EGG VOLUMES AND INCUBATION PERIODS[1]

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INTRODUCTION

IT is common knowledge that the eggs of large birds have, in general, a longer incubation period than those of small birds, but this appears often to be only the most general sort of rule, with many exceptions. The irregularity of the rule can be demonstrated easily by plotting several egg sizes (see below, 'Methods') against their incubation periods on a simple graph (Text-fig. 1).

METHODS

The approximate volume of an egg may be obtained from its average measurements by the formula for an ellipsoid:

$$V = \frac{\pi}{6} ab^2$$

where a is the long axis of the egg and b is the widest transverse axis. Egg measurements are subject to a maximum variability of 20 per cent (Fisher), but since longer eggs are usually narrower, the variability in volume is possibly not so great, whereas the use of *average* egg measurements undoubtedly gives a substantially correct value for average volumes.

An egg is not a true ellipsoid, since it is somewhat narrowed in the maternal oviduct. Among hens' eggs I found volumes by water displacement which were 15 per cent less than those calculated by the ellipsoid formula. On the basis of the following study I have concluded that this is a fairly representative correction for other eggs.

The table shows a list of: egg weights from Bergtold; the volumes calculated from these weights (using a constant specific gravity of 1.07 as in the hen); the volumes calculated by formula from average egg measurements; and the calculated volumes subjected to a correction of -15%. It will be seen that there is a general agreement between the egg-weight volume and the corrected-formula volume.

An examination of this table shows that:

(a) The Ostrich egg, which is more nearly spherical than most eggs, and whose two poles are symmetrical, is apparently more closely represented volumetrically by the uncorrected formula than any of the other eggs. This, however, is probably not true, since the specific gravity of an Ostrich egg is undoubtedly much higher than 1.07, and its volume is therefore less than

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Species	Wt. (oz.)	Wt.-Vol. cu. in.	Form.-Vol. cu. in.	Form.-Vol. −15%, cu. in.
Ostrich	60	94.8	99.07	85.6
Western Robin (2)	.23	.362		
Eastern Robin (1)	.06	.095	.41	.351
Crow	.62	.956	1.34	1.15
Domestic Hen (4)	2.27	3.57	4.25	3.53
Common Tern (1)	.64	1.05	2.03	1.75
W. Mourning Dove (2)	.40	.63		
E. Mourning Dove (3)			.39	.34
Kingfisher	.45	.71	.84	.72
Screech Owl	.58	.92	1.15	.99
Kingbird	.15	.236	.26	.224

(1) Meyer; (2) Bergtold; (3) Forbush; (4) Worth.

that calculated in this way on the basis of its weight. I assume that the pyriform eggs of cliff-dwelling birds are least closely approximated by the formula; the correction in these cases should probably exceed −15%.

(b) The weights of the eggs of the Crow and Common Tern may have been taken after partial incubation had occurred, or else the eggs were smaller than the average for each species.

(c) The Mourning Dove's eggs, weighed by Bergtold (of Denver, Colorado), were undoubtedly of the western subspecies—a decidedly larger bird than *Zenaidura m. carolinensis*.

(d) The other cases come well within 10 per cent of agreement.

(e) The ellipsoid formula, less 15 per cent, therefore gives a fairly true estimate of egg volumes from their primary measurements among eggs of varying sizes and shapes.

Having explained the apparent exceptions to my own satisfaction, I have therefore calculated further egg volumes and corrected each one arbitrarily by −15 per cent, since what I needed for my study was simply a rough approximation to the true egg volume. It need scarcely be observed that, were sufficient egg weights of fresh eggs known, one would conduct such a study as this on egg weights in preference to volumes; or, better still, on the weight of the *contents* of the freshly laid eggs (minus their shells). It appears, however, that even as sketchy a volumetric approximation as this one yields information of sufficient validity to warrant its analysis.

Similarly I have used the average length of the reported incubation period for each species, though as Bergtold has suggested, it might have been better to use the minimum reported period; the latter course, however, would have necessitated the repudiation of many excellent authorities, and since it is quite possible for minimum periods to be reported erroneously, I thought it best to calculate an average period from all reasonable reports.

