

THE EFFECT OF AGE ON LAYING DATES, SIZE OF EGGS, AND SIZE OF CLUTCH IN THE YELLOW-EYED PENGUIN

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IN THE twelve-year period from August 1936 to May 1948 I have carried out a banding study of the Yellow-eyed Penguin, *Megadyptes antipodes*, on the Otago Peninsula, New Zealand. In the course of this study it has been possible to note the behaviour of 162 young penguins from the time when they entered the water as fledglings until they disappeared from my field of operations. The age of individuals under review varied from 1 to 11 years with only 2 birds attaining the age of 11 years. It is obvious, therefore, that by the time the study ended several of the penguins had become aged. Nevertheless, for the purpose of this paper all birds whose age is known are considered 'young penguins.' In addition to the 162 young penguins whose date of hatching could be determined there were also under observation 298 other young penguins which were banded in their first year. It was unknown when and where these juvenals were hatched but as all eggs of the Yellow-eyed Penguin are normally laid within a space of approximately 3 weeks in any one season, the age of these young birds is therefore known to within 3 weeks.

From the study of the behaviour of 460 young penguins in relation to their age, much information has evolved relative to the influence of age on breeding biology. In this paper only 3 aspects will be considered: (1) the influence of age on laying dates; (2) the influence of age on size of eggs; and (3) the influence of age on size of clutch.

Two terms need defining. (1) From the time when a young penguin enters the sea as a fledgling until it moults into its first adult plumage such a bird will be known as a *juvenal*. This period varies from approximately 14 to 18 months. The juvenals are easily recognised by the lack of a sulphur-yellow band of feathers across the back of the head as obtains in adults. (2) In the period between the first and the second adult moults, the penguins will be described as *two-year-olds* and so on for succeeding age-groups.

An outline of the annual cycle of the Yellow-eyed Penguin has already been published (Richdale, 1941). Briefly, the cycle is as follows: Towards the end of August the penguins begin to spend much time ashore in the daytime preparatory to egg-laying. From the middle of September to early October all eggs that are to be laid that season will appear. Since incubation lasts approximately 42 days, by the end of the third week in November practically all chicks which are to hatch, have hatched. For approximately 8 weeks the chicks are continuously guarded by each parent in turn but after that the chicks are left unguarded in

the daytime. Towards the end of February the chicks gradually enter the water and approximately 2 weeks after that, on the average, the parents begin their annual moult. One month previously, on the average, however, juvenals and adults which have not been feeding chicks pass through their moult. In the winter months this species of penguin does not migrate but tends to spend part of its time on the breeding grounds in the evening and during the night. It is at this period that the majority of the new pairs for the ensuing season are formed.

AGE OF BIRD AND LAYING DATES

As the years of the research passed by and as more and more females of known age laid for the first time, it became obvious that age had no influence whatsoever on the date of laying of any particular female. To test the matter statistically the relative data have been tabulated in Table 1. Young birds laying for the first time totalled 59 individuals made up of 34 two-year olds, 23 three-year-olds,

TABLE 1

A Comparison of Laying Dates of Females Laying for the First Time and of Older Females of Unknown Ages

TYPE OF BIRD	NUMBER OF EGGS	MEAN DATE, SEPTEMBER	STANDARD DEVIATION IN DAYS	STANDARD ERROR IN DAYS
Young	104	26.06	5.70	.56
Age unknown	100	27.45	5.37	.54

and 2 four-year-olds. The 52 older birds were of unknown age because they were already adults when first banded. The dates of egg-laying used for these older birds are those when the individual bird was either last seen in its place of breeding or else in the twelfth year of study. This means that the birds ranged in age from at least 7 years to at least 14 years when the data concerning them were taken.

Of the 104 eggs laid by the young birds, 45 females produced 2 eggs and 14 females only 1 egg. Of the 100 eggs laid by older birds, 48 females produced 2 eggs and 4 females only 1 egg. Had these single eggs in both groups of birds been excluded the mean laying dates of the 2 sets of birds would have been much closer but even so the difference as it stands is not statistically significant. From more than 700 records of laying dates in twelve years, the earliest laying date for a young bird is 11 September and the latest is 12 October. For an older bird the earliest laying date is 13 September and the latest is 15 October but the latter date is not included in the data in Table 1 because the laying date of a later season has been used for the particular female penguin concerned.

