BREEDING SEASONS AND SEXUAL DIMORPHISM
IN ROCKHOPPER PENGUINS[1]

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VISITS to Campbell Island (52° 33′ S, 169° 09′ E) from 8 to 26 January 1969 and to Antipodes Island (49° 40′ S, 178° 50′ E) from 28 January to 12 March 1969 permit some comparisons between two breeding populations of the Rockhopper Penguin (*Eudyptes chrysocome*) and supplement data gathered at Macquarie Island between 1959 and 1961 (Warham, 1963). The present paper forms part of a series to deal with aspects of the breeding biology of all the *Eudyptes* penguins.

Bailey and Sorensen (1962) describe the distribution and breeding of the Rockhopper Penguin at Campbell Island, which supports many more Rockhoppers than other penguin species. Small numbers of Erect-crested Penguins (*E. sclateri*) also nest there, and Royal Penguins (*E. chrysolophus schlegeli*) are not rare though not known to breed. The Yellow-eyed Penguin (*Megadyptes antipodes*) is the most plentiful penguin after the Rockhopper, but breeds among thick vegetation well away from the latter bird. At Antipodes Island Rockhoppers share breeding beaches and coastal slopes with large numbers of *E. sclateri*. The latter generally occupy the lower and reasonably flat ground above high water while the Rockhoppers nest higher up, often on steep slopes or within shallow caves. At this island the two species appear to occupy nesting niches equivalent to those Royals and Rockhoppers take up at Macquarie Island where, when the two species are contiguous, the latter again lay higher up among talus debris consolidated by soil, or among tussock grasses.

At Campbell Island the data were collected from live birds at a small colony in Rocky Bay below Mt. Dumas and at a larger one at Penguin Bay. At Antipodes Island Rockhoppers occur mainly on the east and south coasts; the data here were gathered at two colonies in the vicinity of the expedition base at Reef Point on the eastern side of the island. Colony locations with indications of size are being mapped and will appear with a general account of Antipodes Island birds (Warham and Bell, MS.).

THE TIMING OF THE BREEDING CYCLE

Rockhopper chicks on Antipodes Island in 1969 were at a more advanced stage of development than were those on Macquarie Island at the same dates in 1960 and 1961. Thus on 5 February 1969 many were completely feathered and by 9 February some had already left for the sea. The main chick exodus occurred within the next 7 days and all the chicks had gone from the Reef Point colonies by 20 February. Indeed, after about 15 February most colonies were almost deserted for the yearlings had molted and left, although at some of the bigger colonies on the south coast a sprinkling of birds remained, mostly in molt. These probably included a number of failed breeders, but a last check of the nesting areas at Reef Point and at Alert Bay 1 mile farther south on 10 March showed these colonies empty and the breeding birds still at sea feeding in anticipation of their annual molt.

Comparing these data with those from Macquarie Island shows that the season at Antipodes Island is about 12 days earlier. This would set the peak of egg-laying (the date at which 50 per cent of the pairs have laid one egg and 50 per cent have laid two) at approximately 1 November, as this peak is around 13 November at Macquarie Island. This estimate is confirmed by E. G. Turbott who made several landings at Antipodes Island between 4 and 10 November 1950. He reports (pers. comm.) that during this period most birds were sitting on two eggs, the larger one being clean and thus new-laid.

Compared with Macquarie Island chicks, those at Campbell Island were also somewhat advanced but less so than the Antipodes Island birds. Thus 47 chicks on 10 January had a mean weight with one standard deviation of 1312 ± 272 g as compared with a weight of approximately 600 g at Macquarie Island for the same date. Similarly 41 chicks from the same group weighed 1577 ± 339 g on 17 January compared with a mean for that date of about 1150 g at Macquarie (Warham, 1963, Figure 3). These data, in conjunction with the dates listed by Bailey and Sorensen for various episodes of the breeding cycle, indicate a peak of egg-laying at Campbell Island about 4 days earlier than that at Macquarie, i.e. about 9 November.

Many years ago Murphy (1936) drew attention to the wide variations in the breeding seasons of the different populations of this penguin and noted that these were correlated with latitude. The breeding islands lie on both sides of the Antarctic Convergence and between 36° and 53° S. The data available to Murphy were rather fragmentary but later work enables this variation to be examined more precisely.

Breeding data are given by Paulian (1953) for Amsterdam Island and Kerguelen; by Elliott (1957) for Tristan da Cunha; by Swales

(1965) for Gough Island; by Murphy (1936), Pettingill (1960), and Strange (1965) for the Falklands; by Murphy (1936) for Ildenfonso Island, Cape Horn; by Downes et al. (1959) for Heard Island; and by Rand (1954) and La Grange (1963) for Marion Island.

I have either taken the dates for the peaks of egg-laying from these authorities or, where they do not give them, have calculated the dates by assuming that the lengths of the various stages of the breeding cycles do not vary appreciably from those at Macquarie Island as detailed in my previous paper and also that the breeding dates have not altered appreciably in recent years. At Macquarie Island for instance the timing of the season today seems to be the same as it was 50 years ago.

When these dates are plotted against latitude a rough correlation is revealed, but with Heard Island and Kerguelen lying well away from the trend line; the birds breed later here than at other colonies in similar latitudes. Plotting the peak of egg-laying dates against mean annual sea temperature produces the linear relationship shown in Figure 1. These temperatures have been taken from Stonehouse (1967) who derived them from the isotherm charts for February, May, August, and November rather than from actual determinations at sea near the islands, although they agree with data from other sources where these are available.

