SEASONAL FLUCTUATIONS IN WEIGHTS OF PENGUINS AND PETRELS

BY L. E. RICHDALE

FROM August 1936 to May 1946 I carried out a banding study of the Yellow-eyed Penguin, *Megadyptes antipodes,* on the Otago Peninsula, New Zealand. In all, I paid 973 visits to the breeding areas, which are 20 miles from the city of Dunedin with the outermost colonies 20 miles apart. The observations concerned 88 male and 96 female penguins which were found breeding for at least one season. A total of 292 matings was noted.

Weights were recorded as often as possible throughout the year. Finally, in the tenth season, weights were taken at 7-day intervals, from a point 56 days before the deposition of the first egg to the end of the guard stage, when the chicks are abandoned in the daytime and the two parents fish simultaneously.

In addition, seasonal weights were taken of two species of petrels—the Broad-billed Prion, *Pachyptila vittata* [= *forsteri*] and the Diving Petrel, *Pelecanoides urinatrix.* These weights were taken with much less thoroughness, but even so, the results should indicate general tendencies and serve for comparison. The petrel research was carried out on the tiny island of Whero off the southeast corner of Stewart Island.

In conclusion, I have compared the weights of the petrels and penguins with the findings of other workers on other species. This paper owes its inspiration largely to the researches of Wolfson (1945). My thanks are due to Mr. R. K. Wilson, who drew the graphs.

Weight Fluctuation in the Penguin Megadyptes

The weekly weights of the penguin *Megadyptes* are given in Tables 1 and 2; their differences are worked out statistically in Table 3. There is little difference from week to week; only 7 of the 42 differences are significant.[1] Four other types of interval were worked out. In weights taken at two-weekly intervals (Graph 1), 9 differences out of 20 are significant; at three-weekly intervals, 5 out of 12; and the division of each stage into two equal parts gives 5 significant differences out of 10. It will be observed that as the intervals are widened the differences in weight tend to become statistically more significant. A further tendency, however, is for significant phases in the breeding cycle to be obscured.

[1] Before allowing that a difference between means is significant, I have followed the ruling that it must be at least four times the value of the probable error of the difference.

In an endeavor to obviate this factor, I made a final broad grouping, as shown in Graph 2. All but one of the eight differences are significant, and the one exception is nearly so. One important point, however, is hidden. This is the fact that the females are heavier than the males for four weeks preceding the laying of the first egg, a phenomenon best appreciated by the use of weekly intervals as shown in Tables 1 and 2. Graph 2 shows several points between 56 days before the first egg and 48 days after hatching where a change in weight occurs that is significant statistically. Moreover, a close study of the behavior of the sexes during this period shows a correlation with the statistics.

The period from 42 days before laying to the laying of the first egg is best discussed in weekly intervals, since wider intervals fail to reflect important changes in behavior. In the interval 42–36 days before egg-laying, the males have reached their heaviest weight, after which a steady decline occurs till the end of the pre-egg period, when

TABLE 1

MEAN WEEKLY WEIGHTS OF MALE PENGUINS FROM 56 DAYS BEFORE EGG TO END OF GUARD STAGE

Stage	Class interval	n[1]	Mean	σ[2]	PE_m[3]	Range
	days		lbs.	lbs.		lbs.
Pre-egg	56–50	4	14.13	.70	.23	13 –14¾
	49–43	2	13.38	.22	.10	13¼–13½
	42–36	9	14.22	.45	.10	13½–14¾
	35–29	10	13.82	.83	.17	12½–15½
	28–22	7	12.50	.77	.20	11¾–14¼
	21–15	13	11.96	.46	.08	11 –12¾
	14– 8	17	11.57	.72	.11	10½–13
	7– 1	17	11.47	.50	.08	10½–12¼
Post-egg	0– 6	20	12.04	.61	.09	10¾–13
	7–13	33	11.93	.84	.09	10½–14¾
	14–20	16	11.90	.73	.12	11 –13¾
	21–27	18	11.79	.59	.09	10¾–12½
	28–34	21	12.33	.91	.13	11¼–14
	35–41	25	12.57	.60	.08	11½–13¾
	42–48	20	12.27	.61	.09	11 –13½
Guard	0– 6	31	12.51	.85	.10	11 –14¾
	7–13	26	12.59	.84	.11	11½–14
	14–20	27	12.12	.91	.11	10½–14
	21–27	25	11.74	.58	.07	10¾–13
	28–34	22	11.47	.59	.08	10¼–13¼
	35–41	21	11.62	.97	.14	10½–14¼
	42–48	12	11.91	.83	.16	10½–12½

[1] n = number of weights taken.
[2] σ = standard deviation.
[3] PE_m = probable error of mean.

