The influence of developmental environment on the evolution of olfactory foraging behaviour in procellariiform seabirds

R. W. VAN BUSKIRK & G. A. NEVITT

Center for Animal Behavior, Section of Neurobiology, Physiology and Behavior, Davis, CA, USA

Abstract

The evolutionary origins of foraging behaviour by procellariiform seabirds (petrels, albatrosses and shearwaters) are poorly understood. Moreover, proximate factors affecting foraging ecology, such as the influence of environment on the development of sensory systems, have yet to be addressed. Here, we apply comparative methods based on current procellariiform phylogenies to identify associations between sensory modalities and the developmental environment that may underlie the evolution of complex foraging behaviour. We postulate that, for burrow-nesting species, smell is likely to dominate the sensory world of the developing chick. Alternatively, for ground-nesting species, chicks receive exposure to a range of visual, auditory and olfactory cues. We employ maximum likelihood to test models of correlated trait evolution between nesting habit and olfactory foraging style and to reconstruct the ancestral states of these characters when coded as binary states. Our results suggest that nesting behaviour has evolved in conjunction with foraging style. Based on this analysis, we propose that nesting on the surface was a life-history innovation that opened up a new developmental environment with profound effects on the foraging ecology of procellariiform seabirds.

Introduction

Procellariiform seabirds (petrels, albatrosses and shear-waters) spend nearly most of their lifetime foraging over the ocean, coming to shore for only a few months each year or in alternate years to breed. Finding prey at sea is complicated by the widespread and patchy distribution of target species such as krill, squid and fish (for review, see Prince & Morgan, 1987; Rodhouse *et al.*, 1987; Boyle & Boletzky, 1996; Siegel, 2000). Understanding how these birds efficiently search thousands of square kilometres to locate and exploit ephemeral prey patches has prompted many investigations of procellariiform flight styles (Savile, 1957; Cone, 1964; Wilson, 1975; Pennycuick, 1982), provisioning schedules (Weimerskirch, 1998; Croxall *et al.*, 1999; Philips & Croxall, 2003) and foraging strategies (Hutchison *et al.*, 1984; Jouventin & Robin, 1984; Lequette *et al.*, 1989; Weimerskirch *et al.*, 1993;

Correspondence: Gabrielle A. Nevitt, Center for Animal Behavior, Section of Neurobiology, Physiology and Behavior, One Shields Ave, UC Davis, Davis, CA 95616, USA.
Tel.: +1 530 752 5929; fax: +1 530 752 5582;
e-mail: ganevitt@ucdavis.edu

Nevitt *et al.*, 1995, 2004; Nevitt, 2000; Nevitt & Bona-donna, 2005). Although adaptations for long-distance flight clearly underlie the radiation of tube-nosed sea-birds (reviewed by Warham, 1990, 1996), the origins of and interactions among foraging adaptations (sensory ecology and flight style) remain poorly understood. Moreover, proximate factors such as the influence of the developmental environment on sensory systems have been largely ignored. Here we apply comparative methods based on current phylogenies to examine any associations between identified foraging strategies and the developmental environment.

Foraging strategies based on the exploitation of widely dispersed prey require complementary adaptations in a species' morphology and breeding biology because the energy and time required to locate distant prey place severe constraints on the incubation and provisioning of young (Houston, 1995). Most procellariiforms produce only one offspring per breeding season (Lack, 1967, 1968; Ashmole, 1971; Jouventin & Dobson, 2002) and have evolved alternating bouts of incubation and for-aging that balance their energetic needs with those of their partner and offspring (Weimerskirch *et al.*, 1997;

Catard & Weimerskirch, 2000; Cherel *et al.*, 2002). Although a parent is always present during incubation and brooding, the demands of a growing chick eventually require that it be left alone while both parents travel greater distances to utilize more energetically profitable foraging grounds (Weimerskirch *et al.*, 1993; Chaurand & Weimerskirch, 1994).

The need to leave a chick unattended probably played a role in the choice of breeding habitat (remote islands with few predators) and the evolution of nesting strategies (reviewed by Warham, 1996). Species that are either small or produce more vulnerable chicks (e.g. shearwaters, diving petrels, prions and storm petrels) construct deep nesting burrows that offer protection from predators and the elements. Other typically larger species (e.g. albatross and giant petrels) nest at the surface, as their chicks are less vulnerable to avian predation and thermoregulatory stress by virtue of their size. This difference in nesting strategy creates important differences in the developmental environments that burrow- and surface-reared chicks experience. Chicks raised in burrows develop in the dark for the first several weeks or months of their lives, depending on the species. These chicks fledge only after their parents have abandoned them and yet must learn to locate and exploit distant ephemeral prey patches without aid or instruction from the parents. By contrast, chicks reared on the surface are exposed to light early in their development, as well as to a variety of visual cues such as skylight polarization patterns (Able & Able, 1993; Munro & Wiltschko, 1995; Åkesson & Backman, 1999), rotation of the night sky (Wiltschko & Wiltschko, 1994) and conspecific activity in the colony.