The egg-laying data for most of these islands are still imprecise and errors of several days may be involved owing to the necessity of deducing egg-laying peaks from hatching dates, for instance. The information for the Falklands illustrates this. Murphy (1936: 423) stated that the first eggs are laid in the last days of October, that within 3 days a colony will be well sprinkled with them, and that before a week has passed there will be at least one egg in practically every nest. From this I estimate a peak of laying around 6 November as at Macquarie most eggs are laid over a 10-day period. Murphy's figures suggest therefore that laying at the Falklands is about a week earlier than at Macquarie, as plotted in Figure 1. At Beauchene Island, about 60 miles south of the main group, Strange (1965) found the birds with young only a few days old on 2 to 6 December, 1964, perhaps as much as a fortnight in advance of those at Macquarie. Yet Pettingill (1960) working at New Island, estimated that on 29 December 80 per cent of the birds had chicks varying from day of hatching to 1 week old, 10 per cent chicks older than that, and 10 per cent with eggs. Thus hatching there seems to have been at a peak around 25 December which, allowing for an incubation period of 33 days and 4 days between first and second eggs would give a peak of egg-laying of about 20 November —considerably later than at Macquarie Island.
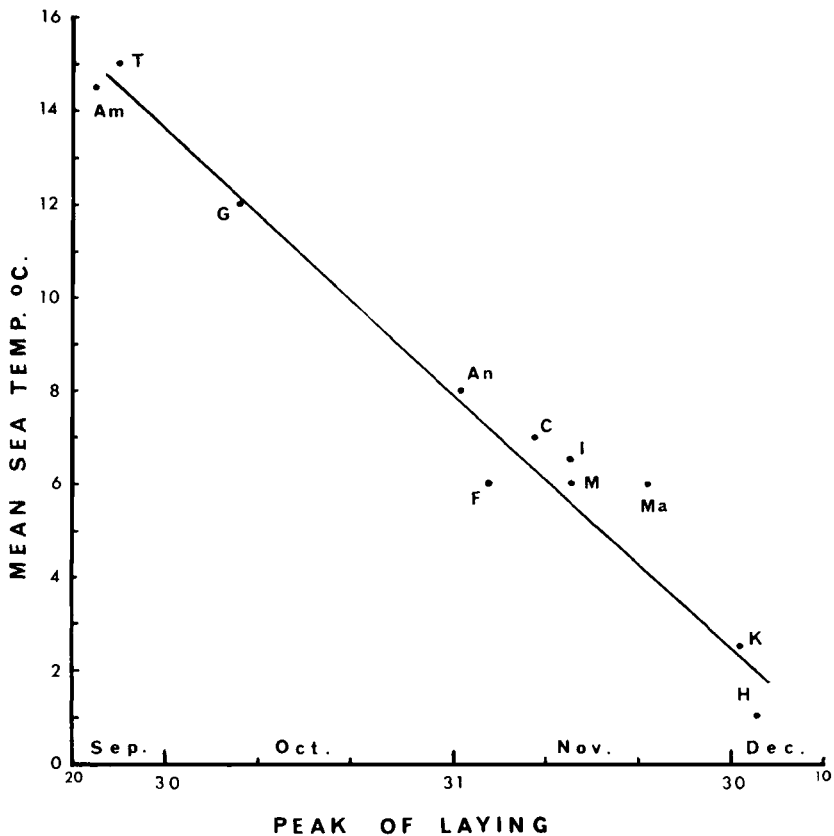
Figure 1. The relationship between the date of peak of egg laying and mean annual sea temperature. Am, Amsterdam Island; An, Antipodes Island; C, Campbell Island; F, Falklands Islands; G, Gough Island; H, Heard Island; I, Ildenfonso Island; K, Kerguelen; M, Macquarie Island; Ma, Marion Island; T, Tristan da Cunha.

Possibly Pettingill's chicks were older than he thought, but he also drew attention to differences in the ages of chicks in different sections of a colony that was broken up into discrete parts by headlands. Hence laying dates may perhaps vary even on the same island from one colony to another. A variation in the development of chicks between colonies on the same breeding station has also been noted in *Eudyptes chrysolophus* (Downes et al., 1959: 13; Warham, 1971).

Despite such inconsistencies it is clear that the peaks of laying differ by over 3½ months between islands at the extremes of the species range, and Figure 1 suggests that the dates of laying advance about 10 days for each degree centigrade rise in mean sea temperature.

Such a correlation is not surprising for a bird spending most of its life in the sea, but whether the link is a direct one and temperature, for example, influences gonad resurgence via sensory input to the hypothalamus, or is indirect, perhaps by way of the food supply, can only be conjectured. We know little of the food spectra of the birds at various breeding stations nor of their wintering areas at sea. Stonehouse (1967) discusses the physical factors that may affect penguins at sea. Being highly specialized animals, not least in their temperature regulatory mechanisms, each species may well be imprisoned within a narrow span of isotherms for which it is physiologically adjusted—to use his phraseology. Swales (1965) also suggests that small differences from year to year in penguin landing dates at Gough Island may be related to differences in the position of the subtropical convergence and hence of sea temperature.

According to Stonehouse's figures the mean sea temperature at South Georgia resembles that at Heard Island, although at South Georgia the extremes of sea temperatures are greater and these may have a bearing on the absence of the Rockhopper from South Georgia as a breeding species (Carrick and Ingham, 1967).

Marion Island seems to show a considerable divergence from the correlation with sea temperature. Judging from the information given by Rand (1954) egg-laying is at a peak there about 10 days later than it is at Macquarie Island although both places have similar mean sea temperatures. His data are supported by those of La Grange (1963) whose figures suggest a peak of laying around 21 November. That the birds should lay late here is particularly anomolous as Stonehouse's data show air temperatures at Marion are appreciably higher than at Macquarie Island.

While the bird's late arrival at Kerguelen and Heard Island may well be influenced by the cold local conditions induced by their extensive ice sheets, there appear to be no physical barriers preventing earlier landings, and the congeneric Macaronis (*E. c. chrysolophus*) arrive about 14 days before the smaller Rockhoppers do.

Interspecific competition with larger Eudyptids could also be a factor affecting laying dates, for wherever two Eudyptids breed abundantly on the same island, it is the smaller Rockhopper that arrives and lays last. At Amsterdam, Tristan da Cunha, Ildenfonso, and Gough Islands there are no other Eudyptids, at the Falklands only a few Macaronis, and at Campbell Island only a few Erect-crested Penguins. Large numbers of *sclateri* breed at Antipodes Island and *chrysolophus* at Macquarie, Marion, Kerguelen, and Heard Islands. At such places there seems to be little overt competition between the two species except possibly for

nesting sites, although some fighting does occur. On the other hand, competition may be important at sea. As all three species seem to feed their chicks almost daily, the feeding range during chick rearing must be limited. Competition seems quite likely to occur then and perhaps at other times during the year, and the later laying of the Rockhopper could have evolved in response to this kind of competitive pressure.

