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Evidence that dimethyl sulfide facilitates a tritrophic mutualism between marine primary producers and top predators

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Tritrophic mutualistic interactions have been best studied in plant–insect systems. During these interactions, plants release volatiles in response to herbivore damage, which, in turn, facilitates predation on primary consumers or benefits the primary producer by providing nutrients. Here we explore a similar interaction in the Southern Ocean food web, where soluble iron limits primary productivity. Dimethyl sulfide has been studied in the context of global climate regulation and is an established foraging cue for marine top predators. We present evidence that procellariiform seabird species that use dimethyl sulfide as a foraging cue selectively forage on phytoplankton grazers. Their contribution of beneficial iron recycled to marine phytoplankton via excretion suggests a chemically mediated link between marine top predators and oceanic primary production.

Many plant species interact with carnivores to gain protection from herbivory. Such mutualistic tritrophic interactions have been studied extensively in plant–insect systems, and are frequently mediated by plant volatiles released in response to insect feeding (1). One example that has received detailed study is the interaction between the phytophagous two-spotted spider mite *Tetranychus urticae*, the lima bean plant *Phaseolus lunatus*, and the predatory mite *Phytoseiulus persimilis* (2, 3). In this model system, grazing by the herbivorous spider mite has been demonstrated to elicit a cascade of biochemical reactions within the afflicted plants, stimulating the release of a suite of volatile terpenoids such as (*E*)-4,8-dimethyl-1,3,7-nonatriene, (*E*)- β -ocimene, and (*E,E*)-4,8,12-trimethyl-1,3,7,11-tridecatetraene (3). These volatiles attract olfactory-searching *P. persimilis* that prey upon herbivorous spider mites.

The possibility of tritrophic mutualisms involving plant volatiles has received considerable attention in terrestrial communities (2–5); however, similar interactions have rarely been suggested for marine systems (6). Dimethyl sulfide (DMS) and its precursor dimethylsulfoniopropionate (DMSP) are well-established infochemicals in the marine environment, and as such are good candidate molecules for mediating tritrophic interactions between phytoplankton and carnivores (7–10). DMS arises as a catabolic breakdown product of DMSP, and has been studied extensively for its putative role as a global climate regulator (11). DMSP is produced by marine algae, where it has been proposed to function as an osmolyte (12) and a cryoprotectant (13). When algal cells lyse, due to biotic or abiotic stress, one of the fates of DMSP is catabolism by the enzyme DMSP lyase to DMS and acrylic acid (14–16). This process may also occur during autocatalytic cell death (17). It has been proposed that acrylic acid is the biologically salient product of this reaction due to its antimicrobial properties (18).

DMS production has also been shown to increase during zooplankton grazing (14). It has been previously proposed that this phytoplankton-derived odorant is an important infochemical for marine apex predators including whale sharks (19), harbor seals (20), penguins (21–23), and procellariiform (tube-nosed) seabirds (24). Procellariiform seabirds have been the best-studied

in this regard, and many species have been shown to detect and respond to biogenic concentrations of DMS in foraging contexts (24, 25). Members of this order share highly pelagic lifestyles and are central-place foragers associated with land only during incubation and chick rearing (26). Procellariiforms routinely range thousands of kilometers to forage (27) and have large olfactory bulbs compared with other avian clades (28), and some species have been shown to track their prey using their sense of smell (29). Some procellariiform species are attracted to DMS, whereas others are not (24, 30) (Fig. 1); however, the relationship between DMS behavioral sensitivity and the consumption of herbivorous crustacea has not previously been shown.

The Southern Ocean is the largest marine ecosystem in the world, with the polar front forming a distinct northern boundary to this ecoregion (31). Our rationale for using this system is twofold: (*i*) A majority of the world's procellariiform species breed or forage in the Southern Ocean (32), and (*ii*) food web relationships are relatively simple by comparison with other marine systems. *Phaeocystis antarctica* and several siliceous diatom species are the dominant DMS-producing phytoplankton species in this ecosystem, and Antarctic krill (*Euphasia superba*) and other small crustaceans (copepods, decapods, amphipods, etc.) are their major consumers.

