Biometric studies of birds in the order Procellariiforms

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BIOMETRIC STUDIES OF BIRDS IN THE ORDER PROCELLARIIFORMES.

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BIOMETRIC STUDIES OF BIRDS IN THE ORDER PROCELLARIIFORMES.

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1. INTRODUCTION

The Procellariiformes are mainly pelagic sea-birds inhabiting every ocean. Some are restricted to warm tropical seas while others feed in open leads between ice-floes. One member of the order, Pagodroma nivea, breeds further south than any other vertebrate except its parasite Stercorarius skua and under conditions so severe that few if any invertebrates can withstand them.

The size range among the Procellariiformes is greater than that obtaining in any other order of birds. Smallest are storm-petrels like Hydrobates pelagicus and Halocyptena microsoma with wing spans of about 30 cm and weights of about 30 g; largest Diomedea exulans and D. epomophora whose wing spans approximate to three metres and body weights average some eight kilos. Between these extremes are about 95 species of small, medium-sized and large birds and in most of the oceans, particularly in the Southern Hemisphere where the order is best represented, species of differing size share common feeding and breeding grounds.

The present study was undertaken to examine the extent of this great range in body size and its consequences to certain aspects of morphology, breeding biology and egg size. Investigations of the relationships between body size, egg size and development times are simplified in this order as a single egg comprises the clutch and if that is lost re-laying is very infrequent. With only one egg to hatch and one chick to rear a comparison of facets of the breeding cycle like incubation and nestling periods can be meaningful although data on these are still inadequate or lacking for most species in the order.

It was anticipated that the decrease in size from the Diomedeidae to the Hydrobatidae would be accompanied by correlated changes in egg size and in times needed for development of the young. It was hoped that if regular relationships could be established between the different variables these could be used to predict statistics for species not yet measured or even for some now extinct. To a considerable degree these expectations have been fulfilled but more data are needed before full advantage can be taken of the relationships discovered. The present study is thus a preliminary one which indicates many other profitable lines of research and, as might be expected, exposes more problems than it solves.

2. NOMENCLATURE.

2.1 The use of the word "Petrel".

Throughout this study the words petrels, Procellariiformes and Tubinares have been regarded as synonyms. This reverts to the custom among early workers on the group whereas in recent years there has been a tendency to use "petrel" in a more restricted and often ill-defined sense so that we read of "albatrosses, shearwaters and petrels" rather than of "albatrosses, shearwaters and other petrels".

2.2 Family and Generic Names.

The family and generic names used follow the form and sequence set out in the letter by Alexander et al (1965) which was drawn up by W.R.P. Bourne in conjunction with the writer and other workers on petrels. The scheme is as follows:-

Order PROCELLARIIFORMES

1. Family Diomedeidae
    - *Diomedea*
    - *Phoebetria*

2. Family Procellariidae
    - *Macronectes*
    - *Fulmarus*
    - *Thalassoica*
    - *Daption*
    - *Pagodroma*
    - *Pterodroma*
    - *Halobaena*
    - *Pachyptila*
    - *Bulweria*
    - *Procellaria*
    - *Calonectris*
    - *Puffinus*

3. Family Hydrobatidae
    - *Oceanites*
    - *Garrodia*
    - *Pelagodroma*
    - *Fregetta*
    - *Nesofregetta*
    - *Hydrobates*
    - *Halocyptena*
    - *Oceanodroma*

4. Family Pelecanoididae
    - *Pelecanoides*

3. THE DATA.

3.1 Sources of the Data.

This study leans heavily on published measurements, notably those for standard dimensions. These have been taken from much of an extensive literature relating to the Procellariiformes and have included particularly the taxonomic and anatomical studies of Milne-Edwards (1867-68); Forbes (1882); Loomis (1918); Mayaud (1932); Falla (1940); Fleming

(1941a and b); Fleming and Serventy (1943); Mathews and Hallstrom (1943); Murphy and Irving (1951); Murphy and Harper (1921); Murphy and Pennoyer (1952); Murphy and Snyder (1952); Murphy (1952); Austin (1952); Kuroda (1954); Schönwetter (1960) and of Bourne and Warham (1966). These data have been supplemented by material gleaned from field studies of which those of Falla (1937); Roberts (1940); Bierman and Voous (1950); Sorensen (1950); Richdale (1950, 1952, 1963, 1965a and b); Hagen (1952); Fisher (1952); Paulian (1953); Prévost (1953a and b, 1958, 1964); Rand (1954); Warham (1956, 1958, 1962); Davis (1957); Holgersen (1957); Tickell (1960, 1962); Rice and Kenyon (1962); Brown (1966); Harris (1966); and Pinder (1966) have proved the most useful.

Finally, the standard texts of Godman (1907-10); Mathews (1912); Bent (1922); Murphy (1936) and Palmer (1962) have provided more data. Other information has been made available by colleagues currently active in sea-bird research and by various people who, at the author's instigation, have collected appropriate data when in a position to do so. This assistance is acknowledged in Section 14.

Some major gaps in the data have been filled by the author from museum material, from field observations and measurements, and from work done during the preparation of "A Handbook of Australian Sea-birds" (Serventy, Serventy and Warham, in press). Methods of measuring non-standard dimensions and other variables are described below in the appropriate sections.

3.2. Summary of the Data.

Some of the more important measurements are given in Appendix A. To save unnecessary repetition of scientific names in the text each species has been given a number. Within each genus the largest birds are listed first. Gaps in the sequence of numbers refer to species for which there has been inadequate information for use in the present study.

For the purpose of the kind of comparisons attempted here it is desirable to compare samples from homogeneous populations; where relevant, measurements are given for each sub-species and these are indicated by suffix letters. No investigation of the validity of such sub-species has been made or is implied and further research will probably show that some are invalid and even that some races have been ascribed to the wrong species.

The final data will show many gaps and to take advantage of the figures that are available small samples have sometimes been used - hence some of the scatter about certain of the regression lines. Again, while there are many useful and large samples, it is often not possible to derive standard deviations for them as neither these nor the raw data were given in the original papers. In consequence only the means and ranges have usually been available and the standard deviation of a regression has therefore been calculated from species means. Hence confidence limits around a regression indicate residual differences between species after the regressional component of the difference has been extracted and not the variability of individuals within species around the regression.

4. THE MEASUREMENT OF SIZE IN PETRELS.

How should the size of a bird be measured? By total length, by the length of a single appendage, by surface area, by body weight? All possibilities seem to have some shortcomings but perhaps body weight is the most useful method of measuring size as this is known to show good correlation with metabolic needs and has important bearings on the mode of flight and on the maximum size attainable.

Unfortunately the body weight of a bird is far from constant. Variations occur during the annual cycle and weights can increase dramatically over quite short periods e.g. before migration. For this reason the fat-free weights have been used for some studies of weight variations in small passerines. Petrels show at least as great a range of variation in weight during the course of a year or breeding season and this too seems mostly to be due to the deposition and utilisation of subcutaneous and depot fat. Ideally therefore, body weights should be the fat-free weights of birds with empty stomachs. There are no figures for fat-free weights of petrels and in view of the large size of many of them it seems most unlikely that such figures are going to be available in the foreseeable future although those of beach-wrecked birds may approximate to fat-free weights. In practice, the data for body weights used here are from samples of mixed provenance. A series made on the breeding grounds may consist of birds that have just been relieved of incubation duties by their mates after a week or more of fasting and may thus be underweight, or of others that have recently arrived with full stomachs and extensive fat reserves, or a mixture of these and of non-breeders. Birds caught at sea may have little or much depot fat but those collected exhausted on the beaches are usually thin and underweight. The sort of variation that may occur is indicated by data for the medium sized petrel *Puffinus tenuirostris* (Serventy *et al*, in press).

A sample of 32 females weighed at the start of incubation had a mean weight of 689g and a further sample of 22 females at the end of incubation a mean weight 20% lower at 554g. Fisher (1967) has recently discussed weight variations during the breeding season in one of the North Pacific albatrosses.

Given large enough samples these differences should tend to average out around a mean somewhat above the fat-free value and such a figure seems to be the most practicable measure for comparing body size in petrels. In this study, where data have been available from samples taken at different times of the year, the figures have been pooled in order to smooth out fluctuations due to varying fat content and similar causes.

Other measurements were investigated which might correlate with the mean values for body weights throughout the order. Total body length is not suitable for this purpose as it varies in skins with the manner of preparation. Tail length is a rather small dimension and not easily measured in live birds but standard wing length proved more suitable. This is the distance from the carpal joint to the tip of the longest primary when the folded wing is flattened against a rule and is in effect the length of the most distal of the three segments of the wing, being the length of the hand plus that of the longest attached feather. Successive measurements of a series of wings showed that an accuracy of about ± 2% was achieved when the same person did the measurwing and about ± 3% when different persons made the measurements. Wing length is not subject to much variation during the year or, if this occurs (due to moult and abrasion), it can usually be detected at the time of measuring and such under-sized examples eliminated from the data. Furthermore, there is much good information on wing lengths in the literature that can be utilised.

Nevertheless, this measurement has some disadvantages. The most important is probably the occurrence of shrinkage during drying so that the mean length of a sample taken from live birds may be significantly greater than that for a similar-sized sample of study skins. There is little published information on this but Tickell (1962) gives some figures for the prion Pachyptila desolata which show differences of up to 2% between the values for live and preserved material from the same breeding places. Similar figures have been obtained from material collected recently at the Snares Islands (Warham, 1967a). With the medium-sized petrel Pterodroma inexpectata the shrinkage in wing length after 6 months drying amounts to between 1 and 1½%.

Unless the indications given by these two species are atypical, it seems that errors due to this factor, averaging about 1½%, will have no significant effect on the conclusions drawn here. The degree of error due to shrinkage and to the use of both preserved and live material is of a smaller order than those differences in wing lengths between species that are postulated as having biological significance.

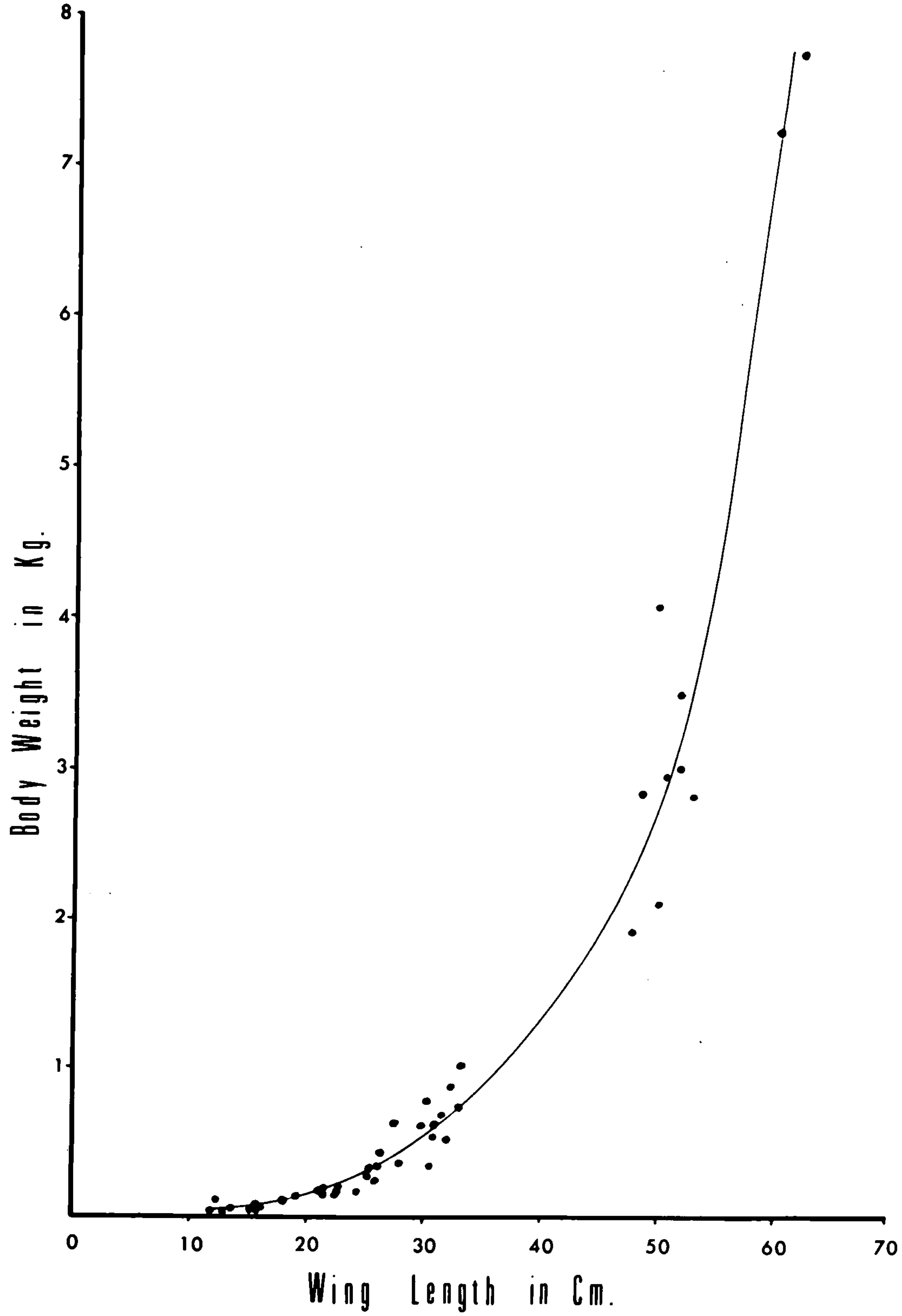

Fig. 1. Wing Lengths & Body Weights in Petrels.

5. RELATIONSHIPS BETWEEN BODY WEIGHT AND STANDARD WING LENGTH.

5.1. Changes in Size of the Wing Elements with Body Weight.

The relationship between mean body weight and mean standard wing length for 44 species of petrel is shown in Figure 1. The data come from Appendix A. Body weights are for adult females except in genera like Puffinus and Pterodroma where long series of measurements have failed to demonstrate sexual differences.

There is a correlation between mean body weight and mean wing length but evidently this is not linear. There is some scatter as expected with biological data and particularly where, as here, many of the sample sizes are small and both living and preserved material has been used. The regression line has been drawn by eye.

The curve indicates that as the standard wing length increases the rate of change of body weight also increases, the ratio of body weight to wing length being much lower with small species than with large ones. This ratio is about 0.3 for a petrel weighing 50g, for one weighing 500g about 1.8, and for one of 5,000 about 8.8. Thus, although with increasing size the distal elements of the wing increase absolutely in length, these increases are progressively smaller in comparison with the increasing body weight.

The wing measurements in Figure 1 represent only a part of the whole wing but despite this, the regular variation in the length of this segment in comparison with the body weight seems likely to be correlated with the modes of flight of the various species.

Small petrels have relatively broad wings which are not excessively attenuated compared with the length of the bird's body. Albatrosses, at the other end of the size range, have narrow wings of high aspect ratio whose total lengths are high compared with the body length. The other groups in the order lie at various points between these two extremes.

The lengths of the three wing elements for a small sample of petrels of various sizes in set out in Table I where data by the anatomist W. A. Forbes (1882) for the lengths of the wing bones are combined with the lengths of the distal segments (= standard wing length) from Appendix A.

TABLE I.

Lengths of wing segments and body weights in petrels.
(Bone lengths from Forbes, 1882, all in mm.)

	Species	a	b	c	d	a:b:c	a:b:d	a+b+d	B.W. g.	B.W. / a+b+d
2b.	*D.e.chionoptera*	428	417	290	601	1.0:1.0:0.7	1.0:1.0:1.4	1446	7270	5.03
6a.	*D.m.melanophris*	259	262	202	521	1.0:1.0:0.8	1.0:1.0:2.0	1042	3515	3.37
14.	*M.giganteus*	243	236	212	498	1.0:1.0:0.9	1.0:1.0:2.0	977	4114	4.21
53.	*P.cinerea*	134	132	127	334	1.0:1.0:0.9	1.0:1.0:2.5	600	1026	1.71
60.	*P.griseus*	81	83	84	304	1.0:1.0:1.0	1.0:1.0:3.6	468	787	1.68
64b.	*P.p.puffinus*	79	72	86	237	1.0:0.9:1.1	1.0:0.9:3.0	388	406	1.05
71c.	*P.m.maoriana*	27	24	37	161	1.0:0.9:1.4	1.0:0.9:6.0	249	47	0.19
74.	*H.pelagicus*	26	24	33	117	1.0:0.9:1.2	1.0:0.9:4.5	167	28	0.17
78a.	*O.l.leucorhoa*	35	35	42	156	1.0:1.0:1.2	1.0:1.0:4.6	266	48	0.18
83a.	*P.u.chathamensis*	43	33	44	123	1.0:0.8:1.0	1.0:1.0:2.9	199	124	0.62

a = humerus; b = ulna; c = manus; d = manus plus feathers.

The table shows the following trends:-

1. The lengths of the humerus and ulna are approximately equal in all species throughout the order as pointed out by Forbes (*loc. cit.*). The position of *Pelecanoides urinatrix* is rather different and is

discussed separately in section 5.3 below.

2. The contribution of the manus to the total length of the arm varies fairly regularly, larger species having relatively shorter hands than the smaller ones.

3. The contribution of the hand plus the attached feathers, i.e. the standard wing length, to the total length of the wing also varies consistently. In the larger species this contribution is relatively small being about equal to the combined length of the two inner segments whereas in the smaller species the lengths of the distal segments are two or three times the combined length of humerus and ulna. The exception is again Pelecanoides.

4. The total length of the wings of petrels from body to wing tip cannot readily be ascertained from skins and there are few field data. However, an estimate of this for comparative purposes can be obtained by adding humeral, ulnal and standard wing lengths as has been done in column a+b+d of Table 1. In the last column of that table the mean body weight in grams has been divided by this estimate of total wing length. It will be seen that unit wing length in the large species carries much more weight than it does in the small ones.

Even ignoring species' variations in the widths of the wings relative to their length, it seems clear that the high figure for the weight per unit length of wing in the large species are correlated with higher wing loadings per surface area. Thus Oceanites oceanicus, one of the smallest petrels and which has a standard wing length of 153mm and weighs 34g has a wing loading of about 0.32 g./cm^2, compared with 1.69 g / cm^2 for Macronectes giganteus and 1.20 g/cm^2 for Diomedea exulans (Mawson, in Falla, 1937).

Mawson also gives mean widths for wings of these species compared with their total length. They are for Oceanites 30% of the total length, for Macronectes 22% and for Diomedea about 14%.

The arm bones of small storm-petrels are strong and little if at all pneumatised. This is presumably a consequence of the low wing loading which would not require a lightening of the skeleton and with the mode of flight which is different to that of large petrels. Storm-petrels are agile and erratic fliers, capable of rapid changes in course and of beating their wings at quite high frequencies and through considerable amplitude. This kind of flight must subject the wing skeleton to considerable bending stress and necessitate strong arm bones.

Because of their low wing loading the wing needs to provide little lift in the small petrels compared to the situation in the large species, so that it is not surprising that the inner elements of the wing - those mainly responsible for lift - are reduced in storm-petrels. However, manoeuvrability is essential for taking the small planktonic organisms that comprise their food from the surface of a restless sea. Hence the importance of the distal elements of the wing which seem mainly responsible for propulsion and, in conjunction with the tail, for steering.

At the other end of the size scale the albatrosses rely on highspeed gliding in zones of strong wind. When they beat their wings it is through shallow amplitudes while in calms, when gliding is impossible, the birds settle onto the surface of the sea. They have high aspect-ratio wings capable of generating considerable lift. The inner elements of the wing, the humerus and ulna with their attached feathers, provide this. The distal element of the wing is reduced, as is the tail, and so too is the manoeuvrability of the bird and its capacity to propel itself by wing beats. Concurrently, and offsetting the increased wing loading, the bones of the forearm and of much of the skeleton are extensively pneumatised.

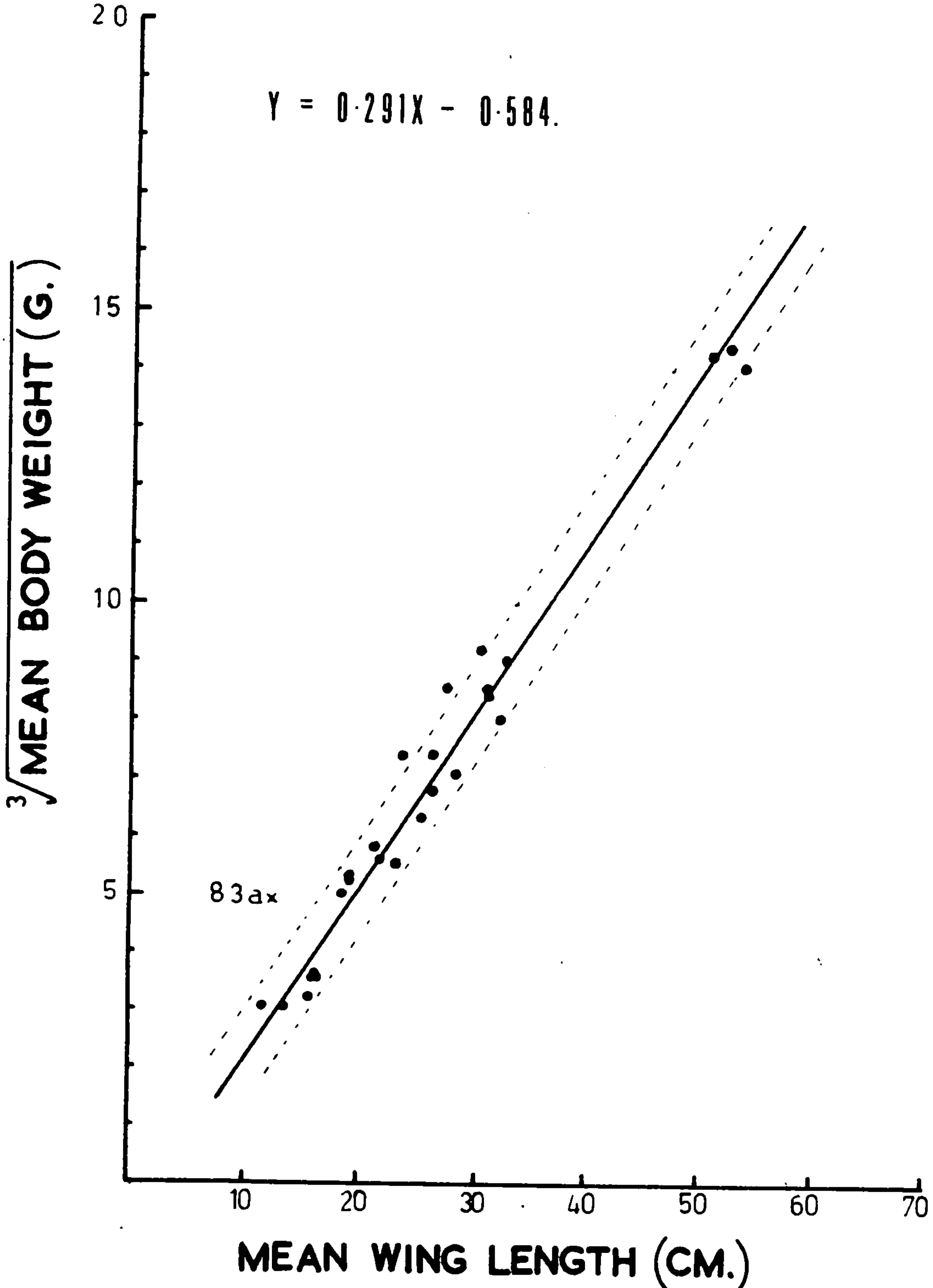

Fig.2. Wing Length: ∛Body Weight. Two standard deviations about the regression line are shown.

TABLE II: WING LENGTHS AND BODY WEIGHTS IN PROCELLARIIFORMES

	Species	Mean Wing Length (cm)	Mean Body Weight (g)	$\sqrt[3]{\text{Body Weight}}$
7.	D.bulleri	52.0 (31♂♀)	3012 (31♂♀)	14.44
8.	D.nigripes	50.6 (49♀)	2934 (138♀)	14.32
12.	P.palpebrata	53.7 (21♂♀)	2838 (10♂♀)	14.16
16.	F.glacialoides	32.9 (21♀)	741 (10♀)	9.05
17a.	F.g.glacialis	31.3 (45♀)	699 (12♀)	8.48
18.	T.antarctica	31.0 (26♀)	627 (21♀)	8.56
19a.	D.c.capensis	26.4 (15♀)	407 (22♀)	7.41
21.	P.incerta	32.1 (54♂♀)	522 (54♂♀)	8.05
32.	P.ultima	28.1 (94♂♀)	360 (13♂♀)	7.11
33.	P.inexpectata	26.2 (100♂♀)	316 (86♂♀)	6.81
35.	P.mollis	25.3 (146♂♀)	254 (146♂♀)	6.33
38a.	P.h.hypoleuca	22.9 (77♂♀)	176 (76♀)	5.60
41.	H.caerulea	21.6 (31♂♀)	181 (10♂♀)	5.66
42a.	P.v.vittata	21.4 (42♂♀)	196 (70♂♀)	5.81
43.	P.d.banksi	19.2 (12♀)	153 (12♀)	5.35
44.	P.salvini	19.0 (18♂♀)	154 (18♂♀)	5.36
45.	P.turtur	18.2 (100♂♀)	132 (100♂♀)	5.09
60.	P.griseus	30.4 (100♂♀)	787 (100♂♀)	9.23
62.	P.tenuirostris	27.4 (40♀)	635 (22♀)	8.59
64b.	P.p.puffinus	23.7 (20♂♀)	406 (32♀)	7.41
69a.	O.o.exasperatus	15.3 (65♂♀)	34.3 (10♂♀)	3.25
70.	G.nereis	13.0 (10♂♀)	29.5 (10♂♀)	3.09
71c.	P.m.maoriana	15.8 (21♀)	47.0 (100♂♀)	3.61
73a.	F.g.leucogaster	16.2 (24♂♀)	46.0 (24♂♀)	3.58
74.	H.pelagicus	11.7 (39♂♀)	28.0 (50♂♀)	3.04
78a.	O.l.leucorhoa	15.6 (94♂♀)	48.0 (66♂♀)	3.63
83a.	P.u.chathamensis	12.3 (100♂♀)	124 (100♂♀)	4.98

5.2. Linear relationships derived from Wing Lengths and Body Weights.

Figure 1 does not reveal any easily computed relationship and it is perhaps unlikely that a measurement of a linear dimension would be directly related to body weight, a three dimensional variable. A better fit for a linear relationship might be expected if the cube of the wing length was compared with body weight or the cube root of body weight with wing length.

This has been done in Figure 2 for the data in Table II and for 27 species. These data have been more critically selected than those used in constructing Figure 1. They are restricted to species for which at least 10 measurements are available of both standard wing length and body weight. For many species the samples are large and as far as possible only data from female birds has been included. However, figures from samples of mixed sex are used in genera like Puffinus and Pterodroma where long series of measurements have failed to reveal any sexual dimorphism in wing length.

The cube root of the body weight and the standard wing length are highly correlated ($r = +0.993$ and $P < .001$). Where Y is the cube root of the body weight in g and X the mean wing length in cm then the equation for the regression line derived by the method of least squares is:-

$$Y = 0.29X - 0.58 \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots \quad (1).$$

or $\sqrt[3]{\text{body weight in g}} = 0.29$ mean wing length in cm $- 0.58$.

This regression line has a standard deviation of $0.41\sqrt[3]{g}$ and 95% confidence limits are shown on either side of the regression line.

Unfortunately, for many species, individual data are not available but only the mean values so that it is not possible to provide standard deviations for each sample but only a figure for the combined samples. The curve would have been more useful had it shown the varying confidence limits over the whole range of body

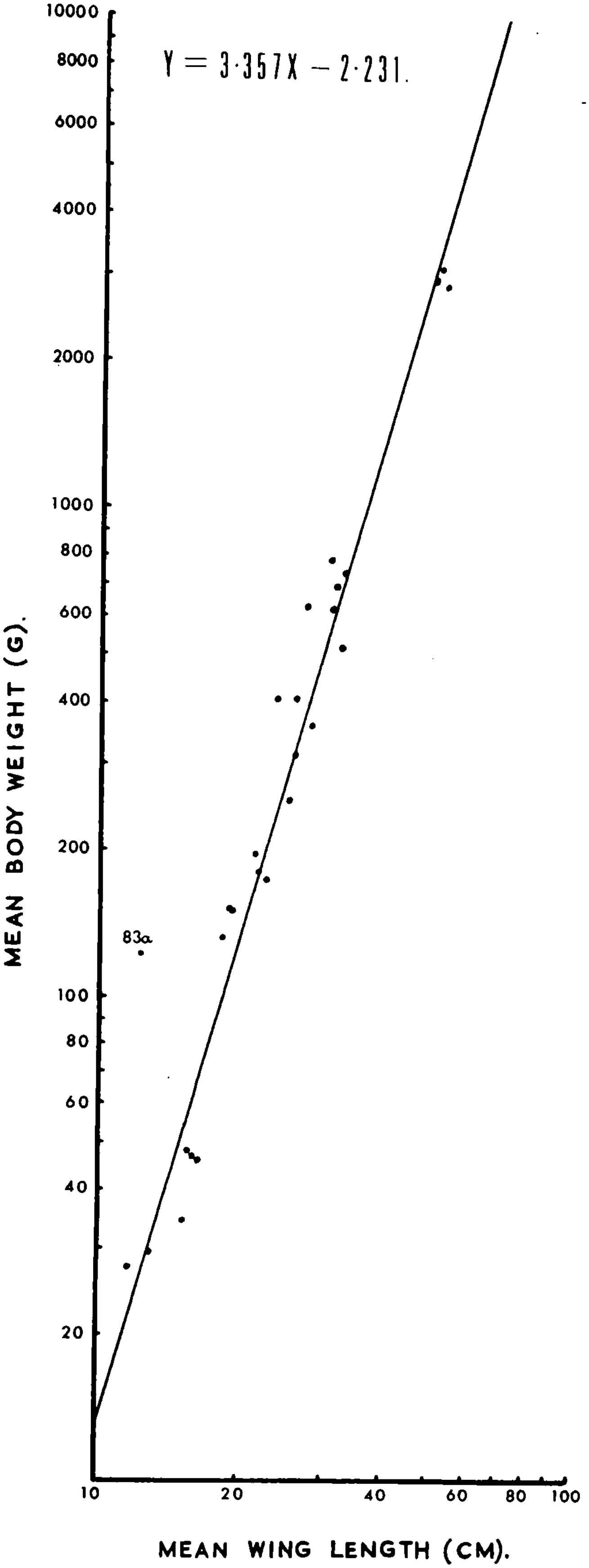

Fig.3. Wing Length: Body Weight

weights.

The regression of X on Y is:-

$$X = 3.38Y + 2.39 \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots \quad (2).$$

or mean wing length in cm = $3.38 \sqrt[3]{\text{mean body weight in g}} + 2.39$.
The standard deviation is 1.34 cm

The wing lengths and body weights of Table II have also been examined after transformation into logarithms. Again a linear relationship obtains as revealed by Figure 3.
The log:log plot tends to spread out the points towards the extremes of the range so that the regression line, while reflecting a highly significant correlation between the two variables, is not identical with that obtained when plotting the cube root of body weight against standard wing length.
When Y = log mean body weight in g, and X = log mean wing length in cm, then

$$Y = 3.357X - 2.231 \ \ldots\ldots \ \text{S.D.} = 0.116 \quad \ldots\ldots\ldots \quad (3)$$

i.e. log body weight in g = 3.357 log wing length in cm - 2.231
and

$$X = 0.287Y + 0.0.690 \ \ldots\ldots \ \text{S.D.} = 0.034 \ \ldots\ldots\ldots \quad (4)$$

i.e. log wing length in cm = 0.287 log body weight in g + 0.690
These two equations can be transformed into the power form giving:-

$$\text{Body weight} = 0.00587 \text{ wing length}^{3.357} \ \ldots\ldots\ldots \quad (3a).$$

$$\text{Wing length} = 4.898 \text{ body weight}^{0.287} \ \ldots\ldots\ldots\ldots \quad (4a).$$

The different estimates relating body weight and wing length given by the series of equations typified by (1) and (3) will be apparent from the following computations:-

Hypothetical wing length (cm)	10	50	100
<u>Equation 1</u>			
Mean body weight (g)	12.6	2724	23188
95% confidence limits (g)	3.4 - 31.1	2271-3232	23187-23189
<u>Equation 3</u>			
Mean body weight (g)	13.4	2974	30470
95% confidence limits (g)	7.8 - 13.7	1743-5074	17840-52020

The plots for four more species of greatly differing size (2b. Diomedea exulans; 24. Pterodroma phaeopygia; 67b. Puffinus lherminieri and 81a. Oceanodroma tethys) for which extensive data became available toward the completion of this study (Tickell, in press and Harris, in press, a, b and c) all fall within the above confidence limits.

5.3. The Position of Pelecanoides urinatrix.

The only species for which adequate data are available and which have been omitted when calculating the above relationships are those for subspecies 83a of the Common Diving Petrel, P. urinatrix, marked separately in Figure 2.

The Pelecanoididae comprise a group of small, fast-flying and mainly coastal species which are the most atypical members of their order in many respects and which show such a series of characters convergent with those of the Alcidae that one investigator believed that they rightly belonged to that family (Verheyen, 1958b). Pelecanoides is short-winged and has a fast whirring flight undertaken close to the surface of the sea and it feeds by diving or flying straight into the water.

An examination of the data in Table I shows that P. urinatrix has the shortest ulna, relative to the other wing bones, of any of the petrels listed. Furthermore, whereas species listed of similar size e.g. Pelagodroma marina have a relatively huge distal element, that of Pelecanoides is considerably reduced in comparison. Thus the short wings characteristic of this species are the result of a relative reduction in length of both the ulna and the hand with its attached feathers compared with other petrels of similar size.

This is well shown in Figures 2 and 3 where the only adequate data for any member of the family, that from Richdale (1965a) is plotted from a sample of 100 animals of mixed sexes. In respect of standard wing length P. urinatrix lies well outside the curve derived from the data from the other 26 species. This is also evident from Figure I but is less obvious there. No doubt data from other members of the genus, when available, would show that all diving petrels share these characters.

5.4. Discussion.

Figures 2 and 3 show that for all families of the Procellariiformes apart from the Pelecanoididae standard wing lengths can be used to measure body size via either the cube root or logarithm of the body weight. The mean body weights per species for a random sample of species each represented by a large sample of birds, will fall in the range:-

$$(0.291 \text{ wing length in cm} - 0.58 \pm 0.82)^3 \text{g}.$$

Body weights are available for only a limited number of petrels but the above formula permits weights to be calculated for the many species whose wing lengths are known.

The main cause of deviations from the regression lines of Figures 2 and 3 seems likely to be real, specific and presumably adaptive differences in the relationships between the two variables. This may apply, for instance, to Macronectes which field observations, Table I, and Mawson's figure given above all suggest, has a rather high wing loading for a bird of its wing length.

Apart from the expected scatter customary with biological data, there are other possible causes of deviation of minor importance here. Thus in some instances sample sizes are small (e.g. body weights for only 10 Phoebetria palpebrata) and these data may have had a skewed distribution about the mean. Occasionally too, where samples of

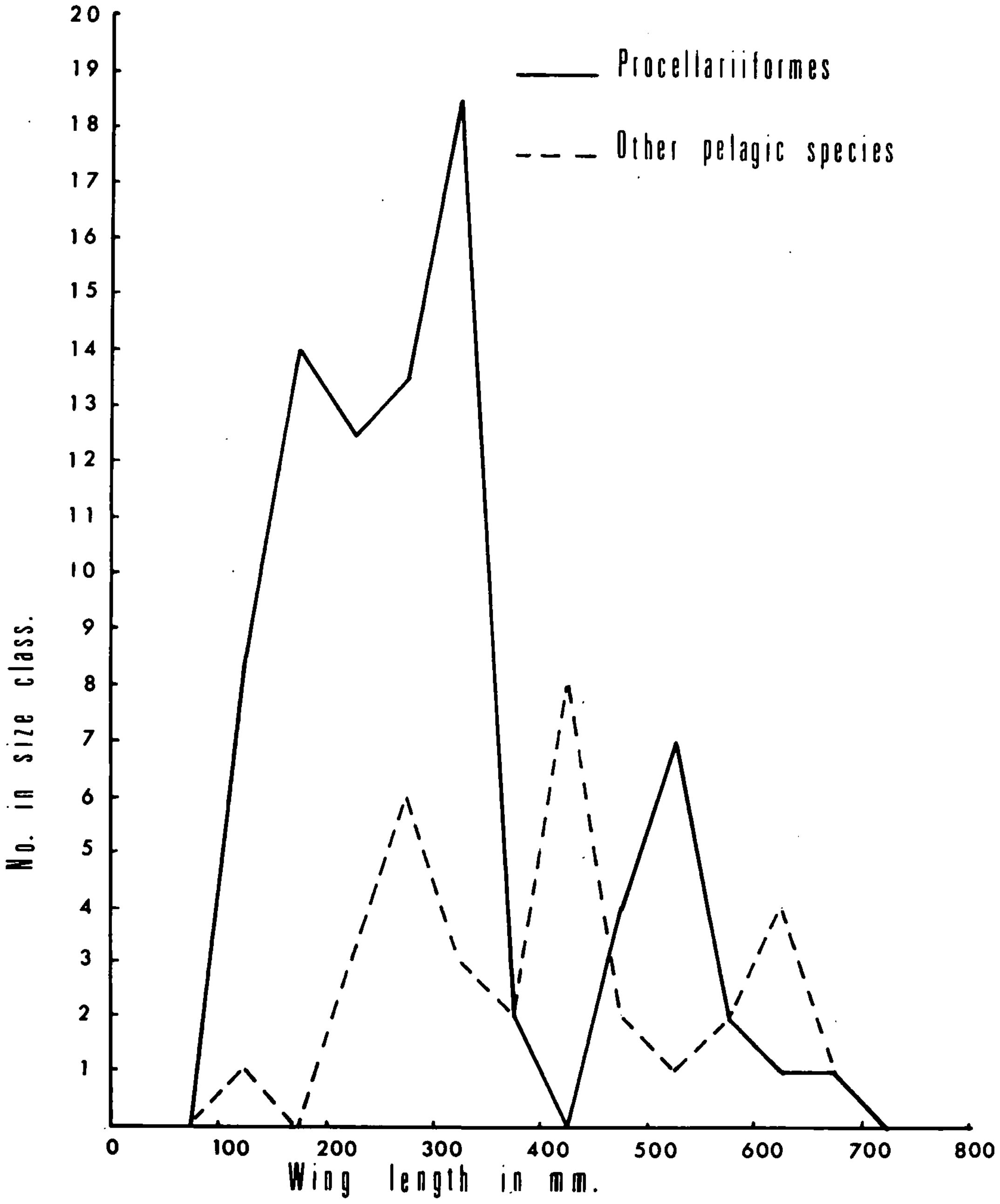

Fig.4. Size variation in the Procellariiformes and other pelagic sea-birds.

mixed sex have been used (e.g. with Diomedea bulleri), the premise that no sexual dimorphism in size exists may be incorrect. However, the inclusion of samples of mixed sexes appears to make little difference to the plots about the regression line in the few instances where the data are adequate to test this.

6. THE DISTRIBUTION OF SPECIES BY SIZE WITHIN THE ORDER.

The sizes of the many species comprising the order Procellariiformes are not randomly distributed over the range. About 70% of them have standard wing lengths of from 150 to 350 mm, whereas the total range of size judged on this variable is from about 110 to 700mm. The distribution of the species by size, using standard wing length as an index of size for 84 species of petrel, is shown in Figure 4 whose data are taken from Appendix A. Class intervals of 50mm have been used and where a species consists of several races whose wing dimensions place them in different class intervals, each interval has been allocated a "half animal", as appropriate.

The frequency polygon shows a marked bimodal form with no species at all in the class 375 to 425 mm. Nichols (1914), who was perhaps the first to attampt an explanation for the great diversity in size among the petrels, also presented a frequency polygon (based on body length minus tail) for 97 of the birds then considered distinct species. He omitted the Pelecanoididae but these are included in Figure 4. His polygon has the same form as in my figure but while he describes how in mixed feeding flocks the smaller species are satisfied "with the crumbs left by the larger ones" and how the smaller species nest in the protection of holes and crevices while the larger ones, not needing protection, nest in the open, he makes no comment about the gap in the size classes. To Nichols it was perfectly obvious that the great range of size among the birds relieves pressure of competition. Murphy, who published alongside Nichol's paper a photograph taken in the South Atlantic in which nine petrel species are distinguishable round one food source, elaborated on Nichol's ideas many years later. In his scholarly "Oceanic Birds of South America" (1936 p. 475) he pointed out that the varying range of size and varying styles of flight and feeding shown by the members of the order exemplify Osborn's principle of adaptive radiation. Murphy emphasised that in a relatively uniform environment like the upper surface of the sea, once selection started to sort out different size types, their varying relationship to the available food and to theirenemies would rapidly accelerate trends towards diversification.

That intra-ordinal competition has played a major part in the evolution of the Procellariiformes seems a reasonable hypothesis although other explanations are possible but the evidence that competition is lessened because of the diversity of size among the species is mainly circumstantial. That many species today will feed cheek by jowl but in different ways on a common food source (usually provided by man) does not necessarily mean that the birds also avoid competition in the course of their normal lives at sea and there is certainly quite a large overlap in the foods taken. Nevertheless it is clear that generally speaking, albatrosses eat different things from storm petrels and prions and these differences seem likely to extend, though perhaps to a less marked degree, to all petrels sharing the same foraging range.

A start has been made at comparing the foods of two closely related species of similar size and breeding biology - the mollymawks Diomedea melanophris and D. chrysostoma. These often nest close to each other, sometimes in mixed colonies, without hybridising.

Tickell (1964) has demonstrated significant differences in the foods taken by members of these mollymawks resorting to the same island to breed, although there was a considerable overlap. Other studies of the foods of petrels are in progress.

If the Procellariiformes (except perhaps the Pelecanoididae) are an ancient and monophyletic group, as seems probable, on account of the homogeneity of their behaviour, modes of life and anatomy, then in the course of their radiation there must once have been some species in the missing size range of wing length class 375-425mm. Why did these disappear? Did some other sea-bird group oust those petrels perhaps under conditions quite different from those obtaining now and, having occupied the niche, prevent its reoccupation by any other Procellariiform birds? Was the size-frequency curve once more normal and the bimodality a consequence of the replacement of petrels by other sea-birds?

With a view to investigating the possibility of past inter-ordinal competition an attempt has been made in Figure 4 to establish the present distribution by size of pelagic sea-birds other than petrels. Such birds are potential if not actual competitors for present-day Procellariiformes though their consumption of foods upon which petrels are dependent are in most cases unknown.

This comparison is fraught with difficulties. For flying species standard wing length has again been used as an index of body size and this may not be very reliable for so wide a variety of birds belonging to two different orders - the Pelecaniformes and Charadriiformes. Furthermore, the lack of quantitative data on food and feeding means that the separation of birds in these orders into pelagic and coastal species is difficult and in some cases rather arbitrary as a species may be pelagic at one season and an inshore feeder at another. Nevertheless some fairly clear cut distinctions are possible; gulls and terns, for example, are unlikely competitors for sea-going petrels. The species regarded as pelagic here include all the tropic- and frigate-birds (*Phaethon* and *Fregata* spp.), all the gannets and boobies except *Sula variegata* and *S. nebouxii*, six terns (*Sterna paradisea*, *S.anaethetus*, *S. fuscata*, *Anous stolidus*, *A. tenuirostris* and *A. minutus*), three gulls (*Rissa tridactyla*, *R. brevirostris* and *Larus pipixican*), the skuas *Stercorarius skua* and *S. longicaudus*, and the auks *Alle alle* and *Fratercula arctica*.

Important and highly pelagic in the southern oceans are ten species of penguin whose food include *Euphausia* and *Munida* and cephalopods known to be eaten also by petrels in those regions. However, to bring flightless, water-dwelling penguins into a scheme based on wing-length or any other measure of body size runs into serious difficulties by virtue of these birds' special mode of life and milieux. They must, however, be included in the comparison in view of their concentration, like the petrels, in the southern oceans where both orders may well have originated. Indeed, they may have co-existed for the whole of their history if, as some believe, the petrels and the penguins have arisen from a common ancestor. And although penguins can take prey unavailable to the surface feeding petrels some competition does exist today and may have been more severe in the past.

An attempt has been made to try and equate the ten species of penguins that are significantly pelagic in their feeding range (i.e. omitting *Spheniscus* and *Eudyptula*) with hypothetical petrel species. This has been done by taking the body length of the penguin and working out what standard wing length would sustain a petrel having that body length. This very crude comparison makes a King Penguin *Aptenodytes patagonica* as equivalent in size to a Royal Albatross and it has been counted as a flying bird of wing length of that species.

