



Ammonia emissions from seabird colonies

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[1] Ammonia emissions were measured from two entire seabird colonies with contrasting species assemblages, to ascertain the ammonia volatilisation potentials among seabird species in relation to their nesting behaviour. Emissions were calculated from downwind plume measurements of ammonia concentration using both inverse dispersion and tracer ratio methods. Measured colony emissions ranged 1–90 kg NH₃ hour⁻¹, and equated to 16 and 36% volatilization of excreted nitrogen for colonies dominated by ground/burrow nesting and bare rock nesting birds, respectively. The results were applied in a bioenergetics model with a global seabird database. Seabird colonies are found to represent the largest point sources of ammonia globally (up to ~6 Gg NH₃ colony⁻¹ year⁻¹). Moreover the largest emissions occur mainly in remote environments with otherwise low NH₃ emissions. These ammonia “hot spots” explain significant perturbations of the nitrogen cycle in these regions and add ~20% to oceanic ammonia emissions south of latitude 45°S.

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1. Introduction

[2] The main sources of NH₃ emissions globally are domestic animals (livestock), synthetic fertilisers, oceans, biomass burning and crops [Bouwman *et al.*, 1997]. The magnitude and location of natural sources of NH₃ have received little attention and estimates that have been made are extremely uncertain [Bouwman *et al.*, 1997; Sutton *et al.*, 2000]. The present study highlights the role of seabirds in contributing to NH₃ emissions, with the first measurements of emissions and first global estimates. While NH₃ emissions from seabird colonies are much smaller than total anthropogenic emissions, their importance lies in the magnitude of emissions from individual colonies (with major local impacts) and the fact that most colonies are located in otherwise pristine environments where anthropogenic emissions are small. Seals may be another source of NH₃

emissions in remote areas. However, measurements by Theobald *et al.* [2006] indicate a much lower percentage volatilisation from seals compared to seabirds, owing to differences in excretory behaviour.

[3] Seabirds play an important role in the nutrient cycling of remote coastal ecosystems by transferring nitrogen from the marine to the terrestrial environment [Anderson and Polis, 1999]. Most previous research has focused on the direct effects of seabird excretal input [Mizutani and Wada, 1988]. By contrast, isotopic analyses of soil and water in the vicinity of seabird colonies point to the importance of ammonia (NH₃) volatilisation from excreta [Wada *et al.*, 1981]. While NH₃ emissions from seabird colonies have not previously been measured, limited data indicate enhanced concentrations of associated atmospheric ammonium aerosol (NH₄⁺) near colonies [Legrand *et al.*, 1998]. The emission of NH₃ from seabird excreta facilitates the wider dispersion of nitrogen beyond the colony perimeter, with subsequent effects on atmospheric composition and terrestrial nutrient supply. Any fluctuations in seabird population size may therefore affect the nutrient supply to and ecological functioning of terrestrial habitats adjacent to seabird colonies.

[4] The absence of previous measurements of NH₃ emission from seabird colonies may be partly attributable to the major experimental difficulties involved. Seabird colonies represent complex point sources, often inaccessible, and the relevant measurements require the deployment of sensitive continuous NH₃ detection systems. To address this challenge, we determined emissions for entire seabird colonies from sea-borne measurements of NH₃ and an atmospheric tracer using relatively accessible islands: the Isle of May (56°11'N, 2°33'W) and Bass Rock (56°04'N, 2°38'W) in the Firth of Forth, Scotland. The two colonies are less than 20 km apart but have highly contrasting seabird communities. The Isle of May is a major colony of Atlantic puffin *Fratercula artica* in the North Sea (42,000 pairs, 1998–2002) [Harris and Wanless, 2004], while the Bass Rock is the eponymous location of the Northern gannet *Morus bassanus* (44,110 pairs in 1998–2000) [Wanless and Harris, 2004]. Both species are piscivorous, but the puffin is a burrow breeder, while the gannet nests at high densities on cliffs and un-vegetated slopes. Very few seabirds apart from gannets breed on the Bass Rock, but the Isle of May also holds large numbers of cliff nesting Common guillemot *Uria aalge*, Razorbill *Alca torda* and Black-legged kittiwake *Rissa tridactyla*.