Here we take advantage of a 50-y dietary database of Southern Ocean seabirds (33) to explore whether DMS mediates a mutualistic tritrophic interaction in the Southern Ocean pelagic ecosystem. If this is the case, then we predict that (*i*) carnivorous species, such as seabirds, that are attracted to this infochemical should specialize on primary consumers, such as crustaceans, and (*ii*) primary producers should gain some benefit from this interaction.

Significance

This study demonstrates that dimethyl sulfide, a chemical cue involved in global climate regulation, mediates a tritrophic mutualistic interaction between marine apex predators and primary producers. Our results imply that marine top predators play a critical role in maintaining both ocean health and global climate. Our results highlight the need for more collaboration and discussion between micro- and macroscale biologists working on global issues in the Southern Ocean.

Author contributions: M.S.S. and G.A.N. designed research; G.A.N. developed the initial dataset; M.S.S. performed research; M.S.S. analyzed data; and M.S.S. and G.A.N. wrote the paper.

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Procellariiform species included in analysis

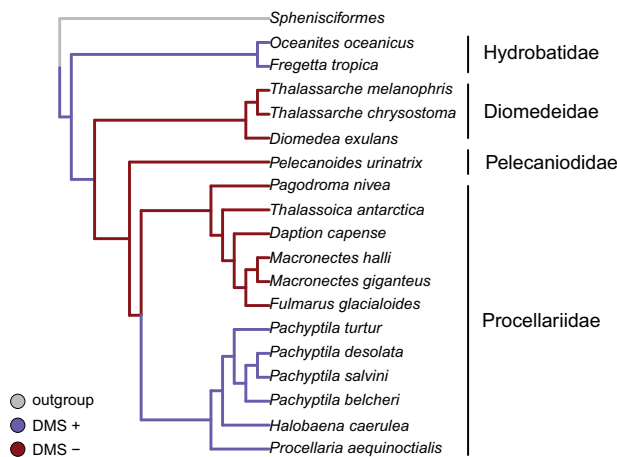


Fig. 1. Phylogenetic relationships between the species included in the meta-analysis, mapped with DMS responsiveness. DMS responsiveness is thought to be ancestral in this lineage (30). Certain species in the outgroup, sphenisciformes (penguins), have also been shown to be responsive to DMS (21–23).

Results

To address our first prediction, we conducted a meta-analysis of diet composition relative to DMS behavioral sensitivity for different procellariiform species. Our meta-analysis included 48 diet studies, which analyzed the stomach contents of over 3,000 individuals of 18 different procellariiform species (Fig. 1 and Fig. S1). Drawing from this extensive database, we found that DMS-tracking species forage mainly on primary consumers, as indicated by a dramatically greater proportion of crustacea in their overall diet [proportion crustacea, 0.814 ± 0.039 ; proportion cephalopod, 0.065 ± 0.019 ; proportion fish, 0.108 ± 0.024 ; averages are weighted by sample size; $F_{2,274} = 62.043$, $P < 0.001$, Tukey honest significant difference (HSD) test; Fig. 2]. By contrast, the diets of non-DMS-tracking species consisted of primary consumers in equal proportions to other food types (proportion crustacea, 0.249 ± 0.035 ; proportion cephalopod, 0.327 ± 0.046 ; proportion fish, 0.316 ± 0.037 ; averages are weighted by sample size; $F_{2,274} = 62.043$, $P = 0.99$, Tukey HSD test; Fig. 2).