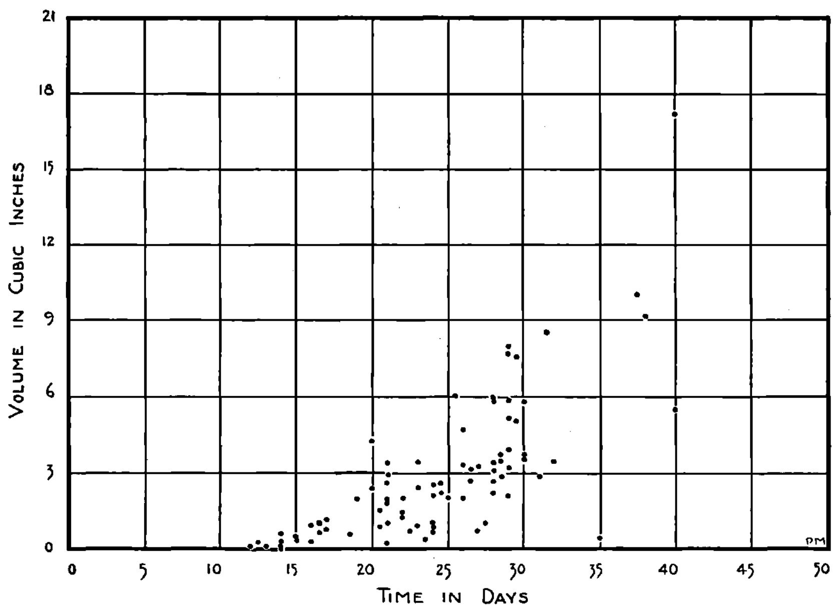
A signal handicap to this study is the lack of information on the incubation periods of very many birds, particularly among the non-passerine orders.

Finally I have, at a later point in the analysis, assigned to these birds an average clutch of eggs, calculating this from the common variation in numbers in the clutch, and disregarding the obviously extreme cases. Where it was possible to determine the usual number in a clutch, I used this figure in preference to the average number.

These various figures are presented in Tables 1 and 2.

Procedure

On examining Text-fig. 1, we find that its apparent irregularity is due to the simultaneous occurrence of two variables, viz., an egg of a given size



TEXT-FIG. 1.—Egg volumes plotted against incubation periods.

may have a variable incubation period, and an incubation period of a given duration may obtain among eggs of variable size.

A further cause of obscurity in Text-fig. 1 is that the range of variability among egg sizes, measured in cubic inches, extends through four logarithmic cycles (0.03 cu. in. to 85.9 cu. in.); if we include the Moas and *Aepyornis*, this variability extends through five cycles, whereas the incubation periods, measured in days, occur within one cycle (10 days to less than 100 days).

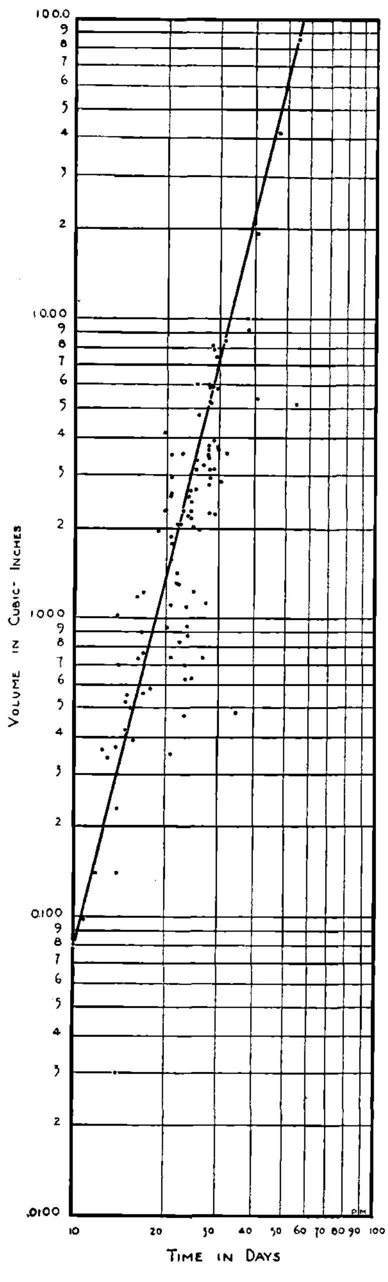
If we plot egg sizes from hummingbird to Ostrich against incubation periods on 'log-log' paper, the apparent random inconsistency of Text-fig. 1 is given a new face; it then becomes apparent that there is a fairly consistent relationship between volume and time which may be represented by a straight line drawn between the two points pertaining respectively to the Yellow Warbler and the Ostrich.

