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Ecological role of the current and abandoned penguin rookeries in the land environment of the maritime Antarctic

ABSTRACT: The results of several years of studies concerning the role of penguin rookeries in the functioning of the land ecosystems in the maritime Antarctic are summarized. The origins of phosphatic ornithogenic soil in the areas of currently active penguin rookeries are presented. In the maritime Antarctic occurs relatively fast microbiological decomposition and mineralization of large amounts of excrements carried into coastal area by penguins during breeding period. Chemically aggressive water solutions of guano react with underlaying rocks. This process brings about the occurrence of wide zones of phosphatization. These processes cause the appearance of the series of phosphate minerals whose composition and properties depend on the changing physical and chemical conditions of the soil environment. It has been discovered that in the rookeries for various reasons abandoned by penguins phosphates are still present in large amounts and, gradually changed and washed out, have been for hundreds, or even thousands years a source of nutrients for plants growing in poor Antarctic land ecosystems. These soils came to be called the relic ornithogenic soils of the maritime Antarctic. The stages of plant colonization in the abandoned penguin rookeries were traced. The differences in the fate of the organic matter carried out from the sea to the coastal area by sea-birds in various climatic zones were discussed.

Key words: Antarctica, ornithogenic soils, penguins, ecological role.

Introduction

The community of birds living in southern polar region is very specific. Almost all species belongs to seabirds of two orders: penguins and tubenosed birds, the best adapted to the life on boundless area of the oceans. The number of species is relatively small (Watson 1975, Croxall 1984). In geographic Antarctic area, in other words south of Antarctic Convergence, only about 30 species of birds are breeding: 6 penguins, about 20 albatrosses and petrels, 1 cormorant, 1 sheathbill, 2 skuas, 1 gull and 1 tern. However, this small number of species characterize a huge amount of individuals.

The numbers of the Adelie and Chinstrap penguins only is estimated for 30 millions of breeding pairs and another 30 millions of nonbreeding individuals of each of these two species (Wilson 1983, Laws 1985).

The competition for food brings about that species breeding in neighbouring places collect their food at different distances from the nesting sites. The foraging radius of pygoscelid penguins amount to several tens of kilometers, those of *Aptenodytes* spp. and smaller Procellariiformes to several hundreds of kilometers, and albatrosses with their excellent ability of flying — even 1.200 — 2.000 kilometers (Williams and Siegfried 1980, Croxall 1984, Pennyncuick, Croxall and Prince 1984, Trivelpiece et al. 1984, Stahl et al. 1985). Krill, squid and fishes are the main food components of these birds and their chicks (Croxall and Prince 1980, Croxall 1984, Croxall and Lishman 1987).

Owing to this the seabirds are playing a very important role in functioning of Antarctic marine ecosystem. In total, these birds, mostly penguins, consume as much as 115—130 millions tons of krill annually (Croxall 1984, Laws 1985).

During the breeding season seabirds bring from the sea to the land huge amount of organic matter and this activity is an important factor in the circulation of matter and energy flow in the land-sea boundary zone. Considerable part of this matter remains as excreta in breeding colonies distributed in many places along the shore line. This organic manure is very rich in nutrients, especially in nitrogen and phosphorus and may fertilize the poor Antarctic land environment.

The problem was studied more closely in the area of continental Antarctic. As a result of his investigations on Haswell Island Syroečkovskij (1959) noticed the fertilizing function of birds excrements and introduced the term of Antarctic ornithogenic soils. In the area of continental Antarctic investigators from New Zealand (Campbell and Claridge 1966, 1987, McCraw 1967, Spellerberg 1970, Speir and Cowling 1984) and from United States (Tedrov and Ugolini 1966, Ugolini 1972) conducted studies for many years. They found that layers of guano (row rank guano) in the areas of penguin rookeries remain there for long periods of time. Very low activity of microorganisms and low air humidity cause that the dry bird excrements, only slightly changed, to be scattered by wind, and thus fertilize nearby land as well as coastal sea waters.

Our investigations on the role of breeding colonies of penguins in the functioning of land ecosystems were carried out in the maritime Antarctic zone.

The distinct features of ornithogenic soils in the maritime Antarctic were not recognized and their similarity to the ornithogenic soils from the continental Antarctic was assumed a priori (Allen and Heal 1970, Ugolini 1972, Everett 1976, Campbell and Claridge 1987). Sometimes it was supposed that melting waters and summer rainfalls wash guano out totally into the sea (Rakusa-Suszczewski 1980), First suggestion concerning certain features of the ornithogenic soils in the maritime Antarctic appeared in the papers described the occurrence of iron-aluminium phosphate containing ammonium and potassium ions in soils from the vicinity of penguin rookeries on Elephant Island (Wilson and Baim 1976, Brien, Romans and Robertson 1979).

The maritime Antarctic is situated in the climatic zone extending from the South Sandwich Islands, South Orkney Islands and South Shetland Islands further south along the western coast of the Antarctic Peninsula, including the adjacent islands. The climate of this zone is milder than on the Antarctic continent (Smith 1984, Walton 1985, Campbell and Claridge 1987). In the King George Island the summer temperature are often above freezing, heavy rains are not rare, and mean soil temperatures are above O°C even to the depth of over 1 m (Cygan 1981, Moczydłowski 1986).

The Antarctic Peninsula and above mentioned islands are almost totally covered with ice. Small strips of land free of ice occur mostly in the coastal zone, and this is the place where large numbers of birds and seals aggregate over the short summer period. During their short stay on the land these animals leave a huge amount of faeces. Among them penguins play the most important role in this natural fertilizing of the coast because of their numbers and their movements far into the land.