Although tube-nosed seabirds have long been thought to hunt by smell (Collins, 1884; Murphy, 1925; Wenzel, 1967; Grubb, 1972; Hutchison & Wenzel, 1980), connections between development, behavioural response to specific odours and foraging ecology have only recently begun to be examined (for review, see Nevitt & Bonadonna, 2005). The most comprehensive studies of foraging behaviour have been conducted in a subantarctic seabird assemblage in the South Atlantic sector near South Georgia Island (Nevitt *et al.*, 1995; Nevitt, 1999a,b; Nevitt *et al.*, 2004; see also Silverman *et al.*, 2004). These studies suggest that procellariiform species differ in their behavioural responses to olfactory stimuli, and that this variation reflects differences in foraging strategies. Moreover, these strategies are adapted to natural cascades of sensory information encountered during area-restricted search (reviewed by Hay & Kubanek, 2002; Nevitt, 1999a; Nevitt *et al.*, 2004; Nevitt & Bonadonna, 2005). Together these results suggest that when prey-related odours are released naturally, either as zooplankton consume phytoplankton or when higher order predators consume zooplankton, they carry information not only about prey type but also about prey state and availability. For example, dimethyl sulphide (DMS) is released during
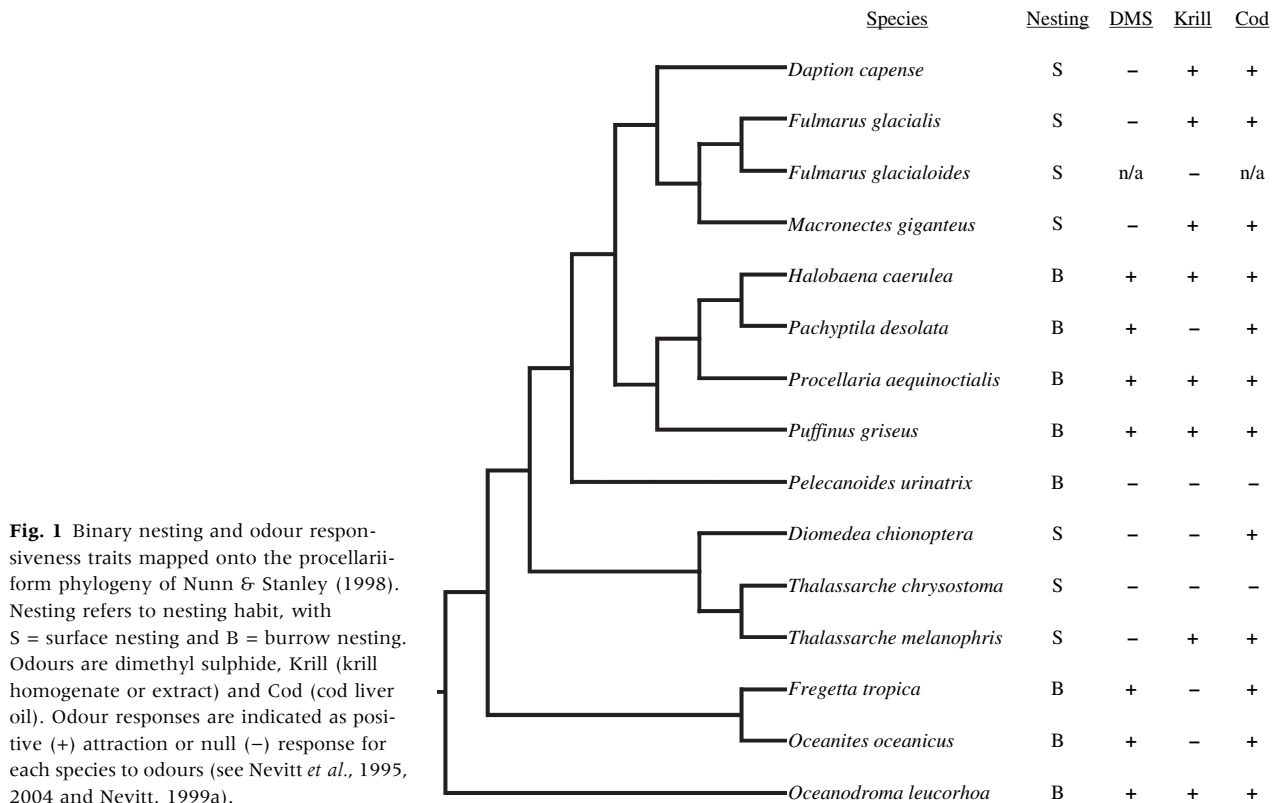
zooplankton grazing and forms as a by-product of the metabolic decomposition of dimethylsulphoniopropionate (DMSP) in marine phytoplankton. When intact zooplankton (e.g. krill) are present and feeding on phytoplankton, the rate of DMSP release is increased (Dacey & Wakeham, 1986; Kasamatsu *et al.*, 2004). This process, in turn, elevates DMS and DMSP in the surrounding water. As DMS in surface seawater is emitted to the air, it can serve as an immediate olfactory indicator of the near-surface availability of aggregating zooplankton. Thus, for opportunistic species, local elevations in DMS indicate an as-yet-unexploited food source. In addition to DMSP, other scented compounds are also released when zooplankton are crushed. These compounds indicate that prey are not only present but are also in the process of being exploited by predators such as marine mammals and seabirds. Extracts of macerated krill and scented components of these extracts (pyrazines) have been shown to attract procellariiforms that typically forage in mixed species feeding aggregations (Nevitt, 1999a; Nevitt *et al.*, 2004). These species tend to use a combination of olfactory and visual cues, including heterospecific networking to locate prey patches (Silverman *et al.*, 2004).