We also investigated morphology as a secondary indicator of olfactory foraging (34). Over the ocean, odors are transported in turbulent plumes and maneuverability is thought to be an adaptation for tracking discontinuous filaments within odor plumes to their source (35). Based on previous studies, we predicted that smaller, more maneuverable birds would be more likely to track DMS (30). We were also interested in how morphology intersected with diet. When controlling for the potential effects of phylogeny (see Fig. 1 for phylogenetic relationships and Table S1 for model performance) on our response variable, we found that smaller and more maneuverable procellariiform species consumed greater proportions of crustacea. A multiple linear regression shows a highly significant negative relationship between log-transformed body mass and DMS behavioral responsiveness as predictors of the proportion of crustacea in the diet ($\beta_{\log wt} = -0.29 \pm 0.046$, $P < 0.001$; $\beta_{DMS \text{ tracker}} = 0.24 \pm 0.046$, $P < 0.001$; Fig. 3A). We report a similar negative relationship between aspect ratio (inversely related to maneuverability) and DMS behavioral responsiveness as predictors of the proportion of crustacea in the diet ($\beta_{\log wt} = -0.09 \pm 0.014$, $P < 0.001$; $\beta_{DMS \text{ tracker}} = 0.27 \pm 0.064$, $P < 0.001$; Fig. 3A).

Both body mass and aspect ratio had far less predictive value for food groups composed of organisms from higher trophic levels. A multiple linear regression for the proportion of cephalopods in the diet showed a positive overall relationship (Fig. 3B), but log-transformed weight was the only significant morphological predictor ($\beta_{\log wt} = 0.12 \pm 0.055$, $P = 0.03$; $\beta_{DMS \text{ tracker}} = -0.10 \pm 0.082$, $P = 0.23$ and $\beta_{\text{aspect ratio}} = 0.06 \pm 0.016$, $P = 0.89$; $\beta_{DMS \text{ tracker}} = -0.03 \pm 0.076$, $P = 0.70$). The multiple linear regression for the proportion of fish in the diet exhibited a weakly positive overall relationship (Fig. 3C), but neither morphological parameter was significant ($\beta_{\log wt} = 0.01 \pm 0.049$, $P = 0.89$; $\beta_{DMS \text{ tracker}} = -0.15 \pm 0.073$, $P = 0.04$ and $\beta_{\text{aspect ratio}} = 0.02 \pm 0.015$, $P = 0.29$; $\beta_{DMS \text{ tracker}} = -0.10 \pm 0.070$, $P = 0.16$; Fig. 3C). Taken together, these results suggest that DMS behavioral responsiveness is linked to the consumption of primary consumers (crustacea) that forage on DMS-producing phytoplankton. As a result, we argue that procellariiform seabirds are playing a similar role to that played by carnivorous mutualists (e.g., *P. persimilis*) in plant–insect interactions.

For this chemically mediated, tritrophic interaction to be mutualistic, it must also carry a benefit to phytoplankton (Fig. 4). Predatory release implies that phytoplankton are “rescued” from grazing pressure when primary consumers are ingested by carnivores. Our results support this hypothesis in that DMS responders were found to preferentially consume phytoplankton grazers (Fig. 2). However, we also considered the possible fertilization benefits that foraging seabirds may provide to phytoplankton. Iron is necessary for electron transfer and ATP production involved in phytoplankton growth (36), but the Southern Ocean is iron-limited (37). This is because the Southern Ocean lacks major land masses to supply new iron via continental (Aeolian) dust or riverine (fluvial) runoff (38). New iron can also enter the surface layer (photic zone) via other abiotic processes, such as upwelling, vertical mixing, or lateral flow, but its overall scarcity contributes to the high-nutrient low-chlorophyll (HNLC) conditions that characterize surface seawater in this region (38, 39). Biologically recycled iron is, therefore, critical in fueling primary production, and iron budget models suggest that at least half of usable iron is recycled (40, 41). Studies of biotic processes contributing to recycling are generally limited to planktonic food web or microbial interactions (42–44), but defecation by marine top