Similarly, the smaller penguins of the large genus Eudyptes become equivalent to smaller albatrosses in size.

The result of this evaluation of the number and size distribution of non-Procellariiform pelagic species that might compete with the petrels is shown in the dotted frequency polygon in Figure 4. It will be seen from the positions of the peaks in the two polygons that the non-Procellariiform species appear to be predominate in size classes not favoured by petrels. This is particularly noticeable in the 350-450mm group where in the absence of any petrels species of small penguins and boobies predominate.

In view of the difficulties involved in making meaningful comparisons, difficulties not restricted to those mentioned above - should one not compare population sizes or even biomass rather than merely the numbers of species? - conclusions drawn from a comparison of the two polygons must be considered as suggestive only. Furthermore the fossil Plotornis delfortrii Milne-Edwards 1878 of the Middle Miocene, believed to be the remains of a petrel (Lambrecht, 1933) may have been a member of the missing size class. The fossil tarsometatarsus is 70.5mm long and this suggests a body weight of around 2,000 g (Figure 30) so that the bird may have been a little smaller than present day mollymawks.

7. RELATIONSHIPS BETWEEN BODY SIZE AND EGG SIZE IN PETRELS.

7.1. Egg weights and Body weights.

Once they have reached maturity and obtained a partner female petrels lay one egg each breeding season. While one race of the tropical Puffinus lherminieri breeds at about nine monthly intervals (Snow, 1965), most petrels breed anually except for the two largest Diomedea exulans and D. epomophora and perhaps D. chrysostoma (Tickell, 1967) which breed biennially. The eggs are large in relation to the birds that produce them, the contrast being most pronounced in the small storm-petrels and prions where the eggs may represent a quarter of the laying bird's weight.

The ratio between egg weight and female body weight varies in a uniform manner throughout the order and ranges from about 6% to 25%. The relationship between these two variates is shown in Figure 5. This is based on the figures from the 19 species for which adequate data are available listed in Table III where the sample sizes are indicated in parentheses. The data include only those species for which at least 5 egg and 5 body weights are available but most samples are considerably larger than this. Female body weights have been used except in such genera as Puffinus and Pterodroma where sexual dimorphism in weight seems to be absent: here the samples are often of mixed sexes.

Table III includes useful data from Richdale (1964) who discussed the relationship between egg weight to body weight among eight species of petrels. Earlier references to this subject include Murphy (1936) and Marshall and Serventy (1956) while Lack (in press), in a discussion of the growth rate in Procellariiformes,

TABLE III. EGG WEIGHTS AND BODY WEIGHTS IN PROCELLARIIFORMES

	Species	Mean Egg Wt. (g)	Mean Body Wt. (g)	Egg Wt. / Body Wt. %	Log. Egg Wt.	Log. Body Wt.	Log. Egg Wt. / Log. Body Wt.
1a.	D.e.epomophora	425(15)	7801(5♀)	5.7	2.6284	3.8927	0.675
2b.	D.e.chionoptera	467(6)	7270(53♀)	6.4	2.6693	3.8615	0.691
7.	D.bulleri	250(100)	3004(31♂♀)	8.3	2.3979	3.4829	0.706
8.	D.nigripes	291(100)	2934(138♀)	9.7	2.4639	3.4675	0.711
10.	D.immutabilis	278(20)	2852(134♀)	10.1	2.4448	3.4551	0.708
14.	M.giganteus	237(12)	4114(5♀)	5.8	2.3747	3.6142	0.657
16.	F.glacialoides	103(13)	741(10♀)	14.0	2.0128	2.8698	0.701
19a.	D.c.capensis	62(42)	407(22♀)	15.2	1.7924	2.6096	0.687
20.	P.nivea	47(21)	244(13♀)	19.3	1.6721	2.3874	0.700
33.	P.inexpectata	53(8)	316(86♂♀)	16.8	1.7243	2.4997	0.690
38a.	P.h.hypoleuca	33(7)	176(76♂♀)	18.7	1.5185	2.2455	0.676
43a.	P.d.banksi	33(23)	153(12♂♀)	21.6	1.5185	2.1847	0.695
44.	P.salvini	32(12)	154(18♂♀)	20.8	1.5051	2.1875	0.688
45.	P.turtur	24(56)	132(100♂♀)	18.2	1.3802	2.1206	0.651
60.	P.griseus	95(25)	787(100♂♀)	12.1	1.9777	2.8960	0.683
62.	P.tenuirostris	85(13)	635(22♀)	13.4	1.9294	2.8028	0.688
64b.	P.p.puffinus	58(10)	406(32♀)	14.4	1.7665	2.6085	0.677
71c.	P.m.maoriana	12(54)	47(100♂♀)	25.1	1.0719	1.6721	0.641
78a.	O.l.leucorhoa	10(100)	48(66♂♀)	21.0	1.0043	1.6812	0.597

also deals with the relationship in general terms. Heinroth (1922) presented a large amount of data on relative egg-weights for many birds which were re-examined by Huxley (1927), but little information on petrels was then available.

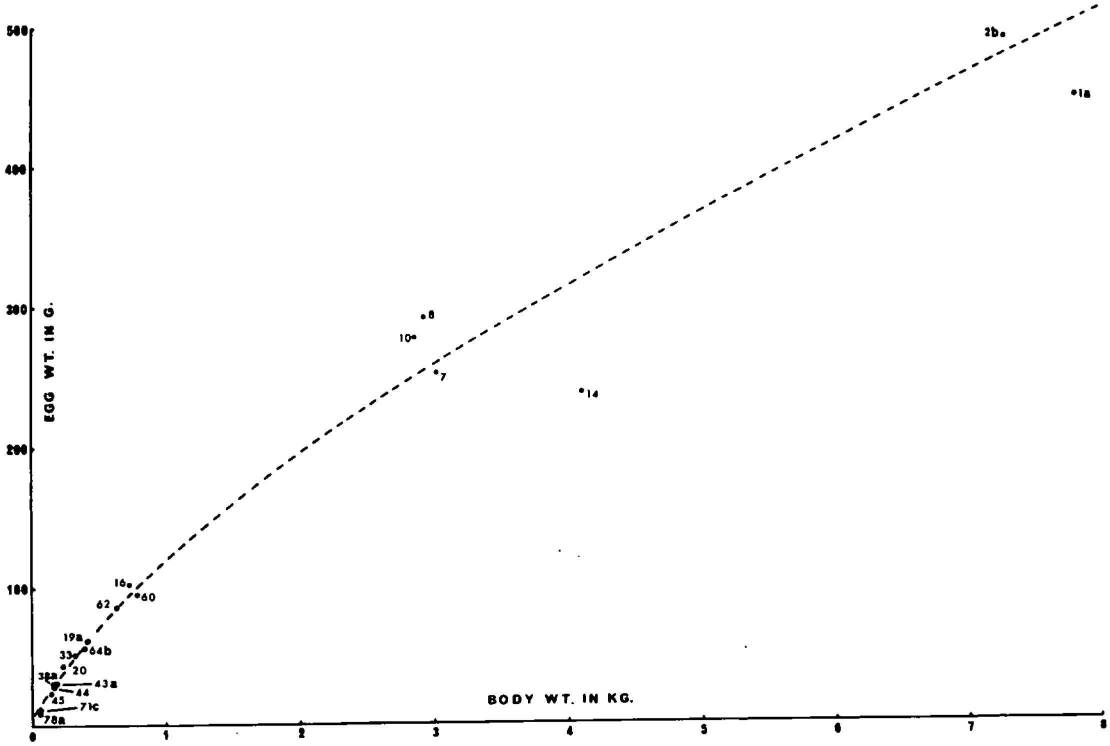

Fig.5. BODY WEIGHTS AND EGG WEIGHTS IN PETRELS.

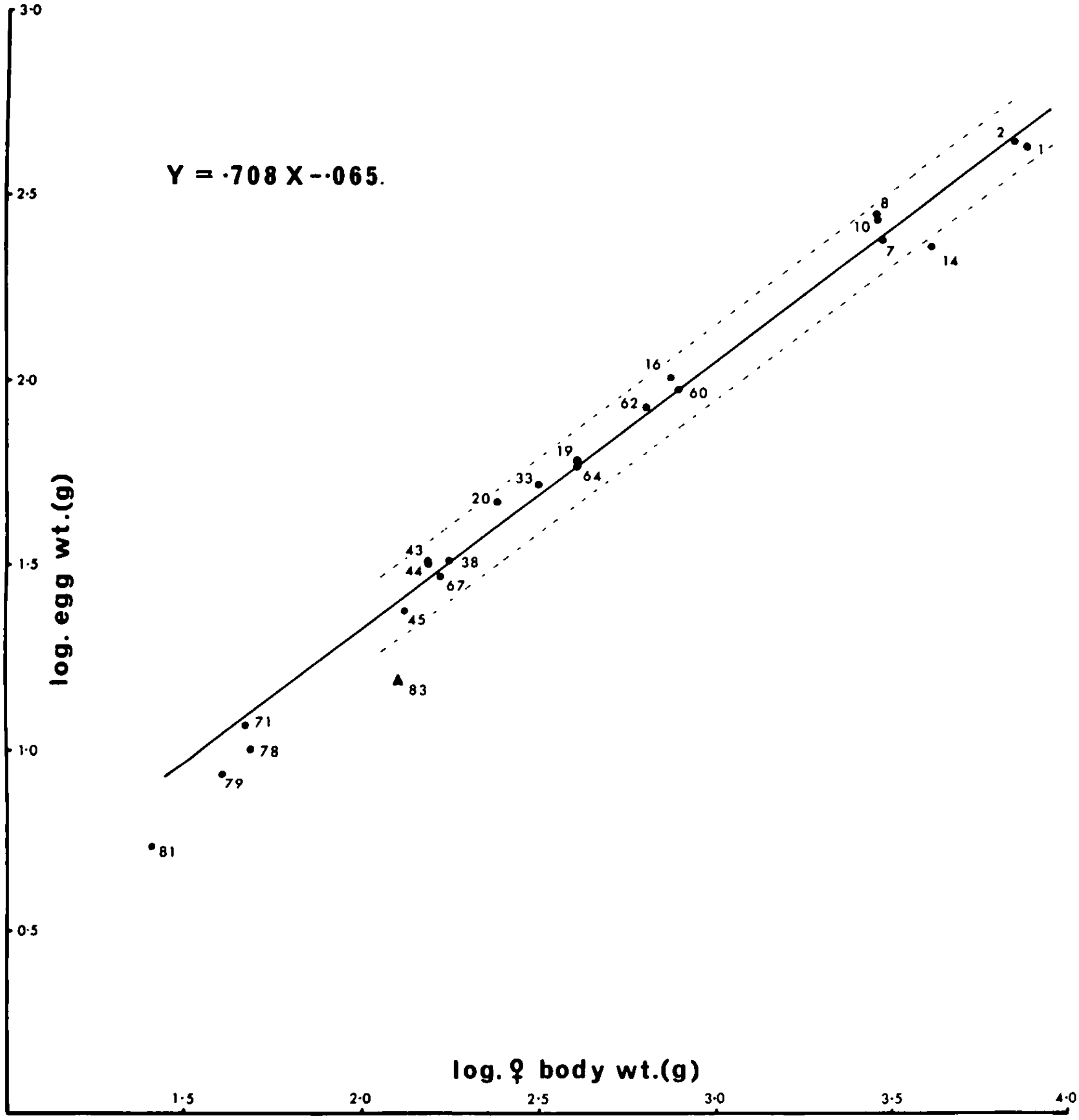

FIG.6. BODY WEIGHTS AND EGG WEIGHTS IN PETRELS

The shape of the curve in Figure 5 resembles that presented by Huxley based on Heinroth's data for 432 species of birds weighing from 2 to 90,000 grams. The points in Figure 5 are not evenly scattered over the size range but reflect the bimodal distribution by size within the order. While there are adequate data for small and medium-sized petrels the figures are fewer and more scattered for the large ones. However, other data from large petrels, though drawn from smaller samples, fit satisfactorily to the upper portion of the curve.

When the logarithms of the data from Figure 5 are examined they are found to be highly correlated ($r = +0.983$; $P < .001$) and they plot about a straight line - Figure 6.

Where Y = log egg weight in g and X = log body weight in g, then the equation of the regression line, calculated by the method of least squares, is:-

$$Y = 0.708X - 0.065 \quad \ldots\ldots\ldots\ldots\ldots\ldots \quad (5)$$

and the points have a standard deviation in log terms about this line of 0.495.

The straight line relationship of these variables plotted logarithmically indicates that the rate of change in egg weight with body weight is constant throughout the order. The relationship appears to be an instance of allometry as described by Huxley (1932) but of the negative kind. The implications of allometric growth and relationships are discussed later in section 12.

Equation (5) can be re-written in the form:-

$$y = 0.859x^{0.708} \quad \ldots\ldots\ldots\ldots\ldots\ldots \quad (6)$$

or egg weight in g = 0.859 mean body weight in g $^{0.708}$.
Thus egg weight in petrels is a function of power of female body weight quite close to that usual where a parameter varies with the area of the body surface (body weight $^{0.667}$). This suggests

that egg size may be a function of the surface area of some organ like the secretory part of the oviduct or perhaps simply egg width, although presumably other factors are also involved.

The last column of Table III shows that:-

$$\frac{\log \text{Egg Weight}}{\log \text{Body Weight}} = 0.680 \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots \quad (7)$$

this being the mean of the ratios for the 19 species listed. The range is 0.597 - 0.711 and the standard deviation about the mean 0.026. Thus 95% of the means of these samples for this ratio lie between 0.680 ± 0.052.

Huxley (1927) found on plotting Heinroth's egg and body weight data on logarithmic axes that the curves for birds in the various orders flattened out at the higher ranges of body weights. At the upper end of the series the relationship of log egg weight (y) in respect of log body weight (x) was of the form $y = bx^{2/3}$ whereas at the lower end it was $y = bx^1$; that is, for the smaller birds the egg size increased linearly up to a limit after which the rate of change was reduced and approximated to a two-thirds power or a "surface area" relationship.

Huxley speculated that two antagonistic processes might be at work here, one favouring growth of egg weight in linear proportion to body weight, the other restricting growth of egg weight to a linear proportion to surface of the body or egg. To maintain an egg size directly proportional to body weight might be biologically advantageous but physiologically impossible so that with larger birds the increase in relative egg size became proportional to the increase in surface area.

At a late stage in the present study additional information became available for two small petrels - 79a <u>Oceanodroma castro</u>

and 81a O. tethys (Harris, in press c). These data have been included in Figure 6 but not used in calculating equations (5) or (7). It will be seen that three of the storm-petrels (78, 79 and 81) lie in positions that suggest a steepening of the curve at the lower end of the size scale and this is strengthened when further data are calculated using equations (3) and (11) for other storm-petrels for which field data are lacking. On the other hand, a cross check by way of the relationship between egg dimensions and body weight that is made in section 7.4 below indicates that the southern genera, Oceanites, Fregetta and Pelagodroma, all long-legged and of which only species 71 is shown in Figure 6, do conform to the general trend among the Procellariiformes. Only the short-legged forms like Hydrobates and Oceanodroma differ and do so in such a way that their eggs represent a lower proportion of the body weight than predicted from equation (5).

It is interesting to note that this change, if real, between a body weight $^{1.0}$ and body weight $^{.66}$ relationship, occurs at around the 100 g figure for body weight. So too does Huxley's curve for birds as a whole. These facts indicate that some basic mechanism may be at work here and effective in many or all orders of birds despite the very different absolute proportions that single eggs bear to the weights of the birds which produce them. Up to about 100 g body weight the members of a series increase their egg sizes linearly with body weight, after which they are adjusted downwards and increase only at a two-thirds power rate of body weight i.e. egg weight becomes a partial function of metabolic rate which varies as the surface area of the body.

Some of the scatter in Figure 6 about the regression line may not be merely a natural consequence of using biological data. That for species 1a and 14 may be due to inadequate sample size but

TABLE IV. WING LENGTHS, EGG WEIGHTS AND EGG CAPACITIES IN PETRELS

Species No.	Mean Wing Length (mm)	$\sqrt[2]{\text{Wing Length}}$	Mean Egg Weight (g)	$\sqrt[3]{\text{Egg Weight}}$	Egg Capacity (ml)
1a	624(8♀)	-	425(15)	-	399(5)
1b	616(12♀)	24.82	416(41)	7.46	-
2c	603(4♀)	-	-	-	365(87)
3a	557(4♀)	-	-	-	242(11)
7	520(31♂♀)	22.80	250(100)	6.30	226(7)
8	506(138♀)	22.49	291(100)	6.66	-
9	504(5♀)	-	-	-	247(9)
10	487(5♂♀)	22.02	278(20)	6.53	-
12	516(14♀)	22.72	240(7)	6.21	219(6)
14	498(5♀)	22.32	237(12)	6.19	220(3)
15	497(10♀)	22.29	232(10)	6.14	216(6)
16	329(21♀)	18.14	103(13)	4.69	-
17a	313(45♀)	-	-	-	92(3)
19a	264(15♀)	16.25	62(46)	3.96	56(3)
22a	317(45♂♀)	-	-	-	78(4)
26	303(28♂♀)	-	-	-	92(3)
27b	290(20♀)	17.03	74(89)	4.20	70(5)
33	262(100♂♀)	16.19	53(8)	3.76	56(11)
38c	228(24♂♀)	15.10	37(41)	3.34	-
42a	214(42♂♀)	-	-	-	33(3)
43a	192(12♀)	13.86	33(23)	3.21	28(5)
44	190(18♂♀)	13.78	32(12)	3.17	-
45	182(100♂♀)	13.49	24(56)	2.88	24(12)
51	374(5♂♀)	19.34	127(9)	5.03	-
57	324(23♂♀)	-	-	-	105(3)
59b	292(208♂♀)	17.09	59(19)	3.90	-
60	304(100♂♀)	17.44	95(25)	4.56	88(13)
62	274(40♀)	16.55	85(13)	4.40	77(5)
64b	237(20♂♀)	15.39	58(10)	3.87	53(14)
68f	173(25♂♀)	-	-	-	32(8)
69a	153(65♂♀)	-	-	-	9.5(6)
71a	157(13♀)	-	-	-	12(3)
71b	158(21♀)	12.57	11.8(54)	2.28	-
74	117(39♂♀)	-	-	-	6(10)
78a	156(94♂♀)	12.49	8.8(45)	2.06	9.2(4)
79b	153(50♂♀)	-	-	-	8.9(4)
83a	123(100♂♀)	11.09	15(27)	2.47	-

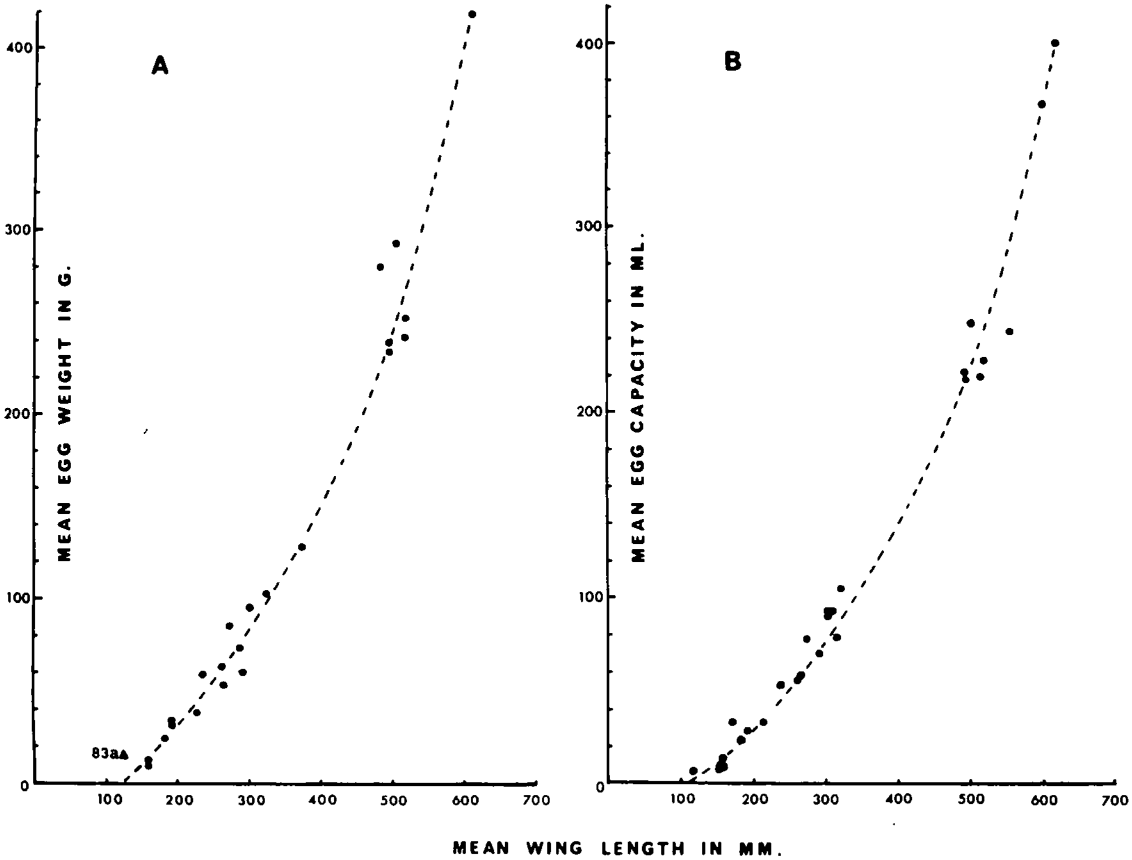

Fig.7. ♀ WING LENGTH, EGG WEIGHT (A), AND EGG CAPACITY (B) IN PETRELS.

could also reflect a real and adaptive deviation from the general trend with these species laying somewhat smaller eggs than other petrels of similar size. The data for 83a Pelecanoides urinatrix are shown separately in the figure and they were not used in calculating equations (5) or (7). Although the figures for egg weights are inadequate, it seems clear that this bird lays eggs smaller than usual for a bird of its body weight. This anomaly is discussed later in sections 7.3, 7.4 and 11.10.

7.2 Egg Weight and Wing Length Relationships.

As a correlation has been established between standard wing length and the cube root of the body weight, there should also be a correlation between some power of the wing length and egg weight. Using data from Table IV (where the sample sizes are in parentheses) a direct plot between mean egg weight and mean wing length for 23 species produces the exponential type curve of Figure 7A. A very similar curve results if mean egg capacity (i.e. the internal volume of the egg shell) is plotted against mean standard wing length for 27 species - Figure 7B. The species represented in the two graphs are rather different but the forms of the curves are essentially the same as would be expected in view of the close relationship of egg capacity to egg weight.

In order to establish a linear relationship it was necessary to convert the variables to equivalent dimensions by comparing the cube root of the egg weights with the square root of the standard wing lengths of female birds. These variates are correlated ($r = +0.967$; $P < 0.001$) and the plot for 22 species is shown in Figure 8. A linear relationship is also obtained when logarithms of egg weight and standard wing length are compared. When $Y = \sqrt[3]{\text{mean egg weight}}$ in g and $X = \sqrt[2]{\text{mean female wing length}}$ in mm, then:-

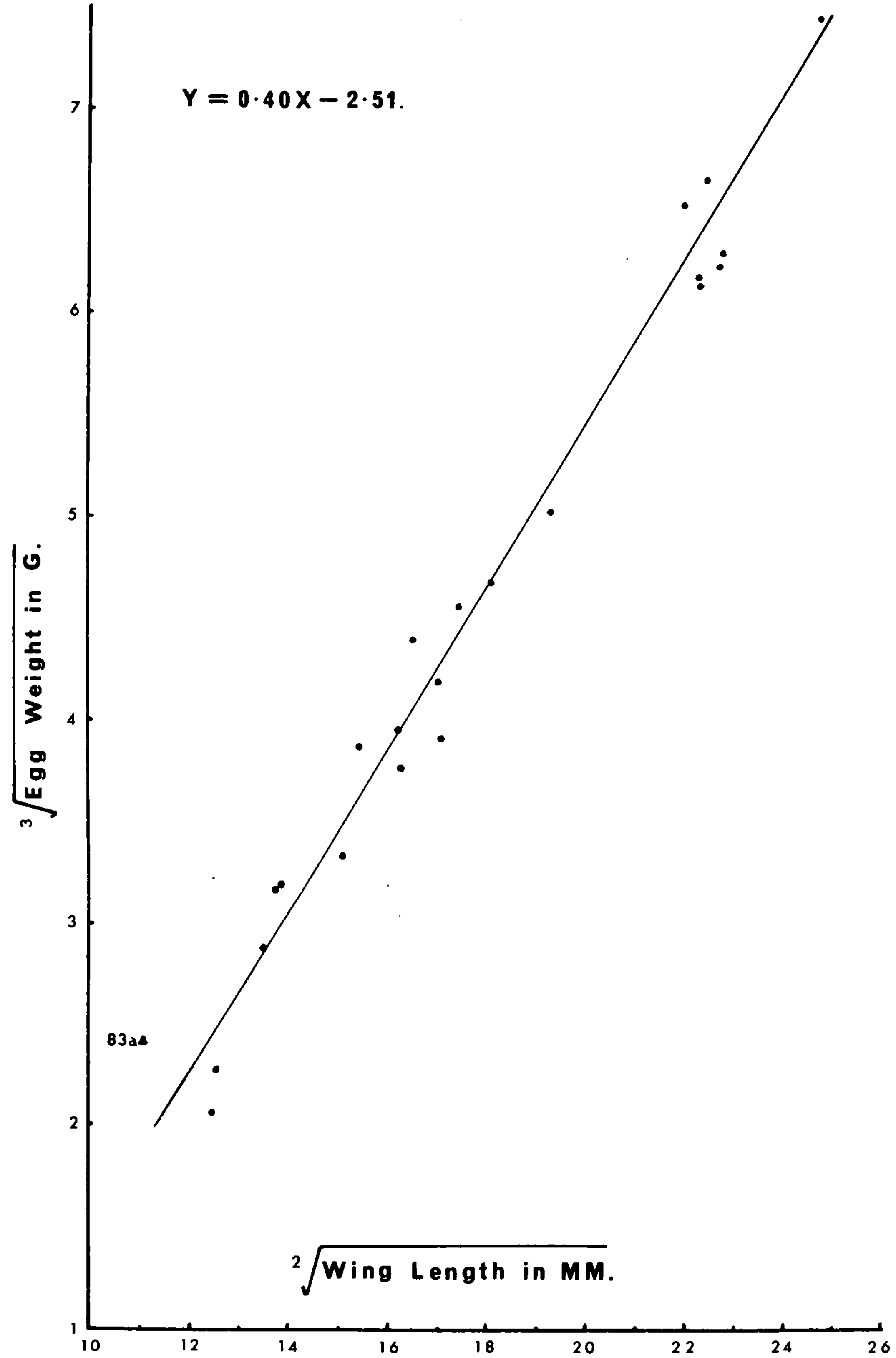

Fig. 8. $\sqrt[2]{\text{MEAN}}$ ♀ WING LENGTH AND $\sqrt[3]{\text{MEAN}}$ EGG WEIGHT IN PETRELS.

$$Y = 0.40X - 2.51 \quad \ldots\ldots\ldots\ldots\ldots\ldots \quad (8)$$

and the points have a standard deviation about the regression of $0.015 \sqrt[3]{g}$.

The scatter about this regression line would be reduced if some of the data for egg weights were more reliable. Sample means for egg weights tend to be lower than the true means for fresh eggs because it is difficult in practice to ensure that all the eggs are new-laid. If incubated eggs are included the value for the mean will be lowered. Recalculation of some of the data from determinations of egg capacities (Table XII) would bring many plots in Figure 8 closer to the line - as explained in section 8. But some values would not be affected in this way. Those for the storm-petrels would not fall closer to the line and although only 2 species of this family are included in Figure 8, Harris's unpublished data for species 81a and 79b also plot well below and outside the 95% confidence limits. The position therefore at this end of the size range appears to be parallel that holding for the egg weight/body weight relationship; that is, there is a marked change in the relationship around the lower limits for body size in petrels. Equation (8) therefore appears to give unsatisfactory estimates for the variates where X is less than 14 and Y is less than 2.5 or where wing length is less than about 19 cm and egg weight less than about 16g.

In Figures 7A and 8 <u>Pelecanoides urinatrix</u> (83a) is also shown. As in previous figures it plots well away from the regression line. This is mainly because of the very low values for wing length which are only partly offset by the low egg weight in relation to body weight already noted. The Pelecanoididae have been omitted when computing Equation (8).

7.3 The Relationship Between the Weights of Petrel Eggs and their Dimensions.

Various formulae have been proposed to relate egg dimensions to egg weight (W) in birds. Most of these involve using the length (L) multiplied by the square of the maximum diameter (B) and are based on the formula for the volume of an ellipsoid.

Bergtold (1929) presented two equations, one for precocial species, particularly the domestic hen, in which $W = 0.5632\ LB^2$, and another based on data from 14 species of altricials where $W = 0.5463\ LB^2$. These equations give estimates of egg weights which he believed accurate to 5%.

Bergtold's formulae assume that the mean density of the eggs in his two main groups do not alter with size. However, the shell is approximately twice as dense as the contents of the fresh egg and the weight of the shell does not represent a constant proportion of egg weight but varies with egg size. Thus in petrels, small species have shells weighing about 5.5% of the total egg weight whereas the shell represents about 9% of the total weight in large ones, according to the data given by Schönwetter (1960). Schönwetter (1925) had earlier proposed a general formula allowing for such variations, $W = 0.5\ (LB^2 + W)$ where w is the weight of the shell, and Nice (1937) found that this formula agreed well with her field data for Melospiza melodia.

Romanoff and Romanoff (1949) and Barth (1953) have discussed Bergtold and others' formulae. Barth pointed out the errors inherent in using axial lengths to determine egg weights and volumes. He obtained data for the weights and volumes of fresh eggs of a number of species and followed the changes in these variables during the course of incubation. He established a formula for egg volume (V) based on its weight at any number of days during incubation (w_n), its density when freshly laid

(d_o) and the loss of weight per day (k):-

$w_n = Vd_o - kn$.

This formula does not involve the use of axial lengths and gave accurate results that were independent of the shape of the egg but the specific gravity and daily loss of weight for each species had to be determined before Barth could derive formulae for the different species. For 41 eggs of Larus canus the specific gravity of the eggs studied varied from 1.056 for Phylloscopus trochilus to 1.087 for Haematopus ostralegus.

As already noted, errors in published figures for egg dimensions would seem to be of a small order in terms of the present study. However, many eggs in museum collections have been donated by oologists who were often biased in their choice of specimens so that atypical eggs are likely to be more numerous here than in similar sized samples gathered at random. It is impossible to judge the importance of this source of error in published data where often only the means and the ranges are given, but as the samples used here are large and heterogeneous, the bias should not be serious. Nor has it appeared important in the samples measured personally, where the infrequent dwarf and giant eggs were omitted.

Another possible source of bias is the proportion of surface-laid eggs in the samples from burrowing species. These are believed to be the products of young birds and there is evidence that these eggs are significantly narrower than those laid by older females (Richdale, 1952; Serventy, 1967). As the eggs of burrowing species are often difficult to collect, it seems probable that a good many eggs in museum collections will have been taken from the surface and will therefore be atypical in respect of breadth. It is again impossible to measure this bias but as the difference between the breadths of surface-laid and burrow-laid eggs seems not to be more than about 1.5% the resulting errors ought not to be important for present purposes.

Despite such shortcomings, a means of determining egg weights from their equatorial dimensions offers several advantages. There is already a great deal of reliable data on these dimensions and they are comparatively easy to obtain in the field. It is far less easy to find and weigh eggs that are really fresh, particularly when dealing with burrowing species, and even more difficult to follow the loss of weight during incubation. To get reliable information on egg weight loss and time for the smaller burrowing species whose tunnels are too narrow to admit a hand would be a difficult undertaking though perhaps worth attempting under suitable conditions. Furthermore, in a group like the Procellariiformes, where the eggs are basically similar in shape, it should be possible to derive a formula for their weights based on their dimensions capable of predicting figures of an accuracy adequate for most purposes. However, owing to the variation within species - in some greater than others - reliance should not be placed on figures derived from formulae where only small series of measurements are available.

Petrels lay elliptical eggs with a noticeable trend for the smaller species to produce more spherical eggs (section 7 below). The egg shape varies from short subelliptical to elliptical and long elliptical in the terminology used by Palmer (1962). In this respect there is a reasonable uniformity throughout the order, and one that is probably greater than that obtaining among the Laridae studied by Barth.

The relationship between mean egg weight in g and the mean value for length x breadth^2 in cm has been investigated using the data for 26 species of petrel. All the samples used include at least five measurements for each variable. Egg lengths and breadths were measured to 0.1mm using vernier calipers, breadth being the mean of two readings taken at right angles to one another at the equator of the egg. Data drawn from the literature may be less

TABLE V: EGG WEIGHTS AND DIMENSIONS

Species No.	Mean Egg Wt(g)	Log B.W.(g)	LB^2 (cm)	Log LB^2	$\frac{\text{Egg Wt.}}{\text{LB}^2}$
1a	425(15)	3.8927(5)	783(48)	2.8938	0.543
1b	416(41)	-	748(54)	-	0.556
2b	467(6)	3.8615(53)	829(9)	2.9186	0.563
3a	238(6)	-	475(52)		0.501
7	250(100)	3.4829(31)	445(100)	2.6484	0.562
8	291(100)	3.4675(138)	538(45)	2.7308	0.541
10	278(20)	3.4551(134)	526(39)	2.7210	0.529
12	240(7)	-	440(32)	-	0.545
14	237(12)	3.6142(5)	448(80)	2.6513	0.529
15	232(10)	-	443(32)	-	0.524
16	103(13)	2.8698(10)	188(13)	2.2742	0.548
19a	62(42)	2.6096(22)	115(46)	2.0607	0.539
20	47(21)	2.3874(13)	86(13)	1.9345	0.546
33	53(8)	2.4997(86)	112(39)	2.0507	0.473
38a	33(7)	2.2455(76)	65(7)	1.8195	0.504
43a	33(23)	2.1847(12)	56(42)	1.7482	0.589
44	32(12)	2.1875(18)	65(16)	1.8129	0.492
45	24(56)	2.1206(132)	48(100)	1.6812	0.500
51	127(9)	-	249(14)	-	0.510
59b	59(19)	-	106(48)	-	0.557
60	95(25)	2.8960(100)	180(78)	2.2553	0.528
62	85(13)	2.8028(22)	157(100)	2.1959	0.541
64b	58(10)	2.6085(32)	107(100)	2.0294	0.542
71c	12(54)	1.6721(100)	24(100)	1.3802	0.500
78a	10(100)	1.0043(66)	18(20)	1.2553	0.555
83a	15(27)	2.0923(100)	33(39)	-	0.457

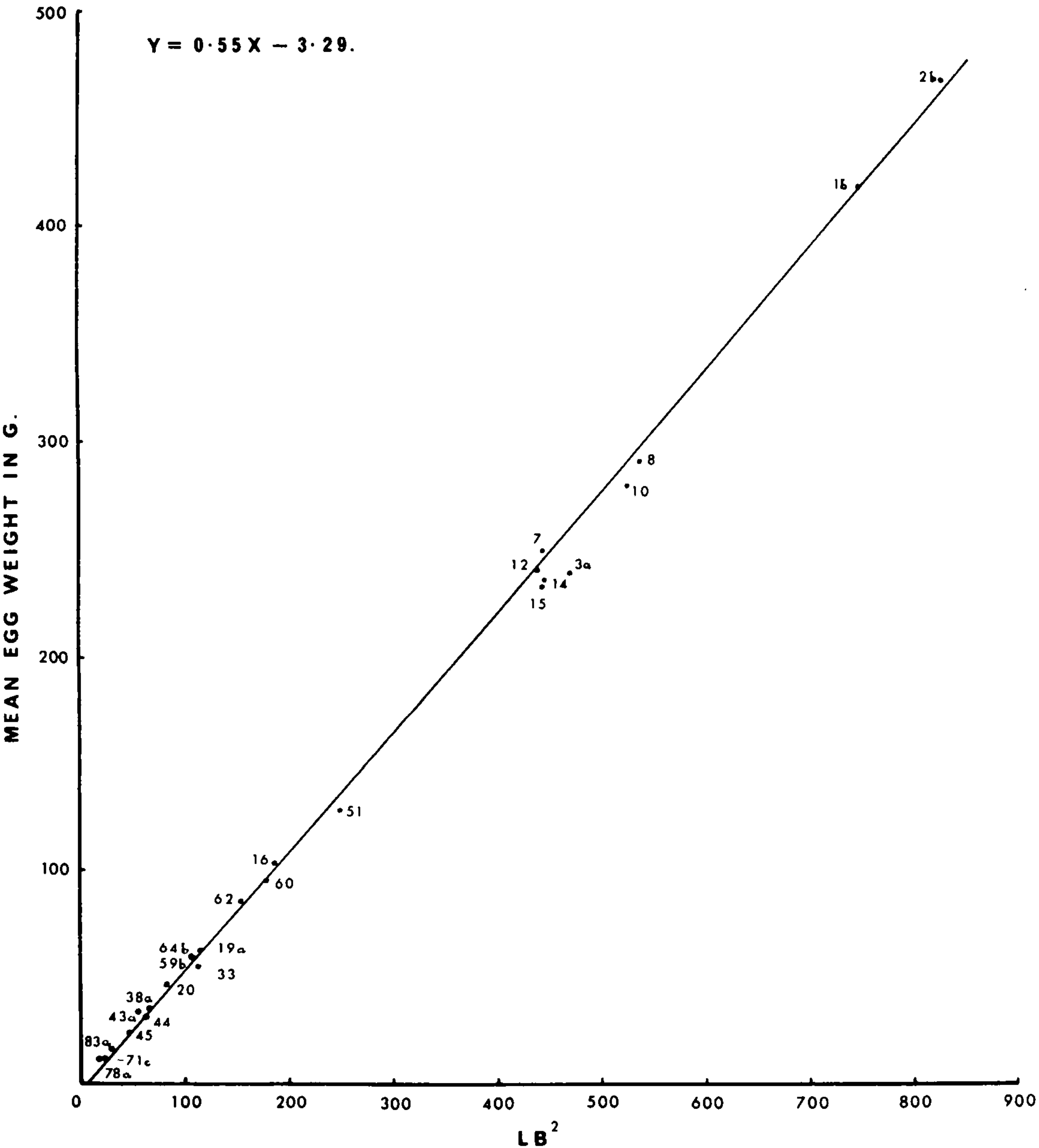

Fig. 9. EGG LENGTH(CM) X BREADTH(CM)^2

v. EGG WEIGHT IN PETRELS.

accurate but errors in measuring seem unlikely to be serious for present purposes.

The data are given in Table V where the sample sizes are shown in parentheses. The variables are plotted in Figure 9 and when $X = LB^2$ in cm and $Y =$ egg weight in g, the regression line, fitted by the method of least squares is:-

$$Y = 0.550X - 3.29 \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots \quad (9)$$

or mean egg weight in g = 0.55 length x breadth^2 in cm - 3.29g. The points have a standard deviation about the regression line of 6.84g.

As the fitted line does not run through the origin a term additional to k LB^2 is included. The data in the last column of Table V however, show the ratios of mean egg weight to mean LB^2 for the 25 species. This ranges from 0.457 - 0.589 with a mean value for all the species of 0.530 or:-

$$\text{Mean egg weight in g} = 0.530\ LB^2 \text{ in cm} \quad \ldots\ldots\ldots\ldots \quad (10).$$

Most of the figures plot close to the regression line and on the data used, equation 10 gives figures accurate to within ± 3% for 16 of the 25 species. The most marked deviations are for species 71c, 78a and 43a where the divergence is -30, -16 and -6% respectively. These, however, are all small species and their divergence seems to be mainly a consequence of the line not passing through the origin. If it were drawn to do that the discrepancies would disappear but there would be a corresponding divergence at the upper end of the size scale. The deviations for these three species disappear if formula 11 is used. The only other figures that fall markedly away from the line are for species 33 and 3a which show a mean variation from the theoretical value for their weights based on egg dimensions of +9 and +8% respectively. These are probably artifacts consequent on the small numbers of egg weights involved,- only 8 and 6 respectively.

Equation 10 also gives estimates for egg weights that are within ± 3% of the known values. Again there are some divergences, the greatest being for Pelecanoides urinatrix (83a) where equation 10 gives an over-estimate by 13% for the weight. The probable reason for this is that the mean weight used (14.9g) is low due to partly incubated eggs being included in the sample and here Richdale (1965a), whose data these are, pointed out that most of the eggs were found addled or deserted so they were almost certainly underweight. Other values that fall off the line are for 71c (+7%), 43a (-9%), 33 (+ 11%), the latter again most likely due to an inadequate sample as suggested by the recalculated figure given in Table XIII. The deviation for species 43a Pachyptila desolata is not readily explicable as the data are based on reasonably large samples and the formula gives an underestimate. Some of the variations could be due to specific differences but it is particularly with small eggs that discrepancies due to loss of weight are likely to be most important as large eggs have smaller weight losses during incubation or exposure per unit weight than do small ones due to the latter's relatively high surface area (Pringle and Barott, 1937).

It is clear that the figures for mean egg weight given in Table V will tend to be underestimates of the true means of large samples of fresh eggs owing to the likelihood of some part-incubated eggs being included. Few of the authorities whose figures have been used make a point of stating that the eggs were absolutely fresh.

No figures for the daily loss of weight of incubated or exposed petrel eggs are available although Harris (1966) found that losses of 12.9%, 10.8% and 9.0% occurred during the first 45 days of incubation of three eggs of Puffinus puffinus. It seems likely that as with other species that have been studied, the daily loss is fairly constant up to the time when the egg is cracked. Furthermore, according to Murray (1926 in Needham, 1963) an infertile egg loses weight at a rate comparable with a fertile one at least for the first 16 days so that an additional bias should not be added if such eggs have been included in the samples.

Barth's figures for loss of weight during incubation for a variety of Charodriiform and Passerine species show that those of *Larus argentatus* and *L. fuscus* lose about 0.5% daily, *Haematopus ostralegus* 0.7%, *Sterna hirundo* 0.8%, *Turdus pilaris* 1.0% and *Phylloscopus trochilus* 1.3% of their initial weights. If comparable losses occur in petrels we might expect that a storm-petrel egg 5 days old would have lost about 5% of its weight and that a medium-sized egg such as that of *Puffinus tenuirostris* would have lost 2.5%. Weight decreases of these orders could well account for a large part of the observed deviations from the predicted weights derived from equations 9 and 10.

Other possible sources of error in these computations are the smallness of some of the samples, that no direct allowaance has been made for inter-specific variations in the proportion of total weight accounted for by the shell and the effects of deviations in shape from the ellipsoid, for pear-shaped or dumbell-shaped eggs, for instance.

However, the two latter have not been ignored; instead their effects have been averaged out throughout the range of the species. To see if greater accuracy would result if individual allowance was made for the weight of the shell the figures for 22 of the species in Table V were recalculated by subtracting the mean shell weights from the total egg weights of the first column. The shell weights were taken from Schönwetter's (1960) data. The new "k" value gained in this way was 0.492 i.e. $W = 0.492LB^2 + w$, where w = weight of the shell). This equation improves only slightly on the margin of error given by equation 10 and makes little difference to the values for the most divergent species, so that on the present data it seems not worthwhile introducing a more complicated equation which in any event has less value for the field worker. For greater accuracy it would be desirable to prepare separate equations for each species based on a sample of at least 100 freshly-laid and weighed eggs. These would allow for any variations in specific gravity from one species to another but would still be only valid when applied to representative samples of eggs rather than to individual ones.

The two equations above have somewhat different applications; equation 9 gives estimates of egg weight with smaller errors than 10 for medium and large-sized species, equation 10, however, is more likely to be reliable for computing the weights of eggs of small petrels.

The following table shows calculated egg weights for various species using the different formulae given above. The data came from Appendix A. The species are those for which good information on wing lengths or egg dimensions are available but for which there are no comparable figures on egg weights.

TABLE VI: FRESH EGG WEIGHTS IN GRAMS CALCULATED FROM DIFFERENT EMPIRICAL FORMULAE

	Species	A	B	C	D	E
4.	*D. albatrus*	342	348	339	-	-
5.	*D. irrorata*	273	273	266	-	-
6a.	*D. melanophris*	258	268	262	276	290
11.	*D. chlororhynchos*	215	201	197	180	245
12.	*P. palpebrata*	243	239	233	237	309
17a.	*F. glacialis*	98	101	100	87	107
18.	*T. antarctica*	95	88	88	80	93
22b.	*P. macroptera*	80	89	88	71	92
25.	*P. lessoni*	96	99	99	78	88
39.	*P. longirostris*	-	30	32	30	38
41.	*H. caerulea*	35	41	43	33	38
42.	*P. vittata*	33	33.5	35.5	35	37
50.	*P. aequinoctialis*	120	123	122	118	142
57.	*P. gravis*	102	113	112	102	103
61.	*P. bulleri*	61	64	65	55	78
69a.	*O. oceanicus*	9.4	7.5	10.4	9.9	14
70.	*G. nereis*	10.7	7.7	10.5	8.8	8.6
73a.	*F. grallaria*	12.0	10.0	12.8	12.3	17

A = calculated from Schönwetter's formula, $W = \frac{1}{2}(LB^2 + w)$.