Here, we investigate the evolutionary relationships between species-specific variation in odour responsiveness and the environment in which procellariiforms develop. We postulate that differences in sensory environment experienced in the nest contribute to different styles of foraging that develop, both proximately (e.g. Wang *et al.*, 1993; Nevitt *et al.*, 1994; Semke *et al.*, 1995; Sneddon *et al.*, 1998; reviewed by Hudson, 1999; Nevitt & Dittman, 2004) and within an evolutionary framework (*sensu* West-Eberhard, 2003, p. 140). Thus, a burrow-nesting life-history trait may be linked to olfactory tracking, whereas ground nesting is not. The following investigation examines the evolution of procellariiform foraging strategies by using phylogenetic relationships to test models of correlated trait evolution between nesting habit and behavioural attraction to DMS.

Materials and methods

Comparative data

We chose fifteen species or species groups within the Procellariiformes for our analysis of foraging behaviour based on the availability of data on species' responses to odours deployed at sea (see Fig. 1 for a list of taxa). We scored the presence or absence of each species' response to DMS, krill homogenate or cod liver oil based on the results of trials performed elsewhere (Nevitt *et al.*, 1995, 2004; Nevitt, 1999a; Nevitt & Haberman, 2003). Cod liver oil is included in at-sea odour trials as it can elicit a response commonly assumed to reflect conditioning to offal discharge by fishing boats (Nevitt *et al.*, 2004). We converted the source data into simple categorical

Species	Nesting	DMS	Krill	Cod
Daption capense	S	−	+	+
Fulmarus glacialis	S	−	+	+
Fulmarus glacialoides	S	n/a	−	n/a
Macronectes giganteus	S	−	+	+
Halobaena caerulea	B	+	+	+
Pachyptila desolata	B	+	−	+
Procellaria aequinoctialis	B	+	+	+
Puffinus griseus	B	+	+	+
Pelecanoides urinatrix	B	−	−	−
Diomedea chionoptera	S	−	−	+
Thalassarche chrysostoma	S	−	−	−
Thalassarche melanophris	S	−	+	+
Fregetta tropica	B	+	−	+
Oceanites oceanicus	B	+	−	+
Oceanodroma leucorhoa	B	+	+	+

Fig. 1 Binary nesting and odour responsiveness traits mapped onto the procellariiform phylogeny of Nunn & Stanley (1998). Nesting refers to nesting habit, with S = surface nesting and B = burrow nesting. Odours are dimethyl sulphide, Krill (krill homogenate or extract) and Cod (cod liver oil). Odour responses are indicated as positive (+) attraction or null (−) response for each species to odours (see Nevitt et al., 1995, 2004 and Nevitt, 1999a).

(+ and −) scores based on statistically significant attraction to the deployed odours.

For our analysis of physical characters related to flight, we obtained morphological data from previously published sources for 67 procellariiform species (Warham, 1977, 1996; Pennycuick, 1982; Spear & Ainley, 1997). We used average values for wing span (63 spp.), wing area (64 spp.), wing load (64 spp.), aspect ratio (63 spp.) and body mass (67 spp.) as indicators of flight performance. Data on flight height were limited to seven species from the southern oceans categorized by Pennycuick (1982) as either low flying (0–3 m above the surface) or high flying (> 4 m above the surface).