Presently it is known that Adelie and Chinstrap penguins are the most abundant species in the maritime Antarctic (Croxall and Kirkwood 1979, Wilson 1983, Croxall 1984, Poncet and Poncet 1987). Penguins in this region feed mainly on krill (Croxall and Furse 1980, Volkman, Presler and Trivelpiece 1980, Jabłoński 1985). Taking into account the food intake of adults and nestlings of different age (Jabłoński 1985, Croxall and Lishman 1987, Trivelpiece, Trivelpiece and Volkman 1987), the chemical composition of excrecta (Burger, Lindeboom and Williams 1978, Pietr, Tatur and Myrcha 1983) and the mean duration of the reproductive period and average value of the breeding success (Trivelpiece et al. 1983, 1984, Croxall 1984), one can calculate that in the maritime Antarctic pygoscelid penguins alone carry out to the land 1.5 — 2.0 $\times$ 10^4 tons of phosphorus annually, over the nestling period. The rate of manuring of vast areas occupied by breeding birds reaches up to 10 kg dry weight of high-protein faeces per 1 m^2 over the season (Tatur and Myrcha 1984).

Current penguin rookeries and formation of the ornithogenic soils

Our main investigations involving microbiological, hydrochemical and geochemical observations in areas surrounding large penguin rookeries were carried out in the region of Admiralty Bay, King George Island (Fig. 1) where

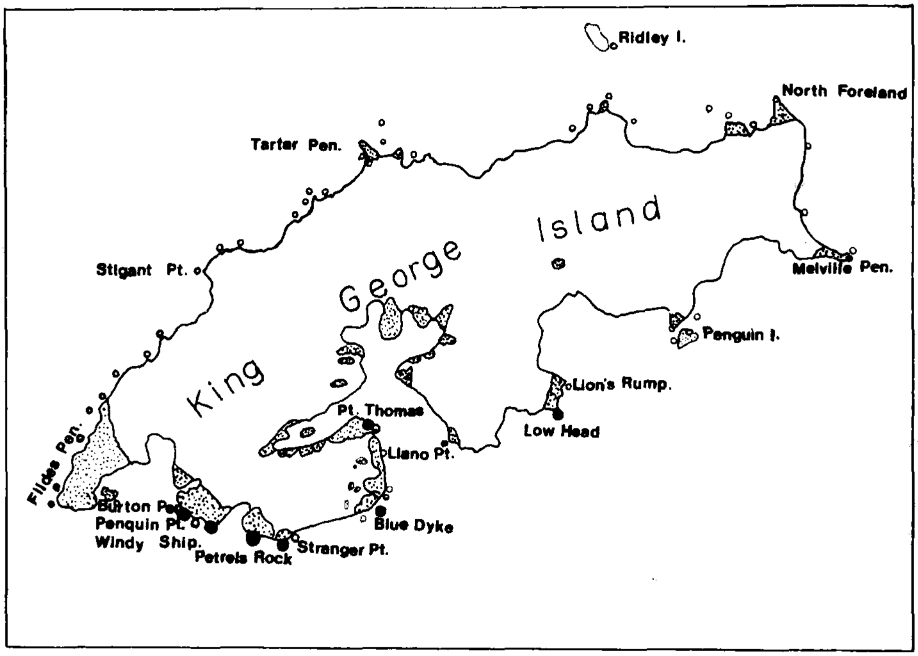

Fig. 1. Distribution of the current and investigated abandoned penguin rookeries on King George Island ○ — actually functioning rookeries, ● — abandoned rookeries

a total of some 45000 pairs of Adelie (*Pygoscelis adeliae*), Chinstrap (*P. antarctica*) and Gentoo (*P. papua*) penguins bred on the seven ice-free strips of the coastline (Jabłoński 1984). The materials were gathered during the IV Antarctic Expedition of the Polish Academy of Sciences (1979/80).

Penguin guano is heterogenous and contains three visible, separated fractions: a "white" fraction (27.7% N) consists of urates, a "red" fraction contains 65.8% of chitin from exoskeletons of krill, *Euphausia superba* and 2.45% of P, and "green" fraction composed mainly of proteins, cholic acids and undigested algal cells (the food of krill) and contains 9.9% N.

Mineralization of this diversified material proceeds in steps. A crucial role in this process is played by microbial activity (Pietr, Tatur and Myrcha 1983, Pietr 1986).

The high activity of microorganisms observed in the maritime Antarctic, which promotes a fast rate of decomposition, is more typical for temperate--climate zones than for the much colder conditions found in continental Antarctica (Boyd, Rothenburg and Boyd 1970, Cameron 1972, Orchard and Corderoy 1983, Ramsay 1983).

In an in situ experiment it was found that under average climatic conditions during the austral summer at King George Island about 50% of the C and N had volatilized to the atmosphere from fresh guano during three weeks, as a result of mineralization processes (Pietr, Tatur and Myrcha 1983). Especially intense microbial processes occur during short periods of solar insolation which warm up the soil surface to the temperature above 10°C. At a temperature of about 16°C the rate of mineralization increased four times. The mineralization of N compounds in fresh faeces was observed as an effect of activity of enzymes (proteases) and microorganisms from the digestive tract of penguins (Pietr, Tatur and Myrcha 1983) and under the influence of proteolitic and ammonifying groups of bacteria developed in guano layer. The high numbers of saprophytic ($30\text{-}42 \times 10^6 \cdot g^{-1}$ dry wt), proteolytic ($0.7\text{-}0.8 \times 10^6 \cdot g^{-1}$ dry wt), spore-forming and the calcium phosphate dissolving groups of bacteria, as well as galatinase, asparaginase, uric acid hydrolase, acid and alkaline phosphatases activities, were characteristic for organic matter from the rookery. Consequently, there is a degradation in the fresh guano of the organic compounds most susceptible to decomposition, and this process is accompanied by the concentration of more resistant compounds, such as chitin, urates and the phosphate minerals (apatite and struvite). These minerals are formed from ions released from decomposing organic matter of guano enriched in marine aerosols. In partly decomposed and washed out guano the rate of mineralization decreased and total microbial activity abruply diminished. However, the activity of bacteria which decompose chitin, urates and apatite, as well as that of the bacteria responsible for the ammonium nitrifying process, increased (Pietr, Tatur and Myrcha 1983, Pietr 1986).

