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# The mineral and energy contributions of guano of selected species of birds to the Marion Island terrestrial ecosystem

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*Guano production by 14 species of surface-nesting birds on Marion Island was determined. The annual production by all species is 3 615 t of dried guano (about 33 000 t fresh) of which 98 per cent is voided by penguins. King penguins, (60,4 per cent), and macaroni penguins, (32 per cent), are the chief producers. Albatrosses, giant petrels, cormorants, skuas, gulls and sheathbills together are responsible for 2 per cent of the total guano production. Most guano is produced during summer and 53 per cent of the annual production occurs in December, January and February. Virtually all of the guano is voided on the coastal plain of the island, particularly on the eastern coast. Only 112 t, or 3 per cent of the annual total of guano is voided in vegetated areas. The remainder falls in penguin or cormorant colonies abutting the sea, which are generally devoid of vegetation. There are no large accumulations of guano on Marion Island, because of the high rainfall. The mineral element and energy content of the guano of selected species is given. Guano appears to be a major source of N and P for the soils of the coastal plain. The island's soils are deficient in these elements and plant growth is enhanced in regions of guano deposition.*

## Introduction

Previous descriptions of the manuring effects of bird guano in sub-Antarctic terrestrial ecosystems (Gillham, 1961) and on Marion Island in particular (Van Zinderen Bakker Sr., 1971; Huntley, 1971; Smith, 1976b, 1977) have been largely qualitative. On Marion Island, primary productivity increases significantly in freshwater and terrestrial localities influenced by the large populations of birds and seals (Grobbelaar, 1974; Smith, 1976a & b, 1978.)

This paper presents quantitative estimates of the mass, energy and nutrient composition of guano deposited on the island by 14 species of diurnally-active, surface-nesting birds. The species are: king penguin, *Aptenodytes patagonicus;* gentoo penguin, *Pygoscelis papua;* macaroni penguin, *Eudyptes chrysolophus;* rockhopper penguin, *E. chrysocome;* wandering albatross, *Diomedea exulans;* grey-headed albatross, *D. chrysostoma;* sooty albatross, *Phoebetria fusca;* light-mantled sooty albatross, *P. palpebrata;* northern giant petrel, *Macronectes halli;* southern giant petrel, *M. giganteus;* imperial cormorant, *Phalacrocorax albiventer;* sub-Antarctic skua, *Catharacta antarctica;* kelp gull, *Larus dominicanus;* and lesser sheathbill, *Chionis minor*.

This list represents 14 of the 16 diurnally-active, surface-nesting species found on Marion Island, the others being the Antarctic tern, *Sterna vittata*, and the Kerguelen tern, *S. virgata*. The breeding populations of both terns amount to fewer than 50 pairs (Berruti & Harris, 1976; Williams *et al.* 1978). The balance of the known breeding avifauna on Marion Island consists of 10 species of small petrels (Procellariidae and Pelecanoididae) which nest underground and are mainly nocturnally active on the island (Williams *et al.* 1979); they were not included in the present research programme.

## Methods and materials

Censuses of the populations of surface-nesting birds on Marion Island were taken during January 1974-June 1975 (Williams *et al.* 1975) and again during January 1976-May 1977 (Williams *et al.* 1979). Counts were made by observers on foot and from aerial photographs of the larger penguin colonies. Estimates, rather than head counts, were made in a few cases.

Information on the body masses of birds and factors affecting the presence and mean density of birds on the island was gathered by monitoring a range of sub-populations of individual species (Williams *et al.* 1975). Where necessary, additional information was obtained from published sources.

The hourly rate of guano production was measured in

several ways. Individual birds were caged for periods of two to 24 hours and guano was collected on aluminium foil or aluminium trays below the cages. All penguins, skuas, gulls and some sheathbills (at night) were treated in this way. Penguin chicks used for guano sampling were selected while they were in creches, following the brood period, since human presence was probably least disruptive in the colonies at this time. Strong plastic sheeting was pegged out around the nests of breeding wandering albatrosses and giant petrels and the guano collected off the sheets. The prevalence of rain and strong winds severely limited the usefulness of this method. The defaecation frequency of free-living sheathbills was determined from focal-animal observations. The mass of guano per defaecation was obtained by collecting droppings off smooth surfaces. The daily guano output by sheathbills was calculated from diurnal and nocturnal rates using the ratio of 11 hours night to 13 hours daylight.

Guano samples were stored in glass vials in a deep-freeze until analysed. The dry mass was determined by drying weighed subsamples in a convection oven at 60-70 °C until a constant mass was obtained. Energy contents were determined using a Gallenkamp ballistic bomb calorimeter. Following digestion of the dried guano samples (Allen *et al.* 1974), the concentrations of calcium, sodium, potassium and magnesium were determined by atomic absorption spectroscopy (Pringle *et al.* 1968) and total phosphorus was determined using the molybdenum blue method (Murphy & Riley, 1962). Inorganic nitrogen ($NH_4^+$–N and $NH_3$–N) was determined using the MgO–Devarda alloy steam distillation method (Bremner, 1965a). Total nitrogen was determined using the regular macro-Kjeldahl method (Bremner, 1965b) and uric acid using the ammonia–silver lactate method (Allen *et al.* 1974). Protein was measured with folin-phenol reagent (Lowry *et al.* 1951) and sulphur by a turbidimetric method.

Two samples were analysed for energy content, and three for mineral element content per species; each sample included guano from three individual birds.

**Table 1**

Mean daily (24-hour) guano production (± standard deviation and range), and output per kg of body mass, by surface-nesting birds on Marion Island.

| Species | *N* | Mean sampling time (hrs) | Fresh (g bird$^{-1}$) | | Dried (g bird$^{-1}$) | | Dried (g kg$^{-1}$) |
|---|---|---|---|---|---|---|---|
| Penguin adults | | | | | | | |
| King | 16 | 2,5 | 404 ± 310 | ( 60–1 392) | 34,4 ± 28,7 | ( 8,8–110,0) | 2,9 |
| Gentoo (feeding chicks) | 12 | 5,3 | 560 ± 250 | (281– 960) | 91,3 ± 44,5 | (23,1–162,3) | 15,2 |
| Gentoo (non-breeding) | 9 | 22,0 | 139 ± 119 | ( 45– 420) | 24,7 ± 17,4 | ( 8,7– 54,2) | 4,1 |
| Rockhopper (feeding chicks) | 9 | 4,0 | 79 ± 54 | ( 15– 162) | 13,2 ± 10,5 | ( 4,3– 36,3) | 4,9 |
| Rockhopper (non-breeding) | 8 | 4,0 | 42 ± 20 | ( 24– 84) | 4,3 ± 2,1 | ( 2,5– 8,9) | 1,6 |
| Rockhopper (moulting) | 22 | 24,0 | 17 ± 18 | ( 3– 66) | 3,4 ± 1,9 | ( 0,8– 9,0) | 1,3 |
| Macaroni (moulting) | 18 | 24,0 | 23 ± 17 | ( 6– 59) | 7,0 ± 4,0 | ( 1,3– 15,0) | 1,5 |
| Penguin chicks in creches | | | | | | | |
| King | 8 | 2,0 | 467 ± 493 | ( 30–1 428) | 63,4 ± 74,5 | ( 4,3–231,2) | — |
| Gentoo | 2 | 2,0 | 534 ± 110 | (456– 612) | 23,6 ± 1,4 | (22,6– 24,6) | — |
| Rockhopper | 16 | 4,0 | 231 ± 143 | ( 30– 542) | 28,4 ± 15,3 | ( 4,1– 51,5) | — |
| Other birds | | | | | | | |
| Giant petrels (adults) | 19 | 18,0 | no data | | 3,2 ± 1,8 | ( 1,1– 7,9) | 0,8 |
| Wandering albatross | | | | | | | |
| (chick 1-2 months old) | 5 | 22,0 | no data | | 10,2 ± 10,2 | ( 2,5– 25,6) | — |
| (chick 4-7 months old) | 6 | 22,0 | no data | | 12,4 ± 5,7 | ( 7,6– 19,5) | — |
| (all chicks) | 11 | 22,0 | no data | | 11,4 ± 7,7 | ( 2,5– 25,6) | — |
| Sub-Antarctic skua (full-grown) | 20 | 4,0 | 194 ± 95 | ( 32– 384) | 24,7 ± 14,6 | ( 5,9– 60,5) | 15,4 |
| Kelp gull (full-grown) | 6 | 4,0 | 181 ± 64 | (120– 294) | 36,1 ± 20,9 | (13,3– 66,6) | 36,1 |
| Lesser sheathbill (full-grown) | 25 | — | no data | | 16,7 ± 10,7 | ( 5,1– 43,8) | 33,4 |

