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Diurnal pattern of changes in the number of penguins on land and the estimation of their abundance (Admiralty Bay, King George I., South Shetland Islands)

[with Plates XIX—XX and 2 text-figs]

Zmiany ilości pingwinów na lądzie w ciągu doby a zagadnienie oceny ich liczebności
(Zatoka Admiralicji, Wyspa Króla Jerzego, Szetlandy Południowe)

Abstract. The most suitable hours for estimating the abundance of penguins in particular phenological periods were determined on the basis of diurnal changes in their numbers. In spite of differences in diurnal behaviour between *Pygoscelis papua*, *P. adeliae* and *P. antarctica* the most suitable time of counting falls between 17.00 and 21.00 of local time in the breeding season and 1 to 1.5 hours before nightfall after breeding. In the incubation period breeding partners of *P. papua* and *P. antarctica* change over at nests usually every 1—3 days. Similar breaks in their stay on land were observed in the post-breeding period.

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I. INTRODUCTION

In ornithological papers the term “diurnal activity” has a very wide comprehension. It appears both in studies of particular phases of activity during a 24-hour period (e. g. sleep, foraging) and in studies of changes in the numbers of birds in their feeding areas or in breeding grounds. We should realize that observing quantitative changes over a 24-hour period, we trace merely the final effect of a complex process which is governed both by a set of factors determining

the physiological state of the birds and by external conditions, which modify the duration of particular diurnal phases. The present paper deals with the changes in the number of penguins on land in a 24-hour period, resulting from the changes in feeding behaviour and phenological changes in the physiological state of the birds (incubation, moult, etc.) and connected with atmospheric conditions (especially in the postbreeding period), for the purpose of the study presented was to establish the optimum time of the day on the basis of the quantitative changes on land in various seasons of the year, for the count of penguins.

LEVICK (1914) and BAGSHAWE (1938) made the first observations on the diurnal activity of penguins. They provided information about the rate of nest building and the frequency at which the parents change over in the breeding season. Their studies were however carried out on a small number of pairs.

The diurnal activity of *Pygoscelis adeliae* was the subject of close studies made by D. MÜLLER-SCHWARZE (1968), D. MÜLLER-SCHWARZE and C. MÜLLER-SCHWARZE (1971), YEATES (1971), CRAWFORD (1975), PAULIN and SAGAR (1977), SPURR (1978) in the Ross Sea area, and by AOYANAGI (1973) in the Prince Claw Coast region. From among the foregoing authors only PAULIN and SAGAR (1977) and SPURR (1978) carried out detailed researches into the changes in the numbers of *P. adeliae* in the region of the colony. The other authors, to be sure, give the periods of the minimum and maximum numbers of these penguins in the study area but their investigations chiefly cover the ethology of breeding pairs.

Ornithological literature provides no information about the diurnal changes in the numbers of Gentoo and Chinstrap penguins and about these changes in Adélie penguins in areas situated out of the mainland. These data are indispensable for the correct estimation of the number of birds, especially in the periods when they stay on land irregularly (i. e. the period preceding breeding, moult and the time of autumn-winter nomadizing). The data about the stay of birds on land are also necessary to determine the amount of food eaten up by the population in particular seasons.

II. METHOD

This study was carried out in the region of Admiralty Bay (King George Island — 62°09'S, 58°28'W) in the colonies at Thomas Point, Llano Point, Shag Island and Demay Point (Fig. 1). The materials covering breeding seasons were collected in 1978/1979, 1979/1980 and 1980/1981 and those of pre- and post-breeding periods in 1979/1980.

Observations of quantitative changes during a 24-hour period and of the time the penguins stayed on land were made on banded specimens. For this purpose 3000 bands (from the Ornithological Station, Polish Academy of Sciences) were fixed on the wings of the birds. 106 penguins banded by Dr W. TRI-

VELPIECE and Dr J. VOLKMAN from the USA in preceding years were also included in the study. In addition, some birds were marked with dyes so that particular parental specimens might be distinguished more easily; the partners from the same nest were marked with different colours. However, the sex of incubating Gentoo and Chinstrap penguins was not marked. The marked

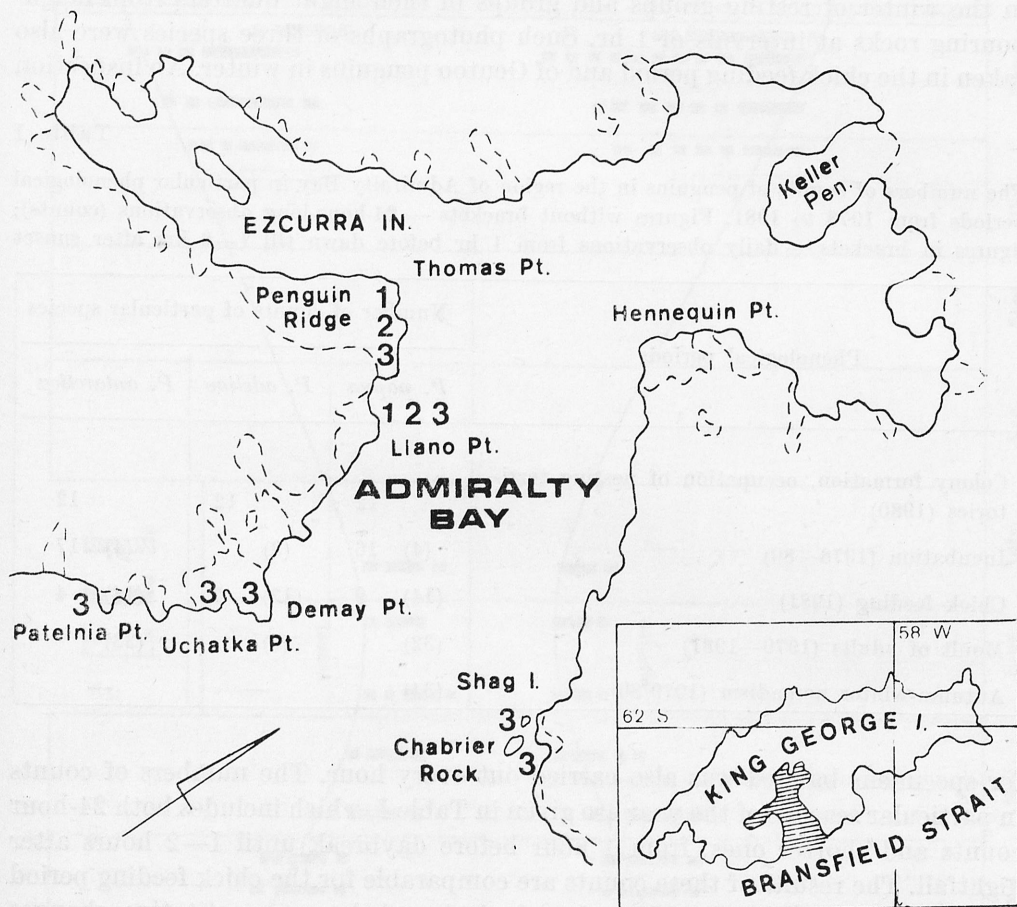


Fig. 1. The distribution of penguin colonies in the region of Admiralty Bay. 1 — colonies of *Pygoscelis papua* (FORSTER 1781). 2 — colonies of *Pygoscelis adeliae* (HOMBRON et JACQUINOT 1841), 3 — colonies of *Pygoscelis antarctica* (FORSTER 1781). The solid line marks the shore-line, broken line the margin of the ice sheet