B = calculated from equation 9.

C = calculated from equation 10.

D = calculated from equation 5.

E = calculated from equation 8.

Tested against the biggest samples for egg weights and egg dimensions from Table V, Schönwetter's formula using his shell weights, gives values from - 7.5% + 4.0% below or above the actual weights.

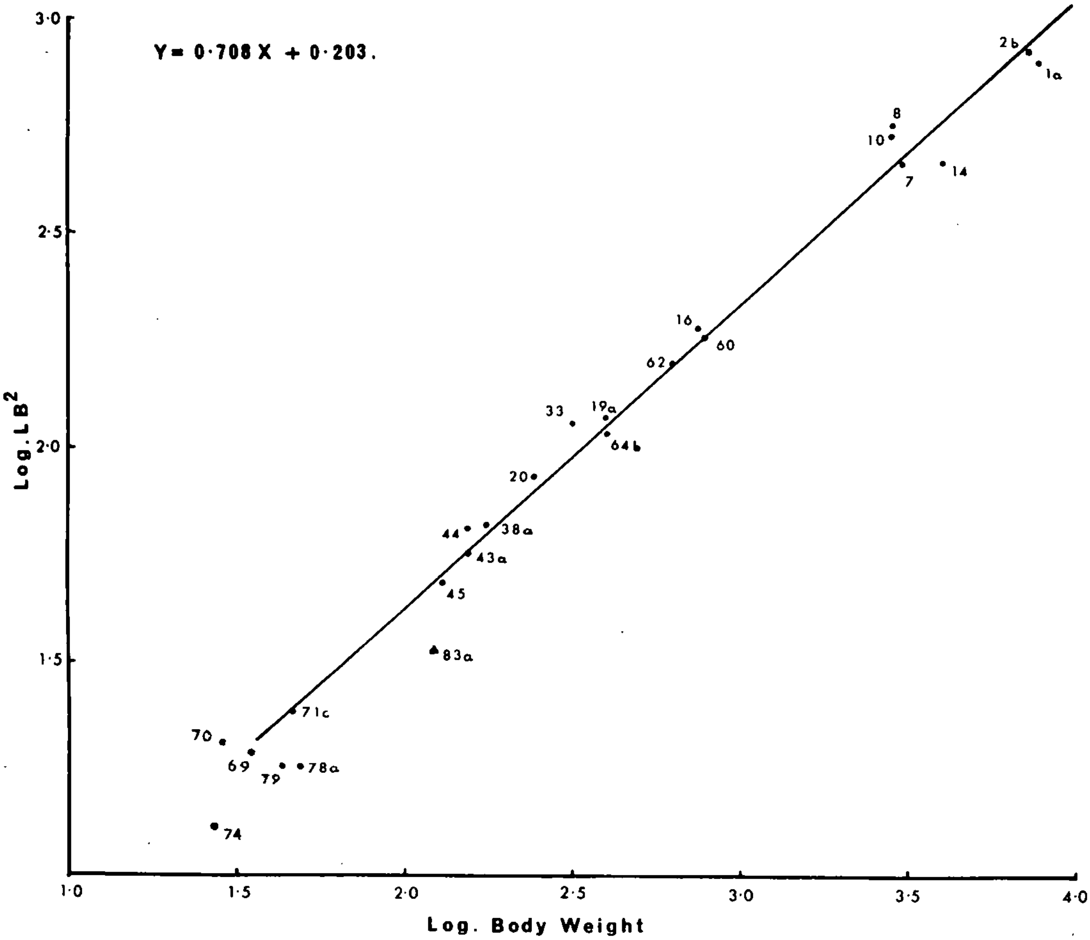

Fig.10. LOG. BODY WEIGHT v. LOG. EGG LENGTH X BREADTH^2.

7.4. Body Weights and Egg Dimensions.

The direct relationship between egg weights and egg dimensions established in the previous section means that a linear relationship also holds between the logarithms of LB^2 and body weight because of the correlation between log body weight and log egg weight.

The relationship between log LB^2 and log body weight for 24 species of petrel is shown in Figure 10. The data come from Table V and Appendix A and show species for which there are at least ten determinations of both variables. The data for species 74, 78, 79 and 83 have not been used in calculating the linear regression of Y (log LB^2 in cm) on X (mean body weight in g) which is:-

$$Y = 0.689X + 0.265 \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots \quad (11).$$

or log LB^2 in cm = 0.689 log body weight in g + 0.265.
This point has a standard deviation in log units about the regression line of 0.03.

The regression of X on Y is:-

$$X = 1.447 - 0.376 \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots \quad (12).$$

or log body weight in g = 1.447 log LB^2 in cm − 0.376.

Equations (11) and (12) can be re-written in the form:-

$$y = 1.841x^{0.689} \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots \quad (11a).$$

or LB^2 in cm = 1.841 body weight in g $^{0.689}$.

and $$X = 0.421y^{1.447} \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots \quad (12a).$$

or body weight in g = 0.421 LB^2 in cm $^{1.447}$.

Examination of Figure 10 shows that although most of the species lie close to the regression line, some, notably species 14, 74, 78, 79 and 83 depart from it. The latter, Pelecanoides urinatrix is again atypical. Richdale (1965a) gave the mean weight of 27 eggs as 14.9 g and the mean weight of 100 adults as 124g. Thus the egg represents only 12% of the body weight, a very low figure for a petrel of that size. On the trend general among petrels the eggs would have been expected to represent about 18% of the body weight. As mentioned in the previous section, this figure for egg weight may be unsatisfactory but there may also be a real difference among birds of the Pelecanoididae: they may normally produce eggs that are smaller than those laid by other petrels of similar size. More information is needed to clarify the position in this species and in other members of the family.

The situation among the Hydrobatidae is interesting particularly in the light of the findings about the relationship of egg weight to body weight in these birds (section 7.1.).

In Figure 10 three storm-petrels - species 69, 70 and 71 - all lie close to the line whereas three others - 74, 78 and 79 - lie well below it. The former are all long-legged forms of the southern seas, the latter all short-legged forms of northern and tropical ones. Less complete data on other storm-petrels e.g. the long-legged Fregetta and Nesofregetta and the short-legged Oceanodroma tethys suggest that this separation is real and not an artifact of inadequate data.

As LB^2 is proportional to egg weight, the implication of the above differences in the relationship of LB^2 to body weight is that in the long-legged storm-petrels (Pelagodroma, Oceanites, Garrodia and Fregetta) the rate of change of egg size with body size is the same as that holding among larger members of the order whereas with the short-legged storm-petrels (Hydrobates and Oceanodroma) the relationship changes so that their egg weights bear a lower ratio to their body weights. Thus in Hydrobates pelagicus the egg amounts to 23.5% of the body weight of 28g while in the long-legged Garrodia nereis, with a body weight of 29g, the egg weight, calculated from its dimensions, represents no less than 36% of the body weight.

As the data on body weights are mainly drawn from small samples caution is needed in interpreting from them and before any firm conclusions can be drawn on the differences between the two groups of storm-petrels (segregated into separate families before the work of Lowe, 1926) better figures for body and egg weights are needed together with additional data for the remainder of the species, i.e. 72, 75, 76, 77 and 80, so that the position can be evaluated for the storm-petrels as a whole.

The plot for Macronectes, species 14, is based on only 12 determinations of egg weight so that small sample size could be important here. Otherwise, either the mean body weight is unusually high or LB^2 unusually low. However, the value for LB^2 seems to be well correlated with that for egg weight (Table V and Figure 9) and as the figures for egg weights and dimensions have been derived from different eggs it appears that egg weights at least are not atypical in respect of their dimensions. It has also been noted in section 7.2 that Macronectes lies well below the line relating body weight to egg weight (Figures 5 and 6). If this were due solely to the small sample of body weights used (5 females only) then the mean body weight would have to drop from just over 4 kg to about 2.5 kg in order to fall on to the line. It seems very doubtful if the estimated mean can be so far from the true mean since the mean weight of eight males of that species is 4.2 kg while four females and five males of the sibling M. halli average 3.6 kg and 4.4 kg respectively. Thus the divergence from the general trend may be due, not to inadequate data, but to these birds actually laying eggs that are smaller and lighter in weight than other petrels of equivalent size. This needs testing against larger samples of birds and their eggs.

Amadon (1943) plotted log LB^2 against log body weight for two dissimilar bird groups, the Emberizinae in the passeriform family Fringillidae and the American quail Odontophorinae of the Phasianidae.

Using data on body weights and dimensions for eleven species of the buntings and seven of quail he obtained linear relationships:-

$$LB^2 = 0.413 \text{ B.W.}^{0.786} \quad \text{(Emberizinae)}$$

$$LB^2 = 0.577 \text{ B.W.}^{0.669} \quad \text{(Odontophorinae)}$$

$$\text{c.f.} \quad LB^2 = 1.841 \text{ B.W.}^{0.689} \quad \text{(Procellariiformes)}$$

His formula for the Emberizinae was based on better data than that for the quail and the maximum deviations from the known egg weights given by the formula were ± 4% while even for the quail the errors in the calculated weights exceeded 10% for only one species.

Amadon concluded that such formulae have real value in calculating body weights from egg dimensions once the appropriate formula have been determined for each group and he recommended that the relationships should be investigated for other groups of birds. It is notable that whereas his formula for buntings covered a range of body weights of from only 12 to 40 g the present ones for three families of petrels covers a range of from 48 to 7800 g.

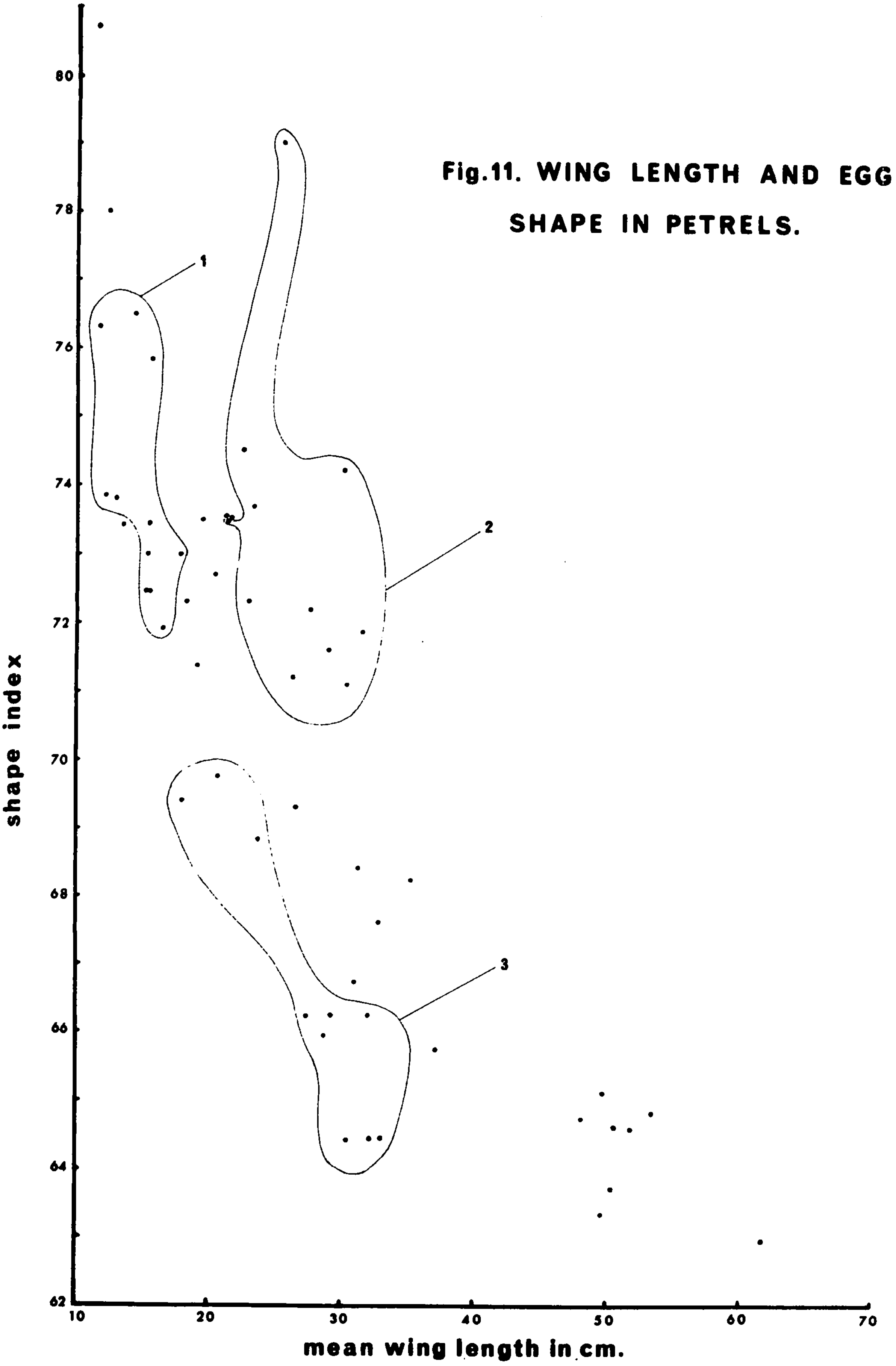
Fig.11. WING LENGTH AND EGG SHAPE IN PETRELS.
shape index
mean wing length in cm.
1
2
3
80
78
76
74
72
70
68
66
64
62
10
20
30
40
50
60
70

8. VARIATIONS OF SHAPE IN PETREL EGGS.

8.1 Egg Shape and Body Size.

As already noted, petrel eggs are usually elliptical in shape but there is a trend for small species to produce more spherical eggs than large ones. Although it is possible to represent the meridian profile of an egg accurately by mathematical formulae (Preston, 1953) the method adopted in the present study has been to use the ratio of the maximum breadth and length for calculating the "shape index" -

$$\frac{\text{breadth}}{\text{length}} \times 100.$$

This measure has some disadvantages, particularly if used to compare eggs of very different shapes, but it seems quite appropriate for comparing eggs among birds as homogeneous as the Procellariiformes.

Egg shape changes in a fairly regular manner throughout the order and is associated with body size. Figure 11 shows the relationship between female wing length and mean shape index for 55 species, where group 1 comprises the Hydrobatidae, group 2 species of Pterodroma, and group 3 species of Puffinus. The data are listed in Appendix A and only those species are plotted for which there are at least 10 measurements for both variables. The average sample contains 46 measurements for egg shape and 40 for wing length so that the considerable scatter seems likely to reflect true differences rather than to be a product of inadequate data.

The points in Figure 11 suggest an underlying curvilinear trend in shape index throughout the order. The most spherical eggs (a sphere has a shape index of 100) are laid by the Pelecanoididae, the most elongate by the Diomedidae so that whereas eggs of D. epomophora have a shape index of 62.0 those of Pelecanoides georgicus have one of 80.7. The position of the Pelecanoididae is not an artifact of their abnormally short wings: birds of this family still retain their extreme position if body weight is plotted against shape index. It is interesting to note that 100 eggs of the Little Auk Alle alle, which Verheyen (1958b) considered a relative of the diving petrels, have a mean shape index of 70.3 so that this species would lie well away from the Pelecanoididae if plotted on Figure 11. After the Pelecanoididae the next most rounded eggs (short sub-elliptical in the terminology of Palmer, 1962) - are those of the small storm-petrels Hydrobates and Oceanodroma and Pterodroma bnevirostris.

Within a genus there is a tendency for the smaller species to lay eggs having higher shape indices but the correlation is not high. Nevertheless, the points for a genus often lie together. Thus the 10 species of Puffinus (group 3) lie to the left of the main trend, that is, birds in this genus lay, on average, eggs that are more elongate than others of comparable size. Similarly the birds in the genus Pterodroma (group 2) lie to the right of the main trend because their eggs are rather more spherical than would be expected. The storm-petrels, Hydrobatidae, (group 1) also occupy a fairly discrete range and between these and Pterodroma lie the genera Pachyptila and Halobaena. The three species of Pelecanoides plotted lie in a straight line above and below the storm-petrels. The group at the lower right hand of the graph comproses the Diomedeidae with Macronectes and the rest of the fulmars with Pagodroma lie in a graded sequence to the right of Puffinus. The one plot for Bulweria places this bird close to Pterodroma and both Calonectris and Procellaria fall close to Puffinus.

The position of Pterodroma brevirostris is anomalous. A sample of 19 eggs measured on Marion Island by Rand (1954) has a mean shape index of 79.0, a figure that is extremely high for a bird of this size and quite atypical for a Pterodroma - note its high placing in group 2 of Figure 11. The only other data available ar dimensions for two eggs listed by Schönwetter (1960) which have a mean shape index of 78.1. Rand identified his eggs as those of a dark-phase form of Pterodroma mollis but it seems probable that they were really eggs of P. brevirostris (Bourne, in litt.) and they are used here on that assumption. Even were they those of P. mollis they would still plot in the same place relative to the rest of the birds in the genus as the wing lengths of those two petrels are almost the same. Little is known of the biology of P. brevirostris but it exhibits some anatomical peculiarities and the unusually spherical eggs may be connected with these. The matter is discussed further in section 8.3.4.

The variation in shape from egg to egg within a species is considerable and some idea of the range of variation involved may be gained from the following table where the species means, standard deviations and coefficients of variation are given for representative samples from different genera. The variances for the shape indices of species 43, 45, 71 and 83 have been calculated from those of the mean egg lengths and breadths given by the authorities cited using the method for estimating the variance of a general function of variables described by Davies (1949).

TABLE VII: INTRA-SPECIFIC VARIABILITY IN EGG SHAPE.

Species	No.	Shape Index	S.D.	Coeff. of var.	Authority.
1a. *D. epomophora*	48	62.07	1.79	2.88	Present study
3a. *D. cauta*	52	63.92	3.83	6.00	" "
25. *P. lessoni*	26	70.93	2.84	4.00	" "
27b. *P. neglecta*	95	71.49	3.59	5.02	" "
43a. *P. desolata*	42	73.46	3.87	5.27	Tickell, 1962.
45. *P. turtur*	100	72.28	3.39	4.69	Richdale, 1965b
54a. *C. diomedea*	46	66.33	3.72	5.62	Present study
58a. *P. carneipes*	55	65.45	4.03	6.16	" "
60. *P. griseus*	62	64.08	2.76	4.31	" "
71c. *P. marina*	100	72.42	3.14	4.34	Richdale, 1965a
83a. *P. urinatrix*	39	78.08	3.95	5.06	" "

It will be seen that, in general, the amount of variation in shape is about the same from one species to another. Why the sample for *Diomedea epomophora* shows less variability than the others is not known. All the eggs came from Campbell Island and might therefore have been expected to be rather homogeneous, but other samples in the table e.g. those for *Pterodroma neglecta* and *Pelagodroma marina* also came from a single breeding place and these seem to be no more variable than mixed samples derived from several colonies.

How does mean egg shape vary between different populations of a particular species? Suitable petrels for examining this are those cosmopolitan forms that have split into a series of faces e.g. *Puffinus puffinus*, *Puffinus assimilis*, *Pelagodroma marina* and *Oceanodroma leucorhoa*. Unfortunately a comprehensive comparison is not possible because for none of these species are adequate data available for all the populations but if a size effect on egg shape is present it must be slight as the available data in the following table show.

TABLE VIII. VARIATIONS IN EGG SHAPE BETWEEN POPULATIONS.

(Sample sizes in parenthesis)

	Wing length mm	Shape index
Puffinus puffinus		
mauretanicus	246 (10)	69.8 (23)
opisthomelas	237 (49)	67.2 (46)
puffinus	237 (20)	68.8 (100)
yelkouan	233 (21)	70.3 (100)
Puffinus assimilis		
haurakiensis	192 (16)	69.1 (7)
elegans	190 (94)	70.0 (?)
kermadecensis	190 (8)	68.9 (9)
assimilis	183 (5)	68.2 (28)
baroli	179 (15)	69.4 (55)
tunneyi	173 (25)	68.7 (13)
Pelagodroma marina		
hypoleuca	161 (20)	73.5 (25)
maoriana	158 (21)	72.4 (100)
dulciae	157 (13)	72.8 (28)

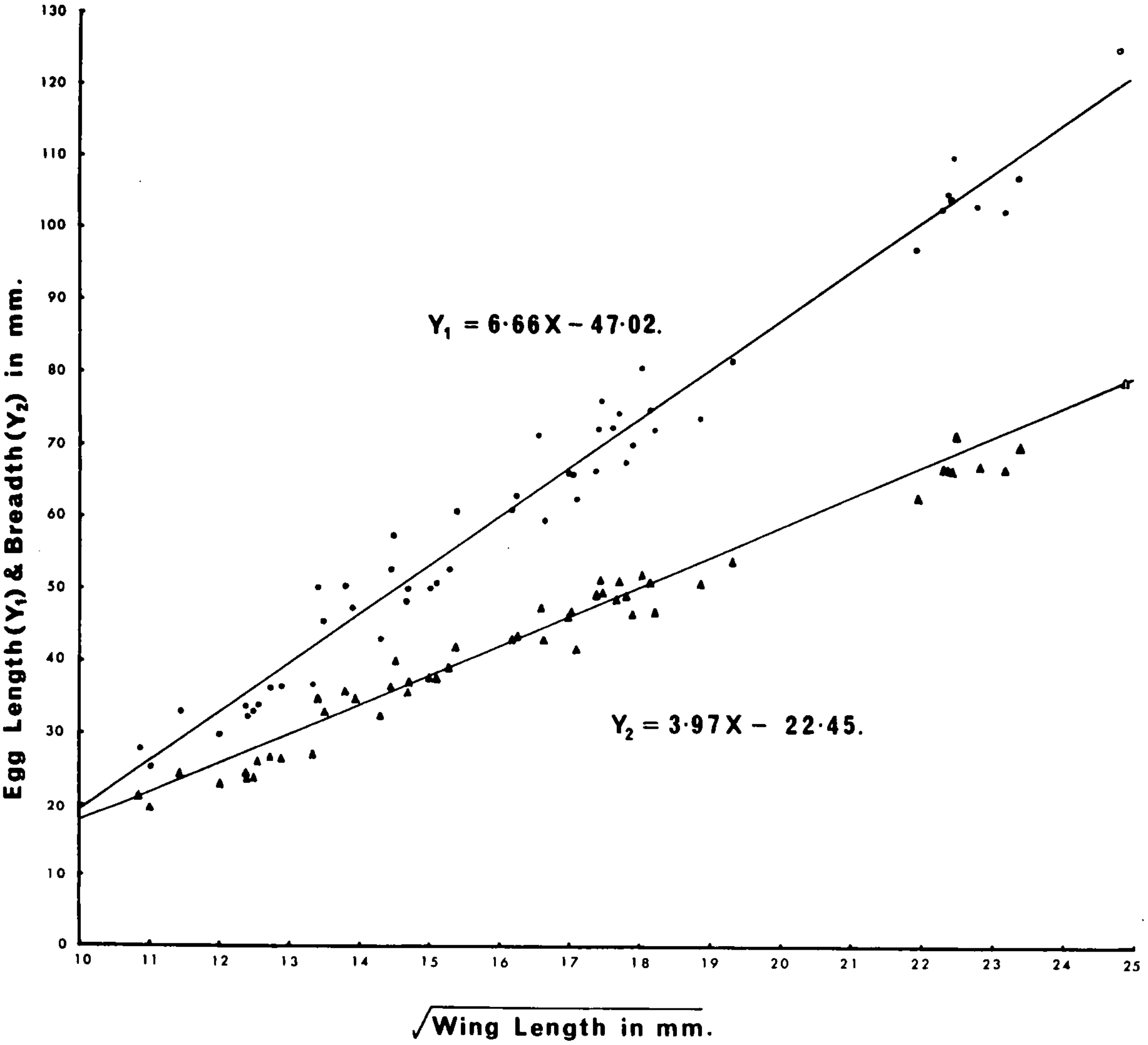

Fig.12. EGG DIMENSIONS v. $\sqrt{\text{WING LENGTH}}$ IN PETRELS.

8.2. Variations in Egg Lengths and Breadths.

To examine the variations in egg shape with body size further, the mean egg lengths and breadths from which the shape indices used in Figure 11 were derived have been plotted against female mean wing length. A curvilinear relationship was indicated which could be transformed to linearity by plotting the square roots of the wing lengths against egg lengths and breadths - Figure 12. The same 52 species are represented here as in Figure 11, except that the three Pelecanoides included in that figure have been omitted. A linear relationship is also apparent when egg dimensions and wing lengths are plotted on logarithmic axes because of the linear relationship that exists between the logarithms of egg weight and wing length (section 7.2. above).

While there is a good deal of variation about the regression lines of Figure 12, the two egg dimensions and the square roots of female mean wing lengths are highly correlated ($r_{\text{breadths}} = +0.987$; $r_{\text{lengths}} = +0.986$; $P < 0.001$ in both.
When Y_1 = mean egg length in mm, Y_2 = mean egg breadth in mm and X = square root of female mean wing length in mm, then

$$Y_1 = 6.66X - 47.02 \qquad (13)$$

and the points have a standard deviation around this line of 3.96mm.

$$Y_2 = 3.97X - 22.45 \qquad (14)$$

where the points have a standard deviation about the line of 2.44mm.

The slopes of the regression lines differ and the greater the distance between the two slopes for any particular value of wing length, the smaller the shape index.
Where the two lines cross when produced, length equals breadth and shape index = 100. The hypothetical petrel laying such an egg has $X = 9.33$ mm, i.e. a wing length of about 87 mm.

The regressions of X on Y_1 and Y_2 based on the same data are:-

$$X = 0.146\ Y_1 + 7.310 \qquad \text{(13a)}$$

or mean female wing length = 0.146 mean egg length in mm + 7.310 and the line has a standard deviation of 0.583mm.

Similarly

$$X = 0.245\ Y_2 + 5.957 \qquad \text{(14a)}$$

or mean wing length = 0.245 mean egg breadth + 5.957 and this equation has a standard deviation of 0.600mm.

If the egg lengths and breadths are plotted against wing lengths using logarithmic axes, they also fall along straight lines but as in Figure 12 the line for egg length/wing length has a steeper slope than the corresponding one for egg breadth. Egg length increases at a greater rate in passing up the size scale than does egg breadth. Thus egg shape index decreases with increasing body size because the lengths of the eggs increase at a more rapid rate than their breadths.

Within the different genera however, the relative importance of variations in lengths and breadths differs. This accounts, for instance, for the positions of birds of the genera <u>Puffinus</u> and <u>Pterodroma</u> in Figure 11. If mean egg lengths and breadths are calculated from equations 13a and 14a from their wing lengths it is found that 9 out of the 11 species of <u>Pterodroma</u> plotted in Figure 11 have egg lengths that are shorter than those predicted from the formula while egg breadths are greater than those predicted. Thus the shape indices are higher than expected for birds of their size. Both length and breadths are involved here in placing these birds to the right of the general trend in Figure 11.

The situation is different in <u>Puffinus</u>. Here both lengths and breadths are greater than given by formulae 13a and 14a but the deviations from the predicted figures for lengths are about three times those for breadths, hence these eggs are, on the whole, longer than predicted and their shape indices are lower.

The presence of such variation suggests that rather than attempt to construct general equations relating body size to egg dimensions for the whole order, it would be more profitable to do this on a generic or family basis. This does not seem worthwhile at the present time but might be feasible when better figures are available allowing tight confidence limits to be established.

In the following table, however, an attempt has been made to calculate standard wing lengths for various petrels for which good data on egg sizes exist (Appendix A) but for which published information on wing lengths are inadequate.

Column A is the calculated figure using equation 13
B " " " " " " 14
C " " " " " " 13a
D " " " " " " 14a
Sample sizes for wing lengths are in parentheses.

TABLE IX. FEMALE WING LENGTHS (mm) CALCULATED FROM EGG DIMENSIONS USING EMPIRICAL FORMULAE.

Species	A	B	C	D	Actual
1a. *D.e. epomophora*	656	638	643	626	624 (8)
2c. *D.e. dabbenena*	683	626	668	615	603 (4)
4. *D. albatrus*	599	592	588	583	550 (2)
6b. *D.m. impavida*	504	497	496	492	511 (3)
10. *D. immutabilis*	550	535	546	527	487 (5)
46. *P. belcheri*	201	208	203	210	178 (6)
51. *P. westlandica*	377	381	374	378	367 (2)
68d. *P.a. assimilis*	220	212	221	213	183 (5)

The same equation can also be used to calculate mean egg dimensions providing that adequate data are available on wing lengths. The following are some predicted dimensions for species about which little or nothing is published on their eggs:-

TABLE X. SOME PREDICTED EGG DIMENSIONS CALCULATED FROM WING LENGTHS USING EMPIRICAL FORMULAE.

Species	Wing length	Egg Dimensions	Shape Index.
3c. *Diomedea cauta*	556 (32)	110.6 x 71.5	64.6
21. *Pterodroma incerta*	321 (54)	72.3 x 48.7	67.3
32. *Pterodroma ultima*	282 (44)	64.8 x 44.2	68.2
48. *Bulweria fallax*	242 (9)	56.6 x 39.3	69.4
65. *Puffinus huttoni*	222 (17)	52.2 x 36.7	70.3
- *Oceanodroma matsudeirae*	184 (127)	43.3 x 31.4	72.5
- *O. markhami*	173 (53)	40.6 x 29.7	73.3
- *O. tristrami*	182 (130)	42.7 x 31.0	72.7

(All dimensions in mm; sample sizes in parentheses.)

8.3. Factors influencing Egg Shape in Petrels.

Whether similar trends correlating egg shape with body size occur in other bird orders has not been investigated. Suitable groups for such an examination would be the Anseriformes and Strigiformes. In the Sphenisciformes the trend is either absent or ill defined. As in the petrels, the largest penguin Aptenodytes forsteri lays the longest eggs, shape index 69.2, but the one laying the most rounded eggs, shape index 83.5, is also a large species, Pygoscelis papua. Indeed, all the Pygoscelid penguins lay eggs with higher shape indices than those of the smallest member of the order - Eudyptula minor.

In the petrels there may well be no direct causal explanation of the correlation, but it seems appropriate to consider factors that could be operating to link body size and egg shape. Perhaps the most likely are:-

1. Small petrels lay rounded eggs to conserve heat loss, this being most necessary with small eggs owing to the operation of the "surface-volume law".

2. That the increasingly elongate eggs in the bigger species is a consequence of anatomical and physiological restrictions concerned with making, transporting and laying eggs which are large in respect of the size of the bird.

3. That egg shape is a by-product of anatomical adaptations for specialised modes of flight and swimming, and particularly of the shape of the pelvis.

8.3.1.

Egg Shape and Heat Loss.

The importance of this factor can only be discussed in general terms because data are lacking on heat loss in petrel eggs.

In the domestic hen, experimental evidence shows that heat loss is proportional to surface area and unless the porosity of petrel eggs varies with their size, as is quite possible, it seems reasonable to suppose that heat loss will also be reduced in spherical as opposed to elongate eggs of the same weight which have different surface areas. However, the difference in the rate of heat loss between eggs of the same weight but of shape index 60 and shape index 80 - the range found in the Procellariiformes - would seem to be small.

Nevertheless it has been established that the eggs of these sea-birds are unusually resistant to chilling (Matthews, 1954) and this may well have survival value for eggs which are sometimes left uncovered. In the burrowing species, incubation stints are generally long, shared by both sexes, and a delay in nest relief is often followed by the on-duty partner's disappearance, presumably to feed. The egg does not necessarily suffer if the other partner arrives within a reasonable time and in temperate climates such eggs can be left uattended for several days without being killed. The situation is different with Antarctic species where the exposure of the egg in the burrow may result in freezing of the embryo in a relatively short time. In these extreme circumstances, a spherical egg, with better heat retention may be marginally better adapted to the chilling that results from perhaps quite short delays during changeovers between partners and which could readily result in nesting failure.

Rounded eggs are not specially characteristic of hole-nesters among petrels as they tend to be among land birds. Compare from Figure 11 the position of the surface-nesting fulmars with those of the burrowing shearwaters: the latter lay longer eggs than do cliff-nesting Pagodroma, Daption and Fulmarus of similar sizes while species of Pterodroma, a genus including numerous surface nesters, lay eggs that tend to be more spherical than those laid underground by similar-sized shearwaters.

Despite such theoretical considerations there seems to be no evidence that the production of eggs of high shape index is an adaptation to colder climatic conditions. On the contrary, most of the present-day species producing rounded eggs inhabit temperate regions; whether this applied also during the main radiation of the order is unknown.

8.3.2. Egg Shape and the Mechanics of Egg Production.

How and where the egg is shaped in the oviduct has been the subject of much discussion and there is no data for petrels. Romanoff and Romanoff (1949) reviewed the work done on the subject up to that date. The oviduct has an inner circular muscle and an outer longitudinal one and their operation on the plastic egg before the shell is secreted could explain most of the variations in shape but just which part of the oviduct is primarily responsible for giving the egg its final form is not clear, even in the much-studied hen. Some researchers e.g. Pearl (1909) thought that even though the egg is ovoid before reaching the "uterus" or shell gland, the muscular activity of the latter region determined its final shape. Curtis [(1914) in Needham, 1963] believed that the shape was determined continuously throughout the oviduct during and after the addition of the albumen. Bradfield (1951) suggested that as the muscles at the end of the isthmus (where the shell membranes are laid down) adjacent to the shell gland are sphincter-like, there would be a tendency for the egg, after having received its albumen in the magnum, to be squeezed to a point at its caudal end during the secretion of the shell membranes.

It has often been pointed out that the diameter of the oviduct could be important in determining the egg's final shape. A small egg passing loosely down the oviduct might retain the original spherical shape of the yolk core around which the albumen and subsequent layers are secreted. An egg passing down a tight oviduct would tend to be squeezed into an elongate shape due to the pressure of the oviduct muscles and that of the surrounding tissues and organs. This could explain why the first eggs laid by a bird on breeding for the first time are often narrower than those it lays in subsequent seasons, e.g. in the Kittiwake (Rissa tridactyla) as shown by Coulson (1963), the passage of the first clutch slackening the oviduct so that subsequent eggs are less compressed but would not explain why the last egg of a clutch tends to resemble the narrow egg laid by a young bird.

It has been shown in previous sections that in passing from small to large species in the Procellariiformes, the lengths of the distal segments of the wings increase in a negatively allometric manner. So too do their egg sizes; that is, although bigger birds lay bigger eggs, these are progressively smaller relative to the size of the birds that produce them.

The diameter of the oviduct may well change in a similar way throughout the order. Everything else being equal, if this change were exactly parallel to the change in egg size, then egg shape might remain the same, but if not, the oviduct would be either progressively tighter or looser with increasing size. Thus the decrease of shape index with size could be a consequence of the eggs being passed down oviducts where the lateral pressures from the muscles and surrounding organs were increasingly great, moulding the eggs into an increasingly elongated form. Support for this hypothesis is given by the way in which the fall in shape index with increasing body size is more a consequence of increasing length then of decreasing breadth (8.2 above).

Here the finding of Pearl and Curtis (1916) seem relevant. They noted that in the domestic fowl the smaller the egg the broader it was in proportion to its length so that dwarf eggs with small yolks tended to be spherical. They considered that one reason for this was that the oviduct, a tube with elastic walls, offered more resistance to the passage of a large than of a small body. They considered that the degree of pressure applied to the egg depended on the diameter of the cross section of the duct and on the relative tonus of the two sets of muscles in the oviduct wall. In hens there was no correlation between egg length and breadth and this led Pearl and Surface (1914) to conclude that the two sets of muscles acted independently.

The mechanics of the laying process itself may also be indirectly involved. In the hen, and in a number of other birds, the egg passes down the oviduct with its pointed end leading (i.e. caudal) but it is nevertheless laid blunt end first (Ernst, 1885 and other references in Needham, 1963). Bradfield (1951) using radiography, has shown that in the hen the egg enters the shell gland pointed end caudal where it lies high up in the pelvic cavity and close to the vertebral column. When the shell has been deposited the egg is lowered until clear of the pubes and swung through 180° in the horizontal plane. It is then raised again, this time with the blunt end caudal, and is laid ~~down~~ from this position about an hour later.

Whether rotation occurs before egg laying with petrels is not recorded and although egg collectors in the past often expressed eggs from petrels that were ready to lay, they have not recorded whether the eggs were delivered blunt end first. It may be that their elliptical shape makes rotation unnecessary, though why this occurs in the hen has not been adequately explained. However, if rotation is necessary, it would be in the smaller species where the egg is relatively huge 20 to 25% of the body weight - that rotation might be most difficult, if only on account of the sheer size of the object to be moved. A spherical egg would then be advantageous because its relative shortness would not only require less lowering to clear the ischia and pubes (and although the pelvis is deeper in the smaller species it is also more open caudally) but less energy would also be involved in turning such an egg in the oviduct.

8.3.3. Egg Shape and Pelvis Shape.

Nicholsky (1893) suggested that birds laying round eggs usually maintain a vertical posture in which the weight of the egg counteracts the pressure of the walls of the ovary and that those which lay oval eggs usually maintain a horizontal posture during which the weight of the egg "assists the pressure of the ovary". Rensch (1947) pointed out that this trend was also associated with the shape of the pelvis; birds like owls, buzzards and kingfishers that lay near-spherical eggs and maintain vertical postures also have deep pelves. In contrast, birds like grebes and geese, that lay elongate eggs, have shallower pelves and a horizontal carriage.

The connection between posture and pelvic shape in petrels is almost the reverse of that described by Rensch. Here the species that have the most upright posture, the albatrosses and giant petrels, have rather elongated pelves whereas the birds that have the most horizontal carriages tend to have deep pelves that are also very wide and open caudally.

On the other hand the connection between pelvis shape and egg shape in the Procellariiformes agrees with that of Rensch's examples; the petrels that lay the most spherical eggs also have the deepest pelves and vice versa.

The condition of the pelvis has been examined in 27 species from all the four families of the order. Skeletal material in the

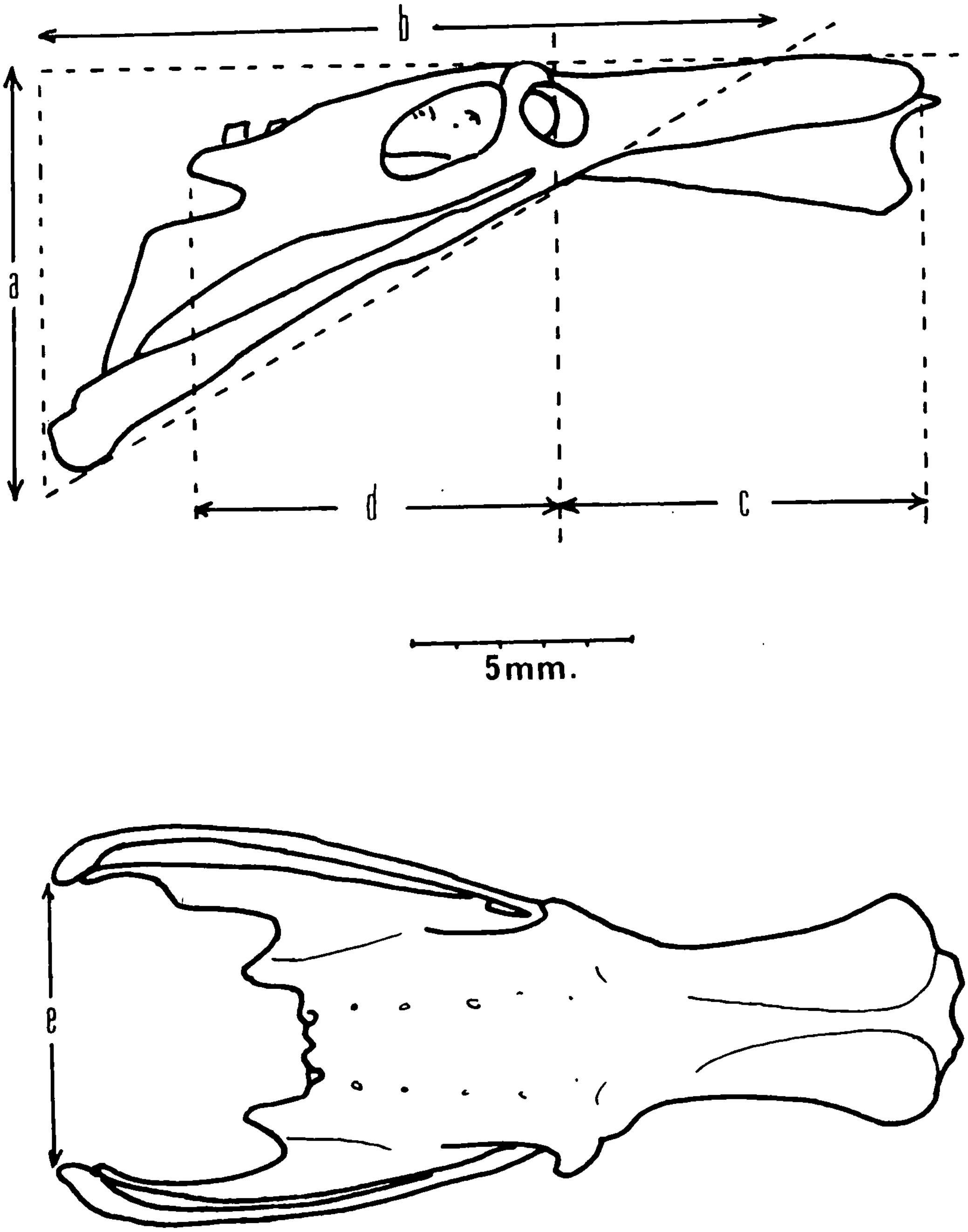

Fig.13. Pelvis of *Diomedea exulans* in lateral & dorsal view showing method of measuring pelvic depth and lateral spread, and position of the acetabulum.

British Museum (Natural History) and the Canterbury Museum has been measured and published diagrams by Milne-Edwards, (1867-68); Forbes (1882); Mayaud (1932) and Kuroda (1954, 1955) have also been utilised.

Figure 13 shows the dimensions that have been measured. Thus a/b has been taken as an index of the depth of the pelvis and e/b as an index of its width and lateral spread. The higher the value of e/b the greater the spread of the pubes and distal portions of the ischia.

The data are not derived from large samples and there is a considerable amount of variation between skeletons of the same species. This is partly due to natural variation but also to distortion of the skeletons during and after their preparation. Another source of error arise from the fact that much of the data is from unsexed skeletons.
How much sexual dimorphism there is in the size of the pelvis in petrels is not clear, but this could be relevant in groups like the fulmars where the sexes are of different sizes.

The data are given in Table XI and in Figure 14 the depths and spreads of the pelves are plotted against the mean shape indices.