alopods in the diet showed a positive overall relationship (Fig. 3B), but log-transformed weight was the only significant morphological predictor ($\beta_{\log wt} = 0.12 \pm 0.055$, $P = 0.03$; $\beta_{DMS \text{ tracker}} = -0.10 \pm 0.082$, $P = 0.23$ and $\beta_{\text{aspect ratio}} = 0.06 \pm 0.016$, $P = 0.89$; $\beta_{DMS \text{ tracker}} = -0.03 \pm 0.076$, $P = 0.70$). The multiple linear regression for the proportion of fish in the diet exhibited a weakly positive overall relationship (Fig. 3C), but neither morphological parameter was significant ($\beta_{\log wt} = 0.01 \pm 0.049$, $P = 0.89$; $\beta_{DMS \text{ tracker}} = -0.15 \pm 0.073$, $P = 0.04$ and $\beta_{\text{aspect ratio}} = 0.02 \pm 0.015$, $P = 0.29$; $\beta_{DMS \text{ tracker}} = -0.10 \pm 0.070$, $P = 0.16$; Fig. 3C). Taken together, these results suggest that DMS behavioral responsiveness is linked to the consumption of primary consumers (crustacea) that forage on DMS-producing phytoplankton. As a result, we argue that procellariiform seabirds are playing a similar role to that played by carnivorous mutualists (e.g., *P. persimilis*) in plant–insect interactions.

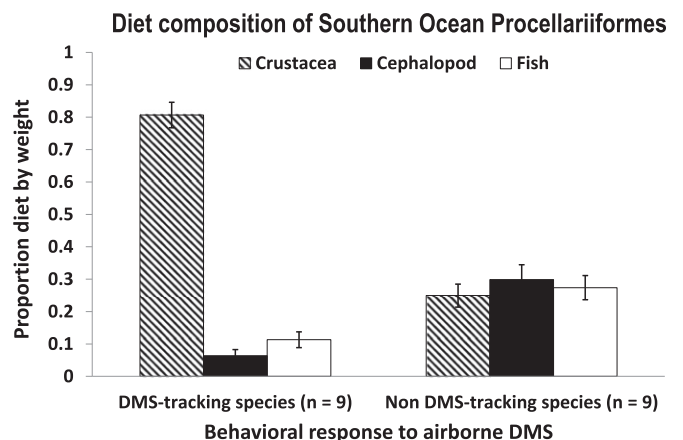


Fig. 2. Diet composition of Southern Ocean procellariiform seabirds relative to DMS responsiveness. Differences in diet among DMS-tracking and non-DMS-tracking species were tested with a GLMM (fit with the package blme in R version 2.15). To control for pseudoreplication, each study and study species was specified as a random effect. To determine the strength of the interactive effect (DMS tracker*food type) compared with the simple main effects on the response (proportion diet), we computed a two-way ANOVA on the fit model. DMS-tracking species' diets contain significantly higher proportions of crustacea than cephalopods or fish ($F_{2,274} = 62.043$, $P < 0.001$; Tukey HSD) in this analysis. Results are shown \pm SE. All reported averages are weighted by the sample size.

