

Proximate and ultimate determinants of clutch size in Anatidae

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In a stimulating analysis, Lack (1967, 1968a) reviewed waterfowl clutch size and egg size data, and concluded that inter-specific variations in average clutch size are generally inversely related to those of relative egg size. Thus, he suggested that the average clutch size of each waterfowl species has evolved in relation to the average availability of food to the female around the time of nesting. He hypothesized that in waterfowl, relatively large eggs have probably evolved to provide the newly-hatched young with a large food supply (an idea he subsequently (1968b) questioned) or with an adequate insulating layer of fat. He also suggested that, since annual, seasonal, and local variations in clutch size exist, proximate factors, such as the food supply of individual females, may be more likely to influence a bird's date of laying than either its egg size or clutch size. Since the publication of Lack's study, several additional reviews of avian clutch sizes have appeared, notably those of Klomp (1970), von Haartman (1971) and Cody (1971). Klomp considered the problems posed by the Anatidae in some detail, and generally agreed that the food supplies available to the female are probably the ultimate factor influencing clutch size in this group.

Because of the large amount of information available for waterfowl, and since Lack did not concern himself with proximate influences on clutch sizes of individuals, I have given these matters some attention and have reached somewhat different conclusions. No simple single explanation for inter- and intraspecific variations in clutch sizes seems possible at present, but a summary of the evidence relating to these phenomena nevertheless appears worthwhile.

Proximate factors influencing clutch sizes of individual birds

It is well established that intrapopulation variations in clutch size of waterfowl do exist, which probably reflect proximate environmental influences that vary with time. Klomp (1970) listed thirteen species of Anatidae that have been reported to

exhibit declines in average clutch size during a single breeding season, and Bengtson (1972) reported this trend in all of ten species of ducks in his study. Except for Koskimies' (1957) suggestion that such individual clutch size variations might be the result of genetic polymorphism having adaptive value, it has been generally believed that these seasonal differences are mainly the result of proximate influences. The lowered hormonal levels after the reproductive peak (Hilden, 1964), or the reduced stimulating by temperature or photoperiod effects (Dane, 1966), might reduce the clutch size of late-nesting birds. Their smaller clutch sizes might also simply reflect reneating, since repeat clutches are generally smaller than the original ones (Sowls, 1959). This, in turn, may result from exhaustion of the female's reserves (Wagner, 1960). Again, the smaller, later clutches may be produced by younger females nesting for the first time and thus not in peak reproductive condition (Lemieux, 1959). Kossack (1950) provided some data for the Canada Goose *Branta canadensis* favouring this view.

Variations in average clutch of a single population in different years also occur in the Anatidae, and clearly must be controlled by proximate factors. The possibility that these might be related to annual variations in food availability has recently been supported by Bengtson (1971) who observed that during a year of relative food scarcity, four species of diving ducks and the European Wigeon *Anas penelope* produced significantly smaller clutches than normal. This finding clearly runs counter to Lack's suggestion that annual variations in food supply influence laying date rather than clutch size, but does support his view that the average clutch size may be basically attuned to normal food availability.

Annual variations in clutch size and non-breeding, related to weather conditions during the egg-laying period, have also been established for the Anatidae, particularly among arctic breeders. Evidence on this point has been provided for the Atlantic Brent Goose *Branta bernicla hrota*, the White-fronted Goose *Anser albifrons*, Black Brant *Branta bernicla orientalis*

and Lesser Snow Goose *Anser caerulescens caerulescens* by Barry (1962), for the Lesser Snow and 'Blue' Geese by Cooch (1961), and for the Ross' Goose *Anser rossii* by Ryder (1970b).

If females breeding for the first time tend to have smaller clutches than experienced breeders, then variations in the percentage of young females in a population might result in between year variations in average clutch size. Mendall (1958) suggested this possibility for the Ring-necked Duck *Aythya collaris*, when he found a limited correlation between poor hatching success in one year and large average clutches of Ring-necked Duck. Hilden (1964) provided supporting evidence among Tufted Ducks *Aythya fuligula* and Greater Scaups *Aythya marila*.