**Table 2**

Annual production of guano (dry mass) by surface-nesting birds on Marion Island.

| Species | Guano (t) | % |
|---|---|---|
| King penguin | 2 182,20 | 60,37 |
| Gentoo penguin | 45,60 | 1,26 |
| Macaroni penguin | 1 145,40 | 31,69 |
| Rockhopper penguin | 179,10 | 4,95 |
| All penguins | 3 552,20 | 98,28 |
| Wandering albatross | 5,33 | 0,15 |
| Grey-headed albatross | 2,10 | 0,06 |
| Sooty albatross | 0,85 | 0,02 |
| Light-mantled sooty albatross | 0,08 | 0,00 |
| Northern giant petrel | 0,13 | 0,01 |
| Southern giant petrel | 0,92 | 0,03 |
| Imperial cormorant | 11,81 | 0,32 |
| Sub-Antarctic skua | 13,51 | 0,37 |
| Kelp gull | 6,08 | 0,17 |
| Lesser sheathbill | 21,50 | 0,59 |
| All except penguins | 62,31 | 1,72 |
| Total | 3 614,51 | 100,00 |

## Results

The daily output of fresh and dried guano for nine species is given in Table 1. Data for adult king penguins include guano from birds feeding chicks, and probably also from non-breeding birds. Guano was collected from 17 northern giant petrels and two southern giant petrels but the data have been combined. Most measurements of guano output were

made during daylight. Guano output at night possibly may be lower than by day and the total daily (24-hour) outputs estimated here should therefore be treated as preliminary estimates.

Details on the numbers and occurrence on the island of the 14 species considered are given in the Appendix. These birds produce a total of 3 615 t of guano (dried mass) per year (Table 2). This amounts to about 33 000 t of fresh guano. About 98 per cent of the annual guano production was voided by penguins, mostly by king and macaroni penguins.

Guano was deposited in 142 of the 1 km² quadrats at Marion Island (Fig. 1). About 87 per cent (3 153 t) of the total annual production occurred within seven of these quadrats. These seven quadrats included the largest of the king and macaroni penguin colonies. Virtually all guano was voided on the coastal lowlands, within 1 km of the shore, and most of it fell in penguin colonies abutting the shore. The leeward east coast received more than the west coast. Very little guano (0,016 t) from surface-nesting birds was deposited in the mountainous interior of the island. Of these birds, only the light-mantled sooty albatross nested further than 3 km from the coast.

Little guano was deposited directly on vegetated areas. The colonies of imperial cormorants and king, macaroni and rockhopper penguins are largely devoid of plants and are often eroded down to bed-rock. Guano deposited there generally does not contact vegetation. During their annual moult, small groups of king penguins may wander away from their colonies to deposit guano on vegetated areas. It was estimated that about 5 per cent of the moulting king penguins do this. Gentoo penguins and all the other non-penguin species on the island generally breed and moult on vegetated areas. A total of 112 tonnes (dried mass) of guano, or 3,1 per cent of the annual production by surface-nesting birds, was estimated to be deposited on vegetated areas. Distributed over about 100 km² of coastal lowlands, this amounts to an average of 1,12 kg $ha^{-1}$. In addition, appreciable amounts of the volatile components of guano, especially nitrogen compounds (Allen *et al.* 1967), may be deposited by rain on vegetated inland areas near the larger penguin colonies (Lindeboom, 1979). There were significant seasonal variations in guano production with the greatest output occurring during summer (Fig. 2), when most of the birds considered here breed. Over 50 per cent of the annual guano production occurs in three months: December, January and February (see Appendix). During the winter most of the guano is deposited by king penguin chicks and their attendant parents, and by gentoo penguins.

The amount of guano which is actually deposited on to vegetated areas shows little seasonal variation (Fig. 2). During early summer much is deposited here by moulting king penguins which wander inland, and during winter gentoo penguins produce most, during their breeding season.

The energy content and concentrations of selected elements in guano of surface-nesting birds on Marion Island are given in Tables 3 and 4 respectively. The concentrations of N and nitrogenous compounds in this guano are given in Table 5. An attempt has been made to estimate the total energy and nutrient contribution by the guano of surface-nesting birds to the Marion Island ecosystem (Table 6). Where possible, the energy and nutrient contributions by

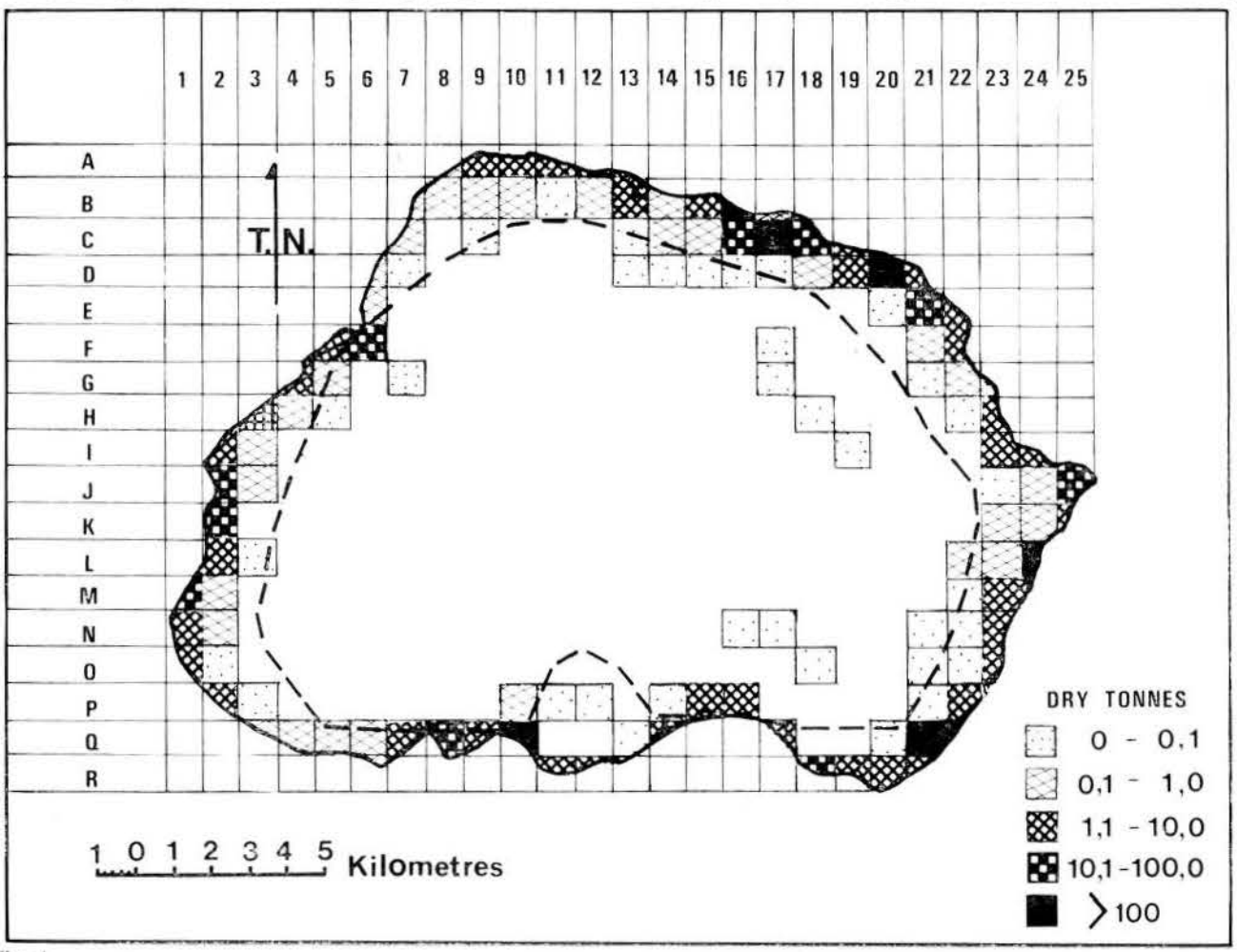
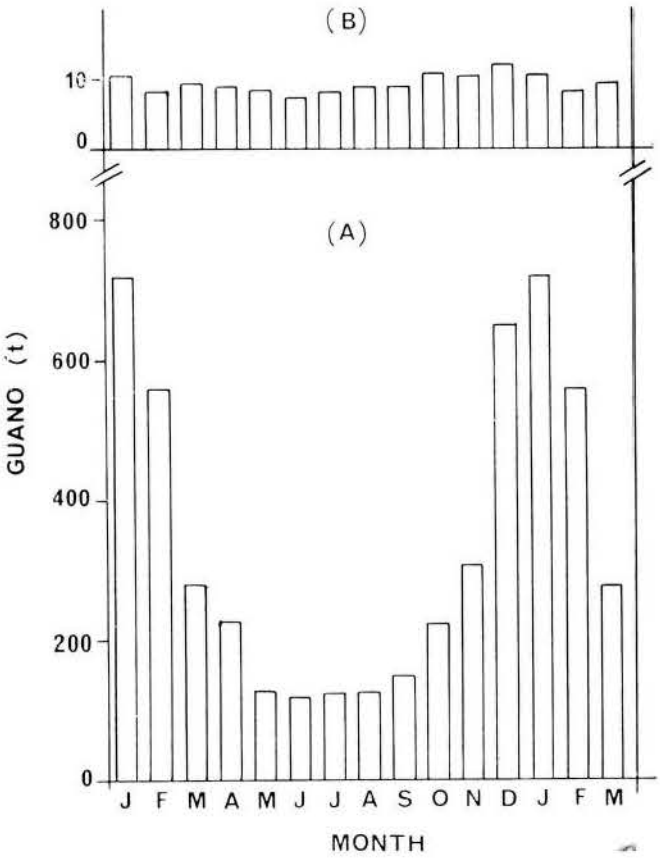