If such an effect exists it is not immediately apparent from the data. For example, laying at Campbell and Ildenfonso Islands, where Rockhoppers have little or no Eudyptid competitors, is not particularly early. Furthermore where the Rockhopper breeds in company with a larger Eudyptid, the feeding periods for the chicks of the two species overlap for about a month despite the later laying of the smaller species. Competition would be reduced, of course, if the two species took different sized prey, as they may well do judging from interspecific differences in bill size.

The later laying of the Rockhopper could be due simply to later arrival in consequence of its smaller size and a reduced capacity for heat retention in comparison with the larger species.

The role of sea temperature in the timing of the laying season is thus by no means clear, and this discussion draws attention to the need for more precise information on the breeding seasons and food preferences at the different islands.

SEXUAL DIMORPHISM

It has long been known that adult male Rockhoppers are bigger and heavier than adult females, and Murphy (1936) gave comparative dimensions based on small samples. During my previous studies of this penguin the reality of the difference in bill size was repeatedly confirmed because the birds could be sexed at copulation, by a sex-specific display and other behavior, and occasionally by dissection, but no birds were measured. This sex-specific display was termed the "male display" in my earlier paper. In it the bird swings its head back until the crown is vertical and then shakes its head rapidly through a narrow arc while calling loudly. In my experience this action is used exclusively by male Rockhoppers, these same birds being the ones that were uppermost during copulation, the most aggressive partners in defense of the nest and the ones that mantled over the chicks during the guard stage (Warham, 1963: 248).

Sexual dimorphism appears also to extend to tarsal and midtoe with claw lengths, but in order to make the best use of the limited time available in the present study it was decided to concentrate on body weights and on the dimensions of beaks and flippers in attempting to
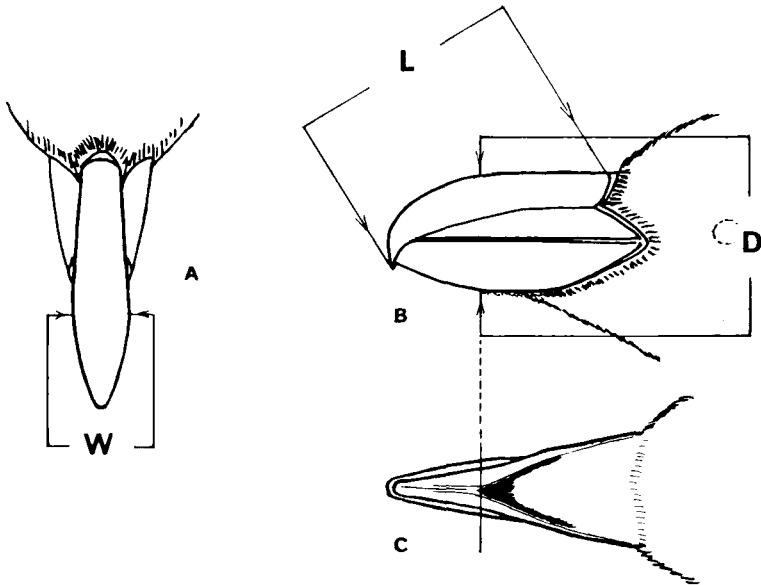
Figure 2. Methods used for bill measurements; A, culmen width (W); B, culmen length (L) and bill depth (D); C, underside of bill showing point just proximal to diverging mandibular rami at which depth was measured.

evaluate the differences and to ascertain whether they could be detected in younger birds.

The length of the flipper was determined by pressing it along a rule butting against the body at the axilla. The bill was measured with vernier calipers taking the length of exposed culmen (L), the maximum width of the culminicorn (W), and the depth of the bill (D) taken at a point just proximal to the tip of the triangular inter-ramal feather patch as shown in Figure 2. A beak shape index was then calculated as

$$\frac{LWD}{10}$$

in mm. This gives a measure of the gross size of the bill. Weights were taken using a spring balance accurate to $\pm$ 25 g.

Data were collected from 10 pairs of live adults at Campbell Island on 17 January, from a further 59 adults at Campbell Island at that date, and from 94 adults at Antipodes Island on 9 February. Yearlings measured included 24 at Campbell Island on 13 and 17 January and 32 at Antipodes Island between 9 and 14 February. Finally 72 chicks were measured at Antipodes Island between 9 and 12 February.

TABLE 1

MEASUREMENTS OF TEN PAIRS OF ROCKHOPPER PENGUINS
AT CAMPBELL ISLAND ON 17 JANUARY 1969[1]

	♂ ♂	♀ ♀	$\dfrac{♂\ ♂}{♀\ ♀} \times 100$
Bill length mm	46.4 ± 1.37 (2.95)	41.1 ± 2.05 (4.98)	113
Culmen width mm	10.6 ± 0.23 (2.17)	9.2 ± 0.25 (2.71)	115
Bill depth mm	20.7 ± 1.07 (5.17)	17.8 ± 0.67 (3.76)	116
Beak shape index	1017 ± 73 (7.18)	670 ± 64 (9.55)	152
Weight g	2757 ± 274 (9.94)	2395 ± 52 (2.17)	115
Flipper length mm	167 ± 4.4 (2.63)	167 ± 3.4 (2.04)	100

[1] Mean, one standard deviation (coefficient of variation).

The 10 pairs measured on 17 January either had chicks or were standing together at nests. In three instances the smaller bird was wet, for the guard stage of the chicks was ending and there was a fairly steady traffic of wet birds entering the colony to feed chicks and of dry ones leaving it, but few pairs to be seen with chicks. One bird of each pair measured looked heavier billed and was the more aggressive when captured. Some of these also gave the male display on reaching their nests after release. The dimensions of these paired birds are summarized in Table 1.

With the exception of flipper length, the male values for each parameter differed significantly ($P < 0.001$) from those for the females. In no dimension except flipper length was any female larger than her mate, the ranges also being mostly nonoverlapping. It might have been expected that some females would weigh more than their mates with the females going to sea daily at this date, whereas some of the males had probably only just been released from their long fasts during their guarding of the chick and thus should have been quite thin, but even in body weight the dimorphism was complete. It will be noted, however, that the males' weights were more variable, mainly due to three that weighed 3000, 3050, and 3250 g. None of these wore the dull plumage usual in birds ready to molt.