TABLE 2

MEAN WEEKLY WEIGHTS OF FEMALE PENGUINS FROM 56 DAYS BEFORE EGG TO END OF GUARD STAGE

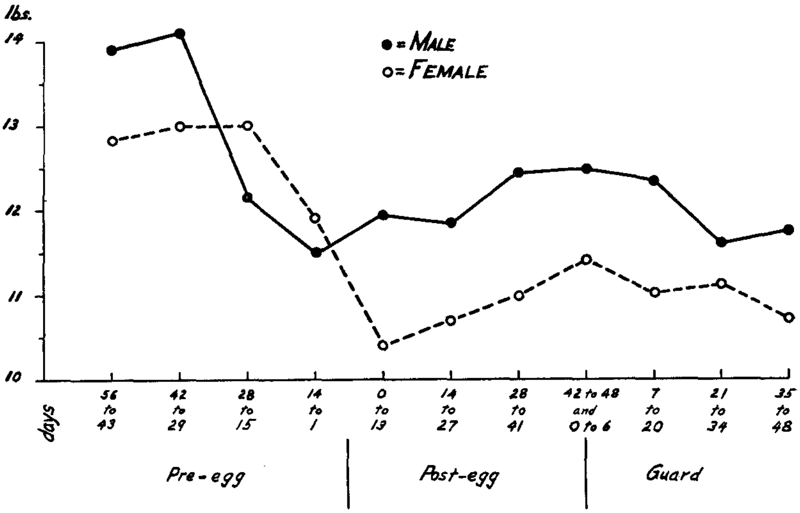
Stage	Class interval	n[1]	Mean	σ[2]	PE_m[3]	Range
	days		lbs.	lbs.		lbs.
Pre-egg	56–50	3	12.58	.33	.13	12¼–13
	49–43	2	12.75	—	—	12½–12¾
	42–36	3	11.92	.66	.25	11 –12½
	35–29	4	13.81	.72	.24	12¾–14¾
	28–22	5	13.30	.56	.17	12¾–14¼
	21–15	11	13.05	.62	.12	12 –14
	14– 8	21	12.20	.62	.09	11 –13¼
	7– 1	18	11.57	.63	.10	10½–12¾
Post-egg	0– 6	39	10.42	.52	.06	9 –11½
	7–13	17	10.40	.48	.08	9¾–11
	14–20	22	10.76	.55	.08	10 –12¼
	21–27	16	10.59	.53	.09	9½–11½
	28–34	16	10.94	.79	.13	10 –12¼
	35–41	19	11.19	.63	.10	10¼–12
	42–48	21	11.29	.61	.09	10¼–12½
Guard	0– 6	34	11.46	.62	.08	10 –12½
	7–13	26	11.26	.85	.11	9¾–13
	14–20	24	10.84	.67	.09	9¾–12¼
	21–27	17	11.88	.62	.10	10 –12
	28–34	27	11.27	.94	.12	9¾–13½
	35–41	20	10.87	.51	.08	10 –12
	42–48	22	10.43	.52	.07	9¾–11½

[1] n = number of weights taken.
[2] σ = standard deviation.
[3] PE_m = probable error of mean.

their weight tends to increase. From 40 days before the egg appears, the males begin to stay ashore in the daytime, and they remain there for much longer periods than the females. Although some of the females begin to stay ashore quite early, they spend far more time than their partners at sea, fishing. Because of this fact, the females continue to increase in weight till the 35–29 day interval.

The result is that the weights of the two sexes in the 35–29 day interval are nearly equal. After this interval the males are lighter than the females till the last week of the pre-egg period, when the weights are once more equal. In the 21–15 day interval, females are on the average slightly over one pound heavier than males.