Fig. 1

Fig. 1. Annual total of guano from surface-nesting birds deposited in 1 km² quadrats on Marion Island. The dashed line indicates the upper limit of the coastal plain (150 m a.s.l.).

Fig. 2. Monthly production of guano (dried mass) by surface-nesting birds at Marion Island (a) and the amount of guano which falls on vegetated area (b). Note that the vertical axes of (a) and (b) have different scales. Data from Appendix 1.




adult and chick penguins were first calculated separately and then combined. The nutrient contribution by macaroni penguins was calculated using nutrient concentrations in rockhopper penguin guano. Contributions by all albatrosses and giant petrels were calculated using the mean values from wandering albatross and giant petrel guano. The contribution from the imperial cormorants, sub-Antarctic skuas, kelp gulls and lesser sheathbills was calculated using mean values from skua, gull and sheathbill guano.

## Discussion

About 3 615 t (dried mass) of guano is deposited annually on Marion Island by three million birds. Although many estimates have had to be made in calculating guano production, the final total compares favourably with available data from the guano platforms of Namibia/South West Africa. In this arid region an average of 1 694 t (sun-dried mass) of guano is harvested annually from platforms used throughout the year for breeding and roosting by one million Cape cormorants, *Phalacrocorax capensis* (Berry, 1976).

**Table 3**

Energy content (kJ $g^{-1}$, dried mass) of guano from selected bird species on Marion Island. The mean ± one standard deviation is given.

| Species | Energy content | *N* |
|---|---|---|
| King penguin (adult) | 14,39 ± 2,20 | 2 |
| King penguin (chick) | 15,29 ± 2,08 | 2 |
| Macaroni penguin (moulting adult) | 13,80 ± 0,93 | 14 |
| Rockhopper penguin (adult) | 11,81 ± 0,19 | 2 |
| Rockhopper penguin (moulting adult) | 13,57 ± 0,81 | 8 |
| Rockhopper penguin (chick) | 16,65 ± 0,94 | 2 |
| Gentoo penguin (adult) | 12,31 ± 0,37 | 2 |
| Wandering albatross (chick) | 17,39 ± 0,29 | 2 |
| Giant petrel (adult) | 17,78 ± 1,00 | 2 |
| Sub-Antarctic skua (full-grown) | 17,66 ± 0,30 | 2 |
| Kelp gull (full-grown) | 17,28 ± 5,05 | 2 |
| Lesser sheathbill (full-grown) | 17,05 ± 1,87 | 3 |

**Table 4**

Nutrient element concentrations (mg $g^{-1}$ of dried mass) in guano of selected species of birds on Marion Island. Each concentration is the mean of three determinations.

| Species | Total *P* | Ca | Mg | K | Na | $S^{--}$ |
|---|---|---|---|---|---|---|
| King penguin | | | | | | |
| adult | 17,5 ± 8,8 | 46,7 ± 28,2 | 7,0 ± 2,4 | 30,5 ± 6,8 | 23,8 ± 3,5 | 0,55 ± 0,24 |
| chick | 38,6 ± 13,4 | 78,0 ± 25,3 | 2,1 ± 0,4 | 9,4 ± 2,8 | 11,4 ± 1,5 | 0,05 ± 0,05 |
| Gentoo penguin | | | | | | |
| adult | 33,8 ± 24,3 | 57,9 ± 14,8 | 7,8 ± 3,4 | 35,9 ± 6,9 | 9,7 ± 5,2 | 0,20 ± 0,21 |
| Rockhopper penguin | | | | | | |
| adult | 31,9 ± 10,1 | 38,4 ± 17,9 | 9,7 ± 8,0 | 32,8 ± 11,8 | 8,3 ± 1,3 | 0,17 ± 0,12 |
| chick | 15,2 ± 2,3 | 21,9 ± 4,4 | 3,5 ± 0,4 | 14,1 ± 1,3 | 10,6 ± 3,7 | 0,11 ± 0,07 |
| Wandering albatross | | | | | | |
| chick | 10,8 ± 2,0 | 4,6 ± 3,6 | 3,8 ± 2,0 | 18,1 ± 2,3 | 24,3 ± 8,5 | 0,14 ± 0,01 |
| Giant petrel | | | | | | |
| adult | 9,0 ± 1,6 | 8,8 ± 7,9 | 3,5 ± 2,9 | 28,7 ± 5,5 | 7,5 ± 5,5 | 0,08 ± 0,14 |
| Sub-Antarctic skua | | | | | | |
| full-grown | 10,9 ± 6,0 | 41,4 ± 27,0 | 2,3 ± 1,3 | 16,0 ± 4,2 | 10,5 ± 2,9 | 0,05 ± 0,09 |
| Kelp gull | | | | | | |
| full-grown | 4,7 ± 2,6 | 158,3 ± 143,0 | 2,9 ± 0,6 | 6,1 ± 3,1 | 14,7 ± 6,1 | 0,05 ± 0,09 |
| Lesser sheathbill | | | | | | |
| full-grown | 13,0 ± 6,5 | 43,7 ± 5,2 | 6,5 ± 6,1 | 14,0 ± 9,1 | 16,7 ± 8,3 | — |

**Table 5**

Concentrations of nitrogen, protein and uric acid (mg $g^{-1}$ of dried mass) in guano of selected species of birds. The mean ± one standard deviation is shown.