AGE OF BIRD AND SIZE OF EGGS

In Table 2 are given details of egg weights at various ages from 2 to 11 years of age. In some instances the number of eggs weighed has not yet reached an adequate sample, especially for the later years, but the investigation is still continuing. All eggs were weighed shortly after being laid. As the figures stand for first and second eggs laid by two-year-olds there is no significant difference, but the sample is small.

It is interesting to note that three-year-old females laying for the first time do not produce eggs lighter than those by three-year-olds which had already laid as two-year-olds. As two-year-olds lay eggs which are significantly ($P < .005$) smaller than those produced by both types of three-year-olds, it is

TABLE 2
A Statistical Comparison of Weight of Eggs at Successive Ages of Females

TYPE OF EGG	NUMBER OF EGGS	MEAN	STANDARD DEVIATION	STANDARD ERROR
		<i>grams</i>	<i>grams</i>	
First egg of two-year-olds	34	115.12	6.06	1.04
Second egg of two-year-olds	19	118.68	7.86	1.85
All eggs of two-year-olds	53	116.39	6.61	0.91
Eggs by three-year-olds laying for first time	47	130.04	5.70	0.83
Eggs by three-year-olds laying for second time	42	131.36	7.74	1.19
All eggs of three-year-olds	89	130.66	6.41	0.68
All eggs of four-year-olds	64	135.31	5.46	0.68
All eggs of five-year-olds	40	137.07	7.29	1.14
All eggs of six-year-olds	29	136.69	7.80	1.44
Eggs by birds 7 to 11 years old	35	139.91	7.91	1.34
Eggs by other birds 8+ to 14+ years old	100	139.19	10.17	1.02

obvious that age is the main factor in the smallness of the eggs laid by two-year-olds and that if two-year-olds do not lay until a year later they are physiologically able to lay eggs as large as those females which have already laid as two-year-olds.

On comparing the three-year-olds and the four-year-olds it may be observed that egg weights increase still further significantly but between successive years no significant increase is registered again. If, however, the four-year-olds are compared with the grouped ages from seven to eleven years another significant difference seems apparent. This means that by the age of four years the egg weights have almost reached their maximum and that over a course of several years a slight significant increase may possibly obtain. More data are required to say exactly when the increase ceases and when, if any, there is a decline in weight due to age.

As a further check, statistics from 100 eggs laid by birds whose ages ranged

from at least 8 years to at least 14 years were worked out. When compared with these, the eggs laid by four-year-olds indicated a significant difference but those laid by five-year-olds did not so that egg weights, on the average, probably reach their maximum when the females are in their fourth and fifth years.

In Table 3 statistical data for the length of the egg have been worked out in the same way as for the weight in Table 2. An endeavour has been made also

TABLE 3
A Statistical Comparison of Length of Eggs at Successive Ages of Females

TYPE OF EGG	NUMBER OF EGGS	MEAN	STANDARD DEVIATION	STANDARD ERROR
		<i>mm.</i>	<i>mm.</i>	
First egg of two-year-olds	34	74.7	3.36	.58
Second egg of two-year-olds	19	76.6	2.57	.59
All eggs of two-year-olds	53	75.4	3.28	.45
Eggs by three-year-olds laying for first time	47	76.5	2.02	.29
Eggs by three-year-olds laying for second time	42	76.1	2.34	.37
All eggs of three-year-olds	89	76.3	2.17	.23
All eggs of four-year-olds	64	76.7	2.63	.33
All eggs of five-year-olds	40	76.2	1.93	.31
All eggs of six-year-olds	29	76.5	1.75	.32
Eggs by birds 7 to 11 years old	35	76.7	1.95	.33
Eggs by old birds 8+ to 14+ years old	100	76.0	2.64	.26

to discover if there are any significant differences in the various age-groups for lengths but in no instance is any difference significant. It is noticeable, however, as far as the study has proceeded, that in eggs laid by two-year-olds there is a greater spread of egg lengths which lessens with age. With birds in the group at least eight years old and more the length again becomes irregular, suggesting an interesting problem to investigate when penguins of a known age become older.

