A POSSIBLE FACTOR IN THE EVOLUTION OF CLUTCH SIZE IN ROSS' GOOSE

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About 25 years ago David Lack advanced the theory that clutch size, in birds which feed their young, has evolved in relation to the size of the brood producing the greatest number of young that reach sexual maturity, the ultimate limiting factor being the availability of food required by the young (Lack, 1954, 1966*a*). According to another major viewpoint (Wynne-Edwards, 1955, 1962), clutch size has evolved in relation to, and compensates for, the average mortality of a population. This idea, based primarily on the theory of "intergroup" selection, says that clutch size increases in a depleted (low density) population and decreases as the population density increases. Wynne-Edwards (1962) gives many examples of this "density-fecundity" relationship in most animal groups. The ultimate limiting factor in his proposal is food, whereas the proximate limiting factor is the regulation of population density by social behavior.

Arguments for and against both theories are now in the literature (Brown, 1964; Cody, 1966; Lack, 1954, 1965, 1966*a*; Perrins, 1964; Skutch, 1967; Smith, 1964; Wiens, 1966; Wynne-Edwards, 1955, 1962, 1963).

Few ideas have been published on the limitations or on the significance of clutch size in birds which do not feed their young, for example the family Anatidae (ducks, geese, and swans).

The purpose of this paper is to suggest that the clutch size of Ross' Goose (*Chen rossii*), a nearctic anserine, has evolved in relation to the food reserves which the female accumulates before arriving on the breeding grounds. I suggest that an important factor in the evolution of the clutch size is the number and size of eggs which provide enough food reserves for the newly hatched young until they are able to feed themselves (see Kear, 1965), and which also leave enough for the female to give maximum attentiveness to the eggs during incubation. The amount of food the female stores is limited by the total increase in body weight she can carry during the spring migration and maintain long periods of flight.

Lack (1966*b*) published one of the first suggestions concerning the significance of clutch size in waterfowl. He states that the average clutch size for each species has been evolved in relation to both the average availability of food for the female at the time and place of egg laying, modified by the relative size of the egg. He expresses essentially the same idea in a recent, more detailed review of waterfowl clutch sizes (Lack, 1968). My hypothesis

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Frontispiece: The larger birds are Lesser Snow Geese (*Chen hyperborea*).

ROSS' GEESE *(Chen rossii)* nesting on an island at Karrak Lake, Northwest Territories, 24 June 1967. Note males standing, females incubating and the paucity of vegetation within the nest territory.

FIG. 1. Ross' Goose nesting island at Karrak Lake, NWT., 25 June 1966.

follows closely that of Lack (1966*b*, 1968) with modification to apply to Arctic nesting geese. It is based on the assumption that the breeding female goose is independent of the food supply at the time and place of egg laying.

Each spring Ross' Geese migrate from their California wintering area in the Sacramento and San Joaquin Valleys to the nesting grounds in the Canadian Arctic, a distance of about 4,000 miles. Most of the population nests on islands in shallow tundra lakes in the Perry River region of the central Arctic (Ryder, 1969) (Fig. 1, 2). Small segments also nest in the Hudson Bay area (Cooch, 1954; Barry and Eisenhart, 1958; MacInnes and Cooch, 1963).

Before and during the spring migration the geese feed extensively and by the time they arrive in the north, their body weights and fat reserves are at a maximum compared to any other time of year. Lack (1966*b*) does not account for this weight increase and large amounts of fat found in Ross' and other Arctic nesting geese at the time of arrival on the nesting grounds (see Hanson, 1962 for Canada Geese (*Branta canadensis*); Barry, 1962 for Brant (*Branta bernicla*); Cooch, 1958 for Blue Geese (*Chen caerulescens*); Barry, 1967 for recent data on the Anderson River, N.W.T. population of Black Brant (*Branta nigricans*), Lesser Snow Geese (*Chen hyperborea*), and White-fronted Geese (*Anser albifrons*); Hanson et al., 1956 for Canada Geese, Lesser Snow Geese and White-fronted Geese from the Perry River region; Macpherson and Manning, 1959 for Canada Geese from Adelaide Peninsula, N.W.T.). Hanson (1965) states that the peak fat reserve in