The other points of the graph are fairly equally distributed on either side of the line. The line itself has a slope slightly exceeding 4 : 1. This means, mathematically, that among a series of eggs of increasing size, the incubation periods and the egg volumes are related in a geometric ratio of a surprisingly high order; a linear increase of one unit of time is accompanied by a corresponding fourth-power increase in the added egg increment.

I call this revelation "surprising" for two reasons. When one considers the growth of a three-dimensional organism, one expects to find relationships between linear and solid dimensions which are expressed by the third, rather than the fourth, power. Further, one expects the actual eggshell surface to influence metabolism in the embryo by virtue of its limiting influence upon respiratory potentialities; and therefore it becomes conceivable that increase in egg size might easily stand in only a second-power relationship to increases in any linear factor. The explanation of this fourth-power relationship must therefore be made on other grounds, and I hereby invite embryologists and physiologists to give further consideration to the problem.

A further inspection of Text-fig. 2 reveals another relationship, namely, that eggs of the same volume may have different incubation periods in more than a random way. Assuming that the average line of the graph represents the average or expected incubation period in a series of eggs of increasing size, we find that among small eggs there is a maximum normal deviation of about four days on either side of the average incubation period, while among larger eggs the deviation may be about five days on either side of the average. Since the deviation usually falls within such limits, one may hazard a fair guess at the incubation periods of birds whose egg dimensions are known, but whose incubation periods have not been discovered. For example, the Great Auk's egg measured 4.67 by 2.91 inches (Chapman). Its volume was therefore 17.82 cubic inches. Plotting this in Text-fig. 2, we find an incubation period of about 39 days. The Great Auk's incubation period was therefore probably 39 $\pm$ 5 days. The question remains: which is the more likely direction of the deviation? Or is it likely that there was any deviation at all in this species?

Returning to Text-fig. 2 for the answers to these questions we find that many birds fall on the line, while others fall at varying distances on either side. I have prepared a list showing: (a) the species on the line itself or



TEXT-FIG. 2.—Logarithmic plotting of egg volumes against incubation periods.

within a day on either side of it; (b) all species further above and to the left of the line; and (c) all species further below and to the right of the line (Table 2).

The birds in the left-hand column of the table have incubation periods longer than the average. In the center column the periods may be accepted as the average. On the right the periods are shorter than the average. An examination of the groupings into which the species fall by this analysis shows a moderate degree of taxonomic overlapping, but at the same time a singular degree of ecological uniformity. First, the birds with a short incubation period (right-hand column) are chiefly species subject to predation or some other type of environmental onslaught. It will benefit them to hatch out their eggs with the greatest possible dispatch, for a bird a-wing is a less easy mark for a predator than an egg or a brooding parent. (Bergtold has also concluded that a shortened incubation period brings *benefit* to a species.) Thus no gulls occur in the left-hand column, and no terns except the Sooty Tern, a tropical species. Among these beach-breeding birds the threat of high tides may act as the stimulus for accelerated incubation, inasmuch as the young are hatched in a precocious state, and the egg stage is the chief danger period. Second, the birds of prey tend to be concentrated in the left-hand column. There are many in the center column, but none at all on the right. These altricial birds, having adequate means of offense and defense, have not felt the press of embryonic speed—there has been less premium on rapid incubation and fledging during centuries of hawk and owl evolution than there has been among other orders. (Is it more than coincidence that the Ptarmigan, White Gyrfalcon, and Snowy Owl—each one an albinistic form—all occur in the left-hand column? There seems to be a preponderance of boreal forms in this group.) Third, the birds in the left-hand column which are subject to predation compensate for their long incubation periods by laying large clutches of eggs (Ingersoll states that the number of eggs laid by a species is in direct ratio to the dangers which it ordinarily encounters). No matter how many of their clutches are destroyed, a single successful one will result in bringing forth a distinct addition to the population.