With the appearance of the first egg, the story changes abruptly. In the 7–1 day interval before egg-laying, the males begin to seek food more often and the females tend to remain ashore. For some days after the first egg is laid the females rarely enter the water and the males seldom stay ashore in the daytime. (There are, of course, exceptions to this general rule.) Thus the females reach their lowest



Graph 1. Mean weights of Yellow-eyed Penguins at two-weekly intervals from 56 days before egg-laying to the end of the guard stage.

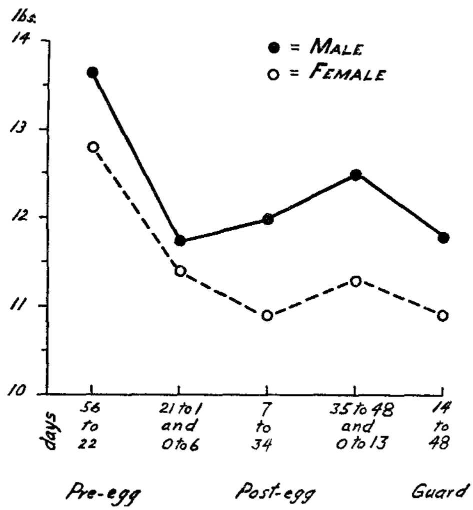
TABLE 3

DIFFERENCES IN WEEKLY MEANS TAKEN FROM TABLES 1 AND 2

Intervals	Male		Female	
	Difference	PE$_d$[1]	Difference	PE$_d$[1]
	lbs.		lbs.	
56–50 and 49–43	.75	.251	.17	.130
49–43 and 42–36	**.84**	.141	.73	.250
42–36 and 35–29	.40	.197	**1.89**	.346
35–29 and 28–22	**1.32**	.262	.51	.294
28–22 and 21–15	.54	.215	.25	.208
21–15 and 14– 8	.39	.136	**.85**	.150
14– 8 and 7– 1	.10	.136	**.63**	.134
7– 1 and 0– 6	**.57**	.120	**1.15**	.116
0– 6 and 7–13	.11	.127	.02	.100
7–13 and 14–20	.03	.150	.36	.113
14–20 and 21–27	.11	.150	.17	.120
21–27 and 28–34	.54	.158	.35	.158
28–34 and 35–41	.24	.152	.25	.169
35–41 and 42–48	.30	.120	.10	.134
42–48 and 0– 6	.24	.134	.21	.144
0– 6 and 7–13	.08	.149	.20	.136
7–13 and 14–20	.47	.162	.42	.142
14–20 and 21–27	.38	.130	.04	.134
21–27 and 28–34	.27	.106	.39	.156
28–34 and 35–41	.15	.163	.40	.144
35–41 and 42–48	.29	.213	.34	.106

[1] PE$_d$ = probable error of difference.

Statistically significant differences are given in boldface.



Graph 2. Mean weights of Yellow-eyed Penguins at wide intervals from 56 days before egg-laying to the end of the guard stage.

weight level during the first two weeks after the egg is laid, whereas the males reach theirs before the egg is laid.

From these respective depression points the weights of both sexes gradually increase during incubation until the highest peak in weight for the post-egg period is reached in both sexes (during the interval from 42–48 days post-egg to 0–6 days guard). Soon after the parents begin to feed the chicks, a decline occurs. This seems to indicate that even though the parents themselves acquire food daily (which they did not during the incubation stage), the additional task of feeding the chicks has an adverse influence on their weight. At the end of the guard stage, weights of the adults have once more reached a low level.

The graph for the guard stage tends to be irregular. This is the most difficult period for which to obtain an even sampling, since there is a great disparity in weight between a bird that has been ashore for nearly 24 hours and one that has just returned from feeding. The true test would be to weigh the birds at a definite period, say five or six hours after they had returned home. This, however, would be an almost impossible task.