2. Methods

[5] NH₃ emission estimates were made using two conceptually independent techniques – an inverse dispersion (ID) method and a tracer ratio (TR) method. Ship-borne measure-

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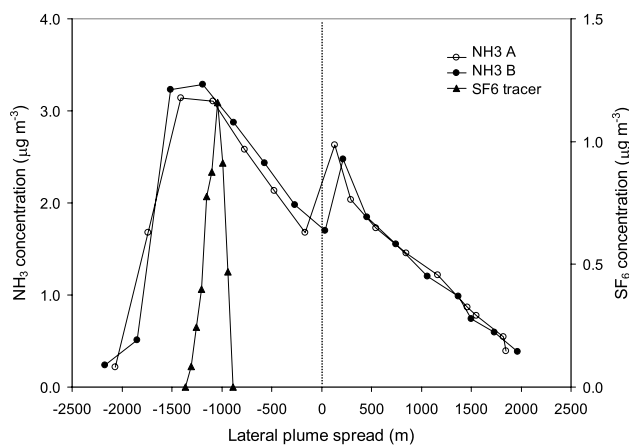


Figure 1. Example cross-section of measured NH_3 and SF_6 plumes from measurements made 1.9 km downwind of the Bass Rock at 16:50–17:40 GMT on 18 July 2002 using two replicate continuous denuders for NH_3 and bag sampling for SF_6 (see Methods). Results for NH_3 are shown at 2 minute intervals and for SF_6 at 30 second intervals. The wind speed was 4.6 m s^{-1} from the south-south-east.

ments of atmospheric NH_3 concentrations were undertaken 80–2500 m downwind from the Isle of May and Bass Rock during May–July 2000–2002. Concentrations of NH_3 were measured using a dual channel ‘AMANDA’ continuous wet denuder system [Wyers *et al.*, 1993]. Coupled with meteorological information and estimated background NH_3 concentrations, this permitted estimation of NH_3 emissions using the ID method. To implement the TR method, a controlled release of sulphur hexafluoride (SF_6) at 1.0 l min^{-1} was made from line-sources on each island, with SF_6 concentrations in the downwind plumes sampled, simultaneously to NH_3 , into inert Tedlar bags for subsequent analysis by gas chromatography with Electron Capture Detection (ECD). The location of the boat was determined continuously using a global positioning system logged to a notebook PC. Measured plume NH_3 and SF_6 concentrations (χ_p) above background (χ_{bg}) were integrated for each tangential transect (y) for the measurement distance downwind of the colony (x).

[6] The Inverse Dispersion (ID) method estimated the NH_3 emission by application of a Gaussian plume dispersion model (GPDM) [see e.g., Seinfeld and Pandis, 1998]. Cross-wind NH_3 concentration profiles were predicted using the GPDM, based on wind speed, lateral and vertical plume spread (using Pasquill-Gifford estimation). These predicted plume concentrations were compared with boat-based measurements to estimate whole colony NH_3 emissions. Meteorological measurements were made on the Isle of May, supplemented by UK Meteorological Office data. Whilst land-based meteorological measurements may introduce a source of error to the plume dispersion modelling, they provide our best estimate at NH_3 dispersion from the seabird colonies, owing to the logistical difficulty of marine meteorological measurements.