The group of the center or 'average' column contains members of practically all the taxonomic divisions. Possibly there is a greater concentration of highly specialized forms here than elsewhere (viz., woodcock, osprey, oystercatcher, nighthawk, kingfisher, etc.), though otherwise it is generally characterized as an 'overlapping' group. The highly specialized birds may perhaps be thought of as finding their specialization a mixed benefit, bringing with its advantages also distinct limitations which closely balance each other, so that incubation time is in the end neither accelerated nor retarded. The birds in the right-hand column which exhibit both increased incubation speed *and* large clutches of eggs are compensating *doubly* for some environmental adversity whose exact nature it would be most interesting to investigate. The Redhead, in fact, is having difficulty in maintaining its status in eastern United States, despite its rapidly incubated clutch of 12.5 eggs. My ornithological friends blame the bird's failure to adapt itself to sportsmen and fire-arms, and no doubt this stupidity extends to other phases of its conduct. If that is so, it has been subject to environmental inroads over a long period of time and has saved itself from extinction only by the double compensation which we have noted.

Therefore in calculating the incubation periods of extinct birds, or of modern birds whose incubation periods are unknown, one may, on ecological grounds, and to a lesser extent on taxonomic grounds, suspect that the deviation, if any, from the calculated average incubation time is positive or negative, depending on the habits of birds occupying similar niches and the type of deviation which such birds exhibit. With this in mind, I think it probable that the Great Auk's egg hatched in 44 days, the deviation from 39 days being in the direction of delayed hatching (see Table 2 for isolated boreal or Antarctic island birds laying a single egg; they occur principally in the left-hand column, i.e., Wilson's Petrel, Leach's Petrel, Fulmar, Gannet, and Dovekie).

A further examination of Text-fig. 2 shows that there are two cases in which the incubation period falls *behind* the expected limit of deviation from the average. The Fulmar is the more noteworthy example of this, while the Gannet shows a less abnormal condition. The cause for such long incubation periods is obscure to me, though it may be the result of long isolation from predation or other adversities. If these incubation periods are really as markedly retarded as this, the Fulmar and the Gannet would be interesting subjects for physiological study. But there is a possibility that the incubation period has been wrongly observed and recorded in each case. In checking these aberrant data I find that Evans stands alone in ascribing to the Fulmar an incubation period of "about a month" instead of 55 days. Evans's estimate falls exactly on the line! So far as the Gannet is concerned, the minimum reported incubation period is 39 days, which still gives it an extraordinary deviation beyond the expected limit of retardation. To come within the limits at all, its incubation period should not exceed 33 days. It would be well for field ornithologists to check up on both these birds again, noticing especially whether the Gannet regularly *suspends* incubation, when the eggs would become chilled and their hatching delayed. On the other hand the Caspian Tern offers an extreme case of accelerated embryonic growth, and one wonders at the accuracy of the reported incubation period (20 days).

In the case of the Domestic Fowl, I asked a housewife to select a few 'average-sized' eggs; I calculated their average volume as 3.47 cubic inches. The incubation period, 21 days, again represents an acceleration of the embryonic growth rate. Under domestication this bird has been bred selectively for the production of larger eggs, for the volume of the Red Jungle Fowl's egg is only 1.56 cubic inches—less than one-half of the figure for the domestic bird (Beebe). On the other hand no artificial selection has been practiced upon the fowl's incubation period; no change of incubation period has been noted among any of man's domesticated birds (Bergtold), for the time element is exactly the same as that of their wild congeners. Since the incubation period is a constant specific character in the fowl, the rate of embryonic growth must have been raised automatically by the artificial enlargement of the egg under domestication. We may test this startling hypothesis by plotting the Red Jungle Fowl's egg on Text-fig. 2. A volume of 1.56 cubic inches and an incubation period of 21 days fall exactly upon the line, while the domestic bird's egg falls far from it. This proves that under domestication the egg has not only been enlarged, but that the growth rate of its embryo has been accelerated as well. This means that the domesticated egg material must experience a more rapid series of cell divisions than did the egg material of the wild ancestors, for we believe that a large animal consists of more cells than does a small one. Byerly, however, has been unable to detect different rates of cell cleavages among breeds of Domestic Fowl of various sizes. It is also puzzling that the basal metabolic rate is lower in large animals than it is in small ones. Could it be, then, that a greater degree of mitotic activity can obtain in the presence of a lower metabolic rate?