| Species | $NH_4^+$-N | $NO_3^-$-N | Total N | Protein | Uric acid | *N* |
|---|---|---|---|---|---|---|
| King penguin (adult) | 14,6 ± 7,2 | 1,5 ± 0,8 | 140,6 ± 232,4 | 370,0 ± 232,4 | 270,9 ± 246,4 | 4 |
| King penguin (chick) | 24,6 ± 4,1 | 1,4 ± 0,5 | 76,3 ± 6,1 | 164,0 ± 77,1 | 69,3 ± 51,5 | 3 |
| Macaroni penguin (adult) | 12,3 ± 1,4 | 1,5 ± 0,2 | 194,0 ± 18,3 | 392,0 ± 168,2 | 445,7 ± 128,4 | 3 |
| Macaroni penguin (moulting) | 17,3 ± 7,3 | 0,1 ± 0,2 | 200,8 ± 47,5 | — | — | 27 |
| Rockhopper penguin (adult) | 16,9 ± 5,2 | 2,9 ± 2,0 | 186,7 ± 44,1 | 379,3 ± 306,2 | 381,0 ± 231,1 | 3 |
| Rockhopper penguin (moulting) | 21,3 ± 1,0 | 0,1 ± 0,1 | 211,1 ± 35,0 | — | — | 25 |
| Rockhopper penguin (chick) | 36,6 ± 3,2 | 1,2 ± 1,7 | 208,5 ± 47,4 | 159,0 ± 2,8 | 336,5 ± 74,3 | 2 |
| Gentoo penguin (adult) | 21,1 ± 4,1 | 4,2 ± 3,0 | 121,3 ± 59,2 | 96,3 ± 18,8 | 339,3 ± 120,2 | 3 |
| Wandering albatross (chick) | 42,8 ± 22,1 | 1,8 ± 2,7 | 151,9 ± 18,0 | 210,7 ± 97,3[2] | 69,7 ± 42,6[2] | 10 |
| Giant petrel (adult) | 18,5 ± 7,1 | 2,0 ± 1,1 | 205,0 ± 112,5 | 311,0 ± 251,1 | 296,3 ± 262,0 | 3 |
| Sub-Antarctic skua (full-grown) | 14,7 ± 2,4 | 4,4 ± 4,8 | 127,0 ± 64,2 | 227,7 ± 43,9 | 45,0 ± 77,9 | 3 |
| Kelp gull (full-grown) | 18,1 ± 26,8 | 0,2 ± 0,3 | 73,3 ± 95,1 | 70,0 ± 36,6 | 68,3 ± 87,2 | 3 |
| Lesser sheathbill (full-grown) | 7,6 ± 4,2 | — | 76,5 ± 24,1 | — | 46,0 ± 45,3[1] | 7 |

[1] $n=2$; [2] $n=3$.

**Table 6**

Approximate amounts of energy and selected elements deposited annually in the guano of surface-nesting birds on Marion Island.

| Species | Energy (kJ × $10^8$) | Total N (t) | P (t) | Ca (t) | Mg (t) | K (t) | Na (t) | S (kg) |
|---|---|---|---|---|---|---|---|---|
| King penguin | 323 | 237,77 | 60,71 | 135,30 | 9,97 | 43,94 | 38,76 | 665 |
| Gentoo penguin | 6 | 5,53 | 1,54 | 2,64 | 0,35 | 1,64 | 0,44 | 9 |
| Macaroni penguin | 160 | 226,10 | 26,96 | 34,53 | 7,53 | 26,82 | 10,80 | 160 |
| Rockhopper penguin | 24 | 35,92 | 5,19 | 6,37 | 1,54 | 5,29 | 1,55 | 28 |
| All penguins | 513 | 505,32 | 94,40 | 178,84 | 19,39 | 77,69 | 51,55 | 862 |
| Albatrosses & giant petrels | 2 | 1,68 | 0,09 | 0,06 | 0,03 | 0,22 | 0,15 | 1 |
| All other birds | 9 | 4,88 | 0,50 | 4,29 | 0,21 | 0,64 | 0,74 | 3 |
| Total | 524 | 511,88 | 94,99 | 183,19 | 19,63 | 78,55 | 52,44 | 866 |

Approximately 97 per cent of the guano deposited on Marion Island falls on bare rock or mud in penguin or cormorant colonies, and is diluted to form pools and streams of liquid or semi-liquid guano which ultimately drain to the sea. Very little guano appears to accumulate in permanent deposits. While the guano is on the floors of penguin colonies, it supplies large concentrations of micro-organisms with energy and nutrients. Lesser sheathbills also eat appreciable quantities of freshly voided penguin guano (Burger, in preparation). Much of the guano returns rapidly to the marine ecosystem. The primary producers in the intertidal kelp beds and offshore areas probably benefit from the nutrients in the guano produced on the island.

The amount of guano deposited directly on vegetated areas appears insignificant relative to the total production. This portion, together with the nutrients from guano which reaches vegetated areas by lateral seepage from penguin colonies and from precipitated volatile components, appears to be a major source of essential nutrient elements.

The soils and vegetation in many areas on Marion Island are deficient in certain elements. In wet mires many elements appear to be deficient and in other areas N, P and sometimes Ca are deficient (Smith, 1976a). Nutrients enter the island's terrestrial ecosystem from the atmosphere, volcanic rocks, the sea and from animal deposits. Algal mats found in many mires have been found to fix atmospheric N (Croome, 1973), but the amounts fixed have not been accurately determined. Weathering of rocks is believed to contribute some elements, notably Fe (Smith, 1976a). The sea is an important source of Na, K, Ca, Mg, Cl and $SO_4$, which are blown ashore in sea-spray during the frequent gales (Grobbelaar, 1975; Smith, 1976a).

The excreta of seals can be seen to stimulate plant growth in the vicinity of wallows. The amount and composition of seal excreta deposited has yet to be determined, but should be far less than that deposited by birds. Avian deposits, other than guano, including carcasses, eggs and feathers, occur in substantial amounts on Marion Island and are rich in many nutrients (Siegfried *et al.* 1978; Williams & Berruti, 1978; Williams *et al.* 1978). Guano however, represents about 85 per cent of the dry mass of all avian deposits and the nutrients in eggs and carcasses frequently enter the island's ecosystem via the guano of predatory and scavenging birds.

The major inputs of N, P and, in some areas, Ca and S, to the island's terrestrial ecosystem appear to be from guano. In the Antarctic, most of the organic matter, N and P in the soils originates from penguin guano and other avian deposits (Tedrow, 1966; Allen *et al.* 1967). Elsewhere, N and P in guano were found to cause increased primary productivity in areas where many birds were concentrated (Leentvaar, 1967; McColl & Burger, 1976).

Superficially, the effects of guano deposition on Marion Island can be seen in the vigorous plant growth and prevalence of coprophilous plant species in the immediate vicinity of penguin colonies and around the nests of other birds. In slopes of tussock grassland containing the nests of burrowing

petrels, Smith (1976b) found increased concentrations of N and P, relative to C content, in the soil and increased concentrations of N, K, Fe and Na in the vegetation, relative to other vegetated areas on Marion Island. The concentrations of Ca and Mg remained unchanged.

Smith (1978) also showed that manuring by gentoo penguins, wandering albatrosses, giant petrels and kelp gulls modified the soil chemistry and vigour of plant growth near nests and roost sites on Marion Island. Manuring was important in maintaining N and P levels in the soil which were compatible with vigorous plant growth.

In general, because precipitation greatly exceeds evaporation on Marion Island, guano deposits are diluted and seldom chemically 'scorch' vegetation as they do on more arid islands frequented by seabirds (Gillham, 1977).

The areas around albatross and giant petrel nests invariably have a more luxuriant vegetation than adjacent areas, dominated by such coprophilous plant species as *Poa cookii*, *Callitriche antarctica* and *Cotula plumosa*. During one year, 2,88 kg of guano (dry mass) is deposited at each wandering albatross nest. Within an area of $5 \times 5$ m centred around the nest, guano deposition is thus 115 g $m^{-2}$. This compares favourably with the agricultural deposition of fertilizer: in the USA artificial fertilizer is applied to pastures and general field crops at the rate of 11-110 g $m^{-2}$ per year (Collings, 1955).

**Acknowledgements**

Scientific research at Marion Island is carried out under the auspices of the South African Scientific Committee for Antarctic Research. Financial and logistical support is provided by the Department of Transport. Valdon Smith kindly analysed guano for certain elements and Valerie Burger, Dawid Mostert and Tim O'Connor helped with other analyses.

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## APPENDIX

### Calculation of the annual guano production by each species

Daily guano production by species for which no data were available was estimated, in proportion to body mass, from the measured guano production of closely related species. Where no data were available for penguins, rockhopper penguins (body mass 2,7 kg) were the data source. For all Procellariiformes, giant petrels (body mass 4,0 kg) and wandering albatrosses (adult body mass 9,0 kg) were the data source for adult and chick guano, respectively.

During the incubation and brood periods, one adult was assumed to be present per nest. Unless otherwise specified, the number of occupied nests during the incubation and fledgling periods was taken to be the average of occupied nests at the start and at the end of each period. The moulting periods of penguins on Marion Island were estimated from data given by Stonehouse (1960), Richdale (1957) and Warham (1963, 1971). The guano output by chicks of imperial cormorants, sub-Antarctic skuas, kelp gulls and lesser sheathbills was not calculated separately, but an estimate was made of the output by the entire population.

Unless otherwise specified, the spatial distribution of the annual guano production of each species was assumed to occur in proportion to the number of breeding pairs per 1 km² quadrat, as given by Siegfried *et al.* (1978). Further details on the specific distribution of guano are on file at the FitzPatrick Institute.