An examination of the data relative to the width of eggs (Table 4) reveals a situation comparable to that for weights with the exception that the difference in egg-width between the four-year-old birds and those birds for the group from 7 to 11 years old is not quite significant statistically. The above means therefore that there are 3 significant differences for egg-width involving the same age-groups as for weights. These are (1) birds 2 years old lay narrower eggs than birds 3 years old and older (2) birds 3 years old lay narrower eggs than those 4 years old and older (3) birds 4 years old apparently lay slightly narrower eggs than birds of age ranging from at least 8-14 years.

Two other points are of interest. (1) Between three-year-olds laying for the first time and those three-year-old birds which laid as two-year-olds there is, as with weights, no significant difference in their egg-width. (2) The differ-

ence in egg-width between the four-year-olds and the last 2 age-groups mentioned in Table 4 is not quite significant for the group from 7-11 years but the difference is significant for birds at least from 8-14 years old. This information suggests that birds may lay slightly wider eggs after 4 years of age, but, as with the data for weight, more details are required for definite decisions.

TABLE 4
A Statistical Comparison of Width of Eggs at Successive Ages of Females

TYPE OF EGG	NUMBER OF EGGS	MEAN	STANDARD DEVIATION	STANDARD ERROR
		<i>mm.</i>	<i>mm.</i>	
First egg of two-year-olds.....	34	53.31	1.49	.26
Second egg of two-year-olds.....	19	53.34	1.46	.33
All eggs of two-year-olds.....	53	53.32	1.48	.20
Eggs by three-year-olds laying for first time.	47	55.95	0.94	.14
Eggs by three-year-olds laying for second time.....	42	56.36	1.17	.18
All eggs of three-year-olds.....	89	56.15	1.08	.12
All eggs of four-year-olds.....	64	56.98	1.14	.14
All eggs of five-year-olds.....	40	57.52	1.37	.22
All eggs of six-year-olds.....	29	57.25	1.35	.25
Eggs of birds 7 to 11 years old.....	35	57.75	1.35	.23
Eggs of old birds 8+ to 14+ years old.....	100	58.05	1.59	.16

TABLE 5
Age in Relation to Size of Clutch

	AGE OF BIRD IN YEARS				
	2	3	4	5-10	7-14
Number of females.....	40	53	39	63	63
Number of eggs.....	67	104	78	124	123
Mean eggs.....	1.68	1.96	2.00	1.97	1.95

AGE OF BIRD AND SIZE OF CLUTCH

The normal clutch size for the Yellow-eyed Penguin is 2 eggs. In collecting data for this investigation I have included only those clutches from breeding areas in which I was working frequently in the period when the eggs were being laid. It is not safe to wait until the eggs have been incubated for a time for, in the interval since the eggs were laid, a number certainly disappear for various reasons.

Table 5 lists 258 females and the number of eggs laid by them according to age. All records were taken soon after the eggs were laid. Of 40 two-year-olds, 13 (32.5%), laid only 1 egg to the clutch; of 218 older penguins, 7 (3.2%) as far as I could ascertain, laid only 1 egg to the clutch. A further point of interest is that of 31 three-year-olds which did not lay as two-year-olds, only

1 bird failed to produce the normal complement of 2 eggs to the clutch. Of an additional 22 three-year-olds which had already laid the previous season as two-year-olds, only 1 did not produce 2 eggs. As this bird suddenly changed its mate (a most unusual happening) some 2 weeks before laying, my impression was that this unusual procedure was the cause of the single egg to the clutch. Further, the egg did not hatch.

DISCUSSION

As for other species of birds not much information is available relative to the effect of age on laying dates, size of eggs, and size of clutch. In connection with the effect of age on laying dates Nice thinks (1937: 106) that in the Song Sparrow, *Melospiza melodia*, the earliest sets of eggs are laid by adult birds and that the young females probably lay later. She also quotes authors who indicate that in the Starling, *Sturnus vulgaris*, and in the Grey Heron, *Ardea cinerea*, old birds tend to lay earlier than young females.