There may be a new clue in this query to the decadent tendencies so frequently found among the giant forms of an evolutionary series of animals. Perhaps their tissues, the seat of a constantly increasing cellular activity, are starved through the equally increasing metabolic inertia which accompanies great physical enlargement. Decadence, so unexpected in giant forms when we consider the potentialities for integrated activity among these great multitudes of cells, is therefore a function of the decrease of the animal's surface area relative to its bulk. Decadence, on the other hand, is not a consequence of cellular degeneracy, the cells being more active than ever before and being overwhelmed finally by sheer gigantismal suffocation.

But to return to our primary data: a mathematical analysis of it yields the following relationship between egg volumes and incubation periods:

$$V = .0063\left(\frac{1000\ V}{T}\right)^{1.30}$$

Let us test this formula by calculating the probable incubation period of any egg simply from its dimensions. The following case is an example, selected at random from the list of birds which fall on the line of Text-fig. 2, and for which, therefore, no ecological correction need be made.

The Black Vulture's egg averages 3.15 by 2.02 inches in its diameters. What is its incubation period?

$$V = .85\left(\frac{\pi}{6}ab^2\right) = 5.81 \text{ cu. in.}$$

$$5.81 = .0063\left(\frac{5810}{T}\right)^{1.30}$$

$$\log 5.81 = 1.30 \log\left(\frac{5810}{T}\right) + \bar{3}.80$$

$$.76 = 1.30 \log\left(\frac{5810}{T}\right) - 2.20$$

$$1.30 \log\left(\frac{5810}{T}\right) = 2.96$$

$$\log\left(\frac{5810}{T}\right) = 2.28$$

$$\frac{5810}{T} = 190.5$$

$$T = 30.5 \text{ days.}$$

Forbush gives 30 days as the incubation period of the Black Vulture.

Extending the line of Graph 2 for another logarithmic cycle (from 100 cubic inches to 1000 cubic inches), I have calculated some additional incubation periods from their egg volumes.

Several of these figures, as well as others below the 100-cubic-inch limit, warrant a few comments.

In the case of the cassowaries and Emu, I found dimensions of *Casuarius sclateri* and calculated an incubation period of 46 days for them. I could not find dimensions of eggs of *Dromiceius novae-hollandiae*, and therefore do not know how they compare in size with eggs of *C. sclateri*. However, these birds are both large, and their eggs are probably of nearly the same size. Newton gives the incubation period of *D. novae-hollandiae* as 70 to 80 days (average 75 days), while Brasil gives 35 to 42 (average 38.5). Since Brasil's data come within a week of my calculation for *C. sclateri*, I would accept his observation on *D. novae-hollandiae* rather than Newton's.

At the Philadelphia Zoo, seven young Rheas were successfully reared in 1937. Their keeper told me the eggs hatched in 45 to 50 days; most authorities state that this period is 35 to 40 days. An average of 47.5 days is, however, much more in accordance with my graph.

The incubation period of the Ostrich is given as 55 days by Coues (50 to 60 days) and as 42 days in the 'Encyclopedia Britannica.' Coues's median value, 55 days, falls within three days of my extended logarithmic curve, so that I am inclined to accept his estimate. Bergtold states that the Ostrich suspends incubation frequently, upon which the eggs take longer than normal to hatch; many conflicting reports of incubation periods are probably due to this habit among certain birds.

The Whooping Crane's incubation period is calculated as 34.5 days. Forbush states his belief that the period is "at least 33 days." My formula gives *Apteryx* an incubation period of 42 days; Evans gives exactly the same figure.

It is amusing to speculate on the incubation periods of extinct birds. By my formula *Aepyornis* would have taken 85 days to hatch, several Moas would have taken 77, 73, 71, and 67 days to hatch, and a fossil ostrich from China would have taken 65 days. Eighty-five days in *Aepyornis* approaches the upper limit of 100 days set by the mechanism of shell structure and gas exchange in large eggs (Needham).

COMMENT

With the aid of these various tables and graphs, it is possible to see a constant relationship among the eggs of all birds, from the hummingbird to the Ostrich. What, really, is this relationship? It is an extension to all birds of the known course of embryonic growth of individual birds. The embryo increases in size according to a known daily pattern which can roughly be called a geometric rate of increase. For all birds the early developmental stages require a certain fairly uniform period; that much is also known for the progressive stages in the gestation of mammalian embryos. For the first six days the embryos of birds cannot be distinguished from mammalian or reptilian embryos (Beebe). But the later stages of avian embryological growth progress at higher and higher absolute speeds. This is why a sparrow's egg, though only 0.07 cubic inches larger than a warbler's egg, takes two days longer to hatch, while a Trumpeter Swan's egg, fully 7 cubic inches larger than a Whistling Swan's egg, takes only a little over two days longer to hatch.