Population density is, theoretically, another factor controlling clutch size. Hilden (1964) found no evidence for this among the two *Aythya* species just mentioned. The only example I have encountered is that of Marshall (1967), who reported that increased clutch size (but reduced nesting success) was associated with increased nesting densities in the European Eider *Somateria m. mollissima*. Ryder (1970b) found that Ross' Geese nested earlier in high-density concentrations, but that clutch size was not influenced by the breeding density.

Interpopulation variations in clutch size might, of course, be a reflection of either proximate or ultimate factors. If the populations are geographically well isolated, the probability of genetic control for these differences would seem to be higher, and indeed Lack (1967) provided some examples among various races of certain

ducks. However, continuous clines in clutch size might well be geared to such proximate factors as photoperiod or temperature gradients. Weller (1964) was unable to find any evidence for such geographic variation in the clutch size of the Canada Goose. The suggestion of Paynter (1951) that the American Eider *S.m. dresseri* has intraspecific clinal variation was based on data from various investigators and, as Weller indicated, is therefore of questionable value as well as being only over a range of less than ten degrees of latitude. A more general comparison of average clutch size of this species (Table 1) is not indicative of increased clutch size with increasing latitude; if anything, the average clutch size is largest at intermediate latitudes.

To summarize, it would appear that proximate factors are as likely to influence anatid clutch size as to account for variations in laying dates, at least in temperate or arctic species.

Ultimate factors influencing average clutch sizes of anatid species

Lack (1967) advanced the view that the average clutch size of each anatid species has evolved in relation to average available food supplies for the female, as influenced by the size of the species' eggs. He and, earlier, Heinroth (1922) have also pointed out that larger-bodied birds channel relatively less food material into the production of individual eggs, resulting in a negative correlation between average adult female weight and the weight of the species' eggs. An even clearer negative correlation

Table 1. Breeding latitude and reported clutch sizes of the Common Eider *S. mollissima*

Latitude (°N)	Average Clutch-size	Total nests	Locality	Authority
79	2.95	2,993	Kongsfjord, Spitzbergen	Ahlen & Andersson 1970
65	2.74	42	Iceland	Gudmundsson, 1932
64	3.44	1,598	Cape Dorset, NWT	Cooch, 1965
63	4.6*	193	Valassaaret, Finland	Hildén, 1964
62	4.89	89	Yukon-Kuskokwim Delta	Lensink (personal communication)
61	4.32	734	Green Is., Que.	Lemieux (cited in Cooch, 1965)
60	3.13	73	Payne, Bay, Que.	Edwards (cited in Cooch, 1965)
56	4.47	120	Belcher Is., NWT.	Freeman, 1970
51	3.6	60	Amchitka Is., Alaska	Kenyon, 1961
48	4.04	1,131	Saquéenay Co., Que.	Lewis, 1939
45	3.53	134	Kent Is., Me.	Gross, 1938
44	3.25	44	Penobscot Bay, Me.	Paynter, 1951

*Excludes clutches of less than three eggs.

may be seen between the average adult female weight and the proportional weight of the average total clutch. This ratio provides a useful index to the relative energy drain on the female during laying. Lack's (1968a) tabular data indicate that in eight taxa (species or subspecies) of swans, the equivalent of from 16 to 34% (average 24%) of their adult weight is deposited in an average clutch of eggs. For sixteen taxa of true geese the calculated range is from 20 to 40% (average 28%), for forty-seven surface-feeding ducks from 35 to 106% (average 60%), and for sixteen sea ducks from 20 to 109% (average 63%). The larger species, geese and swans, which have the greatest available energy reserves of body fat, thus actually experience the smallest relative energy drain from egg-laying. Their generally small clutch size is therefore unlikely to be attributable to limited food supplies during laying.

Several hypotheses have been proposed to explain this problem. Ryder (1970a) has suggested that, at least in the Ross' Goose, the total pre-breeding food reserves needed by the female for both egg-laying and during incubation might limit the average clutch size of this unusually small goose, which usually lays only four eggs. Thus, for this and perhaps other arctic nesting geese, the female's energy supplies must allow the female to provide maximum protection to the clutch during incubation and ensure the survival of the young until they can forage. This theory is essentially an extension of Lack's basic views on clutch size controls.