Weight Fluctuation in Petrels

Before attempting to interpret Tables 4, 5, and 6 it will be advisable to summarize briefly the behavior of the species concerned; more detailed accounts have already been published (Richdale, 1943, 1944, 1945). *Pachyptila* will be dealt with first. The period from May 12

TABLE 4

SEASONAL WEIGHTS OF THE BROAD-BILLED PRION

Periods	Remarks	n[1]	Mean	σ[2]	PE_m[3]	Range
			gms.	gms.		gms.
May 12 to 20	Winter months	13	206.6	14.75	2.73	177 to 227
Aug. 24 to Sept. 2	Laying begins end of August	19	189.4	16.65	2.54	160 to 220
Dec. 6 to 16	End of chick-feeding stage	27	189.8	17.65	2.26	170 to 234
Feb. 7 to March 7	All in molt	22	197.2	13.70	1.92	172 to 225

[1] n = number of weights taken.
[2] σ = standard deviation.
[3] PE_m = probable error of mean.

to May 20, as shown in Table 4, is the middle of the off-season. All the birds handled during this period had completed their molt, but their breeding status was unknown. In the winter months *Pachyptila* visits the shore at irregular intervals.

August 24 to September 2 marks the end of the pre-egg stage and the beginning of laying. One or two of the 19 birds weighed during this period were incubating; the breeding status of the others was unknown.

The adults caught between December 6 and 16 were all feeding chicks (which were near the end of their stay in the burrows). Some adults were caught before they had fed their young and others afterwards. Since chicks may receive up to 80 grams of food in a night (Richdale, 1944:194), the range in weight of feeding adults is very wide.

Finally, the span between February 7 and March 7 is the time the molt occurs. On February 7, 1942, I was present when *Pachyptila* made its first appearance on the island since the completion of the breeding season a little more than a month earlier. All individuals inspected were molting, and all showed considerable wear on the toes—

TABLE 5

DIFFERENCES IN SEASONAL WEIGHTS OF THE BROAD-BILLED PRION

Periods	Difference	PE_d[1]
	gms.	
Between May and August	17.2	3.73
" August and December	.4	3.40
" December and February	7.4	2.96
" February and May	9.4	3.35
" December and May	16.8	3.54

[1] PE_d = probable error of difference.

indicating that they were old birds. Their breeding status was unknown.

For *Pelecanoides* (Table 6) only two periods are available. The first extends from August 23 to 26, which probably represents the beginning of the pre-egg period. The birds were all caught and weighed at night just after they had landed. Some were known to be breeding birds, but others were unbanded. Those handled between December 22 and January 30 were all attending chicks and were caught sometimes before and sometimes after they had fed the chicks. For this reason a wide range in weights is apparent.

TABLE 6

Seasonal Weights of the Diving Petrel

Periods	Remarks	n^1	Mean	σ^2	$PE_m{}^3$	Range
			gms.	gms.		gms.
Aug. 23 to 26	End of winter months	26	136.15	6.25	.83	125 to 152
Dec. 22 to Jan. 30	Chick-feeding stage	100	124.10	10.27	.68	108 to 158
	Difference		12.04	±1.07		

[1] n = number of weights taken.
[2] σ = standard deviation.
[3] PE_m = probable error of mean.

The difference between the December and February weights of *Pachyptila*, as shown in Table 5, is not significant as it stands. When it is realized, however, that the December weights include, in some cases, a quantity of undelivered food for the chicks, it is clear that the real difference would be much greater and possibly significant. This suggests that the month at sea during which the molt commences is a period of recovery from the stress of feeding young.

During the period of molt, February 7 to March 7, individuals were weighed on four occasions. These weights did not show any significant difference. If this represents the true state of affairs, *Pachyptila* does not lose weight while molting.

In *Pachyptila* the difference between the May and December weights is significant. May is the middle of the off-season, and the weights would probably be much higher at the beginning of the pre-egg stage, about the end of July. This is the case in *Pelecanoides,* which also shows a significant difference between the early pre-egg stage and chick stage weights (Table 6). It would seem, then, that weights in *Pachyptila* and *Pelecanoides* rise during the off-season to a peak at the beginning of the pre-egg stage and drop to a low point during the feeding of the chicks.

Finally, Table 4 also indicates that, as in *Megadyptes,* there is a depression point at the end of the pre-egg stage in *Pachyptila.* This is corroborated by the fact that there is a significant difference between the May and the late August weights.