(a) *Guano production by king penguins*

There were 215 234 pairs of king penguins at Marion Island at the start of incubation, and based on Mougin's ratios (Prèvost, (1976), there were 274 458 immature birds. The following data, from Stonehouse (1960) and Barrat (1976), were used to calculate the number of adults and chicks present at each stage of the breeding cycle: both members of the pair are ashore during 17 days of courtship; one bird per pair is ashore during 53 days of incubation and 33 days guarding the chick; the fledgling time is 44 weeks; adults come ashore for a period of three days every three weeks to feed chicks after the guard phase; egg mortality is 35,7 per cent; and chick mortality during the guard phase is 14,8 per cent. Chick mortality during the post-guard period is unknown but was estimated at 30 per cent, based on observations at a colony studied on Marion Island. There were thus, on average, 430 468 adults courting, 176 815 adults incubating, 128 155 adults guarding a similar number of chicks and, during the post-guard period, 14 318 adults and 100 226 chicks present.

King penguins breed asynchronously, laying between 15 November and 20 February (Barrat, 1976). For the purpose of this study, laying was assumed to have occurred on December 15, hatching on 6 February and fledging on 11 December. Adults and immature birds come ashore to moult for 30 days (Stonehouse, 1960) and the timing of moult was estimated from data given by Barrat (1976).

The daily output of guano (dry mass) by an adult is 34,4 g and by a chick aged 3-4 months, is 63,4 g (Table 1). The overall mean daily output of chicks of all ages was taken to be half of this value (31,7 g).

The output of moulting adults and immature birds was estimated to be 15,1 g, based on the output of moulting rockhopper penguins. Adult king penguins have a mean mass of 12,0 kg.

Spatial distribution of king penguin guano.

| Quadrat | No. of birds | | Guano output (t) | | |
|---|---|---|---|---|---|
| | No. of pairs | No. of moulters | Breeding adults & chicks | Moulting ad. & imm. | Total (t) |
| B16 | 14 702 | 46 718 | 127,2 | 21,16 | 148,40 |
| C16 | — | 20 000 | — | 9,06 | 9,06 |
| C17 | 78 835 | 231 453 | 682,3 | 104,85 | 787,16 |
| C18 | 7 871 | 25 420 | 68,1 | 11,52 | 79,64 |
| D20 | 9 581 | 30 916 | 82,9 | 14,00 | 96,93 |
| E21 | — | 20 000 | — | 9,06 | 9,06 |
| 125 | 3 000 | 9 619 | 26,0 | 4,36 | 30,32 |
| 023 | 200 | 687 | 1,7 | 0,31 | 2,04 |
| Q21 | 80 000 | 252 784 | 692,4 | 114,51 | 806,90 |
| Q10 | 21 045 | 67 329 | 182,1 | 30,50 | 212,64 |
| Total | | | 1 862,8 | 319,33 | 2 182,15 |

(b) *Guano production by gentoo penguins*

There were 1 343 pairs of gentoo penguins at Marion Island at the start of incubation and, using Mougin's ratios (Prèvost, 1976), there were 2 760 immature birds. Gentoo penguins are resident and come ashore at night (Van Zinderen Bakker Jr, 1971) for an estimated time of eight hours per day in summer (September to February) and twelve hours per day in winter (March to August). Adults and immature birds come ashore to moult for 30 days. During the 36 days of incubation, starting on 21 July, the number of adults ashore was calculated from the mean egg mortality of 22 per cent (Siegfried *et al.* 1978). The nestling period is 105 days including a 26-day brood period (Williams, in preparation). The number of occupied nests at this time is calculated from monthly chick mortality data given by Williams *et al.* (1978).

The average production of guano (dry mass) per 24 hours by non-moulting adults and immature birds was 58,0 g (Table 1). The daily output by chicks of all ages was taken to be 11,8 g, estimated at half the output of chicks aged 50-60 days (Table 1). The estimated daily output of moulting adults and immature birds which have a mean mass of 6,0 kg was 7,6 g, based on the output of moulting rockhopper penguins.

(c) *Guano production by macaroni penguins*

There were 449 892 pairs of macaroni penguins at Marion Island at the start of incubation and, using Mougin's ratios (Prèvost, 1976), there were 891 905 immature birds. The numbers of breeding adults ashore in each month was calculated using the percentage of a sub-population seen ashore during regular censuses (Williams,

in preparation). The number of chicks present in each month was calculated from mortality data given by Williams *et al.* (1978). Adults and immature birds come ashore to moult for 28 days.

The estimated daily production of guano (dry mass) by an adult courting, incubating and brooding (October-December) was 7,3 g, during the post-guard period (January and February) it was 22,5 g and the output by a chick was 24,2 g, based on the output of rockhopper penguins of similar age and breeding status. Adult macaroni penguins have a mean mass of 4,6 kg. The daily output of guano by moulting adults and immature birds was 7,0 g (Table 1).

(d) *Guano production by rockhopper penguins*

There were 93 286 pairs of rockhopper penguins at Marion Island at the start of incubation and, using Mougin's ratios (Prèvost, 1976) there were 342 359 immature birds. The numbers of breeding adults and chicks present in each month were estimated in a similar manner to the macaroni penguins. Adult and immature rockhopper penguins come ashore to moult for 28 days.

The daily output of guano (dry mass) by an adult during courtship, incubation and brooding was taken to be 4,3 g, which is the output obtained from loafing adults (Table 1). The daily output by an adult feeding chicks (i.e. in February and March) was 13,2 g and by a moulting adult or immature bird was 3,4 g (Table 1). The daily output by chicks of all ages was taken to be 14,2 g per bird, half of the output by chicks aged 50-60 days (Table 1).

(e) *Guano production by wandering albatrosses*

There were 1 852 pairs of wandering albatrosses at Marion Island at the start of incubation. The following data, from Tickell (1968), were used to calculate the number of adults and chicks present in each month: courtship period 27 days when two birds were present per nest for 45 per cent of the time; incubation 78 days; nestling period 278 days including a 32-day brood period; chick mortality 19 per cent; after the brood period each chick is fed for three days when the parent remains for about 30 minutes. At Marion Island the mean laying date was 30 December and egg mortality was 30,4 per cent (personal observation).

The daily production of guano (dry mass) by an adult was estimated to be 7,2 g, based on the output by adult giant petrels. Adult wandering albatrosses have a mean mass of 9 kg (Tickell, 1968). The daily production by chicks was estimated to be 10,2 g during March to May and 12,4 g during June to December (Table 1).

Monthly production of guano by wandering albatrosses

| | No. of bird-days | | Guano output (t, dried) | | |
|---|---|---|---|---|---|
| Month | Adults | Chicks | Adults | Chicks | Total |
| Jan. | 48 701 | — | 0,351 | — | 0,351 |
| Feb. | 43 988 | — | 0,317 | — | 0,317 |
| Mar. | 43 449 | 15 171 | 0,313 | 0,155 | 0,468 |
| Apr. | 22 263 | 35 010 | 0,160 | 0,357 | 0,517 |
| May | 253 | 36 177 | 0,002 | 0,369 | 0,371 |
| Jun. | 245 | 35 010 | 0,002 | 0,434 | 0,436 |
| Jul. | 253 | 36 177 | 0,002 | 0,449 | 0,451 |
| Aug. | 253 | 36 177 | 0,002 | 0,449 | 0,451 |
| Sept. | 245 | 35 010 | 0,002 | 0,434 | 0,436 |
| Oct. | 253 | 36 177 | 0,002 | 0,449 | 0,451 |
| Nov. | 245 | 35 010 | 0,002 | 0,434 | 0,436 |
| Dec. | 46 747 | 24 507 | 0,337 | 0,304 | 0,641 |
| Total | | | 1,492 | 3,834 | 5,326 |

(f) *Guano production by grey-headed albatrosses*

There were 3 370 pairs of grey-headed albatrosses at Marion Island at the start of the incubation period. The following data, from Tickell and Pinder (1975), were used to calculate the numbers of adults and chicks present in each month: courtship 26 days, when both members of the pair were at the nest for 50 per cent of the day; incubation period 72 days starting on 19 October; nestling period 141 days including a brood period of 23 days; egg mortality 46 per cent; and chick mortality 15 per cent.