Guano disappeared fast from the soil surface in the rookery (Fig. 2). During heavy rainfall the solutions with guano suspension were displaced down-slope,

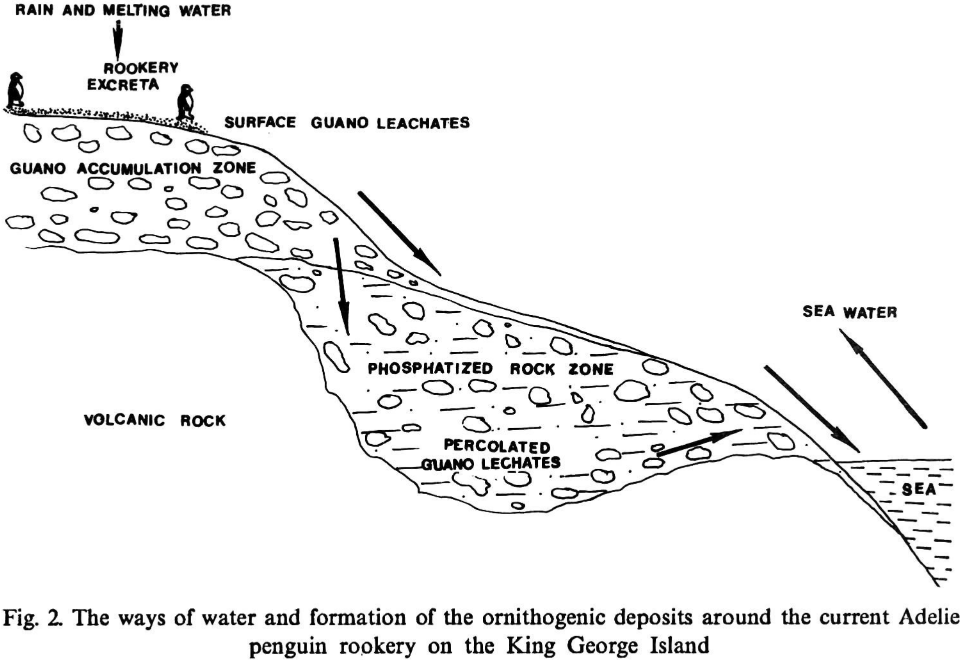

Fig. 2. The ways of water and formation of the ornithogenic deposits around the current Adelie penguin rookery on the King George Island

mainly onto the surface of the soil. During small rainfall or melting of the snow cover, most of the solution percolated through the soil. Such a situation is very typical for the Adelie penguin breeding places (Myrcha, Pietr and Tatur 1985).

Guano is washed partly into stony detritus of the rookery itself, and the remainder is smeared as a thin layer over the slopes around the nesting places of penguins. However, the guano leachates react with stony loams surrounding the rookeries (mainly andesites, basalts and their tuffs), forming a large zone of phosphatized rock. The phosphatized zone show a typical morphology for the soil and, consequently, was described by us as the "ornithogenic soils of the maritime Antarctic Zone" (Tatur and Myrcha 1984). The division of the soil profile into horizons is easily noticable in the field and results from different mineral compositions involving phosphates in various layers. The phosphates play a key role in the genesis of the soil. They are formed either as a product of the precipitation from ornithogenic waters, or as a result of metasomatic reactions on the border of aquatic and silicate phases. The vertical distribution of these phosphates in the profile must remain in a close relationship with the chemical composition of the soil solution. Thus, changes in the chemical composition of the guano leachates percolating through and reacting with the soil proved to be a main factor controlling the vertical distribution of the phosphates in the profiles of the ornithogenic soils (Fig. 3).

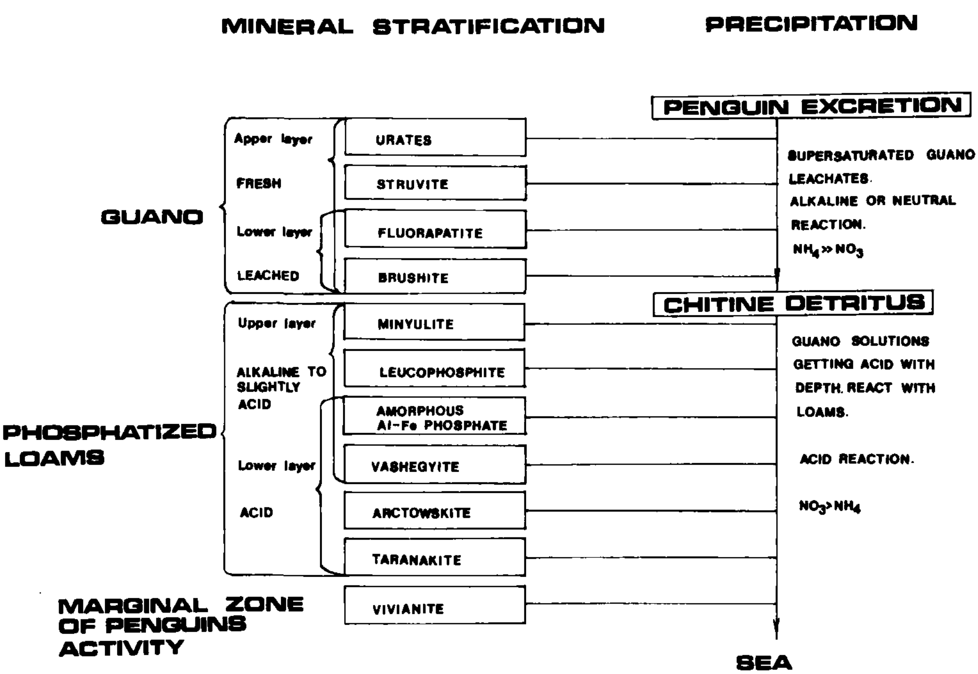

Fig. 3. The water relations and composition of the phosphate deposits in the ornithogenic soils of maritime Antarctic

The surface waters running off the penguins breeding area are alkaline or neutral and contain changeable, often very highly concentrated, mineral forms of P and N (Tatur and Myrcha 1983). Among mineral forms of N, the ammonium form strongly predominates over the nitrate one. After percolation through the soil, the chemical composition of these waters undergoes stabilization and the reaction becomes acid (pH 4 or somewhat higher), and now among mineral forms of N, the nitrates prevail over the ammonium ion. Increase of acidity during percolation is probably due mainly to volatilization to the atmosphere, binding into phosphates, and nitrification of the alkaline ammonium ions. The acid reaction is enhanced also by forming oxalic acid processes of organic matter mineralization. The final pH of the soil water results from the solubility equilibrium constant which is set during the reaction with phosphates occurring in the bottom of the ornithogenic soils.

