The significance of clutch-size in waterfowl

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Summary

1. The average clutch-size of the different species of waterfowl varies inversely with the relative size of the egg. This applies to the Anatidae as a whole, to each of the four genera which can be tested separately, and to four subspecies of the Mallard.
2. It is suggested that the average clutch of each species has been evolved in relation to the average availability of food for the female around the time of laying, modified by the relative size of the egg.
3. The specific differences in clutch-size and egg-size are mainly hereditary and variations in the food supply for a particular female perhaps influence mainly the date of laying.
4. The inverse relationship between clutch-size and egg-size is only broad, probably because the average availability of food differs greatly in different species.
5. The advantage of a relatively large egg is that the newly hatched chick has a relatively large reserve of food.

Twenty years ago, I advocated that the clutch-size of birds which feed their nestlings has been evolved in relation to the size of brood from which, on average, most young survive, the limit being set by the amount of food which the parents can bring to the young; and this view, with minor modifications, has been supported by later observations (Lack 1947, 1966). However, it cannot apply to those birds in which the young feed for themselves from hatching, notably the family Anatidae. Yet, if one believes in natural selection, the normal clutch of each species of waterfowl should be that which, on average, results in the parent concerned leaving the greatest number of surviving offspring.

Why, then, should different species of ducks lay clutches of such different size, ranging from two to three in the Musk Duck *Biziura lobata* to about a dozen in some species of *Dendrocygna*, *Tadorna*, *Anas*, *Aythya*, *Aix* and *Bucephala*? H. J. Frith suggested to me some fourteen years ago that the number might be limited by the food reserves of the adult female, but I dismissed this. However, I later found evidence that the food reserves of the female can modify the clutch-size of the Swift *A. apus* and perhaps of gallinaceous birds (Lack 1956, 1966).

The figures for the weight of the fresh egg and the adult female of many species of Anatidae given by Schönwetter (1960-61), and extensively supplemented by J. Kear (pers. com.), show that the weight of the egg in proportion to the weight of the bird differs greatly in different species, ranging from 2½ per cent in the White-winged Wood Duck *Cairina scutulata* to a little over 20 per cent in two stiff-tails *Oxyura maccoa* and *O. dominica*. Part of this variation is due to a general trend, found within every family of birds, and also within each genus and tribe of ducks, for the smaller species to have proportionately heavier eggs (Heinroth 1922), but this is not the only factor concerned. For instance, though the female Pintail *Anus acuta* and White-headed Duck *Oxyura leucocephala* are of similar weight, their eggs weigh 45 and 96 grams respectively. Again, though the Black Swan *Cygnus atratus* is nearly nine times as heavy as the Bahama Pintail *Anas bahamensis*, the eggs of both are about six per cent of their body-weight.

When proportionate egg-weight is plotted against body-weight for all the available species of waterfowl, a mean curve can be fitted by eye to show the average increase in proportionate egg-weight with decreasing body-weight. The points for some species, notably swans *Cygnus* and stiff-tails *Oxyura*, come well above this mean line, while those for certain other species, notably in the genera *Dendrocygna* and *Anas* and the tribe Cairinini, come well below it, and these species can be said to have relatively large and relatively small eggs respectively (Figure 1).

By drawing lines parallel to the mean line, I separated off all the species with relatively large or small eggs, and relatively fairly large or fairly small eggs, respectively, in such a way that there were a nearly equal number of species in each of these four categories. As there is not space to publish here the weights for each species and the egg-size category to which it has been allocated, copies of this information have been deposited at the Wildfowl Trust and the Edward Grey Institute, together with the usual clutch of each species, based on Delacour (1954-64) and modified by J. Kear (pers. com.).