At neither island were banded birds available and it is difficult to capture pairs once chick guarding has ended. For closer examination of the size differences, data from individual birds tending chicks or believed from their behavior to be breeders had to be used. Therefore the samples of 94 Antipodes Island and 59 Campbell Island birds probably included a few prebreeders (birds in adult plumage not yet mature enough to breed) and failed breeders.
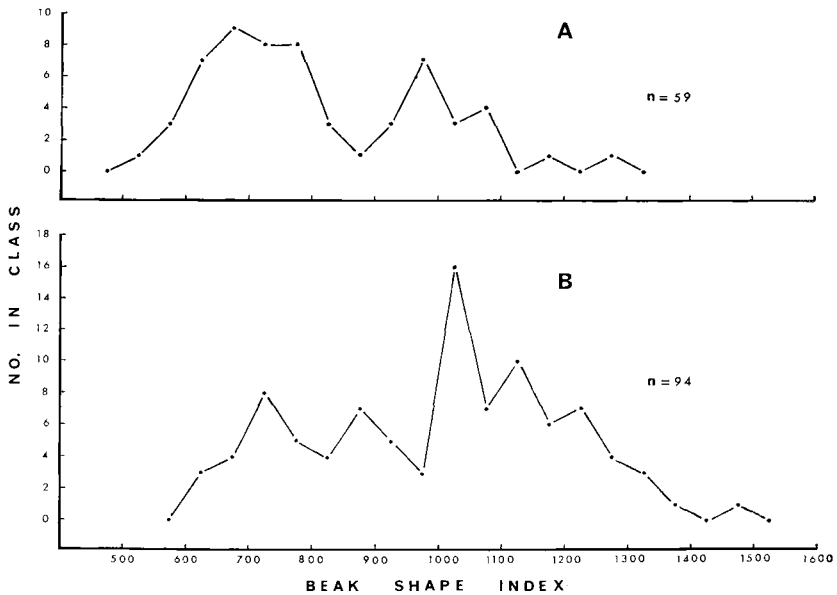
Figure 3. Distribution of adult beak shape indices, A from Campbell Island, B from Antipodes Island.

When capturing these birds it was usually impracticable to sex them by behavioral characters and none was dissected. In 11 instances measured birds were seen to give the male head shaking display. Ten of these birds were later judged to be males from their beak shape indices; the other had a value for this parameter lying in the zone of overlap.

The data from the two islands had to be handled separately as the birds' dimensions showed significant differences, Antipodes Island birds being bigger billed but lighter in weight.

ADULT BEAK SIZE

Figure 3 shows the distribution of beak shape indices in the two samples. Both polygons appear to be bimodal suggesting that two normal distributions may be involved, one for each sex, but the peaks for the two islands do not coincide. Each distribution is projected on probability paper in Figure 4.

In these graphs the points of inflexion indicate that about 43 per cent of the birds in the sample from Antipodes Island lay in the lower size class and were presumably females, whereas about 66 per cent of those in the other sample were in that category. Replotting the points that fell on either side of the inflexions on the premise that the bimodality was due to the interaction of two normal distributions, one for each sex, according to the methods of Harding (1949), produced lines CD and EF for the Campbell Island birds and GH and IJ for those
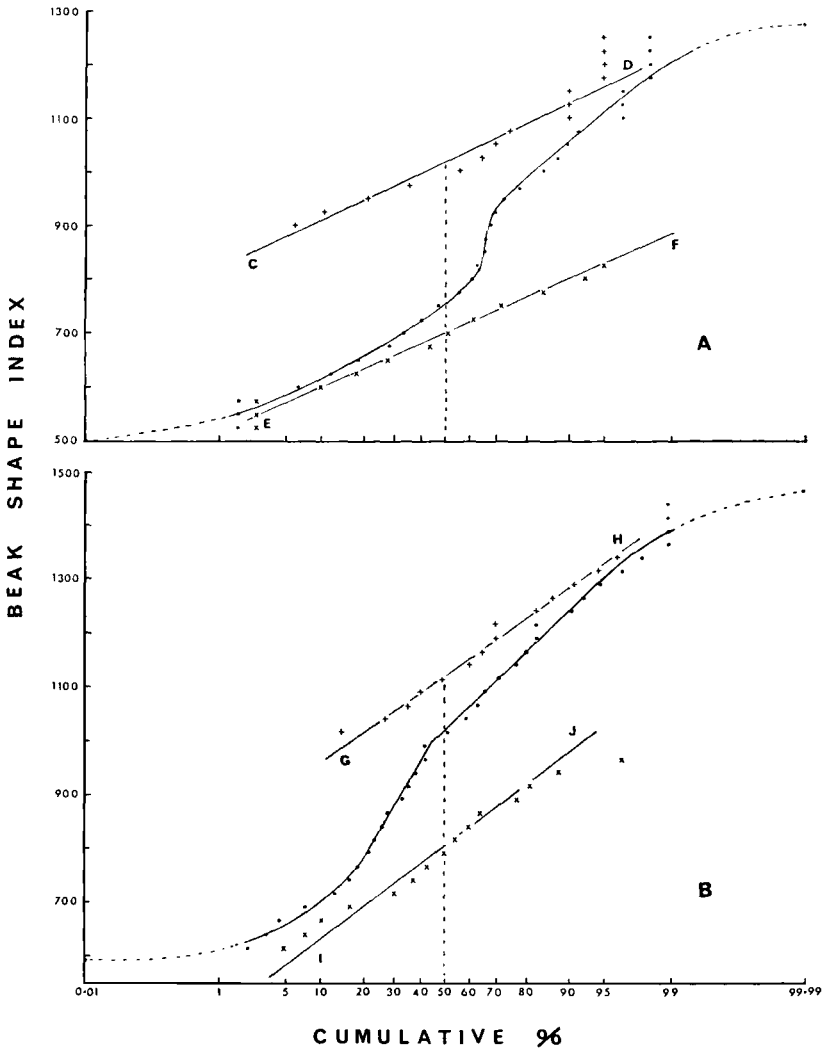
Figure 4. Polymodal frequency analysis of adult beak shape indices, A from Campbell Island, B from Antipodes Island.

for Antipodes. From these the means (50 per cent level) plus or minus one standard deviation (84.1 and 15.8 per cent levels) were read off. They are given in Table 2. In the Campbell Island sample the overlap between the sexes was quite small and at the point of inflexion includes only 2 per cent of females and 3 per cent of males whereas in the Antipodes Island sample the point of inflexion includes 8 per cent of the females and 16 per cent of the males.