[7] In the Tracer Ratio (TR) method, the cross-wind-integrated values of ($\chi_p - \chi_{bg}$) for NH_3 are compared with

the equivalent values for SF_6 to estimate the NH_3 emission rate, given the known source strength of SF_6 (E_{SF_6}):

$$E_{\text{NH}_3}(\text{TR}) = E_{\text{SF}_6} \cdot \int (\chi_{p\text{NH}_3} - \chi_{\text{NH}_3\text{bg}}) dy / \int (\chi_{p\text{SF}_6} - \chi_{\text{SF}_6\text{bg}}) dy \quad (1)$$

[8] A simple bioenergetics model was used to estimate the ‘at colony’ species-specific excretion of nitrogen by seabirds N_{excr} ($\text{g N bird}^{-1} \text{ day}^{-1}$). A detailed explanation of this model is given by Wilson *et al.* [2004]. In order to assess the global significance of NH_3 emissions from seabirds, we compiled a database of seabird populations across the world based on population estimates provided by regional experts. A more detailed analysis of the global seabird database is available from T. D. Blackall *et al.* (manuscript in preparation, 2007). These data were used in conjunction with the bioenergetics model of Wilson *et al.* [2004] to estimate global seabird bioenergetics demands and subsequent nitrogen excretion.

[9] In order to support the wider application of our estimates, we measured NH_3 concentrations at 0.5 m above contrasting seabird colonies around the globe (Isle of May, Scotland; Bird Island, South Georgia; Bird Island, South Africa; Funk Island, Newfoundland) using passive samplers (CEH ALPHA passive NH_3 samplers). Triplicate samplers were exposed at 0.5 m above the surface for a period of between 1 and 30 days duration, after which they were retrieved for laboratory analysis. A full description of the CEH ALPHA passive sampling method is given by Tang *et al.* [2001].

3. Results

[10] The measured plumes of SF_6 were narrower than those of NH_3 (Figure 1) because the SF_6 line sources (up to 240 m long) were not the maximum length of each island (Isle of May, 2 km; Bass Rock, 500 m) and because of a slower response time of the continuous NH_3 detector. The AMANDA NH_3 system shows a fast to respond to NH_3 entering the system, but is slower to return to background levels of detection after passing through the plume (T. D. Blackall, personal observation, 2000). The emissions are derived from cross-wind integration of the measured plumes, and therefore the degree of plume spread would not have appreciably affected the calculated emissions.

[11] Overall, 13 successful NH_3 measurement transects were obtained for the Isle of May and 12 for the Bass Rock. Of these, 11 transects at the Isle of May and 5 at the Bass Rock also successfully measured SF_6 plumes (Table 1). Plume NH_3 concentrations of up to $8 \mu\text{g m}^{-3}$ were recorded at distances between 80–2500 m downwind, which in all cases were distinguishable from NH_3 background values of 0.1 – $1.5 \mu\text{g m}^{-3}$ (median = $0.5 \mu\text{g m}^{-3}$). These NH_3 background values are comparable to those measured over the North Sea, off the Dutch coast [Sorensen *et al.*, 2003].

[12] The ID technique estimated a mean NH_3 emission for the Isle of May of $4.5 \text{ kg NH}_3 \text{ hour}^{-1}$ (range = 1.0 – $15.5 \text{ kg NH}_3 \text{ hour}^{-1}$, $\sigma_{n-1} = 3.9$, $n = 13$), whilst the TR technique estimated a mean of $8.0 \text{ kg NH}_3 \text{ hour}^{-1}$ (range = 0.9 – $54.3 \text{ kg NH}_3 \text{ hour}^{-1}$, $\sigma_{n-1} = 15.6$, $n = 13$). For the Bass Rock, the mean values were $26.1 \text{ kg NH}_3 \text{ hour}^{-1}$ by the ID

Table 1. Summary of Measured Ammonia Emissions From the Isle of May and the Bass Rock, Scotland, Using the Inverse Dispersion Method and the Tracer Ratio Method