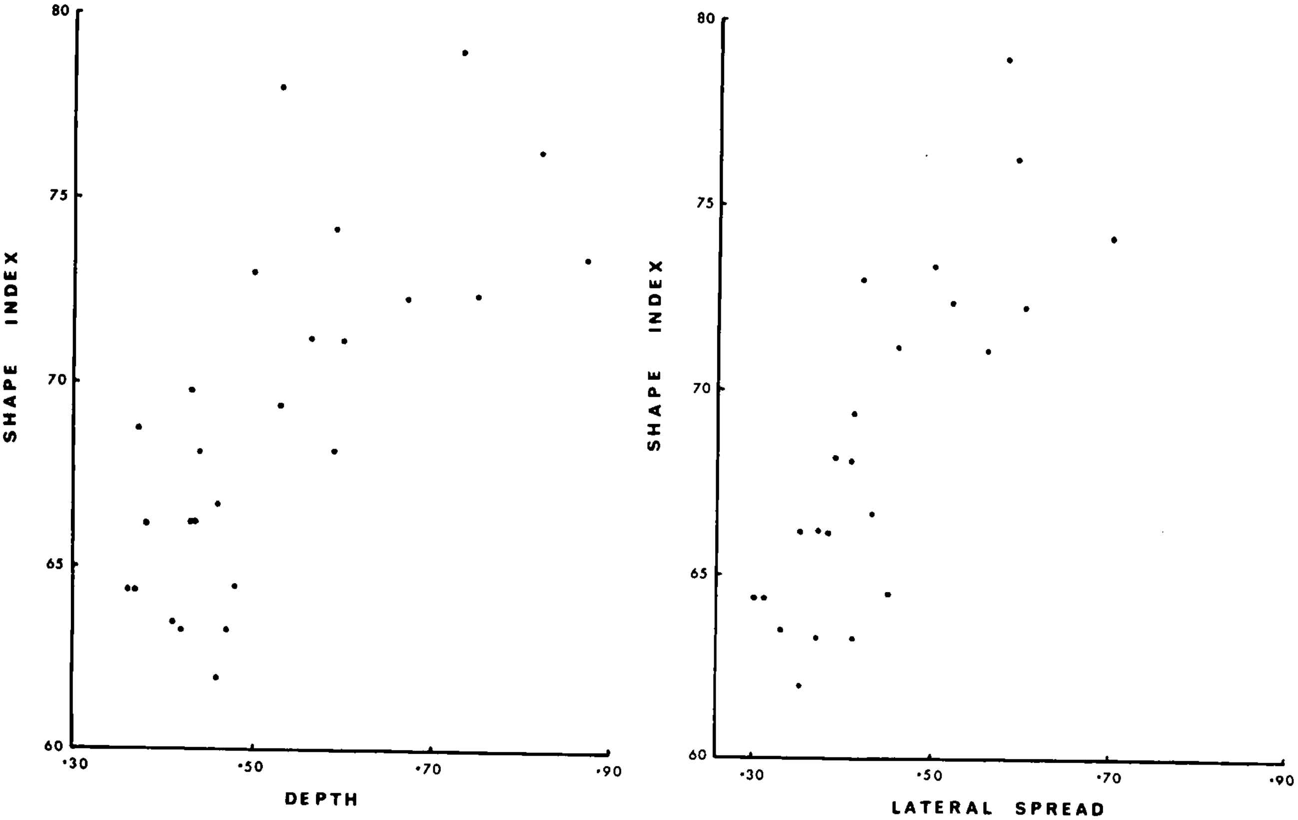

Fig.14. PELVIS SHAPE & EGG SHAPE IN PETRELS.

TABLE XI. PELVIC ANGLES OF PETRELS.

Species		No. in Sample	Depth (a/b)	Lateral spread (e/b)	Egg Shape index.
1a	*D. epomophora*	4	0.46	0.35	62.0
3a	*D.c. cauta*	4	0.42	0.37	63.3
10	*D. immutabilis*	1	0.41	0.33	63.5
14	*M. giganteus*	5	0.47	0.41	63.3
17	*F.g. rodgersi*	1	0.44	0.41	68.1
25	*P. lessoni*	1	0.60	0.56	71.1
26	*P. solandri*	1	0.59	0.70	74.2
33	*P. inexpectata*	3	0.66	0.46	71.2
34	*P. brevirostris*	1	0.73	0.58	79.0
45	*P. turtur*	4	0.67	0.60	72.8
50	*P. aequinoctialis*	1	0.43	-	65.8
51	*P. westlandica*	2	0.46	0.43	66.7
54a	*C.d. borealis*	1	0.59	0.39	68.2
55	*C. leucomelas*	2	0.48	0.45	64.5
57	*P. gravis*	1	0.36	0.31	64.4
58	*P. carneipes*	2	0.43	0.35	66.2
59b	*P.p.chlororhynchos*	1	0.43	0.38	66.2
60	*P. griseus*	6	0.37	0.30	64.4
62	*P. tenuirostris*	6	0.38	0.37	66.2
64b	*P.p. puffinus*	1	0.37	-	68.8
64c	*P.o. mauretanicus*	1	0.43	-	69.8
68e	*P.a. baroli*	1	0.53	0.41	69.4
71c	*P.m. maoriana*	4	0.75	0.52	72.4
74	*H. pelagicus*	1	0.82	0.59	76.3
78a	*P.l. leucorhoa*	1	0.87	0.50	73.4
79b	*O.c. castro*	1	0.50	0.42	73.0
83a	*P.u. chathamensis*	3	0.53	-	78.0

Despite a wide scatter to the points, pelvis depth and breadth are correlated with shape index (r = +0.731 and + 0.820 respectively; $P < .001$ in both instances). That is, species laying the most spherical eggs have generally deeper pelves which are spread more widely caudally, whereas those laying elongate eggs mostly have shallow pelves which are also narrow caudally.

The trend is not wholly consistent. Although the birds that lay the eggs with the lowest shape indices have shallow and narrow pelves, these are neither as shallow or as narrow as those of certain medium-sized petrels of the genus Puffinus, notably gravis, tenuirostris, griseus and puffinus. These are all birds whose egg lengths place them along the upper limit for wing length in Figure 12; they have unusually long legs with low shape indices for birds of their sizes.

Kuroda (1952) correlated the form of the pelvis in petrels, and particularly in the shearwaters, with their modes of life. He showed that the shearwaters with long narrow pelves are those that actively swim and dive for food. These have a long postacetabular ilium to act as attachment for the large muscles needed to provide a powerful back stroke for the feet. These aquatic forms include P. griseus, P. tenuirostris and P. puffinus. At the other end of the range are shearwaters having relatively short and broad pelves and short post-acetabular ilia. These birds are highly aerial, seldom dive when feeding, and show adaptations in the arm bones and elsewhere for a primarily aerial life. This category is best exemplified by Calonectris.

Kuroda has two intermediate categories (a) the partially aquatic shearwaters pacificus and gravis with long narrow pelves and long post-acetabular ilia but better adapted to gliding and sailing than the griseus-tenuirostris group and (b) an intermediate group, particularly carneipes, whose pelvis is fairly narrow but whose post-acetabular ilium has proportions intermediate between the aquatic and aerial condition.

Bearing in mind that both Kuroda's and my data are often based on small samples, his categories fit in quite well with the egg shape - pelvis shape relationships shown in Figure 14. The most aquatic species, griseus, tenuirostris and puffinus all have low shape indices in respect of wing length and pelvis depth, and to a lesser extent, pelvis breadth. The partially aquatic and intermediate species have slightly higher shape indices in relation to wing length and pelvis shape while Calonectris has still higher shape indices relative to these variables.

Thus it would seem to be a reasonable hypothesis that egg shape in shearwaters is associated with the shape of the pelves which in turn have been modified during evolution to fit the birds for an aquatic, aerial or intermediate mode of life at sea.

In the small storm-petrels and prions the advantage of a deep and open pelvis is not clear and examination of further material seems to be required, but the condition may be associated with the need for giving wide attachments to the leg and tail muscles particularly in the long-legged species. These use their feet to fend off the water when "walking on the waves" during feeding and their tails, capable of rapid twistings, are clearly of value when making the erratic, dancing actions involved in snatching small food items from the surface of the sea. In addition, the deep pelvis may help in providing a wide fastening for muscles of the ventral body wall supporting the viscera and particularly the huge egg which may have to be held there for some time before laying.

Why albatrosses and giant petrels have shallow pelves is again not clear. For both these groups walking is important, so that good movements of pronation of the legs are required. Although they can swim well, they seldom submerge deeply nor do they burrow, so that the very strong retractors found in the burrowing and diving species would not be necessary. Furthermore their tails are short and apart from Phoebetria little used for steering. Thus the more generalised form of pelvis may reflect the more generalised function-

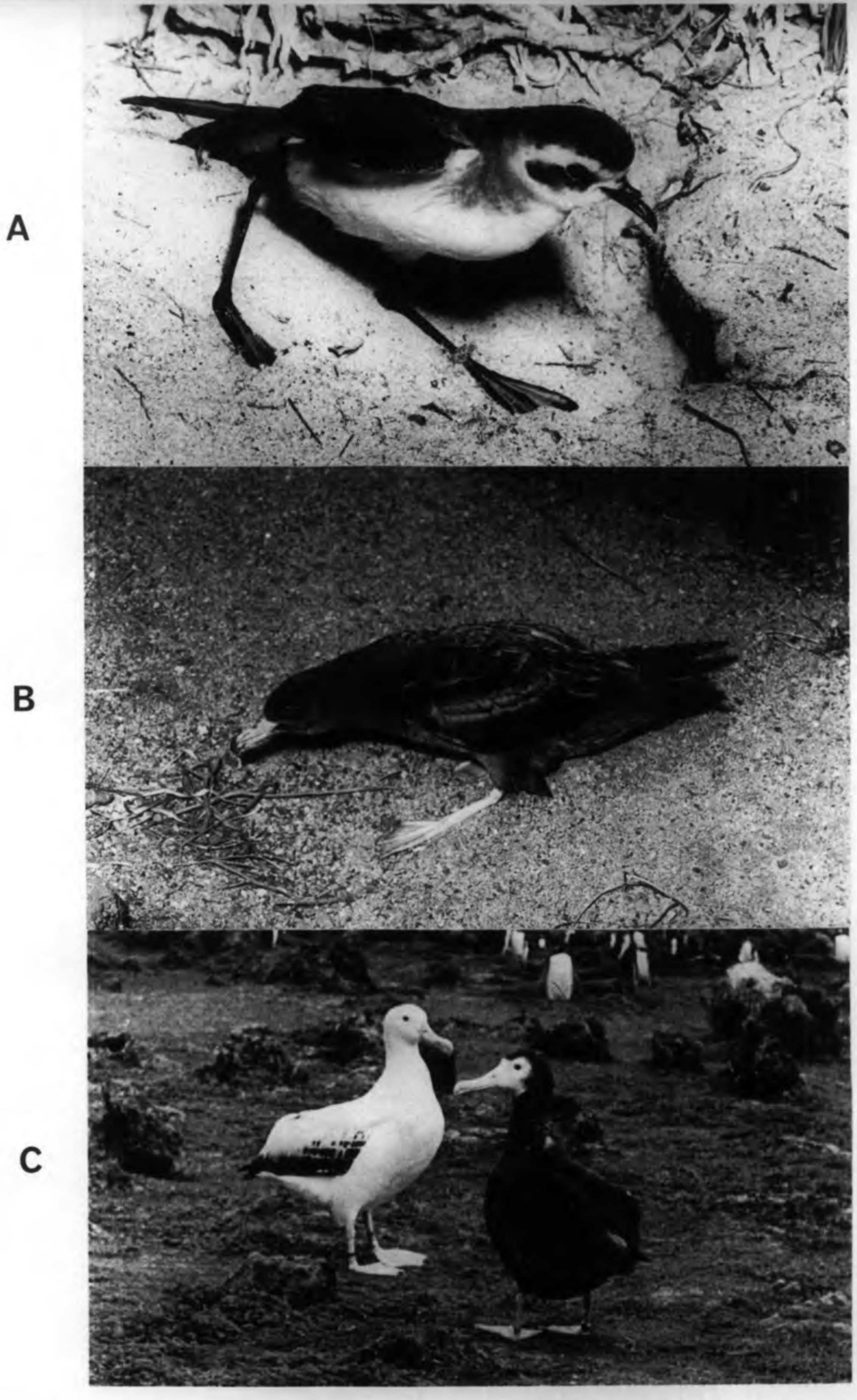

Fig. 15. THE STANCES OF PETRELS.

A–*Pelagodroma marina* walking. B–*Puffinus carneipes* walking. C–*Diomedea exulans* standing.

ing of the legs in these birds.

The relationship between pelvis shape and egg shape in *Pterodroma brevirostris* is particularly interesting. For a *Pterodroma* the shape index is very high but so too is the pelvic depth and the lateral spread of the pubes and ischia. The data do not plot atypically in Figure 14. Not only the pelvic girdle is unusual. The sternum is short, very deeply keeled and deeply notched anteriorly, while the hypapophyses of the dorsal vertebrae are very long, compared with *P. inexpectata* and *P. solandri* (figured by Kuroda, 1955) though no longer than those of *P. macroptera* (pers. observations). The hypapophyses are bigger even than in *Puffinus tenuirostris* and *P. griseus*. If Kuroda's reasoning is correct, this should reflect a diving mode of life in this species.

The larger petrels are usually better adapted for walking whereas the smaller ones either flutter across the ground often resting on the tarsi - the pattern with storm-petrels and diving petrels - or they shuffle along in a rather duck-like fashion and in a highly unstable manner with their wings folded but raised and often outspread as if to improve their balance (Figure 15).
This is the usual pattern with shearwaters. The large albatrosses, on the other hand, can stand erect for considerable periods, an ability they share only with the giant fulmars of the genus *Macronectes*. The smaller fulmars, while able to stand, do not remain standing for long, but soon subside onto their tarsi. With albatrosses the erect posture is usually restricted to standing or "marking time" during displays; when moving directionally they adopt a more horizontal posture. *Macronectes* can move quite fast without doing that. The species best adapted to walking are those spending the greatest length of time ashore and *Macronectes* is the only Procellariiform bird that feeds on land.

Owen (1866) pointed out that walking and perching birds usually have short and broad pelves which provide broad bases for the legs. It might therefore be expected that the width of the pelvis at the acetabulae would be proportionally greater in albatrosses and giant petrels than in smaller species but this is not so in the range of material examined during the present study. Nevertheless, in view of the lack of mobility of the femur, the distance apart of the legs and feet may be controlled not so much by the distance apart of the hip joints i.e. the pelvis width, but in the distance apart of the knees. The latter may be relatively greater in large species because the femora are more outwardly directed to clear the short wide rib cage than applies in some of the smaller birds such as the shearwaters where the rib cage is narrower.

The postures of petrels on land are affected by a variety of factors. For stability the centre of gravity must lie behind the toes and is dependent on the relative lengths of the leg bones, the movements of which these are capable, the position of the acetabulum on which the body is pivoted and other factors like the thickness and strength of the leg bones. The general shape of the skeleton as it affects the underslinging of the viscera may also be important.

A dead petrel's legs are usually stretched back stiffly to lie along-side the tail while the femora are pulled down until they are at right angles to the body axis. This is a consequence of the greater strength of the leg retractors to that of the protractors. This applies to the dead <u>Pachyptila turtur</u> but in life the movements of this bird's femora are far more restricted. They are directed forwards but can move downwards only through about 10 degrees in the sagittal plane. Very little adduction or abduction is possible. The tibio-tarsi have greater mobility and can be brought forward until at about 90 degrees to the long axis of the body, but because of the short femur and the placing of the acetabulae rather to the rear of the pelvic girdle, the legs are in effect pivoted well back towards the caudal end of the body. Pachyptila turtur cannot therefore stand erect with its tibio-tarsi and tarsi-metatarsi in line without falling forward. Instead it adopts a squatting position and rests on its tarsi as an extension of the webbed feet. This and other prions cannot adopt an erect posture like that figured for P. vittata by Milne-Edwards, (1867-68), plate 50.

The situation in other petrels has not been examined but the importance of the lengths of the leg bones in determining posture are particularly evident in the long-legged genera of storm-petrels like Pelagodroma (Figure 15). Here the femur is very short but the tibio-tarsus very long. The ratio of femur:tibia:tarsus:mid-toe and claw is 1.0:3.4:2.3:2.1. This may be compared with, for instance, the gull Larus hautlaubi (1.0:2.0:1.0:0.9), which stands erect with its legs at right angles to the body axis or Pachyptila turtur where the ratios are 1.0:2.4:1.5:1.8. If the femur has as little freedom of movement in Pelagodroma as in Pachyptila, then its crouching posture is understandable. The legs are placed so far back that the tibiae and tarsi need to be flexed to swing the centre of gravity behind the toes.

In albatrosses the femora are relatively long and the post-acetabula ilia fairly short so that the leg as a whole occupies a rather forward position relative to the trunk. In D. epomophora the leg element ratios are 1.0:2.1:1.1:1.5 (c.f. those of the gull above). Other factors may also be involved in giving the increased stability on lamd such as the large webbed feet and the thick legs; the carriage is rather goose-like, as shown in Figure 15.

If there is a causal connection between pelvis shape in petrels and their postures on land, the nature of this connection is not clear.

It seems likely that the variations in proportions of the pelvic bones are part of a range of modifications to a basic structure to fit the birds for different modes of life. At the one extreme are small forms well adapted for life at sea, almost incapable of walking on land but able to dig burrows there using motions rather similar to those employed when swimming; at the other extreme are large forms adapted to sailing in the air and swimming on the surface of the sea and to a life ashore there they breed and move about freely but do not burrow.

Variations in pelvis shape may in turn have influenced the shape of the eggs but how could this be brought about? Rensch (1947) stated that the pelvic cavity was involved but did not elaborate. However it seems possible that the egg before acquiring its hard shell could be moulded by the ventral part of the pelvic girdle. Bradfield (1951) found that a "membraneous" egg removed from the oviduct when the shell membranes had been secreted and held together only by these, is shaped similarly to other eggs laid by the same fowl so that the factors affecting egg shape in the hen apparently operate during or before the egg reaches the isthmus. As already mentioned, Bradfield thought that an important factor was the muscle at the end of the isthmus next to the shell gland which is somewhat sphincter-like and could shape the caudal end of the egg at this stage. The hen's egg remains in this part of the oviduct for about an hour whereas it remains in the adjacent shell gland for about 20 hours during the first part of which the egg undergoes a 25% increase in volume probably due to the uptake of water by the albumen.

If the shape of the egg is given a final adjustment while lying in the pelvic cavity, this must occur during or after the final swelling. It is not clear if while in the isthmus the egg is far

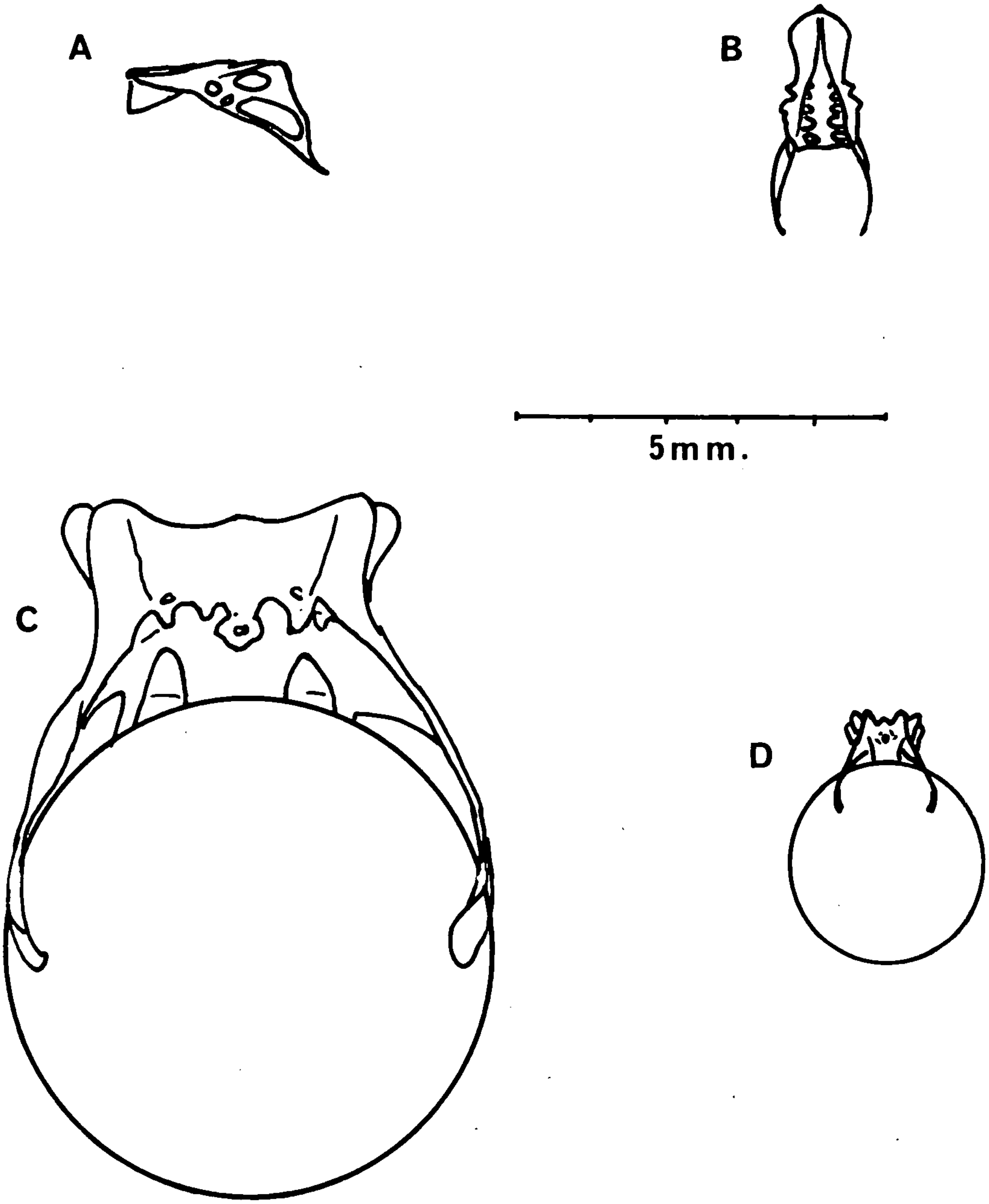

Fig. 16. Pelves of *Pelagodroma marina* in lateral and dorsal view (A & B).

Pelves of *Diomedea cauta* & *P. marina* in caudal view in relation to the breadths of their eggs (C & D).

enough caudal to experience pressure from the pelvis but if the process in petrels is similar to that in the domestic hen, it certainly could be affected during its first hours in the shell gland when the egg is pressed up against the curved ventral region of the sacrum and between the pubes.

Figure 16 attempts to relate the size of the egg to the size of the pelvis in two examples at the extremes of the size range. In C the diagram shows how the egg of an albatross can fit into the pelvic cavity. It is embraced for much of its girth by the arms of the pubes. That the pelvis may be involved in shaping the egg seems feasible here but as the egg is symmetrical, it would seem necessary that it should be rolled on its long axis during the shaping process perhaps concurrently with the swelling. According to Greenwood (1964) the twisted chalazae are formed during rotation of the egg in the shell gland.

In contrast, in the small species like the storm-petrel figured in 16 a, b and d, the egg is so large compared with the pelvic girdle that it is difficult to see how this part of the skeleton could influence the forming egg. But while the posterior arms of the pelvis are relatively stiff in skeletal preparations they are not so in life or in specimens preserved in spirit. Here they are flexible and readily pressed open. Thus they could conceivably be involved in moulding the egg even in these small forms, though this seems less likely than in the large ones.

Whether the pelvis is directly involved in shaping the eggs of petrels or whether these have already attained their final shapes before reaching the pelvic cavity cannot be determined on the present evidence. It may be that the pelvis only has an effect with the larger species and that in the small ones the initial,

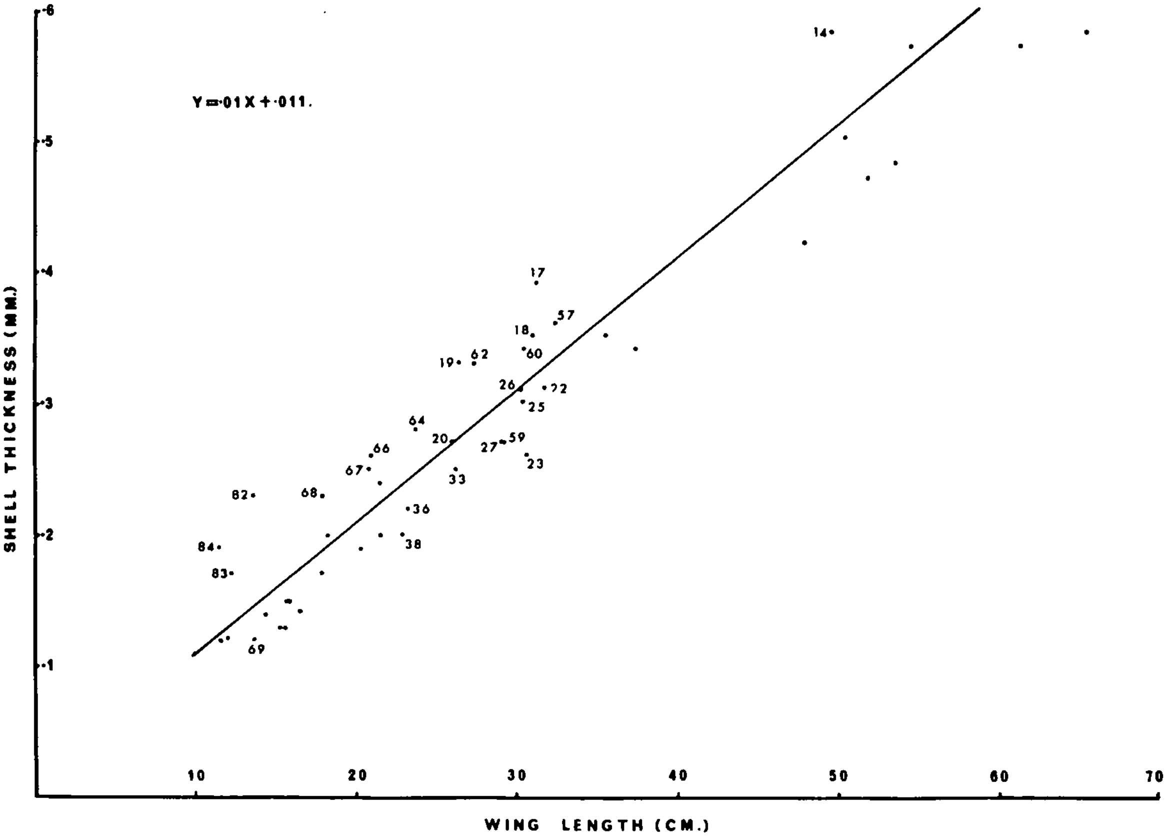

Fig. 17. SHELL THICKNESS v. WING LENGTH IN PETRELS.

TABLE XII: STANDARD WING LENGTHS (cm) AND SHELL THICKNESSES (mm) IN PETRELS.

Species	Mean Wing Length	Shell Thickness	Shell Wt. / Egg Wt. %
1b	61.6	.57	7.8
2b	65.7	.58	8.0
5	54.7	.57	8.9
8	50.6	.50	7.7
11	48.0	.42	7.5
12	53.7	.48	7.9
14	49.8	.58	9.3
17a	31.3	.39	8.3
18	31.0	.35	7.5
19a	26.4	.33	8.5
20	26.0	.27	7.2
22a	31.7	.31	7.1
23b	30.6	.26	5.9
25	30.3	.30	6.3
26	30.2	.31	6.9
27b	29.0	.27	6.2
33	26.2	.25	6.6
36	23.3	.22	5.8
38a	22.9	.20	5.8
41	21.6	.20	5.9
42a	21.4	.24	7.1
43a	19.2	.23	6.7
45	18.2	.20	6.4
49	20.3	.19	6.5
50	37.3	.34	6.9
54a	35.5	.35	7.5
57	32.4	.36	7.5
59b	29.2	.27	6.9
60	30.4	.34	7.2
62	27.4	.33	7.6
64b	23.7	.28	7.4
66	20.9	.26	7.1
67a	20.8	.25	7.5
68e	17.9	.23	7.1
69b	13.7	.12	5.5
71c	15.8	.15	6.0
72	16.5	.14	5.7
74	11.7	.12	5.7
75	12.1	.12	6.7
76	17.8	.17	6.4
77	15.7	.15	6.0
78a	15.6	.13	5.5
79b	15.3	.13	5.5
80	14.4	.14	6.3
82	13.6	.23	7.1
83a	12.3	.17	6.8
84	11.4	.19	6.5

9. VARIATIONS IN SHELL THICKNESS AMONG PETREL EGGS.

Schönwetter (loc.cit) listed the thicknesses of the eggshells for most species of Tubinares and in Table XII his data are given together with the mean female wing lengths. The latter are taken from Appendix A except for those for species 2b, Diomedea exulans chionoptera, which are from Tickell (in litt). There is a close correlation between shell thickness and standard wing length ($r = +0.963$; $P < .001$) and when the data are plotted (Figure 17) it will be seen that they suggest the existence of a linear relationship between the two variables, at least for small to medium-sized species. The points for the large species show a considerable scatter and more data would be required to show whether the relationship continues to be linear at this end of the size range. On the assumption that it is and omitting the three species of Pelecanoides, the relationship between the 44 remaining species is given by:-

$$Y = .011 + .01X \qquad (15)$$

where Y = shell thickness in mm, and X = female wing length in cm. A study of Figure 17 shows that:-

1. The Pelecanoides, species 82, 83a and 84, lie rather away from the plots for other petrels in the same size range. This is a consequence of their unusually short wing lengths: as will be shown below, their shell thickness are similar with those of other petrel eggs of similar size.
2. The shearwaters, Puffinus, species 57, 60, 62, 64, 66, 67 and 68, are plot above the trend line except 59 i.e. they have thicker shells than other petrels of similar wing lengths. The reverse is true of the gadfly petrels, Pterodroma, species 22, 23, 27, 33, 36 and 38 except 25 and 26 which lie on the line: they have slightly thinner shells than other petrels of similar wing lengths. These differences are borne out by the ratios of shell weight to egg weight in column 4 of the table. For Puffinus these ratios range from 6.9 to 7.5% whereas for Pterodroma they lie between 5.8 and 7.1%.

It is difficult to see how these differences can be adaptive. Birds of both genera normally lay on soil either on the surface (many Pterodroma and some Puffinus species) or underground (many Puffinus species and some Pterodromas) and shells of similar thickness and therefore strengths would seem to be required. However, it has been shown (Section 6.2) that shearwater eggs tend to be rather long and thin whereas gadfly petrels lay more spherical eggs. Egg shape and shell thickness may thus be causally linked. If, for example, the egg in the shell gland of a shearwater experiences greater pressure than does the egg of a Pterodroma then the calcium secretory cells may be stimulated to produce more shell material while the forming egg itself is experiencing greater compression. Thus a thicker shell could become associated with a more elongate egg. A similar reasoning might explain the increase in shell thickness with increasing size throughout the order, as the bigger birds lay longer eggs (Figure 11 above). Furthermore Bourne (in litt) points out that the shape of a shearwater egg might be affected by increased pressure generated during swimming at the time of formation of the egg in these aquatic species as contrasted with the situation in the more aerial gadfly petrels.

It seems unlikely that these variations in shell thickness are concerned with permeability to water though they may have some effect on the passage of carbon dioxide and oxygen to and from the embryo. The shearwaters with their thicker shells lay mostly underground where the humid conditions in the burrows would appear to decrease moisture loss through the shell pores compared with that experienced by eggs laid on the surface.

3. Three of the fulmars, Macronectes, Fulmarus and Daption, species 14, 17a and 19a, show the greatest deviations from the trend line. Their shells are unusually thick. The data for Thalassoica, species 18, are inadequate, being based on only one egg. Pagodroma, species 20, however, shows no divergence from the norm in respect of shell thickness.

Fulmars are surface nesters, often laying on hard rocky ledges lacking soft nesting material for cushioning their eggs. Macronectes, whose eggs have the thickest shells of any petrel, often nests in shallow pits on the ground but may also lay among rocks. The value of a thick eggshell here could be in giving the egg greater strength, a requirement that is necessary with fulmars breeding on hard substrates but unnecessary for other large species of petrels like the albatrosses as their eggs are cradled in peat or earthen cups whose shapes make it difficult for the birds inadvertently to apply their whole weight to the egg.

There are no data on shell strengths for petrels but Romanoff (1929) established a direct relationship between breaking strength and shell thickness in the domestic hen. Furthermore he also found that the breaking strength of the shell was lower when pressure was applied along the short axis of an egg than when applied along the long axis. Thus the elongate egg of Macronectes giganteus, shape index 63, would be more easily broken than the more rounded eggs of the smaller fulmars, shape indices 67-71, and would accordingly need greater strengthening.

The greater body weights of the larger species have also to be considered here. Egg breakage is one cause of nesting failure and while some losses arise through eggs rolling out of nests on steep hillsides, more often the pressure that causes breakage arises through the birds themselves. An albatross that accidentally allows its foot to rest on the egg and transfers its weight to that foot, squashes the egg immediately, at least if the egg is at an early stage of development and the viscosity of its contents low. Such accidents are likely to arise in the colonies during intraspecific disputes. The larger the species the greater the danger from such accidents for even if the strength of petrel shells per unit thickness is not uniform throughout the order it seems most unlikely that the larger birds have eggs constructed of materials so much stronger than the small ones as to offset the differences in body weight e.g.:-

Hydrobates pelagicus,	body weight 28g;	shell thickness 0.12mm.
Puffinus puffinus,	body weight 406g;	shell thickness 0.28mm.
Diomedea exulans,	body weight 7270g;	shell thickness 0.58mm.

It would be useful to have further data for Thalassoica and some for Fulmarus glacialoides to see whether these cliff-nesting petrels also lay thick-shelled eggs. Pagodroma also nests among rocks and the apparent exception as regards shell thickness here is perhaps surprising. This may be a consequence of its low body weight, but fresh determinations of shell thickness would seem desirable here. It is interesting to note that Kartaschew (1960, cited by Kuroda, 1963) states that the egg shells of the auk Uria aalge are thicker in those

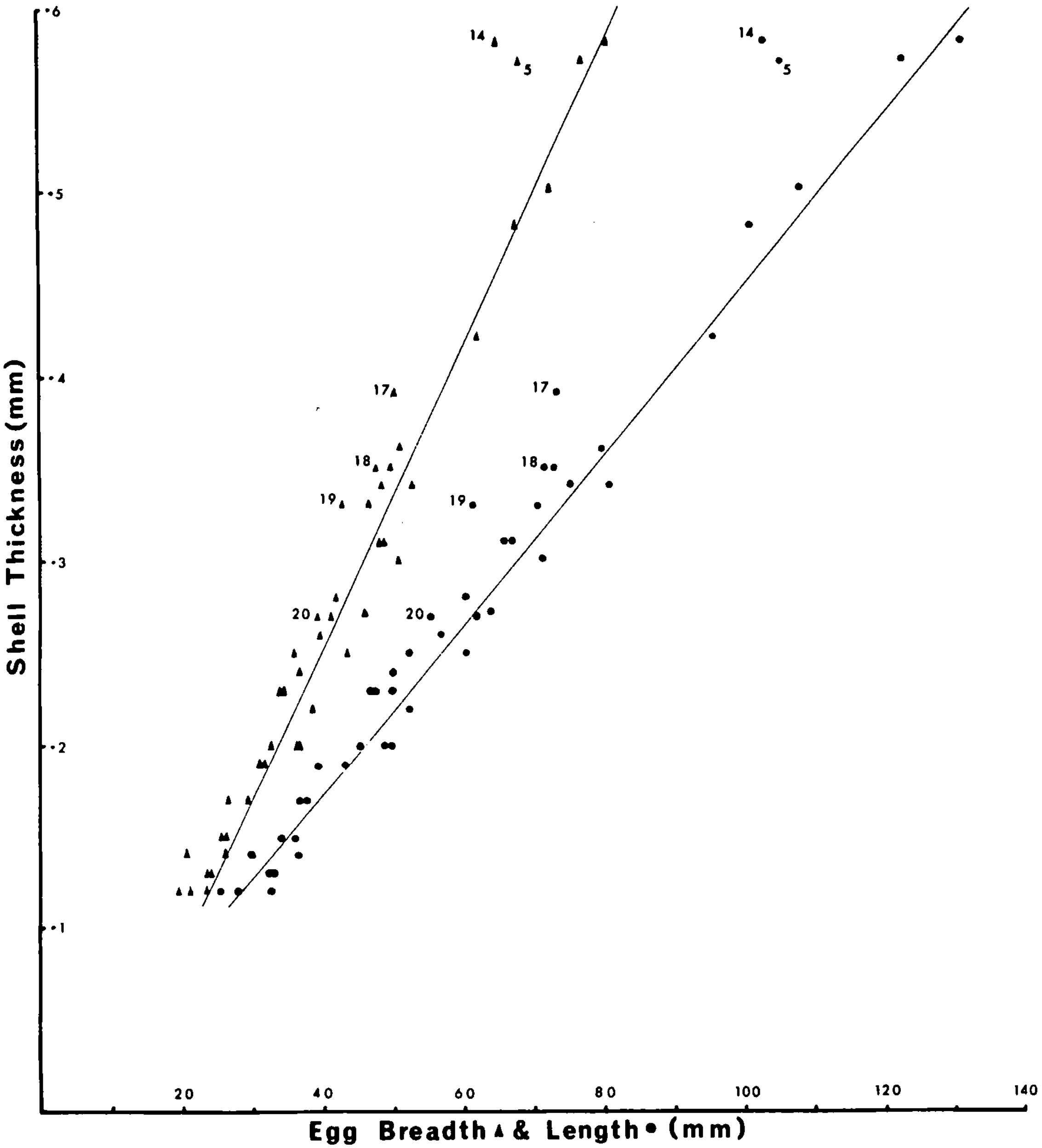

FIG.18. SHELL THICKNESS & EGG DIMENSIONS IN PETRELS.

populations nesting on rough rocky substrates than in those that nest on smooth rocky substrates.

Thick shelled eggs must also be better insulated against heat loss than thin shelled ones of the same size, shape and composition and Belopol'skii (1961) considered the thick calcium layer in the shell of the Northern Fulmar to be an adaptation to breeding at sub-zero temperatures. As fulmars are primarily polar species, this reasoning could apply generally to these birds, the obvious anomaly being Pagodroma which breeds in colder conditions than any other fulmar, suffers considerable nesting losses through the cold (Brown, 1966), and yet appears to have an eggshell no thicker than other petrels of the same size. Oceanites oceanicus, (species 69) the most southerly breeding burrowing petrel, also lays an egg that is not abnormally thick-shelled; indeed, like most of the storm petrels, the plots for shell thickness in Figure 17 lie below the trend line, rather than above it.

In Figure 18 shell thicknesses have been plotted against egg lengths and breadths for the species in Table XII. It will be seen that the relationships between these variables and shell thickness are linear. The Pelecanoididae now plot in accordance with the other petrels but again the fulmars, species 14, 17a, 18 and 19a tend to lie off the trend lines because of their thick shells. Diomedea irrorata, species 5, also seems to lay a thick-shelled egg. Perhaps this too is an adaptation to counter increased risk of breakage for this is a ground nesting albatross which lays on a rocky substrate (Loomis, 1918).

10. THE CAPACITIES OF PETREL EGGS.

The shell of an egg is not an inert container for the developing chick but becomes increasingly permeable to carbon dioxide as incubation proceeds and contributes calcium to the embryo during the ossification of cartilage. Nevertheless, in the hen, the shell loses only about 6% of its initial dry weight during incubation (Tangl and Hammerschlag, 1908) so that measurements of the contents of the egg seem more appropriate than weights of intact eggs when comparing the rates of development between species.

The weights of the egg contents are readily obtained by subtraction of the shell weights from the total weights of fresh eggs but, as has been pointed out, much of the data on weights is derived from eggs that were not known to be new-laid or that were tested for this by flotation or other means. The sample means are therefore underestimates of the true means for the populations concerned. Egg capacities or internal volumes are, on the other hand, readily measured in the laboratory from intact eggshells. This has been done in the course of the present study for samples of eggs from 36 petrel species or sub-species by running alcohol into their shells from a burette. To ensure that air was not trapped between fragments of membrane, the egg was shaken vigorously with a finger over the opening, when about two thirds full of alcohol. Successive measurements of the same eggs gave readings not varying by more than ± 0.2 ml.

Rather than use the means of the capacities so obtained it was thought better to estimate the capacity of the hypothetical mean-sized egg for each species and sub-species, i.e. of eggs having the mean dimensions listed in Appendix A.

The method used was that of Coulson (1963) which is based on modifying the equation of an ellipsoid:-

$$V = \frac{4}{3}\pi . \frac{B}{2}^2 . \frac{L}{2} \qquad \text{or} \quad V = 0.5236B^2L$$

by a correction factor K which allows for the egg being of less volume than that of a true ellipsoid, i.e.

TABLE XIII. EGG CAPACITIES (ml), EGG WEIGHTS (g), INCUBATION AND NESTLING PERIODS (days) IN PETRELS

(Sample sizes in parentheses)

SPECIES	EGG CAPACITY	EGG WEIGHT	INCUBATION PERIOD	NESTLING PERIOD	INCUBATION + NESTLING
1a.	381(48)*	430(48)*	79(5)	240(2)	319
1b.	370(41)*	416(41)	79.3(35)	236(17)	316
2b.	436(28)*	488(28)	78.4(163)	278(35)	356
2c.	373(87)	420(87)*	68(1)	-	-
3a.	242(11)	273(11)*	-	-	-
4.	305(43)*	343(43)*	-	-	-
7.	226(8)	250(100)	-	-	-
8.	261(50)*	291(100)	65.6(75)	c.140	c.206
9.	247(9)	278(9)*	-	-	-
10.	254(14)	285(14)*	64.4(95)	c.165	c.229
12.	219(6)	246(6)*	c.65	139(2)	c.204
14.	213(80)	243(80)*	59.4(11)	c.105	c.164
15.	205(10)*	232(10)	-	108(7)	-
16.	91(13)*	103(13)	43.5(7)	51(6)	94.5
17a.	92(3)	103(3)*	48.3(9)	47(24)	95
19a.	56(3)	62(42)	45(47)	48.9(15)	94
20.	42(21)*	47(21)	43.2(12)	51(7)	94
22a.	78(4)	87(4)*	53(1)	c.105;131(2)	155-184
25.	92(3)	101(3)*	c.59	102(1)	c.161
27b.	70(5)	74(89)	c.51	-	-
30.	50(?)*	56(?)	c.53	-	-
31b.	50(3)*	55(3)*	52.4(15)	92(32)	144
33.	56.5(11)	61(11)*	-	-	-
41.	31(16)*	34(16)*	46(1)	-	-
42a.	33(3)	37(3)*	c.56	-	-
43a.	28(5)	33(23)	44.8(10)	50.5(22)	95.3
45.	24(12)	26(12)*	-	50.0(139)	-
57.	105(3)	116(3)*	c.55	c.105;84	139-160
58b.	70.5(2)	79(2)*	-	92(3)	-
60.	88(13)	95(25)	c.56	96.7(53)	c.153
62.	77(5)	85(13)	53(24)	94(18)	147
64b.	53(14)	58(10)	51.3(43)	69.3(53)	121
67b.	27(11)*	29(30)	49(54)	75(41)	127
68f.	26(10)*	28.5(10)*	54(4)	72(3)	126
69a.	9.6(6)	10.4(6)	c.40(9)	52(1)	c.92
71c.	12.3(10)	13.4(10)*	c.50	57.3(40)	c.107
74.	6.0(10)	6.6(10)*	39.8(36)	62.8(32)	103
78a.	9.2(4)	10.0(100)	41.5(?)	66.5(5)	108
79b.	8.9(4)	9.8(4)*	42(61)	64(53)	106
82.	22(6)	25(6)*	-	-	-
83a.	13.5(27)*	15(27)	c.56	53.7(54)	c.110

* Corrected figure.

$$V = 0.5236\ B^2LK \ldots\ldots (16)$$

For each egg, therefore, the capacity in ml (V), breadth in cm (B) and length in cm (L) were measured and hence K was determined. The mean values of K for 36 species are given in column 13 of Appendix A together with the capacity of their average egg. It will be noticed that the K values approach quite closely to unity, i.e. the eggs themselves are nearly true ellipsoids.

The determinations have been cross-checked in various ways and corrected values for egg weights and egg capacities are shown in Table XIII. In the first place, as the petrel egg sinks when fresh, its capacity must be less than its weight when fresh. Some of the data in Appendix A indicate the reverse and have had to be corrected. Secondly, on the assumption that the specific gravity of the contents of a fresh egg is the same in petrels as in the hen, i.e. 1.035 (Romanoff and Romanoff, 1949), the capacities and weights can be cross-checked if the shell weights are known. The latter were obtained either by direct measurement of museum specimens or from Schönwetter (1960). Then:-

$$\text{Egg weight (g)} = 1.035\ \text{Egg Capacity (ml)} + \text{Shell Weight (g)} \ldots (17)$$

Thirdly, the validity of the corrected figures was confirmed by the use of equations (9) and (10) above:-

(9) Egg Weight = $.55LB^2 - 3.29$ (for eggs weighing more than 20g.)

(10) Egg Weight = $.53LB^2$ (for eggs weighing less than 20g.)

The figure finally used has been determined on the basis of the relative sizes of the samples involved and on their reliability; whether, for example, the weights were known to be those of new laid eggs as with Richdale's data for Diomedea bulleri and for some of the information collected by the writer.

Recalculated figures are indicated by an asterisk in Table XIII but many have needed no adjustment. Thus for species 7, Diomedea bulleri, the egg weights from the measured capacities are 252g as opposed to a mean weight of 250g for 100 eggs measured in the field, and for species 78a, Oceanodroma leucorhoa, the weight calculated from (17) is 10.1g, from (10) 10.0g, whereas field data from 100 eggs gave a mean value of 10.0g.

The most obvious discrepancies in the raw data listed in Appendix A are those in which egg capacities are the same or greater than egg weights. Thus for species 45, Pachyptila turtur, either weight or capacity must be wrong and despite the large size of the sample it was concluded that part-incubated eggs must have been present. A new "best-estimate" has been made from the measured capacities. Species 33, Pterodroma inexpectata, is a similar example: the new calculated weight of 61g based on 11 capacity measurements compares with a figure of 58.5 g deduced from equation (9).