Discussion

According to Baldwin and Kendeigh (1938:431, 435) most species of birds show a maximum weight in winter and early spring and a decrease at the approach of the breeding season. Nice's observations (1937:25–26) on Song Sparrows, *Melospiza melodia,* were similar. Marples (1942 and 1945) indicates a similar trend in the Little Owl, *Athene noctua,* and in the Wax-eye, *Zosterops lateralis.*

Wolfson (1945:109–121), however, objects that these generalizations are only partially true. He states that there is in Oregon Juncos, *Junco oreganus,* and other passerines a significant correlation between an increase to a maximum body weight and the beginning of the spring migration. He produces convincing evidence in support of his contention. His impressive graph (p. 120) indicates that, in the spring, migrants increase rapidly in weight, whereas residents continue to decrease. Further, he points out that the increase in weight of the migrants is due to the deposition of fat, subcutaneously and intraperitoneally (p. 109).

The statements of Wolfson are interesting in view of what happens in *Megadyptes.* Not only is there a tendency to follow the same pattern of weight fluctuations as migrant passerines, but also, heavy deposits of fat develop as the breeding season approaches.

From the beginning of winter to six weeks before egg-laying, there is a gradual steady increase in weight and fat deposition in both sexes. This is true not only of the group of penguins as a whole recorded in Graph 1, but is also true, in the main, of the individuals that I was able to weigh several times during the period. Further, although no birds were collected for autopsy, it was obvious that the males, in particular, were extremely fat by August 24, the beginning of the pre-egg stage. Even their ability to walk was impaired.

Side by side with this gradual development there is manifested a growth in the testes and presumably in the ovary. Dissection of two males killed by a fall of rock toward the end of the winter period showed that the testes were much enlarged. The physiological state of the penguins eventually reached a condition that allowed them to stay ashore for a time without food.

Doubtless there are external as well as internal factors which help to bring about these changes culminating in the pre-egg stage. If so, these external factors, one of which is probably the increase in daylength, apparently act differently on the two sexes. The females reach their peak weight and fat deposition later than the males and are later in beginning to stay ashore in the daytime; they do not, at first, fast as frequently as the males. Wolfson (p. 110) found a comparable situation in migrant passerines, a fact which explains why females arrive on the breeding grounds later than the males.

To sum up, it will be seen that in *Megadyptes* a steady increase in body weight and fat deposition precedes the pre-egg stage and that the females lag behind the males. The sexes, in this way, are prepared for the behavior patterns which will be released in the succeeding period. This preparation occurs at the correct time presumably because of the response of the endocrine glands to external factors in the environment. The response of the endocrine system then causes a change in the metabolism which results in an accumulation of surplus fat.

During the last four weeks of the pre-egg stage the female *Megadyptes* is heavier than the male (Tables 1 and 2). The reason for this is noted above and is not caused by the advent of the eggs, which average about 136 grams and are laid four days apart. In the third week before laying, occurs the greatest disparity in weight between the sexes, when the females average a little more than one pound heavier.

This advantage in female weight in species in which the male is the heavier during most of the year has been recorded elsewhere. When occurring just before laying it has been thought to be due to the presence of the eggs (Nice, 1937:27;1938:7. Marples, 1942:247). Another possibility is that the male's weight may tend to fall because of his greater activity, especially noticeable in species which are highly territorial. Such a possibility is suggested by Nice (1937:25).

In species in which only the female incubates there are records that she continues to be heavier even after the eggs are laid and during the subsequent incubation. Nice (1937:26–27; 1938:7) found this tendency in Song Sparrows. She also quotes Riddle and Braucher as stating that there is an eight per cent rise in weight during incubation in pigeons and doves. From this it would seem that incubation is not the arduous task that some people think. As for the male, in species in which he does not share the task of incubation (so far as records are available), his weight continues to fall. This is recorded in Song Sparrows (Nice, 1937:22) and in the Little Owl (Marples, 1942:247).

In *Megadyptes,* incubation is shared equally by the sexes. The female remains lighter than the male throughout, and, in fact, at the beginning of the period she reaches one of her two lowest depression points. This is due to an increase in fasting toward the end of the pre-egg stage and particularly during egg-laying. From this low level she rises steadily till the eggs are hatched. The male's weight also registers a steady rise. These facts support Nice's view that incubation is a recuperative period. It would seem that in species in which both sexes incubate both male and female gain in weight. If the female alone incubates, the female alone becomes heavier. A knowledge of what happens if only the male incubates, as in the phalaropes, would be of considerable interest.

