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Protection of eggs and chicks against flooding as a part of nesting strategy of pygoscelid penguins at King George Island, South Shetlands

ABSTRACT: In colonies situated at the southern coast of King George Island the nesting areas of penguins of the genus *Pygoscelis* were investigated with respect to the protection of eggs and chicks against flooding. Relationships between the nesting strategy determined by the characteristics of breeding grounds, degree of colonization and breeding time, and the climatic conditions of zones in which majorities of particular species populations breed were presented. It was recorded, that interspecific differences in nesting strategy of pygoscelid penguins enable species which breed sympatrically to avoid competition for the nest-sites, and also seem to be responsible for various population dynamics of species in the maritime Antarctic.

Key words: Antarctic, pygoscelid penguins, nesting strategy.

Introduction

"A central problem in microclimatic terms for all Antarctic birds is how to keep the incubating eggs warm in a cold climate" (Walton 1984). This problem becomes still more pronounced in case of the eggs or chicks being flooded with water, because in water it is particularly difficult for an organism to retain its body temperature different from that of the surroundings (Collier et al. 1978).

In case of Antarctic penguin species, the choice of drained terrains and the protective function of the nests themselves are the only known forms of protecting the eggs and chicks against flooding (Carrick and Ingham 1967, Tenaza 1971, Yeates 1975, Walton 1984).

A majority of populations of penguin species of the genus *Pygoscelis* nests in different climatic zones (Watson et al. 1971). It might thus be expected that variability in environmental conditions of these zones is reflected in varying nesting strategy of particular species.

The aim of this paper is to answer the question: in what way and with what efficiency given penguin species of the genus *Pygoscelis* protect their eggs and chicks against flooding in the conditions of the maritime Antarctic?

Study area and methods

Measurements and observations were conducted in fourteen breeding colonies of penguins of the investigated genus which were situated at the southern shores of King George Island in the period from December 1979 to January 1981 (Fig. 1). The main study object was the Thomas Pt. colony, situated deep inside the Admiralty Bay (Fig. 2).

In fourteen colonies the following characteristics of breeding areas were determined:

1) Azimuths of lines of the slopes of breeding areas located on the slopes. Measurements were made using a compass to the nearest 2°.
2) Coverage of the terrain (so called horizon altitude). A theodolite was used to measure round the horizon at five degree angular distances the vertical angle between the horizontal level and the top edge of hillocks surrounding the measurement site. Then figures in the scale: vertical axis 1 mm = 0.5° of vertical angle, horizontal axis 1 mm = 2,5° of horizontal angle, were drawn. The surface area of the figure between broken line joining values of the vertical angles and the horizontal axis was considered the measure of the terrain coverage. The terrain coverage, expressed in square mm was calculated for the whole horizon (0°—360°) and in the northern quarter (315°—045°).
3) Observations of microrelief concerned the drainage of the terrain and its accessibility for given species, as well as the possibility of forming breeding groups of a degree of coloniality typical for the species.

In the areas of the colonies situated in the region of the Admiralty Bay the characteristics of the snow cover was observed in the winter of 1980. Due to a low variability of this factor only a single series of measurements of snow cover thickness was carried out in the Thomas Pt. colony, on 20 August 1980.

In the Thomas Pt. colony the values of the surface albedo of various breeding groups of each of the species were recorded. The measurements were made twice; in the "normal" conditions at the turn of January and February 1980, and on 12 November 1980, 24 hours after the end of