The above consideration brings out the well-known correlation between the size of the egg and the state of the young when hatched. Altricial young have relatively shorter incubation periods than precociously cursorial or natatory young; birds whose young can run or swim at hatching lay relatively larger eggs, but the size factor adds time to the incubation period.

The Brush-turkey, *Lipoa ocellata,* has an incubation period of 38 days, to average the conflicting reports of Le Souëf and Campbell, while for an egg of its size (9.06 cubic inches) the theoretical incubation period is only 32.5 days, i.e., the deviation is 5.5 days from the average, or a half day more than the expected maximum deviation. This retardation can perhaps be explained on two bases: (a) the relative isolation and lack of predation in its natural habitat; (b) the lowered incubation temperature (about 90° F.).

This study might be pushed further to the correlation of birds' geographical distribution, egg sizes, and incubation periods. Bergtold's theory of "ascent," correlating taxonomic superiority and the resultant increase in temperature with an increase in the speed of incubation is only a vague empiricism which finds few exact applications to individual species of birds. Naturally the entire physiology of any bird—or of any egg-laying organism—must extend itself to the period of the embryonic life of that creature. Thus temperature becomes more or less of a constant in any reckoning of this sort, and one expects to find a certain metabolic increase for each additional degree of heat. It is in cases where the incubation period departs from the expected interval which a certain temperature would predicate that one must search for a factor that can modify developmental sequences apart from thermal dictates. This is the point where ecology operates, within the limits shown in Table 2.

The Megapodes, which presented such an obstacle to Bergtold's theory, fall smoothly into line with my graphs, tables, and reasoning, showing again that egg size and ecology determine incubation periods.

CONCLUSIONS

1. The volume of any egg may be fairly approximated from its primary measurements by the formula:

$$V = 0.85\left(\frac{\pi}{6}ab^2\right),$$

a being the long axis and b the greatest transverse diameter of the egg.

2. The incubation period increases in parallel with the fourth power of the increase in egg volume.

3. A study of relative incubation periods shows that, for an egg of any given size, there is an average incubation period as well as a probable limit to the positive and negative deviations from that average.

4. Given the size of an egg, it is possible to state the limits within which its incubation period is likely to fall; the period is given roughly by the formula:

$$V = .0063\left(\frac{1000V}{T}\right)^{1.30},$$

and an ecological correction not exceeding five days in either direction, may be made, if necessary, by the use of a table which has been presented in this paper.

5. The embryos of predacious birds have relatively slower growth rates than the embryos of many other birds.

6. Birds which have been preyed upon or otherwise harassed may: (a) acquire shorter incubation periods; (b) lay larger clutches of eggs without

shortening the period; or (c) lay larger clutches *and* shorten the period at the same time. In the last case the birds have probably been particularly frequent objects of destruction—there must have been, and perhaps still is, some particularly vulnerable point in their ecological adjustments to bring about such a doubled effort for embryological compensation.

7. Our present knowledge of the incubation periods of small birds in terms of days—not hours—precludes an accurate application of this study to their comparative embryonic growth rates.

8. Incubation periods vary according to the sizes of eggs and the ecological niches of the birds which lay them.

TABLE 1

EGG VOLUMES AND INCUBATION PERIODS (LISTED IN ORDER OF THEIR VOLUMES)

Species	*Volume (cu. in.)* (*V*)	*Incubation Period* (*days*) (*T*)
1. Trumpeter Swan	17.13	40
2. Whistling Swan	9.90	37.5
3. *Lipoa ocellata*	9.06	38
4. Little Brown Crane	8.41	31.5
5. Common Loon	7.98	29
6. Canada Goose	7.81	29
7. White Pelican	7.52	29.5
8. American Eider	5.96	25.5
9. Glaucous Gull	5.94	28
10. Common Murre	5.87	29
11. Brünnich's Murre	5.87	28
12. Black Vulture	5.81	30
13. Gannet	5.39	40.5
14. Brown Pelican	5.23	28
15. Lesser Snow Goose	5.18	28.5
16. Fulmar	5.15	55
17. Herring Gull	4.70	26
18. Caspian Tern	4.16	20
19. Skua	3.86	29
20. Great Blue Heron	3.73	28
21. Red-tailed Hawk	3.71	30
22. Ruddy Duck	3.65	30
23. Osprey	3.64	28
24. Redhead	3.49	23
25. Snowy Owl	3.48	32
26. (Domestic Fowl	3.47	21)
27. American Merganser	3.46	28
28. Red-breasted Merganser	3.46	28
29. Goshawk	3.42	28
30. Swainson's Hawk	3.35	26.5
31. Black Duck	3.19	27
32. White Gyrfalcon	3.14	29