A second hypothesis is that egg predation during the egg-laying period may limit effective clutch size. Thus the dangers of leaving the nest exposed prior to incubation may outweigh the advantages of adding additional eggs. The probability of this occurring increases with increasing clutch size, especially in species vulnerable to pre-incubation predation of the entire clutch. Lack has rejected predation as an ultimate control of avian clutch size, on the grounds that natural predation levels are normally too low to be effective and in general this would seem to be true. Bengtson (1972) provided data for ten Icelandic duck species, showing that pre-incubation nest predation caused 55% of the nest failures in 2,889 nests, or a total of about 19% of the nests under study. This would suggest a daily predation rate of little more than 2% per day during a 10-day egg-laying period, too low effectively to limit clutch size. However, Choate's (1967) study of American Eiders indicated that 66% of the entire nest

predation in 1 year (totalling 58% of 448 nests) occurred on incompleting nests, implying a 12–15% daily nest loss during the 3- or 4-day period required to complete a clutch. If they are at all typical, such predation rates might easily account for the low average clutch size of this species.

Thirdly, it is possible that average clutch size may be limited by decreasing parental effectiveness. Mendall (1958) reported decreased hatching success among large clutches of Ring-necked Duck. Hilden (1964) had similar results for Tufted Ducks and Greater Scaups, and Bengtson (1972) for Greater Scaups. Ryder (1970a) has cited some additional examples. Likewise, larger than normal broods may suffer relatively higher mortality rates than normal sized ones, as indicated by Eygenraam (1957) for Mallard *Anas platyrhynchos*. Cooch (1961) noted that Lesser Snow Goose goslings hatched from eggs laid late in large clutches survived less well. Similarly, Parsons (1970) reported that Herring Gulls *Larus argentatus* hatched from smaller eggs, usually the third-laid ones, exhibited the poorest survival. If this trend is general, it might well be a source of increasing selective disadvantage for enlarging the clutch size.

Fourthly, a restricted optimum breeding period, or the need to synchronize hatching with an optimum hatching date, may limit average clutch size. Koskimies (1957) found laying date and clutch size to be individually constant among female Velvet Scoters *Melanitta fusca*, and believed this ensured uniform hatching times of different-sized clutches. Cooch (1961) similarly pointed out that, in the Lesser Snow Goose, smaller clutches are 'necessary' in retarded breeding seasons or towards the end of normal ones if reproduction is to be efficient. Hilden (1964) mentioned that, since the period of both egg-laying and hatching are undesirably prolonged in large clutches, and since late-hatched broods generally survive poorly, selection may limit clutch size below the female's physiological limits or her incubation abilities. Dane (1966) similarly pointed out that each egg added to a duck's clutch delays hatching another day, both increasing the problems of egg and chick survival and shortening the available time for maturation prior to migration. There is considerable evidence from a variety of waterfowl species that broods hatching relatively late usually survive more poorly than those hatched fairly early in the season (Grice & Rogers, 1965; Bengtson, 1972).

This influence of a restricted optimum

breeding period is most likely to be exerted in arctic or subarctic areas. If one compares the average clutch size of a number of northern hemisphere waterfowl as given by Lack with average July isotherms ($^{\circ}\text{F}$) representing the northern limit of these species' breeding ranges primarily as reported by Voous (1960), an interesting relationship may be seen (Figure 1). Species having small average clutches nearly all are arctic or subarctic breeding, while those with large average clutches tend to be more temperate or subtropical. If one calculates clutch weight as a percentage of adult female weight for such species and again plots the results against July isotherms at the northern limits of distribution, a greater taxonomic spread may be seen (Figure 2). Although collectively there is a strong tendency to reduce the relative amount of energy put into the clutch the further north they breed, the trend is clearer in some groups than in others. This may be due to restricted breeding periods, possibly to

increased egg-predation dangers, to other demands on energy reserves associated with breeding in arctic environments, or to other factors.

In general, those anatid species having the smallest average clutch size (swans, geese, eiders) are not likely to encounter food shortages at the time of laying. Nor are their clutch sizes likely to be limited by ecological needs for relatively large eggs. Increased average food availability seem to play little part in the evolution of increased average clutch size in waterfowl. Instead, I would suggest that, where food supplies are not a limiting factor, clutch size is likely to be limited by decreasing parental effectiveness, decreased available optimum breeding time, and increased probability of nest predation. These four selective factors are in turn further obscured by proximate factors which produce the individual, seasonal and local variations in clutch size encountered by field biologists.