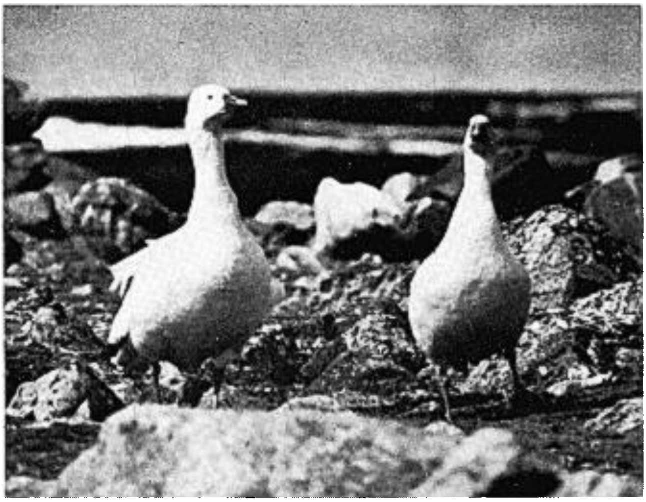

FIG. 2. Ross' Goose mated pair at Arlone Lake, NWT., July 1964.

Canada Geese at the time of arrival on the nesting grounds in northern Ontario is probably an evolutionary development which insures survival of the adult until spring breakup. This type of reasoning is prevalent in the literature of Arctic goose biology (see above references) and what little data we have indicates that it is most likely true. However, none of the literature suggests that the food reserves of the female goose are of evolutionary significance in allowing her to spend more time on the nest.

During the egg laying period Ross' Geese remain on the nesting islands for long periods, only occasionally visiting the mainland feeding marshes. It is hard to believe that the purpose of these visits to the mainland is to prepare her for the fasting period ahead, especially in late seasons when the vegetation is covered with snow or still frozen in the ground and food is scarce.

Ross' Geese usually lay four eggs (Ryder, 1967). Attentiveness increases with each egg in the clutch and incubation begins after the last egg is laid (Fig. 3). During egg laying and incubation, the breeding female can lose up to 800 grams (44 per cent) of body weight. Of this, about 100 grams are lost by ovary regression. During incubation she leaves the nest for short periods to obtain what little food is available near the nest site and rarely will she, accompanied by the male, fly to the mainland marshes to feed. It appears that throughout the incubation period the female is relying heavily on food reserves stored before the nesting season. It is also apparent that the short pre-egg stage and egg laying period (about 10 days) are too short to allow enough food intake to last through the 22-day incubation

FIG. 3. Ross' Goose nest on island at Karrak Lake, NWT., 13 June 1966.

period, even with occasional supplementary feedings. Hanson (1962) states that the resistance to fasting is frequently associated with the nutritive condition at the start of the fast. In Arctic geese this resistance is likely acquired before arrival on the nesting grounds.

The hatching time for a Ross' Goose clutch of three or four eggs is one or rarely more than two days. The goslings and adults leave the nest site within a few hours and begin the post-nuptial period during which the family spends most of its time feeding and later the adults complete the annual molt. Although some body weight is lost during the molt (Ryder, 1967), it is regained before the southward migration in late August and early September.

I propose that the differential utilization of stored food during the nesting season has been most important in the evolution of the clutch size in Ross' and other Arctic nesting geese. Figure 4 presents three possible "cases" which attempt to explain graphically the mechanisms by which present clutch size may have arisen.

Case 1 depicts a situation in which the female, with enough food reserves in her body, is able to maintain attentiveness to the eggs throughout the entire incubation period. Concurrently, the ova are supplied with a sufficient food reserve for the young until they are able to feed themselves. The total reserve allocated to the female and to the eggs is limited by the amount stored before the breeding season. The number of mature ova is limited so that the female can give maximum protection to the clutch. Case 1 proposes that the female is independent of a food supply at the time and place of nesting. Breeding biology studies of Ross' Geese and other Arctic nesting geese suggest to me that average clutch sizes have been evolved in relation to the conditions outlined for Case 1.

