

Olfactory detection of dimethyl sulphide in a krill-eating Antarctic penguin

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ABSTRACT: In response to zooplankton grazing, phytoplankton release dimethylsulphoniopropionate in the seawater, which is then catabolized to dimethyl sulphide (DMS) that is emitted to the air. This molecule therefore signals areas of high productivity in the oceans, and it can be used by predators for locating foraging areas. Detection of this compound has been described in several species of procellariiform seabirds and non-Antarctic fish-feeding penguins. However, there is no evidence of DMS detection by krill-feeding penguins. The mechanisms of krill detection by its predators are especially relevant in Antarctica, where trophic webs are mainly based on krill. We explored for the first time whether a krill-feeding penguin species, the chinstrap penguin *Pygoscelis antarctica*, is able to detect DMS. We examined whether chinstrap penguins could detect DMS by locating DMS or control recipients in pathways that penguins used when moving between the colony and the sea. We also analysed the attraction of nestling penguins to DMS in a T-shaped experimental enclosure. Our results showed that adult penguins are attracted to DMS on land. Nestling penguins also tended to be attracted to the scent of DMS. Further research is needed to examine whether chinstrap penguins use natural DMS concentrations as a foraging cue at sea.

KEY WORDS: Dimethyl sulphide · Avian olfaction · Antarctic penguin · *Pygoscelis antarctica*

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INTRODUCTION

The role of chemical signals in both intra- and interspecific relationships of birds was first studied in birds with larger than average olfactory bulb sizes, such as Procellariiformes (Bang & Cobb 1968). However, subsequent evidence suggests that birds with smaller bulbs, such as Passeriformes, can also detect odours in different contexts and with several functions. At the intraspecific level, olfaction based on chemical compounds emitted by birds may play a key role in social behaviour (Hagelin 2007a,b, Caro & Balthazart 2010). Birds have been shown to use chemical cues to identify their own nest (e.g. Bonadonna et al. 2004, Caspers & Krause 2011). Procellari-

iformes are able to discriminate the scent of their partners from the scent of other conspecifics (Bonadonna & Nevitt 2004). Recently, it has been shown that birds of diverse groups, including Procellariiformes (Bonadonna & Sanz-Aguilar 2012), Passeriformes (Krause et al. 2012) and Sphenisciformes (Coffin et al. 2011) use scent for kin recognition. Psittaciformes (Zhang et al. 2010) and Passeriformes (Whittaker et al. 2011, Amo et al. 2012) can discriminate the sex of conspecifics by using chemical cues alone. It further appears that chemical cues affect how birds interact with other species and their abiotic environment. For example, blue tits and starlings can use sense of smell to discriminate aromatic plants (Petit et al. 2002, Mennerat et al. 2005, Gwinner &

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Berger 2008). Homing pigeons use their chemosensory abilities for orientation and navigation (Wallraff 2004). Zebra finches (Kelly & Marples 2004) and chickens (Marples & Roper 1996) can use the sense of olfaction to accept novel foods. Passerines such as blue tits, great tits and house finches are also able to use chemical cues released by predators to assess the level of predation risk (Amo et al. 2008, 2011, Roth et al. 2008). These results show that birds have the ability to detect chemical cues in both intra- and inter-specific interactions (Hagelin 2007a, Hagelin & Jones 2007).

Some of the most interesting interactions mediated by chemical cues are those affecting several levels of a food web. In response to zooplankton grazing, phytoplankton (e.g. *Phaeocystis* algae) release dimethylsulphoniopropionate (DMSP) to the seawater (Pohnert et al. 2007). This compound attracts the predators of zooplankton, such as pelagic fishes (DeBose & Nevitt 2007, DeBose et al. 2008). DMSP is catabolized to dimethyl sulphide (DMS) that is emitted to the air from the water surface (Pohnert et al. 2007). DMS production is also higher when there is a high productivity of algae (Nguyen et al. 1988), which is especially patent in polar areas (Crocker et al. 1995). Hence, DMS signals areas of high productivity in the oceans (Nevitt 2000, 2011). Recently, it has been demonstrated that several seabird species are able to use DMS to locate these productive areas (Nevitt et al. 1995, Nevitt 2000, 2011). Therefore, with this mechanism, phytoplankton might attract the predators (fishes and birds) of the zooplankton that is feeding on it (see Nevitt 2011 for a review).

