at sea. *Notornis* **34**, 169-192.

Hutchison, L. V. and Wenzel, B. M. (1980). Olfactory guidance in foraging by procellariiforms. *The Condor* **82**, 314-319.

Jouventin, P., Mougin, J. L., Stahl, J. C. and Weimerskirch, H. (1985). Comparative biology of the burrowing petrels of the Crozet Islands. *Notornis* **32**, 157-220.

Martin, G. R. and Prince, P. A. (2001). Visual fields and foraging in procellariiform seabirds: Sensory aspects of dietary segregation. *Brain Behav. Evol.* **57**, 33-38.

Minguez, E. (1997). Olfactory nest recognition by British storm-petrel chicks. *Anim. Behav.* **53**, 701-707.

Nevitt, G. A. (1999). 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. and Dittman, A. (1998). A new model for olfactory imprinting in salmon. *Integr. Biol.* **1**, 215-223.

Nevitt, G. A., Veit, R. R. and Kareiva, P. (1995). Dimethyl sulphide as a foraging cue for Antarctic procellariiform seabirds. *Nature* **376**, 680-682.

Porter, R. H., Hepper, P. G., Bouchot, C. and Picard, M. (1999). A simple method for testing odor detection and discrimination in chicks. *Physiol. Behav.* **67**, 459-462.

Prince, P. A. (1980). The food and feeding ecology of Blue petrel (*Halobaena caerulea*) and dove prion (*Pachyptila desolata*). *J. Zool.* **190**, 59-76.

Prince, P. A. and Copestake, P. G. (1990). Diet and aspects of Fairy Prions breeding at South Georgia. *Notornis* **37**, 59-69.

Ridoux, V. (1994). The diets and dietary segregation of seabirds at the sub-Antarctic Crozet Islands. *Mar. Ornithol.* **22**, 1-192.

Roper, T. J. (1999). Olfaction in birds. *Adv. study Behav.* **28**, 247-332.

Routh, M. (1949). Ornithological observations in the Antarctic seas 1946-1947. *Ibis* **91**, 577-606.

Semke, E., Distel, H. and Hudson, R. (1995). Specific enhancement of olfactory receptor sensitivity associated with foetal learning of food odors in the rabbit. *Naturwissenschaften* **82**, 148-149.

Shibuya, T. and Tucker, D. (1967). Single unit responses of olfactory receptors in vultures. In *Olfaction and Taste*, Vol. 2 (ed. T. Hayashi), pp. 219-233. Oxford: Pergamon.

Sneddon, H., Hadden, R. and Hepper, P. G. (1998). Chemosensory learning in the chicken embryo. *Physiol. Behav.* **64**, 133-139.

Steele, W. K. and Klages, N. T. (1986). Diet of the Blue petrel at sub-Antarctic Marion Island. *S. Afr. J. Zool.* **21**, 252-256.

Strange, I. J. (1980). The Thin-billed prion, *Pachyptila belcheri*, at New Island, Falkland Islands. *Gerfaut* **70**, 411-445.

Tucker, D. (1965). Electrophysiological evidence for olfactory function in birds. *Nature* **207**, 34-36.

Turro, I., Porter, R. H. and Picard, M. (1994). Olfactory cues mediate food selection by young chicks. *Physiol. Behav.* **55**, 761-767.

Vargas, A. and Anderson, S. H. (1996). Effects of diet on captive black-footed ferret (*Mustela nigripes*) food preference. *Zoo Biol.* **15**, 105-113.

Warham, J. (1996). *The Behaviour, Population Biology and Physiology of the Petrels.* London: Academic Press.

Weimerskirch, H., Zotier, R. and Jouventin, P. (1989). The avifauna of the Kerguelen Islands, Indian Ocean. *Emu* **89,** 15-29.

Wenzel, B. M. (1967). Olfactory perception in birds. In *Olfaction and Taste*, Vol. 2 (ed. T. Hayashi), pp. 203-217. Oxford: Pergamon.

Wenzel, B. M. (1986). The ecological and evolutionary challenges of procellariiform olfaction. In *Chemical Signals in Vertebrates* 4 (ed. D. Duvall, D. Muller-Schwartze and R. M. Silverstein), pp. 357-368. Plenum Publishing Corporation.

Zar, J. H. (1996). *Biostatistical Analysis*, Third Edition. Upper Saddle River, NJ: Prentice Hall.