TABLE 1 (continued)

EGG VOLUMES AND INCUBATION PERIODS (LISTED IN ORDER OF THEIR VOLUMES)

Species	*Volume (cu. in.)* (*V*)	*Incubation Period* (*days*) (*T*)
33. Red-shouldered Hawk	3.11	26.5
34. Rough-legged Hawk	3.10	28
35. Ring-billed Gull	2.95	21
36. European Cormorant	2.94	28.5
37. Hooded Merganser	2.80	31
38. Duck Hawk	2.76	28
39. Mallard (Wild)	2.65	26.5
40. Harlequin Duck	2.63	24.5
41. White Ibis	2.59	21
42. Black Guillemot	2.56	21
43. Parasitic Jaeger	2.52	24
44. Oystercatcher	2.43	24.5
45. Long-tailed Jaeger	2.28	23
46. Laughing Gull	2.28	20
47. European Widgeon	2.26	24.5
48. Gadwall	2.24	28
49. Broad-winged Hawk	2.21	24
50. Wood Duck	2.20	29
51. Old-squaw	2.14	24.5
52. Pintail	2.05	22.5
53. Shoveller	2.05	22
54. Black-crowned Night Heron	2.01	25
55. Sooty Tern	1.95	26
56. Franklin's Gull	1.94	19
57. Cabot's Tern	1.86	21
58. Common Tern	1.75	21
59. Glossy Ibis	1.75	21
60. Northern Raven	1.48	20.5
61. Blue-winged Teal	1.40	22
62. Green-winged Teal	1.31	22
63. Barn Owl	1.29	22.5
64. Willow Ptarmigan	1.22	25
65. Canada Spruce Partridge	1.21	17
66. American Crow	1.15	16.5
67. Kestrel	1.13	27.5
68. Pigeon Hawk	1.10	21
69. Dovekie	1.09	24
70. Clapper Rail	1.00	14
71. Screech Owl	.99	23
72. Purple Gallinule	.93	24
73. Woodcock	.93	20.5
74. Green Heron	.89	17
75. Ruffed Grouse	.86	24
76. Sharp-shinned Hawk	.82	22.5
77. Fish Crow	.75	17

TABLE 1 (concluded)

EGG VOLUMES AND INCUBATION PERIODS (LISTED IN ORDER OF THEIR VOLUMES)

Species	*Volume (cu. in.)* (*V*)	*Incubation Period* (*days*) (*T*)
78. Killdeer	.73	27
79. Burrowing Owl	.73	21
80. Kingfisher	.72	16.5
81. Pied-billed Grebe	.69	23.5
82. Passenger Pigeon	.69	14
83. Wilson's Plover	.62	24.5
84. Sanderling	.62	23.5
85. Northern Pileated Woodpecker	.57	18
86. Black Tern	.55	17
87. Least Tern	.54	15
88. Least Bittern	.51	15
89. Spotted Sandpiper	.49	15.5
90. Leach's Petrel	.48	35
91. Wilson's Petrel	.48	35
92. Bob-white	.47	23.5
93. Red Phalarope	.42	15
94. Nighthawk	.39	16
95. Yellow-billed Cuckoo	.37	14
96. Black-billed Cuckoo	.37	14
97. Eastern Robin	.36	12.5
98. Saw-whet Owl	.35	21
99. Mourning Dove	.34	13
100. Kingbird	.23	14
101. Snow Bunting	.14	14
102. Song Sparrow	.14	12
103. Yellow Warbler	.08	10
104. Ruby-throated Hummingbird	.03	14

TABLE 2

GROUPING OF SPECIES ACCORDING TO TEXT-FIGURE 2 (WITH AVERAGE CLUTCH OF EACH)

