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The Egg-Laying and Incubation Periods of Rockhopper, Macaroni and Gentoo Penguins

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INTRODUCTION

It might be supposed that the subject matter of this paper has already been fairly well covered, at least in outline, but in fact precise data on the egg-laying of most penguin species is lacking, and accounts even in recent literature contain many inaccurate statements. This is particularly true of the question of relaying, i.e., what happens when the first clutch is lost? No serious attempt appears to have been made to study this question experimentally in penguins, and the few remarks published on the subject are highly misleading.

The most thorough accounts of the life-histories of individual species are those of Bagshawe (1934) on the gentoo penguin, of Richdale (1949) on the yellow-eyed penguin of New Zealand, and of Gain (1914) and Levick (1915) on the Adélie penguin. But no adequate study of any of the crested penguins *(Eudyptidae)* has yet been published, which is the more suprising as they all live in relatively low latitudes.

The experiments detailed in the following pages were carried out at Macquarie Island and Heard Island where the author was stationed with A.N.A.R.E. parties during 1949 and 1950.

Throughout the present paper "incubation period" is taken to be the interval between the beginning of incubation and the final emergence of the chick from its shell. This accords with current practice (Moreau 1946). As incubation does not begin till some time between the laying of the first and second eggs in the gentoo, and till the laying of the second egg in the rockhopper and macaroni, only second eggs have been considered in determining incubation periods[1]; but since observations could be made only once a day even those were not completely accurate. Eggs might have been laid at any time during the 24 hours preceding discovery and chicks might have been hatched during a rather shorter period, except in a few cases where they were still moist or were just about to hatch. Newly-hatched penguin chicks were not infrequently found sitting in halves of their old shells; these were recorded as fully hatched.

[1] In nests under observation eggs were marked when first noted with the date in Indian ink.

Bergtold (1917) in a paper entitled "The Incubation Periods of Birds" states that "there is a true or specific length of incubation, which can be shortened (artificially) with extreme difficulty, but prolonged with ease", and that it is "a deep-seated, inelastic, and persistently unchanging character". He defines the true length of incubation as "the minimum number of days, under optimum conditions, necessary to hatch a normal bird". With this definition the writer is in complete agreement, and is of the opinion that among penguins optimum or near optimum conditions are realised in a large proportion of cases. All periods much in excess of this period should be suspect as either inaccurate or due to delay because of unfavourable circumstances.

THE ROCKHOPPER, *Eudyptes chrysocome* (Miller)

The observations on this species were made chiefly at Macquarie Island, supplemented to some extent by observations at Heard Island. There is no essential difference in behaviour at the two places[1], apart from earlier nesting at Macquarie Island (the difference is two weeks), but the origin of particular observations is indicated by the letters MI and HI respectively.

Rockhoppers normally lay two eggs of different sizes. Falla (1937) states correctly: "The range of size . . is due to the fact that in many clutches of two the first egg laid is much smaller that the second". Murphy (1936) also mentions, though rather tentatively, the report that the first egg is smaller; and goes on to quote a suggestion that the difference in size is a matter of sex (!). The true extent and significance of this size difference has not apparently been previously studied.

Period between Eggs. Though few accurate records are available, the interval between the laying of the first and second egg is evidently rather long compared with the macaroni and gentoo penguins. Both at Heard Island and Macquarie Island intervals of 5 days were recorded (four cases), and in four others it was at least 4 days. Among two-egg clutches only one interval of 3 days was definitely recorded, but in both of two three-egg clutches observed the intervals were shorter. In one, three eggs were laid with an interval of 5 days between the first and last; in the other the second egg was laid 2 days after the first, and a third within the next 4 days.

Incubation Period. In only three cases (MI) was sufficient data available to calculate the incubation period for the second egg. In one

[1] At Macquarie Island the rockhoppers often nest close to, if not actually among, the tussocks and sometimes build quite substantial grass nests, though there is great variation in this respect. Such nests are not often seen at Heard Island, but this difference is probably simply a question of opportunity.

it was just 33 days. In another, the egg was girdled, but the halves not yet separated 33 days after the first egg was first recorded. The third nest, which was next to this, had exactly the same dates as the second nest for first and second eggs and for the first early signs of chipping, and the chick may be assumed to have hatched a few hours later. This gives an incubation period of 33 days for the first, and of 33-34 (i.e., hatching on the 34th day) for the other two. Other records are compatible with an incubation period of 33 or 34 days.

In six cases the second egg was taken soon after laying, leaving the bird to incubate the first. In five of these the incubation period from the completion of the clutch was 33 or 34 days, and in one apparently 32 days. This last suggests that incubation of the first egg may occasionally begin before the second is laid (c.f. Falla 1937). The data for the other five eggs is not sufficiently accurate to say whether their incubation period was longer than that for the second eggs already mentioned.

Period of Hatching. Of four eggs in which the shell was just starred when hatching was first noticed, one had girdled its shell 24 hours later, but the other three had still only a window 24 hours later, and in one case 33 hours later. Of two others noted as "just chipping", one had hatched the next day and the other was sitting in half of its old shell. From this it seems that the rockhopper may have a rather shorter hatching time than the gentoo, for which more accurate data is available.

The First Egg. The most remarkable fact emerging from this study is that the first egg of the rockhopper is normally wasted. Its fate is extremely varied, but only when the second egg is lost does it produce a viable chick, and as the larger egg always receives preferential treatment, this rarely happens under natural conditions. Out of seventeen nests in which the details were known the following were found:—

In three the first egg was lost during incubation (in one of these it became lost in the structure of the nest before the second was laid, was replaced, but was finally lost during incubation).

In all the remaining fourteen nests the second egg hatched first. In two of these both eggs hatched, but in both cases the second chick was puny and survived only for a short while. In two the unhatched first egg was removed from the nest 3 and 7 days later, and in both cases found to be infertile. In two the nest was empty when next visited. In the remaining cases the nest was occupied by a single chick a few days later and, where the facts were known, the first egg had been ejected soon after the second had hatched. Two of these were recovered and

found to contain dead, fully developed chicks, one of which had actually begun to chip its shell.

The same order of hatching was observed in many other nests not under regular observation, and this is undoubtedly the general rule among the rockhoppers. In every case in which the first egg began to be chipped, it occurred about 24 hours after the second.

It is of course the parent, not the newly-hatched chick, which ejects the unwanted first egg. It appears that once the first chick hatches, all interest in the remaining egg is lost; and even if the second chick succeeds in hatching, there is room for only one offspring in the stormy life of the rockhopper. The series considered is perhaps exceptional in the proportion of pairs which retained both eggs up to the end of incubation. At Heard Island and in some areas at Macquarie Island, the proportion of first eggs rejected during incubation seemed much higher than this.

A simple explanation as to why the first egg hatches after the second suggests itself: In the interval between the laying of the first and second eggs the rockhopper crouches over its egg but does not brood it, and if the egg is handled it is found to be dead cold. Therefore when incubation starts it takes some time to warm up, whereas the second egg gets away to a flying start[1].

Twice the writer saw a rockhopper with two recently hatched chicks of equal size and vigour (MI: This would happen if the smaller egg hatched first). In one case one had disappeared when the area was next visited; in the other both flourished till they were at least three days old, but their subsequent fate was not known. If two chicks are ever reared, it must be a very rare occurrence. Reports of rockhoppers with two well-grown chicks must be received with caution, as is well illustrated by the following instance (HI):—

On 26 January, 1950, two chicks of identical age (24 days) were seen huddled together with an adult bird standing protectively by them. To the uninitiated this would have appeared as an obvious example of a rockhopper with a family of two half-grown chicks, but they were in fact the chicks from two neighbouring pairs, each of which had hatched a single egg, the only successful pairs in a small group of marked nests.