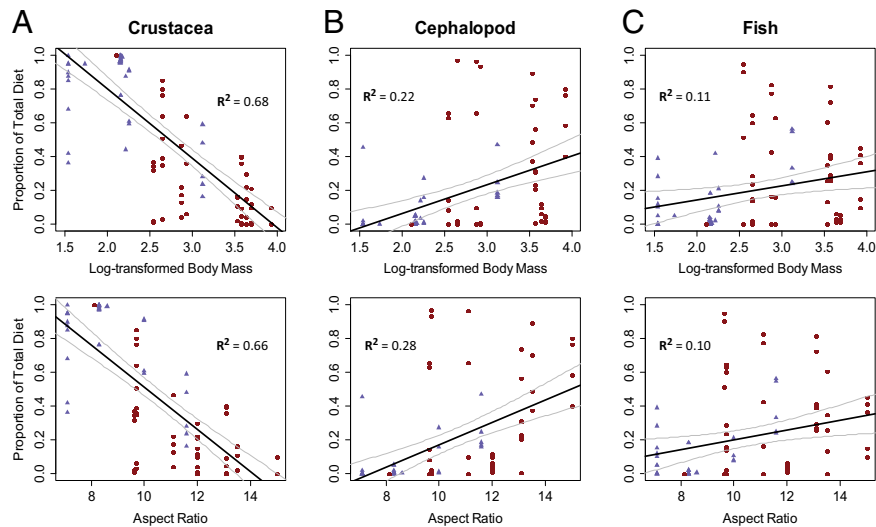


Fig. 3. Morphological relationships for Southern Ocean procellariiforms in relation to diet and DMS attraction. Each point (blue, DMS-tracking species; red, non-DMS-tracking species) represents a species average value within a particular diet study included in the meta-analysis. The black line in each panel depicts the best-fit regression line; gray lines depict upper and lower 95% confidence intervals. (A) A multiple linear regression shows a highly significant negative relationship between log-transformed body mass and the proportion of crustacea in the diet ($F_{2,91} = 96.61$, $R^2 = 0.68$, $P < 0.001$) and, similarly, between aspect ratio (inversely related to maneuverability) and the proportion of crustacea in the diet ($F_{2,83} = 81.45$, $R^2 = 0.66$, $P < 0.001$). (B) A multiple linear regression shows a positive relationship between log-transformed body mass and the proportion of cephalopods in the diet ($F_{2,89} = 11.89$, $R^2 = 0.22$, $P < 0.001$) and, similarly, between aspect ratio (inversely related to maneuverability) and the proportion of cephalopods in the diet ($F_{2,81} = 15.77$, $R^2 = 0.28$, $P < 0.001$). (C) A multiple linear regression shows a weakly positive relationship between log-transformed body mass and the proportion of fish in the diet ($F_{2,91} = 5.52$, $R^2 = 0.11$, $P = 0.005$). The positive relationship between aspect ratio (inversely related to maneuverability) and the proportion of fish in the diet explains even less of the variability in the dataset ($F_{2,83} = 4.544$, $R^2 = 0.10$, $P = 0.013$).

predators has also recently been proposed (45, 46) and investigated with reference to cetaceans (47, 48). It has previously been shown that Antarctic krill play a role in recycling iron (49) and also represent a biological reservoir for iron, sequestering roughly a quarter (~24%) of the total iron in the surface waters of their range (47). Iron sequestered in krill can be made accessible to phytoplankton

through ingestion and subsequent defecation by top predators. Vertebrates excrete iron in feces as ferrous salts (50). As the ferrous salts dissolve, the iron readily binds to ligands (51). It has been suggested that this process increases the residence time of excreted iron in the surface layer of the ocean (51), where it serves as a potential source of recycled iron for phytoplankton (47).

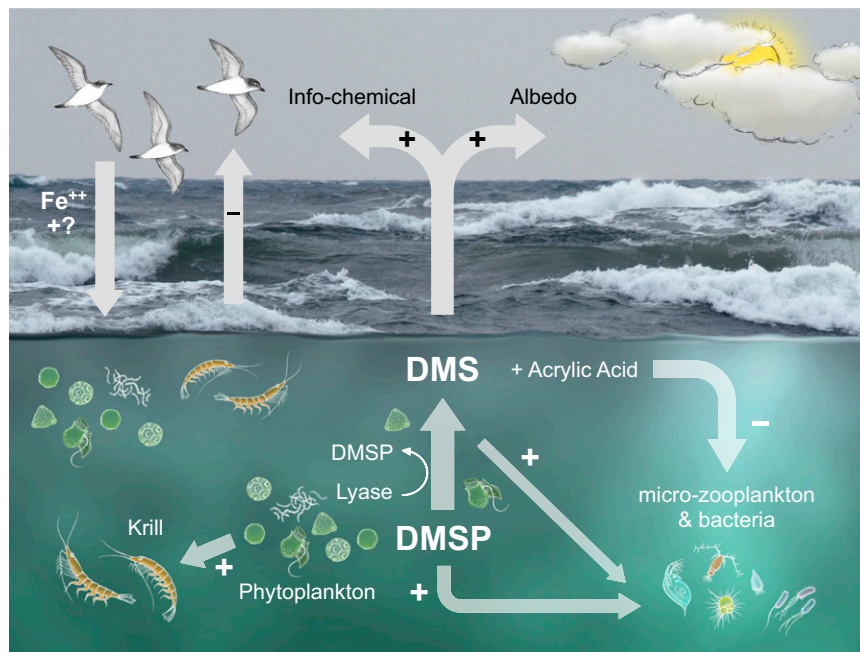


Fig. 4. In this tritrophic mutualism, phytoplankton are grazed by crustacea, catalyzing an enzymatic reaction that converts DMSP to DMS and acrylic acid. DMS, in turn, attracts procellariiform seabirds that forage on primary consumers (crustacea), thereby reducing grazing pressure on phytoplankton. Once attracted, the procellariiforms may benefit the phytoplankton by adding limiting nutrients via excretion. (Figure credit: Allison Bruce.)