Incubation Slow		*Incubation Average*		*Incubation Fast*	
GAVIIFORMES					
				Common Loon	2
COLYMBIFORMES					
Pied-billed Grebe	6				
PROCELLARIIFORMES					
Leach's Petrel	1				
Wilson's Petrel	1				
Fulmar	1				
PELECANIFORMES					
Gannet	1	Brown Pelican	2.5	White Pelican	3
European Cormorant	5				

TABLE 2 (continued)

GROUPING OF SPECIES ACCORDING TO TEXT-FIGURE 2 (WITH AVERAGE CLUTCH OF EACH)

Incubation Slow		*Incubation Average*		*Incubation Fast*	
CICONIIFORMES					
Black-crowned Night Heron	3.5	Great Blue Heron	3.5	Green Heron	4.5
		Least Bittern	4.5	Glossy Ibis	3
				White Ibis	4
ANSERIFORMES					
Trumpeter Swan	6	Whistling Swan	5.5	Canada Goose	7
Mallard	9.5	Pintail	8.5	Redhead	12.5
Green-winged Teal	9.5	Shoveller	10	American Eider	6.5
Blue-winged Teal	10.5	Old-squaw	8		
Gadwall	9.5	European Widgeon	7.5		
Black Duck	9	Harlequin Duck	7.5		
Wood Duck	10.5	Lesser Snow Goose	6.5		
Ruddy Duck	10				
Hooded Merganser	8.5				
American Merganser	11.5				
Red-breasted do.	9				
FALCONIFORMES					
Goshawk	3.5	Black Vulture	2		
Red-tailed Hawk	2	Sharp-shinned Hawk	4.5		
Rough-legged Hawk	3.5	Red-shouldered Hawk	3		
White Gyrfalcon	4	Broad-winged Hawk	3		
Duck Hawk	4	Swainson's Hawk	3		
Kestrel	4.5	Osprey	3		
		Pigeon Hawk	5		
GALLIFORMES					
Ruffed Grouse	10.5			Canada Spruce Grouse	12
Willow Ptarmigan	10.5			(Domestic Fowl)	(?)
Bob-white	13.5				
GRUIFORMES					
Purple Gallinule	8	Little Brown Crane	2	Clapper Rail	10.5
CHARADRIIFORMES					
Wilson's Plover	3	Oystercatcher	2.5	Herring Gull	3
Killdeer	4	Woodcock	3.5	Ring-billed Gull	3
Sanderling	4	Spotted Sandpiper	4	Laughing Gull	3
Skua	2.5	Red Phalarope	4.5	Franklin's Gull	3
Sooty Tern	2	Glaucous Gull	2.5	Least Tern	2.5
Dovekie	1	Common Tern	2.5	Caspian Tern	2
		Cabot's Tern	1.5	Brünnich's Murre	1
		Black Tern	2.5	Black Guillemot	2
		Common Murre	1		
		Parasitic Jaeger	2		
		Long-tailed Jaeger	2		
COLUMBIFORMES					
		Mourning Dove	2	Passenger Pigeon	1
CUCULIFORMES					
		Yellow-billed Cuckoo	4		
		Black-billed Cuckoo	4		

TABLE 2 (concluded)

GROUPING OF SPECIES ACCORDING TO TEXT-FIGURE 2 (WITH AVERAGE CLUTCH OF EACH)

Incubation Slow		*Incubation Average*		*Incubation Fast*	
STRIGIFORMES					
Snowy Owl	7	Barn Owl	6.5		
Screech Owl	4				
Burrowing Owl	7				
Saw-whet Owl	5				
CAPRIMULGIFORMES					
		Nighthawk	2		
MICROPODIFORMES					
Ruby-throated Hummingbird	2				
CORACIIFORMES					
		Kingfisher	6.5		
PICIFORMES					
		Northern Pileated Woodpecker	4.5		
PASSERIFORMES					
		Northern Raven	6	Crow	4
		Fish Crow	4	Robin	4
		Kingbird	3		
		Snow Bunting	6		
		Song Sparrow	5		
		Yellow Warbler	4		
In this column: 38 species; average clutch	5.94	In this column: 43 species; average clutch	4.13	In this column: 21 species; average clutch	4.41

The predators in the left-hand column, including hawks, owls, and skua, average 4.27 eggs per clutch; the non-predators in the left-hand column, including all the others, average 6.65 eggs per clutch.

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