Phylogenetic comparative methods

The phylogenetic relationships that underlie our comparative analyses are based on the results of Nunn & Stanley (1998), who conducted a maximum parsimony analysis of sequence data (mtDNA) from 85 species of procellariiforms, using the penguins (Aves: Sphenisciformes) as an outgroup. We also incorporated the supertree of Kennedy & Page (2002) as a check on the effect of tree topology on our analyses. We reconstructed the ancestral state of nesting habit using the tree topologies of Nunn & Stanley (1998) and Kennedy & Page (2002) for those species that could be scored dichotomously as either surface nesting or burrow nesting and that were resolved as dichotomous branches. For the analysis of correlated trait evolution, we pruned Nunn and Stanley's tree to the 15 species or species groups with branch length information retained. Prions and diving petrels were grouped by genus due to difficulties discriminating species at sea (Fig. 1). The pruned supertree of Kennedy and Page was also examined, but differed only in the placement of *Puffinus griseus* as a sister group to *Procellaria aequinoctialis* when constrained to the 15 species or species groups for which olfactory data were available.

We conducted tests for correlated evolution among binary characters using the software DISCRETE (Pagel, 1994), which implements a Markov model in a maximum-likelihood framework. We tested nesting habit (surface vs. burrow) against responsiveness to DMS, krill homogenate or cod liver oil. A likelihood ratio test of fit under independent and dependent models of evolution was used to test for correlated trait evolution. We determined the likelihood of each model given the data using DISCRETE, and calculated a likelihood ratio test-statistic. Simulation studies by Pagel (1997) have shown that the likelihood ratio test-statistic follows a chi-squared distribution with four degrees of freedom. In the case of small phylogenies, however, the degrees of freedom may actually be fewer than four, indicating that this test is overly conservative (Pagel, 1994). For this

reason, simulations were also performed (500 iterations for each) to provide an additional assessment of statistical significance.

Global optima for likelihood scores in DISCRETE were obtained by running 20 repetitions of each model to check the stability of the maximum-likelihood estimate. In cases where the likelihood values varied considerably, we estimated the parameter kappa (κ) via maximum likelihood to differentially stretch or compress branch lengths within the phylogeny (Pagel, 1994). The value of kappa that provided the best maximum-likelihood score was estimated using the dependent model of evolution, then fixed within the competing models for generating a likelihood ratio test-statistic and for simulations.

We investigated combinations of discrete and continuous characters for 67 procellariiform species using methods based on independent contrasts (Felsenstein, 1985; Harvey & Pagel, 1991) as implemented by the BRUNCH algorithm of the program CAIC (Purvis & Rambaut, 1995). Nesting habit was investigated by analysing only those species that were either burrow or surface nesters (0 or 1) or by including crevice nesters ranked as an intermediate category (0 = burrow, 1 = crevice and 2 = surface). Log transformations of body mass, wing span and wing area were used to eliminate significant associations between the absolute value of the standardized contrasts and the estimated nodal values for these traits (Purvis & Rambaut, 1995). Tests for associations between the absolute value of contrasts and their standard deviations indicated that untransformed branch lengths could be incorporated in all analyses (Garland *et al.*, 1992, Purvis & Rambaut, 1995). No outliers due to assumption violations or confounding variables were detected for any of the independent contrasts.

Ancestral state reconstructions follow the continuous time Markov model of Pagel (1994, 1999), as implemented by Jackson (2004) in the software LASRDISC, a plug-in module for the Mesquite system (Maddison & Maddison, 2003). Nesting habit (burrow vs. surface) and DMS response (attraction vs. nonattraction) were coded as binary characters. The ancestral state of each character was reconstructed using the global and local approaches of Pagel (1999) that are based on maximum likelihood. Log-likelihood scores were calculated under a Markov *k*-state one-parameter model (Mk.1), where forward and backward transition rates are assumed to be equal, and under an asymmetrical Markov *k*-state two-parameter model (Asym. 2.) where the transition rates may vary independently. The two-parameter model was considered an improvement if a likelihood ratio test-statistic exceeded the critical value of the chi-squared distribution with one degree of freedom. A likelihood ratio test was also used as a measure of support for the reconstruction of ancestral states. However, as the two alternative state hypotheses were not nested, a chi-squared distribution could not be used to generate a significance threshold (Pagel, 1999). Instead, a rule of thumb of two log units

was used as the threshold for determining whether the log likelihoods for each hypothesis were significantly different (Edwards, 1972). Joint reconstructions, where the likelihood was maximized simultaneously over all nodes, and marginal reconstructions, where one node was fixed while the likelihood was summed over all state assignments at the other internal nodes, were also performed using LASRDISC (Jackson, 2004).