The relationship between changes in chemical composition of guano leachates and the variability of mineral composition of the phosphates in the ornithogenic soils have been analyzed in detail (Tatur and Barczuk 1984, 1985, Tatur 1989, Tatur and Keck 1990) — see Appendix 1. Struvite is present exclusively on the surface of the soil. This mineral crystalizes from alkaline waters rich in ammonium ions and enriched with Mg. Fluoroapatite is common in the whole surface layer guano. It is the main mineral deriving there from the decomposing organic matter of penguin faeces. Leucophosphite occurs in the shallowest horizon of the phosphatized zone, often under a thin guano layer. This mineral is formed as the precipitate from neutral or slightly acid solutions still holding the ammonium ion. Commonly occurring in the examined ornithogenic soils are taranakite and minyulite. Occurrence of the minyulite is typical in the upper and middle part of the phosphatized rock zone, where iron was entirely leached from the soil by strong action of guano solutions, which simultaneously supplied also high quantities of fluorine. Taranakite is typical for the deepest and acid, always wet layer. It is formed as a precipitate from acid and most diluted solutions. Aluminium-iron phosphates, holding ammonia and potassium ions dissolve in rain and melting waters that are poor in alkali. At first incongruent dissolving lead to liberation of potassium ions and releasing of simple aluminium phosphate. Relatively most constant phosphate is amorphous aluminium phosphate, which, with elapse of time, can change ultimately into crystalline forms — arctowskite and vashegyite, founded in the relic ornithogenic soils (Tatur and Keck 1990).

In nonornithogenic soils surrounding penguin rookeries small amounts of vivianite are sometimes formed. It is probably the most durable form of phosphorus in soils of the maritime Antarctic.

Phosphate minerals in ornithogenic soils of maritime Antarctic form an unstable paragenesis. The observed state of minerals results from unbalanced equilibrium between reverse processes: formation of phosphates in the result of cyclically recurring organic fertilization and their dilution at the lack of manuring. Lack of manuring, gradual disappearance of a fresh guano from the soil surface and washing of the soils with rain and melting waters, all bring about acidification of the soil environment and diminishing of salt concentration in the soil solutions. These are main factors that enhance dissolution of soil phosphates. Occurrence of particular soil phosphates are thus controlled by processes of alternated washing of soils with waters of different origin and chemical composition: (1) rich in nutrient and other ions guano leachates that become acidified when percolate through the soil, (2) very poor in salts of melting or rain origin.

Together with phosphorus in ornithogenic soils there are also accumulated partially: ammonia ions, potassium, calcium, magnesium, strontium and fluorine. Fluorine form even characteristic minerals — fluoroapatite and minyulite (Tatur 1987). Simple, nonidentified organic compounds connected probably with phosphates are also present.

All these processes are leading to the formation of phosphatic ornithogenic soils (Tatur and Myrcha 1984, Myrcha, Pietr and Tatur 1985). Differential mineral composition of genetic horizons of these soils reflects physico-chemical conditions during their development and transformations (Tatur and Barczuk 1984, 1985, Tatur 1989).

The above papers are the first to describe in detail ornithogenic soils in the maritime Antarctic. But the study was carried out on a small area, so the conclusion could not be generalized for the whole region. The purpose of further studies, carried out in 1984—1986 during IX Antarctic Expedition of the Polish Academy of Sciences, was to characterize the diversity and specific features of ornithogenic soils developed in different places, on different parent materials, throughout the maritime Antarctic, including the Antarctic Peninsula, where climatic conditions are different. These studies confirmed results acquired earlier in the region of Admiralty Bay (Tatur 1989).

Accumulation of phosphorus in ornithogenic soils was observed by us on many islands of maritime Antarctic up to the Antarctic Circle as well as on the west coasts of the Antarctic Peninsula and on its northern end. Phosphatic soils of ornithogenic origin occurring in whole maritime Antarctic are comparable rather to those in humid temperate zone. However, in maritime Antarctic such phosphate mineralization is more common and intense due to huge number of penguins, it maintains many specific traits (eg. presence of phosphates with fluorine, most often lack the humus of plant origin in the soil).

Abandoned penguin rookeries and the relic ornithogenic soils

Study sites

These studies revealed an interesting phenomenon of the occurrence of ornithogenic soils in the areas of old, abandoned penguin rookeries in different places of the West Antarctic (Tatur and Myrcha 1989). They have so far been unnoticed since typically they are hidden under plant cover, and their common yellow-brown colour camouflages enormous concentrations of phosphates.

The old ornithogenic soils which we propose to call relic ornithogenic soils, were found in seven different places on the southern coast of the King George Island from Burton Peninsula to Lions Rump (Fig. 1). Penguins could abandon these places for different reasons. One of them is the movement of breeding colonies to lower situated areas, emerging from sea water as a result of isostatic uplift. A good example of this movement can be the areas situated above the current rookeries at Point Thomas and Stranger Point. Another reason for abandoning breeding sites by penguins can be drastic changes in the morphology of the coast line or moraine systems, blocking the passage to the nesting places. Such a situation could have place on King George Island, in the case of abandoned rookeries at Low Head and Blue Dyke.