To date, detection of this compound has been described in several species of procelariiform seabirds (Nevitt et al. 1995, Nevitt & Haberman 2003, Bonadonna et al. 2006, Nevitt 2008) and in the African penguin *Spheniscus demersus* (Cunningham et al. 2008, Wright et al. 2011), and it has also been suggested for Humboldt penguins *S. humboldti* (Culik 2001), which all forage on fish. As yet there is no evidence of DMS detection in krill-feeding penguins. Therefore, to obtain generalizations that allow a better understanding of how multitrophic interactions are mediated by chemical cues in natural ecosystems and of the response of birds to these cues, it is essential to extend the knowledge about this mechanism to krill-feeding penguin species.

The mechanisms underlying prey detection in krill-feeding species are especially relevant in Antarctica, where trophic webs are mainly based on krill *Euphausia* spp. Krill feed on the phytoplankton that lives at the sea-ice interface. There is a clear rela-

tionship between temperature increase, a consequence of climate change, and the reduction in sea ice coverage, the decrease in phytoplankton and the decrease in krill density (Atkinson et al. 2004, Trivelpiece et al. 2011). As a consequence of such a decrease, populations of predators, especially krill-feeding penguins, have also been affected (Fraser & Hofmann 2003). The strong correlations between penguin numbers and krill abundance suggest that penguins may live under an increasingly krill-limited system that negatively affects juvenile birds (Hinke et al. 2007). Within this context, it is especially important to study the factors affecting the foraging success of Antarctic penguins. Among these factors, it is important to identify the mechanisms underlying the detection of prey, especially krill, which constitute 90% of the diet in some species (Williams 1995), reaching up to 99% of the diet in the chinstrap penguin *Pygoscelis antarctica* (Rombolá et al. 2006, Polito et al. 2011).

Here we explored for the first time whether the chinstrap penguin is able to detect DMS. The chinstrap penguin is an Antarctic species that depends mainly on local krill resources for the daily provisioning of chicks during the breeding period. This krill dependence is so strong that chinstrap penguins increase the distance of their foraging trips in order to obtain krill, whereas other pygoscelid species such as the gentoo penguin *Pygoscelis papua* are more flexible and able to change their diet in response to the availability of prey instead of increasing distance of their foraging trips (Kokubun et al. 2010, Miller et al. 2010).

The chinstrap penguin is one of the major consumers of Antarctic krill in the Southern Ocean marine ecosystem (Croxall & Lishman 1987, Williams 1995, CEMP 2004), and it has been included in the Ecosystem Monitoring Programme of the Convention for the Conservation of Antarctic Marine Living Resources (CEMP, CCAMLR) to monitor changes in krill populations (Rombolá et al. 2006). Therefore, the use of DMS for locating krill may be especially important for optimizing foraging during the austral summer. Although sphenisciform chinstrap penguins may have a reduced olfactory bulb size compared to Procellariiformes (Bang & Cobb 1968), in chinstrap penguins the recognition of DMS could be under strong natural selection, as chinstrap fledglings must find suitable food resources without prior foraging experience (Hinke et al. 2007). The first few weeks of independence for fledgling penguins represent a potential bottleneck to recruitment (Moreno et al. 1999, Hinke et al. 2007). Thus, the use of DMS for

finding krill may be relevant for recently independent fledglings. We examined whether chinstrap penguins could detect DMS by locating DMS or control recipients in pathways that penguins used to go from the colony to the sea and vice versa (Cunningham et al. 2008). We also analysed the attraction to DMS of nestling penguins in a T-shaped experimental enclosure (Cunningham et al. 2008). We hypothesized that naïve nestlings of chinstrap penguins may be able to detect DMS.

MATERIALS AND METHODS

Study site

We performed an experiment in natural conditions at a breeding rookery (12 000 breeding pairs, A. Barbosa et al. unpubl.) of chinstrap penguins *Pygoscelis antarctica* in the Vapour Col rookery on Deception Island, South Shetlands (63° 00' S, 60° 40' W), during the austral summer (January/February) of 2011. Experiments were performed from 11:00 to 17:00 h.