We tested the direction and order of changes in olfactory attraction and nesting habit for traits that showed significant evidence for correlated evolution using the transition rate parameters estimated within DISCRETE (Pagel, 1994). This method can be used to determine if a particular evolutionary pathway between the two traits is more likely given the data. The transition rate parameters estimated by DISCRETE were tested for significance by comparing the likelihood score of the full model against the score for a model in which a transition is excluded by forcing it to zero. The test follows an asymptotic chi-squared distribution with one degree of freedom. Pagel (1994, 1997) provides a detailed description of the model and the tests.

For comparison, we also performed a series of analyses that were either uncorrected for phylogeny or involved conversion of continuous data to categories. The Markov chain model of DISCRETE, for example, is unlikely to have the same statistical power as the contrasts employed in BRUNCH, complicating the interpretation of negative results across these two methods. Performing phylogenetically uncorrected analyses and using converted data allowed us to compare results with the same level of statistical power. For the relationship between body size and odour response, we used logistic regression. To allow for direct comparisons among results from DISCRETE and BRUNCH, we converted body mass into the categories 'small' (< 1000 g) or 'large' (> 1000 g). This division allowed us to lump species that were within an order of magnitude of each other in terms of their mass. With this system, we could apply DISCRETE to questions relating body size to odour responsiveness and flight height.

Results

The presence or absence of a response by each seabird species to at-sea odour deployments is presented alongside their phylogenetic relationship in Fig. 1. Of the 15 species or species groups for which experimental data were available, we scored 14 for DMS responsiveness, 15 for krill responsiveness and 14 for cod liver oil responsiveness. Species or species groups differed in their responsiveness to the different odours, with seven of 14 (50%) scored as responsive to DMS, eight of 15 (53%) scored as responsive to krill scent (homogenate or pyrazines) and 12 of 14 (86%) scored as responsive to cod liver oil.

Log-likelihood scores and parameter estimates for each of the pairings of nesting strategy and odour

Table 1 Model parameters (κ), likelihood scores and results of chi-squared and simulation tests for correlated trait evolution between nesting habit and responsiveness to odor cues.

Nesting habit vs. (responsiveness to)	κ	Independent likelihood	Dependent likelihood	LR test-statistic	Chi-squared P-value	Simulation P-value
DMS	0.005	−12.53	−7.92	9.21	0.056	0.006
Krill Homogenate	0.200	−15.65	−15.59	0.12	0.998	0.924
Cod liver oil	0.250	−10.96	−10.96	0.10	0.999	0.950
Body size	0.000	−12.89	−8.82	8.13	0.080	0.076

Likelihood scores were calculated using Pagel's (1999) DISCRETE software. DMS, Dimethyl sulphide.
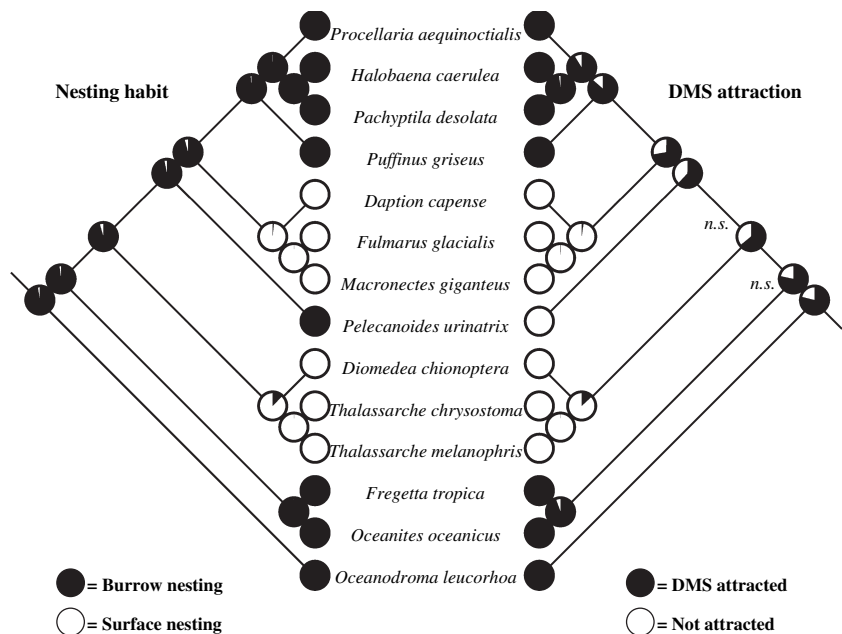
responsiveness are presented in Table 1. DMS responsiveness and burrow nesting showed a significantly better fit under the model of correlated trait evolution using either a chi-squared test or simulations. Responsiveness to krill homogenate and cod liver oil, however, were no more likely to fit a correlated model than one allowing for independent trait evolution. Body size, when categorized as 'large' or 'small', showed no significant relationship with nesting strategy (Table 1) or responsiveness to DMS ($-2LR = 6.76$, d.f. = 4), krill ($-2LR = 0.334$, d.f. = 4) or cod liver oil ($-2LR = 0.769$, d.f. = 4). Transition rate parameters for changes among the states of the correlated traits (nesting habit and DMS responsiveness) were also calculated using DISCRETE. Full models incorporating transition rate parameters provided no improvement over reduced models (with transition rates set to zero) using a likelihood ratio test-statistic.