TABLE 2

BEAK SHAPE INDICES FOR ADULT ROCKHOPPER PENGUINS

	Campbell Island	Antipodes Island
Females	690 ± 80 (11.6)	805 ± 135 (16.7)
Males	1010 ± 85 (8.4)	1120 ± 120 (10.7)
$\dfrac{\text{Males}}{\text{Females}} \times 100$	146	139

Using the product of length, width, and depth to measure bill size tends to emphasize differences in this character and it is not surprising that the curves for beak indices separate so clearly, the differences in the means of the two size groups being highly significant ($P < 0.001$). However when the distributions of the three components were examined separately by the same graphic technique, the bimodalities were less clear-cut and the points of steepest slope that mark the transition from one distribution to the other did not always lie close to those found when the beak index data were analyzed.

Beak widths segregated clearly, depths less so but sufficiently for analysis, whereas the tails of the curves for beak length evidently overlapped considerably, requiring larger samples for the separation of the sexes on this character. Unfortunately it was not possible to sex all these birds on anything but beak characters, and so to get a better estimate of bill lengths the examination was restricted to those birds that could be sexed confidently on beak shape indices. Antipodes Island birds were judged to be females when their beak shape indices were less than 940 (n = 34), males where these were greater than 1020 (n = 49); Campbell Island birds with indices less than 780 were taken to be females (n = 33), those having these greater than 870 to be males (n = 20). From these reduced samples, means and standard deviations were derived using standard formula.

Table 3 shows the results of combining the information for beak depths and widths derived from the graphical analyses using all the data, with those from beak lengths using the more restricted data. The shape indices calculated from the separate estimates of the three components agree well with the indices derived directly from Figure 4. The Campbell Island figures also agree satisfactorily with the small samples analyzed in Table 1. Bill lengths may be compared with the figures given by Westerskov (1960) for freshly killed birds from Rocky Bay, Campbell Island—means for 6 males and 13 females were 44.1 and 40.3 mm respectively.

Table 3 thus gives a best estimate of the mean values for the beak components in the two samples and the differences between the means for the sexes at an island and between islands are all significant with $P < 0.001$ in each instance. As some of the variability in the samples was eliminated by discarding intermediate values in selecting the data, the values for beak length will be slightly below the true mean for the females and slightly high for the males.

This analysis shows that the Campbell Island birds were clearly smaller billed than those at Antipodes, but the degree of difference between the sexes for each bill component was very constant, the values for the males being between 11 and 14 per cent higher in all instances.

TABLE 3

DIMENSIONS OF BILL COMPONENTS IN MM AND BEAK SHAPE INDICES FOR
ADULT ROCKHOPPERS

	Length	Width	Depth	Beak index
Campbell Island				
33 females	40.5 ± 1.91 (4.7)	9.2 ± 0.4 (4.9)	18.0 ± 0.7 (3.9)	670
20 males	46.3 ± 1.92 (4.1)	10.4 ± 0.4 (4.3)	20.3 ± 0.8 (3.9)	977
$\frac{\text{Males}}{\text{Females}} \times 100$	114	113	113	146
Antipodes Island				
34 females	41.8 ± 1.86 (4.5)	9.7 ± 0.6 (6.5)	18.8 ± 0.8 (4.3)	762
49 males	47.8 ± 2.32 (4.9)	10.8 ± 0.5 (4.7)	21.1 ± 1.6 (7.5)	1089
$\frac{\text{Males}}{\text{Females}} \times 100$	114	111	112	143

ADULT FLIPPER LENGTH

The raw data on flipper lengths when plotted on probability paper suggested the existence of bimodalities but with a considerable degree of overlap. Consequently analysis was restricted to data from birds sexed on their beak shape indices, the criteria being the same as those used when estimating bill lengths.

In the sample from Antipodes Island, 50 birds were judged to be males, 34 to be females. Their flipper lengths were found to be distributed almost normally around means of 167.8 ± 3.75 mm for the males and 162.8 ± 3.98 mm for the females. These values are significantly different, $P < 0.001$.

Of the Campbell Island birds 33 were judged to be females (beak shape indices <780) and 20 to be males (beak shape indices >870). The data for the males were not normally distributed and had a mathematical mean of 168 mm. Those for the females approached a normal distribution with a mean of 164.6 ± 3.6 mm, a figure hardly different ($0.5 > P < 0.01$) from that of the similarly sized sample from Antipodes Island. The Campbell Island figures may be compared with the means given by Westerskov (1960) for 6 males and 13 females of 164.3 and 161.8 mm respectively.

These data suggest that the sexual dimorphism also extends to flipper lengths, those of the males being longer, but with a considerable degree of overlap, some adult females having flippers as long as or longer than some adult males. Those of the Antipodes Island males averaged only 3 per cent longer than those of the females.