Case 2 shows that although the total increase in body weight has remained the same, the allocation of food reserves has been decreased to ova and increased to non-ovarian tissues. The direct result here is a smaller reproductive output and an overabundance of food reserve for the female. One obvious "advantage" of this case is that it allows for greater attentiveness to a smaller clutch and increased survival of young. A number of factors might decrease the frequency of this case occurring in a natural population. Firstly, there is no need for the female to retain a food reserve for the post-hatching stage. During this stage, food is abundant in the Arctic, and food storage is not generally considered to be a limiting factor. Secondly, the excess food reserve could have been allotted to the young, by increasing the amount of yolk and size of the egg, to further increase their chances of survival until they are able to feed on their own. Thirdly, low natality added to annual mortality may eventually result in a depletion of the population below recuperable levels, and fourthly, Case 2 favors increased survival of the adult, by supplying more food than is required, and a lowered reproductive output, which is incompatable with the theory of natural selection. Mayr (1963) reminds us that "reproductive success rather than survival [of the adult] is stressed in the modern definition of natural selection." I suggest that Case 2 is rare in natural populations and may be found in two situations: where young geese, breeding for the first time, possibly lay smaller than average clutches (Delacour, 1964); and where a late season in the Arctic delays exposure of nesting habitat. This latter situation forces the female to use some of her reserves while waiting to start nesting. By the time of nest initiation, her reserve is decreased and to give maximum protection to the eggs, allocation to the ova has to be decreased. Smaller clutches in late starting Arctic seasons have been observed in Blue Geese, Brant, Black Brant, and White-fronted Geese (Cooch, 1958; Barry, 1962 and 1967). Atresia of the ovary and resorption of (the contents of) the ova release food reserves to the breeding female.

Case 3 depicts a situation where the number of mature ova is increased in relation to the total increase in body weight. This allows for a larger reproductive output but reduced food reserve for the breeding female. Under these conditions, the females' food storage may be depleted before the eggs hatch, forcing her to leave the nest to feed, allowing for increased exposure of the eggs to weather and predation. The direct result would be high embryo and nestling mortality. Case 3 applies in situations where larger than average clutches are laid. Various workers have reported increased nest and egg loss in such instances (Williams and Marshall, 1938; Hanson and Browning, 1959;