Reaction to Loss of Second Egg. In six nests the second egg was

[1] However some observations already quoted suggest that occasionally the order may be reversed. This would happen if incubation began sufficiently long before the second egg was laid.

removed soon after laying. In each case the bird continued to incubate the first egg, and successfully hatched a chick. In one the newly hatched chick was noted as "puny and isabelline" but nine days later it was "healthy . . . rather light coloured". Four of the other nests were in an isolated group with a fifth pair which had a chick from a second egg. Six weeks after hatching, this group contained five healthy chicks.

It is therefore clear that if anything happens to the second egg, the first can take its place without detriment.

Loss of Both Eggs. If both eggs were lost, the rockhopper in these colonies did not attempt to lay again, but the birds continued to guard their empty sites. Whether they would react in the same way if the eggs of an entire colony were systematically removed, as happens where they are harvested for food, is another matter. Vallentin (1924) states that in the Falkland Islands they do re-lay, and the same is reported by other reliable observers. The extent to which this is true, however, could only be determined by the systematic study of a large number of marked nests as it is very easy to be misled by the natural variation in laying times between different pairs. It would be possible to make two or three large collections in succession from the same area which would merely be the eggs of pairs which had not completed their clutches when the earlier collections were taken.

Haysom, A.N.A.R.E. biologist at Macquarie Island during 1949, took four two-egg clutches and marked the sites. Two days later one of these was found to contain a third egg, but this was probably a case of a true three-egg clutch and the egg would have been laid anyway. The other three pairs did not lay again.

Three-egg clutches. In addition to the case just quoted, two three-egg clutches occurred in areas under observation by the writer (MI). One of these pairs lived in an inaccessible crevice and two of the eggs were kicked out during incubation. The other pair incubated two eggs. At Heard Island a clutch was collected (See Plate 2; Clutch 29.11.E) at the beginning of egg-laying which was almost certainly a true three-egg clutch, as there did not seem to be any other nest from which the third egg could have come and the shape of the eggs was consistent with their having all been laid by the same bird. The order of laying was plainly indicated by the degree of cleanliness, though the size difference between consecutive members of the clutch was decidedly less than usual. The weights and measurements of this clutch were as follows:—

	Weight in gm.	Measurements in mm.
First Egg	69.8	60.0 x 46.2
Second Egg	76.4	62.0 x 47.2
Third Egg	99.2	67.7 x 41.7

It would appear that three-egg clutches are less uncommon among the rockhoppers than in either of the other two species studied.

THE MACARONI PENGUIN, *Eudyptes chrysolophus*, Brandt.

At the end of a survey of the published accounts of the macaroni penguin, Murphy (1936) remarks: "The more northerly colonies at Kerguelen, South Georgia, and elsewhere have been reported on by many observers", yet neither Murphy nor the observers he quotes make any reference to the basic fact that a macaroni clutch consists of two eggs of very unequal size. Gain (1914), Matthews (1929) and Falla (1937) have visited colonies while the birds were incubating, and reported that they lay only one egg. It is interesting to find that the hearsay of sealers during the Nineteenth Century has proved more accurate than the observations of trained scientists in the Twentieth. Sclater and Salvin (1881) quote John Murray, naturalist of the "Challenger" expedition, as follows:— "The sealers told us that they (macaronis) usually lay three eggs, but pitched the first two out of the nest for the Sheathbills to eat: These first eggs were generally much smaller than the other eggs". This statement has waited over half a century for confirmation. It is wrong only in attributing to the macaronis one egg more than their normal complement, and even this error can be readily explained.

The fact that macaronis lay two eggs of unequal size was recognised by A.N.A.R.E. parties at Heard Island from the first, but it was left to the writer to undertake a systematic investigation of the matter.

At Heard Island the macaronis begin to return from their pelagic wanderings towards the end of October and by the second week of November the return is largely complete. In 1950 the first eggs were found on 10 November, and a fortnight later laying was virtually over. There was no late laying among the macaronis, with the possible exception of occasional pairs which nested in the rockhopper rookeries and whose laying was perhaps synchronised with their neighbours[1].

The macaronis are an extremely social species, living in closely packed rookeries. For the most part they live in extremely large colonies, but the one at which most of the following observations were made was a small rookery of about 240 pairs (Plate 1).

Period between Eggs. The egg interval was approximately determined in ten clutches. In eight it was 3 days (including three cases in which the first egg was fresh and warm when found) and in two it was 4 days.

(1) Rockhoppers lay a fortnight later than macaronis at Heard Island.

Plate 1.—Macaroni Penguin Rookery at Erratic Point, Heard Island.

Incubation Period. Data for eight nests is available, but in several cases only the date of chipping, not of final emergence of the chick, was recorded. In the nest for which the most accurate details are known the chick was found with head and flippers out of its shell on the 35th day after laying. In most of the other cases incubation was about 35 days, but in one it was over 36 days. Hatching time was not accurately determined.

The First Egg. While waiting for the second egg the bird crouches over the first rather than broods it, and the egg can very often be seen sticking out in front of the bird. It becomes very dirty and if handled during this interval is found to be quite cold. Often it is lost even before the second is laid, presumably being kicked out of the nest during the fights with passers-by which are such frequent occurrences in these rookeries. Even if it survives it is usually lost after the second egg is laid, though whether it is deliberately ejected or not is difficult to tell.

A few birds continue to brood two eggs till incubation is well started, but no cases were observed in which both eggs were successfully guarded for long. It is probably rare for both eggs to survive for more than a few days after the completion of the clutch.

As the first eggs get kicked out of the nests, they are harvested by the watching skuas and sheathbills, unless they roll into another nest lower down the slope. This not infrequently happens, especially if the rookery is under snow[1], with some of the birds sitting in icy hollows. The birds below will add such eggs to their clutches for a time, which no doubt explains the sealers' belief that macaronis lay three eggs[2]. However a strange egg can usually be distinguished by its difference in shape from the other two.

Loss of the Second Egg. Occasionally a bird will be found incubating a small first egg, presumably having lost the second, but in the only case observed it was also lost before the end of incubation.

Loss of Both Eggs. A substantial proportion of macaronis lose their second eggs during incubation, probably to the sheathbills which in some cases actually nest within the macaroni rookeries. In the rookery under observation (containing 240 pairs) only 68 chicks were reared to their seventh week.

If both eggs are removed as soon as they are laid, the birds make no attempt to lay again, but continue to occupy their empty sites. Some birds will find a stone to brood. Others continue to brood an empty nest (one did so for three weeks, and only the empty look of its "apron" betrayed the fact that the nest was empty). After a short interval most birds merely stand by their empty sites. Both birds are present at first, but interest gradually wanes and during the second half of incubation many such sites may be found unguarded. When hatching begins there is a tendency for all birds to return to the rookeries, and the empty sites are re-occupied, usually by both birds.

THE GENTOO, *Pygoscelis papua*, Forster.

This species lays a clutch of two eggs of approximately equal size, with an interval of about three days. Incubation does not usually start when the first egg is laid, but at some time before the clutch is complete, so that the first egg hatches about 24 hours before the second. For this reason it offers an interesting comparison with the unusual egg-laying habits of the crested penguins.

(1) Chittleborough and Ealey, A.N.A.R.E. biologists at Heard Island in 1949, observed this on several occasions.

(2) They correctly observed that two of the eggs were small.

The following studies were carried out at Heard Island in two rookeries containing about 700 pairs. A complete record was kept of the first 35 nests to lay.

Period Between Eggs. The interval between the laying of the first and second egg was ascertained in 17 nests in which the first egg was not disturbed. In eight the interval was 3 days; in three, less than 3 days; in five, 4 days; and in one, 15 days, which was plainly abnormal. The records for a considerable number of other nests, where the date of laying of one egg was known only within 48 hours, also indicate that 3 to 4 days was the usual interval. In at least four of these the interval was over 3 days.