Date	Range of Transect Distances Downwind of Source, m	Modelled Nitrogen Excretion, kg N hr ⁻¹	Range of ID NH ₃ Emission Estimates, kg N hr ⁻¹	Range of TR NH ₃ Emission Estimates, kg N hr ⁻¹	Mean Fraction of Available Nitrogen Volatilised as NH ₃ ^a
<i>Isle of May</i>					
19 July 2000	664–1023	32	1.5–3.4	1.1–2.7	0.07, 0.05
21 June 2001	611–1297	39	2.2–7.1	1.8–6.7	0.11, 0.10
3 July 2001	59–751	39	0.8–1.5	0.7–1.1	0.03, 0.02
18 July 2002	262–1583	32	4.1–12.8	7.6–44.7	0.22, 0.82
<i>Bass Rock</i>					
6 August 2001	77–1307	67	13.2–72.9	5.3–52.7	0.54, 0.44
21 August 2001	821–2460	65	10.7–25.7	ND ^b	0.25, ND ^b
18 July 2002	1545–2472	68	5.2–36.2	8.9–33.7	0.25, 0.34

^aThe first figure is from the Inverse Dispersion (ID) method, the second is from the Tracer Ratio (TR) method.

^bND, not determined.

technique (range = 6.3–88.6 kg NH₃ hour⁻¹, σ_{n-1} = 22.0, n = 11) and 30.8 kg NH₃ hour⁻¹ by the TR technique (range = 6.5–64.0 kg NH₃ hour⁻¹, σ_{n-1} = 23.4, n = 5). The wide range of estimates is indicative of the high temporal variability in emission, related to the interactive effects of water availability, temperature and wind speed on the hydrolysis of bird excreta (uric acid) and subsequent volatilisation as NH₃. Using the two different techniques allowed validation of the results, since the main uncertainties concern the emission calculations rather than determination of atmospheric concentrations. Although there was considerable scatter, based on the available paired sampling periods, the ID and TR methods yielded consistent estimates overall (Figure 2).

[13] The bioenergetics model of *Wilson et al.* [2004], used in conjunction with the total number of seabirds associated with each colony and their attendance, provided N excretion estimates of 101 Mg N yr⁻¹ and 494 Mg N yr⁻¹ for the Isle of May and Bass Rock, respectively. Based on the modelled excretion estimates for the month prior to each measurement campaign, measured NH₃ emission can be expressed as a fraction of total N excreted available for volatilisation as NH₃. This yielded estimates of 0.16 (standard error = 0.07) and 0.36 (standard error = 0.09) for the Isle of May and Bass Rock, respectively. These contrasting volatilisation factors for the two colonies are consistent with an expected effect of habitat on NH₃ volatilisation. It is known that overlying vegetation and absorption of NH₃ by soil can reduce NH₃ emissions [*Misselbrook et al.*, 2000], so that vegetation or burrow nesting species on the Isle of May result in a lower proportion of N volatilisation than the gannets on the Bass Rock which breed on bare ground. The volatilization rate was found to be larger at the Bass Rock than at the Isle of May, but due to temporal variability was only significant to P = 0.1 (one-tailed unpaired t-test).

[14] There is a substantial difference in excretion density between the two islands. Accounting for the projected surface areas of the Isle of May and Bass Rock (~70 and 9 ha, respectively), this equates to annual excretion estimates of 1,430 and 52,200 kg N ha⁻¹ yr⁻¹ for the Isle of May and Bass Rock, respectively. To our knowledge, the second of these values is the highest N input rate ever reported, although more densely populated seabird colonies at other global locations may exhibit higher N input rates. However, most papers referring to guano deposition do not

make quantitative estimations [e.g., *Crawford and Jahncke*, 1999], whilst those that do report considerably lower guano input rates of up to 1,000 kg N⁻¹ ha⁻¹ [e.g., *Schmidt et al.*, 2004].