Response of adult penguins to DMS

We located 13 separate observation points in different pathways that penguins used to go to forage from the colony to the sea and vice versa. These points were in different parts of the colony to minimize the proportion of resampled individuals. The colony was situated in several hills, and penguins needed to go down from the colony to the sea. The slope of the pathways differed between observation points. At each observation point, we placed a Petri dish and marked the point with 2 metal rods situated 1 m from the Petri dish in each direction along the path. We deployed DMS or control solution in the Petri dish for a period of 30 min. After that, we changed the Petri dish for a clean new one and added the other treatment in order to do repeated measurements at each point. The order of treatments was randomised across sampling points. We added 7.85 ml of a DMS solution ($0.002 \text{ mol ml}^{-1}$) to 17.15 ml of water in a Petri dish to obtain a volume of 25 ml. The control solution was prepared with 7.85 ml of vegetable oil and 17.15 ml of water. The vegetable oil has a detectable scent to humans, suggesting that birds had to discriminate between 2 scented compounds rather than the presence or absence of odour. An observer, with knowledge of the treatment, was situated approximately 20 m from the observation point

and recorded the time that randomly selected penguins ($n = 1084$) spent within the 2 m sector. In order to have independent data and because many penguins were continuously walking close to the points, we recorded the behaviour of only one penguin at a time, and when it passed, we recorded the behaviour of the next penguin that entered within the 2 m sector. We distinguished between penguins going to forage at sea or returning to their nest after a foraging trip. We measured wind speed (mean 20 km h^{-1}), and temperature (mean 3°C) with a Kestrel Weather K3000 Wind Meter. We noted the wind direction (from sea to land or from land to sea).

We used a general linear mixed model (GLMM) to analyse differences between treatments (DMS vs. control) in the time spent close to the stimuli. We included the direction in which birds travelled (from the colony to the sea versus from the sea to the colony), the direction of the wind (from sea to land versus from land to sea) and the order of treatment presentation in the model as a fixed factors, and sampling location as a random factor. We also included the interactions between treatment and the direction of penguins, between treatment and direction of wind and between treatment, direction of penguins and direction of wind in the model. Data were log transformed to ensure normality.

Response of nestlings to DMS

We performed an experiment to examine the attraction of nestling penguins to DMS. The experiment was performed in a T-shaped mesh enclosure, built with 50 cm high chicken wire (mesh size 1.3 cm) and located in front of and 50 m from the closest breeding sub-colony, and also in front of and 300 m from the sea coast (Fig. 1). In that way, both experimental arms of the enclosure were equally distant from the colony and the sea, and we avoided any confounding effect due to the possible attraction of nestlings to these areas. We used a mesh enclosure, since chinstraps are not burrow nesters. Both the 'vertical' and 'horizontal' segments of the T were $150 \times 50 \text{ cm}$ corridors (Fig. 1). Just outside these arms, on the farthest side from the central arm, we placed 2 Petri dishes, one with DMS and one with a control solution. Therefore, nestlings were offered a simultaneous choice between 2 stimuli: DMS and a control (vegetable oil). Both DMS and the control solution were prepared following the same methodology as in the previous experiment. The location of treatments in the enclosure was balanced between

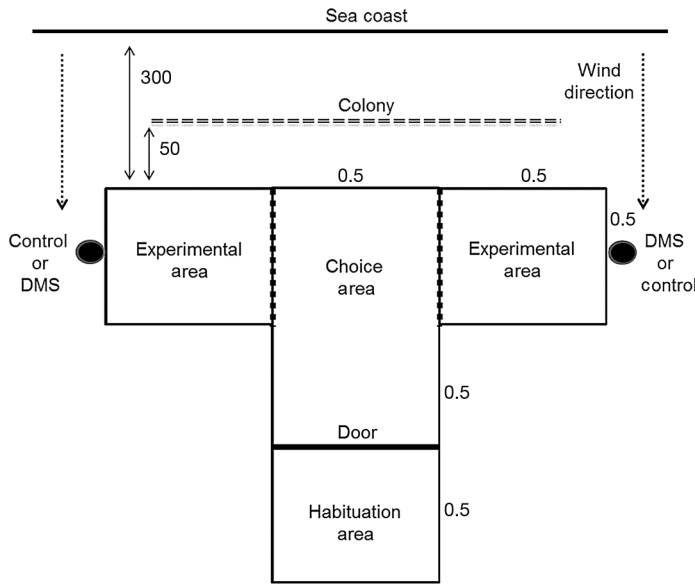


Fig. 1. Enclosure in which the experiment was carried out, with sizes indicated in meters. Black points represent the Petri dishes where the corresponding treatment was added (dimethyl sulphide, DMS, vs. control). The enclosure was perpendicularly located at 50 m from the nearest sub-colony and 300 m from the sea coast

both sides of the enclosure between trials. After each trial, the enclosure was cleaned with ethanol. We performed the experiment on days with no or low wind that always blew from sea to land. The location of the maze, which was situated cross wind, ensured that both Petri dishes were equally exposed to the wind (Fig. 1).