With the hatching of the chicks there seems to be a general drop in weight for at least those parents which feed the young. This applies to *Megadyptes*. (In this penguin there is a rise again, however, after the end of the guard stage, a condition characteristic of this species and probably of all penguins.) Nice (1937:27) states that feeding young is strenuous in the two sexes for both Song Sparrows and Tree Sparrows, *Spizella arborea*. The same conditions appear to apply in the Little Owl (Marples, 1942:pl. 20).

Finally, weights connected with the molt will be considered. Immediately following the breeding season in autumn, the molt commences for most penguins of both sexes. The greatest amount of fat is developed (being greater than at the end of the winter months) and the heaviest weight of the yearly cycle is attained just as the molt commences, but on completion of the molt the birds register the minimum weight for the year.

As regards other families of birds, Nice (1937:22) indicates that Song Sparrows are "undoubtedly" at their lowest weight in August and September, when the molt occurs. Beck found a heavy loss at this time in four domestic fowls (Nice, 1938:7). In the Little Owl, Marples (1942:247) thinks that the minor loss in weight he recorded in the autumn was due to molt.

The contrary view is held by Baldwin and Kendeigh (1938:463), who say that "molting and renewal of feathers in August and September is not joined with a decrease in weight; rather there is an increase in weight at that time." In support of this, Laskey (Nice, 1938:7) reports the "highest weight during the inactive period of molting" in male Mockingbirds, *Mimus polyglottos*.

In petrels, it would seem from the meagre evidence available that they reach peak weight at the beginning of the pre-egg stage and decrease steadily till the egg is laid. They are again low in weight at the end of the chick stage, and up to this point the graph of their weight closely resembles that of *Megadyptes*. During the molt *Pachyptila,* at least, does not lose weight.

In conclusion, it is obvious that not all species of birds reach their maximum weight in the winter months and then decrease as the breeding season approaches. Some, like the migrant passerines, penguins, and at least some petrels, reach a peak at the beginning of the pre-egg stage. The weight of incubating birds tends to rise; if a bird does not incubate, its weight tends to fall. Parents that feed the young also lose weight, but no data are available on parents that do not feed the young. As regards the molt, some birds—particularly penguins—certainly lose weight during the process. On the other hand, there is evidence that some birds do not and that others even gain weight. It is abundantly clear that data collected on bird weights are of inestimable value in clarifying many physiological and psychological problems.

Summary

In the course of a 10-year study (1936–1946) of the Yellow-eyed Penguin, *Megadyptes antipodes,* weights were taken at 7-day intervals from 56 days before the egg was laid to 48 days after hatching—a period of about 146 days.

Males reach their peak weight at the end of the off-season and drop steadily during the pre-egg stage until just before egg-laying.

Females reach their peak in weight a week later than the males, and for four weeks are heavier than the males, which again exceed the females in weight as the eggs appear.

As incubation progresses, both sexes steadily increase in weight, but another drop occurs during the 48 days after the hatching of the chick.

Weight fluctuations in two species of petrel, the Broad-billed Prion, *Pachyptila vittata* [=*forsteri*], and the Diving Petrel, *Pelecanoides urinatrix,* were also examined. The same pattern of fluctuation seemed to occur in these two species as in the penguin *Megadyptes.*

The results of the study were compared with the findings of other workers on other species. They were found to follow closely the deductions of Wolfson, who studied migrant Oregon Juncos, *Junco oreganus.* They differ, however, from data on non-migratory birds, most of which apparently reach peak weights in the winter.

Megadyptes resembles Juncos in that a heavy deposit of fat develops as the pre-egg period approaches. In both species this is coincident with growth of the gonads.

The pattern of weight fluctuation indicates that incubation in birds is not the arduous task that it is supposed to be, but that feeding of young is a time of stress.

The penguin *Megadyptes* reaches its peak weight for the year at the beginning of the molt, its minimum weight at the end; the petrel *Pachyptila* apparently does not lose weight during the molt. Evidence from other workers on other species indicates that in some birds there is a gain of weight during the molt; in others, a loss; in still others, no significant change.

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