[15] The global seabird energy demand data were used to predict species-specific NH₃ volatilization rates. Based on our measurements, volatilization rates of 0.36 and 0.16 were applied for bare rock breeding species and vegetation/burrow breeding species, respectively. On this basis, the global emission of NH₃ from seabirds was estimated to be 242 Gg NH₃ year⁻¹. Table 2 shows that more than 50% of the total estimated emission occurs in the Antarctic and sub-Antarctic, where large seabird colonies are supported by energy from the productive Southern Ocean. Out of 178 seabird species included in our database, it is remarkable that just 10 species contribute over 80% of the estimated global ammonia emissions, with the largest estimated contributions

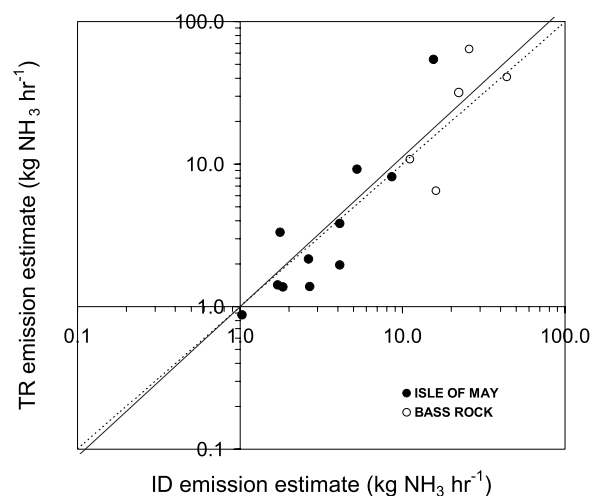


Figure 2. Comparison of the Tracer Ratio (TR) and Inverse Dispersion (ID) method estimates of ammonia emission for measurement transects downwind of the Isle of May and the Bass Rock, Scotland. Sixteen runs were successful in providing simultaneous estimates by the two methods. The solid line indicates the linear regression of the log transformed data: $\log_{10}(\text{TR}) = 1.05 \log_{10}(\text{ID})$, $R^2 = 0.83$; intercept not statistically significant.

Table 2. Estimated Global Seabird Energy Demands, by Region, as Calculated From a Database of Global Seabird Populations^a

Region	Total Estimated Energy Demand, 10^9 kJ yr^{-1}	Estimated Terrestrial N Excretion, Gg N yr^{-1}	Estimated NH_3 Emission, $\text{Gg NH}_3 \text{ yr}^{-1}$	Contribution to Global Seabird NH_3 Emissions, %	Dominant Emitting Bird Group	Contribution of Dominant Bird Group, %
Antarctic	47672	329.9	129.6	53.6	Penguin	97.8
S. America	12329	85.3	30.7	12.7	Cormorant	81.5
N. America	8568	59.3	21.8	9.0	Auk	73.2
Europe	7608	52.6	18.4	7.6	Auk	53.0
Russia	7185	49.7	15.6	6.5	Auk	59.1
Africa	6587	45.6	9.0	3.7	Penguin	87.4
Pacific	3466	24.0	8.8	3.6	Tern	85.9
Greenland	1983	13.7	5.4	2.2	Auk	79.5
Other regions	1504	10.4	2.3	1.0	Tern	39.1

^aEstimates are included for the total terrestrial N excretions and subsequent NH_3 emissions to the atmosphere in these regions.

from Macaroni penguin *Eudyptes chrysolophus* (28%) and Chinstrap penguin *Pygoscelis antarctica* (16%). These species dominate NH_3 emissions as a result of their large population sizes and their nesting behaviour (bare ground breeders). The dominance of emissions by a small number of species means that any fluctuations in their population size would have a dramatic effect on nutrient supply to ecosystems that are reliant on NH_3 deposition from a seabird source.