As observations were made only once a day, it is only possible to conclude that about 3 days is the usual interval, but that it is often more, and sometimes less. Bagshawe (1934) records one case in which the egg interval was accurately known — 77 hours. In another it appears to have been about 52 hours. His average for seven cases was 3.2 days.

Clutch Size. Single-egg and three-egg clutches are both exceptional. The former must always give rise to the suspicion that one of the eggs has been lost. In the nests under regular observation only three single eggs were noted. All were laid early, so the possibility of their being cases of second laying can be excluded, and all were rather small. In one case, after the birds had guarded the egg for a few days, incubation was apparently begun, but the nest was abandoned half-way through the incubation period. In another, the egg was taken when found. Nine days later a normal-sized egg was laid, and a clutch of two eventually completed, but whether or not by the original occupant it was not possible to say. In the third case the egg was found embedded in the wall of the nest four days after laying, but was restored to a proper position. A second egg was laid fifteen days after the first, but it was so strikingly different in shape that the possibility of its being laid by another bird must be admitted[1]. Both eggs were incubated, and the second hatched in normal time, but the first was addled. Such records suggest that small single eggs may be laid by young females laying for the first time (c.f. Richdale 1949).

Three-egg clutches have been recorded by nearly all observers, but they must occur in less than 1% of cases. In some hundreds of nests examined, the writer has only once seen a clutch of three eggs[2] — a

(1) However, the fact that the first egg was still present is proof that the nest had been continuously guarded.

(2) But he has observed families of three chicks on two occasions at Macquarie Island.

freshly completed clutch in the group of late layers discussed below. The eggs were large, and the order of laying was plainly indicated by the degree of soiling, the colour ranging from reddish brown to pure white. (See Table 5). Bagshawe records a number of three-egg clutches, and one of four.

Incubation Period. If the first egg is handled in the interval before the second is laid, it is usually found to be cool. In two sets of eggs the yolks were examined with a hand lens 48 hours after the clutch had been found to be complete. In both sets, the first egg was found to be the more advanced of the two, the germinal area measuring about 20 mm. in diameter as against 9 mm. in the second eggs. No vascular elements were yet visible in either. In one clutch, examined 24 hours after it was found to be complete, the first egg was at about the same stage as the second eggs in the other clutches.

With these facts in mind it was not unexpected to find that in marked clutches the first egg always hatched first, the interval between the hatching of first and second eggs being normally 24 to 48 hours, more often the shorter interval. As it is not possible to know how much incubation to allow the first egg before the clutch has been completed, the only estimate of incubation period available is the interval between the laying of the second egg and its hatching. Of 15 cases, six hatched on the 36th day after the egg was first recorded and nine on the 35th day. In two of the latter, the chicks were partly out of their shells and would presumably have been altogether free within two or three hours. As the eggs may have been laid nearly 24 hours before they were first noted, this gives these an incubation of just 35 days which is probably the natural incubation period under optimum conditions. In one of these cases the two eggs of the clutch were laid with an interval of less than three days, and were just 48 hours apart in reaching the stage described. In this case incubation probably began with the laying of the first egg, each egg taking 35 days or a little less to hatch. The birds in this nest always sat very closely.

Bagshawe records seven carefully determined incubation periods, ranging from 35 days to 39 days, but three of them are based on first eggs and no allowance is made for the interval between when the egg was laid and the beginning of incubation. The remaining cases are all 35 or 36 days. It is interesting that under the more rigorous conditions of the Danco Coast the true incubation period of the gentoo should be identical with that observed at Heard Island.

In each of seven of the nests under observation one of the eggs failed to hatch. One of these had been cracked and contained a dead partly-

developed chick, but in the other six (four were first eggs and two were second) incubation had apparently never started. Some observations made at another gentoo rookery at Heard Island suggest that such infertility cannot be attributed to artificial influences. In this rookery containing about 250 nests five infertile eggs were picked up on 19 December from nests which each contained one growing chick. In none of these eggs was there any indication that development had ever started, and in two the yolk was still intact.

Period of hatching. In four cases, where the shell was only just starred when chipping was first recorded, only the bill could be seen through a small hole in the shell 24 hours later but the chick was hatched at the end of 48 hours. In other cases where the time of final hatching was fairly accurately known, no sign of chipping was noted 48 hours earlier. One or two cases in which hatching lasted more than 48 hours were probably exceptional.

Reaction to Loss of Eggs. The gentoos' reactions to the loss of their eggs are considerably more complex than the rockhoppers' or macaronis' and their capacity to re-lay under certain circumstances is far greater. This is however complicated by various factors, not least by the gentoos' natural timidity, which causes them to frustrate the efforts of the experimenter by abandoning sites where there is too much interference.

The effects of the following experiments were tried:—

a) The removal of each egg as it was laid.
b) The removal of the first egg only.
c) The removal of the second egg only.
d) The removal of both eggs as soon as the clutch was completed.
e) The removal of all eggs from a section of the rookery.

The nests selected for the experiments were all individually marked and situated amongst nests at which other birds were incubating undisturbed to induce a sense of security in the pairs under observation.

a) *The Removal of Each Egg as it was Laid.* This was done in eight nests in an area under daily observation. One nest was abandoned after the second egg was taken and never re-occupied. At another, one of the birds remained on guard for six days, after which the site was abandoned[1]. At a third, one bird was sitting three days later, but the site was then abandoned. The fourth nest was occupied intermittently for some time, and both birds were present and building 16 days later, but nothing came of this. At the remaining four nests a third egg was laid within five days of the removal of the second.

[1] These two nests were in an isolated area where the birds were rather nervous.

In two of the four sites which were abandoned conditions for the birds were discouraging, and in the other two the first egg was removed more than 24 hours after it had been laid, whereas at the four nests in which a third egg was laid, the first egg was removed soon after laying.

b) *Removal of the First Egg Only.* This experiment was carried out in an area previously little visited, and special care was taken to reduce disturbance to a minimum, as it was thought that failure to re-lay in the earlier experiment might have been due to excessive interference. The eggs were taken on the days they were laid (7 November U.V. b, 8 November U.V. c and U.V. d and 10 November U.V. h and U.V. i) and the area was not visited again till 18th November. Egg laying was a few days later than in the earlier groups. Pair b had laid two more eggs by 18 November, the second being abnormally narrow and pairs c, d and h had laid a second egg which they were content to incubate alone. On 18 November pair h were incubating two small angular stones, whose size and shape bore no resemblance to eggs. These they continued to incubate diligently at least until 7 December. It seems possible that this pair had laid and lost a second egg which was not recorded.

In three other nests under observation the first was stolen by skuas before the second was laid. Two of these laid and incubated only one more egg, but the third laid two more eggs and hatched both.

c) *Removal of the Second Egg Only.* In ten nests the second egg was removed within 24 hours after laying, the first egg being left undisturbed. All of these continued to incubate the remaining egg, and did not lay again. Eight hatched single chicks, one egg was infertile, and one was robbed before the end of incubation.

d) *Removal of Both Eggs as soon as the Clutch was Completed.* In four marked nests the clutch was taken within 24 hours of completion. In three other nests the clutch was taken 24 or 48 hours later. None of these pairs laid again in the same nests, though most of them continued to visit their empty sites intermittently. K5 may be quoted as an example. This nest was in a part of the rookery otherwise little disturbed, and the site could be observed from a distance. A newly completed clutch was taken on 4 November and the next day it was deserted. It remained so on all subsequent visits up to 23 November, when a pair were seen standing at the site. On 24 November it was again deserted, but on 29 November a pair were present, peering into the empty hollow, and one was seen to fetch a piece of nesting material. On 30 November it was deserted but a week later one bird was again present lying in the hollow.