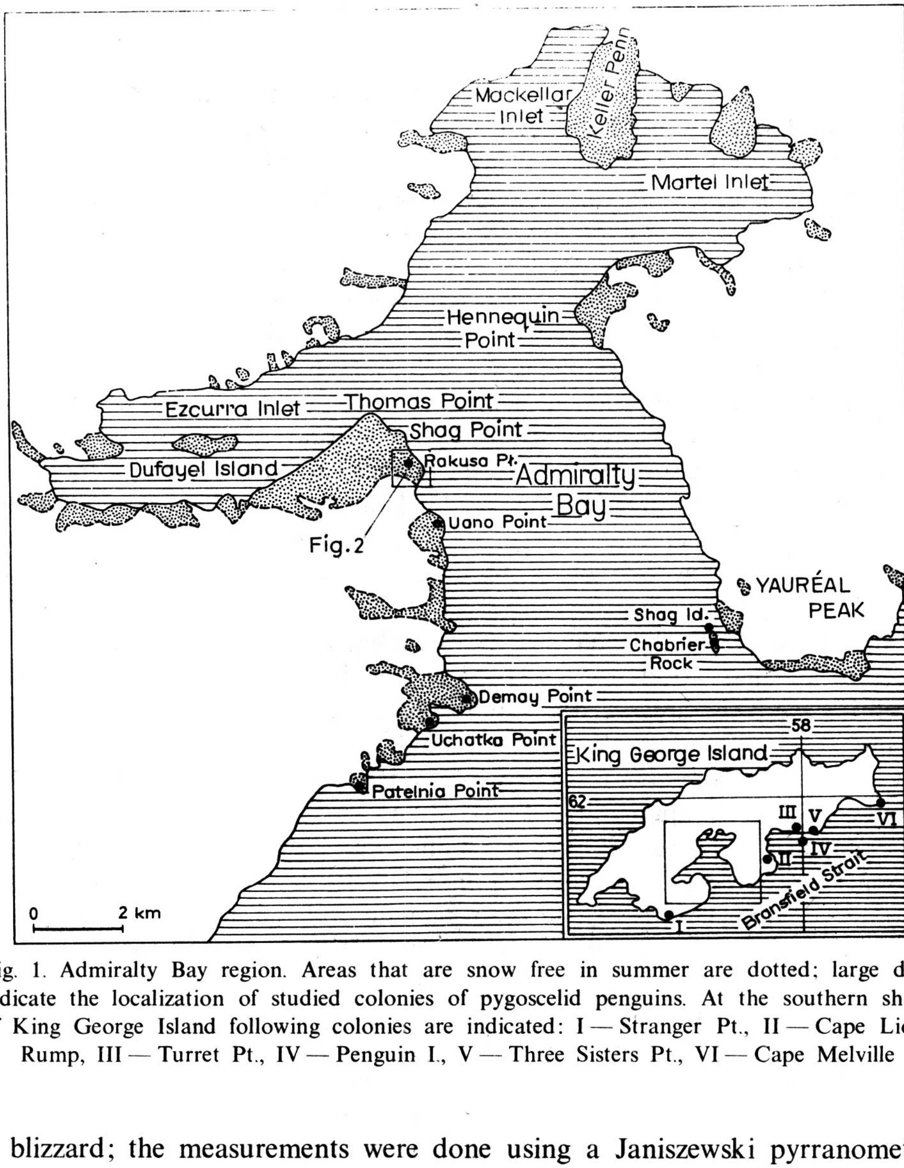


Fig. 1. Admiralty Bay region. Areas that are snow free in summer are dotted; large dots indicate the localization of studied colonies of pygoscelid penguins. At the southern shore of King George Island following colonies are indicated: I — Stranger Pt., II — Cape Lions Rump, III — Turret Pt., IV — Penguin I., V — Three Sisters Pt., VI — Cape Melville

a blizzard; the measurements were done using a Janiszewski pyrranometer type M80-M.

The statistical significance of differences between the mean values was determined with the t-Student test.

The terms "breeding colony" and "breeding group" were used in the present work in congruence with their meanings defined by Oelke (1975).

The zone of the Antarctic coast in the case of *Pygoscelis adeliae*, the maritime Antarctic for the *P. antarctica*, and subantarctic islands for the *P. papua* were considered as their main breeding ranges (Watson et al. 1971, Croxall and Prince 1980, Croxall 1984).

Results

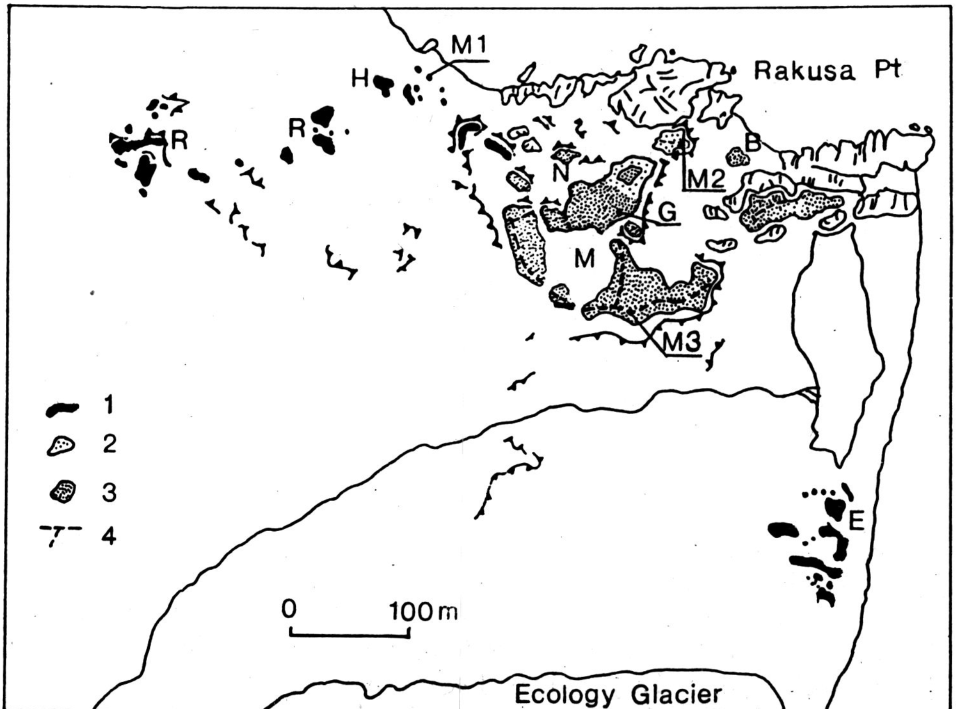
The common feature of nest-sites of the investigated penguin species was a good water run-off. In all the fourteen investigated colonies (Fig. 1) the nesting areas were located in well drained slopes, ridges of storm bars and moraines, cliff shelves and solitary rocks. Most of these terrains were cut by lines of watersheds (Fig. 2). The gentoo penguins bred sometimes in solitary nests located on flat terrain. These were dry places, in which no running water was observed. Some borders of the Adelie and gentoo penguins breeding groups were flooded by thaw water, e.g. around Point G (Gutter), in the Thomas Pt. colony (Fig. 2).