We used a long-handled net to capture 35 nestlings during the crèche phase. To minimize time in captivity, after a brief habituation period of 3 min at the base of the central arm (habituation area, Fig. 1), nestlings were released into the choice area, from which they could enter the left or right arms (experimental areas, Fig. 1) of the T-maze.

In order to determine whether the number of nestlings that selected the DMS-scented arm differed from the number of nestlings that selected the control arm of the enclosure, an observer situated 20 m from the enclosure and blind to treatments recorded the time that nestlings spent in each sector of the enclosure during 5 min. After trials, nestlings were marked with an indelible pen on 1 foot to avoid recapture and were immediately released at the exact place where they had been captured. Birds were kept in captivity a maximum of 15 min. All birds showed normal behaviour after being released, i.e. nestlings joined some other nestlings forming a crèche in the breeding sub-colony as before capture.

We calculated the number of birds that spent more time in the DMS than in the control sector during the experiment. We built generalized linear models with binomial errors and a logit link function to analyse whether the number of birds that spent more time in the DMS sector was significantly different from the number of birds that spent more time in the control sector. We included the side of the enclosure (left vs. right) where the DMS was located as a fixed factor. Statistical analyses were performed with STATISTICA 8.0.

Although we performed the same experiment with adult penguins, we will not report the results of the study because most adult penguins spent a fair amount of time trying to escape from the enclosure. Comparison with previous studies suggests 2 methodological issues that may have exacerbated the problem of stress and should be avoided in future experiments. First, we used adult, recently caught birds, whereas Cunningham et al. (2008), for instance, used penguins from a rehabilitation centre. Second, the use of a chicken-wire enclosure that allowed penguins to see their colony could increase their motivation to escape. In contrast, in the previous study with adult penguins (Cunningham et al. 2008), as well as in other studies with procellariiforms (e.g. Nevitt & Bonadonna 2005, Bonadonna et al. 2006), the experiments were performed in opaque closed enclosures, where subjects could not see their environment, possibly decreasing their stress response (Cockrem et al. 2008).

RESULTS

Response of adult penguins to DMS

Adult penguins spent more time within 1 m of the Petri dish when it contained DMS solution than when it contained a control solution (GLMM, $F_{1,1037} = 12.85$, $p = 0.0004$, $n = 1084$; Table 1). However, the time spent close to the DMS was affected by the interaction between wind direction and penguin direction (interaction between treatment, wind direction and penguin direction: $F_{2,1037} = 17.27$, $p < 0.0001$). When penguins faced the wind, they spent more time close to the DMS solution than to the control solution, but the time spent within 1 m of the Petri dish did not differ between treatments when penguins moved with the wind (Fig. 2). The order of treatment presentation did not influence the time spent close to the stimuli ($F_{1,1037} = 0.36$, $p = 0.55$). There were differences among observations points

Table 1. Analysis of time spent by adult chinstrap penguins *Pygoscelis antarctica* close to the stimuli (dimethyl sulphide, DMS; or vegetable oil, control) in several observation points along the pathways when they were going to sea to forage or returning to the colony from the sea (penguin direction) and when they walked with the wind or into the wind (wind direction)

Factor	Effect	df	F	p
Treatment (DMS vs. control)	Fixed	1,1037	12.8460	0.0004
Order of treatment presentation	Fixed	1,1037	0.3646	0.55
Observational point	Random	12,1037	12.9528	<0.0001
Penguin direction (from vs. to the sea)	Fixed	1,1037	13.1241	0.0003
Wind direction (from vs. to the sea)	Fixed	1,1037	2.5252	0.11
Treatment × Penguin direction	Fixed	1,1037	4.9286	0.03
Treatment × Wind direction	Fixed	1,1037	5.9322	0.02
Treatment × Penguin direction × Wind direction	Fixed	2,1037	17.2655	<0.0001

(random factor; $F_{12,1037} = 12.95$, $p < 0.0001$). These differences between points were due to the differences in the slope of the pathways where the observation points were located, as penguins walked more slowly in some points than in others. However, such differences between points did not influence the effect of treatment, because the interaction between treatment and point was not significant ($F_{9,1028} = 0.81$, $p = 0.60$) when we considered it in a previous model.