More often, one or both birds were usually at the site for about a fortnight after the eggs were taken, one sometimes sitting in the nest. After that they gradually lost interest.

e) *Removal of All Eggs from a Section of the Rookery.* The experiment was tried of removing all eggs every second day from the beginning of laying, in a section of the rookery containing 51 pairs (one of which was left to nest in peace). The following table sets out the number of eggs collected:—

Date	No. of Eggs Collected	No. under 120 gm. in weight
31 October	6	
3 November	9	
4 November	15	
6 November	13	1
8 November	24	5
10 November	10	2
13 November	22	5

The number of eggs under 120 gm. is little more than might be expected in any random collection of fifty clutches and does not suggest that many third eggs had been laid. The two smallest (103.8 and 91.4 gm., collected on 8 and 13 November) were of a rather peculiar shape and might have been laid by the same bird. This section was not visited again till 18 November, when it was found that a considerable part of the area had been abandoned. The 34 birds still present were in a very nervous state and fled when approached. The next visit was on 2 December, when only 13 birds were sitting (at least one on an empty nest and one standing by an empty site). However it was found that an entirely new sub-section containing 17 pairs had been established a short distance up the hill. The birds were just beginning to lay and two had already completed clutches. Eight days later ten clutches had been completed, seven nests containing single eggs, and three further nests had been established. No more eggs were laid after this, the seven settling down to incubate single eggs and the three last pairs failing to lay. A further 14 pairs had established a similar late group as an annexe to another section close by. The first group had been established entirely, the second mainly, since the previous visit on 18 November.

There can be little doubt that these groups were fugitives from the section which had been systematically robbed. This second attempt was just a month after the first, and a month after the average time of laying in the main colony. Their eggs were of good size and included the only clutch of three eggs ever seen by the writer.

Factors Affecting the Times of Laying. These experiments should be considered in the light of normal variation when free from human interference. Egg-laying among the gentoos is not quite as highly synchronised as in species such as the macaroni which live in closely packed colonies, although the dates of normal laying are within fairly narrow limits. In 1950 first eggs were found on 26 October in all three gentoo rookeries within easy reach of the A.N.A.R.E. Station, and in the earliest section of one rookery laying was almost complete 12 days later.

Many observations indicate that at Heard Island the appearance of snow-free ground is an important factor in determining just when gentoos in any particular section of the rookery begin to lay. On 4 November in the earliest section 29 out of 35 nests contained eggs while in one portion of another rookery only 5 out of 32 nests contained eggs. The terrace on which the first group was established was almost free of snow from the beginning of egg-laying, while the hummocks on which the second group was established were only just appearing through the snow drifts at that date. Further, while no more nests were subsequently added to the former, nearly 30 additional nests were later established in the latter.

It is interesting to contrast this with Macquarie Island where the question of snow-cover does not arise. There egg-laying begins more than six weeks earlier.

Thus two distinct factors control the date of laying. The first is the inherited rhythm and habits of the species which are themselves perhaps a compound of several climatic factors; their net effect is fairly constant from year to year. The second, operating where the nesting grounds are snow-free for a limited season only, is the immediate accessibility of the desired nesting-sites, and this may vary from one part of a rookery to another. At Heard Island the nesting grounds probably become snow-free at approximately the same date each year, but it would be interesting to know what happens in exceptional years.

Although these two factors determine the dates for most laying, a certain amount of late laying normally occurs in every rookery. Such late laying may of course be the second attempt of birds which have already lost clutches. It almost invariably occurs in special groups, and isolated cases of late nesting are very rare. Groups of late nesters were first noted at Macquarie Island, associated with rookeries that were substantial distances from the sea. These birds gathered near the beaches, at times in very exposed places where they were liable to be over-run by elephant seals. As these sites were also the gathering places for unemployed and non-breeding birds, it seems probable that the late nesters may have been inexperienced young birds nesting for the first time who had mistaken this collection of birds for the main colony (c.f.

Richdale 1949). At Heard Island the segregation of late groups was less marked and they were often interspersed among groups which had laid at the normal time. The latest group seen was one of five pairs, one of which was sitting on a newly hatched chick on 26 January eight weeks after the first chicks had hatched.

One case of isolated late laying was observed in the centre of a rookery which contained no late section. A nest with a freshly completed clutch was found on 16 December when all the surrounding pairs had chicks, or eggs that were just about to hatch. On 2 February one of this pair was still guarding a fortnight old chick surrounded by a mob of moulting chicks. One suspects that the chick's chances of growing up were slight.

Finally, mention should be made of birds which prepare sites but do not lay. These are birds which are late in selecting their sites, probably because they have already abandoned earlier ones, and which start building at a time when their neighbours are starting to incubate. They complete nests and brood them for several days, but apparently lacking the stimulation of breeding behaviour among their neighbours they fail to lay, though they continue to visit their sites at intervals.

Conditions Required for Re-laying. It is evident from the experiments described that while a natural clutch of three eggs is rare, a gentoo will in certain circumstances lay a third egg in an attempt to complete its clutch after the loss of the first egg. But once the clutch has been completed, even if it is taken immediately, the stimulus to continue laying is lost, and the bird's subsequent reactions depend a great deal on the behaviour of its neighbours. A pair which lose a clutch in a group where the rest are peacefully incubating, will generally continue to guard their empty site, and will perhaps make sporadic attempts at rebuilding[1]. On the other hand if they and their neighbours all lose their eggs they will abandon their original sites and seek to establish others[2]. If a pair leave a robbed nest and settle beside birds which have just finished laying, they may build a nest, but will fail to lay again; but if they find themselves in the company of other pairs in a similar position, they may join them to form a late nesting group. If this happens second clutches may be laid after an appropriate interval.

(1) Their original nesting material is of course pilfered on the first occasion on which it is left unguarded. The late collecting of nesting material is not confined to unsuccessful pairs, for on several occasions birds have been observed piling nesting material around their sitting partners. Among both successful and unsuccessful pairs recrudescence of the desire to collect is seen chiefly toward the end of the incubation period.

(2) Goodridge (1847) quotes a sealer (wrecked on the Crozet Islands in 1820) as saying:— "We observed, when we robbed those [gentoos] which formed their nests on the plain, that they rebuilt their nests higher up" which exactly describes what happened at one of the Heard Island rookeries in 1950.

Such behaviour is a good example of the necessity of mutual stimulation for successful breeding, a subject discussed by Roberts (1940) in his analysis of the exteroceptive factors affecting the reproductive cycle in penguins. It is perhaps significant that the single case of isolated late laying observed at Heard Island occurred during hatching, which is a time of renewed emotional excitement in the colony after the torpid days of incubation.

Exploitation. The writer is cautious about accepting the reports quoted by Murphy (1936) that from five to eight or even ten layings by gentoos may result from repeated robbing of the nests. Allowance may not have been made for the natural scatter in the dates of laying. Casual observers do not realise that clutches collected on different dates (unless from marked nests) are generally not repeated layings but rather the products of pairs which had not yet laid at the times of the earlier visits. Furthermore, birds which lay again as a result of losing completed clutches do so only after a considerable interval.

The best method of harvesting gentoo penguins' eggs is probably to collect all eggs from as large an area as possible for the first few days of laying only. There will then be a sufficient number of birds which have not laid to encourage those which have lost eggs to continue.

THE EGGS OF THE ROCKHOPPER AND MACARONI PENGUINS

The first eggs of the rockhopper and macaroni penguins are considerably smaller than the second eggs but in both species the two eggs of a clutch are of similar shape. The shape varies from clutch to clutch but in all cases it is elongate and more or less tapered, the taper being more pronounced in the macaronis which is no doubt related to the fact that they nest on stony slopes with little or no pretence at a nest. A selection of four two-egg and one three-egg rockhopper clutches is shown in Plate 2 and one two-egg macaroni clutch in Plate 3.