The daily output of dry guano by an adult and by a chick was estimated to be 3,0 g and 4,7 g respectively. Adult grey-headed albatrosses have a mean mass of 3,7 kg (Tickell & Pinder, 1975).

Monthly production of guano by grey-headed albatrosses.

| | No. of bird-days | | Guano output (t, dried) | | |
|---|---|---|---|---|---|
| Month | Adults | Chicks | Adults | Chicks | Total |
| Oct. | 127 280 | — | 0,382 | — | 0,382 |
| Nov. | 90 270 | — | 0,271 | — | 0,271 |
| Dec. | 68 940 | — | 0,207 | — | 0,207 |
| Jan. | 41 170 | 55 490 | 0,124 | 0,261 | 0,385 |
| Feb. | — | 48 524 | — | 0,228 | 0,228 |
| Mar. | — | 51 956 | — | 0,244 | 0,244 |
| Apr. | — | 48 510 | — | 0,228 | 0,228 |
| May | — | 32 907 | — | 0,155 | 0,155 |
| Total | | | 0,984 | 1,116 | 2,100 |

(g) *Guano production by sooty albatrosses*

There were 2 030 pairs of sooty albatrosses at Marion Island at the start of the incubation period. The following data, from Berruti (1977 and personal communication), were used to calculate the numbers of adults and chicks present in each month: courtship 25 days during which both members of the pair were present for 50 per cent of the day; incubation period 68 days starting on 10 October; nestling period 170 days including a brood period of 21 days; mean egg mortality 35 per cent and chick mortality 54 per cent. Egg and chick mortality were calculated for 10-day periods using unpublished field data (Berruti, personal communication). Guano output by adults returning to feed chicks after the brood period was negligible.

The daily output of guano (dry mass) by an adult and by a chick was estimated to be 2,0 g and 3,2 g respectively. Adult sooty albatrosses have a mean mass of 2,5 kg (Berruti, 1977).

Monthly production of guano by sooty albatrosses.

| | No. of bird-days | | Guano output (t, dried) | | |
|---|---|---|---|---|---|
| Month | Adults | Chicks | Adults | Chicks | Total |
| Sept. | 32 514 | — | 0,065 | — | 0,065 |
| Oct. | 58 692 | — | 0,117 | — | 0,117 |
| Nov. | 49 860 | — | 0,100 | — | 0,100 |
| Dec. | 42 683 | 14 757 | 0,085 | 0,047 | 0,132 |
| Jan. | 6 930 | 31 351 | 0,014 | 0,100 | 0,114 |
| Feb. | — | 26 149 | — | 0,084 | 0,084 |
| Mar. | — | 26 192 | — | 0,084 | 0,084 |
| Apr. | — | 22 731 | — | 0,073 | 0,073 |
| May | — | 20 667 | — | 0,066 | 0,066 |
| Jun. | — | 5 481 | — | 0,018 | 0,018 |
| Total | | | 0,381 | 0,472 | 0,853 |

(h) *Guano produced by light-mantled sooty albatrosses*

There were 176 pairs of light-mantled sooty albatrosses at Marion Island at the start of incubation. The following data, from Berruti (1977 and personal communication) were used to calculate the number of adults and chicks ashore in each month: courtship period 19 days, during which both members of the pair were ashore for 50 per cent of the day; incubation period 67 days starting on 29 October; nestling period 170 days including a 20-day brood period. Egg and chick mortality were assumed to be similar to those of the sooty albatross. Guano output by adults returning to feed chicks after the brood period was negligible.

The daily output of guano (dry mass) by an adult and by a chick was estimated to be 2,2 g and 2,8 g respectively. Adult light-

mantled sooty albatrosses have a mean mass of 2,8 kg (Berruti, 1977).

Monthly production of guano by light-mantled sooty albatrosses.

| Month | No. of bird-days | | Guano output (t, dried) | | |
|---|---|---|---|---|---|
| | Adults | Chicks | Adults | Chicks | Total |
| Oct. | 3 866 | — | 0,009 | — | 0,009 |
| Nov. | 4 770 | — | 0,010 | — | 0,010 |
| Dec. | 4 061 | — | 0,009 | — | 0,009 |
| Jan. | 2 370 | 2 948 | 0,005 | 0,011 | 0,016 |
| Feb. | — | 2 342 | — | 0,008 | 0,008 |
| Mar. | — | 2 354 | — | 0,008 | 0,008 |
| Apr. | — | 2 047 | — | 0,007 | 0,007 |
| May | — | 1 881 | — | 0,007 | 0,007 |
| June. | — | 1 085 | — | 0,004 | 0,004 |
| Total | | | 0,033 | 0,045 | 0,078 |

(i) *Guano production by northern giant petrels*

There were 208 pairs of northern giant petrels at Marion Island at the start of incubation. The following data, from Williams *et al.* (in preparation), were used to calculate the number of adults and chicks present in each month: incubation period 60 days starting on 15 August; nestling period 116 days, including a 22-day brood period; egg mortality 23,8 per cent and nestling mortality 14,3 per cent. The guano output by adults feeding chicks after the brood period was negligible and the output of non-breeding and courting birds was not considered.

The daily output of guano (dry mass) by an adult was 3,2 g (Table 1) and the output of a chick, based on the output of nestling wandering albatrosses, was 5,1 g. Adult northern giant petrels have a mean mass of 4,0 kg.

Monthly production of guano by northern giant petrels.

| Month | No. of bird-days | | Guano output (t, dried) | | |
|---|---|---|---|---|---|
| | Adults | Chicks | Adults | Chicks | Total |
| Aug. | 2 760 | — | 0,009 | — | 0,009 |
| Sept. | 5 704 | — | 0,018 | — | 0,018 |
| Oct. | 4 944 | 2 368 | 0,016 | 0,012 | 0,028 |
| Nov. | 888 | 4 440 | 0,003 | 0,023 | 0,026 |
| Dec. | — | 4 588 | — | 0,023 | 0,023 |
| Jan. | — | 4 588 | — | 0,023 | 0,023 |
| Feb. | — | 1 184 | — | 0,006 | 0,006 |
| Total | | | 0,046 | 0,087 | 0,133 |

(j) *Guano production by southern giant petrels*

There were 1 337 pairs of southern giant petrels at Marion Island at the start of incubation. The following data, from Williams *et al.* (in preparation), were used to calculate the number of adults and chicks present in each month: incubation 60 days starting on 27 September, nestling period 119 days, including a 24-day brood period; egg mortality 26,3 per cent; and nestling mortality 12,5 per cent. The guano output by adults returning to feed chicks after the brood period was negligible and the output by courting and non-breeding birds was not considered.

The daily production of guano (dry mass) by an adult was 3,2 g (Table 1) and the output by a chick, based on the output by wandering albatross nestlings, was estimated to be 5,7 g. Adult southern giant petrels have a mean mass of 4,5 kg.

Monthly production of guano by southern giant petrels.

| Month | No. of bird-days | | Guano output (t, dried) | | |
|---|---|---|---|---|---|
| | Adults | Chicks | Adults | Chicks | Total |
| Sept. | 4 644 | — | 0,015 | — | 0,015 |
| Oct. | 35 991 | — | 0,115 | — | 0,115 |
| Nov. | 33 645 | 4 620 | 0,108 | 0,026 | 0,134 |
| Dec. | 17 556 | 28 644 | 0,056 | 0,163 | 0,219 |
| Jan. | — | 28 644 | — | 0,163 | 0,163 |
| Feb. | — | 25 872 | — | 0,147 | 0,147 |
| Mar. | — | 22 176 | — | 0,126 | 0,126 |
| Total | | | 0,294 | 0,625 | 0,919 |

(k) *Guano production by imperial cormorants*

There were 647 cormorants present all year at Marion Island The daily production of guano (dry mass) was estimated to be 50 g per bird, based on the daily production of 56,2 g for the guanay *Phalacrocorax bouganvillii* (Avila, 1954) which has body dimensions about 10 per cent larger than those of the cormorant (Murphy, 1936). The annual dry guano production is 11,811 tonnes or 0,984 t per month.

(l) *Guano production by sub-Antarctic skuas*

The summer population of sub-Antarctic skuas at Marion Island was 2 516 birds. The number of birds present on the island in any month was calculated using the percentage of a sub-population (mean summer count was 63 birds) which was present in each month in the area between Transvaal Cove and East Cape. The daily production of guano (dry mass) was 24,7 g per bird (Table 1).