Gentoo specimens formed 18.1—22.8% of all the specimens from particular breeding groups in different seasons, the Adélie penguins 1.8—20.3% and the Chinstrap penguins 10.4—29.7%. In the moult period the banded Gentoo penguins formed 8.6—10.7% and the Chinstrap penguins 2.5—7.6% of all the birds. In the winter only the Gentoo penguins occurred regularly and then 1.5—45.2% of all the specimens of this species from various night quarters in the region of H. Arctowski Station and Llano Point were banded.

I assumed that the changes in the number of specimens banded were representative of the whole population. In order to verify the reliability of the estimates of changes in the number of specimens banded, an analysis of these changes was additionally made as exemplified by whole breeding groups. Collection of these materials consisted of taking photographs of breeding groups, in the winter of resting groups and groups in their night quarters from neighbouring rocks at intervals of 1 hr. Such photographs of three species were also taken in the chick feeding period and of Gentoo penguins in winter. An inspection

Table I

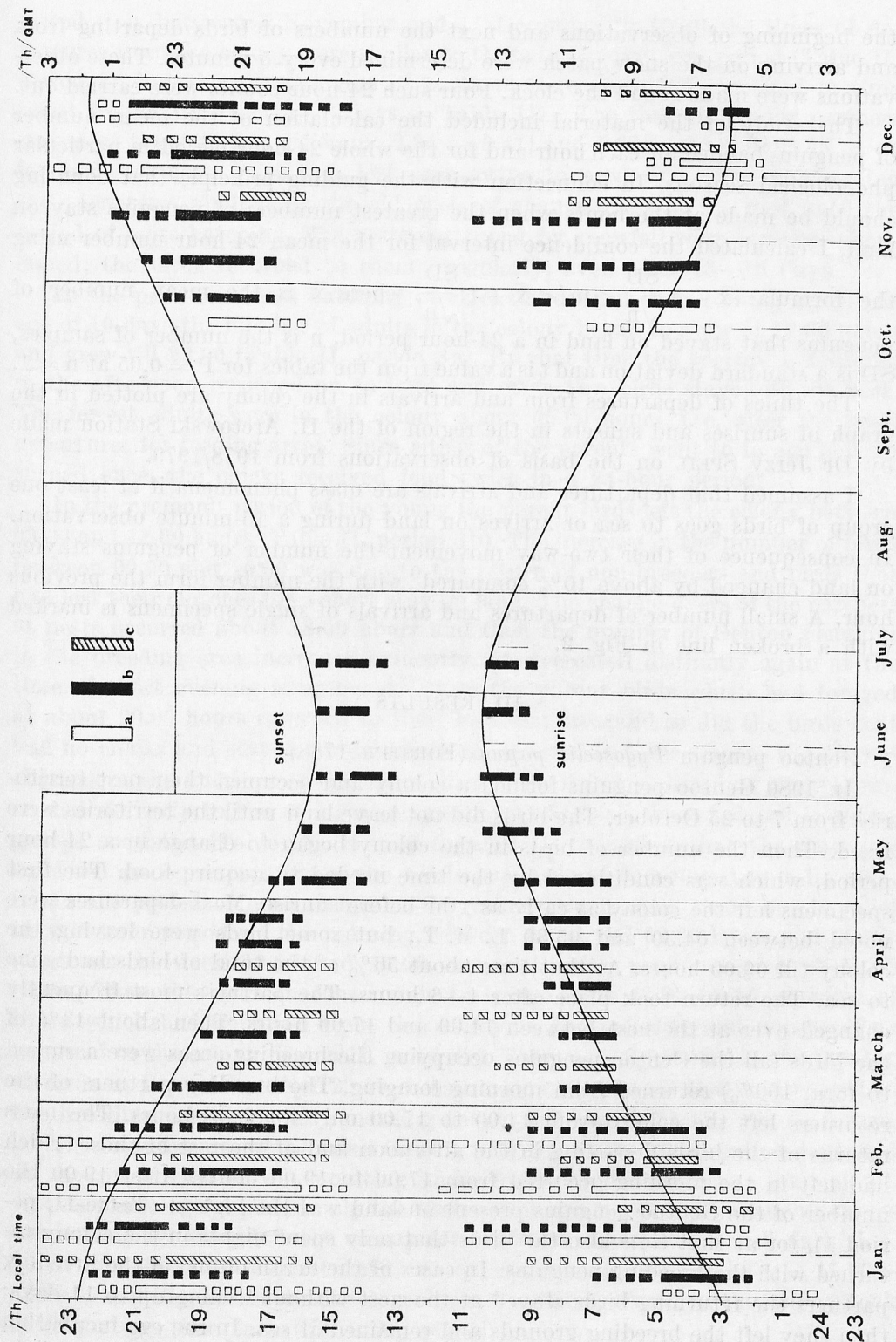
The numbers of counts of penguins in the region of Admiralty Bay in particular phenological periods from 1978 to 1981. Figures without brackets — 24-hour-long observations (counts); figures in brackets — daily observations from 1 hr before dawn till 1—2 hrs after sunset

Phenological periods	Number of counts of particular species		
	<i>P. papua</i>	<i>P. adeliae</i>	<i>P. antarctica</i>
Colony formation, occupation of nesting territories (1980)	12	12	12
Incubation (1978—80)	(4) 16	(3)	(4) 17
Chick feeding (1981)	(14) 9	(13) 2	(14) 4
Moult of adults (1979—1981)	(32)	(6)	(33)
Autumn-winter nomadism (1979/80)	(34)	—	—

for specimens banded was also carried out every hour. The numbers of counts in particular seasons of the year are given in Table I, which includes both 24-hour counts and shorter ones, from 1 hour before daybreak until 1—2 hours after nightfall. The results of these counts are comparable for the chick feeding period was nightless and in the other phenological periods no quantitative changes were found after dark. The local time for King George Island is used in the tables illustrating quantitative changes.

Observations of changes in the number of non-breeders staying on snow patches at a distance from the colony were carried out in the seasons 1979/1980 and 1980/1981. In view of the greater agility of non-breeders, their numbers were estimated in the following way: the birds in a grouping were counted at

Fig. 2. Times of the morning departures from colonies and evening returns of the species of the genus *Pygoscelis*: a — *P. adeliae*, b — *P. papua*, c — *P. antarctica*. The solid blocks represent the time of mass departures from or arrivals in colonies, the broken ones the time of sporadic departures and arrivals



the beginning of observations and next the numbers of birds departing from and arriving on the snow patch were determined every 5 minutes. These observations were made round the clock. Four such 24-hour counts were carried out.