In the following work weight was used as a measure of egg size. This proved satisfactory as long as the eggs were freshly laid and weighed within a reasonable time after collection, partially incubated eggs being excluded. Weights and measurements of unselected[1] clutches of rockhopper eggs from Heard Island are given in Table 1 while measurements of additional clutches selected because of their unusual sizes or shapes are given in Table 1a. Similar figures for macaroni eggs are given in Tables 2 and 2a. A summary of similar measurements on rockhopper eggs from Macquarie Island is given in Table 3. In Figures 1 and 2 are plotted the weights of first eggs against the weights of second eggs.

[1] These were taken from marked nests chosen purely because of convenience of site and are considered a random sample of clutches.

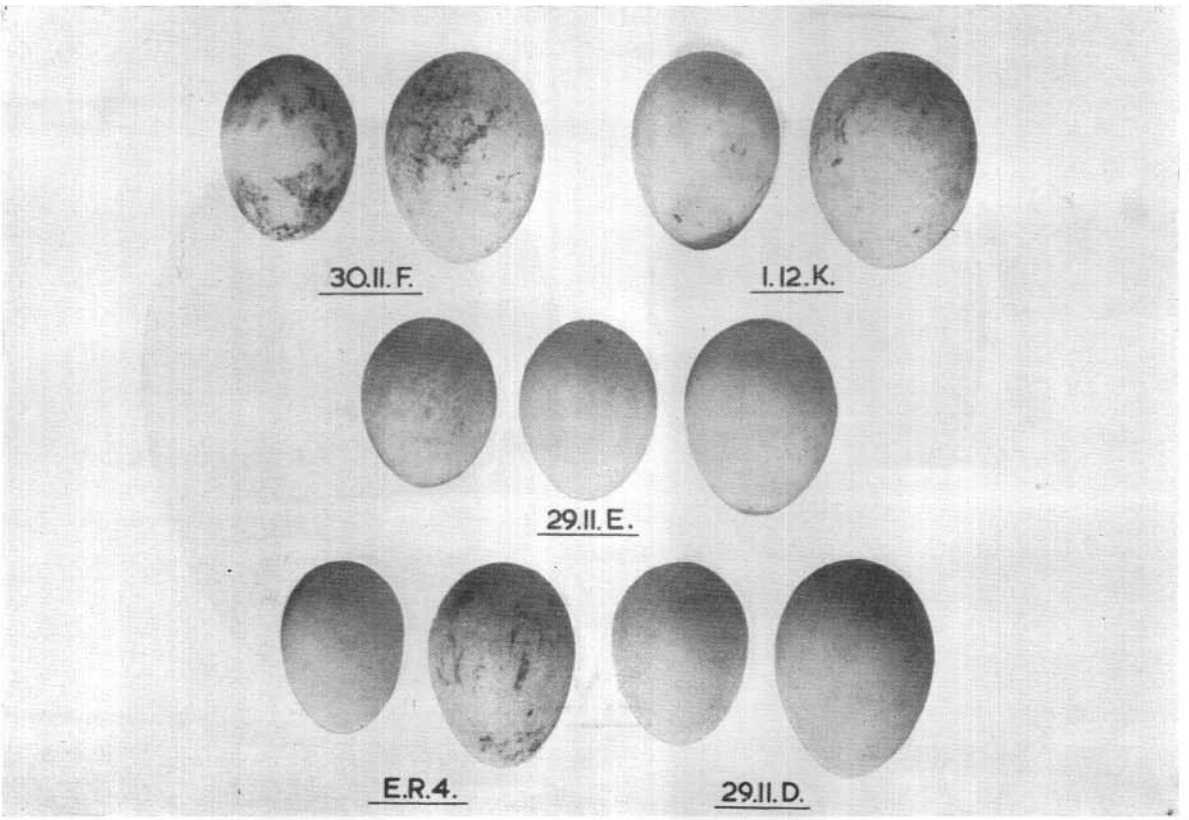

Plate 2.—A Selection of Rockhopper Penguin Clutches.

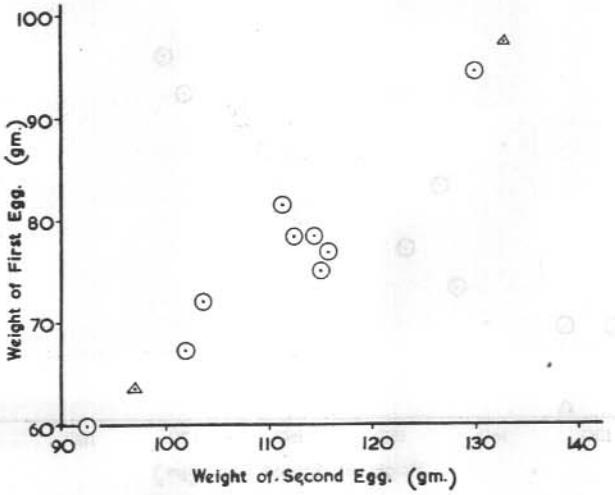

Fig. 1.—Weight of First Egg plotted against Weight of Second Egg for Rockhopper Penguins. Points in circles from Table 1, points in triangle from Table 1a.