It was determined that in winter of 1980 in seven colonies situated in the region of the Admiralty Bay there occurred a low snow cover in comparison with surrounding areas. In the Thomas Pt. colony the mean thickenss of cover in areas M1, M2, M3, Holm and Ecology on 20 August, 1980 was twice lower than that in the Gutter region and five times lower than in the Meadow and other non-colonized regions close to the colony (Fig. 2, Tab. 1).

In almost all of the colonies the breeding areas of chinstrap penguins were rocky and covered with pebbles, boulders and stones. The only exception were the areas of the NE Penguin I. and Cape Mellville colonies, which were similar to the main nesting areas of the Adelie penguins. They differed from the nest-sites of adelie penguins by steep slopes, narrow and stony apporaches. Most of the investigated chinstrap colonies were situated on steep slopes and cliffs. Parts of the Uchatka Pt. and Patelnia Pt. colonies were located on relatively flat erroded rocky plates. Certain breeding groups of chinstrap penguins on the Thomas Pt. and SW Penguin. I. colonies occupied the edges of cliffs, the eroded tops of which were inhabited by the Adelie penguins (Fig. 2).

Most of the Adelie penguins on the King George Island nested in multithousand groups situated on the tops and mild slopes of hills of relatively plain surface (e.g. M3, Fig. 2). This refers to the Thomas Pt., Llano Pt., Cape Lions Rump and Stranger Pt. colonies (Fig. 1). In the Thomas Pt., Llano Pt. and particularly Stranger Pt. and Three Sisters colonies, they nested also on storm bars on which they formed approximately circular groups of nesting birds including from several dozens to several hundred pairs each.

Fig. 2. Location plan and view of the Thomas Pt. colony of pygoscelid penguins. 1 — breeding groups of *Pygoscelis papua* (H — Holm, E — Ecology, M1, R — Rock), 2 — breeding group of *P. antarctica* (M2), 3 — breeding groups of *P. adeliae* (N — North, B — Beach, G — Gutter, M3), M — non-colonized area — Meadow, 4 — watersheds. Location plan according to Furmańczyk (unpubl.), phot. E. Moczydłowski


M1
H
Rakusa Pt
R
R
B
N
M2
G
M
M3
1
2
3
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Ecology Glacier

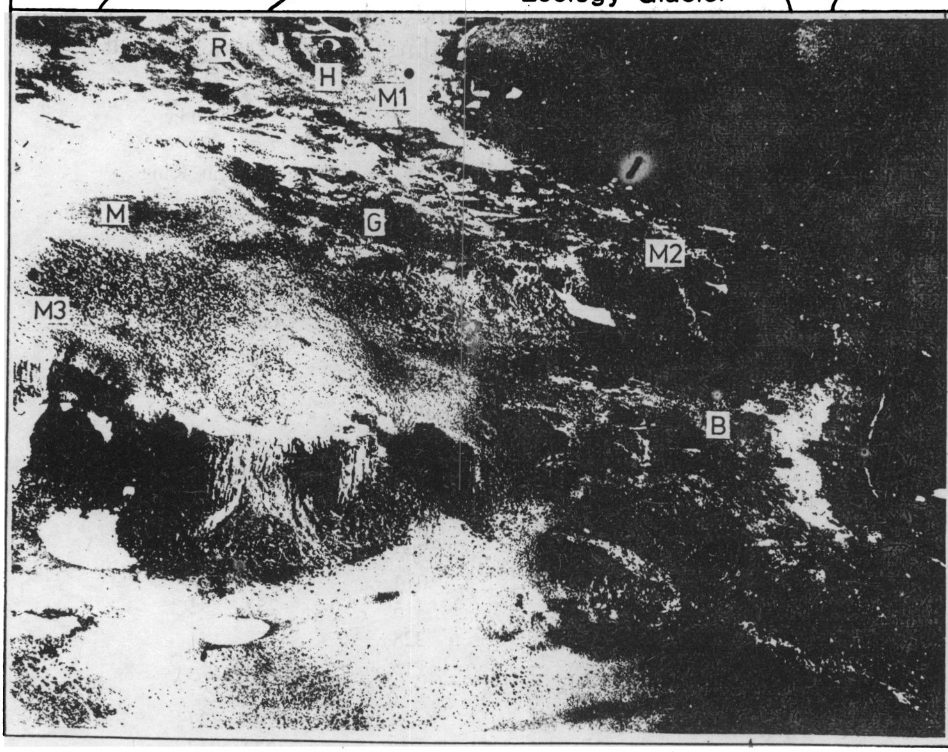
R
H
M1
M
G
M2
M3
B

Table 1

Mean thickness of snow cover at Thomas Pt. on 20 Aug. 1980

Area		Thickness of snow cover (cm) n = 50	
M3	summer nest-site of Adelie	11.8	(0–38)
M2	summer nest-site of chinstrap	11.3	(0–35)
M1	summer nest-site of gentoo, "Storm Ridge"	19.6	(8–30)
H	summer nest-site of gentoo, "Holm"	11.7	(2–25)
E	summer nest-site of gentoo, "Ecology"	9.4	(0–32)
G	edge of Adelie summer nest-site	25.3	(7–48)
M	noncolonized between Adelie summer nest-sites, "Meadow"	63.1	(28–130)
	in vicinity of summer gentoo nest-sites	74.4	(39–130)
	in vicinity of Adelie and chinstrap nest-sites	85.7	(42–220)
	meteorological station	70.0	

The gentoo penguins in four colonies on the King George Island nested mostly on storm bars and ridges of moraines. In the Thomas Pt. colony they also nested on clumps of peat and solitary rocks (Holm and Rock, respectively; Fig. 2), and in the Cape Lions Rump colony on a mildly sloping rocky ridge. They usually formed breeding groups of several to several dozens pairs. On storm bars and ridges of moraines the gentoo penguins nested sometimes in one, sometimes in two rows of nests.