Marginal reconstructions for the ancestral states of nesting habit and olfactory responsiveness using the pruned Nunn and Stanley tree and Pagel's global method with a one-parameter model are presented in Fig. 2. Marginal and joint reconstructions yielded similar patterns of ancestral state reconstructions at each node, with

burrow nesting and attraction to DMS the more likely ancestral conditions for this group of procellariiforms. Reconstructions of nesting state using data for 78 species from the Nunn and Stanley topology and 92 species from the Kennedy and Page supertree also support burrow nesting as the ancestral state of the Procellariiformes. In all cases, use of a two-parameter model did not yield a statistically significant improvement over the one-parameter (i.e. equal forward and backward transition rates) model in log-likelihood scores. The global and local methods of reconstruction also yielded similar results for ancestral state assignments, and each showed similar levels of support. Log-likelihood scores for the various combinations of global vs. local, one parameter vs. two, and marginal and joint reconstructions are presented for nesting habit and olfactory responsiveness in Appendix 1.

Finally, we found no significant relationships between adult morphology (body mass or wing measurements) and either nesting strategy or attraction to odours when using phylogenetically corrected methods. Independent contrasts of body mass show predictable allometric relationships with wing span ($t = 5.817$, $P < 0.001$), wing

Fig. 2 Marginal probability reconstructions of ancestral states for nesting habit and olfactory responsiveness using the topography of Nunn & Stanley (1998). Both trees employ a global analysis and a Markov k-state one-parameter model (Pagel, 1999). Areas of pie charts indicate relative support for each ancestral state. Dimethyl sulphide (DMS) attraction refers to those species that showed a statistically significant behavioural response to DMS slicks during previous at-sea trials (Fig. 1) Log-likelihood scores for the trees are −6.869894700 for nesting habit and −7.607159452 for olfactory responsiveness. All reconstructions are significant for the ancestral state occupying the majority of each node, except for two nodes labelled as not significant (NS).

Nesting habit

Procellaria aequinoctialis
Halobaena caerulea
Pachyptila desolata
Puffinus griseus
Daption capense
Fulmarus glacialis
Macronectes giganteus
Pelecanoides urinatrix
Diomedea chionoptera
Thalassarche chrysostoma
Thalassarche melanophris
Fregetta tropica
Oceanites oceanicus
Oceanodroma leucorhoa

DMS attraction

n.s.
n.s.

● = Burrow nesting
○ = Surface nesting

● = DMS attracted
○ = Not attracted

Flight height vs. (responsiveness to)	κ	Independent likelihood	Dependent likelihood	LR test-statistic	Chi-squared P-value	Simulation P-value
DMS	0.30	−7.07	−4.83	4.48	0.345	0.069
Krill Homogenate	0.25	−8.26	−7.19	2.14	0.710	0.622
Cod liver oil	0.35	−7.95	−7.32	1.26	0.868	0.730
Body size	0.00	−10.90	−6.12	9.56	0.0485	0.0437

Table 2 Model parameters (κ), likelihood scores and results of chi-squared and simulation tests for correlated trait evolution between flight height and responsiveness to odour cues.

Likelihood scores were calculated using Pagel's (1999) DISCRETE software. DMS, dimethyl sulphide.

area ($t = 5.583$, $P < 0.001$) and wing aspect ratio ($t = 5.614$, $P < 0.001$). Standard logistic regression (uncorrected for phylogeny) of body mass on attraction to odours did, however, reveal a significant relationship between mass and DMS responsiveness ($P = 0.041$; $\beta = -2.459$; SE = 1.205). Independent contrasts showed a marginally significant ($t = 7.61$, $P = 0.052$) relationship between flight height and body mass, a result consistent with Pennycuick's (1982) observation that small procellariiforms tend to fly closer to the ocean surface than large procellariiforms. However, neither nesting habit nor odour responsiveness showed a significant relationship with body mass. Contrasts of wing measurements (span, area, aspect ratio and load) with nesting habit and odour attraction (DMS, krill and cod liver oil) were nonsignificant in all instances. Results from likelihood analysis indicate a relationship between flight height and odour responsiveness. Likelihood scores from DISCRETE for the dichotomous characters flight height and attraction to odour slicks revealed significant simulation evidence for correlated trait evolution between flight height and DMS attraction, but no support for relationships between flight height and attraction to krill- or fish-related odours (Table 2).