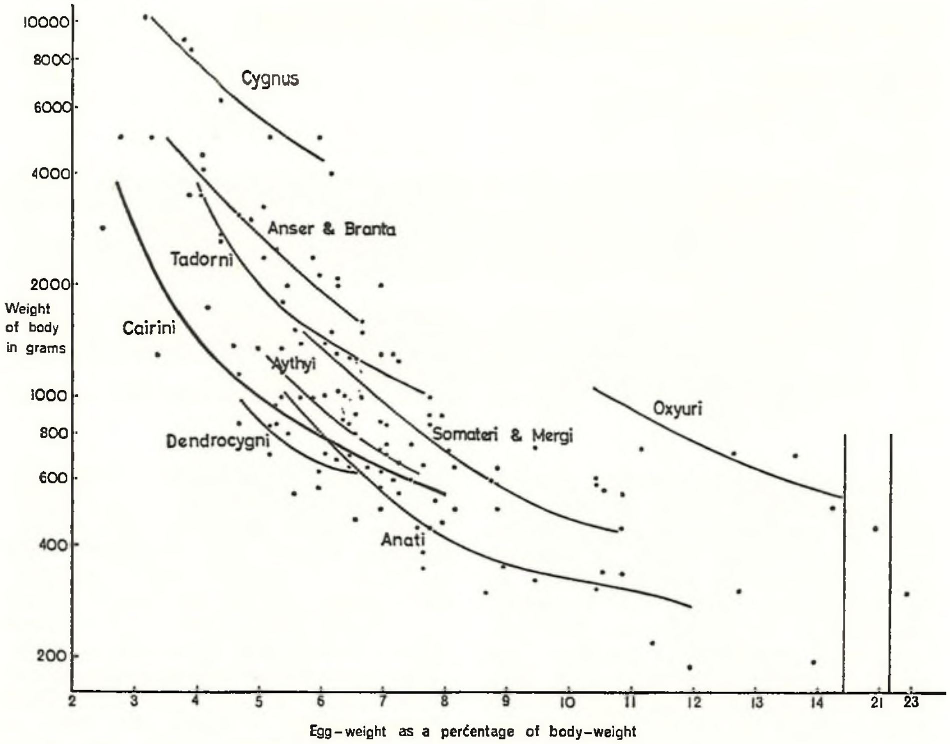

Figure 1. Proportionate egg-weight in relation to body-weight in Anatidae.

Table I shows that the average clutch-size is just over five for the species with relatively large eggs, about seven and a half for those with fairly large eggs, eight for those with eggs of medium size, and nearly nine and a half for those with relatively small or fairly small eggs. Hence clutch-size and the relative size of the egg are inversely related. This suggests that the female has limited food reserves which can be used to form either a few large eggs or more smaller ones. Since both clutch-size and the size of the egg are relatively constant in each species, the main differences between species are probably due to hereditary factors, evolved through natural selection. It is reasonable to suggest that they have been evolved in relation to the average availability of food for the female around the time of laying.

The inverse relationship between clutch-size and relative egg-size is only broad, as shown by the wide limits in the average clutch-size of the species in each egg-size category in Table I. But this is to be expected if the relationship depends on the average availability of food for the laying female, as the latter must be expected to differ greatly in different species. A few species lay about their own weight of eggs in a clutch, including the Shelduck *T. tadorna*, the Ruddy Duck *Oxyura jamaicensis* and the three species

Table I. Clutch-size and relative size of egg in the Anatidae as a whole. Separate figures are included for a few well-marked subspecies of the same species.

Relative size of egg	*Number of species (or subspecies)*	*Average clutch*	*Limits of average clutch*
large	18	5.1	2-8
fairly large	20	7.6	4-12
medium	55	8.0	4-13
fairly small	20	9.4	6-12
small	21	9.3	6-11

of goldeneyes *Bucephala*, while at the other extreme, the clutch is only about 16 per cent of the body-weight in the Trumpeter Swan *Cygnus c. buccinator*.

It might be objected that the different tribes of Anatidae are so different that the figures for all species of waterfowl should not be grouped together as in Table I. However, Table II shows that there is a similar inverse relationship between clutch-size and the relative size of the egg in each of the four genera for which there are enough species with eggs of different size for a separate analysis, namely *Anser*, *Branta*, *Anas*, and *Aythya*. Moreover a similar relationship holds among four races of a single species, *Anas platyrhynchos*, as the egg is relatively smallest in the Common Mallard *A. p. platyrhynchos*, with a clutch of about 11, next smallest in the Florida Duck *A. p. fulvigula*, with a clutch of nine, rather larger in the Hawaiian Duck *A. p. wyvilliana*, with a clutch of eight, and relatively largest in the Laysan Duck *A. p. laysanensis*, with a clutch of five. Again the Auckland Island Flightless Teal *Anas a. aucklandica*, with a clutch of three to four, has a relatively larger egg than the New Zealand form *A. a. chlorotis*, with a clutch of six.