Monthly production of guano by sub-Antarctic skuas.

| Month | % present | No. of bird-days | Guano output (t, dried) |
|---|---|---|---|
| Jan. | 100 | 77 996 | 1,927 |
| Feb. | 100 | 70 448 | 1,740 |
| Mar. | 65 | 50 697 | 1,252 |
| Apr. | 56 | 42 269 | 1,044 |
| May | 16 | 12 479 | 0,308 |
| Jun. | 5 | 3 774 | 0,093 |
| Jul. | 2 | 1 560 | 0,039 |
| Aug. | 10 | 7 800 | 0,193 |
| Sept. | 64 | 48 307 | 1,193 |
| Oct. | 100 | 77 996 | 1,927 |
| Nov. | 100 | 75 480 | 1,864 |
| Dec. | 100 | 77 996 | 1,927 |
| Total | | | 13,507 |

(m) *Guano production by kelp gulls*

There were 923 kelp gulls present at Marion Island all year. The gulls roost at night and often feed by day at offshore kelp beds, and thus spend only about 50 per cent of their time on land (personal observation). Daily production of dry guano is 36,1 g per bird (Table 1). Annual production is 12,164 tonnes of dry guano, distributed throughout the year, of which approximately 6,082 tonnes, or 0,507 t per month, falls on land.

(n) *Guano production by lesser sheathbills*

There were 3 528 lesser sheathbills present all year at Marion Island. The daily production of guano (dry mass) was 16,7 g per bird and the annual production by the population was 21,504 tonnes or 1,792 t per month.

Monthly guano production by king penguins (t, dried)

| Month | Breeding adults | | | | Chicks | | Moulting birds | | Total |
|---|---|---|---|---|---|---|---|---|---|
| | Courting | Incubating | Guarding chicks | Post-guard | Guarded | Post-guard | Adults | Immatures | |
| Nov. | 29,616 | — | — | 14,776 | — | 95,315 | 65,001 | — | 204,708 |
| Dec. | 222,122 | 97,319 | — | 5,418 | — | 34,949 | 32,500 | 31,082 | 473,390 |
| Jan. | — | 188,556 | — | — | — | — | — | 62,165 | 250,721 |
| Feb. | — | 36,495 | 96,988 | — | 89,375 | — | — | 31,082 | 253,940 |
| Mar. | — | — | 48,494 | 9,851 | 44,688 | 63,543 | — | — | 166,576 |
| Apr. | — | — | — | 14,776 | — | 95,315 | — | — | 110,091 |
| May | — | — | — | 15,269 | — | 98,492 | — | — | 113,761 |
| Jun. | — | — | — | 14,776 | — | 95,315 | — | — | 110,091 |
| Jul. | — | — | — | 15,269 | — | 98,492 | — | — | 113,761 |
| Aug. | — | — | — | 15,269 | — | 98,492 | — | — | 113,761 |
| Sep. | — | — | — | 14,776 | — | 95,315 | 32,500 | — | 142,591 |
| Oct. | — | — | — | 15,269 | — | 98,492 | 65,001 | — | 178,762 |
| Total | 251,738 | 322,370 | 145,482 | 135,449 | 134,063 | 873,720 | 195,002 | 124,329 | 2 182,153 |

Monthly guano production by gentoo penguins.

| Month | No. of bird-days | | | | Guano production (t, dried) | | | | Total |
|---|---|---|---|---|---|---|---|---|---|
| | Breeding adults | Non-breeding adults & immatures | Moulting birds | Chicks | Breeding adults | Non-breeding adults & immatures | Moulting birds | Chicks | |
| Jan. | — | 28 520 | 40 290 | — | — | 1,654 | 0,306 | — | 1,960 |
| Feb. | — | 25 760 | 40 290 | — | — | 1,494 | 0,306 | — | 1,800 |
| Mar. | — | 84 413 | — | — | — | 4,896 | — | — | 4,896 |
| Apr. | — | 81 690 | — | — | — | 4,738 | — | — | 4,738 |
| May | — | 84 413 | — | — | — | 4,896 | — | — | 4,896 |
| Jun. | 39 000 | 41 400 | — | — | 2,262 | 2,401 | — | — | 4,663 |
| Jul. | 57 970 | 42 780 | — | — | 3,362 | 2,481 | — | — | 5,843 |
| Aug. | 57 970 | 42 780 | — | — | 3,362 | 2,481 | — | — | 5,843 |
| Sep. | 31 850 | 27 600 | — | 4 864 | 1,847 | 1,601 | — | 0,057 | 3,505 |
| Oct. | 27 477 | — | 41 400 | 18 240 | 1,594 | — | 0,315 | 0,215 | 2,124 |
| Nov. | 26 591 | — | 41 400 | 18 848 | 1,542 | — | 0,315 | 0,222 | 2,079 |
| Dec. | 27 477 | 28 520 | — | 608 | 1,594 | 1,654 | — | 0,007 | 3,255 |
| Total | | | | | 15,563 | 28,296 | 1,242 | 0,501 | 45,601 |

Monthly guano production by macaroni penguins.

| Month | No. of bird-days (thousands) | | | Guano output (t, dried) | | | Total |
|---|---|---|---|---|---|---|---|
| | Breeding adults | Chicks | Moulting adults & immatures | Breeding adults | Chicks | Moulting adults & immatures | |
| Oct. | 5 035 | — | — | 36,76 | — | — | 36,76 |
| Nov. | 9 808 | — | — | 71,60 | — | — | 71,60 |
| Dec. | 10 765 | 5 094 | — | 78,60 | 123,3 | — | 201,86 |
| Jan. | 6 256 | 8 066 | 12 487 | 140,76 | 195,2 | 87,41 | 423,37 |
| Feb. | 4 155 | 2 253 | 12 487 | 93,48 | 54,5 | 87,41 | 235,42 |
| Mar. | — | — | 12 597 | — | — | 88,18 | 88,18 |
| Apr. | — | — | 12 597 | — | — | 88,18 | 88,18 |
| Total | | | | 421,19 | 373,0 | 351,18 | 1 145,36 |

Monthly production of guano by rockhopper penguins.

| Month | No. of bird-days (thousands) | | | Guano output (t, dried) | | | Total |
|---|---|---|---|---|---|---|---|
| | Breeding adults | Chicks | Moulting adults & immatures | Breeding adults | Chicks | Moulting adults & immatures | |
| Oct. | 19 | — | — | 0,08 | — | — | 0,08 |
| Nov. | 4 467 | — | — | 19,21 | — | — | 19,21 |
| Dec. | 3 847 | — | — | 16,54 | — | — | 16,54 |
| Jan. | 4 394 | 1 205 | 4 793 | 18,89 | 17,10 | 16,30 | 52,30 |
| Feb. | 2 703 | 737 | 4 793 | 35,68 | 10,47 | 16,30 | 62,44 |
| Mar. | 565 | 232 | — | 7,46 | 3,29 | — | 10,75 |
| Apr. | — | — | 4 752 | — | — | 16,16 | 16,16 |
| May | — | — | 472 | — | — | 1,61 | 1,61 |
| Total | | | | 97,86 | 30,87 | 50,35 | 179,10 |