This is an evidence to suggest that relic ornithogenic soils on the sites known so far were developed not earlier than in the Holocene (Tatur 1989). The oldest of the sites examined, the age of which is relatively well documented, is located around the small, covered with mosses, Green Valley at Penguin Ridge, above the currently active Point Thomas rookery (Tatur and del Valle 1986, Tatur and Myrcha 1989). Using the data on the age of the peat covering ornithogenic sediments, as estimated by the C^{14} method (Birkenmajer 1981a), and on the rate of isostatic uplift of King George Island in the Holocene (Birkenmajer 1981b), it can be suggested that Chinstrap and Adelie penguins (bone remains preserved) nested there 5—8 thousands years ago. Nowadays this area is covered with dense, diverse plant communities comprising mosses, lichens, liverworts and vascular plants.

The main investigation was carried out in the area of an abandoned penguin rookery, occupied several hundred or even several thousand years ago, on Low Head oasis. Based on the analysis of bone remains (especially numerous humeri and tarsometatarsi), it can be concluded that the rookery consisted mostly of Chinstrap penguins, with a rather small admixture of Macaroni penguins (*Eudyptes chrysolophus*). This material is dominated by bones of young individuals (Bocheński 1985, Tatur and Myrcha 1989).

A much younger abandoned rookery is located at Stranger Point. Based on the rate of isostatic uplift of King George Island in the younger Holocene (Birkenmajer 1981b) and on the growth rate of the lichens *Usnea* sp. in Antarctic (Hooker 1980), it may be expected that Adelie penguins nesting there over the last millenary abandoned the steep coastal cliff and moved into newly emerged beaches, and then kept moving towards the sea as the island moved up and new beaches were formed (Fig. 4). This process has been continued up to now (Tatur and Myrcha 1989). In this way, on raised sea teraces and on the coastal cliff, a sequence of identical nesting sites was developed in the form of convex lenses, which were abandoned at different time by individual groups of breeding penguins. This creates a particularly suitable situation for analysing successive stages of the succession of plant communities (Myrcha 1989).

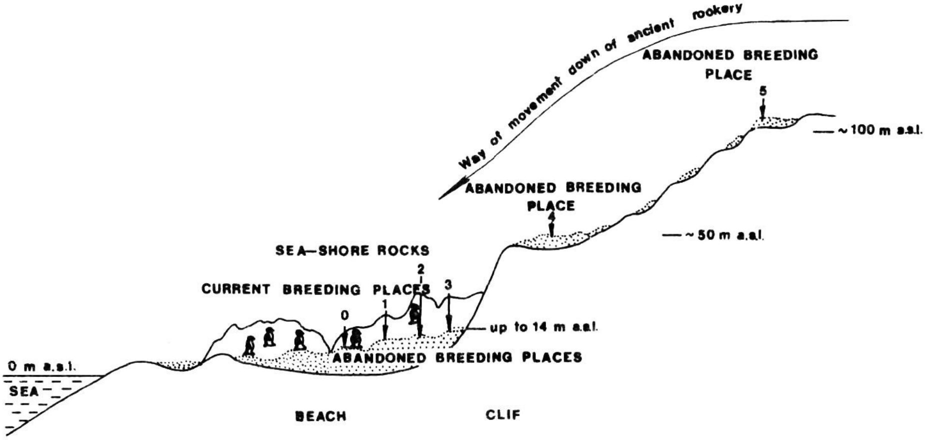

Fig. 4. Current and abandoned breeding places in Stranger Point pygoscelid penguins rookery (King George Island) 0—5 — sampling places

Relic ornithogenic soils in maritime Antarctic

Characteristics of the relic ornithogenic soils and level of their development in maritime Antarctic are strongly different in comparison with the soils from abandoned penguin rookeries founded at few places in the region of the Ross Sea (Campbell and Claridge 1966, Spellerberg 1970, Speir and Cowling 1984).

As shown earlier, ornithogenic soils on and around the current penguin rookery in maritime Antarctic are formed as a result of guano mineralization processes and phosphatization of the underlying rock due to the action of aggressive guano solutions (Tatur and Myrcha 1983, 1984, Myrcha, Pietr and Tatur 1985, Tatur 1987). Soils of the penguin rookeries abandoned several hundreds or even several thousands years ago preserve their chemical and mineralogical properties (Tatur 1989, Myrcha and Tatur 1990). With the time, however, they are being transformed as a result of chemical and mechanical weathering, gravitational movements, frost action, and growth of a plant cover.

In the area abandoned by penguins, that is in relic ornithogenic soils, the surface layer of guano is heavily reduced as a result of chemical and mechanical erosion, and under the plant cover a horizon of humus accumulation of plant origin is gradually developing. Due to phosphate weathering, minyulite disappears from the relic phosphatized zone. Also the occurrence of leucophosphite becomes less common. The most frequent minerals are taranakite and either amorphous or crystalline aluminium phosphates.

The chemical analysis of water soluble elements in ornithogenic soils of the abandoned Low Head rookery leads to the conclusion that as a result of

gradual washing of phosphates, soil solutions are permanently enriched not only with phosphate ions but also with ions of many other elements (Tab. 1). Clearly more soluble are phosphates present in the remains of guano, still preserved at several points in small amounts, than phosphates from the loam containing Al-Fe phosphates.
The analyses of the water extracts of soil provide evidence that phosphate ornithogenic soils are a rich source of nutrients for plants growing on them. It should be noted, however, that the main source of nutrients in the area of current colonies are alkaline guano solutions containing phosphates of calcium, magnesium and ammonium, and also sea salt. In the areas abandoned by penguins, the source of nutrients are less water soluble aluminium-iron phosphates containing K and NH_4 ions. Only in some places of these areas solutions containing nutrients released from relic guano can appear, which are rich in calcium phosphates.

Relic ornithogenic soils and vegetation

Chemical analysis of green parts of grass, *Deschampsia antarctica,* was conducted in order to investigate direct influence of relic ornithogenic soils upon plant nutrition. Analyses concerned *D. antarctica* growing in three geomorphologically similar, but differing in abundance, places: vicinity of current Point Thomas rookery, area of the abandoned Low Head rookery, and Italian Valley (Admiralty Bay) where penguins never bred, as control (Tatur and Myrcha 1989).