Seabirds defecate at foraging sites in viscous, liquid form on the surface layer of the ocean. Iron is generally toxic to birds, and roughly 90% of ingested iron must be excreted (52). Reported iron concentration in seabird feces is 185 ± 9.3 ppm dry weight (53), which is similar to the iron concentration in baleen whale fecal plumes (166.6 ± 155.2 ppm dry weight) (47). This is roughly 10 million times the average iron content of Southern Ocean seawater (0.2–0.3 nM) (54), even in historically productive regions of the Southern Ocean where iron concentrations are highest (0.1–0.6 nM) (55). Local enhancements of only 0.1–0.5 nM iron can stimulate phytoplankton growth in vitro (39). This suggests that the deposition of excrement during foraging could elevate iron levels enough to locally stimulate phytoplankton growth, especially when considering that productive areas consist of heterogeneously productive patches that can be rapidly exploited and fertilized by seabirds. Moreover, experimental results show that DMS-responsive species act as scouts for locating transiently productive patches that may be disassociated from upwelling areas (24). This behavior can initiate mixed-species feeding aggregations of seabirds and potentially other predators (24, 34, 56).

Thus, we next considered the contribution of Southern Ocean seabirds to iron supplementation. For our initial analysis, we focused on population data from 20 seabird species breeding on South Georgia Island, located 1,500 km northeast of the Antarctic Peninsula at the northern edge of the circumpolar frontal zone. We chose this microcosm because seabirds in this region forage in a krill-dominated system, detailed dietary data are available from long-term studies, and extensive investigation of DMS responsiveness has also been conducted in this region (24). Species known to respond to DMS make up 76% of seabirds breeding on South Georgia (Table S2), and it has been suggested that this behavior contributes to the formation of mixed-species feeding aggregations at krill swarms (34). Over 31 million seabirds breed in this region and their annual consumption of krill has been estimated at 5.69 million metric tons (t) (57), representing a biological iron reservoir of ~ 226 t (Table S3). These birds forage sympatrically with marine mammals, leading to an additive effect on localized fertilization.

Considering the entire Southern Ocean, the biomass of ~ 250 million breeding seabirds (both sphenisciformes and procellariiformes) is estimated at 228,578 t (58). These pelagic seabirds spend most of their lives at sea, and are associated with land only during the breeding season. Consequently, most of their defecation occurs at sea, suggesting that their potential for recycling iron and other nutrients needs to be more carefully considered in maintaining ocean health. For instance, biomass estimates for the blue whale (*Balaenoptera musculus*) population are comparable for the region (59), and their iron contribution is considered to be ecologically significant (47). Taken together, our data support the proposed beneficial effect that seabird excrement has on phytoplankton and provide evidence for a chemically mediated tritrophic mutualistic interaction between primary producers and foraging assemblages of top predators in the Southern Ocean.

Discussion

Effects of marine top predators on phytoplankton chemical and community ecology have rarely been considered (9, 60). Our study highlights a need to better understand how chemical signals regulate interactions between marine top predators and primary producers by providing evidence that DMS plays a similar role to volatile terpenoids in terrestrial plants in attracting olfactory-searching carnivores. This study supports the hypothesis that DMS release, stimulated by herbivore grazing, attracts procellariiform species specializing on primary consumers (Fig. 2). Furthermore, we consider the potential positive impacts that foraging seabirds have on phytoplankton through predatory release and iron recycling via defecation.