Further evidence on the matter under discussion is as follows: From 9 January to 26 February 1948 I spent 48 days on the sub-Antarctic islands, The Snares, which are situated some 64 miles south-west off the end of the most southerly of the 3 main islands of New Zealand. Among other things it was possible to study the laying period of Buller's Mollymawk, *Diomedea bulleri*. Females of this species began to lay on 16 January and had almost completed laying for the year when we left on 26 February so that the span of laying is approximately 7 weeks. A total of 132 eggs was weighed and measured (only 1 egg forms the clutch). There was no tendency for large eggs to be laid first and for smaller eggs to appear later. All sizes were scattered indiscriminately throughout the entire laying period. Therefore, if my surmise is correct that young birds in Buller's Mollymawk lay small eggs, age is not a factor in determining laying dates of individuals in that species.

In conclusion, it would seem that in penguins and petrels which tend to have restricted laying spans and which tend to breed at a relatively late age, that age does not affect the date of laying. Age at breeding in species of petrels which I have studied has varied from the end of the second year as in the Diving Petrel, *Pelecanoides urinatrix*, to as long as the end of the eighth year as in the Royal Albatross, *Diomedea epomophora sanfordi*. It should be noted, however, that all species of penguins and petrels may not have a restricted laying period. For example, from my own observations the Little Blue Penguin, *Eudyptula minor minor*, has a laying span of several months.

In species of birds like the Song Sparrow which may breed more than once in a season and may re-nest if a nest is destroyed, it is possible that the breeding rhythm in young females has not developed fully by the time the old birds are ready to reproduce early in the season. This would mean that young females would tend to lay subsequently to the older females which had bred previously.

In connection with the effect of age on size of eggs it is well known that the young birds of the domestic fowl produce small eggs. Nice (1937: 113-121) in her study of the Song Sparrow indicates a comparable situation to that which obtains in the Yellow-eyed Penguin. For example, in the Song Sparrow, egg-width and egg-weight increase with age, being 3% for width and 7% for weight; egg-length is variable. Reduced egg-width and consequently reduced egg-weight would seem to be governed in young birds by the lack of a fully developed oviduct due to youth.

As for the effect of age on size of clutch in birds in general, some information is available in the literature but, although probably many of the statements are valid, little statistical support is offered. Nice (1937: 108-111) and Lack (1947: 313-314) summarise the known data and opinions. Much more research is needed. In the Yellow-eyed Penguin, as already noted, two-year-old birds definitely tend to produce a clutch less than the normal complement of 2 eggs. After that, unless advanced age has an influence, age does not affect size of clutch. In conclusion, it may probably be found that young birds of many species tend to produce small clutches. As regards aged birds, the position is somewhat doubtful and may not be so general. Lack (1947), for instance, quotes species which are apparently not affected.

SUMMARY

In the course of a 12-year study (1936-48) of the Yellow-eyed Penguin, *Megadyptes antipodes*, it was possible to study the effect of age of bird on laying dates, size of eggs, and size of clutch.

From 104 eggs laid by 59 young penguins which laid for the first time the mean date of laying was 26.06 September; from 100 eggs laid by 52 older birds the mean date of laying was 27.45 September. The difference is not significant statistically. In practice eggs laid by young penguins may appear at any time in the short laying period of approximately three weeks—age does not affect date of laying.

Two-year-old Yellow-eyed Penguins produce significantly lighter and narrower eggs than older birds but although the difference in length is not significant, individual measures are dispersed over a wide range. Three-year-olds lay much heavier and wider eggs than two-year-olds but not so heavy nor so wide as do four-year-olds. Subsequently there is possibly a further slight significant increase in width and weight. In old age there appears to be a tendency towards a reduction in weight and towards irregularity in length but width of eggs seems to increase.

Of 40 two-year-old Yellow-eyed Penguins, 32.5% laid only 1 egg to the clutch whereas of 218 older birds only 3.2% did so. Youth, therefore, in this species, does affect size of clutch.

In Buller's Mollymawk, *Diomedea bulleri*, age does not appear to affect date of laying.

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