The study of the material included the calculation of the mean number of penguins banded for each hour and for the whole 24-hour period in particular phenological seasons. In connection with the guiding principle that counting should be made at the hours when the greatest numbers of penguins stay on land, I calculated the confidence interval for the mean 24-hour number using

the formula: $\bar{x} - t \frac{SD}{\sqrt{n}} < m < \bar{x} + t \frac{SD}{\sqrt{n}}$, where \bar{x} is the mean number of penguins that stayed on land in a 24-hour period, n is the number of samples, SD is a standard deviation and t is a value from the tables for $P = 0.05$ at $n = 1$.

The times of departures from and arrivals in the colony are plotted in the graph of sunrises and sunsets in the region of the H. Arctowski Station made by Dr Jerzy SPEIL on the basis of observations from 1978/1979.

I assumed that departures and arrivals are mass phenomena if at least one group of birds goes to sea or arrives on land during a 15-minute observation. In consequence of their two-way movement the number of penguins staying on land changed by above 10% compared with the number from the previous hour. A small number of departures and arrivals of single specimens is marked with a broken line in Fig. 2.

III. RESULTS

1. Gentoo penguin *Pygoscelis papua* (FORSTER 1788)

In 1980 Gentoo penguins formed a colony and occupied their nest territories from 7 to 25 October. The birds did not leave land until the territories were fixed. Then the number of birds in the colony began to change in a 24-hour period, which was conditioned by the time needed to acquire food. The first specimens left the colony as early as 1 hr before sunrise. Mass departures were noted between 04.30 and 05.30 L. M. T., but some birds were leaving the colony till 09.00 hours. At that time about 56% of the total of birds had gone to sea. The return took place after 4—6 hours. The partners most frequently changed over at the nest between 14.00 and 17.00 hours. Then about 43% of the birds (all the Gentoo penguins occupying the breeding areas were assumed to form 100%) returned from morning foraging. The breeding partners of the returners left the colony from 14.00 to 17.00 only for 2—3 hours. The mass returns of the birds departing in the afternoon and of the rest of those which had left in the morning occurred from 17.00 to 19.00 hours. After 19.00 the number of the Gentoo penguins present on land was the highest (Table II, period 1), for at that time also the birds that only spent nights in the colony returned with the breeding penguins. In cases of the death of one of the breeding partners the returning birds stayed at the nest without feeding up to 14 days; then they left the breeding grounds and remained at sea. In the egg incubation

period (i. e. between 5 November and 17 December in 1980) the times of departures from the colony were similar to those in the previous period (Table II, period 2), but the change-overs of partners were more differentiated in time (most frequently every 1—3 days — Table III). The time particular partners stayed at the nest was different: 2.84 (± 0.41) and 5.62 (± 0.94) days ($N = 81$ for each partner). Pairs that lost eggs owing to predation went on guarding their territory, abiding by the old cycle of change-overs at the nest until the period of mass hatching. The nests destroyed by snowfall were however abandoned; the birds returned to them irregularly, even after 13—15 days.

In the period of mass hatching of chicks and until their coming up to the age of 10 days the number of adults in the colony began to grow at 17.00 hours and grew till 22.00 (Table II, period 3a). At that time the specimens foraging in the afternoon returned on to land and often two birds stayed at the nest. The fewest adults were in the colony about 05.00 hours, i. e. after the mass departures for feeding areas. Since either of the parents went to forage and returned once, the chicks received food twice in a 24-hour period.

In the premoult period of the young the parent birds left the colony between 03.00 and 11.00 hours (Table II, period 3b). The increase in the number of birds between 09.00 and 10.00 was due to the return of non-breeders and birds that had lost their clutches for a short stay on land. The change-overs of the partners at nests occurred about 18.00 hours and then the number of Gentoo penguins in the breeding area increased evidently. It decreased distinctly again at the time of short evening foraging. At 21.00 the parent birds which had foraged at about 20.00 hours returned to their breeding area and so did the birds that had no chicks and stayed irregularly in the colony. In three seasons the diurnal changes in the numbers of specimens banded in different breeding groups proceeded similarly to the changes in specimens of which three isolated breeding groups consisted (Table II). It may therefore be admitted that the materials collected are representative of the whole population inhabiting Admiralty Bay.

In the period of mass moult of the young two minima stood out in relief in a 24-hour period: in the morning between 04.00 and 09.00 hours and in the afternoon between 12.00 and 15.00. A quantitative peak occurred at 19.00 hours. Then the birds that had gone to forage from 13.00 to 15.00, some of those which had departed from the colony in the morning and non-breeders returned to the colony (Table II, period 3c). There was a decrease in the number of birds in the colony after 22.00, because some specimens that had stayed in the breeding areas since the morning return left again for the sea to forage.

The total number of the adult Gentoo penguins in the moult period depended on the proportion of the moulting birds, for these did not leave land at all. In this phenological period only the birds in the premoult and postmoult stages went foraging. They left the colony for the shore when it was still dark (i. e. about 06.15—06.30) and returned in the largest numbers as late as 17.00—18.00 hours. In this season the departures from and returns to the colony took a very short time each (Table II, period 4).

Table II

The mean numbers of *Pygoscelis papua* present on land in successive hours in different phenological periods: 1 — colony formation and occupation of nesting territories until laying of eggs, 2 — incubation, 3 — feeding of chicks (3a — chicks up to ca 10th day of life, 3b — chicks up to period of their moult, 3c — period of chick moult), 4 — period of adult moult, 5 — autumn/winter nomadizing (5a — 1/2 Apr. — 1/2 May, 5b — 1/2 May — 1/2 July); "+" — values over, and "-" — values below confidence limits of mean number for 24 hrs.