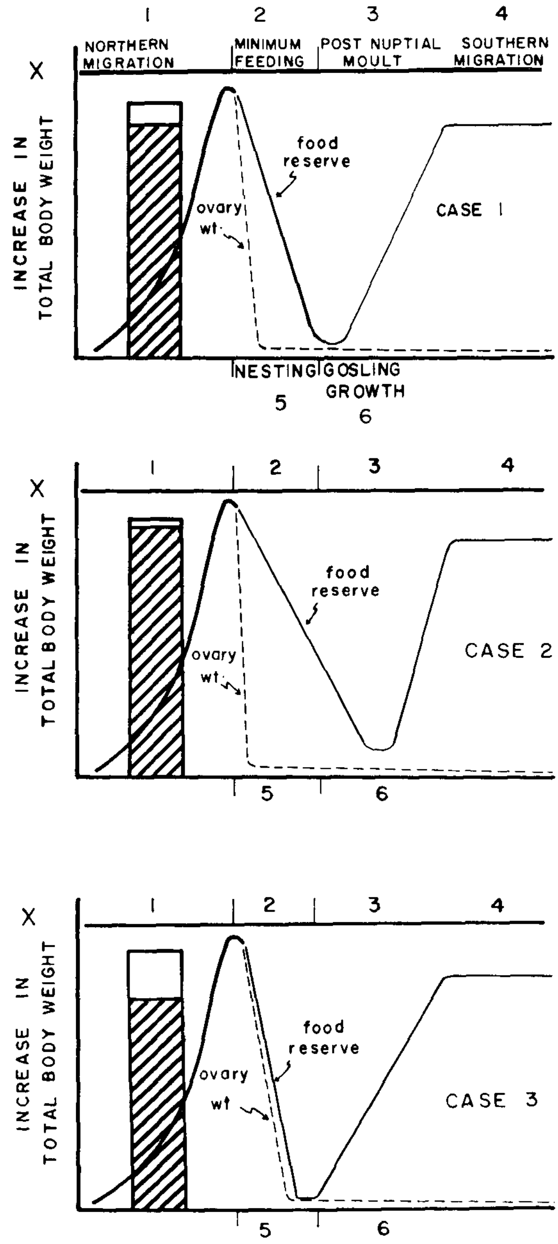

FIG. 4. Proposed mechanism for the evolution of clutch size in Ross' Goose. The vertical bar represents the proportion of spring food reserves acquired by the breeding female before arrival on the nesting grounds, which are allotted to non-ovarian (hatch

Cooch, 1961; Hilden, 1964; Perrins, 1964; Barry, 1967). Poor success of large clutches is attributed to incubation difficulties, possible discomfort to the female resulting in her moving the eggs from the nest; eggs accidently rolling out the nest when she changes position (Delacour, 1964), and increased breakage when the eggs are layered in the nest, a situation I found common in large clutches of Ross' Geese. Cooch (1961) noted that the larger clutches of Blue Geese take longer to hatch than those of average size and that the individuals which hatch last are weak, often unable to keep up to the older members of the brood. The "prognosis of survival for such goslings is poor." Hilden (1964) points out that in large broods of *Aythya* in Finland, the hen experiences difficulties keeping the brood intact when threatened by an enemy and when brooding in cold weather. This results in increased brood mortality. Eygenraam (1957) cited in Hilden (1964) showed that the largest broods of the Mallard (*Anas platyrhynchos*) are reduced at a relatively faster rate than those of normal size. In Arctic nesting geese, the larger clutch, in addition to presenting the problems outlined above, take longer to complete development. Time to complete the reproductive cycle is short in the Arctic (see Cooch, 1961; Ryder, 1967) and any individual that takes excessive time fails to rear offspring. Late seasons can have the same effect on large broods in terms of development of young. Barry (1962) found 21 young Brant frozen in the ice in the spring of 1957. These geese had hatched in the late season of 1956 and were in perfect shape except that feather development was four to five days short of allowing them to fly.

More intense studies of embryonic, nestling, and fledgling mortality in relation to clutch size are required for most species before definitive statements are made regarding the credibility of Case 3. The investigations of Cooch (1958) on Blue Geese and the reviews of long term studies in Lack (1966*a*) strongly support the contention that larger than average clutches do not necessarily produce the greatest number of young which survive to sexual maturity. I suggest that Case 3, although existing in current populations of Arctic nesting geese, contributes less than Case 1 to the natural rate of increase of a population.

The mechanisms I have presented to explain the evolution of clutch size in Arctic nesting geese are, for the most part, speculative. I hope that in the future, collection of breeding biology data from the Anatidae and other groups which do not feed their young, will illustrate the validity of the ideas expressed in this paper.

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lines) and ovarian tissues. The horizontal X-line represents the weight above which the female cannot sustain long periods of flight during the spring migration. Weights are relative but nesting season phenology is based on data collected during the 1963 and 1964 nesting seasons (Ryder, 1967). See text for further explanation.

SUMMARY

Three possible cases or alternatives are presented to explain the evolution of clutch size in Ross' Geese and other Arctic nesting geese, which do not feed their young. It is suggested that food reserves, acquired by the breeding female goose before the time and place of nesting, are allotted to ova and non-ovarian tissues. The number and size of eggs is limited to provide enough reserve food material to the young until they are able to feed themselves, and also to provide the breeding female with food so that she can give maximum protection to the clutch. The total amount of food stored before the breeding season, is limited by the maximum increase in body weight the female can carry during the spring migration.

ACKNOWLEDGMENTS

I would like to thank Drs. W. J. Maher, R. S. Miller, G. M. Sutton and Mr. A. Dzubin for reviewing drafts of this paper. Special appreciation goes to Dr. Sutton for underwriting the costs of the color plate. Financial support for this and related research was supplied by the Canada Department of Indian Affairs and Northern Development, Canadian Wildlife Service.

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