Table 2

Azimuths of the slopes in colonies of pygoscelid penguins at King George Island

Colony	Chinstrap (deg)	Adelie (deg)
Thomas Pt.	290	340–012
Llano Pt.	112–030	342–357
Shag I.	320–020	
Chabrier Rock	320–050	
Demay Pt.	217	
Uchatka Pt.	112	
Patelnia Pt. "NW"	082	
Patelnia Pt. "SW"	302	
Patelnia Pt. "SE"	300	
Stranger Pt.	014	300–312
Turret Pt.	315	252–292
Cape Melville	228	
Penguin I. "NE"	215	
Penguin I. "SW"	287	
Three Sisters		297–327
Cape Lions Rump		272–012

The surface of the investigated penguin breeding grounds received various amount of solar energy. The amounts were the highest on the surface of the main breeding areas of the Adelie penguins since the azimuths of the sloping surfaces of these areas were exclusively northern ones (Tab. 2). Besides, the mean value of the total coverage of the colony area was lower by 40%, and the coverage of the area in the northern quarter of the horizon was lower by 100% then the respective values for uncolonized areas (Tab. 3).

Table 3

Total horizon altitudes (T: 0—360°) and northern quater horizon altitudes (CNQ: 337.5°—22.5°) at colonies of King George Island

Chinstrap			Adelie		
Colony	T (mm^2)	NQ (mm^2)	Colony	T (mm^2)	NQ (mm^2)
Thomas Pt. M2	998	161	Thomas Pt. M3	811	176
Stranger Pt.	750	264	Stranger Pt.	1166	575
Turret Pt.	425	248	Turret Pt.	972	470
Chabrier Rock	2099	443	Llano Pt.	1143	89
Shag I.	1440	485	Cape Lions Rump	1941	168
Demay Pt.	2148	1301	Three Sister	497	188
Patelnia Pt.	558	434	Mean	1088	278
Cape Melville	1468	530	Noncolonized areas		
Penguin I. "NE"	612	159	Cape Vaureal	1577	949
Penguin I. "SW"	1434	750	Hennequin Pt.	2019	3
			Keller Pen.	1665	483
Mean	1193	477	Mean	1754*	593

$\bar{T}$* differs statistically from $\bar{T}$ Adelie and $\bar{T}$ chinstrap ($p < 0.05$)

The measurements of albedo in the Thomas Pt. colony indicate that the highest amount of the solar radiation was absorbed by the breeding grounds of the Adelie penguins. In the period with no snow cover the mean value of the albedo of the Adelie penguins breeding areas was lower by 6% and by 14% from values for the breeding areas of the chinstrap and gentoo penguins, respectively (Tab. 4).

The albedo of areas covered with snow depends on the species and number of birds in breeding group. In the most abundant breeding groups of the Adelie penguins (M3) and gentoo penguins (Ecology) the values of the albedo of the surface was significantly lower than that in less abundant groups of these species (Beach, North and M1, Holm; Tab. 5). The lowest albedo of surface of the breeding areas covered with snow was recorded in the breeding group M2 of the chinstrap penguins. It was lower than

Table 4

Mean albedo of the ground surface of pygoscelid penguins nest-sites at Thomas Pt.

Period	Adelie $\bar{A}\% \pm SE\%$	Chinstrap $\bar{A}\% \pm SE\%$	Gentoo $\bar{A}\% \pm SE\%$
12 Nov. 1980	42.4 ± 2.8 n = 20	31.8 ± 1.0 n = 5	68.5 ± 2.9 n = 15
Jan./Feb. 1980	19.7 ± 1.0 n = 40	25.5 ± 1.4 n = 40	33.3 ± 1.1 n = 40

Means differ statistically ($p<0.001$) except means for Adelie and chinstrap in 12 Nov. 1980.

the lowest mean values in the area of the breeding groups of the Adelie and gentoo penguins by 12% and 22%, respectively (Tab. 5).

Table 5

Mean albedo of the ground surface of pygoscelid penguins nest-sites at Thomas Pt. in 12 Nov. 1980, one day after blizzard

Adelie		Gentoo		Chinstrap	
Nest-site	$\bar{A}\% \pm SE\%$ n = 5	Nest-site	$\bar{A}\% \pm SE\%$ n = 5	Nest-site	$\bar{A}\% \pm SE\%$ n = 5
M3	44.1 ± 1.2	Ecology	53.8 ± 1.6	M2	31.8 ± 1.0
Beach	48.1 ± 1.1	Holm	76.5 ± 0.6	snow around colonies	84.1 ± 1.3
North	54.6 ± 2.2	M1	75.3 ± 0.2		
Gutter	22.9 ± 1.5				