Hours (local time)	Phenological periods									
	3a			3b			4	5a		5b
	1	2	3a	Breeding groups in 1979/1980 (56 p.) (64 p.) (150 p.)		Birds marked in 1978—1981		Birds spending night near Station (in 1980)		
				Birds marked in 1978—1980						
1	—	130+	117	112+	128+	300+	117+	64	—	—
2	—	128+	116	110+	127+	298+	115+	67	—	—
3	121+	121+	89—	78—	93—	195—	88—	63	—	—
4	109+	112	88—	73—	91—	183—	88—	43—	—	—

5	70	103	71-	55-	67-	153-	70-	20-	—	—	—	—
6	63-	98	91-	64-	72-	165-	89-	17-	320+	1078+	510+	—
7	61-	89-	79-	71-	80-	192-	79-	12-	262	755	372	—
8	56-	85-	89-	80-	92-	208-	89-	13-	170-	582-	282-	37+
9	54-	84-	115	105+	120+	266	114	16-	169-	582-	272-	12
10	56-	82-	128	96	121+	261	110	44	171-	582-	272-	6-
11	54-	79-	123	68-	85-	186-	72-	52	170-	604-	270-	5-
12	57-	79-	124	91	104	240	102	42-	170-	604-	301-	9-
13	64-	79-	112	91	109	242	102	30-	171-	625-	300-	9-
14	73-	84-	118	97	112+	252	104	30-	170-	625-	304-	29+
15	83	100	122	103	111+	241	111	43-	190-	690	318	30+
16	85	97	127	98	107	258	106	55	215	862	416	31+
17	85	94-	132+	115+	123+	276	110	74	247	1035+	482+	—
18	119+	112	165+	126+	144+	339+	128+	109+	307+	1078+	510+	—
19	139+	124+	140+	91	128+	296+	106	137+	316+	1078+	511+	—
20	141+	128+	124	92	107	243	99	128+	317	—	—	—
21	142+	128+	136+	121+	138+	300+	133+	113+	317+	—	—	—
22	—	130+	140+	121+	138+	302+	134+	122+	—	—	—	—
23	—	130+	126	114+	136+	302+	126+	70	—	—	—	—
24	—	130+	128	114+	133+	302+	128+	79+	—	—	—	—
Mean number in 24 hrs	85,9	105,2	116,7	95,2	120,0	260,0	105,0	60,1	230,1	770,0	365,7	18,7
Confidence limits ($\pm m$)	15,8	8,5	13,6	8,8	9,3	21,6	7,7	16,1	35,0	111,3	57,6	9,8

Table III

The distribution of the numbers of returns of marked penguins on to land after a lapse of different numbers of days in the 1980/81 season. The designation of phenological periods (2, 4, 5) as in Table II

Days	Phenological periods			
	2	5	2	4
	<i>P. papua</i>		<i>P. antarctica</i>	
0 *	1 — 0,6%	—	1 — 0,4%	5 — 6,3%
1	58 — 35,8%	7 — 19,4%	70 — 30,2%	18 — 22,8%
2	37 — 22,8%	11 — 30,6%	51 — 22,0%	29 — 36,7%
3	18 — 11,1%	10 — 27,8%	38 — 16,4%	20 — 25,3%
4	11 — 6,8%	4 — 11,1%	18 — 7,8%	3 — 3,8%
5	7 — 4,3%	2 — 5,5%	16 — 6,9%	1 — 1,3%
6	4 — 2,5%	1 — 2,8%	6 — 2,6%	1 — 1,3%
7	2 — 1,2%	1 — 2,8%	4 — 1,7%	2 — 2,5%
8	1 — 0,6%	—	5 — 2,1%	—
9	5 — 3,1%	—	3 — 1,3%	—
10	3 — 1,8%	—	4 — 1,7%	—
11	3 — 1,8%	—	5 — 2,1%	—
12	4 — 2,5%	—	3 — 1,3%	—
13	8 — 4,9%	—	7 — 3,0%	—
14	—	—	1 — 0,4%	—
Total of specimens	162 — 99,8%	36 — 100%	232 — 99,9%	79 — 100%

* before a lapse of 24 hours.

In the first phase of autumn-winter wanderings, i. e. from the second half of April till the first half of May, 52.9—59.6% of the birds remained on land in the daytime. The changes in the number of penguins banded and photographed proceeded uniformly during a 24-hour period (Table II, period 5a). The departures from land ranged between 07.00 and 08.00 hours and the mass returns from the sea between 16.30 and 17.30. It was established on the basis of 36 birds banded in the breeding season and remaining for winter that the birds most frequently return on to land after 1—4 days (Table III). In the second phase of autumn-winter wanderings, i. e. from mid-May to mid-July only 13.5—24.3% of the birds remained on land in the daytime. The mass departures from land took place between 09.00 and 10.00 and the returns from the sea mainly between 13.30 and 14.30 hours (Table II, period 5b). This diurnal rhythm was maintained by groups going to sea and returning on to land regardless of the fact how many days particular members of the groups had spent at sea.

Apart from the above-presented diurnal quantitative changes, marked changes in the size of the population of Gentoo penguins in dependence on air temperatures were also observed in the autumn-winter season. This dependence is illustrated by the following materials from April and May from the region of the H. Arctowski station: at the time of 12 observations, when minimum temperatures were lower than -10°C , the mean number of birds was 297.5 in a 24-hour period. During 8 days with minimum temperatures reaching $+2^{\circ}\text{C}$ — 1 144.2 specimens in a 24-hour period. On these warm days after the return from the sea the Gentoo penguins formed groups in the breeding areas, where some of them started nest building and courtship.

2. Adélie penguin *Pygoscelis adeliae* (HOMBRON et JACQUINOT 1841)

In 1980 the period of colony formation and occupation of breeding territories lasted from 28 September to 18 October. After the territories were established both birds as a rule stayed at the nest, the female till the laying of the second egg and the incubating male till the hatching of chicks. However, it was found that at that time independently of the size of the breeding group, about 18% of the birds (non-breeders of unidentified sex) left land in early morning hours and returned from 16.00 to 19.00 hours (Table IV, period 1). From among 681 such specimens, 468 did not build nests and 193 took part in courtship and nest building but did not lay eggs. The males that had lost the eggs by predation or by their having been buried in snow, stayed on the empty nest up to the mass hatching of chicks.

In the period of chick feeding, to about the 10th day of their life, the returns of adults began by 16.00 hours but in the season of 1978/1979 the most adult birds stayed in the colony between 19.00 and 21.00 (Table IV, period 3a). Between 23.00 and midnight the Adélie penguins went out of the colony to the shore, where they gathered in groups before swimming out to their foraging areas. The increase in the number of penguins at 03.00 was caused by the late return of specimens, which had gone to sea as early as the previous day. Their breeding partners usually left the colony at about 08.00. The above-presented rhythm of quantitative changes characterized both the birds banded in different breeding groups and a breeding group consisting of 370 pairs (Table IV, period 3a). In the 1980/1981 season the birds left the colony between midnight and 02.00. In that season the quantity peak for the Adélie penguins staying on land was very much extended in duration; it began as early as 11.00—14.00 hours and lasted till midnight (Table IV, period 3a).