Response of nestling penguins to DMS

Most nestlings (66%, 23 of 35) spent more time in the DMS than in the control sector (34%, 12 of 35), although differences only approached significance levels (Wald Stat = 3.41, $df = 1$, $p = 0.06$, $n = 35$). The arm of the enclosure where the DMS dish was located did not influence the preference of nestlings (Wald Stat = 0.35, $df = 1$, $p = 0.56$).

DISCUSSION

Our results show for first time that a krill-eating penguin is able to detect DMS. Adult chinstrap penguins that walked into the wind spent more time close to the DMS deployments than close to the control deployments. These penguins were probably able to detect the DMS before reaching the 2 m sector and they may have been following the DMS-scented trace upon arrival to this sector. However, there were no differences in the time penguins spent close to both olfactory stimuli when they were walking with the wind, probably because these penguins

would not be able to detect the DMS scent until they passed the source of the odour. We performed a repeated measures analysis, applying both treatments at each observation point, so that differences in the response of penguins to the DMS could be attributed to the direction of the wind relative to the direction in which the birds were travelling. Our results also agree with those of Cunningham et al. (2008) and Wright et al. (2011), who showed that African penguins responded to DMS deployments on land. We used vegetable oil as a control scent, so our results clearly show that the attraction of penguins to

DMS seems to be specific to DMS rather than a general response to any novel scent.

Based on our results, we propose the hypothesis that nestlings were able to detect and tended to exhibit a preference for DMS before they experienced it in a foraging context at sea. When offered the choice between a DMS and a control source in an enclosure, most nestlings chose to stay in the DMS-scented part of the enclosure, although our results only approached significance levels ($p = 0.06$). Stress due to recent captivity (Cockrem et al. 2008) may explain why we did not observe a greater attraction to DMS in enclosures. A previous study that has shown a positive response of adult African penguins

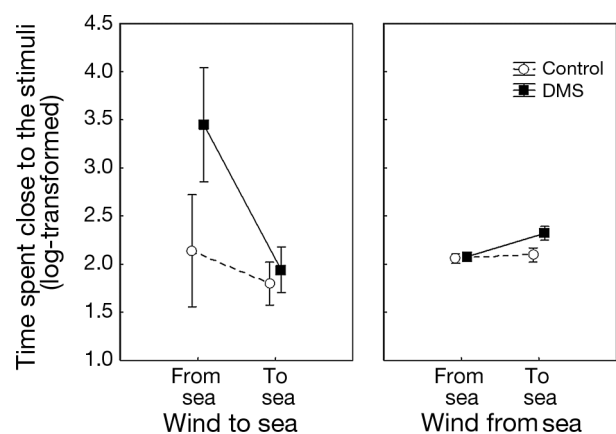


Fig. 2. *Pygoscelis antarctica*. Mean (\pm SE) time (s) spent by chinstrap penguins within 2 m of a Petri dish with 25 ml of dimethyl sulphide (DMS) or control solution. Data are presented separately for penguins that were going from the colony to sea and penguins that were returning from the sea to the colony, and when the wind was blowing from the sea or towards the sea

to DMS in an enclosure (Cunningham et al. 2008) used penguins from a rehabilitation centre. These captive penguins were likely habituated to humans and were not under the stress of having recently been caught, as in our study.

Our results are in accordance with those of Bonadonna et al. (2006), who clearly showed that blue petrel *Halobaena caerulea* chicks were even able to detect DMS at a naturally occurring concentration (<10 pmol l⁻¹). Whether the ability to discriminate DMS from other scents is innate or learned during the nestling period cannot be disentangled in our study, because, although nestlings were not previously exposed to DMS in a foraging context at sea, they may have learnt to recognize the scent from krill fed by their parents (Bonadonna et al. 2006). Regardless of the mechanism, an early ability to detect DMS may be especially important for fledged penguins because once they reach the age of independence (53 to 57 d, Viñuela et al. 1996), they are left unattended by their parents. At that time, young penguins must go to the sea and be able to find suitable food resources without prior foraging experience. Therefore, the use of DMS for finding krill may be relevant for recently independent fledglings.