[16] The major uncertainties in our regional NH_3 emission values are the estimated volatilisation rates, which, based on simple thermodynamics [Sutton *et al.*, 1994], would be expected to be lower in the colder conditions of Antarctica and higher in tropical regions. However, a reduction in surface absorption rates in frozen conditions [Sommer *et al.*, 1991] and a restriction of urea hydrolysis in dry conditions are expected to offset this effect. Direct measurements of NH_3 emissions in Antarctica are not available, but seabird excretal mass budgets have implied volatilisation rates of up to 90% of total excreted nitrogen as NH_3 [Lindeboom, 1984], values that are much higher than our UK measurements. Average monthly NH_3 concentrations measured at the Isle of May showed a substantial monthly variation, with values over Atlantic puffin sites of $0.4\text{--}31.4 \mu\text{g m}^{-3}$, and the highest values in the vicinity of cliff-nesting Common guillemots ($0.5\text{--}168.3 \mu\text{g m}^{-3}$). By contrast, at three sites on Funk Island (Newfoundland) NH_3 concentrations by Common guillemots were in the range $710\text{--}1370 \mu\text{g m}^{-3}$, while at four sites on Bird Island (South Africa), concentrations by Cape gannets *Morus capensis* were in the range $54\text{ to }560 \mu\text{g m}^{-3}$. At Bird Island (South Georgia, South Atlantic), NH_3 concentrations by Black-browed albatross *Diomedea melanophris* and by Macaroni penguin *Eudyptes chrysolophus* were 14 and $55 \mu\text{g m}^{-3}$, respectively. These measurements of elevated NH_3 concentration near seabirds at a range of latitudes illustrates that seabird NH_3 emissions are a global phenomenon and provide some confidence for the use of observed NH_3 emission factors at a global scale. Further measurements of whole colony emissions under a range of climatic conditions would clarify the precise nature of temperature effects on global seabird NH_3 emissions.

4. Discussion

[17] In principle the TR method for estimating NH_3 emissions is considered more robust, since the ID method depends on an empirical parameterisation of dispersion from the complex multi-height sources that seabird colonies

represent. The main uncertainty with the TR method is the co-location of the tracer release with the NH_3 emission, and the errors associated with this should decrease for plume measurements made at greater distances. Further measurements would be necessary to determine the causes of inter-transect variability between the ID and TR methods (see Table 1).

[18] NH_3 emissions from seabirds turn out to be very important in relation to other sources. Based on the bird attendance periods, annual NH_3 emissions for the Isle of May and Bass Rock are estimated to be 19 and $152 \text{ Mg NH}_3 \text{ yr}^{-1}$, respectively. The former is similar in magnitude to a medium sized chicken farm, while the latter would exceed the emission from even the largest industrially farmed chicken complexes ($\sim 10^6$ broilers), based on an emission rate of $0.085 \text{ kg NH}_3 \text{ broiler}^{-1} \text{ yr}^{-1}$ [Misselbrook *et al.*, 2000].

[19] The largest seabird NH_3 emissions occur in remote oceanic environments, where anthropogenic emissions are negligible and where the only other major source of NH_3 is the ocean surface. We compared our spatial estimates with the 1° resolution global ocean emissions of Bouwman *et al.* [1997], allowing for the known interaction of atmospheric NH_3 with the sea-surface NH_3 compensation point, which reduces actual compared with potential ocean emissions [Sutton *et al.*, 1994]. On this basis, for the entire southern hemisphere south of lat. 45° , NH_3 emissions from seabird colonies account for 20% of the total estimated oceanic NH_3 emissions, with over 90% of this arising from penguins on sub-Antarctic Islands.

[20] The highly concentrated nature of the seabird NH_3 emissions shows how individual colonies represent the largest point sources of NH_3 globally, larger than any anthropogenic point sources. For example, estimated NH_3 emissions from a major Macaroni penguin rookery of 2 million birds [Woehler, 1993], Zavodovski Island (area $4 \text{ km} \times 5 \text{ km}$), South Sandwich, would be $\sim 6 \text{ Gg NH}_3 \text{ yr}^{-1}$, equivalent to the net ocean emission from the surrounding area of $1640 \text{ km} \times 1640 \text{ km}$. In recent years (1991–2000), Antarctic penguin populations have shown increases in some areas, whilst decreasing in others [Croxall *et al.*, 2002]. Similarly, in the UK the population of Northern gannets has increased over the last 100 years [Lewis *et al.*, 2001], whilst other species (e.g., Black-legged kittiwake) have seen a decline in their numbers [Ratcliffe, 2004]. These population fluctuations may lead to a destabilised nutrient supply in

many remote coastal ecosystems. The high proportion of seabird-excreted nitrogen volatilised to the atmosphere as NH_3 , together with its dispersion and deposition, increases the ecological footprint associated with this perturbation of marine to terrestrial nutrient flow.