The discrepancies in the data for species 3a, Diomedea c. cauta, seem irreconcilable. 52 egg dimensions and 11 egg capacities were measured by the writer, the six egg weights coming from the literature or from data on museum shells. The weights are clearly too low. They are lower than the figure calculated from (9) and furthermore the measured capacity (242ml.) is greater than the mean weight (238g). However, the corrected weight based on the capacity and a shell weight of 23g is 273g as against that calculated from (9) of 258g. The 6% difference is excessive in view of the relatively large samples used for determining dimensions and capacities. It seems likely that the weight derived from dimensions is nearer the true mean weight but on the data presently available a reliable estimate does not seem to be possible. The figures for this species have therefore been omitted in calculating the mean value for egg capacity to egg weight below.

For species 31 and 41, lacking data on egg weights or capacities but for which there are useful figures on development times needed for discussion in section 11, the egg weights and capacities have been calculated directly from their mean dimensions and Schönwetter's data for the weights of their shells.

The capacities of the eggs of the albatrosses 8 and 10 could not be determined directly owing to the lack of suitable material. They have been estimated from external volumes given by Frings (1961).

He also gave the egg weights listed in Appendix A but as the eggs were 3 and 2 weeks old when measured, their mean weights must have been lowered accordingly. Their capacities have been calculated by subtracting the mean volumes of their shells from their total volumes. In both instances the shell weights are 22g, and with shell density of 2.0 (this being the mean of the data from the eggshells of three petrel species), their shell volumes are 11 ml. The resulting figures cross-check well with weights calculated from equation (16).

Re-calculated egg weights help to explain some of the deviations from trend lines noted in previous sections. Thus in Figure 6, species 14, Macronectes giganteus, would now plot within the 95% confidence limits and four other species would also fall closer to the regression line though one, species 10, would lie further away. In Figure 8, relating wing lengths to egg weights, the positions of petrels 33, 15, 14 and 71c lying below the line would be improved and in Figure 9, relating egg weight to LB^2, all the points below the line would be brought onto or close to it. In Table V, the recalculated egg weight for species 33 would result in an egg weight to LB^2 value of .544 instead of .473, the former being much closer to the mean value for all species.

It is interesting to note that the recalculated weights for the two small petrels 71c, Pelagodroma marina and 74, Hydrobates pelagicus suggest egg weight to body weight ratios of 28% and 24% respectively. The former is the highest value for this ratio so far determined for a petrel.

Finally, the relationship between mean egg capacity and mean egg weight can be calculated from Table XIII. For 37 species the mean value of:-

$$\frac{\text{Egg Capacity in ml}}{\text{Egg Weight in g}} = 0.900 \quad \ldots\ldots\ldots\ldots\ldots\ldots \quad (18)$$

the standard deviation about the mean being ± 0.017.

11. DEVELOPMENT RATES OF PETRELS.

The development of a petrel from zygote to breeding adult takes considerably longer than this does with most other birds and the larger petrels take longer to reach maturity than the smaller ones. Thus while the mean age at first breeding for the medium sized species *Puffinus tenuirostris* is 5.3 years for females and 6.6 years for males (Serventy, 1967), for *Diomedea epomophora* the females do not breed until about 8 years old and the males from 9 to 11 years old (Richdale, 1950; Westerskov, 1963). On the information presently available the main exception to such long periods of immaturity is *Pelecanoides urinatrix*, which Richdale (1965a) found may breed when only 2 years old.

The time elapsing between fertilisation and egg laying in petrels is unknown. This is partly due to the difficulty of establishing when effective coition occurs and partly because, in those species that indulge in pre egg-laying exoduses, copulation possibly occurs at sea, the egg being deposited very soon after the females return to the nesting ground.

The present discussion is restricted to a consideration of the rates of development from egg laying up to the time of the young bird's first flight, that is, during the incubation and nestling periods. Various investigators have attempted to unravel the relationships between these periods and egg weight, body weight, the food reserves of the egg and similar variables but adequate information on the Procellariiformes was lacking. Recent research has provided new data enabling some earlier comments of Warham (1964) and of Lack (1967) to be elaborated.

11.1. Incubation Periods in Petrels.

The incubation periods of birds have been frequently discussed, the most comprehensive compilation on the subject being that of Bergtold (1917), although some of his data are unsatisfactory by present-day standards. Heinroth (1922) discussed implications of the variations in incubation periods found among birds and reptiles and reviewed previous work. Needham (1963) used Bergtold's data to compare development rates of birds with those of mammals. Kendeigh (1940, 1952, 1963), Huggins and Huggins (1941), Skutch (1945), Nice (1954) are among those who have discussed physiological and ecological factors affecting incubation periods and Lack (1954, 1967, and in press) has also dealt with the problem and its significance to population regulation.

With a clutch size of one the incubation period of a petrel egg is readily defined as the time elapsing between egg-laying and the chick's complete separation from its shell where incubation has been regular and uninterrupted (Heinroth, loc. cit.). Because many species are nocturnal when on land, lay underground and desert fresh eggs rather readily when disturbed, it is often difficult to establish accurate laying dates. This is much easier with surface-nesting species although Macronectes, being rather timid, is an exception here (Warham, 1962). An additional complication arises from a tendency for the birds to leave their eggs uncovered for one or more days before resuming incubation. This may increase, decrease, or have no effect on the time to hatching depending on the ambient temperature, the state of development of the embryo at the time, and similar factors. Many authors who have been unable to inspect nests daily make no reference to periods during which the eggs were uncovered but others like Roberts (1940), Richdale (1965a, 1965b), Davis (1957) and Tickell (1962) do, the last making a distinction between "apparent" and "true" incubation periods in the prion Pachyptila desolata. In the cold environment of Signy Island (shade temperature 20-50°F during the summer) where he worked, incubation time was apparently increased by as long as the eggs were left uncovered and without causing hatching failure. Further south, Roberts (1940) found that eggs of Oceanites oceanicus hatched after 2 days desertion. Temporary breaks in incubation occur both among petrels disturbed by man and under entirely undisturbed conditions (Warham, 1956b) and in surface-nesters as well as with burrowers. Surface-nesters that leave their eggs unattended, however, usually lose them to predators. The exceptions here are species breeding on tropical islands lacking suitable predators and include Puffinus pacificus and P. nativitatis. While the eggs of petrels of polar regions left uncovered may be killed by freezing, those of tropical petrels may be killed by overheating.

Thus it is very difficult to make corrections for days when eggs are uncovered. Tickell (loc.cit.) simply deducted the days during which the eggs were uncovered in arriving at the true incubation periods and the same has been done in the present study to adjust the data of Roberts (1940) and Davis (1957) to enable meaningful comparisons to be made. Other variables such as the stage of development of the embryo at the time when the egg is uncovered cannot be allowed for. This may be quite important since with domesticated birds the heat output of the embryo is considerable and increases rapidly from about half way through the incubation period.

The apparent incubation periods are often spread over a wide range. That the spread of true incubation periods is much narrower may be seen from the following table:-

TABLE XIV THE RANGES OF THE APPARENT AND TRUE INCUBATION PERIODS IN PETRELS.

(All times in days: numbers of determinations in parentheses)

Species	Apparent range	Corrected range	True Mean & S.D.	Coeff. of Var.	Authority
1b	-	77-81 (35)	79.3 ± 0.99	1.25	Richdale, 1952.
2b	-	75-82(163)	78.4 ± 1.17	1.49	Tickell, in press
8	-	63-68 (75)	65.6 ± 1.18	1.80	Rice & Kenyon,1962
10	-	62-68 (95)	64.4 ± 1.02	1.58	Rice & Kenyon,1962
14	-	58-61 (11)	59.4		Warham, 1962
20	-	42-44 (12)	43.2 ± 0.85	1.97	Brown, 1966
31b	50-56 (15)	-	-		Wingate,pers.comm.
43a	42-50 (22)	44-46 (10)	44.8 ± 0.56	1.25	Tickell, 1962
62	-	52-55 (24)			Serventy, 1967
64b	47-55 (43)	-	-		Harris, 1966
74	38-50 (36)	38-42 (36)	39.8 ± 0.91	2.29	Davis, 1957

These data indicate that the time required for development of the embryo to hatching is species-specific and that individual variation from bird to bird within a species is not great. This may reflect constancy of incubation (apart from occasional temporary desertions already discussed) resulting in the supply to the eggs of a rather constant amount of heat, or development processes whose rates are not greatly affected by temperature. The data in the table do not suggest any differences in the spread of incubation times between tropical species (8, 10, 31), temperate (16, 62, 74) or polar species (43a, 20) nor between highly migratory ones like 62, 64 and 20 or relatively sedentary ones like 14 and 31, but more information is needed.

Occasionally one of a series of determinations of the lengths of incubation periods in petrels proves to be exceptionally short. Dunnet (pers.comm.) has provided a series of incubation periods for *Fulmarus glacialis*. They were: 43, 47, 47, 49, 49, 50, 50, 50 and 50 days and he noted that the 43 day period was that of the bird that was the last to lay and that the period could have been shorter but could not have been longer. Tickell (1962) discussing a rather similar instance with *Pachyptila desolata* points out that short incubation periods could be a consequence of egg retention in the oviduct.

The narrow spread of incubation periods within a species is not universal among birds. In small passerines, for instance, the spread is relatively wide. Thus for the House Wren *Troglodytes aedon* studied by Kendeigh (1952) it varies from 13-16 days and for the Song Sparrow *Melospiza melodia* 12 to 15 days (Nice, 1937). These variations occur with birds that do not incubate continuously as do petrels. Thus Kendeigh (*loc.cit.*) showed that the attentive periods of House Wrens on their eggs numbered from 24 to 79 per day, the degree of attentiveness being influenced by the air temperature. Such discontinuous incubation and the consequent fluctuations in egg temperature, particularly well shown by Huggins (1941), seems to be one of the main reasons for the variability of incubation periods in these and other small birds.

11.2. Incubation Periods and Egg Capacity.

Table XIII lists the available data on mean incubation periods in the Procellariiformes together with the sample size in each case. The

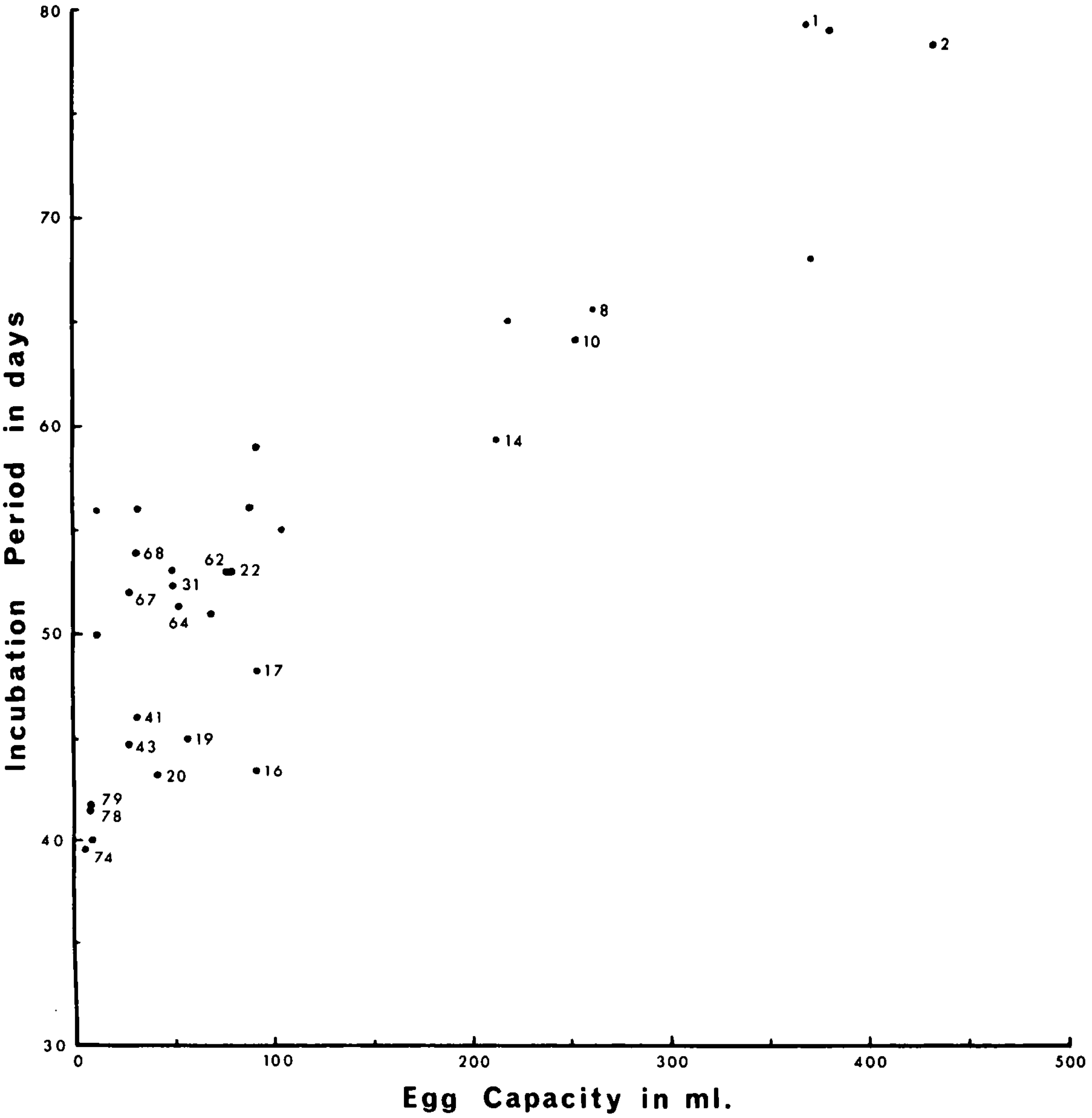

FIG.19. INCUBATION PERIODS & EGG CAPACITIES OF PETRELS

figures have been corrected for intermittent incubation where possible. Data for egg capacities and egg weights corrected as described in section 10 are indicated with an asterisk.

Data for incubation and nestling periods are from the following sources:
1a Sorensen (1950a); 1b Richdale (1952); 2b Tickell (in press); 2c Swales (1965); 8 & 10 Rice & Kenyon (1962); 12 Sorensen (1950b); 14 & 15 Warham (1962); 16 Prévost (1958, 1964); 17a Dunnet (pers. comm.) and Fisher (1952); 19a Pinder (1966); 20 Brown (1966); 22a Warham (1956); 25 Warham (1967); 27b Oliver (1955); 30 Ashmole in Lack (1966); 31b Wingate (pers.comm.); 41 Paulian (1953); 42a Richdale (1965b); 43a Tickell (1962); 45 Richdale (1965b); 57 Rowan (1952) and Elliott (1957); 58b Warham (1958); 60 Richdale (1963); 62 Serventy (1967); 64b Harris (1966); 67b Snow (1965) and Harris (in litt.); 68f Glauert (1946); 69a Roberts (1940); 71c Richdale (1965a); 74 Davis (1957); 78a Huntingdon in Palmer (1962); 79b Allen (1962) and Harris (in litt.); 83a Richdale (1965a).

In Figure 19 mean incubation periods are plotted against mean egg capacity. All the available data are plotted but only those derived from several determinations are numbered. Despite the scatter there is a significant correlation between egg capacity and incubation period ($r = +0.9370$; $P < .001$).

Heinroth (1922) pointed out that while, within a group, there may be a relationship between the length of the period of incubation and the size of the egg as shown by Fürbinger (1888), there are many exceptions. Thus gannets of the genus Sula, that lay eggs weighing 106, 65, 68 and 58g, all hatch these in 41-45 days (Nelson in Lack, 1967). Figure 19 shows that the relationship is not entirely constant within the Tubinares. Thus species 16, Fulmarus glacialoides, although laying almost exactly the same sized eggs as 17a, F. glacialis, has an incubation period averaging 5 days shorter than that bird.

The publication of Prévost's data for glacialoides that brought to light this anomaly in incubation periods was one of the causes that set the present investigation in train. Indeed, all the fulmars (14, 16, 17a, 19a and 20) have rather short incubation periods for eggs of their respective sizes. This is brought out rather better in Figure 20

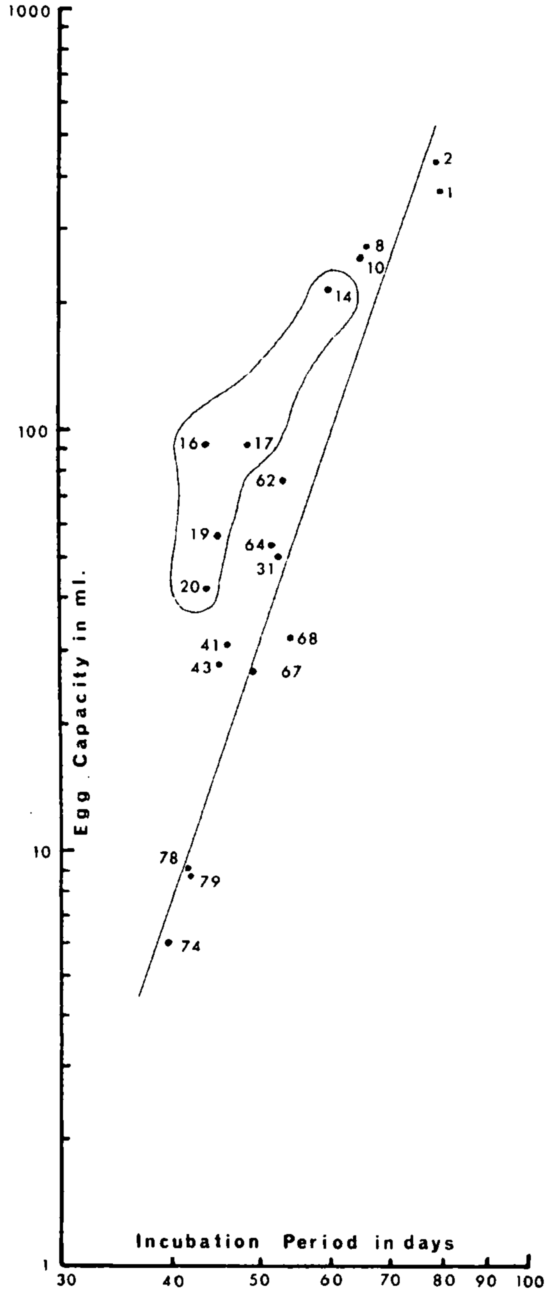

FIG. 20. INCUBATION PERIODS & EGG CAPACITIES OF PETRELS.

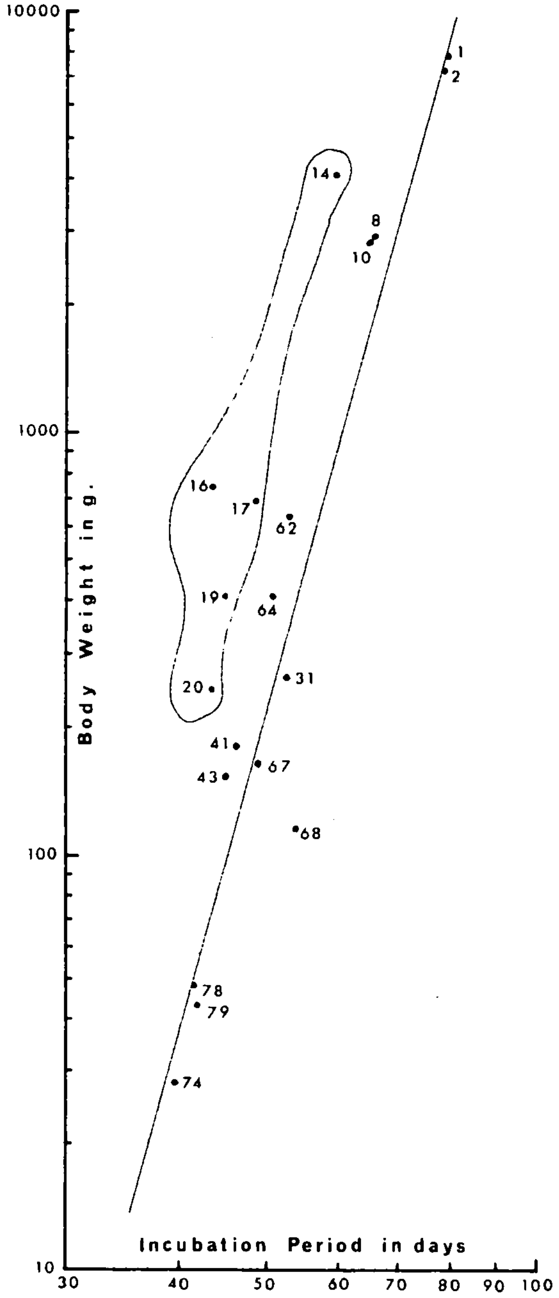

FIG. 21. INCUBATION PERIODS AND BODY WEIGHTS OF PETRELS.

where logarithmic axes are used and in Figure 21 where the incubation periods are plotted against mean female body weight. The situation of the fulmars in this respect is discussed more fully in section 11.12 below. It is interesting to note that another Antarctic species, 69a Oceanites oceanicus, also shows evidence of having an atypically short incubation period. Although laying an egg 60% larger than that of 74, Hydrobates pelagicus, it appears to have a similar incubation period to that bird yet breeds in much more severe climatic conditions. However, the data for Oceanites are based on very small samples and included several instances where incubation was interrupted (Roberts, 1940).

Returning to Figure 19 it will be seen that several species show the reverse tendency to that of the fulmars; having longer incubation periods than other petrels of similar size. Most divergent are 31b Pterodroma hasitata cahow, 67b Puffinus lherminieri subalaris and 68f Puffinus assimilis tunneyi. The data for the latter are not entirely satisfactory and there may well have been some suspension of incubation. On the other hand all three are relatively sedentary birds, the two latter at least visiting their burrows outside the breeding season (Snow, 1965; Warham, 1957). All three are birds of tropical or warm temperate seas; one, P. lherminieri breeds at about 9 monthly intervals at the Galapagos while P. assimilis is a winter breeder in south-western Australia. Thus it seems possible that selection has favoured more leisurely rates of development in these species compared to the other Puffinus species (62 and 64) plotted in the figure, which are migratory. These show highly synchronised patterns of egg laying and desert their young towards the end of the rearing period apparently in order to start their post-nuptial breeding migration (Marshall and Serventy, 1956; Harris, 1966).

Figure 20 enables a comparison to be made with the graph drawn up by Worth (1940) who plotted egg volume against incubation period on logarithmic axes for species from hummingbirds to ostriches and attempted to provide ecological reasons for deviations from his trend line. The regression line in Figure 20 has been drawn up without using the data for the fulmars; these are indicated separately. From the data for the other 14 petrels it is found that when Y = mean egg capacity in millilitres and X = mean incubation period in days then:-

$$\log Y = 6.116 \log X - 8.8536 \quad \ldots\ldots\ldots\ldots\ldots\ldots \quad (19)$$

or log egg capacity in ml = 6.116 log incubation period in days - 8.8536. Likewise the regression of logarithm of incubation period on logarithm of egg capacity is:

$$\log X = 0.1524 \log Y + 1.4666 \quad \ldots\ldots\ldots\ldots\ldots\ldots \quad (19a)$$

i.e. log incubation period in days = 0.1524 log egg capacity in ml + 1.4666.

No species plots more than 5 days away from the regression line but clearly more data from a wider range of birds is needed to show that in petrels generally apart from the fulmars a linear relationship holds between these variables.

Worth's data (partly from Bergtold, 1917) included figures for only three species of petrel and these disagree with those used in the present study for the same birds. Nevertheless, he noted that all three were slow to develop for the size of their eggs and that they plotted well away from his trend line. The latter does not agree with that in Figure 20 which is inclined more steeply to the Y axis than Worth's line. This difference does not arise because he used egg volume rather than egg capacity as has been done in Figure 20. The egg volume exceeds the capacity by the volume of the shell and this, in petrels, amounts to about 3% to 5% of the egg capacity. If volumes were used instead of capacity the slope of the regression line in Figure 20 would not be altered significantly although, owing to their thick shells, the fulmars would plot slightly further away from the trend line.

It is probable that had better data been available Worth would have found that a family of curves was needed to express the relationships between egg volume and incubation period as is shown by the graphs for egg weight against incubation periods for sea-birds presented by Lack (1967). The petrels thus form a separate group when these variables are compared and the penguins too fail to plot near Worth's curve, being also slow to develop. They plot along a regression line paralleling that of the petrels but they have shorter incubation periods relative to the sizes of their eggs. Again, as in the petrels, one group comprising species of the genus Eudyptes stands apart from the others in having shorter incubation periods relative to their egg sizes.

Worth was unable to explain the slope of his curve on biological grounds. The slope relates increase in incubation periods per unit time to a fourth power increase in egg volume. The corresponding line for petrels in Figure 20 is even steeper relating egg capacity to the sixth power of the incubation period. Evidently this is due to a compound rate of change between the two variables but the biological basis of these rates seems obscure. Needham (1931, 1963) had already constructed a similar curve based on egg weights and pointed out that the trend line showed that if egg weight was increased by one thousand times the incubation period is only increased by about four times. For petrels, because of the different slope to the line, the comparable increase in incubation period would be only about three times.

Worth (loc.cit) suggested a number of ecological reasons to explain deviations from the expected times from laying to hatching according to egg volume. He thought that fast rates were largely a consequence of selection in the face of heavy predation and he drew attention to the long incubation period of Fulmarus glacialis, suggesting that this would make an interesting subject for physiological study.

Huggins and Huggins (1941), reviewing previous work, agreed that there was a positive correlation between egg weight or egg volume and incubation periods. They pointed out some of the deficiencies in previous studies and suggested that the considerable variation found in incubation periods for eggs of similar sizes laid by different species were most likely due to the inadequacies in the data rather than being the result of adaptive responses to ecological factors.

The present work confirms that the correlationship between incubation period and egg size applies also in petrels, with the fulmars deviating furthest from the general trend. What is not clear is whether the fulmars have retained a primitive pattern of short incubation periods and have been able to colonise the polar regions because of this pre-adaptation while other petrels have evolved longer incubation periods as they came to colonise temperate and tropical seas (perhaps in the face of a less plentiful food supply); or whether the original petrels had long incubation periods and the fulmars were able to adapt to the polar conditions of short breeding seasons but with long day lengths by speeding up their rates of development.

The latter alternative seems the more probable. That long incubation periods are primitive as proposed by Heinroth (loc.cit.) seems rather likely in view of the long periods involved in the development of reptiles and the trend for more advanced bird groups to shorten incubation periods. Maybe the fulmars represent a relatively recent development in the Procellariidae and are still evolving more rapidly than other petrels. These are the birds that most often prove to be exceptions to general rules relating variables like wing length to body weight, body size, shell thickness and so on, while the only Procellariiform bird known to be expanding its range dramatically in recent times is the Northern Fulmar (Fisher, 1952, 1966).

11.3. Incubation Periods and Body Size.

11.3.1. Incubation Periods and Female Body Weights.

Larger petrels lay larger eggs which take longer to develop to hatching than those of smaller petrels. The correlation between mean female body weight and mean incubation period for 15 non-fulmarine species is highly significant ($r = +0.9586$ and $P < .001$) and the data are plotted on logarithmic axes in Figure 21.

This figure again brings out the special position of the fulmars - Macronectes (14), F. glacialis (17) and F. glacialoides (16), Daption (19) and Pagodroma (20). The regression of body weight in grams (Y) on incubation period in days (X) for the 15 non-fulmarine species is given by:-

$$\log Y = 8.0496 \log X - 11.3270 \quad \ldots\ldots\ldots\ldots\ldots\ldots \quad (20)$$

or log body weight in g = 8.0496 log incubation period in days - 11.3270. Likewise the regression of X on Y from the same data is:-

$$\log X = 0.1141 \log Y + 1.4325 \quad \ldots\ldots\ldots\ldots\ldots\ldots \quad (20a)$$

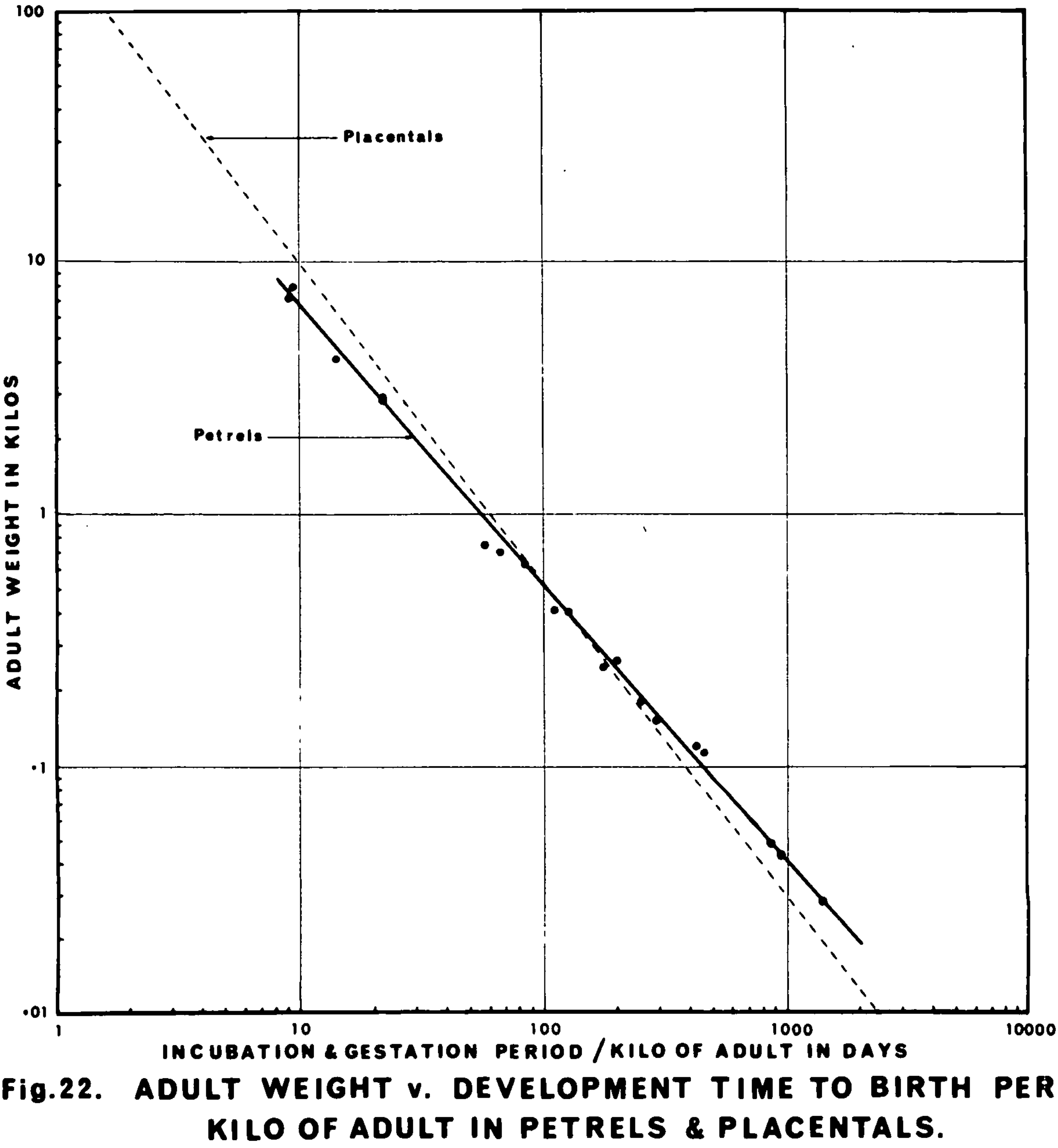

Fig.22. ADULT WEIGHT v. DEVELOPMENT TIME TO BIRTH PER KILO OF ADULT IN PETRELS & PLACENTALS.

or log incubation period in days = 0.1141 log body weight in g + 1.4325.

Allowance can be made for the factor of weight by considering the variations in incubation time per unit weight of adult. The relationship between that variable and female adult weight is shown in Figure 22 which is based on columns 2 and 4 of the following table:-

TABLE XV <u>DEVELOPMENT RATES TO BIRTH OF PETRELS</u>.

Species	Body Wt. (kg)	Inc. Period (days)	Incubation time/kg of adult (days)	Birth Wt. (g)
1a	7.801	79	9.9	-
1b	-	79.6	-	300
2b	7.270	78.4	9.3	340
8	2.934	65.6	22.4	160
10	2.852	64.4	22.6	150
14	4.114	59.4	14.4	215
16	0.741	43.5	58.7	72*
17a	0.699	48.3	69.1	76
19a	0.407	45.0	111	45
20	0.244	43.2	177	33*
31b	0.344	52.4	152	38*
41	0.181	46	256	24*
43a	0.153	44.8	293	23
62	0.635	53	83	59*
64b	0.406	51.3	126	45
67b	0.168	49	292	21*
68f	0.116	54	466	24*
74	0.028	39.8	1421	5
78a	0.048	41.5	865	7*
79b	0.044	41.8	950	7.5

* Calculated value

This figure brings out the difference in development rates between small and large petrels as measured by the times to produce unit weight:

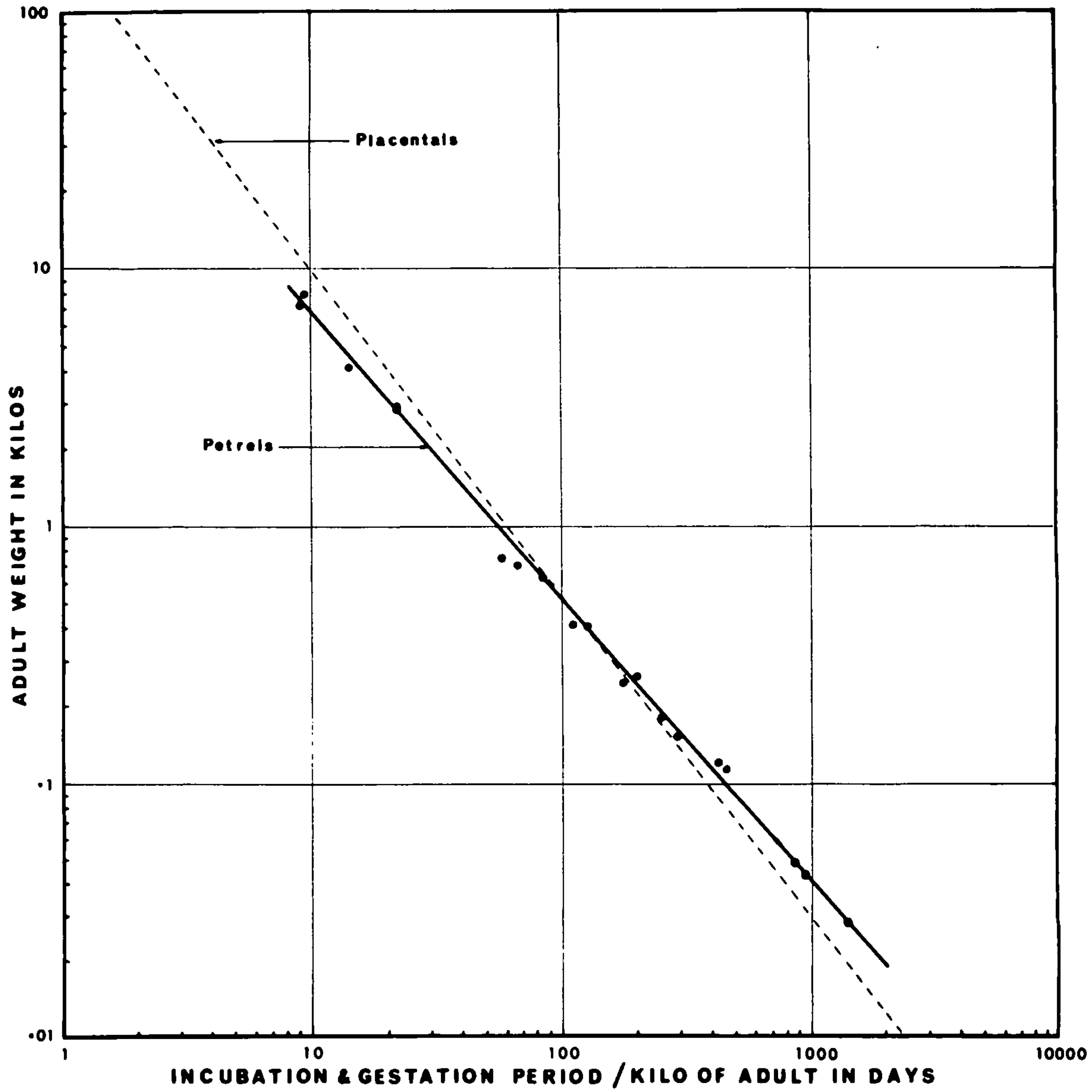

Fig.22. ADULT WEIGHT v. DEVELOPMENT TIME TO BIRTH PER KILO OF ADULT IN PETRELS & PLACENTALS.

it takes far longer for a storm-petrel to produce unit weight of storm-petrel than for an albatross to produce unit weight of albatross. Unit weight of the two animals are not of course equivalent, unit weight of the smaller species including a greater diversity of tissues and organs - more differentiation - than unit weight of the larger species and presumably this difference is mainly responsible for the longer time needed by small petrels to produce unit weight.

This method of plotting the data follows Needham (1963) who worked on the gestation periods of placental mammals. His data were extensive and ranged over six orders of magnitude from mice to elephants and although there was a good deal of scatter, a linear relationship held when the data were plotted on logarithmic axes. His regression line has been dotted in on Figure 22 and it will be seen that the two lines have similar slopes but that they intersect at a point representing a body weight of about 500 grams. On these data, a petrel and a placental weighing about 500 grams will produce unit weight of bird or mammal at the same rate. Within the size range of the petrels, large ones produce unit weight more quickly than do similar sized mammals whereas petrels below about 500 grams body weight take longer to produce unit weight than do placental mammals of equivalent size.

11.3.2 Incubation Periods and Birth Weights.

The relationship between incubation period and body size can also be investigated by comparing birth weights and incubation periods. These are given in Table XV and plotted in Figure 23 which shows, not only the data for petrels, but also similar curves drawn up by Needham (loc.cit.) for birds (using Bergtold's data) and for mammalian birth weights and gestation periods using data from Przibram (1927) and others. Birth weights for petrels have been taken from Brown (1966); Davis, 1957); Harris, (1966); Rice and Kenyon, (1962); Richdale, (1952, 1964); Roberts (1940) and Warham, (1962). Hatching weights for other species have been estimated by taking 70% of the mean value for fresh egg weight as this was found to be the average value for hatching weights for the eleven species whose birth weights have been recorded. Needham's birth weights for birds were calculated as 75%

of the fresh egg weight.

Needham's curves for birds and placentals substantiate his conclusion that (a) the time to make a given weight of bird is always less than that required to make a given weight of mammal and (b) that the prolongation of the incubation time caused by raising the hatching weight a given amount is less than the prolongation of the gestation time caused by raising the birth weight by the same amount. The latter holds too for petrels but Figure 23 shows that in other respects these birds stand in a rather different relationship to the mammals for

i. Placental mammals and petrels of birth weights 30 to 40 grams take about the same time (c.50 days) from conception to birth so that the time to make unit weight of either animal is about the same.

ii. Petrels with birth weights greater than 40 grams take less time from conception to birth than do mammals of equivalent birth weights.

iii. Petrels with birth weights below about 30 grams take longer to develop to hatching than similar sized placentals do to develop to birth. They take longer to make unit weight of bird than do mammals of the same size - the reverse situation to Needham's findings for birds as a whole.

iv. Judging by Bergtold's data, petrels take about twice as long to reach a given hatching weight as do the members of other bird orders.

As has already been pointed out Bergtold's data were not entirely reliable and the curve that Needham drew represents a simplification of the true position. A series of curves is needed, as drawn by Lack (1967) for sea-birds. Nevertheless, better data seem unlikely to upset the above conclusions and although the Casuariiformes, the Megapodiidae (Frith, 1959) and the Fregatidae (Nelson, 1967) also have very long incubation periods, petrels develop more slowly for their size than any other group of birds and it would be interesting to be able to extend the comparison to include the monotremes and reptiles, but this has not been possible in the present study.

11.3.3. Incubation Periods and Female Wing Lengths.

As it has been shown that female wing lengths may be used as a measure of female body weights in petrels, wing lengths also bear a relationship to incubation periods similar to that borne by body weight. The measurement used is the cube of the wing length in decimetres. When incubation period and $(\text{mean female wing length})^3$ are plotted logarithmically the result is a curve similar to that of Figures 20 and 21. The fulmars and the two small shearwaters 67b and 68f again lie to either side of the line whose equation is:-

$$\log Y = 7.1651 \log X - 11.1220 \quad \ldots\ldots\ldots\ldots\ldots\ldots \quad (21)$$

where $Y = (\text{mean female wing length in decimetres})^3$ and X = incubation period in days.

$$\text{and} \quad \log X = 0.125 \log Y + 1.5694 \quad \ldots\ldots\ldots\ldots\ldots\ldots \quad (21a)$$

or log incubation period in days = $0.125 \log (\text{mean female wing length in decimetres})^3 + 1.5694$.

These equations are both derived from the data for the 14 non-fulmarine species and for all 19 species the correlation between log incubation period and $\log (\text{mean female wing length})^3$ is high, $r = +0.813$ and $P < .001$.

11.4. Possible mechanisms for altering incubation periods.

If natural selection has operated on the lengths of incubation periods in petrels, by what means have these changes been effected? There are several possibilities:

i. Increase rates of cell division or increase cell size.

ii. Produce smaller eggs while retaining the same body size: such eggs will then take less time to develop to the hatching stage.

iii. Produce eggs of the same size but with reduced yolks so that hatching must take place sooner than formerly.

iv. Produce eggs with the same sized yolks but hatch the chick at an earlier stage and carrying larger yolk reserves in the yolk sac.

v. Retain the egg in the body cavity before laying.

vi. Increase the temperature of the egg during incubation.

Whether the rates of cell division or the sizes of the cells themselves have been increased in fulmars is not known. The only data relevant to this aspect appear to be those of Byerly, Helsel and Quinn (1938) - cited in Worth (1940) - which suggest that between different breeds of hens and ducks the rates of cell division in the eggs are the same but the sizes of the cells vary from species to species so that the different breeds have different incubation periods. Worth (loc.cit.) however, states that in the evolution of the domestic fowl a bigger egg has been evolved without a concomitant increase in the incubation period.

Fulmars do not seem to have shortened their incubation periods by the device of producing smaller eggs. Apart from Macronectes, which may perhaps lay a smaller egg than normal for a bird of its size (point 14 in Figure 6), the remaining fulmars, including those that have the shortest incubation periods, lay eggs that are quite typical as regards weights and dimensions (points 16, 19a and 20 in Figures 6 and 10). Furthermore, as already emphasised, the low plot for Macronectes in Figure 6 may be a consequence of inadequate data on body weight.

If eggs were hatched at a less advanced stage of embryonic development than customary among other petrels in order to shorten incubation periods an increase in nestling period would be expected unless the chicks also left for the sea in a less advanced state or compensation occurred during that period in the form of accelerated development. There is little evidence that petrel chicks ever fledge prematurely except for the example given by Belopol'skii (section 11.12 below) but it seems quite possible that some petrels are born at a less advanced stage than others. This is indicated by the way that all the surface nesters, the fulmars included, guard their young for far longer than the two or three days customary among the burrowing forms and by other evidence discussed in section 11.6. Some compensation may also occur as among fulmars both incubation and nestling periods are short (11.12).

Egg retention in the body cavity before laying would clearly shorten the apparent incubation period. It is now known that in at least six petrels either the females or both sexes remain at sea until shortly before laying (Warham, 1964) and egg retention might be feasible without impairing the adults' feeding ability, particularly in food-rich areas like the Southern Ocean. Cuckoos are well known for their ability to delay egg laying (Stresemann, 1927-34; Liversidge, 1961) but whether such a device is used by fulmars is unknown. It is perhaps relevant here to note the findings of Brody and Henderson (1927, in Brody, 1945) that, with the domestic fowl, increase in temperature of the egg such as would occur if it were retained in the shell gland has the greatest effect on embryo development when occurring at an early stage. The atypically short period of 43 days for a Northern Fulmar mentioned previously may also be noted. An examination of the embryos of new laid fulmar eggs for comparison with those of other petrels would readily resolve this matter but such eggs have not been available to me in the course of the present study.