When the crèches had been formed, many parent Adélie penguins stayed in the colony only at the time of chick feeding. For this reason the quantitative fluctuations in a 24-hour period were greater than in the period when the birds occupied their breeding territories (Table IV, periods 3a, 3b and 3c). In the first phase of the stay of the young in crèches, that is, till their moult, the mass departures of adult birds from the colony were observed after 04.00 and lasted

Table IV

The mean numbers of *Pygoscelis adeliae* present on land in successive hours in different phenological periods. All designations as in Table II

Hours (local time)	Phenological periods						
	I		3a			3b	3c
	Breeding groups in 1980 1580 p. 77 p.		Breeding group 370 p. in 1978/1979	Birds (1978/ 1979)	marked (1980/ 1981)	Birds marked in 1978— 1981	Birds marked in 1978— 1981
1	—	—	740—	562—	125—	80+	71+
2	—	—	725—	521—	108—	75+	73+
3	3629+	176+	813	614	100—	78+	119+
4	3352	166	765	560	114—	124+	58+
5	3188—	165	760—	576	121—	60+	37
6	3106—	161	740—	524—	123—	38	23
7	3054—	158—	700—	543—	124—	25—	13—
8	3024—	157—	685—	503—	139—	17—	17—
9	3001—	156—	690—	535—	154	19—	12—
10	2978—	155—	696—	526—	153	12—	8—
11	2962—	155—	710—	551—	163+	9—	5—
12	2949—	155—	704—	553—	160	8—	5—
13	2949—	156—	775	606	161	14—	2—
14	2948—	157—	813	608	169+	15—	4—
15	3171—	159	833	595	176+	16—	12—
16	3264	160	854	634+	168+	28—	25
17	3598+	164	900+	649+	174+	39	32
18	3620+	170+	915+	659+	172+	46	27
19	3629+	175+	970+	685+	175+	44	33
20	3629+	175+	1075+	744+	175+	62+	41
21	3629+	170+	980+	703+	175+	78+	38
22	—	—	960+	627+	174+	74+	65+
23	—	—	920+	623+	161+	78+	61+
24	—	—	745—	548—	165+	80+	71+
Mean number in 24 hrs	3246,3	162,6	811,0	593,8	151,2	46,6	35,5
Confidential limits ($\pm m$)	136,9	3,7	47,0	26,6	10,5	13,3	12,4

until 11.00. Between 03.00 and 04.00 there was however an increase in the number of the Adélie penguins owing to the returns of birds which had swum out to sea on the previous day. The returns from the sea occurred chiefly between 19.00 and 21.00 and lasted till midnight (Table IV, period 3c). In the period of moult of the young the same rhythm of 24-hour changes in the number of parent birds persisted. As a result, the young received food once a day.

The largest numbers of non-breeders left their resting areas between 02.30 and 03.30 and their mass returns to the groups resting on snow took place from 15.30 to 21.30 and so earlier than the returns of the breeding penguins.

The moult of the young being over, the adult Adélie penguins left the regions of the colonies. Only a small number of specimens remained for the period of moult. There was no area of mass moult of adult Adélie penguins on King George Island in 1981. Some groups, few in number and consisting of 15—320 specimens (2100 altogether), were moulting on icebergs drifting close to the coast of the island. This number however formed a slight proportion of the population of the island, numbering 59356 pairs in 1980/1981. Some fragmentary data concerning 1979 and 1980 seem to confirm this situation.

Adélie penguins were encountered irregularly and few in number in winter. More numerous groups appeared at the end of June and in the first half of July 1980 and were observed, while they were walking on ice or resting in the vicinity of the unfrozen parts of the bay.

3. Chinstrap penguin *Pygoscelis antarctica* (FORSTER 1781)

The period of colony formation and the establishing of breeding territories lasted from 28 October to 8 November in 1980. When the territories had been established, about 78% of the specimens (of 144 covered by observations) still stayed in the colony till the eggs had been laid. The other specimens (i. e. 32 birds, 22%) swam out to sea, where they usually foraged for 6—7 hours, but some of them did not return on to land before a lapse of 1—3 days. In that period the departures from the colony between 04.00 and 07.00 hours and fairly numerous returns between 16.30 and 18.30 (Table V, period 1). From among those 32 birds swimming out to forage, only 2 participated in breedings; 2 had no territories and 28 took part in courtship and nest building but had no eggs.

In the period of egg incubation the partners usually changed over at the nest every 1—3 days (Table III). The penguins left the colony for the sea gradually between 04.00 and 07.00 hours and the returns took place between 17.30 and 19.30 (Table V, period 2). In the period of chick feeding, until they were about 10 days old, the diurnal rhythm of adults resembled that in the previous period (Table V, period 3a). The increase in the number of birds noted after 05.00 hours was caused by the return of specimens staying at sea longer than a day. In the period of chick feeding, from the 10th day of their life onwards, the lowest number of adults was observed about 05.00 and between 13.00 and 15.00 (Table V, periods 3b and 3c). It was then that the mass departures of birds to forage occurred (one of the parent birds in the morning and the other in the afternoon). Young Chinstrap penguins therefore received food twice daily. The evening maximum numbers falling from 17.00 to 21.00 (Table V, period 3b) and from 19.00 to 21.00 (Table V, period 3c) were caused by the returns of birds which foraged after 09.00 hours and by the lingering of other birds at their nests till the return of the partner. Not numerous penguins that

left the colony after 21.00 returned to it after midnight. This rhythm of diurnal quantitative changes characterized both marked birds in mixed Chinstrap-Adélie colonies in the neighbourhood of the H. Arctowski Station and in an isolated one-species group at Demay Point.

Table V

The mean numbers of *Pygoscelis antarctica* present on land in successive hours in different phenological periods. All designations as in Table II

Hours (local time)	Phenological periods							
	1	2	3a	3b			3c	4
	Birds marked in 1978—1981			Breeding groups in 1979/1980		Bird marked in 1978— 1981	Birds marked in 1978—1981	
				Demay Pt. (156 p.)	Arctowski St. (79 p.)			
1	—	142+	140+	312+	158+	172+	164+	—
2	—	142+	146+	312+	158+	170+	154+	—
3	144+	137+	145+	294	147	162	160+	—
4	137+	134+	111	245	126	146	133	—
5	120	117	139+	153—	76—	95—	90—	—
6	118	106	124	257	130	153	152+	196+
7	116	92	124	275	142	163+	148+	176+
8	102—	90—	106—	281	151	166+	116	99—
9	102—	90—	88—	245	126	140	122	81—
10	101—	91—	89—	239	126	142	124	84—
11	103—	92—	91—	202	107—	113—	102—	79—
12	102—	90—	87—	183	104—	124	119	80—
13	106—	93—	83—	104—	51—	57—	51—	80—
14	114	95—	80—	92—	47—	50—	36—	87—
15	120	97—	103—	122—	79—	89—	82—	98—
16	120	94—	108—	245	124	138	117	145
17	131+	100—	130+	300+	151	167+	131	176+
18	132+	128+	128+	355+	172+	173+	135	180+
19	140+	136+	126	422+	212+	245+	218+	180+
20	140+	136+	139+	330+	163+	190+	146+	180+
21	140+	138+	127+	318+	169+	175+	155+	181+
22	—	137+	133+	281	147	151	133	—
23	—	138+	137+	275	142	147	131	—
24	—	138+	138+	275	142	156+	148+	—
Mean number in 24 hours	120,4	114,7	117,7	254,9	131,7	145,2	127,8	131,3
Confidential limits ($\pm m$)	7,3	9,2	9,0	40,0	20,1	10,6	15,9	25,8

In the moulting period adult penguins stayed in rock recesses sheltered from the wind. The abundance of Chinstrap penguins this time was dependent upon what proportion of the whole population the moulting birds formed. The birds that swam out to feeding areas were in the premoult or postmoult stage. Their diurnal rhythm was marked by their taking a short time to depart from the colony (from 06.30 to 07.30). Between 08.00 and 15.00 the number of penguins present on land was smaller than the mean diurnal number (Table V, period 4). The mass returns to the colony began as early as between 15.30 and 16.30 and included both the birds that had gone to sea in the morning and those which had left a few days before (Table III).