The results of chemical analyses of *D. antarctica* from different places show that on both the current and the relic ornithogenic soils this grass is generally richer in K, Na, P and Ca than the plants from the control area. It may be suggested that this is an effect of the past and current manuring by birds. However, the contents of N, Sr, Zn and Cu are clearly higher only in the samples taken from current soils. Grasses growing on relic ornithogenic soils and on control area have a similar content of these elements. This implies that the effect of ancient manuring on their present availability to *D. antarctica* is disappearing (Tab. 2).

The contents of Mg, Mn, and Fe was the highest in samples of the grass from relic ornithogenic soils. Probably, this was an effect of the lower pH of soil solutions since this factor can largely influence the release of these nutrients. Thus, the samples of the grass from the control site were poorest in most of the elements analyzed.

The chemical degradation of the relic ornithogenic soils may supply nutrients for plants during many thousands of years. Those are very important processes for a poor Antarctic terrestrial environment. Vegetation, however, cannot use all phosphate deposits and sometimes a considerable part of

Table 1

Water soluble elements in the relic ornithogenic soils from Low Head, King George Island (fraction < 1 mm)

	Samples		pH		Total P	Water soluble elements (ppm)						
			4°C after 24 h	24°C after next 24 h	%	P	N/NH_4	N/NO_3	Ca	Mg	K	Na
surface soils	With Ca phosphates		5.2	—	1.5	100	6.0	151	65	25	62	535
	With Al-Fe phosphates		5.0	—	3.0	68	2.2	16	3	4	34	180
soil profiles	No. 27											
	Central part, stones and boulders, *Usnea* sp., nitrophilous lichens,	0–1 cm	6.0	6.6	0.82	61	1.4	119	3	11	32	580
	Prasiola crispa	0–50 cm	4.8	4.7	4.11	58	1.0	9	3	4	14	100
	No. 28											
	Flat hummock	0–2 cm	4.6	4.0	2.63	41	3.9	30	3	6	54	120
	with pebbles,	2–5 cm	4.5	4.3	9.67	40	5.4	21	3	6	47	100
	Usnea sp.	5–50 cm	4.2	4.0	5.67	90	7.0	2	3	4	48	80
	No. 29	0–20 cm	4.9	4.8	2.75	39	0.5	19	3	4	7	60
	Slope of the hill, dominance	20–40 cm	5.6	5.3	3.72	162	2.1	49	99	22	71	160
	Usnea sp.	40–50 cm	6.4	6.1	4.07	57	25.8	34	65	19	82	180

Table 2

Chemical composition of *Deschampsia antarctica* growing on different places of the King George Island (mean values and standard deviations)

Sampling places	Elements										
	N %	P %	K %	Na %	Ca %	Mg %	Sr ppm	Mn ppm	Fe ppm	Zn ppm	Cu ppm
Breeding site, Pt. Thomas rookery, n=5	3.57±0.58	0.59±0.083	2.06±0.30	0.20±0.032	0.37±0.205	0.18±0.042	38.6±20.3	58.4±19.9	196±20	67.4±18.5	12.2±2.3
Abandoned rookery, Low Head, n=5	2.51±0.74	0.36±0.051	1.60±0.16	0.14±0.014	0.16±0.036	0.18±0.055	17.4±3.6	51.0±13.8	596±322	25.4±13.7	9.2±3.3
Control site, Italia Valley, Admiralty Bay, n=7	2.53±0.37	0.48±0.064	2.08±0.32	0.20±0.059	0.22±0.061	0.24±0.031	12.0±2.3	101.7±52.1	610±378	31.3±11.3	99.1±1.8

nutrients released from soils and carried by waters, gets directly into the ocean. During field studies on abandoned Low Head rookery it was observed that phosphorus returns not only in form of orthophosphates soluble in water but also in the form of tender phosphate suspension washed out from old ornithogenic soils. This suspension is composed also of alluminium phosphates holding potassium and ammonium ions, which further incongruent dissolving and thorough one occurs already in the sea water.

Colonization of plants on abandoned Stranger Point rookery

The areas of active breeding colonies of penguins have no plant cover almost at all. Even if the vegetation had been growing there earlier, it was destroyed as a result of permanent trampling by penguins and excess of manuring. The areas receiving high dozes of organic fertilizers are only temporarily covered with thick patches of a coprophilous algae *Prasiola crispa.* Only communities of nitrophilous lichens are abundant on the rocks around penguin colonies. Isolated clumps of higher plants can also occur only on the margins of the rookery, not yet destroyed by birds. The productivity of the areas of active breeding colonies is typically limited to the high microbiological activity.

On Stranger Point, like in another places of the maritime Antarctic, *P. crispa* is a pioneer species growing on newly abandoned, stony nesting sites (Myrcha and Tatur, unpubl. data). Shortly afterwards first crustose lichens appear on stones emerging from the guano washed with water. In places still covered with guano, mosses start growing a little later. As guano is further washed, the top parts of the abandoned breeding hummocks are occupied by fruticose lichens, mostly *Usnea* sp. In places from which guano is deeply washed out, these lichens show a luxuriant growth and become dominant organisms. In places where the surface soil layer is still covered with guano, mosses are increasingly abundant among stones, in addition to *Usnea* sp. At the same time, crustose lichens, first covering almost the whole surface of stones, slowly dissapear almost completely.

In depressions, around and between old breeding hummocks, mosses were present from the very beginning of the plant colonization. Finally they formed a dense carpet, typically with a diverse species composition. Habitat conditions for their growth were suitable in these places not only because they were rich in nutrients but also due to the presence of phosphate clay in the underlaying rock. The presence of this clay accounts for a high soil moisture and acid reaction, in contrast to the alkaline reaction of the guano. The last plants appearing on drier sites in places abandoned by penguins are vascular plants, mostly patches of the grass *D. antarctica,* usually accompanied by the moss *Polytrichum alpinum* and sometimes also by *Colobanthus quitensis.*

In this way, a simple phytocoenosis of the poor ecosystem of Antarctic tundra develops over a long time.