11.5. Egg and Body Temperatures in Petrels.

As differentiation and development involve many chemical processes differences in egg temperatures will affect development rates, at least within limits, and Bergtold (1917) suggested that the body temperature of the parent bird was the most important factor controlling incubation time. He attempted to show that large birds have lower body temperatures than small ones and that members of the more highly evolved groups have higher body temperatures than those belonging to more primitive groups. Kendeigh (1940), who used rates of gaseous exchange of the eggs to measure rates of growth of their embryos, also investigated the effects of temperature on the development of the House Wren. He also thought that inter-specific differences in incubation temperatures might affect the lengths of their incubation periods even though the different species might be adjusted to particular incubation temperatures.

Huggins (1941) determined the egg temperatures of 37 species belonging to 11 orders of birds. The data were obtained under natural conditions and no significant differences were found in the average temperatures from order to order. The mean figure of 34.0°C had a standard deviation of 2.28°C. He concluded that there could be little difference in the average body temperatures of the incubating birds and that other factors must control the lengths of the incubation periods. Irving and Krog (1956) found no significant difference in egg temperatures among 7 species of Arctic birds from those determined by Huggins and they noted the low variability in resting body temperature among the 29 Alaskan birds they studied. Neither they nor Huggins had data for petrels but recently some members of this order have been examined and consideration of their egg and body temperatures seems appropriate.

Unfortunately there is little quantitative data on the effects of differing temperature regimes on incubation periods and none for petrels. Kendeigh (1940) calculated that for a House Wren whose eggs are normally hatched at 35°C in 13 days, the incubation period at 32.2°C and 37.8°C would be 18 and 10 days respectively; that is, a fall and rise of 2.8°C would lead to alterations of +40% and -23% in incubation period. Frith (in Nice, 1962) provides an example of the effect of temperature on incubation in the megapode <u>Leipoa ocellata</u> whose eggs are laid in a mound of decaying vegetation. They hatched in summer after about 57 days at 33°C, took up to 90 days in late autumn but in an incubator at 37.7°C hatched in 44 days, though prematurely and with their yolk sacs still attached. Frith (1959) ascribed such differences in incubation periods to the differences in temperature levels within the mounds. These data from two very dissimilar species suggest that quite small changes in egg temperature may result in substantial changes in incubation periods.

The available data for petrels are given in Table XVI. The figures used are as far as possible those of birds that were incubating or otherwise reasonably inactive.

TABLE XVI. TEMPERATURES OF INCUBATING PETRELS AND THEIR EGGS.

(Numbers of determinations in parentheses)

Species		Body Temp. °C	Egg Temp. °C	Reference
2	D.exulans	39.6 (11)		Eydoux & Souleyet, 1838.
7	D.bulleri	39.5 (3)		Warham, unpublished.
8	D.nigripes	38.1 (10)	36.4	Howell & Bartholomew, 1961a.
10	D.immutabilis	37.5 (10)	36.0	" "
16	F.glacialoides	38.8 (23)	29.3 (4)	Etchécopar & Prévost, 1954; Prévost, 1964.
19a	D.capensis	39.1 (29)	29.6 (10)	Prévost. 1964.
20	P.nivea	38.7 (26)	26.0 (9)	ibid.
38a	P.hypoleuca	38.2 (10)		Udvardy, 1963.
49	B.bulweria	37.8 (10)		"
43a	P.desolata	38.6 (43)		Tickell, 1962.
45	P.turtur	39.9 (28)		Farner, 1956.
59b	P.pacificus	39.5 (11)	34.3 (10)	Howell & Bartholomew, 1961b.
62	P.tenuirostris	40.9 (37)		Farner & Serventy, 1959.
	P.nativitatis	38.1 (10)		Howell & Bartholomew, 1961b.
64a	P.puffinus	37.0 (4)		" "
69a	O.oceanicus	38.8 (10)		Roberts, 1940.
78a	O.leucorhoa	37.2 (14)	22.5 (9)	Folk, 1951.

In discussing early work on body temperatures Simpson (1912) pointed out that determinations made on birds dragged on board at the end of fishing lines were likely to be abnormal because protracted struggles involve heat production. Nontheless, the data obtained by these methods do not show any marked rise compared with those in Table XVI. Thus two specimens of Procellaria aequinoctialis had rectal temperatures of 40.8 and 39.7°C, five of Daption capensis averaged 40.7°C, two of Procellaria cinerea 39.6°C, two of Macronectes 39.7°C, while 9 specimens of Diomedea exulans and D. chlororhynchos had mean temperatures of 40.7°C. A single specimen of Hydrobates pelagicus that alighted on the deck of a ship was found by Simpson to have a cloacal temperature of 39.8°C. Folk (1949, 1951), Farner (1956), and Farner and Serventy (1959) have shown that there is a significant difference in the body temperatures of petrels that are incubating and those on the surface shortly after arrival or shortly before their departure in the early morning. Incubating birds have lower temperatures than active ones and it is the temperature of the inactive bird that will be closest to that of the incubated egg.

An analysis of the body temperatures given in Table XVI suggests that petrels have significantly lower body temperatures than other birds for which data are available. Indeed, the only other bird group to show lower body temperatures than the petrels are penguins of which the four species listed by King and Farner (1961) have body temperatures ranging from 37.7 to 38.1°C. These birds also have long incubation periods.

The mean body temperature with standard error of the 17 species of petrel listed in Table XVI is 38.65 ± 0.2425°C .... (A)
and the sample means have a normal distribution about that figure.

The mean temperature with standard error of the 28 species of non-Procellariiform birds listed in King and Farner's Table VIII is
40.02 ± 0.1313°C .... (B)

The mean temperature with standard error of the 70 species of non-Procellariiform birds listed in King and Farner's Table IX is
41.25 ± 0.1410°C .... (C)

If A and B are compared the difference between the means is 1.37°C and the standard error of the difference is 0.2758°C. This difference is thus highly significant, $P < .001$. Likewise if A and C are compared, the difference between the means if 2.60°C while the standard error of the difference is 0.2806°C, and here again the mean temperatures are significantly different with $P < .001$.

On this evidence therefore, it seems that petrels do have lower body temperatures when at rest than other birds apart from penguins and for both these groups of sea-birds Bergtold's hypothesis, that body temperature is an important factor controlling incubation periods, seems to require further investigation. Nice (1962) using data from fewer species than given in Table XVI also commented on the association of protracted incubation periods with low body temperatures in petrels while Brown-Séquard (1854) had long before drawn attention to body temperatures of petrels captured off the Cape of Good Hope which he thought surprisingly low in view of their active habits.

Few determinations of the temperatures at which petrels' eggs are incubated have been obtained. Determinations reported by Etchécopar and Prévost (1954); Prévost (1964) and Folk (1949, 1951) suggest that the egg temperatures of petrels may be considerably lower than those of the species studied by Huggins (loc.cit.). With Prévost's birds, all Antarctic species, the ranges of egg temperatures were wide - 21.4 - 31.6°C for Pagodroma; 22.9 - 33.6°C for Daption and 27.2 - 33.0°C for Fulmarus glacialoides. These were much greater than the ranges of the body temperatures and suggest that the eggs were getting cooled, perhaps as a result of human interference, shortly before measurements were taken. The ambient temperatures were slightly below zero and the wind strengths about 6 to 8 metres per second so that cooling effects could have been highly important and, in conjunction with difficult field conditions, may explain the variations and low figures obtained.

It seems probable therefore that the true egg temperatures for these three species when undisturbed were closer to the maxima recorded by the French workers. This belief is reinforced by the data on the albatrosses Diomedea nigripes and D. immutabilis and the shearwater Puffinus pacificus given by Howell and Bartholomew (1961a; 1961b) who found that egg temperatures were not significantly different from those of the incubation patches. The ambient temperatures under cloudy skies were about 21°C when the measurements were made so that cooling effects would have been much less important here. Furthermore, the tropical species studied by Howell and Bartholomew may have been more accustomed to the near approach of human observers and therefore less prone to lift from their eggs than Etchécopar and Prévost's birds.

If egg temperatures of the order given by Folk and Etchécopar and Prévost are really typical of petrels then the whole question of the temperature range within which petrel eggs develop calls for investigation. These egg temperatures are close to the physiological zero for the domestic hen of 26.7°C given by Funk and Biellier (1944). Such low temperatures, if not artifacts, would make the abbreviated incubation periods of the southern fulmars even more remarkable. In discussing his results Folk (1951) pointed out that they helped to explain the long incubation periods he found for Oceanodroma leucorhoa.

Data on the Antarctic Skua Stercorarius skua maccormicki, a bird that also incubates at low ambient temperatures, are perhaps relevant here. The birds had a mean body temperature of 41.2°C and their eggs a mean temperature of 35.9°C at Wilkes Station, Antarctica. That is, the eggs were only about 5.3°C below that of the body temperature of the incubating bird (Eklund and Charlton, 1958).

The range in temperature of the skua eggs was quite wide, some 16.5°C, which the authors ascribed to the frequent changes of the adults on the eggs, i.e. to cooling by the ambient air. The range of temperature is less than that found by Etchécopar and Prévost, the difference perhaps reflecting in part the more severe climatic conditions at Point Géologie than at Wilkes.

Embryos developing within an egg and within a placenta clearly have many features in common but it is nevertheless rather surprising to find animals as dissimilar as mammals and petrels having such similar weight-specific development rates in the period before birth. However Nice (1962), who compared the development of behaviour in the Song Sparrow with that of the domestic mouse, found many correspondences in the lengths of the stages through which both progressed to independence. Again, the similarities and differences in the relationships between metabolic rates of passerine and non-passerine birds and of mammals (the curve of body weight to standard metabolic rate on logarithmic axes for non-passerines closely approximates that of mammals) also suggest that the relationships between these variables are fundamentally similar in the two animal classes (Brody, 1945; Lasiewski and Dawson, 1967). That an albatross has a faster rate of development than a placental of similar size may be a response to the restrictions of the cleidoic egg and particularly to the bird embryo's inability to eliminate waste products which are excreted in the mammal through the maternal kidneys, as Needham (loc.cit.) suggested for birds in general.

It might appear that the relatively low body temperatures of placentals and petrels compared with those of higher bird groups could account for some of the similarities seen in Figures 22 and 23. Petrels, with a mean resting body temperature of 38.6°C, compare with the mean value of 37.8°C given by Morrison and Ryser (1952) for 56 species of placental mammals and 41.2°C for 70 species of birds (King and Farner, 1961). Placentals thus approach more nearly to petrels in their body temperatures so that it seems possible that body temperature controlling the temperatures of homologous chemical processes in the embryo mammal and petrel, could be an important factor in determining their developmental rates. Nevertheless the data do not enable a clear-cut conclusion to be drawn. In the first place, while the body temperatures of the two groups are rather similar suggesting a difference in resting metabolism of only about 10% (Rodbard, 1950), the temperatures of their embryos may be rather different for whereas the mammalian ones are jacketed at a constant temperature within the maternal body the petrel embryos lie externally. Even though the egg fits snugly into what almost amounts to a pouch and probably lies on the feet of the parent rather than directly on the often cold substrate, the egg must develop at a temperature below that of the parent.

Unfortunately the egg temperature data in Table XVI are somewhat ambiguous. Even if those of Folk and Prévost are too low it will be seen that the temperatures of the eggs of species 8 and 10, both tropical albatrosses, are above that of 34.0°C determined by Huggins (1941) for birds in general. These data suggest that, at least in these two species, low egg temperatures cannot explain their long incubation periods. Yet for a third species, 59b, *Puffinus pacificus*, breeding on the same island as the albatrosses, the egg temperature was two degrees lower. The anomaly may be more apparent than real. The albatross eggs were well incubated so that their embryos may have been producing a considerable amount of metabolic heat and it is suggestive that the body temperatures of brooded, recently hatched young were significantly higher than those of the brooding adults (Howell and Bartholomew, 1961b). The shearwater egg measurements were made on eggs lacking visible embryos; this may explain their markedly lower temperatures.

Furthermore, even were the mean egg temperatures for petrels significantly lower than the mean egg temperatures for other birds, this would not enable a meaningful comparison to be made. For one thing Huggins (loc.cit.) showed that with most of the birds studied by him, the eggs were subjected to a fluctuating temperature regime as were those of the Antarctic Skua studied by Eklund and Charlton already discussed. These conditions are quite different to those under which the petrel egg develops. Petrels sit very tightly and incubation is continuous apart from the occasional absences already discussed. Howell and Bartholomew (1961b), for instance, found that the eggs of Puffinus pacificus varied by only 0.6°C in three hours' continuous recording. Thus a comparison of the effect of temperature on incubation between petrels and other birds would involve comparing fluctuating with steady states. Furthermore, due to the increasing liberation of metabolic heat by the embryo, the temperature of the egg tends to rise throughout incubation (Ecclesmeyer, 1907 in Needham, 1963; Kendeigh, 1940) and petrels, unlike some other birds, do not seem to apply themselves any less closely to their eggs in the later stages of incubation than they do at the start of this process. And in some sea-birds this rise may be considerable, though again there are no data for petrels. During the 28 days incubation of the Antarctic Skua, Spellerberg (1966) recorded a gradual rise in mean egg temperature from about 28°C to 39°C.

Recently McNab (1966) has revived the idea that small birds have higher basal metabolic rates and temperatures than large ones (as proposed by Bergtold, 1917) and he has modified the equation relating basal metabolism to body weight of King and Farner (1961) to relate body weight and body temperature. The data in Table XVI, however, do not support the idea that smaller petrels have higher resting temperatures than large ones ($r = + 0.151$; $P > 0.1$), although any such tendency might be expected to show particularly clearly in a group with so wide a range of body size. Similarly Udvardy (1953) could find no relationship between body temperature and body weight in the 541 specimens of 67 species that he measured. Likewise there seems to be no correlation between body temperature and weight in placental mammals (Morrison and Ryder, 1952 modifying Rodbard, 1951) whereas Figure 23 would suggest that, if temperature is an important factor affecting gestation periods, small mammals would have higher body temperatures than large ones, and even higher perhaps than those of small petrels.

An additional complication in comparing development rates between mammals and petrels is that the mammalian foetus, at least in the rat, has a similar weight-specific metabolic rate to that of the adult but lower than that of the newly born rat (Kleiber, Cole and Smith, 1943), whereas the petrel embryo is initially poikilothermic and only gradually attains a measure of homeothermy during incubation and at the same time must raise its metabolic rate accordingly.

It seems therefore, that despite the significantly lower body temperatures of petrels and the conjunction of low temperatures with extended incubation periods found among reptiles and monotremes, the present data are insufficient to determine to what extent long incubation periods are the result of low temperatures during development within the egg and to what extent to genetical, size and other factors. Measurements of petrel egg temperatures throughout incubation would be revealing while attempts at artificial incubation at different temperature regimes would also throw light on this aspect of the problem.

11.6. Incubation Periods and Egg Composition.

As the yolk comprises the main food reserve for the embryo the latter cannot remain for long within the shell once the yolk has been consumed. Both altricial and precocial chicks hatch before this stage is reached but the yolk reserves carried by the hatchlings in their yolk sacs are generally far larger in altricial than in precocial species of similar body weights.

Pycraft (1914) seems to have been one of the first to suggest that the size of the yolk supply largely governed the length of the incubation period.

The composition of birds' eggs and the relative proportions of yolk, albumen and shell have been examined by several workers, whose findings were discussed by Heinroth (1922), Romanoff and Romanoff (1949) and Nice (1962).

The Romanoffs gave a table for 10 altricial and 10 precocial species relating the weights of the egg components to the weights of the intact egg. These data may be summarised as follows:-

	% Yolk	% Albumen	% Shell
Altricials	12-27	68-79	5-10
Precocials	32-40	50-56	8-14

These authors also pointed out that the proportions of the component parts vary with the size of the egg. In general, for both precocials and altricials, larger eggs have relatively smaller yolks and more white and shell than smaller ones. This evidently applies both intra- and inter-specifically for with the domestic hen large eggs contain smaller yolks relative to total egg weight than do small ones (Curtis, 1911).

Data for 12 species of petrel are listed in Table XVII and plotted in Figures 24 A and B. The first figure shows how the weights of the parts vary with the weights of the eggs and the second figure presents the same information on a percentage basis. The graphs are based on small samples and the trend lines are drawn in by eye. The correlations are good. For egg weight to yolk weight $r = + 0.9977$, for egg weight to albumen weight $r = + 0.9988$ and for egg weight to shell weight $r = + 0.9523$. $P < .001$ in each instance.

My data and those obtained by colleagues were taken from freshly laid eggs which were hard boiled, cooled, and then separated into shell with its underlying membrane, the albumen, and the yolk. Each component was then weighed. Boiling resulted in a loss of weight of about 1-3% of the total egg weight and as this loss is believed to be mainly due to loss of water from the albumen the figure for that component was increased by the difference between the fresh egg weight and the boiled egg weight as recommended by Curtis (1911). The latter author also discussed ways of assaying egg composition and although her methods gave greater accuracy than that adopted here, they would be difficult to use in the field. The hard-boiling procedure gives results that seem adequate for an initial examination of trends and the data for the eggs analysed by me do not show much variation although all the samples are small.

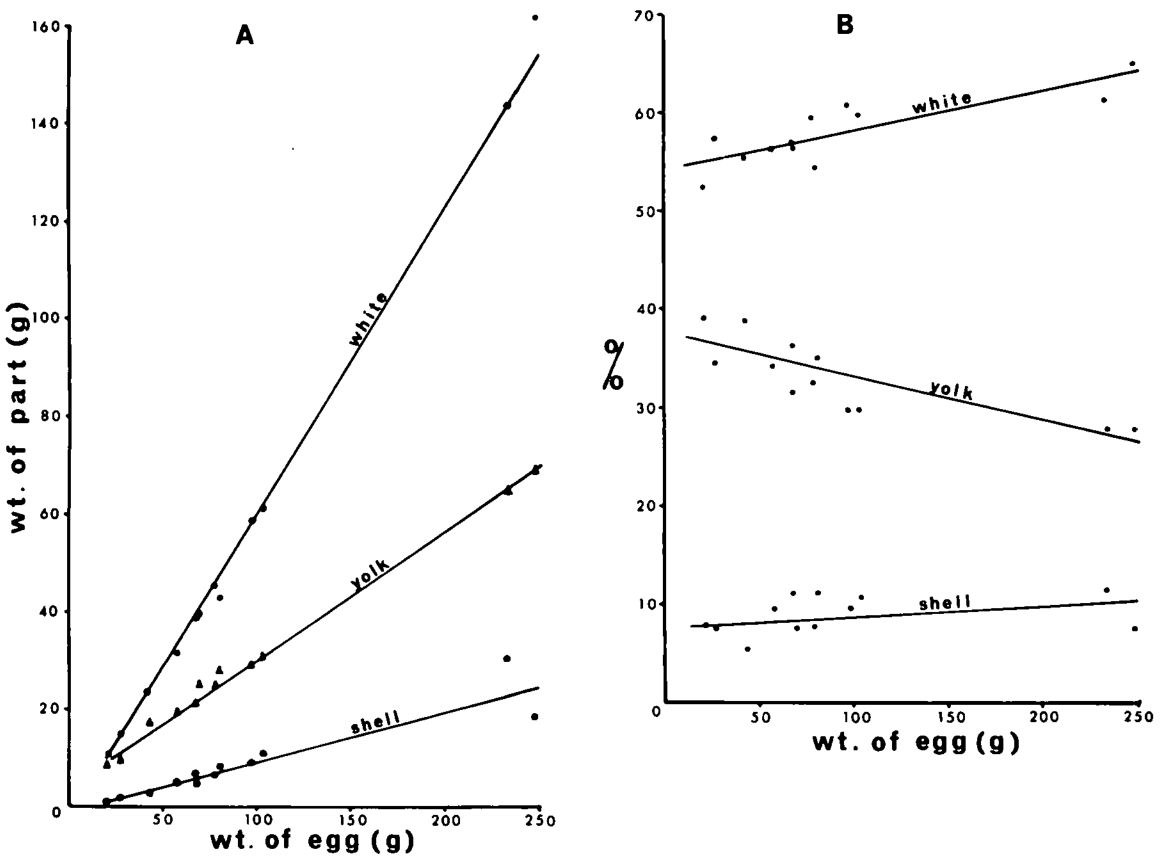

FIG. 24. CONSTITUENTS OF PETREL EGGS.

TABLE XVII: THE COMPOSITION OF SOME PETREL EGGS

	Species	No.	Fresh wt(g)	Shell (g)	Shell %	White (g)	White %	Yolk (g)	Yolk %
7	D.bulleri	3	247.5	18.2	7.4	160.8	64.9	68.5	27.7
14	M.giganteus	5	233.8	26.2	11.2	142.5	61.0	65.0	27.8
16	F.glacialoides	9	103.4	11.2	10.9	61.6	59.6	30.5	29.5
17a	F.glacialis	4	97.0	9.6	9.9	58.7	60.6	28.7	29.5
19a	D.capensis	10	67.3	7.6	11.2	38.5	57.0	21.4	31.8
20	P.nivea	6	56.8	5.5	9.7	31.9	56.2	19.4	34.1
27b	P.neglecta	3	68.7	5.2	7.5	38.5	56.2	25.0	36.3
38c	P.nigripennis	1	42.6	2.4	5.6	23.6	55.4	26.6	39.0
59a	P.pacificus	3	76.9	6.1	7.9	45.7	59.5	25.1	32.6
62	P.tenuirostris	1	80.0	8.5	10.6	43.5	54.4	28.0	35.0
67	P.lherminieri	6	25.7	2.0	7.8	14.8	57.5	8.9	34.7
71c	P.marina	2	20.6	1.6	8.0	10.9	52.7	8.1	39.3

(Data for species 14, 16, 19a and 20 from Etchécopar and Prévost (1954); those for 17a, 62 and 67 in personal communications from Drs. Dunnet, Serventy and Harris respectively; the remainder determined by the author.)

Figure 24 shows that the trends noted by the Romanoffs in other bird groups also apply among the Procellariiformes. Increasing egg size is accompanied by increase in absolute weight of all the three components but relative to the fresh weight of the intact egg the amounts of albumen and shell increase whereas that of the yolk decreases.

Nice (loc.cit.), commenting on Etchécopar and Prévost's data for penguins and petrels, states "We do not know whether the large amount of yolk is an adaptation to extreme cold or is a characteristic of these orders throughout their range. It may indicate that penguins and albatrosses and perhaps petrels are really more semi-precocial than semi-altricial". The data in Table XVII do not suggest that habitat temperatures have any bearing on yolk quantity among the Tubinares. On the basis of their egg composition these birds lie nearer to the precocial category than to that of the altricials. But these terms are difficult to define precisely for the states of maturity of newly-hatched chicks form a continuum between the extreme precocity of the young megapode that can fly within a few hours of birth, is homeothermic and receives no parental care, to the passerine wholly dependent on its parent for food and most of its warmth for some considerable time before the acquisition of homeothermy and independence.

These two categories have been subdivided in various ways e.g. by Portmann (1938), Verheyen (1948), Needham (1950), Nice (1962) and others. King and Farner (1961) consider them in respect of thermoregulation only, pointing out that from the start of incubation there is a gradual change in the thermoregulatory contributions of the adults and the young to the eggs or young. Nice (loc.cit.) used additional criteria: whether the eyes were open at birth, the body naked or down covered, the chick able to move about within the first day or so, and so on. For Farner and Serventy (1959) the burrowing Puffinus tenuirostris and Pachyptila turtur are precocials as they attain homeothermy within a day or so after hatching. Nice, on the other hand, categorised the petrel chick as either "semi-precocial" or "semi-altricial", the latter being down-covered and unable to leave the nest for some time after birth, the former being born with eyes open, down-covered and staying in its nest though able to walk, e.g. gulls and terns.

The Tubinares are precocial in acquiring homeothermy soon after hatching, usually being born bright-eyed, clad in down, soon able to perform a variety of comfort and exploratory movements and not, as far as is known, learning from their parents how to find food for themselves. They are altricial in being able only to shuffle around during their first few days in the nest, born with limbs poorly developed, needing a little warmth and a considerable amount of care from their parents, while growth, maturation and learning are necessary before the chick can fend for itself.

Thus it is a matter of what characters are used and what weight is given to these as to how petrels should be classified in respect of their maturity at birth. Their relative immobility in their early days seems to be mainly a consequence of the need for a sea-bird to nest on land whereas most precocials nest and feed on the ground. For the present purpose I propose to treat the petrels as semi-precocial.

Even within this rather homogeneous order there are differences among species in the degree of maturity at birth. Whereas many burrowers acquire homeothermy within 2 days of emerging from their eggs, the surface nesters seem to take longer, perhaps weeks to reach this stage, and they also tend to be born with rather thinner coats of down than the burrowing species (Richdale, 1943 and pers. observations). The young Pelecanoides is likewise clad initially in thin down with a bare patch on the crown and is brooded for at least a week (Richdale, 1965a). The state of the down of the albatross hatchling suggests that it is born at an earlier stage of development than the chick of a burrowing petrel. This, and the increase in the length of the guard stage with increase in body size, may be a consequence of the concomitant reduction of yolk relative to egg weight. Small petrels with yolky eggs may thus be said to be more precocial in both these features as well as in their ability to control their body temperatures. Unfortunately, although there are good data on the length of the guard stage for surface nesters (16 days for Daption; 18 for F.glacialoides; 9 for Pagodroma; 20 for Macronectes; 17 for D.immutabilis; 19 for D.nigripes; and 40 for D.epomophora) there is little information on the period during which brooding is necessary. Towards the end of the guard stage and sometimes long before this, chicks are found sitting beside their parents. Prévost (1964) believes that homeothermy in the southern fulmars is only attained shortly before the end of the guard stage. If this should be so then these petrels are born at an earlier physiological stage of development, at least as far as thermo-regulation goes, than burrowing species. On the other hand Howell and Bartholomew (1961) provide data that indicate the attainment of homeothermy in the young *Diomedea nigripes* and *D. immutabilis* within a few days of hatching and well before guarding has ceased.

The data in Table XVII do not suggest that the relationships between egg size and egg composition among petrels are markedly different from those existing among other precocials. The yolk weights of seven of the ten precocials listed by the Romanoffs are very similar to those predicted from the curves in Figure 24 for petrel eggs of similar sizes: they conform quite well with those of duck and game birds, for instance. But two species, Emu (*Dromaius novaehollandiae*) and Ostrich (*Struthio camelus*), have substantially larger yolks than would be expected for hypothetical petrel eggs of similar weights. Another precocial species with a much bigger yolk supply than a petrel's egg of similar weight is that of *Megapodius* whose eggs, containing 62% of yolk by weight, are more yolky than those of most reptiles (Meyer, 1930).

From the direct determinations of yolk weights given above and by calculating the values for other species using the trend line of Figure 24A it is possible to gain some idea of the relationship between the initial weight of the yolk and the length of the incubation period in petrels. The calculated data are as follows:-

TABLE XVIII: CALCULATED YOLK WEIGHTS FOR PETREL EGGS.

	Species	Yolk Wt. (g)	Incubation period(days)
2b	*D. exulans*	132	78
8	*D. nigripes*	80	66
10	*D. immutabilis*	79	64
31b	*P. hasitata*	18	52
43a	*P. desolata*	12	45
64b	*P. puffinus*	19	51
74	*H. pelagicus*	5	40
78a	*O. leucorhoa*	6	41.5
79b	*O. castro*	6	42
67b	*P. lherminieri*	12	52

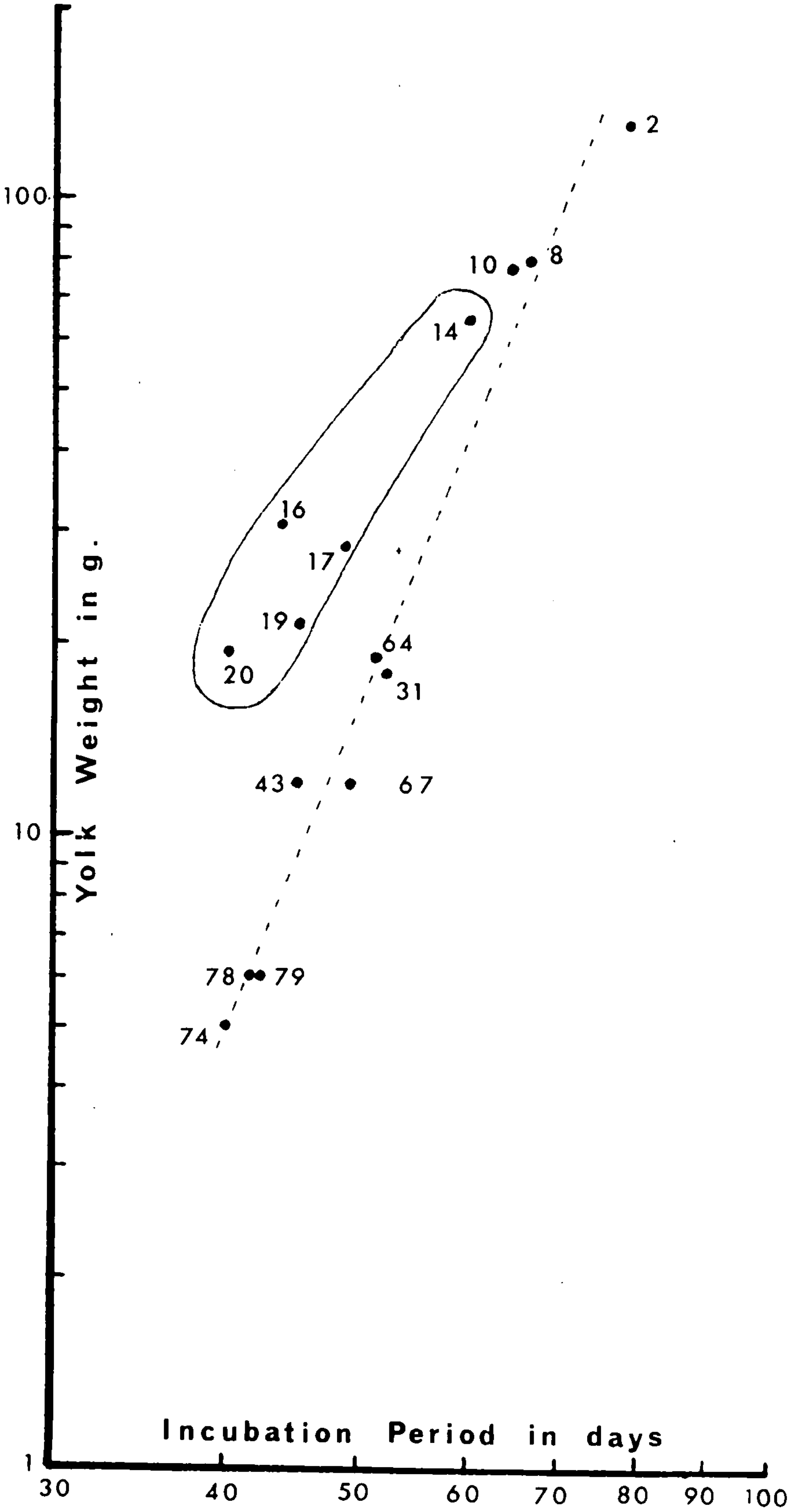

FIG.25. INCUBATION PERIODS & YOLK WEIGHT IN PETRELS.

The combined data are set out on logarithmic axes in Figure 25. The fulmars are again indicated separately while the incubation period for Pagodroma is that given by Prévost (1964) for the large form studied by him of about 40 days and not for the smaller one studied by Brown (1966). It will be seen that there seems to be a linear relationship between the log of yolk weight of the newly laid egg and the log of the time between laying and hatching at least for the non-fulmarine species whereas the latter have shorter incubation periods than the rest relative to yolk size. The similarity of this figure to those of Figures 20 and 21 will be noted. Figures 24 and 25 show that the short incubation periods of the fulmars are not a consequence of their eggs having relatively small yolks which would force hatching to occur earlier. Either the rate of development of these eggs is faster or the chicks hatch carrying larger reserves in their yolk sacs than do other petrels of equivalent size or one or more of the alternatives discussed in section 11.4 above apply.

The relationship indicated by Figure 25 could reflect a causal association between yolk weight and incubation period but any such association must be quite different from that of other precocial species as these hatch eggs of sizes similar to those of petrels in much less time than the latter. Thus while the size of the yolk supply may have an important bearing on inter-specific variation in the length of incubation periods this does not explain the abnormal length of these periods in petrels generally. It must be pointed out, however, that no investigation of the quality of the yolks of petrel eggs has been made; conceivably these could have a higher fat and energy content than those of other birds and enable the embryo to remain longer within its shell. It is known that there are differences in the lipid contents of yolks (Romanoff and Romanoff, 1949; Kuroda, 1963) even though it has been possible to exchange yolk and albumen between eggs of different species without interfering with normal development (Ermanov, 1934 in Needham, 1950).

Assessment of the role of the yolk in the development time to hatching of the petrel egg is hindered by the lack of information concerning the proportion of yolk still unused and retained in the yolk sac at the time of hatching. In the previous discussion it has been assumed that comparable proportions are retained by the different hatchlings. Clearly it would be better to relate the lengths of the incubation periods with the weight of yolk actually consumed between laying and hatching, or to some more precise measure of energy consumption.

Petrel chicks contain a yolk reserve at birth and this could be of particular value to the young of burrowing forms that are left unattended at two or three days old. Parental visits for the purpose of feeding the chick tend to be erratic perhaps because long distances are covered in the quest for food, so that an energy reserve early in life when the small chick is probably losing heat at a higher rate than at any subsequent time (due to its high surface area to body weight ratio) could be of survival value. Reid and Bailey (1966) have demonstrated a similar function for the yolk reserves held by the young Adelie Penguin (Pygoscelis adeliae). This can survive for 6 days if its parents are delayed from feeding the chick by rough seas or by long treks over fast ice.

The albumen of an egg holds in its colloidal matrix about two-thirds of the developing embryo's water supply (Gray, 1926 in Needham, 1963) as well as important store of protein. By the time of hatching this water supply is exhausted. Birds' eggs, unlike the highly lecithal eggs of reptiles, cannot absorb significant amounts of water through their shells. Needham (loc.cit.) believed that bird embryos are short of water, not only needing all that can be held in the albumen, but also utilising the fatty acids of the yolk as energy sources because these produce water on combustion.

Personal observations of newly hatched petrels do not suggest that the young storm petrel or prion, born from an egg with a low albumen content, and the albatross, born from an egg with a high albumen content, differ noticeably in the wetness of their down. Nor have I ever noticed any surplus water in the discarded eggshells at this time. Thus it seems probable that in petrels too the water supply is exhausted by the time that incubation is complete.

Several possible advantages are gained by the larger species in secreting larger amounts of albumen around their egg yolks. Despite a slight reversal of the tendency among the fulmars, it seems clear that the larger the bird the longer must be the time taken to reach a given stage of development. Increased time within the shell means increased time during which uncontrollable loss of water through the shell occurs. Thus the larger the egg the greater the water store required for development. In addition, the larger the egg and the longer the development before hatching the greater the quantity of water needed to dilute the nitrogenous and other toxic products of combustion. Acting to lessen water loss in larger eggs are their thicker shells, which may perhaps retard passage of water outwards, and the reduced ratios of surface area to weight (Dunn, 1922 in Needham, 1963). In addition, low egg temperatures would be expected to lessen water loss as demonstrated by Kendeigh (1940) in his study of the House Wren.

The proximate cause of the regular trends in egg composition demonstrated here may lie in the mechanics of egg production. Although there appear to be no data on oviduct size in birds, it is known that the relationships of many organ weights to body weights conform to allometric formulae but that the slopes of the curves relating these variables differ (Brody, 1945; Rensch, 1966). That is, the different organs do not increase in size at the same rate with increasing body size. The albumen of an egg is secreted in response to pressure on the epithelial cells of the magnum so that the insertion of a foreign object like a ball bearing results in the production of an "egg" with the object at its centre. Thus if the larger yolks released by the larger petrels are passed into oviducts that are slightly smaller relative to these yolks there will be more pressure between the extensible walls of the oviduct and the yolk. This will result in increased stimulation of the secretory cells, a greater deposition of albumen and of shell, and a more elongated egg.

11.7. The Nestling Periods of Petrels.

The time that elapses from the liberation of the petrel chick from the eggshell to its first flight - the nestling or fledgling period - varies between about 50 to 280 days. The smaller species usually fly at an earlier age than the larger ones do but those with the shortest nestling periods are not the species that are smallest in size.

The available data are set out in Table XIII. Mean values based on samples of very varied size are given in column 5 and the total time between egg laying and the date of first flight in the final column of the table.

Precise information on nestling periods is not as easily obtained as is that for incubation periods and is seldom determined to within an accuracy of more than half a day; more usually the individual figures are accurate to ± 1 day. Furthermore, the nestling period as defined above may not be the age at which the chick reaches the sea. Most chicks do achieve that on their first flight but sometimes they alight on the breeding grounds and their final departure may be delayed accordingly. This occurs with surface nesters like Macronectes and the albatrosses (personal observations) and can then be easily overlooked. In practice, the nestling period is often taken as the age at which the chick disappears after having reached the appropriate state of development. Errors are even more likely with burrowing species as the young birds leave under cover of darkness and some, failing to get away before dawn, take refuge in burrows at lower altitudes where they may remain for several further days before finally departing. Thus recorded nestling periods probably tend to underestimate the birds' true ages when they reach the sea.

For a given species the nestling periods are more variable than incubation period; ranges and variability are shown in Table XIX. The mean coefficient of variation in nestling times for the 12 species listed is 4.67 which compares with a mean coefficient of variation in incubation periods for 7 species from Table XII of 1.66.

Because of continuous incubation and the limited intra-specific range of body temperature the embryo develops in a very uniform environment and its energy supply is fixed at the time of formation of the egg. The chick, on the other hand, develops for most of its time exposed to a fluctuating micro-climate, its energy intake varying with personal characteristics of its parents and with climatic and other factors affecting their food supply. Thus a greater variability in nestling periods is to be expected. The weather at the time when the

TABLE XIX: RANGES OF VARIATION IN NESTLING PERIODS IN PETRELS.

(All times in days)

Species	N	Range	Mean ± S.D.	Coeff. of Var.	Authority
1b	17	216-252	236 ± 10.6	4.49	Richdale, 1952.
2b	35	263-303	277.7 ± 2.8	1.01	Tickell, *in litt*.
17a	24	41-57	47.1 ± 4.0	8.49	Fisher, 1952.
19a	15	47-52	48.8 ± 1.5	2.99	Pinder, 1966.
20	7	48-54	50.7 ± 2.1	4.14	Brown, 1966.
43a	22	42-54	50.5 ± 2.8	5.64	Tickell, 1962.
45	139	43-56	50.0 ± 2.5	5.00	Richdale, 1965b.
60	53	86-106	96.7 ± 4.7	4.86	Richdale, 1963.
64b	53	62-76	69.3 ± 3.0	4.27	Harris, 1966.
71c	40	52-67	57.3 ± 2.8	4.89	Richdale, 1965a.
74	32	56-73	62.8 ± 3.5	5.57	Davies, 1957.
83a	?	47-59	53.7 ± 2.5	4.65	Richdale, 1965a.

birds are ready to leave also plays a part. Calms or gales tend to delay departure and lengthen nestling periods, an effect that is most readily detected among surface nesting species like *Macronectes* (Warham, 1962) and *Diomedea epomophora*; the latter's chicks may require a wind speed of at least Beaufort Scale 3 for their first flight (Richdale, 1952).

The pattern of growth in the nestling is generally similar to that of von Bertalanffy's third type (where metabolic rate is proportional to a figure intermediate between body weight$^{1.00}$ and body weight$^{0.75}$) in which the curve for weight increase is of a decaying exponential pattern without any point of inflexion whereas the curve for linear growth e.g. that of the wing, is S-shaped with a point of inflexion (von Bertalanffy, 1957). However, the weight of a growing petrel chick generally levels off at a figure well above that of adult weight and then declines somewhat to fledging. Departure generally occurs when the chick is 5 to 10% heavier than the adult. During growth a

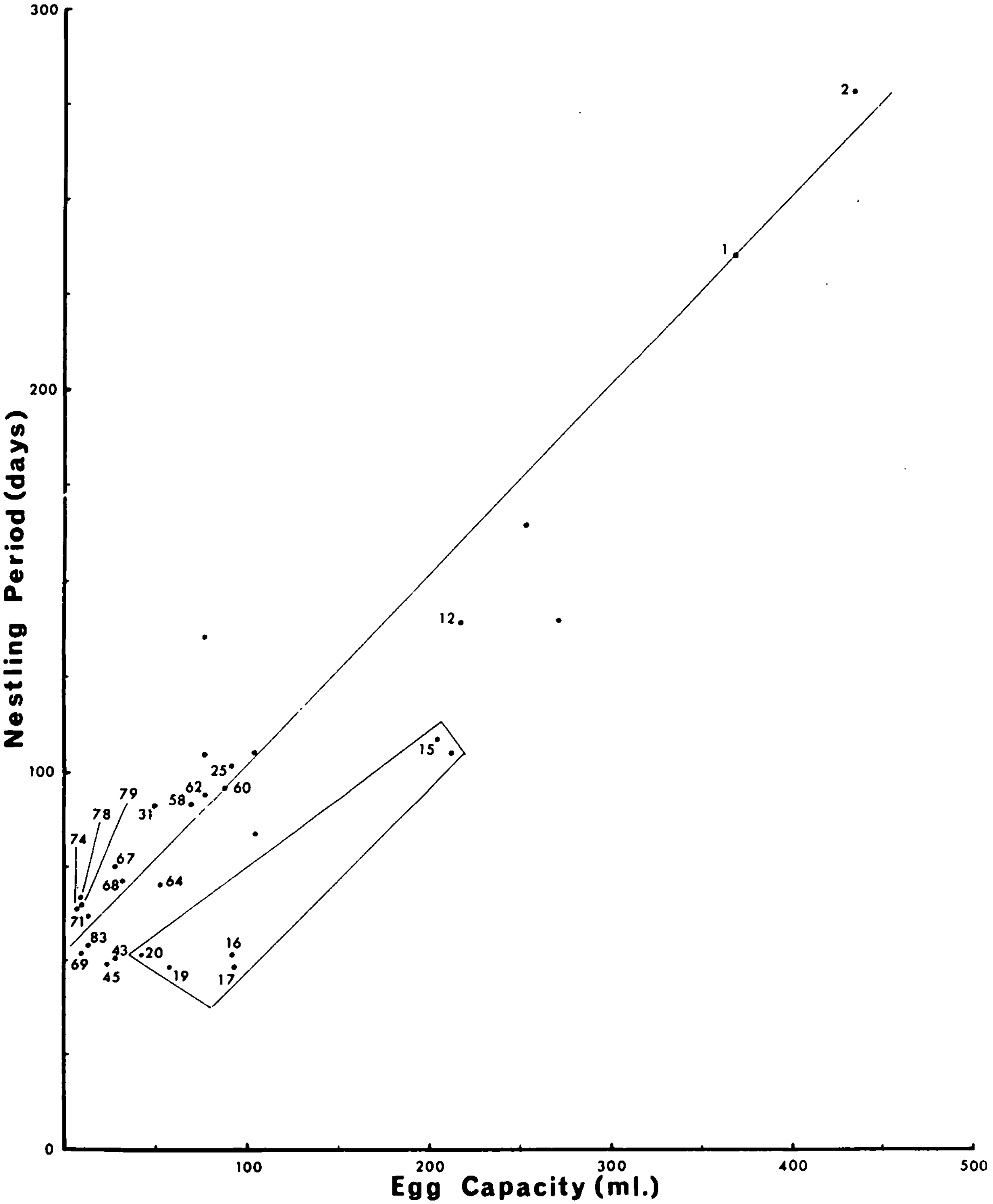

FIG. 26. NESTLING PERIODS & EGG CAPACITIES IN PETRELS.

considerable amount of depot fat is laid down but this does not seem to have been measured precisely in any petrel and in the light of recent work on the Swallow *Hirundo rustica* (Ricklefs, 1968), where the excess in weight reached by the nestlings above that of the adult can all be accounted for by the accumulation of water in the tissues, the question of the peak weights of petrels needs further investigation. Lack (in press) discusses the role of these fat reserves and Harris (in press b) details of growth rates in petrels of the genus *Puffinus*.

Apart from its weight the fledgling's dimensions are almost those of the adult. Some slight feather growth often follows fledging and chicks may fly with down still adhering to their bodies but it seems that the development of the flight feathers is not mainly dependent on the state of nourishment of the young bird but rather to hereditary factors (Lack, in press), at least in *Puffinus puffinus*.

11.8. Nestling Period and Egg Size.

Figure 26 shows the relationship between mean nestling period and mean egg capacity for 29 species. The data come from Table XIII. All available data are plotted but only those points based on exact determinations of nestling period are numbered.

The correlation between these variables for 24 species ($r = +0.9535$; $P < .001$) and the distribution of the points suggest a linear relationship, particularly if the plots for the fulmars (boxed in the figure) are omitted. The equation for the regression line, which is based on figures for the 19 non-fulmarine species, is:

$$Y = 0.496X + 52.61 \quad \ldots\ldots\ldots\ldots \quad (22)$$

where Y is the mean nestling period in days and X is the mean egg capacity in millilitres.