ADULT BODY WEIGHTS

Figure 5 gives the distribution of the body weights of the birds in the two samples. Both graphs show evidence of two modes, but these do not coincide with those seen in Figure 4 where the beak shape indices for the same birds were plotted. Whereas the latter indicate male to female ratios of 57:43 for the Antipodes and 34:66 for the Campbell Islands samples, the weights segregate at 35:65 and 16:84 ratios when analyzed graphically. Evidently the weight distributions at the time of sampling were only partly related to the sexes of the birds. This was further
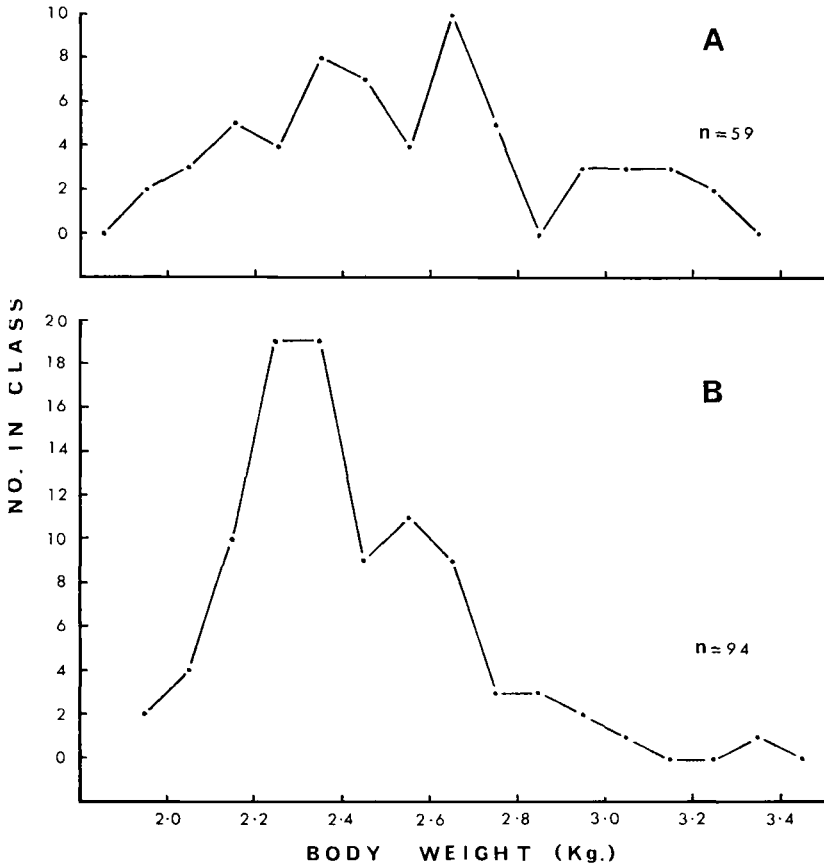
Figure 5. Distribution of adult body weights: A, Campbell Island; B, Antipodes Island.

shown by the relatively low correlation between body weight and beak shape index; $r = +0.321$, $P < 0.01$ and $+0.307$, $P < 0.02$ for the Antipodes and Campbell Island samples respectively.

Penguin weights vary greatly during the time the birds are ashore as the breeding cycle involves both sexes in long fasts. As has already been pointed out the females might have been expected to be in better condition late in the breeding cycle than their mates. Nevertheless when the weights were reexamined using information only from birds sexed on bill size, the males in both samples were found to be significantly heavier than the females ($P < 0.001$). The data are given in Table 4.

Despite the larger bills of the birds from Antipodes Island they prove to be lighter than those from Campbell Island ($P < 0.001$ for the males, $P < 0.01$ for the females). However to compare body weights from two breeding populations, one should either take data gathered at the same stage of the breeding cycle or

TABLE 4

BODY WEIGHTS (G) OF ADULT ROCKHOPPER PENGUINS SEXED ON BEAK SHAPE INDEX

Campbell Island	33 females	2370 ± 280 (11.8)
	20 males	2720 ± 250 (9.2)
	$\dfrac{\text{Males}}{\text{Females}} \times 100$	115
Antipodes Island	33 females	2225 ± 140 (6.3)
	49 males	2425 ± 230 (9.5)
	$\dfrac{\text{Males}}{\text{Females}} \times 100$	109

use fat-free weights to allow for the gain and loss of subdermal fat. The Antipodes Island birds measured on 9 February are being compared with others measured 23 days before and, as the Campbell Island penguins lay about 8 days later than those at Antipodes, the differences are aggravated. The low values for the Antipodes Island birds may reflect the wear-and-tear of chick rearing as the figures were collected very late in the breeding season. The true mean values corrected for varying fat reserves for Antipodes Island birds may well be higher than that of those at Campbell Island, but the present information does not allow these means to be estimated.

YEARLINGS

Young Rockhoppers come ashore at about hatching time as 1-year-olds, and most have molted and departed by the time the chicks fledge. These yearlings are short-crested, usually rather pale on the throat, and with duller bills and eyes than those of the adults. After the molt they are similar except that their throats are now black so that they are difficult to distinguish from 2-year-olds as the latter also tend to be rather short-crested.

Table 5 summarizes data from 24 immatures measured at Campbell Island on 13 and 17 January and 32 measured at Antipodes Island between 9 and 14 February. One or two 2-year-olds may have inadvertently been included, but otherwise all were believed to be yearlings.

The data confirm subjective observations that 1-year-olds are smaller, often lighter in weight than adults at equivalent stages of the annual cycle, and smaller billed. The bills of the 24 birds of mixed sex from Campbell Island were intermediate in size between those of adult males and females but nearer those of the females. The bills of the 32 Antipodes birds were more divergent, being smaller than adults of either sex. Although the mean beak shape index for the Antipodes yearlings was greater than that for the Campbell Island ones, the reverse situation to that of the adults, the differences of the means between islands in Table 5 are not significant for any parameter except for body weight.

The sample from Campbell Island is too small for further analysis, but graphical analysis of the distribution of beak indices from the Antipodes Island birds indicates a 50:50 ratio between two groups, one having a mean beak index of 780 ± 75 and the other of 630 ± 75, which are presumed to refer to the males and females

TABLE 5

MEASUREMENTS OF YEARLING ROCKHOPPER PENGUINS

	Campbell Island	Antipodes Island
Number	24	32
Bill length mm	42.3 ± 2.3 (5.5)	41.7 ± 2.5 (6.1)
Culmen width mm	9.4 ± 0.5 (5.4)	9.2 ± 0.5 (5.5)
Bill depth mm	18.5 ± 1.3 (6.8)	18.5 ± 1.1 (5.7)
Beak shape index	739 ± 99 (13.4)	711 ± 99 (13.9)
Weight g	3132 ± 337 (10.7)	2119 ± 489 (23.1)
Flipper length mm	165 ± 5.0 (3.0)	163 ± 5.1 (3.1)

respectively. These differences are significant, $P < 0.001$ and the values are 71 per cent and 83 per cent below those of the respective adult values given in Table 3.

The data for flipper lengths show that the yearlings in both samples (of mixed sexes) were short-flippered, having mean values closely approaching those for adult females. Neither sample shows any clear bimodality that might be linked to sexual differences.

The mean body weights for the Campbell Island yearlings exceeded those for either adult sex given in Table 4, whereas those for the Antipodes Island yearlings were below the adult values. These anomalies are again almost certainly a consequence of differences in the stages of the annual cycle at which the two populations were sampled. That from Campbell Island included 12 premolt "fats" with a mean weight of 3283 ± 213 g, whereas the one from Antipodes Island included only four similar birds (mean weight 3162 g) but also 19 molted ones ready for the sea that averaged 1884 ± 247 g and which account for a substantial proportion of the variability of that sample. These differences in weight emphasize the role of subdermal fat in tiding the birds over the molt when they are unable to feed and their body insulation is temporarily reduced.