Discussion

Our study suggests that the variation in behavioural attraction to DMS is not distributed randomly among the procellariiforms, but is instead strongly correlated with nesting habit. We found that most burrow-nesting species are attracted to DMS, whereas surface nesters are not. Furthermore, our analysis indicates that the ancestral condition for this group is burrow nesting, with subsequent independent radiations to surface nesting in the albatrosses and the fulmarine petrels. Combining these results with our present knowledge of the sensory ecology of foraging in the procellariiforms, we suggest that these moves to the surface led to the development of an increased use of visual or multimodal (visual + olfactory) foraging strategies and a decreased reliance on tracking odour plumes to locate prey.

To put this hypothesis in context, DMS emissions increase when phytoplankton is grazed by zooplankton (Dacey & Wakeham, 1986; Kasamatsu et al., 2004). Results from empirical studies at sea suggest that DMS

responders opportunistically exploit ephemeral prey patches by detecting these initial elevated emissions by smell (Nevitt et al., 1995). These 'early-detector' species can thus practice a hit-and-run strategy, capitalizing on prey patches before more aggressive predators arrive. However, if the prey patch persists beyond a few minutes, foraging activity increases the types of cues available to other foraging seabirds. As the birds feed, odours from macerated krill are released adding olfactory information about the condition of the prey patch. The physical presence of accumulating birds and other predators adds visual information (see Nevitt, 1999a; Nevitt et al., 2004). These multi-modal stimuli draw in 'late-detector' species, which can aggressively dominate the rapidly growing mixed-species feeding aggregation.

In procellariiforms, as in other animals, odour-tracking behaviour is characterized by zigzag upwind flight to the odour source (Grubb, 1972; reviewed by Dusenbery, 1992). Fluctuations in the odour plume are characterized, in turn, by intermittency (Li et al., 2001) such that the ability to maximize odour detection to locate the source requires a high degree of manoeuvrability within the spatial scale that demarcates the odour plume (Dusenbery, 1992; Nevitt, 2006). As birds get larger and more reliant on dynamic soaring, they reduce their ability to track odour plumes as efficiently or at the same spatial scales as more manoeuvrable species. Thus, this highly efficient mode of flight may work against the manoeuvrability required for opportunistically tracking odour plumes at more limited spatial scales. Instead, an increased dependence on dynamic soaring would allow for the exploitation of a wider habitat range (e.g. Weimerskirch et al., 1997) and a greater reliance on visual cues and network foraging (e.g. Silverman et al., 2004) to find available prey patches.

Size, through its influence on chick predation risk and thermoregulatory ability, is typically assumed to influence which lineages nest underground and which nest at the surface (Warham, 1990, 1996). Size varies greatly within the procellariiforms, ranging from the storm petrels (40–60 g) to the largest albatrosses (6–8 kg), yet our phylogenetically corrected analyses showed no significant associations between body mass and nesting habit or between body mass and DMS tracking behaviour (Table 2). Likewise, the morphology of the procellariiform wing influences both range and manoeuvrability

with respect to flight performance (Cone, 1964; Warham, 1977; Pennycuick, 1982; Spear & Ainley, 1998), but we found no associations between wing span, wing area or aspect ratio and either nesting habit or behavioural sensitivity to DMS. Although the statistical power of the comparative analyses does not allow us to rule out relationships between size and nesting or wing morphology and odour responsiveness, our results suggest that other selective pressures are acting that may have been previously overlooked.

Based on our evidence for correlated trait evolution between nesting habit and DMS attraction, we propose that the move to the surface by albatrosses and fulmarine petrels opened up a new developmental environment with profound effects on foraging ecology. In an evolutionary timeframe, surface nesting provided chicks much earlier access to a broader array of visual cues and, particularly, earlier access to light. The response of the developmentally plastic phenotype to this new environment could be acted upon by selection. Those species that moved to the surface would eventually become less reliant on olfactory cues and more reliant on vision. In the context of foraging, this would mean that surface nesters would become less reliant on olfactory tracking to locate ephemeral prey patches and more reliant on multi-modal and network foraging to exploit productive areas (Waugh & Weimerskirch, 2003). Whereas the present discussion is limited to foraging behaviour, observed differences between burrow and surface nesters with respect to activity patterns (crepuscular vs. diurnal) and nest site relocation (olfactory vs. multimodal) are consistent with this model (reviewed by Nevitt & Bonadonna, 2005).