Spatial distribution of skua guano

| Quadrat number | No. of birds | Guano (t) | Quadrat number | No. of birds | Guano (t) | Quadrat number | No. of birds | Guano (t) |
|---|---|---|---|---|---|---|---|---|
| F21 | 28 | 0,150 | B9 | 10 | 0,054 | R20 | 33 | 0,177 |
| F22 | 28 | 0,150 | F5 | 30 | 0,161 | R21 | 33 | 0,177 |
| E21 | 100 | 0,537 | G4 | 30 | 0,161 | Q21 | 118 | 0,633 |
| D20 | 76 | 0,408 | G5 | 20 | 0,107 | P21 | 17 | 0,091 |
| E22 | 80 | 0,429 | H3 | 12 | 0,064 | P22 | 22 | 0,118 |
| D18 | 96 | 0,515 | I2 | 12 | 0,064 | O21 | 9 | 0,048 |
| D19 | 26 | 0,140 | I3 | 10 | 0,054 | O22 | 13 | 0,070 |
| D21 | 76 | 0,408 | J2 | 30 | 0,161 | O23 | 22 | 0,118 |
| C19 | 52 | 0,279 | J3 | 20 | 0,107 | N21 | 8 | 0,043 |
| C18 | 58 | 0,311 | K2 | 22 | 0,118 | N22 | 8 | 0,043 |
| C17 | 188 | 1,009 | L2 | 20 | 0,107 | N23 | 25 | 0,134 |
| C16 | 108 | 0,580 | M1 | 40 | 0,215 | M22 | 12 | 0,064 |
| C15 | 18 | 0,097 | N1 | 20 | 0,107 | M23 | 25 | 0,134 |
| C14 | 18 | 0,097 | O1 | 12 | 0,064 | L22 | 20 | 0,107 |
| C13 | 18 | 0,097 | P3 | 10 | 0,054 | L23 | 68 | 0,365 |
| B14 | 20 | 0,107 | Q3 | 10 | 0,054 | K23 | 20 | 0,107 |
| B15 | 20 | 0,107 | Q4 | 12 | 0,064 | L24 | 60 | 0,322 |
| B16 | 108 | 0,580 | Q5 | 10 | 0,054 | K24 | 25 | 0,134 |
| B10 | 8 | 0,043 | Q6 | 10 | 0,054 | J23 | 16 | 0,086 |
| A10 | 14 | 0,075 | Q7 | 20 | 0,107 | J24 | 22 | 0,118 |
| A11 | 14 | 0,075 | Q8 | 20 | 0,107 | J25 | 35 | 0,188 |
| B12 | 16 | 0,086 | Q9 | 40 | 0,215 | I24 | 23 | 0,123 |
| B13 | 14 | 0,075 | Q10 | 60 | 0,322 | I23 | 12 | 0,064 |
| A9 | 14 | 0,075 | R6 | 11 | 0,059 | H22 | 7 | 0,038 |
| A8 | 4 | 0,021 | P11 | 16 | 0,086 | H23 | 10 | 0,054 |
| B8 | 12 | 0,064 | P12 | 14 | 0,075 | G21 | 10 | 0,054 |
| C7 | 8 | 0,043 | R18 | 48 | 0,258 | G22 | 25 | 0,134 |
| D6 | 8 | 0,043 | R19 | 19 | 0,102 | | | |
| | | | | | | Total | 2 516 | 13,507 |

Spatial distribution of kelp gull guano.

| Quadrat number | No. of birds | Guano (t) | Quadrat number | No. of birds | Guano (t) | Quadrat number | No. of birds | Guano (t) |
|---|---|---|---|---|---|---|---|---|
| A8 | 2 | 0,013 | J25 | 2 | 0,013 | Q8 | 8 | 0,053 |
| A9 | 2 | 0,013 | K25 | 8 | 0,053 | R8 | 2 | 0,013 |
| A10 | 2 | 0,013 | L24 | 20 | 0,132 | Q7 | 2 | 0,013 |
| A11 | 4 | 0,016 | M24 | 36 | 0,237 | R6 | 6 | 0,040 |
| A12 | 4 | 0,026 | M23 | 6 | 0,039 | Q5 | 6 | 0,040 |
| A13 | 4 | 0,026 | N23 | 8 | 0,053 | Q4 | 3 | 0,020 |
| B14 | 14 | 0,092 | O23 | 8 | 0,053 | Q3 | 8 | 0,053 |
| B15 | 14 | 0,092 | P23 | 2 | 0,013 | O1 | 2 | 0,013 |
| B16 | 58 | 0,382 | P22 | 6 | 0,040 | N1 | 8 | 0,053 |
| C16 | 20 | 0,132 | Q22 | 24 | 0,158 | M1 | 18 | 0,118 |
| C17 | 140 | 0,923 | Q21 | 44 | 0,290 | L1 | 2 | 0,013 |
| C18 | 120 | 0,791 | R21 | 26 | 0,171 | K2 | 18 | 0,118 |
| C19 | 34 | 0,224 | R20 | 2 | 0,013 | I2 | 2 | 0,013 |
| D20 | 4 | 0,026 | R19 | 4 | 0,026 | H3 | 8 | 0,053 |
| D21 | 6 | 0,040 | R18 | 16 | 0,105 | G4 | 8 | 0,053 |
| E21 | 6 | 0,040 | Q14 | 14 | 0,092 | F5 | 8 | 0,053 |
| E22 | 24 | 0,158 | Q13 | 4 | 0,026 | F6 | 8 | 0,053 |
| F22 | 6 | 0,040 | R13 | 2 | 0,013 | E6 | 4 | 0,026 |
| G22 | 18 | 0,119 | R12 | 2 | 0,013 | D6 | 2 | 0,013 |
| G23 | 8 | 0,053 | R11 | 2 | 0,013 | C7 | 2 | 0,013 |
| H23 | 8 | 0,053 | R10 | 6 | 0,040 | B7 | 4 | 0,026 |
| I23 | 6 | 0,040 | Q10 | 6 | 0,040 | B8 | 2 | 0,013 |
| I24 | 8 | 0,053 | Q9 | 10 | 0,066 | F21 | 22 | 0,145 |
| | | | | | | Total | 923 | 6,082 |

Spatial distribution of lesser sheathbill guano.

| Quadrat number | No. of birds | Guano (t) | Quadrat number | No. of birds | Guano (t) | Quadrat number | No. of birds | Guano (t) |
|---|---|---|---|---|---|---|---|---|
| I25 | 60 | 0,366 | A10 | 48 | 0,293 | Q6 | 2 | 0,012 |
| I24 | 40 | 0,244 | A9 | 40 | 0,244 | Q7 | 34 | 0,207 |
| I23 | 17 | 0,104 | A8 | 4 | 0,024 | Q8 | 34 | 0,207 |
| H23 | 40 | 0,244 | C6 | 4 | 0,024 | Q9 | 34 | 0,207 |
| G22 | 30 | 0,183 | C7 | 10 | 0,061 | Q10 | 10 | 0,061 |
| G23 | 10 | 0,061 | D6 | 8 | 0,049 | Q13 | 2 | 0,012 |
| F22 | 30 | 0,183 | D7 | 4 | 0,024 | Q14 | 10 | 0,061 |
| E22 | 20 | 0,122 | E6 | 8 | 0,049 | R13 | 2 | 0,012 |
| E21 | 40 | 0,244 | F5 | 80 | 0,488 | Q17 | 10 | 0,061 |
| E20 | 10 | 0,061 | F6 | 130 | 0,792 | R18 | 50 | 0,305 |
| D21 | 84 | 0,512 | G4 | 60 | 0,366 | R19 | 18 | 0,110 |
| D20 | 162 | 0,987 | G5 | 10 | 0,061 | R20 | 18 | 0,110 |
| C19 | 65 | 0,396 | H3 | 28 | 0,171 | R21 | 18 | 0,110 |
| C18 | 133 | 0,811 | H4 | 10 | 0,061 | Q21 | 120 | 0,731 |
| C17 | 857 | 5,224 | I2 | 44 | 0,268 | Q22 | 40 | 0,244 |
| C16 | 33 | 0,201 | I3 | 10 | 0,061 | P22 | 7 | 0,043 |
| B16 | 159 | 0,969 | J2 | 60 | 0,366 | P23 | 2 | 0,012 |
| B15 | 45 | 0,274 | K2 | 20 | 0,122 | O23 | 7 | 0,043 |
| B14 | 45 | 0,274 | L1 | 10 | 0,061 | N23 | 7 | 0,043 |
| B13 | 25 | 0,152 | L2 | 20 | 0,122 | M23 | 25 | 0,152 |
| B12 | 14 | 0,085 | M1 | 80 | 0,488 | M24 | 5 | 0,030 |
| B11 | 5 | 0,030 | M2 | 15 | 0,091 | L23 | 10 | 0,061 |
| B10 | 10 | 0,061 | N1 | 40 | 0,244 | L24 | 117 | 0,713 |
| B9 | 10 | 0,061 | N2 | 5 | 0,030 | K24 | 10 | 0,061 |
| B8 | 4 | 0,024 | O1 | 40 | 0,244 | K25 | 32 | 0,195 |
| B7 | 10 | 0,061 | O2 | 5 | 0,030 | J25 | 30 | 0,183 |
| A13 | 25 | 0,152 | Q3 | 12 | 0,073 | | | |
| A12 | 14 | 0,085 | Q4 | 12 | 0,073 | | | |
| A11 | 40 | 0,244 | Q5 | 20 | 0,122 | | | |
| | | | | | | Total | 3 528 | 21,503 |