IV. COMMENTS ON RESULTS

Gentoo penguin

Gentoo penguins left land 0.5—2.5 hrs before dawn. Mass departures took 1.5—2.0 hrs. The most numerous returns began 2.5 hrs before sunset and lasted till sunset. In connection with differences in the times of sunrise and sunset between particular seasons of the year the time of departures from and returns on to land changed (Fig. 2). As a result, the highest number of Gentoo penguins present on land occurred from evening to morning (i. e. after the completion of evening foraging and before swimming out to sea in the morning). Night counts, before sunrise, were possible only at the end of December and at the beginning of January, because it was light then. In the other periods counts were possible only in the evening, i. e. 2.5 hrs before sunset. In the period when the birds occupied breeding territories counts in the hours of the maximum abundance were justified in the case of studies of the whole population, that is, including non-breeders. When the breeding territories had been established and at the time of egg incubation the highest number of penguins in the colony was noted from 18.00 hours till night and in the period of chick feeding — until they were 10 days old — from 17.00 to 19.00 and from 21.00 to 22.00. On the other hand, the estimation of the numbers of breeding pairs was possible all over the day, for one of the partners as a rule remained at the nest. The materials collected in the 1980/1981 season however showed that the pairs which had lost their eggs owing to intense snowfall returned to the nest but they maintained the same diurnal rhythm as did non-breeders. To determine the number of such pairs in the season of unfavourable atmospheric conditions it was necessary to carry out counts also in the evening. Moreover, evening counts were expedient in the period when the young stayed outside the nest territory, i. e. in their premoult period, (counts at 18.00—19.00 and 21.00—22.00) and in the moult period, when the maximum number of adults occurred between 18.00 and 22.00 hours. Besides, the evening counts provided the correct appraisal of the number of birds in the autumn-winter periods of nomadic life. In

these phenological periods 52.9—59.6% of the population stayed on land all day and did not forage till mid-May and 13.5—24.3% from mid-May to mid-July. In view of changes in the day length, the times of appropriate counts also underwent changes: the maximum number settled between 16.30 and 17.30 till mid-May and between 14.00 and 15.00 from the second half of May till mid-July. In the autumn-winter period counts should be carried out as frequently as possible also, because the number of birds returning from sea changed according to the changing air temperatures. Although the number of hours with daylight was considerably differentiated in particular seasons of the year, the time designed for foraging did not undergo a change and averaged 3—6 hrs. Foraging was found to be shorter in the evening (2—3 hrs) only in the breeding season. And so my observations of shorter foraging in the evening confirm the data presented by BAGSHAWE (1938). In the breeding season there also happened sporadic shorter excursions to foraging areas connected with the fact of the swarming of *Euphasiacea* shoals deep into Admiralty Bay. Fairly large intervals between the arrival in and departure from the colony in the breeding season, shown in Fig. 1, are only apparent, for the change-over of the parents in the middle of the day is not taken into account in Fig. 1. This is so because the number of Gentoo penguins did not reach maximum values at that time. In order to obtain the average time given by one specimen to foraging in the breeding season, the number of hours between the mass departure from the colony and the mass return should be halved (both parent birds go foraging). The combined return of groups composed of specimens that stayed at sea for different numbers of days (Table III) suggests that particular birds and groups came into contact with each other in the feeding area. This permits the supposition that in particular phenological periods the distribution of feeding areas was rather uniform.

Adélie penguin

After the establishing of breeding territories quantitative estimation was possible through the day till the laying of the second egg, because then the pairs did not leave the colony. Quantitative fluctuations within a 24-hour period were brought about only by the non-breeders, which formed 18% of the population and at that time stayed together with the breeding birds. In that period the hours after 16.00—17.00 turned out to be the most suitable for estimating the size of the whole population. It should however be kept in mind that the results obtained come from two groups from only one season, and so they ought to be checked in several seasons. In the period of incubation the number of birds was rather stable, for even after egg loss the incubating males remained at their nests until mass hatching. This is therefore the most suitable period to estimate the number of breeding pairs. In the period from the completion of hatching of chicks to the formation of their crèches the highest number of Adélie penguins stayed in the breeding area, for then both

breeders, non-breeders and the birds that had lost their clutches were present on land (SAPIN-JALOUSTRE, 1960; TAYLOR, 1962; PENNY, 1968; SPURR, 1975). At that time the size of the whole population could be estimated between 16.00 and 24.00 hours (Fig. 2). In these hours the parent birds changed over at the nest. The pattern of change-overs consisted in that one of the parents stayed at the nest for 24 hours, while the other was foraging. In consequence of this diurnal rhythm of foraging the young Adélie penguins received food once daily. The fact that feeding occurred once in a 24-hour period was connected with the long-distance wanders of birds to the foraging areas (JABŁOŃSKI, 1985). At the time when the parent birds changed over non-breeders and the birds which had lost their clutches also arrived in the colony. The hours in which the maximum number of Adélie penguins occurred underwent changes both in the course of development of the young (Fig. 2) and in different breeding seasons (Table IV). It should be supposed that this was due to changes in the area where *Euphausiacea* shoals appeared in particular seasons (JABŁOŃSKI 1985). When the young abandon the nests and form crèches, the returns of adults on to land are considerably prolonged in time, for with the retention of the 24-hour rhythm of the previous period (feeding by one of the parents once a day) the bird arriving with food stays in the colony only a few hours. The markedly prolonged time of returns caused that the times of departure were also differentiated. As a result of such a 24-hour rhythm only the guarding parents stayed in the region of the crèche all day long. It was found on the basis of three-year observations that the guarding parents occurred in the largest number 3—4 hours before midnight. A scheme of diurnal rhythm, worked out on the basis of materials collected in the seasons 1978/1979 and 1979/1980, was consistent with the opinions expressed by D. MÜLLER-SCHWARZE (1968), D. MÜLLER-SCHWARZE and C. MÜLLER-SCHWARZE (1971), YEATES (1971), AOYANAGI (1973), CRAWFORD (1975), PAULIN and SAGAR (1977) and SPURR (1978), according to whom the greatest numbers of Adélie penguins occurred on land before midnight. In the season of 1980/1981 the quantitative peak in the colonies was however extended in time and differed both from the data in literature and from the author's own materials concerning preceding seasons. SPURR (1978) supposes that the differentiation of the diurnal rhythm of Adélie penguins may be due to different weather conditions. Some modifications of the times of departures from and arrivals in the colony are brought about by the distance of the breeding areas from the shore-line and from the places of *Euphausiacea* shoals, for TAYLOR (1960) described such cases from Cape Royds that Adélie penguins wandered 16 km on ice to reach the sea. The materials gathered in the region of Admiralty Bay support the data from literature about the influence of the distance of the breeding area from the sea on the diurnal rhythm. The Adélie penguins that nested on hills 150—200 m away from the shore left their breeding areas 30—45 minutes before the penguins that inhabited beach-ridges, about 30—40 m from the sea.