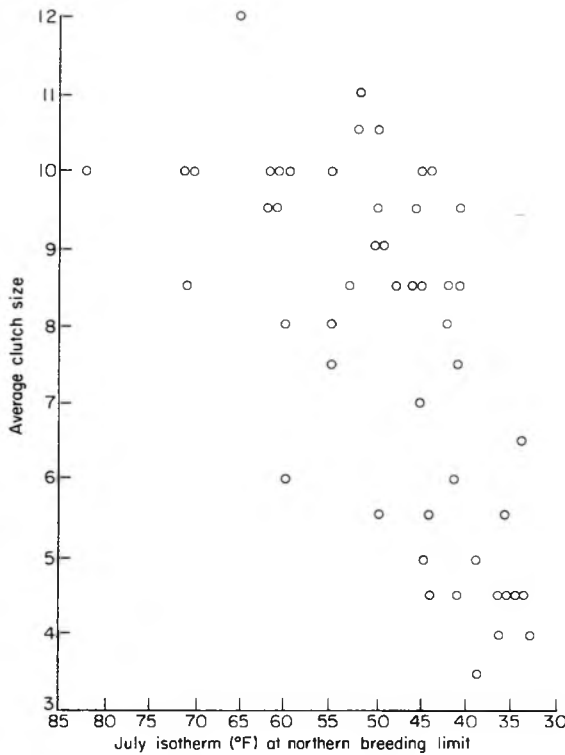


Figure 1. The relationship between average clutch size and northern breeding limits in fifty northern hemisphere Anatidae.

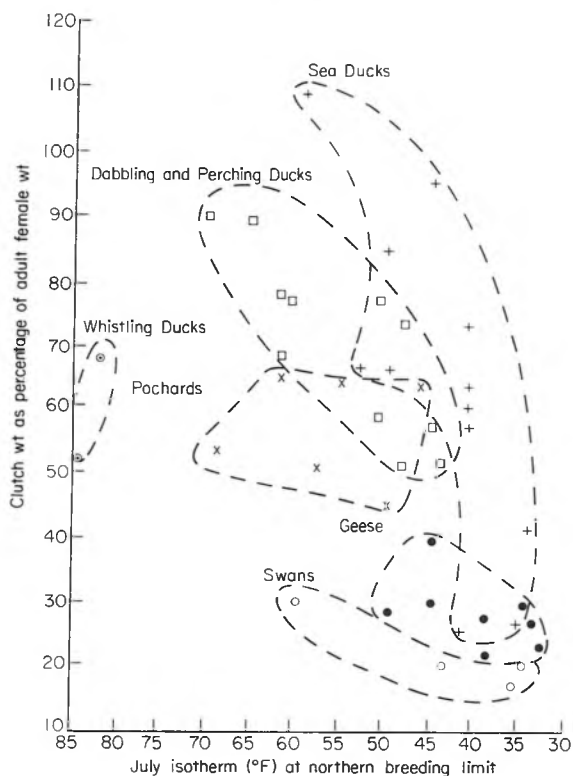


Figure 2. The relationship between the total average clutch weight relative to adult female

weight in the northern breeding limits in forty-three northern hemisphere Anatidae.

Summary

A review of Anatidae clutch-size data and an analysis of David Lack's hypothesis that food availability to the female around the time of her nesting can account for the evolution of average waterfowl clutch-sizes suggest several additions to or modifications of his theory. First, in contrast to Lack's suggestion, proximate factors do influence anatid clutch-sizes and result in measureable seasonal, yearly and perhaps also interpopulational variations in these. Secondly, indirect evidence suggests that several factors in addition to average food supplies may have influenced clutch-size evolution. These include needs for efficient partitioning of energy reserves between the incubating female and her eggs, dangers of pre-incubation clutch losses in those species that are unusually susceptible to nest predation, and decreasing parental effectiveness as well as possible decreased available optimum breeding periods associated with increases in clutch-sizes. Several or all of these may have placed upper limits on anatid clutch-sizes independently of or in conjunction with food supply effects.

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