There is a good deal of scatter about the trend line but the most marked deviations are for the fulmars which plot far below the line. They have much shorter nestling periods than would be expected on basis of their egg sizes judged by the relationship between these variables in other petrels. Thus the Northern and Southern Fulmars

(16 and 17) succeed in rearing their chicks in around 50 days whereas two species that lay eggs of similar sizes to theirs, Pterodroma lessoni (25) and Puffinus griseus (60) require nearly 100 days to do this. The four species of medium-sized fulmars actually take less time to rear their young than do the storm petrels (69-79) although these are much smaller birds laying much smaller eggs. Other species that plot well below the line are the two prions (43 and 45) and an albatross (12). The plot for the latter (P. palpebrata) is based on only two nestling period determinations and the true picture may be different but it is interesting to note that apart from one of the prions, all the petrels that plot well below the trend line are breeders in high altitudes where the seasons are short but days long.

Figure 26 does not show the lowest nestling periods recorded in petrels. These also concern fulmars. They are the mean value of 46 days for the large form of Pagodroma nivea studied by Prévost (1964) and the range of 35 to 45 days for Fulmarus glacialis breeding in the Barents Sea region according to Belopol'skii (1961) and discussed in section 11.12 below.

The birds that plot furthest above the line consist of three storm petrels (74, 78 and 79), a shearwater (67) and a gadfly petrel (31). All inhabit temperate or tropical seas and all are non-migratory, dispersing rather than moving rapidly after breeding to contra-nuptial areas. The only storm petrel to plot below the line is Oceanites oceanicus (69), a highly migratory Antarctic breeder. Although this lays an egg of substantially the same size as Oceanodroma leucorhoa, the Antarctic bird succeeds in rearing its chick to flying in only 78% of the time needed by the other species. However, only one determination of nestling period has been made. The data for Pterodroma macroptera are unsatisfactory. Elliott (1957) estimated the nestling period at about 105 days against which the two determinations of 128 and 134 days given by Warham (1956) seem very high. They were obtained with the help of lightkeepers and could represent the upper extreme of a wide range of values but a mean closer to Elliott's estimate seems more likely to be correct. The petrels whose plots lie close to the line show an intermediate condition between the rapid development of the fulmar chick and the slow develop-

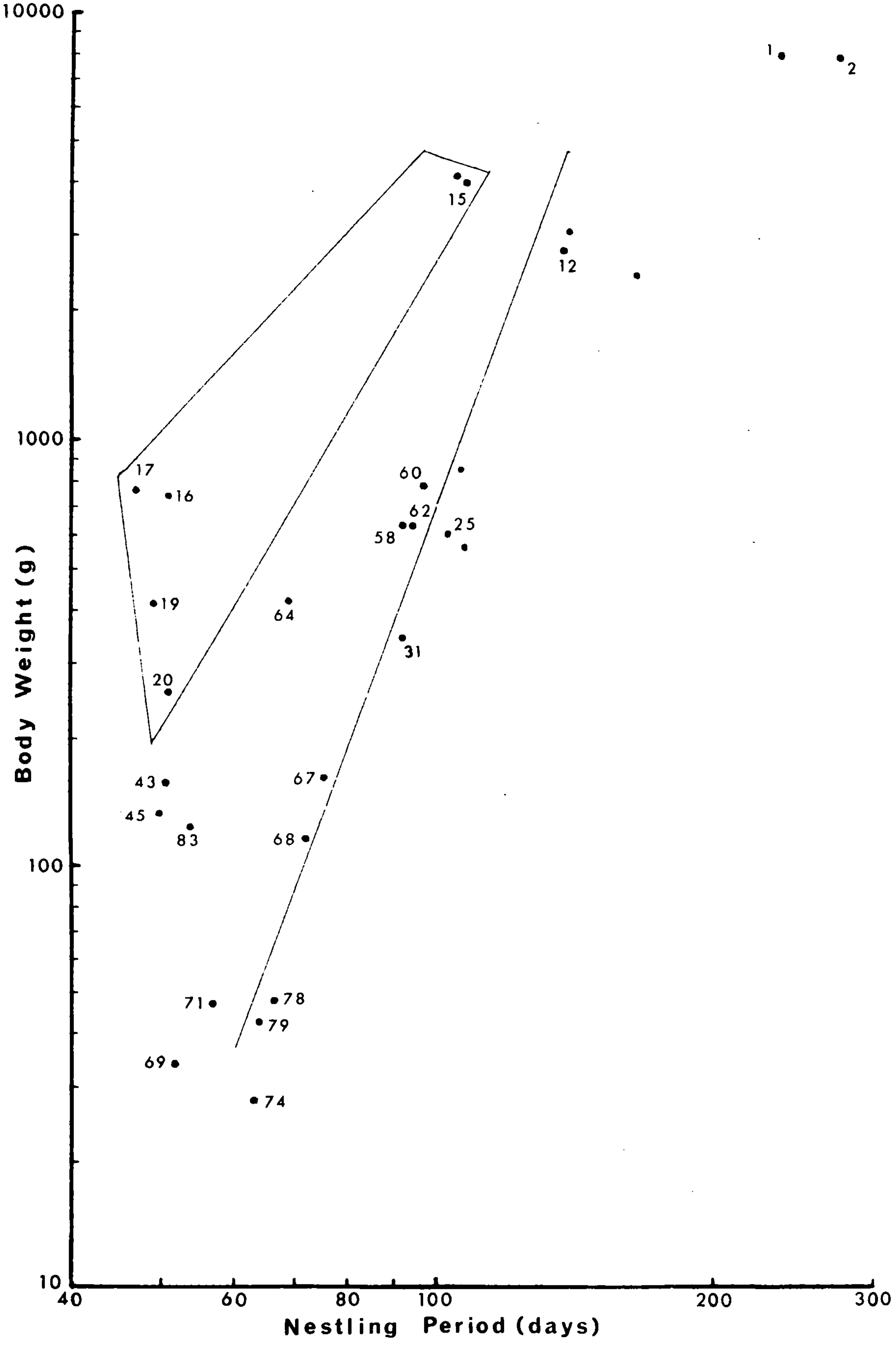

FIG. 27. NESTLING PERIODS & BODY WEIGHTS IN PETRELS.

ment of non-migratory warm-water species. They include four highly migratory shearwaters (58, 60, 62 and 64) at least three of which desert their chicks towards the end of the nestling period apparently in order to begin their great migrations. Puffinus gravis (57) would probably also plot in this category but the available data for nestling period (c. 105 and 84 days) are anomalous. Pterodroma lessoni (25), which falls close to the trend line, is probably best regarded as non-migratory as, like P. macroptera, it is absent from its nesting grounds for only about two months (Warham, 1967). Its position is however only based on a single determination for nestling period.

Because of the wide scatter about the regression line, equation 22 is unlikely to have much predictive value. More information is needed particularly from the larger petrels of the genus Procellaria and from the mollymawks in the genus Diomedea for the relationship between egg size and nestling period to be adequately elucidated.

11.9. Nestling Periods and Body Size.

Large petrels take longer to rear their young to fledging than small ones do and for 14 species for which there are adequate data on body weight and nestling period $r = +0.9508$; $P < .001$. These two variables are not, however, linearly related. Plotted on arithmetic axes the points appear to lie along a curve but the relationship is complicated by the situation among the fulmars which rear their chicks more rapidly than do other petrels of similar weights. The same picture emerges when (mean wing length)^3 is plotted against nestling period.

The data are plotted on logarithmic axes in Figure 27. Body weights are from Table XX and Appendix A but the figures used are the means for adults of both sexes, not for females only as in previous diagrams. This makes no significant difference to the species plots but does provide larger samples for the factor of body size. Some weights have been calculated from standard wing lengths using equation 3. Only the points based on accurate determinations are numbered.

Logarithmic plotting emphasises the data at the extremes of the ranges of values and it will be seen that for species with nestling periods of 50 to 60 days there is little, if any, correlation between the two variables. The fulmars are indicated separately: in respect of body weights these birds have very short nestling periods. Their position is similar to that obtained when incubation periods and body weights are compared - Figure 21.

A trend line has been inserted by eye using the data for all species except the fulmars. In relation to this line it will be seen that while most of the shearwaters (58, 60, 62, 67 and 68) and two gadfly petrels (25 and 31) lie close to the line, the large albatrosses (1 and 2), the prions (43 and 45), one shearwater (64) and a diving petrel (83) do not.

The large albatrosses take far longer to produce flying young from their hatchlings than they would if the growth rate conformed to the trend line. The prions, diving petrel and <u>Puffinus puffinus</u> show the reverse tendency, raising their young more quickly relative to their body size than would be expected. Furthermore, two of the five storm petrels (71 and 69) have relatively short nestling periods while the others (74, 78 and 79), as Figure 26 also indicates, have relatively long ones. These variations tend to follow those found with incubation periods but it is not clear why <u>Puffinus puffinus</u> should be so atypical compared with other migratory shearwaters. The unexpectedly short nestling period of <u>Pelecanoides</u> is discussed in the next section.

In general, the relationship between nestling period and adult weight tends to reflect that between nestling period and egg capacity but partly because egg size and body size are not linearly related, neither are body size and nestling period.

To allow for the factor of body size the relationship between nestling time per unit weight of adult and adult weight has been examined in Figure 28 where the line relating incubation time per unit weight of adult to the same variable is also shown (see Figure 22). The data are from Table XX.

A linear relationship exists between the two variables but the regression line relating nestling period per unit weight to body weight, which is

$$Y = 2.3549 - 1.200X_n \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots \quad (23)$$

(where Y = log mean adult weight in g and X_n = log mean nestling period per kilo of adult in days) does not coincide with that representing the relationship between incubation period per unit weight and adult weight. This is

$$Y = 1.9145 - 1.099X_i \quad \ldots\ldots \quad (24)$$

where X_i = incubation period per kilo of adult in days. The two lines have different gradients, that for nestling time corresponding with a power relationship of $X_n^{-1.20}$, that for incubation times corresponding with one of $X_i^{-1.10}$. The data for nestling times per unit weight are also more dispersed about the regression line ($r = -0.9978$ for incubation times, $n = 20$; $r = -0.9075$ for nestling times, $n = 24$).

This difference in slope means that the rate of production per unit weight of petrel during the nestling period is less than that during incubation. Figure 28 shows also that the fulmars (16, 17, 19 and 20) produce unit weight more rapidly than other petrels of similar sizes. The two large albatrosses (1 and 2) diverge most markedly for whereas during incubation they produce unit weight of albatross more rapidly than any other petrel and the data plot very close to the regression line, in the nestling period they produce unit weight more slowly, taking about 30 days per kilogram instead of the 18 days per kilogram needed to conform with the regression line. That they plot so far from that line is not due to inadequate data. Those for species 2 are good and while only two nestling periods are available for subspecies 1a they show a close agreement with a longer series for the subspecies 1b and they could not possibly be short enough to bring the point for this species onto or near the regression line. Even so, these birds still produce more efficiently on a weight-specific basis than smaller petrels which is one advantage of large size. The storm petrels (69 - 79) also all lie to one side of the regression line and suggest that at this end of the size scale also efficiently falls away.

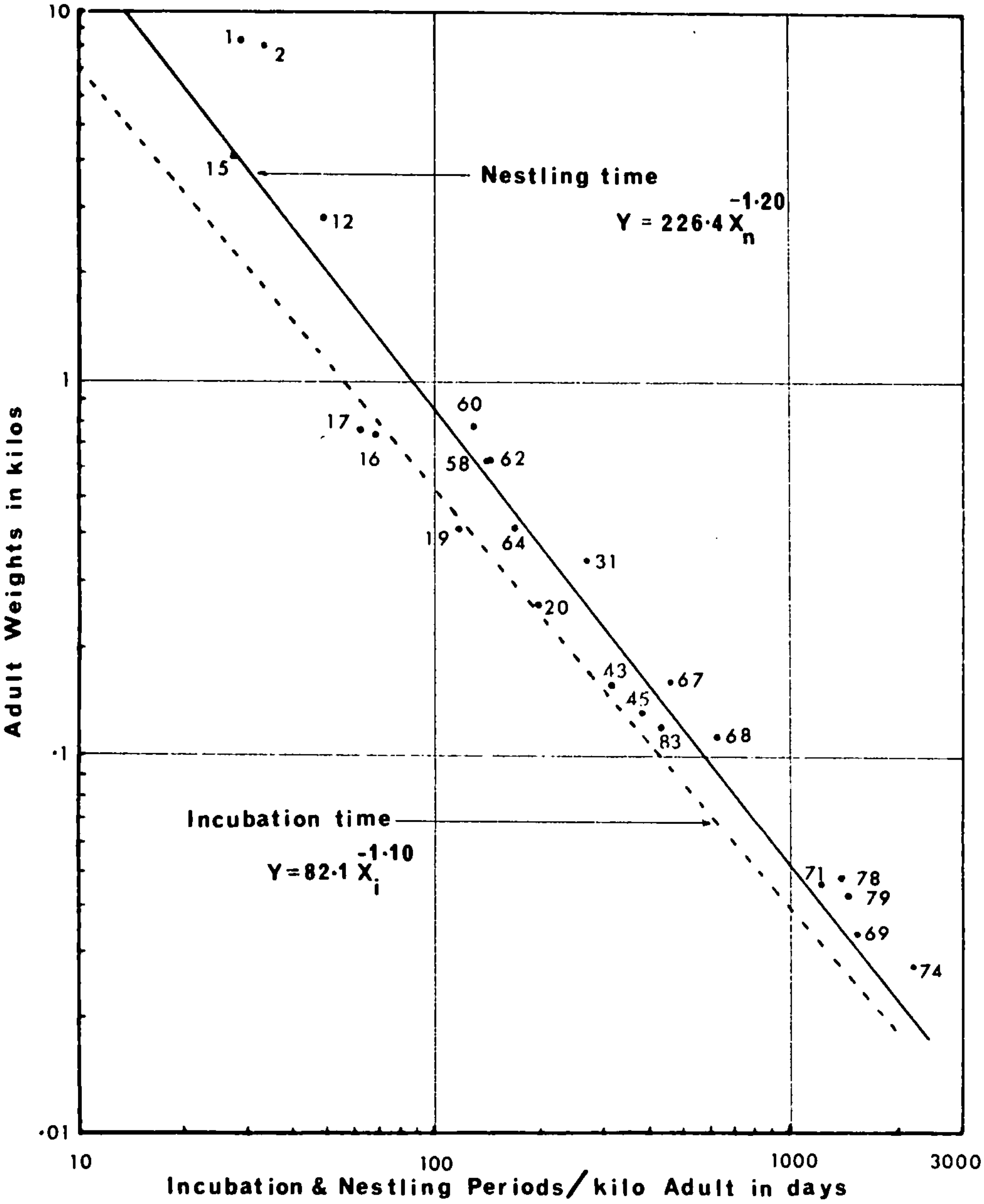

FIG.28. ADULT WEIGHT v DEVELOPMENT TIME PER KILO OF ADULT IN PETRELS

TABLE XX: DEVELOPMENT RATES TO FLEDGING IN PETRELS.

(Sample sizes in parentheses)

Species	Body Weight (kg)	Nestling Period (days)	Nestling Time / kg Adult (days)
1a	8.389 (14)	240 (2)	28.6
2b	8.190 (105)	278 (35)	33.9
12	2.838 (10)	139 (2)	49.0
15	4.052 (9)	108 (7)	26.7
16	0.739 (18)	51 (6)	69
17	0.762 (32)	47 (24)	62
19	0.415 (45)	49 (15)	118
20	0.260 (27)	51 (7)	196
31	0.344 (1*)	92 (32)	267
43a	0.159 (124)	50.5(22)	318
45	0.132 (100)	50 (139)	379
58	0.632 (19*)	92 (3)	146
60	0.787 (100)	97 (53)	123
62	0.635 (54)	94 (18)	148
64b	0.423 (18)	69 (53)	164
67b	0.163 (13)	75 (41)	460
68f	0.116 (25*)	72 (3)	621
69	0.034 (10)	52 (1)	1529
71c	0.047 (100)	57 (40)	1219
74	0.028 (50)	63 (32)	2243
78a	0.048 (66)	66.5 (5)	1385
79b	0.043 (12)	64 (53)	1488
83a	0.124 (100)	54 (54)	433

* Calculated Value.

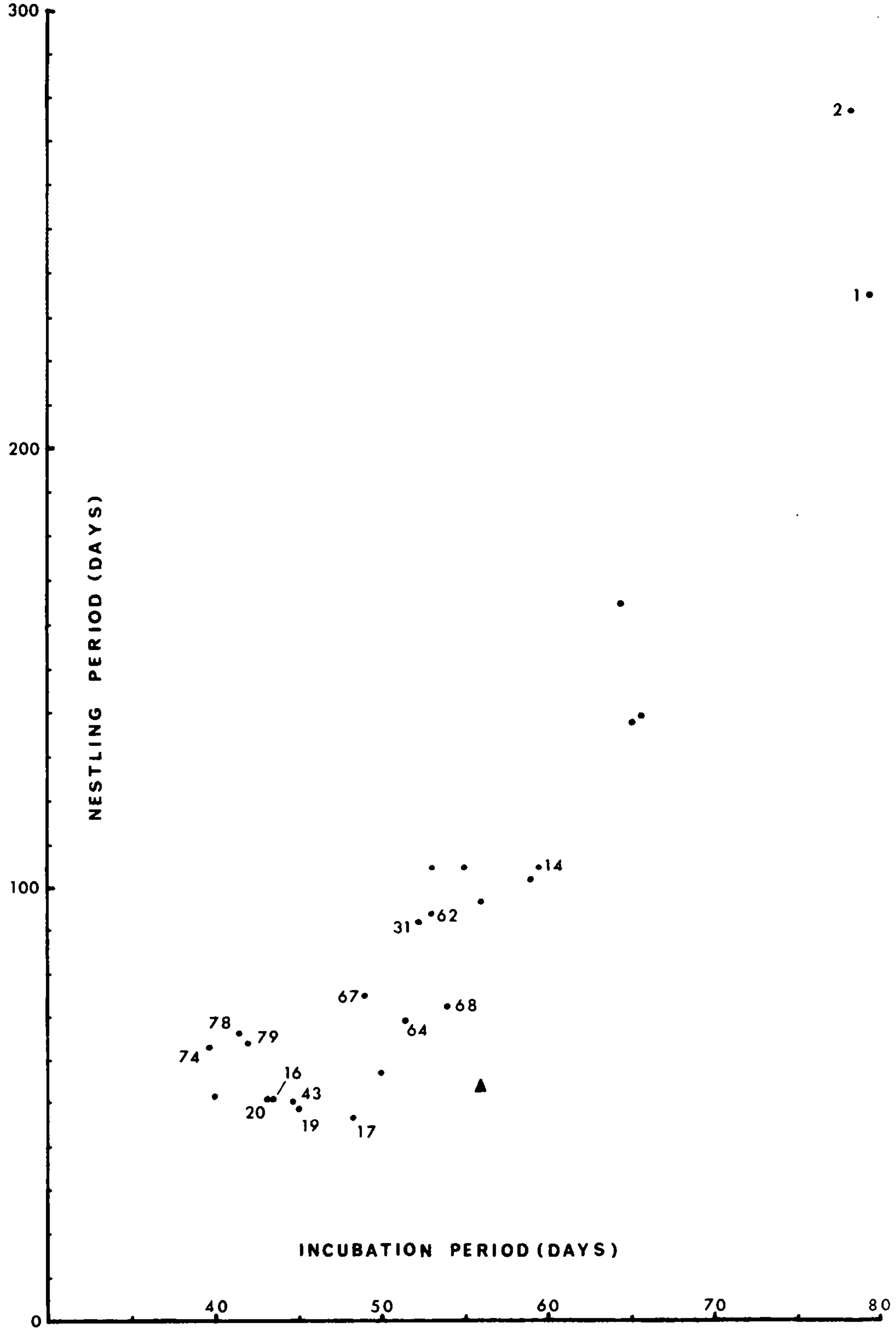

FIG.29. INCUBATION & NESTLING PERIODS IN PETRELS.

11.10. Nestling Periods and Incubation Periods.

Petrels with short nestling periods also tend to have short incubation periods, as shown by Lack (1967). For 14 species for which adequate data are available (Table XIII) the correlation between these two variables is significant with $r = +0.9508$; $P < .001$. The data are displayed on arithmetic axes in Figure 29. They suggest a curvilinear relationship.

The correlation between incubation and nestling periods shown in the preceding sections may reflect direct causal relationships. Thus a small egg would be expected to hatch sooner than a large one if only because less material has to be converted into living tissue. Likewise, the size of the hatchling will vary according to the size of the egg from which it is produced and other factors being equal, the time to complete development to adult size would be expected to relate to this initial size at hatching. Hence with small petrels that produce large eggs relative to their body sizes a greater proportion of the total time from laying to fledging would be expected to be devoted to incubation than with a large petrel which lays an absolutely larger egg but one that is smaller relative to body size and therefore produces a relatively small chick. In that case the proportion of time spent in incubation should be smaller in respect of total development time.

Figure 29 indicates that this is generally true, so that the larger species lie to the right of and above the smaller ones. Thus for the large species 2 (D. exulans) the nestling period is about 3.6 times that of the incubation period; for medium-sized species 62 (P. tenuirostris) only about 1.8 times as long, while the chick of the small species 79 (O. castro) is in the nest only 1.5 times as long as it is in the egg. Nevertheless, this cannot be the whole story as otherwise the points in Figure 29 would all plot neatly along a curve of an ascending exponential type.

It will be seen that the species that lie close to the origin include not only the smallest ones - the storm petrels (74, 78 and 79) - but also the much larger medium-sized fulmars (20, 16, 19 and 17) with Pachyptila desolata (43). Oceanites oceanicus (69) may rightly belong among this group but the data are inadequate.

It is interesting to note that on the evidence available, the closely related fulmars F. glacialis (17), and F. glacialoides (16), each of which requires about 95 days from egg laying to produce a fledged chick, do not achieve this in quite the same way. With glacialoides the nestling period is shorter than the incubation period whereas in glacialis the reverse seems to hold. Their egg and body weights, however, are almost exactly the same.

Pelecanoides occupies a peculiar position. It is unnumbered in Figure 29 as the data are only approximate but is indicated there by a triangle. With this bird the ratio of the nestling to incubation periods is about 1.0 despite the small egg relative to body size (section 7.1). On the basis of its egg capacity this species should have an incubation period of around 44 days (equation 19) rather than the 56 days of Richdale's estimate. Again, while the plot for the nestling period against egg capacity places Pelecanoides quite close to the trend line, this too is unexpected. As the egg is small, the hatchling must also be small so that longer time should be needed for development to adult size. Part of the explanation for the latter anomaly may be that the chick does not fledge above adult weight as most petrel fledglings do (Richdale, 1965a; Lack, in press) so that its state on departure may not be truly comparable with those of other Procellariiformes. Furthermore, according to Lack's reasoning (1967 and in the following section) the inshore feeding of this bird allows more frequent chick meals leading to a rapid growth rate during the nestling period.

11.11. Discussion on Development Rates.

It has been shown in the previous section that there are underlying regularities in the times taken by different species of Tubinares to produce fledged young. These times are correlated with body size and egg size. No petrel, as far as is known, can raise a flying chick from the egg in less than about 95 days. For the very large species about a year is required.

If it is assumed that the relationships demonstrated above reflect fundamental ordinal characteristics of the petrels controlled by a common genetic constitution that is also responsible for their common morphological features, then it would seem that the lengths of these developmental phases are capable of modification in the course of natural selection.

The most notable exceptions to general trends in development rates are shown by the fulmars, species 14, 15, 16, 17, 19 and 20. Unfortunately there is little information for *Thalassoica* (18) but Orton (1968) indicates that 13 weeks elapse from egg laying to chick departure, so that evidently in *Thalassoica* development is also rapid. These are all birds that breed in or close to the polar regions although the Arctic *F. glacialis* has spread south in recent years while *Macronectes* may have speciated and spread north recently to lower latitudes in the Southern Ocean. All these birds breed in the open on flat ground or on cliff ledges and cavities among rocks that provide limited shelter from the weather. In these high latitudes summers are short but the summer days are long.

Recent studies of two Antarctic species, *Daption capensis* by Pinder (1966) and *Pagodroma nivea* by Brown (1966) show that while the dates of re-occupation of the breeding sites are correlated with the dates of break up of the pack ice, the peak of egg laying is remarkably constant from year to year, all the eggs being laid within a week on either side of the mean date. This synchrony is also seen in the hatching dates. The rigid time table suggests that the period during which breeding is possible (when day length is adequate, surface plankton plentiful, the feeding grounds available at a convenient distance from the nest site and the latter safe from icing or snowing up) is limited. Maher (1962), Prévost (1964), Brown (1966) and Pinder (*loc.cit.*) have all discussed aspects of the environmental problems faced by these birds and Prévost also examined the micro-climate of the nesting sites.

Such restricted breeding seasons are paralleled by those of highly migratory petrels like *Puffinus tenuirostris* which seem to be able to perform their vast flights only by speeding up the breeding cycles and actually deserting their unfledged chicks. The *Daption* chick flies at the end of February and the *Pagodroma* and *Thalassoica* chick flies about the same time and these, together with those of F. glacialoides (Prévost, 1964) and Macronectes giganteus (Warham, 1962) seem to reach the sea when the food supply is at a maximum if the state of the surface plankton sampled in Foxton's study (Foxton, 1956) applies also to the foods of these species.

Polar conditions appear to give the petrels little room for manoeuvre in breeding timetables. They are prevented from laying any earlier than they do by the danger of ice or snow blockage of their nest sites, by the short days and extensive sea-ice that curtails photo-synthesis and, at the end of the season, by the return of these conditions and the annual descent of the plankton. Were these birds to require the normal times for development characteristic of other petrels of the same size it seems unlikely that successful breeding could occur. A shearwater or gadfly petrel the size of F. glacialoides requires about 150 days to produce flying young from its new laid egg; the fulmar does this in about 60% of that time. Such abbreviated breeding seasons appear to be adaptations developed for breeding in a marginal environment whose exploitation is possible only on the basis of prompt exploitation of a seasonal flush of food and nest sites.

There is evidence too that among the fulmars there are differences in the development times; that the adjustment to local conditions has not been uniform. For Daption capensis there is apparently little evidence of variations with latitude, the birds studied by Prévost (1964) at Pointe Géologie (66°S) having similar incubation and nestling periods to those at Signy Island (60°S) investigated by Pinder (1966). On the other hand there may be significant differences between the populations of Pagodroma at Pointe Géologie and at Mawson and Davis (68°S) as may be seen when Brown's and Prévost's data for these two birds are compared (Table XXI). Whereas Daption at the two breeding places does not differ in body size, Pagodroma at the two Antarctic mainland sites does. Relevant data are:-

TABLE XXI: DEVELOPMENT TIMES IN TWO POPULATIONS OF PAGODROMA

(Sample sizes in parentheses)

Site	Body Wt. (g)	Egg Wt. (g)	Incubation period (days)	Nestling period (days)
Pointe Géologie	347 (6)	59.6 (6)	c.40	46 (6)
Mawson and Davis	244(13)	47.4(21)	43.2	51 (7)

Despite the small size of the samples the data do indicate that a real difference exists between the two populations. The Pointe Géologie birds succeed in raising their young in less time than the birds of the smaller form. The data are reinforced by the annual time table at the two stations, for the birds at Pointe Géologie succeed in getting their chicks to sea by about the same date (6 March) as those at Mawson and Davis despite the former's laying about 5 days later than the latter. Even were the rearing periods of the two forms identical, that the larger form takes the same time would indicate an effective acceleration of development since larger petrels take longer to develop. There is no evidence that the chicks at either station fly at different stages of development and although the eggs of the larger form are larger, producing larger hatchlings they bear a lower ratio to the body weight of the birds that lay them (16%) than obtains with those of the smaller form (19%). The reason for the later laying at Pointe Géologie appears to be due to somewhat more severe climatic conditions at that time than at the two other breeding places.

It seems clear that Pagodroma, the smallest of the fulmars and yet the most southerly breeding perhaps of all birds - flocks have been seen around a mountain top about 415 km. from the sea by Fuchs and Hillary (1958) - has exploited a considerable capacity to speed up both incubation and chick rearing. The latter could be a consequence of parental access to a rich food supply but this could hardly affect incubation periods unless particularly high energy materials are incorporated in the egg. It seems more likely that the major factor is genetic, that selection has been severe and operated on a species with the potential to adjust development times to a considerable extent. It would be interesting to have data on the breeding cycles at the inland colonies of Pagodroma such as those seen by Lovenskiold (1960) to learn if these birds, faced with energy consuming flights of 200 km and more between their nests and the sea, have modified their development rates still further.

Inspection of Figure 26 shows that relative to egg size (or capacity) Pagodroma (20) does not deviate from the regression line more than do other small or medium sized fulmars which all have very similar nestling periods. Perhaps this means that in this respect adaptation has proceeded to its limit and that any further acceleration is impossible unless the chicks leave the nest at an earlier stage of development, as may perhaps obtain with fulmars of the Barents Sea discussed later. As regards incubation periods (Figure 20) it will be seen that relative to egg size Pagodroma (20), Daption (19) and F. glacialoides (16) show equivalent degree of adaptation whereas F. glacialis (17) shows less. However, data on incubation periods for the form of the latter bird breeding at the northern fringe of its range at about 80°N are not available.

These conclusions run counter to those of Maher (1962) who discussed food and climate in relation to the breeding cycle of Pagodroma at Cape Hallett. He collected no data on incubation or nestling periods but estimated the total time involved as being from 100-120 days. He was apparently unaware of Prévost's determinations and does not seem to have appreciated the importance of body size or he would not have compared development rates of Pagodroma with Oceanites and concluded that Pagodroma has not shortened its incubation period or rate of development in adapting to the Antarctic.

Evidence from the Arctic also suggests that fulmars in that region have speeded up their development rates in adapting to a marginal habitat. The data, summarised by Belopol'skii (1961) are unfortunately rather inadequate and not always consistent. According to work quoted by this author the nestling period of F. glacialis in the Barents Sea ranges from 35-45 days which is considerably shorter than the European data given in Table XIII. Furthermore, it seems that the duration of the nestling period may be longer for early hatched chicks than for later hatched ones. This shortening of the nestling period seems to be in part at least due to the descent of the chicks to the sea before they reach adult size and before they are able to fly.

It is not clear what advantage this system offers as it seems most unlikely that the parents feed their chicks once they leave the nest and unlikely too that self-feeding could be effective in the absence of flight. Perhaps it is better to experience a period of fasting at sea and remain in open water during the final stages of maturation rather than freeze on the nesting ledges while the belt of sea ice widens below even though the parents may continue bringing food. On the other hand these colonies apparently experience conditions more extreme than those in much of the Antarctic for Belopol'skii reports that laying takes place with ambient temperatures as low as -25°C. The possibility of early nesting in Novaya Zemlya is attributed to the flying powers of the fulmars which give them access to adequate high energy foods beyond the edge of the ice and at great distances from the nesting places. This author also states that the nestling period of the F. glacialis is shorter in regions with more severe climates and this he believed applies not only to this sea bird but to others breeding in the Barents Sea region such as the Kittiwake.

Macronectes appears to have accelerated both its egg and chick development. This is less Antarctic in its range than the other fulmars previously discussed and the main populations breed at lower latitudes on either side of the Antarctic Convergence. At Macquarie Island at least M. giganteus is present at its nest throughout the year so that these birds would seem to be subject to comparatively little pressure for accelerating development at the present time. Yet once acquired the benefits of shortened nestling periods seem unlikely to be relinquished. It seems possible that during the Pleistocene Macronectes experienced selection pressures similar to those operating on the Antarctic species today and that the shortened nestling periods evolved then have since been retained.

Lack (1967) has suggested that it is the inshore feeding sea birds which have the shortest incubation and nestling periods. He has extended this hypothesis to the Procellariiformes by assuming that the frequency of feeds given to the chicks is a measure of the feeding range of the parents. He draws attention to the frequency of chick feeding in Pelecanoides, the chick's rapid rate of growth and its departure at only about adult weight.

This hypothesis cannot be tested at present as far as it applies to petrels generally owing to inadequate data but while a high frequency of visits to the chicks by the parents certainly implies a limited feeding range, the reverse is not necessarily true and Serventy (1967) provides evidence that in Puffinus tenuirostris (which does not feed its chick frequently) much of the food in the adult's stomach on arrival has been caught only a few hours before. Furthermore, the fulmars, with their outstandingly rapid development rates, are not necessarily inshore feeders. At least one of these breeds 200 kilometres inland and it seems most unlikely that birds at these high-latitude nesting places have longer incubation or nestling periods than those breeding on the Antarctic coastline.

Lack (in press) has taken his investigation of the growth rate in petrels further particularly in respect of the food supply available during the breeding seasons. He believes that these birds, as an alternative to altering their clutch size, have adapted their growth rates to the local food conditions. Development is discussed in the light of the fat reserves laid down by the chick, the presence or otherwise of a desertion period, body size and other factors. He comments on the rapid development of the fulmars and interprets this, as I do, as an adaptation to polar conditions.

The evidence on development rates for petrels of warm and tropical seas suggests a different situation. It has been shown in section 11.2 that relative to egg size at least two non-migratory warm water petrels have long incubation periods while five non-migratory tropical or temperate zone species also take unusually long to rear their chicks relative to their egg size.

Very recent information (Harris, in press, b) indicates the plasticity of the nestling period in Oceanodroma castro. At the Galapagos Islands he found that 19 chicks flew at a mean age of 70 days in the hot season whereas 25 chicks were ashore for a mean period of 78 days in the cold season, this being a species that breeds throughout the year at this station (Snow and Snow, 1967). Yet at Ascension Island 53 chicks of the same species flew on average at age 64 days (Allan, 1962). Incubation periods, on the other hand, are the same at both places.

The above considerations indicate that the times needed for incubation and chick rearing have been subjected to modification in the course of evolution at least in some petrel genera. Incubation period appears to be less pliable than nestling period but modifications of the one are often accompanied by modifications to the other so that common genetic factors may be involved. It seems likely that long incubation periods are the original condition in this order and that the fulmars have been helped in their invasion of the polar regions by their ability to speed up development times. Indeed it may well be that this trend to shortened development times has operated widely during the evolution of the order and that the situation with sedentary tropical species represents a retention of the primitive state rather than its modification from one where development rates were faster.

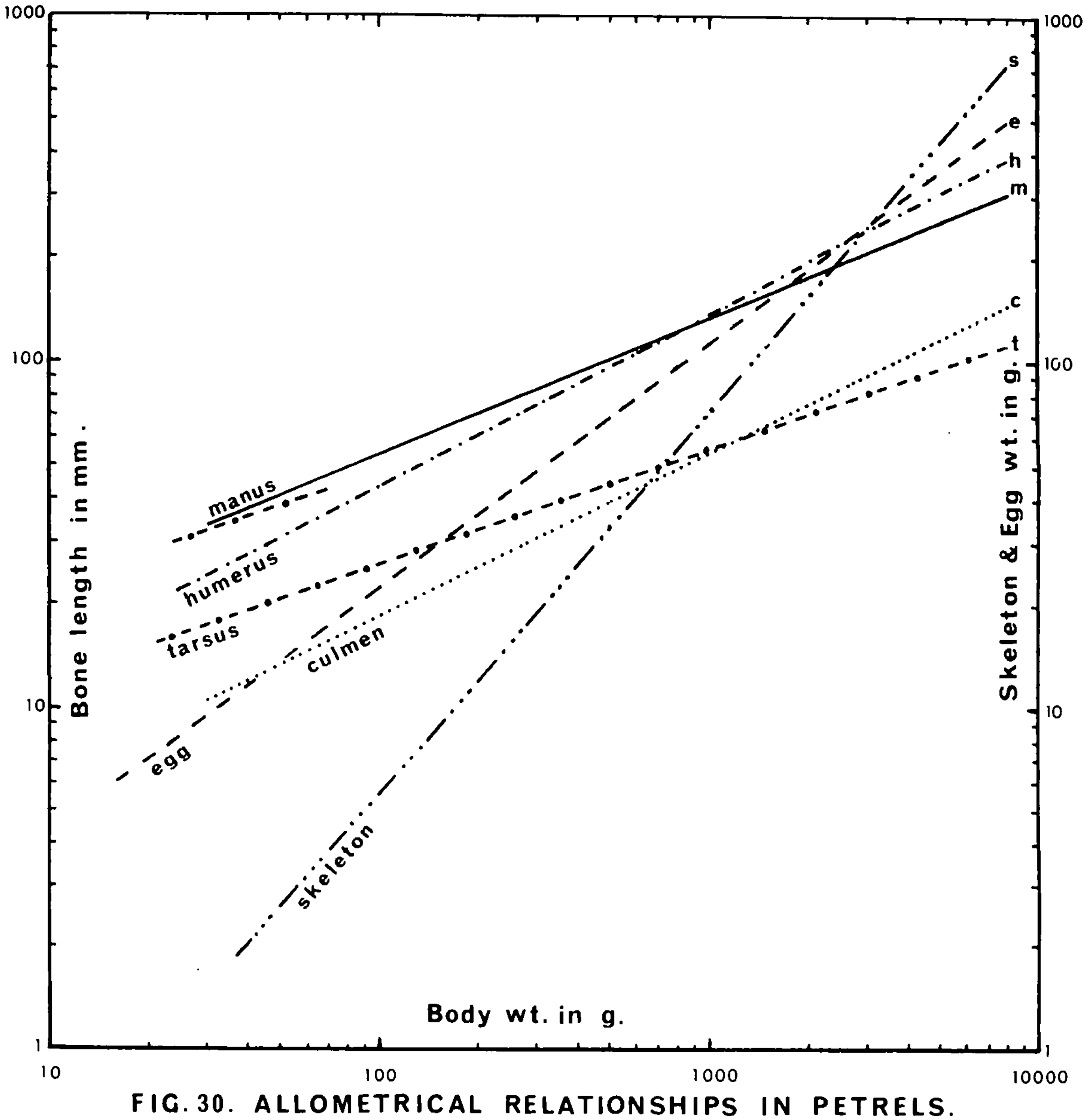

FIG. 30. ALLOMETRICAL RELATIONSHIPS IN PETRELS.

12. GENERAL DISCUSSION

It has been shown in previous sections that throughout the Procellariiformes harmonious relationships exist between body size and a number of variables such as the dimensions of body parts, egg weight and growth rates: these relationships can be described by a series of empirical equations. Some variables are linearly related to body size but more usually the part is a parabolic function of the whole and the relationship can be represented by means of a logarithmic or power equation. Thus the relationship of standard wing length in centimetres (y_w) to mean female body weight in grams (x) is given by equation 4a:-

$$y_w = 4.90x^{0.29} \quad \dots\dots\dots\dots\dots\dots \quad (4a)$$

while fresh egg weight in grams (y_e) is related to mean female body weight in grams (x) as follows:-

$$y_e = 0.859x^{0.71} \quad \dots\dots\dots\dots\dots\dots \quad (6)$$

The importance of body size in determining the dimensions of parts and organs is explored further in Figure 30 where a series of variables is plotted against body weight on logarithmic axes in addition to the curve relating egg weight and body weight from Figure 6. These additional curves relate the weights of the dry skeleton in grams (y_s); the standard lengths of tarsus and culmen in millimetres (y_t and y_c); the lengths of the cleaned bones of the forearm: humerus (y_h), ulna (y_u) and manus (y_m) in millimetres, to mean body weight (x) in grams. The regression lines are:-

$$y_s = 0.035x^{1.1} \quad \dots\dots\dots \quad (25) \qquad n = 10 \text{ species}$$

$$y_t = 5.7x^{0.31} \quad \dots\dots\dots \quad (26) \qquad n = 43 \text{ species}$$

$$y_c = 2.1x^{0.47} \quad \dots\dots\dots \quad (27) \qquad n = 41 \text{ species}$$

$$y_h = 4.3x^{0.53} \text{ .... } (28) \qquad n = 20 \text{ species}$$

$$y_m = 8.6x^{0.40} \text{ .... } (29) \qquad n = 16 \text{ species}$$

Thus the sizes of at least seven body components are related to body size by means of allometric equations of the form

$$y = bx^a$$

where "b" is the intercept on the y axis (the value of y when x is unity) and "a" is the value of the ratio of rate of change of organ size with body size, the "equilibrium constant" or "partition coefficient" between the part and the body.

The data on which Figure 30 is based are somewhat heterogeneous. Further study will undoubtedly show that the values of both constants in the allometric equations need some slight modification. The number of species from which the data have been drawn are indicated beside each equation but whereas for some variables like tarsal and culmen lengths the figures used are the means from long series, for others such as skeletal weights and lengths of the wing bones only a single determination has been made for some species. The data for standard wing lengths and bone lengths come from the literature cited in section 3, from Table I and Appendix A. These data have been supplemented with additional measurements including determinations of skeletal weights.

Of the eight variables egg weight shows negative allometry ("a" < 1) and so too do wing and tarsal lengths ("a" $= 0.33$ for isometry when comparing lengths and a three-dimensional variable). The remaining lengths show positive allometry ("a" > 0.33). Skeletal weight also shows slight positive allometry with "a" $= 1.1$. Here the skeletal weight increases relative to body size with increasing body size. But the exponent figure is only slightly above the value of unity at which the part bears a constant ratio to body size, i.e. is isometric.

The spread of the points about the regression lines varies. For skeletal weights and the lengths of the bones of the forearm the spread is small, for culmen and tarsal lengths, much greater. The variations for tarsal lengths are only partly due to the long-legged species in the Hydrobatidae and further work may show that there is a change of gradient at the lower end of the size range in this variable. Culmen lengths vary too as species of similar weight can have significantly different values for this variable, reflecting differences in bill form not adequately described by a single measurement. For instance, in Puffinus the bill tends to be long and slender, in Pterodroma shorter and deeper, hence in birds of similar size from the two genera, even if the same amount of material has gone into making the bill, this is not revealed by a single linear measurement. Here is another instance where closer study and further measurement may be expected to reveal generic differences in the allometric constants.

The lengths of the humerus and ulna are so close that on the data for the 20 species measured in compiling equation 28, a common regression line seems adequate. The only species ignored in working out that relationship is Pelecanoides urinatrix. This bird, so short-winged for a petrel of its body size, has abnormally short humerus, ulna and manus as pointed out in section 5.2 above.

It is interesting that skeletal weights vary almost isometrically with body weight. Skeletal weights were also isometrically related to body weights in the Felidae studied by Davis (1962). However, in the petrels the larger species have increasingly pneumatised bones and these must play a major part in keeping down skeletal weight. The main bones still unpneumatised in the albatrosses are those of the hind limb. In view of the severe stresses to which these are subject during landings ashore in the absence of strong winds (due to imperfect flight control and high wing loadings), further reduction of skeletal weights by pneumatisation may well be impossible without an unacceptable increase in casualties due to limb breakage. The partition coefficient of 1.1 suggests that this is barely possible up to the present limit of body size.

Figure 30 also shows how the contributions of the separate wing bones vary in a series of petrels of increasing size. All three segments increase with positive allometry with increasing body size but the manus increases more slowly than the other two major bones so that a point is reached where the lengths of humerus and ulna exceed that of the complex of bones comprising the hand. In consequence, while the wings of the larger species are longer than those of the small ones, the relative contributions to this result of the humerus and ulna are greater than those of the manus, as established in section 5.1. This seems to be an example of a widespread tendency in serial organs for the distal parts that develop last to grow at a lower rate than the proximal ones and to be more variable in size. There seem to be proximal-distal gradients of differentiation controlled by growth genes so that the parts of the organ closest to the body obtain more material for growth during ontogeny than do the distal parts. Examples of similar compensation effects are given by Rensch (1966) who points out that this is also evident in the proportions of the bones of the hand in man analysed by Whitely and Pearson (1900). The tendency for the distal wing elements to be more variable while the proximal ones are more stable and less "responsive" to environmental effects, has been noted among other bird groups (Fisher, 1955).

Such changes in the form of the wing skeleton with changing body size have resulted in alterations to the modes of flight which are thus correlated with body size. The small species have a more generalised type of flight, beating their wings frequently and gliding less and for shorter distances than the larger ones. Compare, for instance, the relatively high wing-stroke frequency of small shearwaters like _Puffinus assimilis_ with that of a large shearwater such as _Calonectris diomedea_ which glides so well that in the words of Meinertzhagen (in Lowe, 1925) "When they rise from the water they simply open their wings and glide. Not once did I see a wing flap when taking the air." There may be some minor deviations from this trend (see Murphy, 1936 and Kuroda, 1954 for descriptions of the modes of flight in these birds) but generally, both within families and genera and throughout the order as a whole, the larger the bird the more progression is by planing and gliding and the less frequently are the wings actually beaten for this purpose.