DMS is typically studied for its role in contributing to albedo via the formation of cloud condensation nuclei (11). Our results suggest a second climatic role for DMS in stimulating primary production through natural ecosystem processes. Since Martin's seminal work proposing the iron-fertilization hypothesis (39), there has been much interest in artificially fertilizing HNLC oceanic regions to stimulate phytoplankton growth to reduce atmospheric carbon dioxide. It is becoming more apparent, however, that conserving pelagic ecosystems, including marine top predators, may also be critically important to stimulating primary production through trace-nutrient recycling (45–48, 61). Our results contribute to this conclusion by identifying a role for DMS in mediating tritrophic interactions between primary producers and top predators. Our results also point to a pressing need for more interdisciplinary research spanning marine microbial and macroscale ecological processes (62, 63).

To our knowledge, no studies have definitively resolved how marine ecosystems will respond to the extinction of marine top predators and the loss of their contribution to trace-nutrient recycling. Procellariiform seabird numbers are declining rapidly: Nearly half (46.5%) are listed as vulnerable, endangered, or critically endangered (58). Results presented here illustrate a fundamental, albeit understudied, link between apex predators and the base of the pelagic food web, suggesting that a decline in seabird populations could negatively affect overall marine productivity.

Materials and Methods

Diet and Sensory Data Analysis. To test for differences in diet among DMS-tracking and non-DMS-tracking species, we used a generalized linear mixed-model (GLMM) fit using the package *blme* in R (version 2.15, www.R-project.org). In this hierarchical model, we specified each study ($n = 48$ studies) and each species ($n = 18$ species) as a random effect. We did this to avoid pseudoreplication and to make more precise parameter estimates. Additionally, sample size from each individual study was considered, to make the proportion diet estimates as accurate as possible. The two predictor variables considered were DMS tracker (binary: yes/no) and food type (crustacea, cephalopod, and fish). Both predictor variables were categorical. The response variable was percent diet by weight (continuous, bounded at 0 and 1). Fixed effects, random effects, and interactive effects were considered. We used a Bayesian linear mixed-effects regression with weakly informative priors to fit the model. This was done so that the intercept estimates for all random effects were nonzero. Parameters were fit with maximum-likelihood estimation computed using the Laplace approximation (64). To determine the strength of the interactive effect (DMS tracker*food type) compared with the simple main effects on the response (proportion diet), we computed a two-way analysis of variance (ANOVA) on the fit model. After evaluating the factorial ANOVA, we ran a Tukey HSD post hoc analysis to investigate differences between groups. Reported results are \pm SE. Significance was determined at $\alpha = 0.05$.

Morphological Analyses. Multiple linear regressions were performed for the diet and morphological data available for each species. For the first set of models, the predictor variables were log-transformed weight of each seabird species ($n = 18$) and DMS tracker (binary: yes/no) and a weight*DMS tracker interaction. The response variable was proportion diet by weight (continuous, bounded at 0 and 1). Because the difference in body mass was so great between the seabird species considered in the meta-analysis, we log-transformed their body weights to make the data fit a linear model. Three different models were considered to account for the three major food types (crustacea, fish, and cephalopod).

For the next set of regressions, examining maneuverability measures, the predictor variables were the aspect ratio for each seabird species on which we had data ($n = 16$) and DMS tracker (binary: yes/no). The response variable was proportion diet by weight (continuous, bounded at 0 and 1). Again, three different models were considered to account for the three major food types (crustacea, fish, and cephalopod).

It has already been shown that attraction to DMS evolved multiple times during the evolutionary history of the procellariiformes, including several times within the largest family, the procellariidae (30); therefore, it was unnecessary to conduct a systematic analysis to determine whether a behavioral response to DMS was independent of phylogeny.

Phylogenetic Analyses. To investigate the degree to which phylogeny influenced the morphological regression values, we ran phylogenetic least-squares regression

models on each species' mean value. We chose to do this because models that account for multiple measurements within each species in the dependent variable are still in the developmental stage. To incorporate phylogeny into the model, we used the Adams consensus tree (65), downloaded via treeBASE (www.treebase.org). Branch lengths were not provided, so they were created via the Grafen method (66) using the `compute.brln()` function of the R package `ape`.

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