Means differ statistically except M1 — Holm and North — Ecology:
M3 Beach p<005
North — Beach p<0.05
Ecology — Beach p<0.02
North — M3 p<0.01
all other p<0.001

Discussion

Water outflow and snow cover

Does snow cover constitutes a significant danger for the embryos or nestlings of the polar species of birds? Belopolskij (1957) describes a situation from the vicinities of Murmańsk, in which the development of the embryo of Brünnich guillemot (*Uria lomvia*) occurs properly only when the egg remains in icy water. This is the only known case of this kind of adaptation to polar conditions. In the case of penguins as well as other species of Antarctic birds nesting in open terrain it is believed that only continuous protection of the parents makes early stages of ontogenesis possible (Sapin--Jaloustre 1960, Goldsmith and Sladen 1961, Spellerberg 1969, Boyd and Sladen 1971, Derksen 1977, Weinrich and Baker 1978, Burger and Williams 1979, Taylor 1985).

The above opinion was formulated by the results of investigations of bird adaptations to air cooling. However, water cools much more intensively than air. According to Collier et al. (1978) animal body transfers heat five times faster to water than to air. Wet body loses heat at the rate of 25 kJ per gram of evaporated water. Besides, the cooling of eggs and nestlings with water connot be compensated with the supply of heat from the body of parents. This is so because heat more quickly outflows than inflows due to the twice higher value of the heat coefficient conductivity for water than for skin (Burton and Edholm 1955).

The above facts allow one to assume that water flooding of eggs and nestlings is a lethal factor for them. The protection of nests against flooding is thus of fundamental importance for the reproduction of pygoscelid penguins.

As it is the case on the King George Island, also in other colonies penguins of the genus *Pygoscelis* prefer those forms of terrain microrelief which protect their nests against being flooded (e.g. Matsuda 1964, Tenaza 1971, Oelke 1975, Starck 1980). In certain colonies the terrain microrelief itself sufficiently protects nests against being flooded (bare rock, steep cliff). Nests of such colonies are small sometimes built of only several stones (C. Müller-Schwarze and D. Müller-Schwarze 1975, own unpubl. data).

Another means of protecting the nests against being flooded is also choosing by penguins the breeding areas of thin snow cover at the end of winter (Tab. 1). Small amount of snow means that also the amount of melted water will be limited. Besides, a thin layer of snow rapidly disappears and thus unveils pebbles necessary for building the nests. On flat surfaces or mild slopes, nests are the basic form of protecting eggs and chicks against flooding due to elevating them above the surface of flowing water.

Attempts at colonizing the Gutter area (Fig. 2), which is characterized by a twice larger thickness of snow cover than the other nesting areas (Tab. 1), were not successful. In the seasons 1978/1979, 1979/1980 and 1980/1981 the breeding success in this area was almost zero. Few chicks hatched from eggs laid in small nests built on snow, and also these were killed by streams of thaw water (Zdzitowiecki, pers. comm., own unpubl. observ.). Probably, the thick snow cover in the Meadow area (Tab. 1, Fig. 2) prevented the Adelie penguins from the colonizing this place, because, in respect to physiography, it did not differ from neighbouring, colonized areas.

The above discussion might be summed up as follows: in the penguin colonies in the Admiralty Bay, the complicated shapes and limits of breeding groups are determined by a low snow cover in winter.

Implication of microclimate

In the colonies on King George Island the surface of the Adelie penguins nest-sites receive an especially large amount of solar radiation due to the northern slope of the hill-sides (Tab. 2), low coverage of the terrain (Tab. 3) and its low albedo value in snowless periods (Tab. 4).

Most of known colonies of the Adelie penguins from the Antarctic coast were also located on hill-sides exposed to the north (Yeates 1975, Aoyanagi 1979, Ainley and DeMaster 1980, Aoyanagi and Tamiya 1983). Results of microclimatic investigations of the nesting places indicate that their microclimate is milder than it follows from standard meteorological recordings (Sapin-Jaloustre 1960, Yeates 1971), but it hardly affects the energetic budget of penguins (Yeates 1975, Moczydłowski 1986). This conclusion seems feasible, because Antarctic penguin species are very well adapted to cold (Stonehouse 1967, Le Maho 1977, Taylor 1985, 1986). On the land overheating of the body may constitute for them a more serious problem than its underheating (Stonehouse 1970). However the energetic cost of staying in the sea is high (Goldsmith and Sladen 1961, Kooyman 1975, Kooyman et al. 1976).

I think that the main reason of choosing for nesting especially insolated places is rather a protection of nests against thaw water, than providing thermal comfort for nesting Adelie penguins. This hypothesis is supported by the following facts.

Solar energy absorbed by the terrain surface causes a greater increase of ground temperature than temperature of the air near the ground (Geiger 1966). This was also confirmed in the case of surfaces of the *Pygoscelis* penguins nest-sites (Moczydłowski 1986). For the Adelie penguins starting to breed in early spring, increase in surface ground temperature **is particularly important for protecting clutches against flooding because it** facilitates building nests and accelerates snow melting and melt water run-off from nesting terrains, when ground temperature at the depth of 0.05 m is below 0°C even in the warm zone of the maritime Antarctic (Moczydłowski 1986).