As all the variables in Figure 30 are related to body size they are also related to each other. In a series of petrels graded according to size the dimensions of their parts change according to a regular pattern; they are a function of body size itself and the form of the adult animal changes accordingly.

The existence of these allometric relationships between certain parts and the whole emphasises the homogeneity of the birds that constitute the order Procellariiformes. An extension of the analysis to other characters would be expected to reveal that many of these are also related allometrically to body size. Then, given the value of any one variable for a particular petrel, the other variables could be determined; Adolph (1959) did this for 32 physiological properties of 6 species of mammal. He found that factors like urine output, ventilation rate, tidal volume, basal oxygen consumption and brain, heart, liver and adrenal weights were all linked to body weight allometrically and were therefore related to each other. Likewise Needham (1934) has shown that in metazoan animals the changes in water and other chemical constituents that occur during growth bear allometric relationships to the body weights at a particular time.

The demonstration of "rules" concerning the relationships between organ size and body size in the petrels is not in itself a demonstration of an intimate phylogenetic relationship between the animals concerned for there is an overall relationship, usually of negative allometry, between the organ weights and body weights of birds and mammals as a whole, sometimes called "Welcker's rule". These relationships have been elaborated by Brody (1945) and Rensch (1948), among others. To establish the uniqueness of the relationships among petrels would require a more detailed analysis to show that the allometric constants are significantly different to those relating the particular variable with body size in other groups. This is not possible here without expanding the present study unduly and because data on other birds, equivalent to those available for petrels, are not readily available.

Some comparisons are possible however. Thus the egg weight to body weight relationship for petrels; $y_e = 0.859x^{0.71}$ may be compared with that determined by Brody (1945) for a wide range of birds of many classes where $y_e = 0.257x^{0.73}$. The partition coefficients here are very similar and the different "b" values may be ascribed to the generally large sizes of petrel eggs relative to those of the birds that lay them compared with the situation with birds in general. Also, as noted (section 7.4), Amadon's allometric equations relating egg dimensions to body weights for buntings and quail have quite different values for both allometric constants than has the corresponding equation for petrels.

Allometry is believed to result from the operation of genes or gene complexes which control development rates (Huxley, 1932). Where the relationships hold throughout growth or throughout a taxon, it is assumed that all the members share a common genetic factor controlling the growth gradients and the point at which they cease to operate, i.e. when growth is complete and anabolism and catabolism are balanced (von Bertalanffy, 1957). The actions of the genes responsible must be mediated through specific growth substances, hormones, enzymes and similar agencies and some common control operates to link their action with body size. In other words, organ size is not only correlated with body size but these two variables may be causally linked.

Thus when natural variation and selection produces a change in body size changes of proportions in individual structures due to the operation of gene-controlled allometry, i.e. to allomorphosis, automatically follow. Although the change in body size is adaptive the altered size or shape of the organ may or may not have adaptive value. Likewise, increase in body size may result in the appearance of structures for which the potential was present in the ancestor but which could not be manifest until body size itself had increased. A well known example is the evolution of excessive horns in the Titanotheres (Osborn, 1929). If such excesses prove to be sufficiently dysgenic they may cancel out the benefits accruing to the species by its increased size and such animals will then be removed by natural selection. Selection may also operate on the allometric rates themselves while organs and tissues may be able to respond directly to the physiological needs of the body and vary allometrically without any change in genetic composition.

Control of body size has been shown in some instances to be through a single gene but according to Rensch (1966) more often there are several genes that initiate growth gradients during ontogeny. Where a mutation causes these genes to lengthen the time during which the growth gradient is operative, for example by permitting a growth promoting hormone to circulate for longer or by delaying the onset of maturity, then a larger animal may result and selection could favour such effects. The larger animal will be morphologically different from its predecessors through the operation of the genes controlling all the growth gradients in the body. Thus a harmonious complex of changes in morphology, anatomy and physiology results.

Mutation and natural selection however, may alter the values of either of the two allometric constants. The slopes of the regression lines and/or the size of the intercept on the y axis may be altered. This is perhaps the rule rather than the exception in allomorphosis so that large species are not merely allometric alterations of smaller ones. The gradients also often change during ontogeny, particularly at birth. Another example is the change of gradient that occurs towards the lower limit of size in the relationship between egg weight and adult weight in birds (Huxley, 1927; section 7.1 above).

In some phylogenetic sequences such as that of the horse, phylogenetic allometry closely follows that of ontogenetic allometry so that the allometric constants during growth of a recent species and between related fossil species are similar (Robb, 1935). This is apparently not usual, and does not seem to apply among petrels where the standard wing length, for instance, of the growing chicks does not follow the same gradient of growth as between species although the "a" value is rather similar up to the point when the chick's weight reaches that of the adult. Further examination and comparisons are needed, however, of other variables before any generalisations in this regard are possible.

It seems likely that many of the curves that have been drawn to relate organ size and similar variables to body size in whole classes of animals are actually composite curves. This is indicated, for instance, in some of the relationships figured by Brody (loc.cit.). These variations in growth gradients suggest that in evolution many lines of animals have been able to deviate to some extent from the straitjacket of allometry. Among storm petrels, for instance, Oceanodroma and Hydrobates have tibiotarsi whose proportions are "normal" for their body size, i.e. agree with the allometric relationship of equation 26 whereas in the genera Pelagodroma, Oceanites, Fregetta and Nesofregetta these bones are greatly elongated and their allometric regression line against body weight is different. It is shown in Figure 30 by the short line for tarsus measurements. Natural selection favoured the development of long-legged forms in the Hydrobatidae evidently as an adaptation to a mode of life that involves a dancing flight close to the surface of the sea. Here stilt-like legs tipped by webbed feet not only act as balancers but also act to fend off from the sea's surface while the body and wings are carried well up and avoid being caught beneath breaking crests. A glance at the two lines for tarsal lengths in the figure suggests that in the evolution of the long-legged forms a change of "b" has occurred without a corresponding change in "a", as has happened in the evolution of other vertebrate and invertebrate lines (White and Gould, 1965). However, the long- and short-legged forms are connected via species of intermediate tarsal lengths. Because no body weights are available for these species their positions are not shown in Figure 30, the data being merely calculated from other known parameters like wing length. Data for long-legged forms were not used in calculating equation 26.

Some of the physiological consequences of increase in body size where allometrical growth ratios are involved have been discussed by Rensch (1966). Large birds have lower basal metabolic rates than small ones and basal metabolism is related allometrically to body weight with "a" = 0.743 for birds above about 100 grams according to King and Farner (1961). Large petrels will likewise have lower basal metabolic rates than small ones and, in consequence of lower oxygen consumption, respiration, heart-beat rates and blood pressure are correspondingly reduced in the large forms while, due to the less intense metabolic processes, the periods of ontogenetic development are longer and postnatal growth slower than with smaller species. This applies not only to petrels (section 11) but to birds generally and to mammals. Rensch also shows that, as a rule, sexual maturity is attained sooner in small animals than in large ones but that the latter have longer life spans. The available evidence for petrels certainly supports the first of these propositions and what little evidence we have on longevity would fit with the idea that albatrosses, for example, live longer than the storm petrels. Newell (1949) pointed out that increase or decrease of body size may be a by-product of selection for delayed sexual maturity on the one hand or for rapid growth on the other.

Bachmann (1943) developed a mathematical formula correlating the tempo of ontogeny and mean age to predict the major events of the life cycles of animals. Williams (1957) also developed a theory of senescence which correlates delayed morphogenesis with delayed senescence and several workers, e.g. Loeb and Northrop (1917), found a connection between the duration of life and the temperature regimes under which animals live, those at the lower temperatures living longer than those at the higher one, the Q_{10} for duration of life being approximately 2.

No determinations of metabolic rates for petrels have been published although it is hoped that some will soon be available. However, if resting body temperatures in petrels are indeed lower than those of other birds, so too will be their metabolic rates. Thus their life processes as a whole may well be running at a reduced tempo compared with more advanced birds and in this event the slow growth rates, long periods of immaturity, low annual mortality and high longevity become more explicable.

Low metabolism would be advantageous in the exploitation of environments with irregular food resources, allowing the birds to cruise for long periods between meals and extensive fast ashore during the breeding season. The larger the bird the lower the basal metabolism, the more efficient energy utilisation.

The concept that petrel structure conforms to a ground plan expressible in part by a series of allometric growth equations and in which body size has been a major determinant has implications in the study of the phylogeny of the order. If this is indeed a monophyletic group, except perhaps for the Pelecanoididae, size changes clearly have been dominant trends in the evolution and these would lead to changes in shape, modes of flight and in the size ranges of the foods available to the different species.

Was the ancestral form large and the radiation mainly towards the evolution of smaller forms; medium-sized, leading to both larger and smaller forms; or small, leading to phyletic size increase?

It seems impossible to judge the correct answer to that question but the last possibility seems to rest on less tenuous evidence than the other two. On this view the ancestor of the order may be envisaged as a small bird having many of the facies of the present short-legged storm petrels such as Oceanodroma or Hydrobates. From this a succession of larger forms evolved probably during quite a short period as radiation rapidly proceeded to exploit a pelagic environment where few other birds offered competition. Selection favouring increased size would be accompanied by associated changes in morphology, development and physiology according to the rules that govern the relationships between body organs and body size in recent species, genera, and families, for these rules must have been operative in their phylogenetic ancestors.

It is well known that there has often been a tendency towards increasing size in the course of evolution. This was investigated by Cope (1896) and "Cope's Rule" has since been found to apply in many lines of descent not only in vertebrates but also in invertebrates (Newell, 1949; Rensch, 1959). In many of these instances of phyletic size increase or "phyletic growth", to use Newell's terminology, the ratio of the part to that of the whole remains constant over long periods of the phylogeny. This is evolutionary allometry or allomorphosis (Huxley, Needham and Lerner, 1945). In a sequence with an adequate fossil record many of the allometric constants can be determined. Likewise the palaeontologist may be able to use allometric formulae to determine the sizes of organs or parts of extinct species whose fossil remains are incomplete, using analysis of a series of recent related animals as a basis for deductions about a related phylogenetic series. Gould (1966) has recently reviewed size changes and other aspects of allometry and summarises the benefits resulting from size increase.

If the hypothesis that phyletic size increase has been the major trend in the evolution of the Procellariiformes is correct, we should expect that present-day small forms would retain more primitive characters in their anatomy, physiology and behaviour than the larger forms. There is some evidence that this is so. Thus it has already been pointed out that anatomists Forbes (1881) and Lowe (1925) concluded that the Hydrobatidae, particularly the short-legged forms, are less specialised than the larger petrels and supposedly retain more of the characters possessed by their extinct common ancestor from which both Procellariidae and Hydrobatidae must have been derived. Lowe described and contrasted a number of anatomical features not noted by Forbes that support the separation of the storm petrels as a whole (including both long- and short-legged genera) from other petrels and which emphasise the generalised characters of storm petrel anatomy. Oliver (1945) discussed further details of petrel osteology, particularly the form of the pelvis and vomer and he too concluded that the storm petrels are the most primitive group with *Macronectes* and the albatrosses representing the extreme points of evolution in the order. Kuroda (1954) emphasised the difficulties encountered in trying to separate adaptive from non-adaptive characters. He suggested that the ancestral petrel may have been a small aquatic type perhaps similar to the Oligocene *Hydrornis natator* and that the Pelecanoididae was an early development in the subsequent adaptive radiation. Kuroda envisaged the Hydrobatidae as being an early development in the phylogeny and points out that though these and the Diomedeidae form contrasted extremes each can be connected with the Procellariidae by some characters. The Diomedeidae he considered to have arisen as an offshoot of the main line before the differentiation of the Procellariidae proper but after the evolution of large sized forms in the line leading to the shearwaters.

There is some evidence too from ontogeny that the storm petrel form of bill is a more generalised and therefore presumably more ancient type. The observations of Fleming (1941b) that the form of the newly hatched prion resembles that of the adult storm petrel, have already been mentioned and other petrels e.g. *Pterodroma inexpectata* also pass through a storm petrel stage in the ontogeny of the bill. The newly hatched chicks of *Diomedea exulans* and *D. epomophora* also have down-curved beaks rather like those of outsize storm petrels.

The fossil record, so valuable in tracing phylogeny in many groups, e.g. the ammonites studied by Newell (1949), seems of little value for the petrels. The oldest may be a shearwater-like form *Hydrornis natator* of the Oligocene while by the end of the Miocene many present-day genera had appeared - *Fulmarus*, *Oceanodroma* and *Procellaria* as well as *Plotornis delfortrii* which may be a member of the now extinct assemblage that linked the large forms like *Calonectris* and *Procellaria* with *Diomedea*. The last is known from the Pliocene. This fossil record is rather poor but does suggest that the evolution of the different genera may have been quite rapid and that most families and genera are relatively old.

Behaviourally, the larger species show the most complex patterns. Thus that of *D. exulans* is more elaborate than that of *D. bulleri* and this in turn is more elaborate than that of the smaller *Phoebetria palpebrata*. The latter genus was regarded as being the most primitive of the albatrosses by Murphy (1936). The storm petrels, though little studied, seem to have very simple displays and their repertoire of vocalisations is not as extensive as that of larger forms though perhaps more so than that of *Pelecanoides urinatrix* which appears to have the least complex song of any petrel - more puffin-like (*sic*) than petrel-like to the author's ear. The medium-sized burrowing forms *Pterodroma* and *Puffinus* also have extensive vocal repertoires, but less complex perhaps than *Procellaria*, while their displays are mainly simple.

That the simple behaviour of nocturnal species is not due merely to their nocturnal habits which would make the evolution of complex displays involving visual stimuli unlikely is supported by the situation among the fulmars. These show a large range of size, are quite active by day but use rather similar gaping, mutual preening and head waving actions to the burrowing species that are active on land only after dark. Here too *Macronectes*, the giant of the fulmars, seems to use more complex behaviour patterns than the smaller species and is the only petrel able to feed both at sea and on land. Nor do my observations of the smaller petrels under good viewing conditions, e.g. *Puffinus griseus* at Snares Island (Warham, 1967a) support the view that the smaller species' apparently less complex behaviour merely reflects the difficulty of watching behaviour after dark.

Brain size may have a bearing on this question of simple versus complex patterns of behaviour. In a phylogenetic series of increasing size brain size generally bears a negatively allometric relationship to body size, the larger animals having relatively smaller but absolutely larger brains. There are no data on petrels but rough measurements of cranial cavities suggest that a similar relationship holds in this order and that the adult Diomedea epomophora has a brain about 20 times as capacious as that of the adult Pachyptila turtur. The difference is also shown by the relatively large heads of small forms like storm petrels and prions as compared with those in albatrosses and giant petrels - compare for instance A and C in Figure 15. Although smaller relative to body size the larger brains of the larger species, with their greater numbers of ganglion cells and dendritic connections, would be expected to allow the control and performance of correspondingly more complex activities and greater learning ability. Few people have succeeded in keeping petrels in captivity and no experimentation has been done on these but there is a considerable body of information supporting the idea that larger animals perform better at learning and memorising than do related but smaller species, and this may well also hold with petrels. Furthermore, while brain size in birds usually exhibits negative allometry with increasing body size, the forebrain may grow with positive allometry thus fitting the larger animals even better for the performance of complex tasks.

This evidence from varied sources fits the view that Cope's Rule has operated in the phylogeny of the petrels. It is suggested that the small, short-legged storm petrels may be closest to the original ancestor from which the various family groups evolved and that within these families increase in size has been the rule during the course of evolution. Whereas in many lines of descent the early, smaller members of the series have tended to disappear, this has happened less frequently with the petrels. Instead, the early members of the order have tended to co-exist with the larger derived forms, presumably because of the considerable range of habitats available and the different styles of flight and feeding that were consequent upon increases in body size.

Partly because of the strong mate and site tenacity in sea-birds in general and in petrels in particular, it is quite conceivable for one population of a form to speciate while another one does not, owing to chance variation and to environmental differences experienced by the two populations. The reality of such isolation is shown by the presence today of two evidently separate populations (one breeding in the dry season, the other in the wet) of Oceanodroma castro at the Galapagos Islands (Harris, in press, c). Once diversity of size has been achieved, inter-specific competition would be expected to maintain or even increase the differences as the birds developed more subtle modifications to anatomy, behaviour and geographical range to fit them still better for their particular niches.

Howard (1950) believed that the common ancestor of the Pelecaniformes and Procellariiformes must have originated well back in the Cretaceous. In view of the long period of time elapsing since then and of the paucity of sea-bird fossils in general, direct evidence for the early origins of the petrels may never be available. That phylogenetic growth has been a mainspring of the evolution in the group is admittedly speculative, with some of the evidence capable of differing interpretations, and the hypothesis is put forward merely as one possibility.

Selection towards decreased body size might be expected to occur as an adaptation to fit species for life in the polar regions where short breeding seasons call for rapid growth in the young. As has been shown, Pagodroma could not have exploited its Antarctic niche unless its young had sufficiently rapid growth rates to complete their development during the ice-free period. Here large size, though favourable for heat balance, would have been detrimental unless growth rates could have been accelerated to an appropriate degree or some behavioural or physiological adaptation evolved (e.g. those adopted by Aptenodytes forsteri) to make life possible in the inclement climates of the Antarctic spring and autumn.

While I know of no evidence for suggesting Pagodroma's descent from a larger ancestor it is noteworthy that this bird exhibits the greatest intra-specific range of body size among petrels. There is a considerable variation too in the size of the birds among the three populations of Fulmarus glacialis. Furthermore, marked sexual dimorphism in body weights and dimensions occurs among fulmars. The males are the larger sex and the difference is marked in Macronectes (Bourne and Warham, 1966) so that the sexes are readily separated in the field on this character. Evidently the potential for changing body size is well developed in the Procellariidae.

The existence of allometric trends among the petrels also has taxonomic implications for if alterations in absolute size bring forth complex changes in shape or proportions of parts then these correlated variables cannot be used as independent taxonomic criteria. Gould (1966) provides some relevant examples. In the petrels, a notoriously difficult group taxonomically, the widespread occurrence of allometry would seem to call for a multivariate approach to the analysis of total shape and Gould (*loc.cit.*) has given reasons why the labour involved in such a method may be justified.

13. CONCLUSIONS.

1. The homogeneity of form and structure among the birds comprising the Procellariiformes that is apparent from an examination of their external anatomy is supported by the results of the present study. The Pelecanoididae however show a number of characters which set them well apart from other petrels.
2. The homogeneity is shown by the harmonious relationships that hold throughout the order between many variables and body size. These relationships can be defined by means of allometric equations whether they concern bone lengths, organ weights or development rates. As all the variables are related to body size, all are related to one another. Because of this it is possible to use a variable like standard wing length as a measure of body weight.
3. This homogeneity is thought to be largely due to a common genetic inheritance which controls growth gradients in ontogeny and during the evolution of size changes. Through the influence of these gradients, harmonious and quantitative shifts of proportions have accompanied changes in body size so that the shapes of animals in evolutionary sequences intergrade.
4. The early petrels may have been small birds from which something akin to the present spectrum of forms arose early in the history of the order when petrels expanded to occupy niches then largely unexploited by birds. The present range of species is thus seen as representing stages in the evolution towards larger forms. Owing to the diversity of niches available and the diversity of feeding and flying methods that became possible with the shifts in proportions of body parts during and after this radiation, representatives of small and intermediate-sized forms were able to persist cheek by jowl with the derived larger ones. Only in the size range between the large <u>Procellaria</u> shearwaters and the small albatrosses is there a gap in the size range today. The roles in the marine ecosystems originally played by that group may perhaps be filled today by gannets and penguins. Interpretations of the processes leading to the present range of size

in the order, other than that of phyletic growth, are possible however.

5. While petrels seem to be a very conservative group with many present-day forms retaining the characters of their fossil ancestors, some lines seem to be more plastic. Among the fulmars active speciation may be proceeding now. In this group of genera, deviations from the ground plan of petrel form and growth are frequent and these are interpreted as the result of selection operating on the genes controlling allometry to fit these birds for life in environments that are only marginally tolerable.
6. The Procellariiformes exhibit some physiological characters that may be primitive. Among these are their low resting body temperatures and probably low basal rates of metabolism. These may be important causes of their slow rates of development, their long pre-breeding periods and their high potential for longevity. Low intensity of metabolism may have been an important factor facilitating their radiation into regions where the food supply is unreliable, permitting long periods of fasting at sea and, during the breeding season, on land. That their embryonic development rates seem to parallel those of mammals rather than those of other birds may be connected with the low body temperatures at which the eggs are incubated.
7. Petrel eggs show a tendency to become more elongate with increasing size. The causes of this tendency and its adaptive value, if any, are not clear.
8. The thickness of a petrel eggshell varies in a regular manner throughout the order but the surface nesting fulmars lay thicker shelled eggs than other species of similar size, perhaps because they lay on rocky substrates where extra strength is beneficial.
9. The composition of the eggs of petrels changes in a regular manner with their size, small eggs containing a high percentage of yolk. With increasing size the proportion of yolk decreases while that of the albumen increases. This change may be necessitated by the water requirements of the embryo which in larger eggs takes longer to reach the hatching stage so that uncontrolled water loss will be correspondingly greater.

10. Incubation periods are much less variable than nestling periods and are partial functions of egg and body size but the petrels having the most rapid rates of development are not the smallest species but birds nesting in polar regions where the breeding season is short but the summer days are long.
11. On a weight-specific basis the larger petrels are more efficient in the production of young than are the smaller ones.
12. Many of the above conclusions can only be tentative at this stage; they emphasise the need for further work and point to the existence of some considerable gaps in the data. These gaps are associated particularly with species in the genera *Halocyptena*, *Fregetta*, *Nesofregetta*, *Bulweria*, *Calonectris*, *Thalassoica* and *Procellaria*.

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15. SUMMARY.

1. A study has been made of the range of body size in the Procellariiformes and of the consequences of this to the sizes of certain body parts, of the eggs and of development rates.

2. Body size may be measured in terms of standard wing length (= manus length + length of longest primary feather), but the correlation between wing length and body weight is non-linear. That between standard wing length (cm) and the cube root of the body weight (g) is linear, however:-

$$\sqrt[3]{\text{body weight}} = 0.29 \text{ wing length} - 0.58$$

and so are the logarithms of body weight (g) and wing length (cm):-

$$\log \text{body weight} = 3.357 \log \text{wing length} - 2.231$$

This can be re-written in the power form as:-

$$\text{wing length} = 4.898 \text{ body weight}^{0.287}.$$

3. The variations in standard wing length, i.e. the distal element of the wing, are regular. Relative to the wing as a whole this element becomes progressively shorter with increasing size. These changes in proportions are in turn correlated with modes of flight. The small storm petrels, with relatively large distal elements in comparison to the inner elements of their wings, exhibit considerable agility in flight and beat their wings frequently; the great albatrosses, with relatively short distal segments, exhibit reduced manoeuvrability but the long inner segments of their wings generate substantial lift and the birds progress mainly by sailing.

4. Petrel species are not uniformly distributed by size within the order. The size-distribution curve is bi-modal lacking any members in the 375-425mm class of wing length. On the assumption - reasonable in view of their many similarities and inter-

grading of characters - that the petrels comprise a monophyletic group (with the possible exception of the Pelecanoididae) then there must once have been petrels in the missing size class. A comparison of the size-distribution curve with that of present day sea bird competitors of petrels suggests that gannets, boobies and medium-sized penguins may now be occupying the niche once available to the missing petrels.

5. Egg weight (g) and female body weight (g) are related, but not linearly. A logarithmic plot shows that:-

$$\log \text{egg weight} = 0.708 \log ♀ \text{body weight} - 0.065$$

which can be re-written in the form of an allometric equation:-

$$\text{egg weight} = 0.859\ ♀\ \text{body weight}^{0.708}.$$

Likewise a linear relationship holds between the cube root of the egg weight (g) and the square root of the standard wing length (mm):-

$$\sqrt[3]{\text{egg weight}} = 0.40\sqrt{♀\ \text{wing length}} - 2.51$$

6. The relationship between egg weight (g) and egg dimensions (cm) for 26 species was found to be:-

$$\text{egg weight} = 0.55\ \text{length} \times \text{breadth}^2 - 3.29$$

and

$$\text{egg weight} = 0.53\ \text{length} \times \text{breadth}^2.$$

The first equation is more accurate when computing weights for eggs greater than 20g, the second giving more accurate estimations for eggs lighter than 20g.

Egg dimensions (cm) are also related to body weights:-

$$\log LB^2 = 0.689 \log ♀ \text{body weight} + 0.265$$

or:-

$$\log ♀ \text{ body weight} = 1.4471 \log LB^2 - 0.376 .$$

7. Egg shape varies in a rather regular manner with body size and egg size. Smaller species have more spherical eggs. However, birds of the genus <u>Puffinus</u> tend to lay more elongate eggs and those of the genus <u>Pterodroma</u> less elongate ones than do other petrels of similar size. Within a species there is no evidence of any consistent variation in egg shape between the different races or sub-species.
8. Egg lengths (mm) and egg breadths (mm) are related to wing lengths:-

$$\text{egg length} = 6.66 \sqrt{♀ \text{ wing length}} - 47.02$$

$$\text{egg breadth} = 3.97 \sqrt{♀ \text{ wing length}} - 22.45$$

and as egg length increases at a greater rate in passing up the size range than does egg breadth, so bigger eggs are more elongate than smaller ones.

9. Factors influencing egg shape in petrels may include (a) the need in those of small species to conserve heat and moisture by reducing surface area, (b) anatomical and physiological restrictions concerned with the making, transport, and laying of eggs which are large in respect of the size of the bird (over 25% of the body weight in the smallest petrels) and (c) anatomical adaptations for specialised flight and swimming. Of these both (b) and (c) seem most relevant and the shape and spread of the pelvis is correlated with egg shape and with body size. The smaller petrels have wide pelves and rounded eggs, the large species narrower pelves and narrower eggs. The eggs may perhaps be given their final shape while held between the pubes during the laying down of the shell. In addition, in large species the oviducts may be smaller relative to total body size and to the sizes of the yolks so that greater pressures are exerted on the forming eggs causing their elongation during their passage

caudally.

10. Larger eggs have thicker shells than smaller ones, the relationship between standard wing length (cm) and shell thickness (mm) being:-

shell thickness = 0.11 + 0.01 ♀ wing length.

Variations within this general trend are that Puffinus spp. have thicker and Pterodroma spp. thinner shells than other petrels of similar sizes. Significantly thicker too are the shells of the fulmarine genera Macronectes, Fulmarus and Daption, possibly as an adaptation to nesting on hard substrates where extra strength in the shell may be advantageous.

11. The internal capacity of a petrel's egg (ml) is correlated with its dimensions and with its weight (g) when fresh:-

egg capacity = 0.900 egg weight .

12. Data on incubation periods are given. These range from 41 to 79 days. If allowance is made for the periods during which the eggs are uncovered, the time from laying to hatching is rather constant for any particular species. Incubation periods (days) are correlated with egg capacity (ml):-

log egg capacity = 6.116 log incubation period - 8.8536

but this relationship does not hold for fulmars which have shorter incubation periods than other species laying similar sized eggs.

13. Incubation periods (days) vary according to body size (g) but non-linearly:-

log ♀ body weight = 8.0496 log incubation period - 11.3270

and:-

log ♀ wing length (decimetres) = 7.1651 log incubation period (days) - 11.1220

On a weight-specific basis the smaller petrels are much less efficient at producing unit weight than are the larger ones. Petrels take about twice as long to reach a given hatching weight as most other kinds of birds.

However, the fulmarine species do not fit these formulae, their incubation periods are shorter than indicated by the general trends for body size. How this speeding up of development is achieved is not clear.

14. Body temperatures of petrels, on the data presently available, are low and average 38.65°C, significantly lower than the mean of 40.02°C for non-petrel species. Data on egg temperatures are scarce and unsatisfactory but it seems probable that these too are low and this may have a bearing on the long incubation periods. Low body temperature seems more likely to be a retention of a primitive condition rather than an evolutionary novelty and is presumably associated with low basal metabolism. If so, the latter may have formed a pre-adaptation fitting petrels for a pelagic existence where a capacity for sustained fasting enables penetration to areas not accessible to birds with higher requirements for energy intake.

15. The composition of petrel eggs varies in a regular manner according to their size. Increasing size is accompanied by an increase in the proportion of albumen and a decrease in that of yolk. Shell composes 7.5 to 11%, albumen 53 to 65% and yolk 28 to 39% of the fresh egg weight. These data are in line with similar sized eggs of precocial species such as ducks. Yolk weights are correlated (in log terms) with incubation periods but again the fulmars are atypical and their rapid development to hatching is not a consequence of reduced yolk reserves.

16. Nestling periods are more variable than incubation periods and range from 50 to 278 days.

The days elapsing from hatching to chick departure are correlated with egg capacity (ml) according to the formula:-

$$\text{Nestling period} = 0.496 \text{ egg capacity} + 52.61$$

and is also correlated in log terms with body weight. In both respects fulmars are atypical having shorter nestling periods than other petrels of similar sizes. As obtains during incubation, the nestling time per kg of adult is much less for large than for small petrels but in general the rate of production per unit weight is less than during the incubation period.

17. The duration of the incubation and nestling periods are related for a particular species, those with short nestling periods have also short incubation periods. The fulmars, breeding in polar regions, develop overall faster than other petrels and this is believed to be an adaptation to a short breeding season with long summer days. In one fulmar (Pagodroma) there is evidence that some differences in development rates occur between populations and these may be connected with local climatic conditions. Nestling periods for non-migratory tropical petrels are long relative to their egg sizes and in general with petrels, development after hatching seems to be more flexible in response to environmental conditions than development rates within the egg.

18. The sizes of at least 7 body components - skeleton weight (y_s), lengths of tarsus (y_t), of culmen (y_c), of humerus (y_h), of ulna (y_u), and of manus (y_m) and egg weight (y_e) are related to body weight allometrically:-

$$y_e = 0.899x^{0.71}$$

$$y_s = 0.035x^{1.1}$$

$$y_t = 5.7x^{0.31}$$

$$y_c = 2.1x^{0.47}$$

$$y_h \ \& \ y_u = 4.3x^{0.53}$$

$$y_m = 8.6x^{0.40}$$

where x is mean body weight in grams.

Egg weight, standard wing length and tarsal lengths exhibit negative allometry while skeletal weights vary almost isometrically with body weight: the remainder show positive allometry. As all these variables are related to body weight they are also related to each other so that petrel structure conforms to a ground plan expressible in part by a series of allometric relationships in which body size is a determining factor. The underlying mechanisms may be a common gene or gene complex which controls growth gradients and the stages at which growth of the various parts ceases.

It is postulated that phyletic size increase has been a dominant feature in the evolution of the order as in some better known lines of descent and that the group may have arisen from some small generalised ancestor perhaps having many of the characters of storm petrels like Oceanodroma but the evidence for this view, based on morphology, ontogeny and behaviour, is rather sparse and mainly circumstantial.

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APPENDIX A: BASIC DIMENSIONS OF THE PROCELLARIIFORMES AND THEIR EGGS

Wing lengths marked * are from live material

FAM. DIOMEDEIDAE

	SPECIES	No.	Sex	Wing (mm.)	No.	Sex	Body Wt (g)	No.	Mean egg size (mm.)	Shape index	No.	K	Capacity (ml)	No.	Wt. (g)
1a	D.epomophora epomophora	8	♀	624	7	♀	7801	48	126.8 x 78.6	62.0	5	.9720	398.6	15	425
1b	D.e.sanfordi	12	♀	616				54	123.6 x 77.8	63.0				41	416
2b	D.exulans chionoptera	4	♀	601	53	♀	7270	9	131.2 x 79.5	60.6				6	467
2c	D.e.dabbenena	4	♀	603	1	♀	6534	87	127.0 x 76.9	60.6	87	.9482	372.8		
3a	D.c.cauta	4	♀	557	2	♀	3585	52	105.9 x 67.0	63.3	11	.9710	241.9	6	238
3c	D.c.salvini	32	♂ ♀	556				8	106.0 x 69.3	65.4					
4	D.albatrus	2		550				43	116.0 x 74.2	63.9	2	.9708	324.6		
5	D.irrorata	40	♀	547				38	106.0 x 68.8	64.9					
6a	D.m.melanophris	7	♀	521	10	♂ ♀	3515	8	110.0 x 67.0	60.9					
6b	D.m.impavida	3	♀	511*	2	♀	2871	26	102.5 x 66.2	64.5					
7	D.bulleri	31	♂ ♀	520*	31	♂ ♀	3012	100	102.1 x 66.0	64.6	8	.9698	225.8	100	250
8	D.nigripes	49	♀	506	138	♀	2934	45	108.8 x 70.3	64.6	1	.9670		100	291
9	D.chrysostoma	5	♀	504	2	♀	2973	40	107.0 x 67.4	63.0	9	.9699	246.8		
10	D.immutabilis	5	♂ ♀	487	134	♀	2852	39	109.2 x 69.4	63.5	14		254	20	278
11	D.chlororhynchos	30	♂ ♀	480	6	♂ ♀	1927	75	96.1 x 62.2	64.7					
12	P.palpebrata	21	♂ ♀	537	10	♂ ♀	2838	32	101.6 x 65.8	64.8	6	.9503	218.9		
13	P.fusca	13	♂ ♀	503	5	♂ ♀	2102	21	103.1 x 65.7	63.7					

	SPECIES	No.	Sex	Wing (mm.)	No.	Sex	Body Wt (g)	No.	Mean egg size (mm.)	Shape index	No.	K	Capacity (ml)	No.	Wt. (g)
14	Macronectes giganteus	19	♀	498	5	♀	4114	80	103.8 x 65.7	63.3	3	.9385	220.2	12	237
15	M.halli	10	♀	497	4	♀	3564	32	101.5 x 66.1	65.1	6	.9323	216.5	10	232
16	F.glacialoides	21	♀	329	10	♀	741	13	74.4 x 50.3	67.6	1	.9333	92.0	13	103
17a	F.g.glacialis	45	♀	313	12	♀	699	100	74.0 x 50.6	68.4	3	.9282	92.1		
18	T.antarctica	26	♀	310	21	♀	627	12	72 x 48	66.7					
19a	D.c.capensis	15	♀	264	22	♀	407	46	62 x 43	69.3	3	.9378	56.3	42	62
20	P.nivea	16	♀	260*	13	♀	244	21	55.5 x 39.4	71.0	1	.9600	43.3	21	47
21	Pterodroma incerta	54	♂ ♀	321*	54	♂ ♀	522	1	69.5 x 52.0						
22a	P.m.gouldi	45	♂ ♀	317	?	♂ ♀	567	37	67.4 x 48.4	71.9	4	.9364	77.6		
22b	P.m.macroptera	26	♂ ♀	309	5	♀	528	12	67.8 x 49.7	73.3	1	.9420	82.6		
23b	P.e.cervicalis	9	♂ ♀	306				8	65.2 x 48.0	73.6					
24	P.p.phaeopygia	68	♀	305				6	61.2 x 42.9	70.1					
25	P.lessoni	28	♂ ♀	303	5	♂ ♀	606	43	71.7 x 51.0	71.1	3	.9439	92.1		
26	P.solandri	58	♀	302	2	♀	475	18	66.0 x 49.0	74.2					
27a	P.n.juana	31	♀	300				10	65.2 x 45.9	70.4					
27b	P.n.neglecta	20	♀	290				96	64.2 x 46.0	71.6	5	.9515	70.2	89	74
28	P.r.rostrata	14	♀	290				2	63.5 x 42.3	66.6					
29a	P.a.arminjoniana	26	♀	285				3	61.4 x 45.5	74.1					
29b	P.a.heraldica	67	♀	277	1	♂ ♀	319	29	59.1 x 42.7	72.2					
30	P.alba	39	♀	276	?		269	8	56.1 x 42.5	75.9				?	56
31b	P.h.cahow	3	♂ ♀	261*				1	58.2 x 43.4						
32	P.ultima	44	♀	282	13	♂ ♀	360								
33	P.inexpectata	100	♂ ♀	262*	86	♂ ♀	316	39	60.5 x 43.1	71.2	11	.9605	56.5	8	53
34	P.brevirostris	17	♂ ♀	255	7	♂ ♀	324	19	56.7 x 44.8	79.0					
35a	P.m.mollis	146	♂ ♀	253*	146	♂ ♀	254	4	62.2 x 46.9	75.4					

SPECIES	No.	Sex	Wing (mm.)	No.	Sex	Body Wt (g)	No.	Mean egg size (mm.)	Shape index	No.	K	Capacity (ml)	No.	Wt. (g)
36 P.c.cooki	16	♂ ♀	233	2	♀	191	21	52.5 x 38.7	73.7					
37a P.l.leucoptera	17	♂ ♀	225	5	♂ ♀	179	31	49.8 x 37.1	74.5					
38a P.h.hypoleuca	77	♂ ♀	229	76	♀	176	7	48.4 x 36.8	76.0					
38c P.h.nigripennis	24	♂ ♀	228				41	51.4 x 37.2	72.3				41	37
39 P.l.pycrofti	24	♂ ♀	215	9	♂ ♀	159	18	48.3 x 35.5	73.5					
40 P.brevipes	22	♂ ♀	212				4	48.4 x 35.1	72.5					
41 H.caerulea	31	♂ ♀	216	10	♂ ♀	181	16	49.9 x 36.7	73.5					
42a P.v.vittata	42	♂ ♀	214*	70	♂ ♀	196	12	50.0 x 36.7	73.5	3	.9449	33.3		
43a P.d.banksi	12	♀	192*	12	♀	153	42	47.1 x 34.6	73.5	5	.9477	28.0	23	33
44 P.salvini	18	♂ ♀	190	18	♂ ♀	154	16	50.3 x 35.9	71.4				12	32
45 P.turtur	100	♂ ♀	182*	100	♂ ♀	132	100	45.1 x 32.6	72.3	12	.9566	24.0	56	24
46 P.belcheri	6	♂ ♀	178				63	47.5 x 34.8	73.3					
48 B.fallax	9	♂ ♀	242	5	♂ ♀	176								
49 B.bulweria	11	♀	203				66	42.9 x 31.2	72.7					
50 P.aequinoctialis	11	♀	373	3	♀	1075	17	81.0 x 53.3	65.8					
51 P.westlandica	2	♀	367	1	♀	1247	14	82.4 x 55.0	66.7				9	127
52 P.parkinsoni	4	♀	348	1	♀	1077	12	70.3 x 49.6	70.5					
53 P.cinerea	11	♀	334	7	♀	1026	6	83.0 x 56.2	67.7	1	.9379	128.7		
54a C.d.borealis	10	♀	355				70	73.3 x 50.0	68.2					
54b C.d.diomedea	10	♀	335				70	68.1 x 45.4	66.7					
54c C.d.edwardsi	6	♀	308				10	62.3 x 44.4	71.3					
55 C.leucomelas	3	♀	315				5	68.8 x 44.4	64.5					
56 P.creatopus	53	♀	330				11	71.7 x 46.2	64.4					
57 P.gravis	23	♂ ♀	324	8	♂ ♀	873	78	80.0 x 51.5	64.4	3	.9468	105.2	1	105
58a P.c.hullianus	28	♂ ♀	320	1	♀	574	49	69.5 x 46.0	66.2					
58b P.c.carneipes	19	♂ ♀	315				55	69.6 x 45.5	65.4	2	.9348	70.5		
59a P.p.pacificus	85	♂ ♀	308	9	♂ ♀	358	13	66.6 x 43.6	65.5				2	74

FAM: HYDROBATIDAE.

	SPECIES	No.	Sex	Wing (mm.)	No.	Sex	Body Wt (g)	No.	Mean egg size (mm.)	Shape index	No.	K	Capacity (ml)	No.	Wt. (g)
69a	O.o.exasperatus	65	♂ ♀	153	10	♂ ♀	34	20	33.4 x 24.2	72.4	6	.9334	9.6		
69b	O.o.oceanicus	51	♂ ♀	137				40	32.7 x 23.3	71.2					
70	G.nereis	10	♂ ♀	130	10	♂ ♀	29	12	33.2 x 24.5	73.8					
71a	P.m.hypoleuca	20	♀	161				25	36.1 x 26.5	73.5					
71b	P.m.dulciae	13	♀	157				28	36.0 x 26.2	72.8	3	.9572	12.4		
71c	P.m.maoriana	21	♀	158	100	♂ ♀	47	100	35.9 x 26.0	72.4	10	.9655	12.3	54	12
72	F.tropica	25	♂ ♀	165				20	36.3 x 26.1	71.9					
73a	F.g.leucogaster	24	♂ ♀	162*	24	♂ ♀	46	6	35.7 x 26.0	72.8				2	14
73b	F.g.grallaria	12	♀	156				3	33.5 x 24.7	73.7					
74	H.pelagicus	39	♂ ♀	117*	50	♂ ♀	28	100	27.8 x 21.2	76.3	10	.9219	6.0		
75	H.microsoma	11	♂ ♀	121				20	25.4 x 19.4	73.8					
76	O.melania	57	♀	178				61	36.6 x 26.7	73.0					
77	O.furcata	19	♂ ♀	157	1	♂	59	40	33.9 x 25.7	75.8					
78a	O.l.leucorhoa	94	♂ ♀	156	66	♂ ♀	48	100	32.7 x 24.0	73.4	4	.9576	9.2	100	10
78b	O.l.beali	57	♂ ♀	151				32	31.7 x 23.2	73.2					
78c	O.l.socorroensis	25	♂ ♀	149				20	30.8 x 23.1	75.0					
79a	O.c.bangi	16	♀	155	20	♀	40	9	31.6 x 22.9	72.6				28	8.5
79b	O.c.castro	50	♂ ♀	153	12	♂ ♀	43.5	44	32.2 x 23.5	73.0	4	.9558	8.9		
80	O.homochroa	58	♀	144				57	29.8 x 22.8	76.5					
81a	O.t.tethys	71	♂ ♀	137	18	♂ ♀	26	4	28.4 x 20.9	73.6				23	5.2
81b	O.t.kelsalli	14	♂ ♀	124				6	27.3 x 19.7	72.3					

	SPECIES	No.	Sex	Wing (mm.)	No.	Sex	Body Wt (g)	No.	Mean egg size (mm.)	Shape index	No.	K	Capacity (ml)	No.	Wt. (g)
59b	<u>P.p.chlororhynchos</u>	208	♂ ♀	292	8	♂ ♀	375	48	62.3 x 41.3	66.2				19	59
60	<u>P.griseus</u>	100	♂ ♀	304*	100	♂ ♀	787	78	75.7 x 48.8	64.4	13	.9315	88.0	25	95
61	<u>P.bulleri</u>	17	♂ ♀	288	4	♂ ♀	374	23	65.7 x 43.3	65.9					
62	<u>P. tenuirostris</u>	40	♀	274	22	♀	635	100	71 x 47	66.2	5	.9435	77.5	13	85
64a	<u>P.p.opisthomelas</u>	49	♂ ♀	237				38	60.9 x 41.2	67.6					
64b	<u>P.p.puffinus</u>	20	♂ ♀	237	32	♀	406	100	60.9 x 41.9	68.8	14	.9421	52.7	10	58
64c	<u>P.p.mauretanicus</u>	10	♂ ♀	246	5	♀	517	23	61.2 x 42.7	69.8					
64d	<u>P.p.yelkoan</u>	21	♂ ♀	233				100	58.0 x 40.8	70.3					
65	<u>P.huttoni</u>	17	♂ ♀	222	17	♂ ♀	364	3	58.7 x 40.2	68.5					
66	<u>P.gavia</u>	55	♂ ♀	209				13	57.3 x 39.9	69.7					
67a	<u>P.l'h. l'herminieri</u>	26	♂ ♀	208				39	52.5 x 36.2	68.9					
67b	<u>P.l'h. subalaris</u>	99	♂ ♀	191	13	♀	163	11	47.8 x 34.0	71.1				30	29
68a	<u>P.a.haurakiensis</u>	16	♂ ♀	192				7	52.6 x 36.3	69.1					
68d	<u>P.a.assimilis</u>	5	♂ ♀	183				28	51.8 x 35.3	68.2					
68e	<u>P.a.baroli</u>	15	♂ ♀	179				55	50.0 x 34.7	69.4					
68f	<u>P.a.tunneyi</u>	25	♂ ♀	173				10	52.3 x 35.6	68.1	8	.9351	32.4		

FAM: PELECANOIDIDAE

	SPECIES	No.	Sex	Wing (mm.)	No.	Sex	Body Wt (g)	No.	Mean egg size (mm.)	Shape index	No.	K	Capacity (ml)	No.	Wt. (g)
82	P.garnotii	40	♂ ♀	136				20	47.0 x 34.5	73.4	6		22		
83a	P.u.chathamensis	100	♂ ♀	123*	100	♂ ♀	124	39	37.7 x 29.4	78.0				27	15
83c	P.u.berard	7	♂ ♀	121				9	38.2 x 30.8	80.6					
84	P.georgicus	85	♀	114	4	♀	134	13	39.2 x 31.6	80.7					