CHICKS

As sexual dimorphism evidently extends to yearlings it might also be expected to show in the dimensions of 72 chicks, almost or completely down-free and ready for departure, measured at Antipodes Island between 9 and 12 February.

The data for body weights and beak shape indices are given in Figure 6. Both polygons suggest the interaction of more than one normal distribution but with much overlap, as would be expected of animals actively growing, not of identical ages, and subject to variables like the differing capabilities of parents at finding and delivering food. The weight polygon has a rather extended tail of low-weight animals that would probably die before fledging. That for beak index appears to be bi- or even trimodal, with the peak between indices 300 and 400 difficult to explain on biological grounds and probably a consequence of inadequate sample size.

Table 6 gives the means and standard deviations for the various parameters when the data were treated as homogeneous. When the cumulative frequencies for weights were plotted on probability paper a change in slope around 1980 g suggested that the distribution can be explained in terms of two normal curves with 74 per cent of the birds lying in a light weight category around a mean of 1750 ± 180 g and 26 per cent being significantly heavier ($P < 0.001$) around a mean of 2200 ± 150 g.
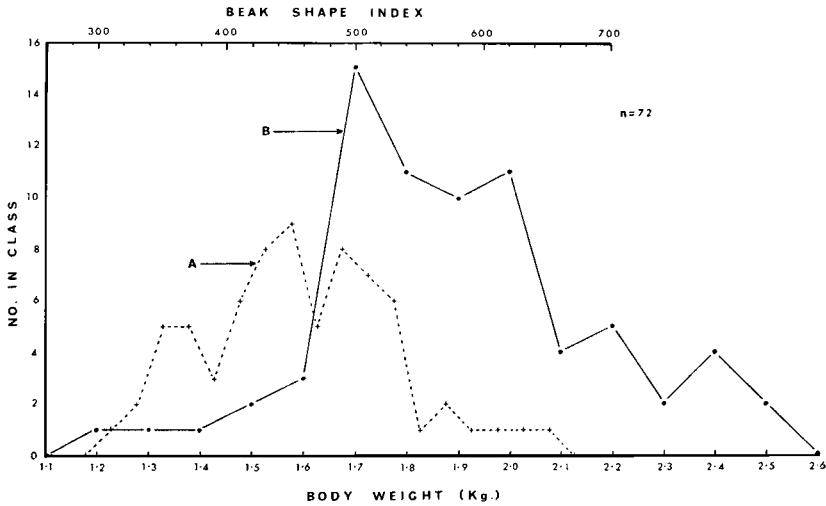
Figure 6. Beak shape indices (A) and body weights (B) of 72 Rockhopper chicks ready to fledge.

Data on beak shape indices are less amenable to further analysis but if the peak around 350 is ignored, the rest of the distribution can be explained as due to two normal curves where 60 per cent of the birds lie about a mean beak index of 410 $\pm$ 50 and the upper 40 per cent around one of 510 $\pm$ 35, values that are again significantly different with $P < 0.001$. Furthermore despite a lot of scatter, heavier chicks tended to have heavier bills ($r = +0.469$, $P < 0.001$).

Compared to a sample of adults of mixed sexes these near fledglings had bills that were 48 per cent as large whereas their flippers were 96 per cent as long so that the chicks evidently go to sea with their flippers better developed than their bills.

That the large-billed and heavy-bodied class were mainly males and the smaller-billed, lighter-bodied birds mainly females seems to be a reasonable hypothesis in view of the size differences among yearlings and adults. As the chicks could not be sexed by any other means and none was dissected, the existence of sexual dimorphism in bill size and body weight of the chicks just before fledging could not be proved, and the results can only be regarded as suggestive. Larger samples seem to be needed together, with corroborative data on sex based on separate characters, e.g. on the behavior of older birds marked and measured as chicks.

TABLE 6

MEASUREMENTS OF 72 ROCKHOPPER CHICKS AT ANTIPODES ISLAND

Bill length mm	38.2 $\pm$ 2.3 (6.0)
Culmen width mm	7.6 $\pm$ 1.0 (13.7)
Bill depth mm	15.3 $\pm$ 2.1 (14.0)
Beak shape index	445 $\pm$ 72 (16.2)
Flipper length mm	157.9 $\pm$ 19.4 (12.3)
Body weight g	1860 $\pm$ 268 (14.3)

DISCUSSION

Sexual dimorphism in bodily dimensions is rather widespread among colonial seabirds, being quite marked in penguins of the genus *Eudyptula* as well as in all five Eudyptids, in some petrels, e.g. *Macronectes,* and in many gulls. In *Eudyptes* it seems to be correlated with a greater aggressiveness by the males, but whether the dimorphism is maintained through selection pressures favoring nest defense, sexual recognition, the reduction of intraspecific competition for food, or serves other functions is unknown. Further comparative data from other species may throw some light on this aspect of the problem.

The data presented here support the idea that sexual dimorphism in the Rockhopper Penguin, starting perhaps in the chick, increases with age and is most pronounced among breeding birds. The age at which growth ceases is unknown and must await the repeated measurements of birds marked as chicks. Such a program would reveal whether the age at which growth ceases is the same for either sex and for each character, or whether bill size, for example, continues to increase even after breeding age is attained.

While the data reveal differences in bill measurements between the sexes of adults at a particular island, are the bill size differences between adults at the two islands really typical of their respective populations, bearing in mind that the data were collected at different stages in the breeding cycles? Significant differences in flipper lengths between the populations could not be demonstrated, and the figures for body weight ran counter to those for bill size.

When working with unmarked birds it is impossible to be sure that the adults measured at the two islands were drawn from strictly comparable age groups. Those at Campbell Island were still tending chicks, as were some of those at Antipodes Island, but others measured at the latter station were merely standing at nest sites with partners and either had no chicks or their chicks had left. Thus more of the birds in the Antipodes Island sample could have been prebreeders. If so, these, being younger, should have smaller bills and their inclusion would lower the mean value for beak shape index accordingly, whereas the means from this island are significantly greater than those from Campbell Island. Thus if such an effect is present it supports rather than invalidates the hypothesis that the breeders at Antipodes Island are heavier billed than those at Campbell Island.