In the coastal Antarctic the Adelie penguins clutches protection is made difficult mainly by low temperature, because it is hard to extract pebbles from the frozen soil. In the maritime Antarctic a considerable amount of snow precipitation is a factor endangering the nests by drowning in the thawing period (Tab. 4). In both cases an additional stream of solar energy coming to the surface of the breeding areas is desirable, because it increases ground temperature and accelerates ablation of snow. Perhaps, this is the cause of the fact that the Adelie penguins are equally careful in choosing insolated nesting places both in coastal Antarctic and in the much warmer maritime Antarctic.

Effect of coloniality

After snowfalls occurring during the nesting period the surface of penguins nest-sites may absorb from 15% to 50% more solar energy than "clear" snow surface (Tabs. 4 and 5). A factor which is responsible for the decrease of the albedo of nesting surface areas is mixing of snow with soil and excrements. The intensity of the mixing depends upon coloniality degree of nesting birds, thus on abundance of breeding group and nest density.

In the Thomas Pt. colony it was recorded that the albedo of the surface of breeding areas covered with snow depended upon the coloniality degree of the Adelie and gentoo penguins. Adelie penguins are strongly colonial (Stonehouse 1975, Volkman and W. Z. Trivelpiece 1981), whereas gentoo are the least colonial among species of the genus *Pygoscelis* (C. Müller--Schwarze and D. Müller-Schwarze 1975, Croxall and Prince 1980). As result, the mean albedo value of the surface of the Adelie penguins breeding areas was lower by 26% than the mean value of the surface albedo of the gentoo penguins breeding grounds (Tab. 4). Influence of the abundance of the breeding group on the surface albedo value occurred in the case of both species. In smaller breeding groups (M1, Holm — *P. papua* and North, Beach — *P. adeliae*) the surface albedo values were higher than in larger breeding groups of the same species (Ecology — *P. papua* and M1 — *P. adeliae*) by 22% and 4%—14%, respectively (Tab. 5, Fig. 2).

In respect to the degree of coloniality chinstrap penguins are an intermediate species. Probably, the particulary low labedo value of this species nest-sites is a result of the physiography and thermal qualities of the substrate. On steep, rocky slopes of the Antarctic penguins breeding areas, dark, free of snow surface is of considerable size due to stones and boulders sticking out of snow, and quickly increases due to fast melting of snow covering the rocky substrate. (The heat conductivity coefficient of basalt is twice higher than these of sand and soil; Staniszewski 1979).

Penguins supply their breeding grounds with large quantities of sodium chloride carried out from the sea with food, and then expelled with excrements (Boyd 1967, Tatur and Myrcha 1983, Tatur and Barczuk 1984). Sodium lowers the temperature of snow melting, consequently, it is probably responsible for snow ablation in breeding areas at temperatures below 0°C.

During nesting period in the region of the Admiralty Bay the author frequently noticed the absence of snow in the penguins nest-sites, while the other areas of oases were covered with snow for many days after the snowfall. Higher concentrations of sodium chloride might be expected in areas of higher coloniality of nesting birds.

There is much evidence that the coloniality degree of nesting penguins of the *Pygoscelis* genus determine the degree of snow ablation in the breeding areas, thus indirectly the efficiency of protecting clutches against flooding. If this is the case, then more clear is that diversity in coloniality degree of populations of the same species breeding in various climatic conditions — e.g. in the maritime Antarctic and in the Antarctic coastal Areas.

A characteristic feature of the structure of Adelie penguins breeding colony in maritime Antarctic is the occurrence of breeding groüps consisting of several thousand pairs (C. Müller-Schwarze and D. Muller-Schwarze 1975, Jabłoński 1984), not recorded in the colonies of coastal Antarctic In the Thomas Pt. (maritime Antarctic) the mean distance between the nests of chinstrap penguins was 0.6 m and that between gentoo penguins 0.75 m (Volkman and W. Z. Trivelpiece 1981), while on South Georgia Island (the zone of subantarctic islands) the distances were by 0.15 m and 0.25 m longer, respectively (Croxall and Prince 1980). In maritime Antarctic during the nesting period the amount of snowfall is almost three times higher than in the zone of coastal Antarctic area and subantarctic islands (rainfalls dominate in the last zone of the above) (Tab. 6). The tendency to increase the coloniality degree in maritime Antarctic may be a response of penguins to greater danger of snowfalls.

Nesting strategy

Accepting a hypothesis of essential importance of nests protection against flooding for the nesting strategy of penguins of the genus *Pygoscelis* emables discovering still other relationships between species strategy and environamental conditions which has formed it.

Chinstrap penguins dominant in maritime Antarctic begin nesting 3 to 4 weeks later than the other species (Conroy, Darling and Smith 1975, Lishman 1985). In the zone of intensive snow precipitation it is a strategy profitable from the point of view of protecting nests against flooding, because with lapse of time the probability of large snowfalls decreases while the amount of solar energy increases (Dolgin, Marchunova and Petrov 1976).

A consequence of late nesting is pushing the chinstrap penguins to the rocky and steep areas by the Adelie penguins which start nesting earlier. These areas lie high above the sea level (Volkman and W. Z. Trivelpiece

1981) and thus are less shaded by the surrounding hillocks (Tab. 3). Good insolation and thermal qualities of the rocky substrate cause fast snow melting in the breeding areas of the chinstrap penguins. Difficulties of approaching and then moving along steep, rocky slopes is not an obstacle for the chinstrap penguins due to their low body weight and good climbing ability.