To sum up, it can be stated that the activity of penguins, leading at first to the devastation of plant cover, than accounts for the development of the new types of soils which are more suitable for plant growth. These are much richer in clay and very rich in nutrients, and also highly differentiated. Thus, penguin rookeries are the factor increasing trophic diversity of the habitat for plant communities of the maritime Antarctic, and also differentiating their productivity and their species diversity.

Although the diversifying effect of seasonal aggregations of birds and seals on trophic conditions of Antarctic soils is emphasized in the geobotanical and pedological literature (e.g. Smith 1985, Walton 1985), the role of relic ornithogenic soils in this zone has been unknown so far. Since these soils extend over large areas in many West Antarctic oases it may be suggested that they play an important role in the development of plant communities in this part of the Antarctic region.

Fate of sea-birds excrements in various climatic zones

The biogeochemical cycle of ornithogenic matter plays different role in marine and terrestrial ecosystems in various climatic zones (Hutchison 1950). In tropical and subtropical arid zone the bird excrements are accumulated and form the thick guano deposits. In the most arid places the easy soluble nitrates and ammonia salts can be found in guano. In more moistured zones such accumulation is lower, simple nitrogen salts are being washed out and mainly phosphates remain in guano, with calcium phosphate as main mineral. In the wet tropical zone these phosphates became dissolved in precipitation waters and chemically aggressive solutions react with underlaying rocks, forming around the colonies zones of phosphatized rocks. On carbonates and marls (often on coral atols) calcium phosphates are a main component of ornithogenic soils. However, typical for this zone final products of phosphatization process of silicate rocks are simple alluminium-iron phosphates, whereas in similar deposits in wet temperate zone the hydrated alluminium phosphates and alluminium-iron phosphates containing ions of potassium and ammonia are characteristic. Biological effects of activity of birds in tropical and temperate zones are relatively inconspicuous against proliferously developing nature in the surrounding areas. Thus, in these zones the ecological consequences of the activity of birds have a clearly local significance only.

Reverse pattern of ornithogenic matter cycling and its ecological consequences are observed in polar zones where the activity of birds became more conspicuous. Due to climatic and ecological differentiation, a very strong dissimilarities are observed between Arctic, coastal zone of Antarctic continent and maritime Antarctic.

In Arctic region, due to probably lower activity of microorganisms and proliferous development of flourishing carpets of tundra vegetation around the bird colonies, the content of phosphorus in waters running off from the breeding places is not enough high to cause the phosphatization of the rocks (Myrcha and Tatur, unpubl. data from Spitsbergen). Nutrients washed out from the excrements are partially assimilated by vegetation, but a considerable part of nutrients being not bound by plants gets into sea, and in the coastal waters near the bird colonies their concentration increase conspicuously enhancing in consequence higher production of phytoplankton (Golovkin and Pozdnjakova 1964, 1965, Golovkin, Širokolobov and Garkovaja 1972, Golovkin and Gurevič 1973, Golovkin and Garkovaja 1975, Bedard, Theriault and Berube 1980). In this way, the bird activity forms the littoral zones of high productivity, situated near the shores with bird colonies. This phenomenon is visible because the waters of Arctic Ocean are generally not so rich in nutrients as those of the Southern Ocean.

In oases situated on the coast of Antarctic Continent the low temperature and air humidity bring about that the penguin guano did not undergo mineralization and the row rank guano is forming (Tedrov and Ugolini 1966, Boyd, Rothenburg and Boyd 1970, Spellerberg 1970, Cameron 1972, Ugolini 1972, Orchard and Corderoy 1983, Ramsay 1983, Speir and Cowling 1984). The lack of water makes washing out the soluble components from this matter not possible. That is why no chemical changes are noted in the weathered cover of rock lying beneath guano. In the areas of present and former Holocene colonies there are layers of row rank guano (ornithogenic soils of Continental Antarctic) differring sharply from the substratum and gradually dispersed by wind.

This ornithogenic matter is very important source of organic matter and nutrients for terrestrial ecosystems, when releasing of nutrients from the parent material as the result of soil forming processes (besides ornithogenic) is extremely slowed down in the climatic conditions of Antarctic Continent. On the contrary to terrestrial ecosystems, the effect of the dispersed by wind, humified guano on the maritime ecosystem has most probably small significance, since ocean waters around the Antarctic Continent are generally rich in nutrients due to the upwellings.

Quite different is the fate of penguin guano in the region of maritime Antarctic, where positive values of temperature and high air humidity are often recorded. The soils are washed out by melting and rain waters in summer. Up to recent time there was an opinion that penguin guano left on the land was very fastly washed out into the sea again without any changes. Our investigations carried out for several years have complicated this simple scheme.

The existing favourable humidity and thermic conditions enable relatively fast microbiological decomposition and mineralization of penguin excrements. As a result of these processes and the reaction of guano leachates with underlaying rocks (mainly andesites, basalts or their tuffs) characteristic phosphatic ornithogenic soils developed. These soils are very important source of nutrients for Antarctic plant communities. The fertilizing significance of these soils does not end with penguins abandoning the rookeries. In many areas where rookeries occurred earlier well developed relic ornithogenic soils still do exist. The chemical degradation of the relic ornithogenic soils supplies nutrients for plants during hundreds or even thousands years. These processes are very important for the functioning of the poor Antarctic terrestrial environments.

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Streszczenie

W pracy podsumowano rezultaty dziesięcioletnich badań nad rolą kolonii lęgowych pingwinów w powstawaniu gleb ornitogennych i funkcjonowaniu ubogich środowisk lądowych w strefie Antarktyki morskiej. Ptaki morskie, głównie pingwiny, rozradzające się w wolnych od lodu przybrzeżnych oazach, wynoszą na ląd w czasie sezonu lęgowego olbrzymie ilości (do 10 kg suchej masy/m^2) materii organicznej w postaci fekalii. Panujące w tej strefie w okresie letnim warunki atmosferyczne sprzyjają szybkiej, lecz przebiegającej etapami, dekompozycji i mineralizacji odchodów. Podstawowe badania, obejmujące analizę procesów mikrobiologicznych, hydrochemicznych i geochemicznych, przeprowadzono na wyspie King George (Fig. 1), a następnie obserwacje te rozszerzono na rejon Półwyspu Antarktycznego i przyległych wysp.