The evening hours (after 17.00) appeared to be the most suitable to determine the number of non-breeding penguins in the period of chick feeding.

Chinstrap penguin

These penguins began to depart from the colony as early as 1 hr before dawn, but left it in the largest numbers at dawn and up to 3 hrs. after dawn. In spite of the variable number of hours with daylight the time of departures from the colony was fairly steady and in the breeding season fell between 03.00 or 04.00 and 06.00 or 07.00 hours. The estimate of the number of birds before morning foraging was possible only from the end of December to the beginning of January, i. e. to the completion of egg hatching. At that time the departures started at dawn and counting was facilitated by light nights. The possibility of morning counts was however limited to 1 hour. During the morning peak of abundance between 06.00 and 08.00 hours, when the parents changed over, nearly exclusively breeding penguins stayed in the colony. In the breeding season therefore the most suitable time of counting occurred at the evening peak of abundance, between 17.00 and 21.00. This peak underwent slight modifications according to the day length and the phenology of Chinstrap penguins (Fig. 2). And so, e. g. in the period of feeding of chicks up to the 10th day of their life the most birds stayed on land from 17.00 to 03.00 on the next day, and in the moulting period of the young from 19.00 to 21.00. In the period of breeding territory defence evening counts appeared useful exclusively for the determination of the total number of the population, for at the time of the evening peak both the parent birds, nonbreeding birds and those which had lost their clutches and irregularly stayed at the nests were present in the colony. The actual number of breeding pairs could be determined throughout the day, because one of the parent birds always remained with the young. In the moulting period of adults only evening counts from 17.00 till night were representative. In the daytime, between 08.00 and 15.00, the mean numbers were lower than the confidence interval of the mean diurnal number.

Observations of the marked penguins of all the three species indicate that in individual cases the stay outside the breeding colony for a few days may be associated with the landing of birds a long way from the colony. This was observed, among others, in connection with the appearance of such predators as killer-whales and leopard seals.

The materials contained in this paper permit the following generalizations:

1. In the breeding season the most suitable time for counting penguins of the genus *Pygoscelis* on King George Island fell between 17.00 and 21.00 hours L. M. T., after breeding 1—1.5 hrs before dark.
2. In the incubation period Gentoo and Chinstrap breeding partners change over at the nest after 1—14 days (most frequently 1—3 days). A similar frequency of arrivals on land was also found in the post-breeding period. In the period of chick feeding each parent bird to these two species swam out to forage once in a 24-hour period and consequently their chicks received food twice

daily. As regards Adélie penguins, only one of the parents brought food and in this connection the chicks received food once a day. This information is significant for the estimation of the quantity of food consumed by a population.

3. The differentiation of the stay of penguins on land and in foraging areas in respect of time and the resulting differentiation of the frequency of chick feeding are most probably conditioned genetically by the derivation of particular species of the genus *Pygoscelis* from different geographical regions. According to KOROTKEVICH (1960) and WATSON et al. (1971), the Gentoo and Chinstrap penguins belong to subantarctic forms and Adélie penguins to antarctic (continental) ones. It may be supposed that the fact of their taking food once daily is conditioned by the existence of a broad ice zone, separating colonies from the open sea, and so by the climate prevailing in the region of the Antarctic continent.

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STRESZCZENIE

Przeprowadzono analizę zmian ilościowych *Pygoscelis papua*, *P. adeliae* i *P. antarctica* w ciągu doby w rejonie Zatoki Admiralicji (Wyspa Króla Jerzego, Południowe Szetlandy) w latach 1978—1981. Ilość liczeń podano w tabeli I. Oceniano stan ilościowy oznakowanych pingwinów z wybranych grup lęgowych i skupień w miejscach odpoczynku co 1 godzinę. W okresach nielegowych liczenia rozpoczynały się przed świtem i trwały do nocy. Na podstawie przedziału ufności średniej ilości dobowej ustalono godziny, w czasie których występuje maksymalna ilość osobników (Tab. II, IV, V). Pomimo różnic w rytmie dobowym badanych trzech gatunków pingwinów oraz zmienności tego rytmu w obrębie gatunku w zależności od okresu fenologicznego, stwierdzono, że: 1. najodpowiedniejszą porą liczeń w okresie lęgowym są godziny 17—21 czasu lokalnego; 2. w okresie połęgowym od 1 do 1,5 godziny przed zmrokiem, tj. od 16,30—17,30 do połowy maja oraz od 14 do 15,30 w okresie od połowy maja do połowy lipca.

Stwierdzono, że zmiany partnerów przy gnieździe wśród *P. papua* i *P. antarctica* w okresie wysiadywania jaj odbywają się po upływie 1—14 dób (najczęściej 1—3 dób), a powroty na ląd w okresie jesienno-zimowym po upływie 1—7 dób (Tab. III).

Stwierdzono też, że u *P. adeliae* jeden osobnik rodzicielski przynosi pokarm młodym jeden raz w ciągu doby, a u *P. papua* i *P. antarctica* oboje rodzice. Wysunięto przypuszczenie, że zróżnicowanie częstości karmienia młodych uwarunkowane zostało na skutek pochodzenia tych gatunków z odmiennych rejonów geograficznych (*P. adeliae* z rejonu antarktycznego, a *P. papua* i *P. antarctica* z rejonu subantarktycznego).