The existence of minor differences in bill size between adults at Campbell and Antipodes Islands suggests that the gene flow between the populations is restricted, although the islands are only about 745 km apart. Such isolation is presumably in part due to the tendency

among Eudyptids for the young to return to their birthplaces. Other minor differences might therefore be expected to develop between such populations, and suggestive observations were made on one such feature, the extent of the pink coloration at the base of the mandible in the adult birds. In about 30 breeders of mixed sexes at Macquarie this pink mark extended forward from the fleshy gape for about one sixth of the length of the lower mandible and ended abruptly, clearly separated from the reddish brown of the rest of the beak. In most Campbell Island adults the mark was much more pronounced, extending from one third to one half of the length of the mandible as in birds figured by Bailey and Sorensen (1962: 106). In some Campbell examples the pink marking also extended along the proximal edge of the maxilla. At Antipodes a minority of breeders resembled Macquarie Island birds in this feature, but in most the pink was more noticeable and showed a condition intermediate between that seen at Campbell and at Macquarie.

Such minor differences suggest that careful comparisons using adequate samples from different breeding stations might reveal enough differences (in crest length and other mensural characters, underflipper patterns, etc.) to enable adults to be identified to particular populations. As the collection of long series is no longer permitted, at least on the New Zealand sub-Antarctic sanctuaries, it would be necessary as in the present study to rely on data drawn from live animals. Despite the obvious disadvantages, their use at least ensures that the data are free from uncertainties caused by shrinkage and fading that can complicate comparisons made from preserved skins, and live birds must in any event be used if repeated examinations of the same individuals are required.

SUMMARY

The laying seasons at 11 breeding stations of the Rockhopper Penguin between 36° and 53° S were examined. Laying is roughly correlated with latitude, being earlier at the more northerly stations, but a better correlation is with mean annual sea temperature. The dates of laying advance about 10 days for each degree Centigrade rise in mean sea temperature. Marion Island appears to be exceptional in that laying is 8 to 10 days later than at other islands with similar sea temperatures. More precise information for many stations is needed to evaluate the correlation and to explain its underlying basis.

In an attempt to establish the degree of sexual dimorphism, culmen length and width, bill depth, flipper length, and body weight were measured in samples of adults, yearlings, and chicks about to fledge at Campbell and Antipodes Islands. No birds were dissected, but some were

sexed on behavioral characters found during a previous study to be specific for males. Bimodal distributions of the measured parameters were assumed to be the result of sexual dimorphism, and those birds sexed as males by behavior fell into the larger size category.

In 10 adult pairs the males were bigger billed and heavier than their mates, but some females had longer flippers. Data from 94 adults at Antipodes and from 59 at Campbell also indicated that the males were bigger billed and heavier. Males also had significantly longer flippers in the Antipodes birds, but this parameter showed more overlap between the sexes than did weight or bill size. Campbell adults were significantly smaller billed than those from Antipodes, and small differences were also noted in the bill color patterns of the two populations.

The 56 yearlings measured were smaller billed and shorter in flipper than the adults, but the bills and flippers of yearlings from the two islands were not significantly different. The 32 from Antipodes included a large and a small billed group believed to be males and females respectively, but none was dissected and behavioral clues to sex were not available.

The Campbell yearlings were heavier than those from Antipodes mainly because the Campbell birds included 12 in premolt condition (average weight 3283 g), whereas the Antipodes sample included many molted birds; 19 of these averaged 1884 g.

At Antipodes 72 chicks about to leave for the sea were measured. The data for weight and bill size were bimodal suggesting that sexual dimorphism in these parameters had already become established. These chicks' bills were only 48 per cent of the adult size, but the flippers were 96 per cent as large as those of the adults.

The function of sex differences in Rockhopper Penguin measurements is not known, nor is the age at which bill growth ceases. Differences in morphological characters between populations on different islands separated by wide stretches of sea probably reflect genetic isolation enhanced in part by the tendency of young birds to return to their natal islands.

LITERATURE CITED

BAILEY, A. M., AND J. H. SORENSEN. 1962. Subantarctic Campbell Island. Proc. Denver Mus. Nat. Hist., No. 10.

CARRICK, R., AND S. E. INGHAM. 1967. Antarctic sea-birds as subjects for ecological research. Japan Antarctic Res. Exped., Sci. Rept. Spec. Issue, 1: 151–184.

DOWNES, M. C., E. H. M. EALEY, A. M. GWYNN, AND P. S. YOUNG. 1959. The birds of Heard Island. ANARE Rept. Ser., B. 1.

ELLIOTT, H. F. I. 1957. A contribution to the ornithology of the Tristan da Cunha Group. Ibis, 99: 545–586.

HARDING, L. P. 1949. The use of probability paper for graphical analysis of polymodal frequency distributions. J. Mar. Biol. Ass. U. K., 28: 141–153.

La Grange, J. J. 1963. Notes on the birds and mammals on Marion Island and Antarctica (S.A.N.A.E.). J. South African Biol. Soc., 3: 27–84.

Murphy, R. C. 1936. Oceanic birds of South America. New York, Amer. Mus. Nat. Hist.

Paulian, P. 1953. Pinnepèdes, Cétacés, Oiseaux des Îles Kerguelen et Amsterdam. Mém. Inst. Sci. de Madagascar, 8: 111–234.

Pettingill, O. S., Jr. 1960. Crèche behavior and individual recognition in a colony of Rockhopper Penguins. Wilson Bull., 72: 209–221.

Rand, R. W. 1954. Notes on the birds of Marion Island. Ibis, 96: 173–206.

Stonehouse, B. 1967. The general biology and thermal balance of penguins. Advan. Ecol. Res., 4: 131–196.

Strange, J. L. 1965. Beauchêne Island. Polar Rec., 12: 725–730.

Swales, M. K. 1965. The sea-birds of Gough Island. Ibis, 107: 219–221.

Warham, J. 1963. The Rockhopper Penguin, *Eudyptes chrysocome*, at Macquarie Island. Auk, 80: 229–256.

Warham, J. 1971. Aspects of breeding behavior in the Royal Penguin, *Eudyptes chrysolophus schlegeli*. Notornis, 18: 91–115.

Westerskov, K. 1960. Birds of Campbell Island. Wellington, New Zealand, Dept. Internal Affairs, Wildlife Publ. 61.

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