Table II. Clutch-size and relative size of egg in certain genera of waterfowl.

Relative size of egg	*Number of species (or subspecies)*	*Average clutch*
Anser		
fairly large	5	5.3
medium	5	6.1
Branta		
fairly large	2	4.3
medium	3	5.7
Anas		
fairly large	2	4.8
medium	13	7.6
fairly small	13	9.6
small	8	9.4
Aythya		
fairly large	2	7.3
medium	7	9.2
fairly small	2	9.0

Since, in waterfowl, a relatively larger egg has been evolved at the expense of a smaller clutch, it must have some compensating advantage. This is probably in providing the newly hatched duckling with a relatively large fat reserve, which is at first in the yolk sac, but is rapidly transferred to the liver and under the skin just after hatching (Kear 1965). The advantage of this fat reserve is that it enables the young to withstand temporary food shortage. For instance, ducks have proportionately larger eggs than gallinaceous birds, and correspondingly a young Mallard can survive without food for longer than a young Capercaillie *Tetrao urogallus*; further, Swedish Mallard have larger yolk sacs and can survive for longer than English ones (Marcström 1966). Again, swans have relatively large eggs, and their newly hatched chicks can survive unusually long without food (Heinroth 1926, Perrins and Reynolds 1967). The other waterfowl with relatively large eggs are the stiff-tails, and the young of *Oxyura leucocephala* have an unusually thick dorsal layer of fat; further their eggs are unusually resistant to changes in temperature, which may be a subsidiary advantage of a large egg (Phillips 1926).

It is presumably because they have a big fat store that newly hatched ducklings can walk a long way from the nest before their first meal, and this has the special advantage that the duck need not nest beside water, and so may select a safer site than might otherwise be possible. A large fat store confers a special advantage on arctic species such as the Goldeneye *Bucephala clangula*, since it can act as an insulating layer. Further, young Goldeneyes maintain their body temperature by metabolising fat, and so can continue searching for food, whereas young Mallard are not cold-hardy and, if cold, have to be brooded by the parent (Koskimies and Lahti 1964). It is therefore suggestive that nearly all the waterfowl which nest in the arctic belong to genera with relatively large or fairly large eggs, namely *Cygnus*, *Anser*, *Branta*, *Somateria*, *Melanitta*, *Bucephala* and *Mergus*. Again, J. Kear pointed out to me that probably the ducklings which find it hardest to obtain food are those which have to dive for it, notably in the tribes Mergini and Oxyurini, and these have relatively large or fairly large eggs; pochards Aythyini do not have relatively such large eggs, but their young at first feed from the surface, except for the New Zealand Scaup which according to Porter (1940) will go down to six feet to feed even at a day old. This species also has relatively the largest egg among the Aythyini. It may be wondered whether conditions are unusually rigorous for ducklings on islands, since the Laysan and Auckland Island ducks have relatively larger eggs than most other species of *Anas*.

Clearly, the extent to which a larger egg, and hence a fatter duckling, is advantageous depends on the conditions experienced by the young soon after hatching. The size of egg evolved by each species is presumably that at which the improvement in the survival-rate of each chick resulting from a larger egg just balances the resulting decline in the number of eggs laid.

If, as argued here, the hereditary differences in clutch-size and egg-size between different species have been evolved in relation to the average availability of food for the laying female, it might be thought that, if food were unusually sparse, a duck would lay either a smaller clutch or smaller eggs than usual. That it does not usually do so is presumably because, if it did, its chances of leaving offspring would be too small to set against the risks and strains of breeding. Further, in many areas a shortage of food at the start of the breeding season is likely to be very temporary. Hence if food is sparse, it is probably most advantageous for a duck to postpone breeding until it can produce a clutch and eggs of the normal size, though there is no direct evidence on this point. Again, if food is unusually plentiful, a duck does not usually lay more or larger eggs; perhaps it lays earlier, though again there is no direct evidence. Early laying might be advantageous when the potential breeding season is short. While these remarks seem true in general, some annual, local and seasonal variations in clutch-size are known in ducks and need study.

Acknowledgements

I must apologise to H. J. Frith for ignoring for so long his suggestion mentioned in the first paragraph. I am extremely grateful to J. Kear for her trouble in helping to assemble the data on weights and clutch-size on which the paper is based.

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