W odróżnieniu od wcześniejszych przypuszczeń o szybkim zmywaniu guana z obszaru kolonii lęgowych do morza stwierdzono, że w wyniku przemywania tej warstwy przez wody pochodzące z opadów deszczu i topniejącego śniegu, powstają agresywne chemicznie roztwory, które w znacznej części przesączają się przez podłoże (Fig. 2). Roztwory te reagują z podległymi skałami, co prowadzi do powstania wokół kolonii szerokich stref fosfatyzacji. W wyniku tych procesów powstaje szereg związków fosforanowych, których skład chemiczny, właściwości i rozmieszczenie zależą od zmieniających się warunków fizycznych i chemicznych (Fig. 3). Opisane w wyniku tych badań fosforany grają kluczową rolę w genezie gleb ornitogennych Antarktyki morskiej, porównywalnych raczej z analogicznymi glebami wilgotnej strefy umiarkowanej, niż wcześniej opisywanymi z obszaru Antarktyki kontynentalnej.

W rezultacie dalszych badań opisano ciekawe zjawisko występowania, w różnych miejscach Antarktyki Zachodniej, gleb ornitogennych na obszarach dawnych, obecnie z różnych przyczyn opuszczonych przez ptaki kolonii lęgowych. Nie zostały one wcześniej zauważone, ponieważ ukryte są zwykle pod bujną pokrywą roślinną, a ich typowa żółto-brązowa barwa maskuje dużą koncentrację fosforanów. Przeprowadzono analizę przyczyn i próbę oceny czasu opuszczenia tych

miejsc przez pingwiny. Szczegółowe badania wykazały, że te reliktowe gleby ornitogenne, pomimo przerwania ciągłego dopływu materii organicznej przed setkami, a nawet tysiącami lat w dalszym ciągu zachowują swoje podstawowe właściwości chemiczne i mineralogiczne. Opisano przemiany zachodzące w tych glebach pod wpływem zmieniających się środowiskowych czynników abiotycznych i biotycznych.

Chemiczna analiza roztworów wodnych tych gleb wskazuje, że w wyniku stopniowego wymywania fosforanów są one w dalszym ciągu źródłem, stale wzbogacającym ubogie środowiska lądowe w szereg nutrientów (Tabela 1), przyswajanych przez porastające je zbiorowiska roślinne (Tabela 2). Badając opuszczane stopniowo przez pingwiny miejsca lęgowe w kolonii Stranger Point, King George Island (Fig. 4), przeprowadzono wstępną analizę etapów kolonizacji tych miejsc przez rośliny.

Na zakończenie pracy porównano losy materii organicznej zawartej w odchodach ptaków morskich, gniazdujących na obszarach przybrzeżnych w różnych strefach klimatycznych.

Appendix 1.

Urates and phosphates from ornithogenic soils of the maritime Antarctic

Urates	$(NH_4 >> K, Na)_{0.8}(Mg, Ca, Fe)_{0.1}C_5H_3O_3N_4$ Evaporation of liquid excretion. Occur only on the surface of the current rookeries, often in pure agglomerations.
Struvite	$Mg (NH_4) PO_4 \times 6 H_2O$ Needs excess of ammonia and magnesium ions in guano leachates. Occur in surface guano layer of the current penguin rookeries. Form crusts on the stones.
Fluorapatite	$Ca_5(PO_4)_3F$ Precipitate directly from solutions leaching mineralized krill remains in guano layer. Alkaline or neutral reaction, abundance of F. Occur in surface crusts on stones. Common in the relic ornithogenic soils.
Brushite	$CaHPO_4 \times 2 H_2O$ (?) Precipitation from solutions leaching mineralized fish remains in guano layer. Slightly acid reaction, poverty of F. Found only around cormorant nests.
Leucophosphite	$(NH_4 > K)_2(Fe > Al)_4(PO_4)_4(OH > F)_2 \times 4 H_2O$ Excess of alkali. Iron present in variable redox conditions. Upper part of the phosphatized zone. Occur also in the relic ornithogenic soils.
Minyulite	$K Al_2(F >> OH)(PO_4)_2 \times 4 H_2O$ Excess of alkali. Abundance of F. Iron totally leached. Upper part of the phosphatized zone. Never found in the relic ornithogenic soils.
Taranakite	$(K, NH_4)_3Al_5H_6(PO_4)_8 \times 18 H_2O$ Excess of alkali. Permanent moist reducing conditions. Lower part of the phosphatized zone. Common also in the relic ornithogenic soils.
Amorphous aluminium phosphates	
Crusts on the stones surface	$Al_{10}F_9(PO_4)_7 \times n H_2O$
grains in the soil	$Al_{10}(F > OH)_3(PO_4)_9 \times 43 H_2O$ Alkali poverty and/or incongruently dissolving of alkali bearing Al-Fe phosphates. Common in the whole phosphatized zone of the current and relic ornithogenic soils.

Crystalline aluminium phosphates	
Arctowskite	$(Al_{8.4}Fe_{0.6})_9$ $(OH)_3(PO_4)_8$ × 27 H_2O Alkali poverty. Formed while aging, may be as the result of taranakite recrystallization. Occur only in the relic ornithogenic soils.
Veshegyite	$(Al_{0.9}Fe_{0.1})$ PO_4 × 3.15 H_2O Alkali poverty. Slowly phosphatization of silicate clay minerals. Found only in the relic ornithogenic soils.
Vivianite	$Fe^{II}_3(PO_4)_3$ × 8 H_2O Diluated ornithogenic solutions react with silicate clay under peat bank. One case.