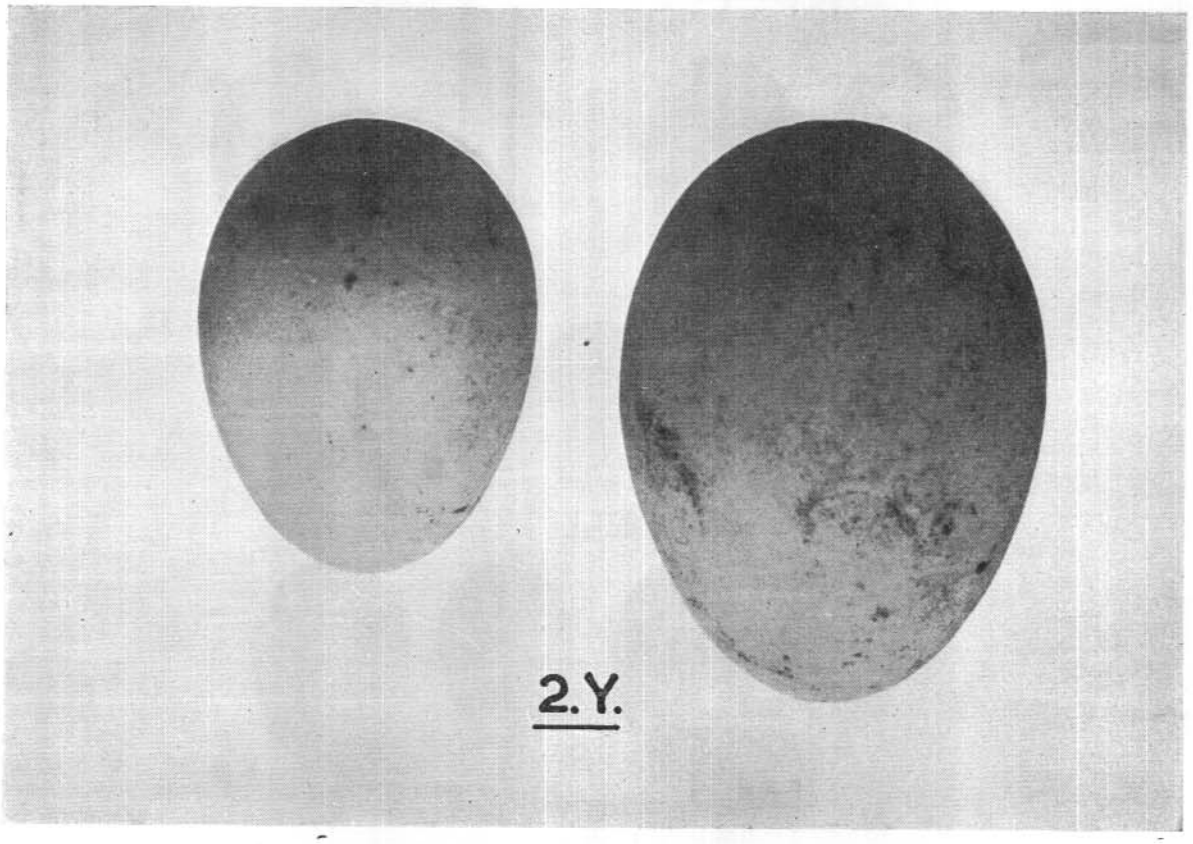

Plate 3.—A Macaroni Penguin Clutch

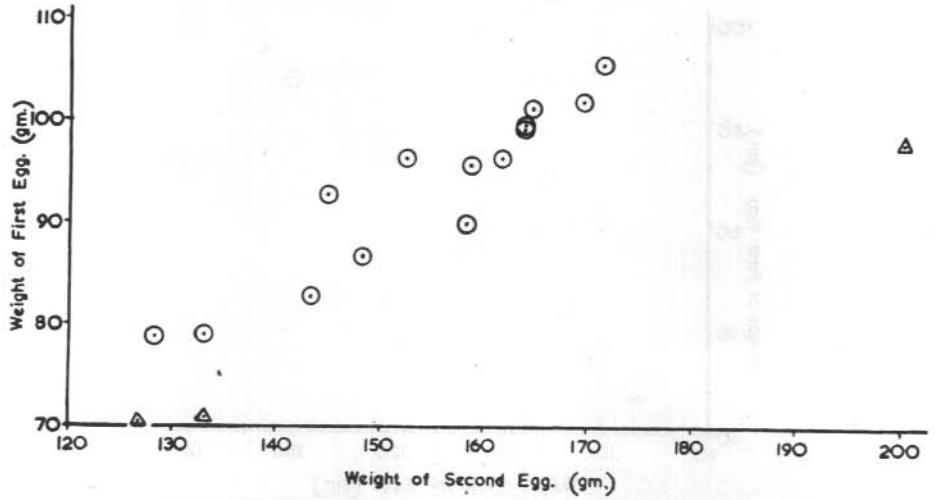

Fig. 2.—Weight of First Egg plotted against Weight of Second Egg for Macaroni Penguins. Points in circles from Table 2, points in triangles from Table 2a.

It is obvious from these figures that the weights of first and second eggs are not independent, for a large first egg is generally associated with a large second egg. This suggests that the egg weights are samples from a bivariate population.

In biological work it is generally found that linear dimensions are normal variates. For this reason the following analysis deals with the cube roots (denoted w_1 and w_2) of the weights of first and second eggs, and assumes the measures w_1 and w_2 to be samples from a bivariate normal[1] population. Using standard statistical procedures, parameters specifying this bivariate normal population were estimated from the data listed in Tables 1 and 2. These estimates and the 95% confidence limits[2] of the population parameters are listed below:—

	Rockhopper Penguin	
	First Egg (w_1)	Second Egg (w_2)
Mean	4.231 (4.094-4.368)	4.798 (4.682-4.914)
Variance	0.032	0.023
Correlation Coefficient	0.95 (0.79-0.99)	

	Macaroni Penguin	
	First Egg (w_1)	Second Egg (w_2)
Mean	4.543 (4.467-4.619)	5.362 (5.273-5.451)
Variance	0.017	0.025
Correlation Coefficient	0.92 (0.76-0.97)	

It will be noted that the difference between mean w_1 and mean w_2 is much greater in the macaroni than in the rockhopper. However the value of the correlation coefficient for macaronis is not significantly different from that for rockhoppers. Combining these two estimates a value $0.94 \pm \frac{0.04}{0.10}$ is obtained as the estimate of the correlation coefficient. It is possible that this particular value of the correlation coefficient between w_1 and w_2 is a characteristic of the genus *Eudyptes* as a whole.

(1) In this case the samples are too small to enable a useful test to be made of the assumption that the cube root of weight is a normal variate.

(2) The probability that these limits include the value of the parameter characteristic of the population is 0.95.

TABLE 1

Measurements of Unselected Clutches of Rockhopper Eggs from Heard Island.

Number of Clutch	First Egg			Second Egg		
	Weight (gm)	Length (mm)	Width (mm)	Weight (gm)	Length (mm)	Width (mm)
29. 11.B	78.6	68.0	46.0	112.4	74.0	53.0
29. 11.C	67.4	62.0	44.0	102.0	72.0	50.5
29. 11.D	75.2	62.5	46.5	115.0	73.7	53.5
30. 11.F	78.6	64.7	46.7	114.4	72.0	53.5
30. 11.G	72.2	60.5	46.0	103.6	68.0	52.5
30. 11.H	77.0	64.7	46.2	115.8	73.0	53.5
1. 12.K	94.4	67.5	50.5	129.8	73.0	56.5
E.R.4	60.0	59.0	42.2	92.6	69.2	49.0
4. 12.M	81.6	63.7	48.0	111.4	70.0	54.0

TABLE 1a

Measurements of Selected Clutches of Rockhopper Eggs from Heard Island.

Number of Clutch	First Egg			Second Egg		
	Weight (gm)	Length (mm)	Width (mm)	Weight (gm)	Length (mm)	Width (mm)
29. 11.A	97.2	65.2	51.5	132.8	72.7	56.7
1. 12.I	63.6	65.0	42.7	97.0	73.7	49.5

TABLE 2[1]

Measurements of Unselected Clutches of Macaroni Eggs from Heard Island.

Number of Clutch	First Egg			Second Egg		
	Weight (gm)	Length (mm)	Width (mm)	Weight (gm)	Length (mm)	Width (mm)
20	79.0	—	—	133.0	—	—
EO	92.8	69.3	49.0	143.4	79.4	57.1
40	99.6	68.5	50.7	164.0	79.0	60.4
14	105.4	72.1	51.4	171.4	79.6	61.7
15	101.2	65.3	52.7	164.8	79.6	61.0
YY	95.6	76.4	47.9	159.0	84.5	57.5
18.11.f	96.2	70.0	49.2	161.8	81.5	59.2
Av 116	96.4	70.4	49.1	152.4	79.0	58.9
Av 117	78.9	66.0	46.0	128.2	78.1	54.8
Av 118	99.1	71.1	50.0	164.0	82.9	59.0
Av 119	92.7	82.4	45.3	145.0	88.0	55.0
Av 121	90.0	69.6	48.0	158.4	81.1	59.2
Av 122	101.8	69.0	51.0	169.6	81.3	60.8
Av 123	86.8	67.1	47.5	148.2	78.2	57.9

[1] All the macaroni clutches were obtained from marked nests by collecting each egg in turn as it was laid, thus obviating the possibility of "foreign" eggs ejected from neighbouring nests being included. The clutches with Av serial number were collected at the writer's request by M. Downes, A.N.A.R.E. biologist at Heard Island during 1951.

TABLE 2a

Measurements of Selected Clutches of Macaroni Eggs from Heard Island.

Number of Clutch	First Egg			Second Egg		
	Weight (gm)	Length (mm)	Width (mm)	Weight (gm)	Length (mm)	Width (mm)
Av 120[1]	97.8	68.0	50.5	200.4	87.5	64.1
70	70.4	58.0	47.0	126.8	73.0	56.0
2Y	71.0	61.7	45.7	133.0	77.0	55.7

TABLE 3

Summary of Measurements of Seven Unselected Rockhopper First Eggs from Macquarie Island.

Mean			Largest			Smallest		
Weight (gm)	Length (mm)	Width (mm)	Weight (gm)	Length (mm)	Width (mm)	Weight (gm)	Length (mm)	Width (mm)
80.9	64.3	47.5	86.2	63.5	49.0	67.2	58.5	45.3

Summary of Measurements of Eleven Unselected Rockhopper Second Eggs from Macquarie Island.