This hypothesis allows us to formulate several testable predictions about the sensory abilities of surface-nesting vs. burrow-nesting species with respect to their foraging ecology. First, as DMS is considered to be a keystone odorant in the marine food web (Hay & Kubanek, 2002), we expect that closely related species that are burrow nesters will also be responsive to DMS. This could include species from orders such as the Sphenisciformes (penguins), a group whose shared ancestry with the Procellariiformes is well supported by fossil and molecular evidence (Slack *et al.*, 2006). Whereas the link to foraging has not been established, it is intriguing that preliminary experiments with African Penguins (*Spheniscus demersus*), suggest that these birds can detect DMS and will orient to it in a Y-maze (Cunningham *et al.*, 2006).

Secondly, we expect that surface nesters and burrow nesters will have different visual capabilities and that these differences will impact foraging behaviour. Although visual fields and their relationship to the pursuit of individual prey items have been explored in the procellariiforms (Martin & Brooke, 1991; Martin, 1998; Martin & Prince, 2001), data are lacking on both visual acuity (the ability to see detail at distance) and sensitivity (the ability to see in low light levels). Both of

these characteristics contribute to how well birds should be able to monitor foraging activity of other birds and marine mammals at sea. An increase in eye size is one evolutionary means of increasing acuity (Land, 1981) and may provide an initial metric for exploring differences in the ability of surface nesters and burrow nesters to detect activity of other birds at sea, particularly in low light levels (*sensu* Thomas *et al.*, 2002). Species that develop in the dark environment of the burrow are in a setting that is conducive to the evolution of heightened visual sensitivity (night vision). Sensitivity improves through increases in the pupil aperture or photoreceptor type (Martin, 1993), and increased sensitivity would be beneficial to species that are crepuscular or nocturnal (see also Miller, 1979; Land, 1981). Thus, the balance between eye size, structure and receptor type should differ between surface and burrow nesters.

Thirdly, we expect burrow-nesting species to show higher levels of in-flight manoeuvrability. Our limited exploration of wing morphology failed to identify evolutionary correlations with either nesting habit or olfactory responsiveness. However, wing shape is only one factor that influences manoeuvrability. Tail plumage is used to generate torque, both with respect to turning and to maintain stability and thus plays a substantial role in determining the speed with which a change in direction can be initiated (Dudley, 2002). A comparative analysis of procellariiform tail morphology may be one means of relating differences in manoeuvrability to foraging strategy. In addition, our analysis indicates that DMS-responsive species fly closer to the surface of the ocean where flux is the highest and odour plumes may be easier to pick up and follow.

Lastly, we expect contrasting selection pressures on surface- and burrow-nesting species to lead to distinct differences in the coloration of their plumage. DMS responders would benefit from being less visible at sea as these birds are exploited by other larger and more aggressive species that may exclude them from foraging opportunities. Flying close to the surface of the water and being cryptically coloured would reduce the visibility of olfactory foraging species. By contrast, species that rely on visual cues when searching for prey are more likely to engage in network foraging behaviour. This is only possible if birds are able to spot conspecifics at great distance. We predict that species utilizing visual cues will have contrasting black and white plumage patterns that increase visibility at sea (Bretagnolle, 1993).

As a signal molecule, DMS provides an important tool for defining olfactory foraging strategies (Hay & Kubanek, 2002). Here, a connection between nesting environment and responsiveness to DMS has allowed us to view differences in the way procellariiforms use their sensory modalities as one consequence of the shift to surface nesting in the albatrosses and fulmarine petrels. By identifying evolutionary associations between behavioural responses to cues such as DMS and the

developmental environment, we can formulate testable hypotheses about the evolution of foraging behaviour within a framework of sensory ecology rather than limiting such investigations to the analysis of flight style alone.

Acknowledgments

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Appendix

Log-likelihood scores for ancestral state reconstructions of nesting habit and olfactory responsiveness based upon the phylogeny of Nunn and Stanley pruned to 15 species. Scores illustrate similarities in support of the reconstruction when the likelihood method, reconstruction method or model of evolution is varied. Joint refers to the maximization of likelihood simultaneously over all nodes, whereas marginal refers to maximizing likelihood with one node fixed. Global and local indicate the use of Pagel's (1999) global and local reconstruction methods. Mk.1 indicates a one-parameter model of evolution and Asym. 2 indicates a two-parameter model of evolution.

Likelihood method	Reconstruction method	Model of evolution	Nesting habit log likelihood	Olfactory response log likelihood
Joint	Global	Mk.1	−7.099761052	−8.461660160
Joint	Global	Asym. 2	−6.624131954	−7.581551890
Joint	Local	Mk.1	−7.078153100	−8.392004551
Joint	Local	Asym. 2	−6.494621352	−7.579192070
Marginal	Global	Mk.1	−6.869894700	−7.607159452
Marginal	Global	Asym. 2	−6.494621352	−7.400094360
Marginal	Local	Mk.1	−6.800940298	−7.564026380
Marginal	Local	Asym. 2	−6.285546154	−7.010795970