[21] Many studies have addressed the direct impacts of seabird excreta on soils and vegetation, with an enrichment of ^{15}N natural abundance occurring near breeding or roosting sites [Mizutani *et al.*, 1986; Mizutani and Wada, 1988] being attributed to the trophic enhancement of ^{15}N in seabird excreta. Such values are almost certainly partly due to preferential volatilisation of $^{14}\text{NH}_3$ over $^{15}\text{NH}_3$ [Mizutani *et al.*, 1986]. Our estimates of extreme rates of NH_3 emission also point to the role of subsequent atmospheric deposition of the volatilized NH_3 and help to explain the unexpected observation of extreme $\delta^{15}\text{N}$ negative values at Antarctic sites, more distant from seabird colonies [Wada *et al.*, 1981]. Our results also point to the importance of such biogenic NH_3 volatilisation, dispersion and deposition on vegetation dynamics of coastal terrestrial ecosystems in remote locations [Erskine *et al.*, 1998; Schmidt *et al.*, 2004]. Seabird ammonia emissions may also explain nucleation events of fine atmospheric particles that have repeatedly been observed around sub-Antarctic islands and along the Arctic coastline [Weber *et al.*, 1998]. Our results therefore support the importance of NH_3 from seabird colonies for ternary nucleation [Weber *et al.*, 1998] and secondary aerosol formation [Legrand *et al.*, 1998] in these remote areas.

[22] In locations where overall seabird numbers have been increasing in recent years [Ratcliffe, 2004], the causes of such increase, although poorly understood, are almost certainly anthropogenic (e.g., interactions with fisheries). Therefore, the results of our study also contribute to the debate on the relative importance of natural and anthropogenic “pollution” sources of NH_3 emissions. In particular, they highlight how the distinction between natural and anthropogenic sources is not clear. Given the blurring between such artificial definitions, our results point to the need for international protocols to consider all emission sources and not just those traditionally viewed as being anthropogenic.

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References

Anderson, W. B., and G. A. Polis (1999), Nutrient fluxes from water to land: Seabirds affect plant nutrient status on Gulf of California islands, *Oecologia*, *118*, 324–332.

Bouwman, A. F., D. S. Lee, W. A. H. Asman, F. J. Dentener, K. W. Van Der Hoek, and J. G. J. Olivier (1997), A global high-resolution emission inventory for ammonia, *Global Biogeochem. Cycles*, *11*, 561–587.

Crawford, R. J. M., and J. Jahncke (1999), Comparison of trends in abundance of guano producing seabirds in Peru and southern Africa, *S. Afr. J. Mar. Sci.*, *21*, 145–156.

Croxall, J. P., P. N. Trathan, and E. J. Murphy (2002), Environmental change and Antarctic seabird populations, *Science*, *297*, 1510–1514.

Erskine, P. D., et al. (1998), Subantarctic Macquarie Island – A model ecosystem for studying animal-derived nitrogen sources using ^{15}N natural abundance, *Oecologia*, *117*, 187–193.

Harris, M. P., and S. Wanless (2004), Atlantic Puffin *Fratercula arctica*, in *Seabird Populations of Britain and Ireland*, edited by P. I. Mitchell *et al.*, pp. 392–406, Poyser, London.

Legrand, M., F. Ducroz, D. Wagenbach, R. Mulvaney, and J. Hall (1998), Ammonium in coastal Antarctic aerosol and snow: Role of polar ocean and penguin emissions, *J. Geophys. Res.*, *103*, 11,043–11,056.

Lewis, S., T. N. Sherratt, K. C. Hamer, and S. Wanless (2001), Evidence of intra-specific competition for food in a pelagic seabird, *Nature*, *412*, 816–819.

Lindeboom, H. J. (1984), The nitrogen pathway in a penguin rookery, *Ecology*, *65*, 269–277.