Mean			Largest			Smallest		
114.2	71.5	53.8	127.6 127.6	76.0 71.5	55.5 56.5	96.2	70.0	50.5

THE EGGS OF THE GENTOO PENGUIN

The gentoo normally lays two eggs, of which the first is usually somewhat larger than the second. In a newly completed clutch it is always possible to tell which is the first and which is the second egg as even in the cleanest grass nests the first egg has always acquired a soiled appearance by the time the second is laid. As from then on the eggs are carefully incubated, this difference persists for a considerable time.

[1] Clutch Av 120 was obtained in an unselected series. It was excluded from Table 2 because of the size of the second egg which was plainly abnormal. It is possible that this was a double-yolked egg.

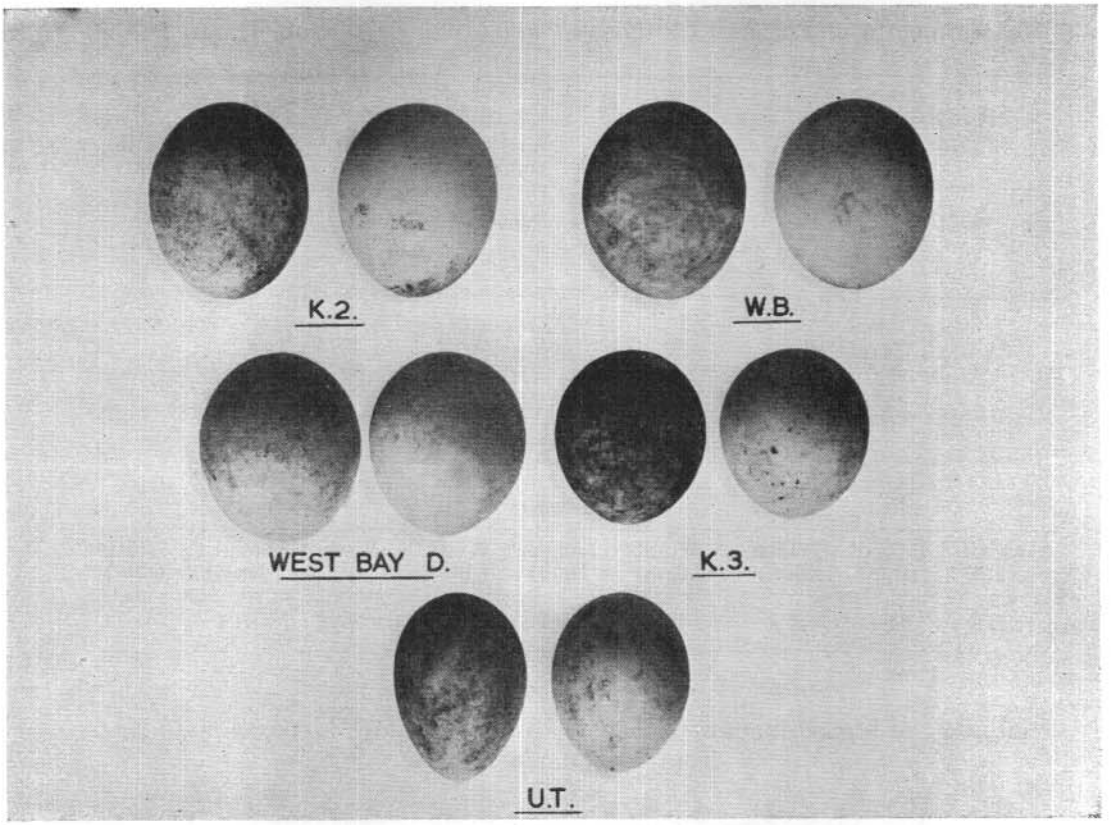

Plate 4.—A Selection of Gentoo Penguin Clutches.

The eggs of the gentoo are very variable both in size and shape but in general tend to be rounded or sub-spherical in their main outline. Usually the two ends are distinguishable and some unusual shapes occur. A selection of clutches is shown in Plate 4.

Eggs of the same clutch are usually similar in shape and an abnormally shaped egg is usually associated with another of similar shape. The main exception is in cases where the first egg is lighter than the second. Here the first egg is usually longer than the second but very narrow or poorly filled. Such a case is clutch U.T. (c.f. Table 4a) in Plate 4. It is interesting to note that Richdale (1949) found that in the yellow-eyed penguin the eggs of the young birds were significantly lighter and narrower than those of older birds while there was no significant difference in length.

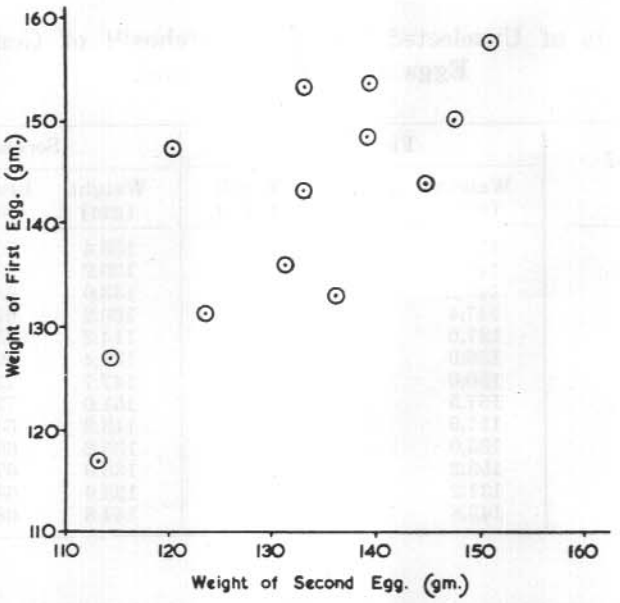

Fig. 3.—Weight of First Egg plotted against Weight of Second Egg for Gentoo Penguins. Data from Table 3.

Weights and measurements of unselected clutches of gentoo eggs from Heard Island are listed in Table 4 and similar figures for the selected clutch U.T. mentioned above are listed in Table 4a. Figure 3 shows a plot of weight of first egg against weight of second egg.

As in the case of macaroni and rockhopper eggs it is apparent that the weight of the first egg is not independent of the weight of the second. It is again assumed that the cube roots, w_1 and w_2, of the weights are samples from a bivariate normal population. The following estimates (from the data of Table 4) of the parameters specifying the population are obtained:—

	Gentoo Penguin	
	First Egg (w_1)	Second Egg (w_2)
Mean	5.209 (5.118-5.300)	5.098 (5.004-5.192)
Variance	0.023	0.025
Correlation Coefficient	0.76 (0.36-0.92)	

Measurements of one natural gentoo three-egg clutch and four artificially induced three-egg clutches are given in Table 5. It will be seen that the decrease in size from first to second egg is continued in the third.

TABLE 4

Measurements of Unselected Two-Egg Clutches[1] of Gentoo Penguin Eggs from Heard Island.

Number of Clutch	First Egg			Second Egg		
	Weight (gm)	Length (mm)	Width (mm)	Weight (gm)	Length (mm)	Width (mm)
WB	153.6	73.5	60.7	139.4	70.5	59.0
L.28.a	148.4	70.5	61.0	139.2	68.5	60.0
B.33.a	143.2	70.5	60.0	133.0	68.5	59.0
B.22.d	147.4	73.0	60.0	120.2	67.2	56.5
B.2.11.(a)	127.0	69.5	57.0	114.2	65.5	55.7
K 1	136.0	70.0	58.7	131.4	70.0	57.7
K 2	150.0	73.7	60.0	147.7	73.0	60.0
B.33(e)	157.5	75.5	61.0	151.0	73.5	60.5
K 3	117.0	66.5	56.2	113.2	64.5	56.0
K 5	133.0	69.0	58.5	136.2	68.5	59.5
U.V. (a)	153.2	71.0	61.5	133.0	67.7	59.0
U.V. (e)	131.2	73.0	57.0	123.6	68.5	56.7
U.V. (g)	143.8	69.2	60.7	144.8	68.5	61.0

TABLE 4a

Measurements of a Selected Abnormal Clutch of Gentoo Eggs from Heard Island.