In contrast the gentoo penguins are well adapted to nesting conditions occurring in the zone of subantarctic islands. Temperatures well above the freezing point, practically unlimited snowless areas (Tab. 6) enable the gentoo penguins to build large nests, distant from one another, with no such obstacles as frozen soil or snow cover.

Table 6

Mean values of air temperature and precipitation for last quarter of year and the share of snow free areas in different climatic zones of Antarctic

Zone	Mean air temperature (°C)	Mean precipitation (mm)	% of snow free areas (Walton 1984)
Subantarctic Islands	3.0 (−3.6 ÷ +9.0)	74.4 (34 ÷ 120)	15 ÷ 100
Maritime Antarctic	−1.5 (−6.0 ÷ +1.0)	62.7 (41 ÷ 158)	5 ÷ 50
Antarctic coast	−9.6 (−25.4 ÷ −0.4)	23.5 (8 ÷ 51)	<3

Means for temperature and precipitation were calculated basing on mean values for October, November and December for the period 1957—1970 from all meteorological stations of particular zone (Dolgin, Marchunova and Petrov (1977, Tab. 1). It was assumed that the stations Signy Island and Orcadas represent the maritime Antarctic zone.

In the zone of subantarctic islands the clutch may be endangered by rain water since during breeding period the amount of precipitation in this zone is higher by 16% than in maritime Antarctic, the precipitation consisting mainly of rain (Tab. 6). I think that the main function of large nests of the gentoo penguins is the protection of eggs and chickness against precipitation water. Under the conditions in the zone of Subantarctic Islands this is a satisfactory kind of protection.

On the other hand, the nesting strategy of the gentoo penguins is not adapted to conditions occurring in maritime Antarctic. Being situated low on the shores the nest-sites of this species are shaded by hills to a larger extent than the nesting areas of related species, and thus are less insolated. Besides, due to their low degree of coloniality the gentoo penguins weakly influence the melting of soil and snow ablation. I think that these penguins breed in maritime Antarctic only when meterological conditions enable them nest building.

In October 1980 in the Thomas Pt. colony the ground temperature in the nesting areas of the three species of the investigated penguin genus was below 0°C (Moczydłowski 1986). The gentoo penguins of the nesting groups M1, Holm and other neighbouring groups (Fig. 2) several times attempted to build their nests. Although there was no snow cover on the terrain, picking out stones from the frozen soil was an essential obstacle in constructing the nests. Only several pairs of the Holm breeding group (largest in this area), built up their nests and laid eggs.

At the same time the Adelie penguins were building their nests with no problems. However, they started the building only when the number of arriving birds had amounted to several hundreds individuals. First penguin newcomers after the inspection of colony area, lay on snow in a prone position (own observ.).

The nesting strategy of the Adelie penguins is effecient in low temperatures and low snow precipitation, which occur in the zone of coastal Antarctic. The careful choosing of insolated terrains for nesting and intense influence exerted by dense, numerous breeding groups upon soil surface and snow support this opinion.

The nesting strategy of the Adelie penguins in maritime Antarctic is less efficient than in coastal Antarctic. This results from the fact that although high nest density enhances snow ablation yet it also causes higher snow accumulation in the nesting areas. In the case of low snow precipitation which occurs in coastal Antarctic snow accumulation is also low. In contrast, in maritime Antarctic (high snow precipitation — Tab. 6), snow accumulation may be catastrophic for the clutches. Being faced with increased danger, the Adelie penguins nest in maritime Antarctic in very numerous breeding groups, which more efficintly than small ones influence snow ablation.

Nest-site selection

In previous studies nest-site preferences of penguin species were determined on the basis of such forms of land physiography as ridge, bar, slope, cliff etc. (Carrick and Ingham 1967, Stonehouse 1970, White and Conroy 1975, Volkman and W. Z. Trivelpiece 1981). In the colonies on King George Island almost any of the above mentioned physiographical forms occurs in the nesting areas of each of the three penguin species. Observations made on King George Island confirm Croxall's (1984) opinion that in respect to terrain physiography the requirements of the pygoscelid penguins are overlapping.

In the colonies on King George Island borders between the nesting areas of the pygoscelid penguins may be determined on the basis of criteria other than physiographical ones.

Chinstrap penguins are "destined" in colonies to occupy rocky peripheries by penguins which start nesting earlier. The Adelie and gentoo penguins are not accustomed to colonize rocky nest-sites of the chinstrap penguins. The reason of this is that the former ones are heavier and less dextrous than the chinstrap in crossing obstacles and steep slopes.

The Adelie penguins choose for nesting rockless areas, in which a high degree of coloniality is possible. These terrains are of large surface area, or smaller ones but of compact circular shape.

The gentoo penguins occupy terrains of the elongated shape, and of comparatively small surface area. These or also other features cause that only a low coloniality degree may occur in these areas. The nesting areas of gentoo penguins would not allow the nesting strategies of Adelie and chinstrap penguins to be realized there and thus they are useless for them.

The borders separating the nesting areas of particular species may change. The nesting areas of chinstrap penguins undergo the process of strong congealing and chemical erosion due to strong acidity of waters in the nesting areas (Tatur and Myrcha 1983). Probably, the processes of erosion make the chinstrap penguins nesting grounds useful for the Adelie penguins. This may be one of the reasons of nest-sites competition described by W. Z. Trivelpiece and Volkman (1979) and W. Z. Trivelpiece, S. G. Trivelpiece and Volkman (1984).