Redaktor pracy: prof. dr Z. Bocheński

for breeding

Phot. 2

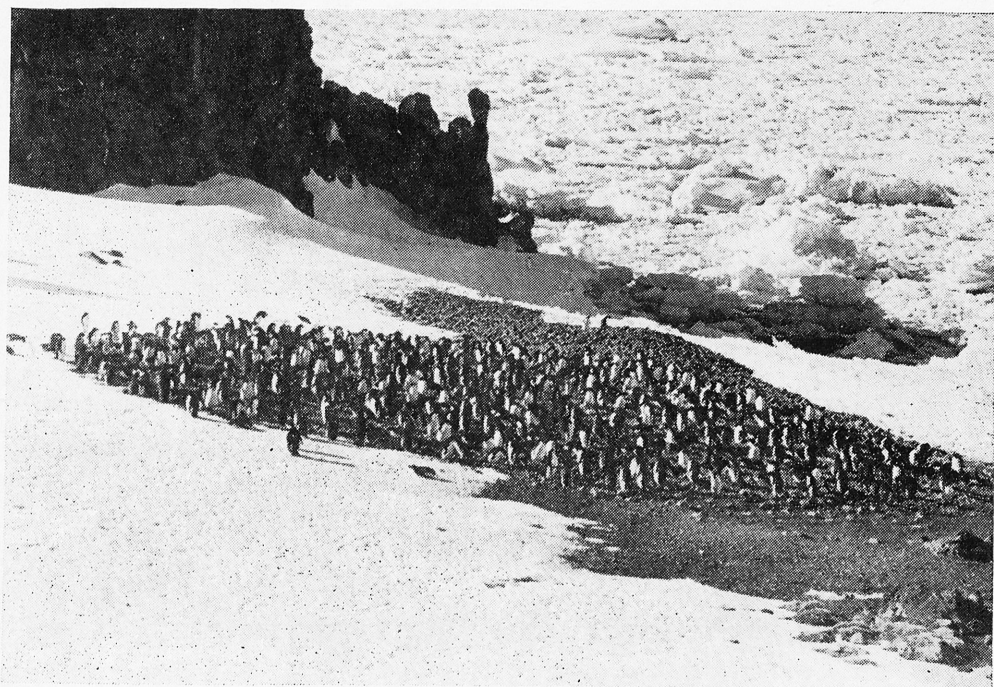
Plate XIX

Phot. 1. The breeding group of *Pygoscelis adeliae* consisting of 384 pairs after the establishing of territories. Picture is taken on 28 Oct. 1980 at 12.00—12.30. On that day the first egg was layed. Such photographs helping in bird counting were taken at intervals of 1 hr.

Phot. B. Jabłoński

Phot. 2. The same breeding group on 7 Dec. 1980 at 12.00—12.30. On that day mass hatching had started. By many nests two birds can be seen because it was the time of changing of partners on the nests after return of females — on the right side of picture the group of males departing for foraging

Phot. B. Jabłoński



Phot. 1



Phot. 2

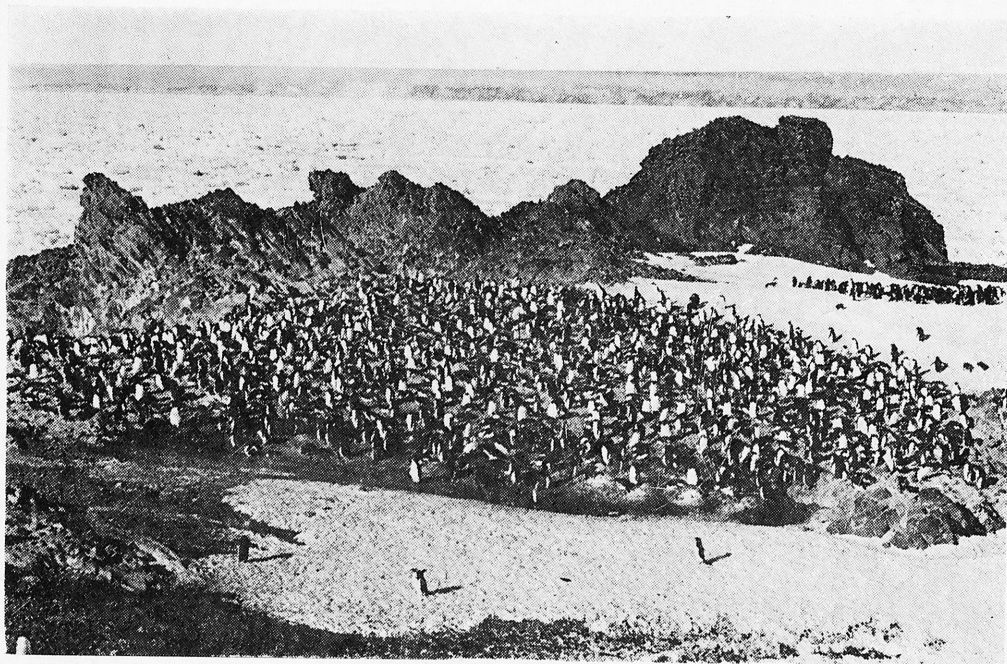
Plate XX

Phot. 3. The breeding group of *Pygoscelis adeliae* consisting of 605 pairs after the establishing of territories. Picture taken on 31. Oct. 1980 at 12.00—12.30. The females incubating the first egg are seen

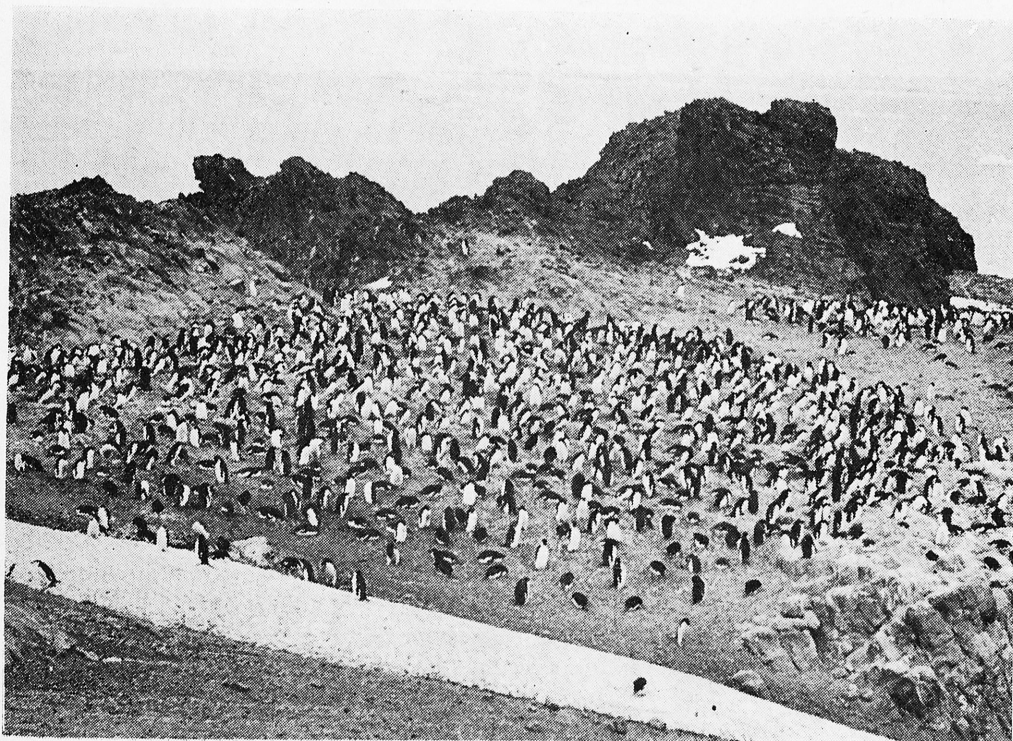
Phot. B. Jabłoński

Phot. 4. The same group on 7 Dec. 1980 at between 15.00 and 16.00

Phot. B. Jabłoński



Phot. 3



Phot. 4