Number of Clutch	First Egg			Second Egg		
	Weight (gm)	Length (mm)	Width (mm)	Weight (gm)	Length (mm)	Width (mm)
U.T.	99.0	70.7	50.0	104.4	67.2	52.5

TABLE 5

Measurements of Three-Egg Clutches of Gentoo Eggs from Heard Island.

Number of Clutch	First Egg			Second Egg			Third Egg		
	Weight (gm)	Length (mm)	Width (mm)	Weight (gm)	Length (mm)	Width (mm)	Weight (gm)	Length (mm)	Width (mm)
B.2.11(a)	127.0	69.5	57.0	114.2	65.5	55.7	—	63.0	53.2
B.33 (e)	157.5	75.5	61.0	151.0	73.5	60.5	—	70.0	55.5
B.33 (c)	—	—	—	129.4	67.2	58.5	—	64.0	55.5
B.33 (d)	—	—	—	125.6	68.0	57.0	—	67.5	54.5
Natural	146.4	73.5	60.0	151.8	72.0	61.5	137.6	70.2	59.0

[1] In two or three of these clutches the possibility that the first egg had been lost and therefore second and third eggs are being dealt with cannot be excluded.

A REVIEW OF EGG-LAYING AND INCUBATION AMONG PENGUINS

Pygoscelidae. From the accounts of Gain (1914), Levick (1915) and Bagshawe (1934) it is clear that the egg-laying of the Adélie and ringed penguins is similar to that of the gentoo. The former has an egg interval of 3 or 4 days and a slightly shorter incubation period than the gentoo. Levick records 37, 33 and 31 days, but the first of these is from the laying of the first egg and, as Levick himself points out, merely demonstrates that incubation does not begin till the second egg is laid. His records therefore should be read as two of 33 days and one of 31 days. Gain records that Adélie penguins may on rare occasions lay a clutch of three and states that they can be made to lay 2 or 3 eggs beyond their normal clutch "by removing the eggs from the nest". It is not clear whether he is dealing with marked nests. He records the incubation period as 33-36 days, but here again this may include records from the laying of the first egg to the hatching of the first chick.

The only adequate study of the ringed or chinstrap penguins is by Bagshawe, whose records of incubation periods are of the interval from laying to hatching. His records of such periods for second eggs vary from 34 to 37 days and the period between first and second eggs averages 3.4 days. He mentions three-egg clutches as very rare.

Megadyptidae. For the yellow-eyed penguin Richdale (1940) records incubation periods of from 40 to 50 days which is a surprisingly wide scatter, but in nearly 70% of the 86 records collected the period was from 42 to 44 days. The period between eggs was usually 4 to 5 days and a clutch of two eggs of very similar size was the rule. Clutches of three eggs are apparently unknown.

Eudyptulidae. The penguins of the genus *Eudyptula* have not been studied in much detail, and are evidently difficult subjects. They lay two eggs and have an incubation period of about 38 days (Richdale 1941a).

Spheniscidae. The most detailed observations on a member of this genus are those of Kearton (conveniently summarised by Murphy 1936) on the South African species, which is remarkable in that it is believed to have two breeding seasons a year. Its normal clutch is two and the incubation period 39 to 41 days (Roberts 1940). It is regularly exploited for its eggs under government license, but no detailed study of the biological economics of this exploitation appears to have been made.

Aptenodytidae. The king and emperor penguins normally lay one egg and incubation in the former lasts about 52 days (Roberts, ibid.).

Eudyptidae. Penguins of the *Eudyptes* genus are the only ones in which all the species which have been studied lay two eggs of conspicuously unequal size, with proportionately dissimilar prospects. Of the five species generally recognised, the rockhopper and the macaroni have been discussed in the present paper. The details concerning the royal, which is essentially a macaroni with a white face, are not yet known[1]. The erect-crested penguin, *E.sclateri* is the subject of two very interesting papers by Richdale (1941b and 1950) who made a careful study of a pair which nested on the Otago peninsula in 1938 and 1939. In 1940 and for six years afterwards the female returned alone, and laid in five of these years. In 1938, when first found, the female was incubating a single egg. On each subsequent occasion it laid two eggs, but always ejected the smaller, apparently deliberately, when the second was laid. Richdale states that in 1939 the second egg was smaller but he refrained from handling either egg before it was found outside the nest for fear of disturbing the bird. On all subsequent occasions the first egg was smaller. From the figures given there is obviously no simple relationship between the weights of first and second eggs in the clutches laid by this particular bird, but it seems clear that otherwise the behaviour of this species tends to resemble that of the macaroni. In the second of the two papers mentioned Richdale gives a table for 50 clutches of the thick-billed penguin, *E.pachyrhynchus.* All are two-egg clutches and in many there is a marked discrepancy in size, though in some clutches the difference is slight. Richdale states that he is not aware which eggs in the clutches were laid first.

A COMPARISON OF THE EGG-LAYING OF THE ROCKHOPPER AND MACARONI PENGUINS

In every aspect of its laying the macaroni penguin is more specialised than the rockhopper.

(a) The "token" first egg is considerably smaller in the macaroni penguin.

(b) The rockhopper frequently incubates both eggs up to hatching time whereas the macaroni rejects the first egg on the completion of its clutch, or not long afterwards, and frequently loses it even before the second egg is laid.

[1] An unpublished manuscript, "Notes on the Royal Penguin, *Eudyptes schlegeli* at North Heard, Macquarie Island 1952-3" by Z. Soucek, A.N.A.R.E. medical officer at Macquarie Island in 1952, shows that the first egg is distinctly smaller than the second, the mean weight of first and second eggs being 102.8 gm. and 162.2 gm. respectively, and the mean length being 68.7 mm. and 80.7 mm. respectively. Soucek also states: "The guarding of the first eggs was careless and all were destroyed or thrown out either before or soon after the laying of the second egg". The incubation period was 35 days. No three-egg clutches were recorded.

(c) The frequency of three-egg clutches among the rockhoppers must be considered a primitive trait, since only one chick is reared. Three-egg clutches are so far unknown in the macaroni.

(d) The macaroni dispenses with anything more than a "token nest", whereas the rockhoppers still on occasion build substantial grass nests.

One curious feature of the egg-laying habits of the rockhoppers and macaronis is that, though their effective clutch has been reduced to one, the laying of the "token" first egg has been retained. Its function is certainly not an insurance against the loss of the larger egg, though it might ensure that the larger egg is properly prepared for and receives prompt and wholehearted attention on its arrival.

Comparison of Laying Dates. One other point brought out by these studies is that the dates on which the first eggs are laid by any one species in one locality is remarkably constant from year to year. This has often been noted, though the tables in Murphy (1936) and Roberts (1940) list in most cases only the month. The following table compares the laying dates at Heard Island and Macquarie Island for the gentoo, rockhopper and macaroni penguins.

	Heard Island		Macquarie Island	
	1949	1950	1949	Falla (1937)
P.papua	22 Oct.	26 Oct.	9 Sept.	13 Sept. 1912
E.chrysocome	—	23 Nov.		11 Sept. 1913[1]
E.chrysolophus	12 Nov.	10 Nov.	8 Nov.	9 Nov. 1912

In every case recorded by the writer, laying was fairly general within two days of the dates given. The exact beginning of laying by the rockhoppers at Heard Island was missed in 1949, but it was between 21 November, when there were no eggs, and 26 November when some pairs already had a clutch of two.

(1) Tulloch reported first eggs on 12 September, 1915.

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