Final remarks

In the maritime Antarctic there occurred a considerable increase of penguins quantity in the course of recent 30 years (Croxall and Kirkwood 1979, Jabłoński 1984a). Increase in the abundance of all animals whose main component of the diet is krill results from a higher abundance of food in the Southern Ocean after overexploitation of the whales population (Sladen 1954, after Conroy 1975).

It has been proved that in the maritime Antarctic the abundance of the chinstrap penguins increased to the highest degree; a certain increase was also recorded in the abundance of Adelie penguins, while the abundance of the gentoo penguins only fluctuated (Croxall and Kirkwood 1979). I suppose that differences in the nesting strategies of particular species are mainly responsible for different abundance dynamics of penguin populations of the genus *Pygoscelis* in the maritime Antarctic. This is the case because nesting strategy determines the choice of nesting terrains suitable for given species, the terrains not being of equal value for various species and being present there in different abundance.

In the colonies on King George Island potentially nesting terrains for the gentoo penguins occur in abundance. However the nesting strategy of the gentoo penguins is weakly adjusted to the climatic conditions of the maritime Antarctic and as a result there are years in which individuals of this species may not be able to nest, even in terrains which have been colonized long time ago. Consequently, I think that the abundance of the gentoo penguins in the maritime Antarctic is not limited by insufficiency of suitable nest-sites. Fluctuations in this species population abundance reflect variability in climatic conditions.

An essential element of the Adelie penguins nesting strategy is careful choice of their nest-sites in respect to insolation, terrain slope exposure, size and shape of surface. Erosion was the only process recorded which might increase the surface area of terrains satisfying the above mentioned conditions. Due to severity of criteria applicable while choosing nest-sites, the Adelie penguin nesting areas are probably rare and constitute a factor limiting the size of this species population.

The chinstrap penguins seem to be in more favourable situation as regards the increase of their number. Due to such elements of nesting strategy as late nesting and good locomotive efficiency the chinstrap penguins may utilize for nesting terrains not accesible for related species. Besides, the recession of glaciers uncovers grounds which may be colonized almost exclusively by this species (Jabłoński 1984b). This cannot be the main cause of their increase in abundance because, as it follows from Croxall and Kirkwood's (1979) study a high increase was also recorded in these colonies of the maritime Antarctic in which the surface area of terrains free of ice and snow did not increase. The abundance of suitable nesting areas enables a general increase of the number of chinstrap penguins. But various abundance dynamics in given colonies is probably a consequence of differences in surface area of potential nest-sites, availability of the food and accessibility of the feeding grounds.

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Streszczenie

W koloniach położonych na południowym brzegu wyspy Króla Jerzego (rys. 1) od grudnia 1979 do stycznia 1981 badano niektóre własności terenów lęgowych pingwinów z rodzaju *Pygoscelis*. Stwierdzono, że dobry spływ latem i niska pokrywa śnieżna zimą są cechami powszechnymi badanych terenów lęgowych. W kolonii Thomas Pt. średnia wysokość pokrywy śnieżnej na terenach latem lęgowych nie przekraczała w końcu zimy 20 cm (tab. 1).

Tereny lęgowe pingwinów Adeli i antarktycznych na wyspie Króla Jerzego otrzymują więcej energii słonecznej niż nieskolonizowane obszary bezśnieżne ze względu na małe zakrycie horyzontu (tab. 3). Dodatkową ilość energii słonecznej otrzymują tereny lęgowe pingwinów Adeli położone na zboczach, dzięki północnej ekspozycji (tab. 2).

W kolonii Thomas Pt., w warunkach bezśnieżnych powierzchnie terenów lęgowych pingwinów Adeli, antarktycznych i papuaskich absorbowały średnio 80, 75 i 67% energii padającej, a przy zalegającym śniegu odpowiednio: 58, 68 i 31% padającej energii promieniowania słonecznego (tab. 4). Ilość energii absorbowanej przez powierzchnie terenów lęgowych pokrytych śniegiem wzrasta ze wzrostem stopnia kolonijności gniazdujących ptaków (tab. 5).

Zdaniem autora, określone w tej pracy cechy terenów lęgowych oraz konstrukcja gniazd, stopień kolonijności gniazdujących pingwinów i czas rozpoczęcia lęgów są elementami strategii gniazdowania poszczególnych gatunków, odpowidzialnymi za ochronę lęgów przed zalewaniem wodą roztopową lub opadową. Zagrożenie dla lęgów stanowią wysokie opady ze względu na dużą ilość spływającej wody i możliwość zasypania śniegiem oraz ujemna temperatura gruntu, gdyż utrudnia budowę gniazd.

Jakościowe i ilościowe zróżnicowanie fizycznych czynników środowiska w strefach „rodzinnych" poszczególnych gatunków (tab. 6) stanowi dobre wytłumaczenie odmienności strategii gniazdowania poszczególnych gatunków.

Na podstawie różnic strategii gniazdowania określono zasady podziału terenów lęgowych pomiędzy sympatrycznie gniazdującymi gatunkami oraz przyczyny różnej dynamiki liczebności populacji pingwinów z rodzaju *Pygoscelis* w Antarktyce Morskiej.