Misselbrook, T. H., et al. (2000), Ammonia emission factors for UK agriculture, *Atmos. Environ.*, *34*, 871–880.

Mizutani, H., and E. Wada (1988), Nitrogen and carbon isotope ratios in seabird rookeries and their ecological implications, *Ecology*, *69*, 340–349.

Mizutani, H., H. Hasegawa, and E. Wada (1986), High nitrogen isotope ratio for soils of seabird rookeries, *Biogeochemistry*, *2*, 221–247.

Ratcliffe, N. (2004), Causes of seabird population change, in *Seabird Populations of Britain and Ireland*, edited by P. I. Mitchell *et al.*, pp. 407–437, Poyser, London.

Schmidt, S., W. C. Dennison, G. J. Moss, and G. R. Stewart (2004), Nitrogen ecophysiology of Heron Island, a subtropical coral cay of the Great Barrier Reef, Australia, *Funct. Plant Biol.*, *31*, 517–528.

Seinfeld, J. H., and S. N. Pandis (1998), *Atmospheric Chemistry and Physics: From Air Pollution to Climate Change*, 2nd ed., John Wiley, Hoboken, N. J.

Sommer, S. G., J. E. Olesen, and B. T. Christensen (1991), Effects of temperature, windspeed and air humidity on ammonia volatilization from surface applied cattle slurry, *J. Agric. Sci.*, *117*, 91–100.

Sorensen, L. L., O. Hertel, C. A. Skjoth, M. Lund, and B. Pedersen (2003), Fluxes of ammonia in the coastal marine boundary layer, *Atmos. Environ.*, *37*, S167–S177.

Sutton, M. A., W. A. H. Asman, and J. K. Schjorring (1994), Dry deposition of reduced nitrogen, *Tellus, Ser. B*, *46*, 255–273.

Sutton, M. A., U. Dragosits, Y. S. Tang, and D. Fowler (2000), Ammonia emissions from non-agricultural sources in the UK, *Atmos. Environ.*, *34*, 855–869.

Tang, Y. S., J. N. Cape, and M. A. Sutton (2001), Development and types of passive samplers for monitoring atmospheric NO_2 and NH_3 concentrations, *Sci. World*, *1*, 513–529.

Theobald, M. R., P. D. Crittenden, A. P. Hunt, Y. S. Tang, U. Dragosits, and M. A. Sutton (2006), Ammonia emissions from a Cape fur seal colony, Cape Cross, Namibia, *Geophys. Res. Lett.*, *33*, L03812, doi:10.1029/2005GL024384.

Wada, E., R. Shibata, and T. Torii (1981), ^{15}N abundance in Antarctica: Origin of soil nitrogen and ecological implications, *Nature*, *292*, 327–329.

Wanless, S., and M. P. Harris (2004), Northern Gannet *Morus bassanus*, in *Seabird Populations of Britain and Ireland*, edited by P. I. Mitchell *et al.*, pp. 115–127, Poyser, London.

Weber, R. J., P. H. McMurry, L. Mauldin, D. J. Tanner, F. L. Eisele, F. J. Brechtel, S. M. Kreidenweis, G. L. Kok, R. D. Schillawski, and D. Baumgardner (1998), A study of new particle formation and growth involving biogenic and trace gas species measured during ACE 1, *J. Geophys. Res.*, *103*, 16,385–16,396.

Wilson, L. J., et al. (2004), Modelling the spatial distribution of ammonia emissions from seabirds in the UK, *Environ. Pollut.*, *131*, 173–185.

Woehler, E. J. (1993), *The Distribution and Abundance of Antarctic and Sub-Antarctic Penguins*, Sci. Comm. on Antarct. Res., Cambridge, UK.

Wyers, G. P., R. P. Otjes, and J. Slanina (1993), A continuous-flow denuder for the measurement of ambient concentrations and surface-exchange fluxes of ammonia, *Atmos. Environ., Part A*, *27*, 2085–2090.

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