We performed the experiment in the colony, on land, an environment where penguins normally do not find DMS. Furthermore, we used a concentration of DMS much higher than that which the birds may encounter at sea (see Nevitt 2000, Nevitt & Bonadonna 2005), and even higher than previously used in studies with procellariiforms (Cunningham et al. 2003, Bonadonna et al. 2006) and other penguin species (Cunningham et al. 2008, Wright et al. 2011). DMS is an irritant chemical compound, so under a high concentration, we might have observed an averse response in penguins, as has been observed with other irritant compounds such as ammonia in other bird species (Kristensen et al. 2000). However, despite this, we found that penguins spent more time close to the DMS than to the control stimuli, and therefore our results give first evidence that this species is able to detect this chemical compound. Further research is needed to determine whether chinstrap penguins can detect DMS at natural concentrations and use it as a foraging cue at sea.

DMS signals areas of high concentrations of krill in the oceans (Nevitt 2000, 2011). Although penguin colonies may be located where local oceanic circulation or bathymetry concentrates food and promotes access to foraging areas (Fraser & Trivelpiece 1996, Trivelpiece & Fraser 1996, Hinke et al. 2007), the use of DMS gradients may help chinstrap penguins

to maximize their foraging efficiency, especially because this species feeds almost exclusively (99%) on krill, and previous studies on its diet and habitat use have shown that when krill is not available close to the colony, chinstrap penguins travel longer distances to find krill instead of capturing other prey as other pygoscelid penguins do (Kokubun et al. 2010, Miller et al. 2010). This may be especially important during breeding, when penguins need to not only find food for themselves but must also provision their chicks daily. When travelling to their feeding areas, penguins emerge to the water surface to breathe, and in that moment they may obtain information about DMS gradients—information that they can use to modify their travelling direction.

Detection of DMS has also been observed in other species, mainly procellariiform seabirds such as blue petrels (Bonadonna et al. 2006) and Antarctic prions *Pachyptila desolata* (Nevitt & Bonadonna 2005). African penguins are also able to detect DMS (Cunningham et al. 2008, Wright et al. 2011); this species feeds predominantly on anchovies *Engraulis* sp. and sardines *Sardinops sagax* (Crawford & Dyer 1995, Wilson et al. 1995). This species, as do many procellariiform species that feed on fishes and squids, may use DMS concentration to locate the fishes that feed on krill, whereas chinstrap penguins may use DMS to directly locate the krill they feed on. From an evolutionary point of view, the phytoplankton that release DMSP, the precursor of DMS, could benefit from attracting krill predators, as they decrease grazing pressure. Therefore, for phytoplankton, the attraction of krill-eating species such as fishes or chinstrap penguins could be better than the attraction of super-predators that feed on fishes that feed on krill, such as procellariiform species or the African penguins. These species remove the predators of krill and, therefore, they may impose a cost to the phytoplankton DMS signalling. A balance between predatory species may occur to make these complex systems evolutionary stable, as has been observed in terrestrial systems (Sabelis & Dejong 1988, Godfray 1995). In terrestrial ecosystems, the role of induced indirect defences mediated by chemical compounds has been largely studied in systems composed of plants, herbivorous insects and predatory insects (Schoonhoven et al. 2005, Dicke & Baldwin 2010). When plants are wounded by herbivorous insects, they release volatile compounds to attract the predators (or parasitoids) of these insects (Schoonhoven et al. 2005). While insectivorous birds can also use the defense of attacked plants to locate their prey (Mäntylä et al. 2004, 2008a,b, 2011), in the terrestrial systems studied

so far, volatiles emitted by attacked plants do not seem to be used by superpredators or hyperparasitoids (Buitenhuis et al. 2005, Poelman et al. 2008). Further research is needed to understand the extent to which superpredators eavesdropping on the signals released by plants or algae to attract predators can destabilize the evolution of induced indirect defences.

In conclusion, although penguins were traditionally thought to be visual hunters (Wilson et al. 1993, Wilson & Wilson 1995, Ryan et al. 2007), our results show that the chinstrap penguin is able to detect DMS. This olfactory capacity seems to be expressed even in nestlings without prior foraging experience. Further research is needed to examine whether chinstrap penguins are also able to detect DMS at naturally occurring concentrations, as are procellariiforms (Nevitt & Bonadonna 2005, Bonadonna et al. 2006), and under natural conditions at sea (see Nevitt et al. 1995, Nevitt 2000, Wright et al. 2011).

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