The significance of territory size in in colonial nesting geese—an hypothesis

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Geese that nest colonially show two attributes which may have important evolutionary implications. Firstly, upon arrival at the nesting grounds, body weights and food reserves (= fat) of such geese are greater than at any other times of year (see Ryder, 1970 for references). Secondly, ganders are territorial and spend a large amount of time defending an area immediately around the nest site (Delacour, 1964).

The ability to carry food reserves on to the nesting grounds would seem to have selective value. Hanson (1962) stated the reserves supply energy from the time the geese arrive on the nesting area until new plant growth is available. Barry (1967) thought the reserves in ganders may serve two functions; to provide energy during the period of food scarcity at the beginning of the nesting season and to act as insulation against cold weather. Here, I contend the gander's reserves are significant in enabling him to effectively defend the territory and later the young. Unlike the female (see Ryder, 1970), the male's reserves are not strictly to enable him to stay on the territory only until the eggs hatch. As Cooch (1958) mentioned, the male becomes the sole protector of the young after they leave the nest site and territory, which they do shortly after hatching, until they no longer require brooding. Consequently, supplementary food within the territory may provide the male with sufficient extra reserves which he may use until the young are relatively independent of his care.

The hypothesis states that in a colonial situation, the size of the territory defended by the gander may have evolved in relation to the reserves accumulated by him before the nesting season. The territory is large enough to provide any supplemental food which may be required and small enough to enable the male to protect the nest site against close-nesting conspecifics. Balance between a large and small territory is realized in the gander spending proportionately more time on the area and directly contributing to nest and reproductive success. As in the female (Ryder, 1970), the total reserves acquired by the male before the nesting season are limited by the increase in body weight he can carry during spring migration and still maintain long periods of flight.

The ideas expressed below were formulated during research in 1966, 1967 and 1968 on the breeding biology of Ross's Goose *Anser rossii* at Karrak Lake, Northwest Territories (67°15′N, 100°15′W) (Ryder, 1972). During the 22-day incubation period, territorial Ross's ganders can lose up to 600 grams weight (Figure 1). This represents a maximum recorded loss of 33 per cent of the body weight at arrival on the nesting ground. Of this total, only about 12 grams are lost through testicular regression. Cooch (1958) reported that territorial Blue Goose *Anser caerulescens* ganders lost about 17% (450 grams) of their spring arrival weight as a result of 'activities associated with reproduction'.

Within the selected territory, the gander appears to have two functions; to ward off potential predators and to protect the female and the nest from intruding conspecifics. Harvey (1971) showed that only one member of a pair of Blue Geese is required on the

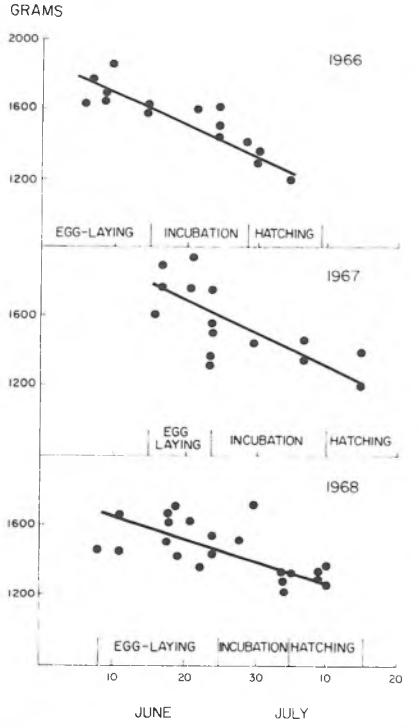

Figure 1. Ross's gander body weights during the 1966, 1967 and 1968 nesting seasons at Karrak Lake, Northwest Territories. Each point represents one gander.

territory to discourage interspecific avian predators. Since the female's presence on the territory appears to be sufficient to prevent clutch destruction, the male's physical condition, as reflected in the total amount of accumulated food reserves, has most likely not evolved in relation to energy required solely to defend the territory against a normal number and species of interspecific predators.

Available evidence suggests that the male's food reserves are important in enabling him to protect the female against intruding members of the same species, especially those which are nesting close by. Ewaschuk & Boag (1972) concluded from their study of Canada Geese *Branta canadensis* in Alberta: 'It appeared that the presence of the gander in the territory during incubation was a major factor influencing nest desertion. The reason was that his presence prevented adjacent ganders from attacking the incubating goose'. Cooch (1958) noted the sole function of the male Blue Goose during incubation was to defend the nest site and Harvey (1971) concluded from his study on Blue Geese that the incubation behaviour of (female) geese determined the nest success.

It follows that for the gander to defend the territory effectively, two conditions must be met; supplementary food must be available within the boundary of the territory so that the male does not have to leave often and for any great length of time, and he must be able to defend the nest site against surrounding territorial males. Based upon these two requisites, I consider there are three possible conditions which have played an important role in the evolution of territory size in colonial nesting geese.

Condition 1 assumes that the gander acquires a territory which is larger than the surrounding territories. The advantage of this situation is that he is in possession of more supplementary food than is perhaps required in relation to his stored reserves. Although this allows him to remain on the area throughout the entire nesting period, the larger territory may result in an increased number of contiguous territories, especially where nests are dispersed toward uniformity. To protect the area effectively, the gander must utilize proportionately more of his energy reserves which may become depleted before the young are independent of his care. This situation is analogous, in its effects on the gander and his mate, to a natural increase in nest density. The consequences will be the same because of a presumed increase in the number of neighbours nesting close-by.

A number of studies have noted that nest and hatching success are adversely affected when nest densities are above normal. Munro (1960) reported that nest desertion in Canada Geese was density dependent whereas Elder (1946) and Wood (1964) showed that crowding could inhibit reproduction in Canada Geese. Weigand *et al.* (1968) reported that the main cause of nest site desertion in Canada Geese was crowding which resulted in interference of nesting activities. Collias & Jahn (1959) concluded from their studies of a confined population of Canada Geese that an observed loss in productivity was largely due to territorial behaviour of the birds resisting crowded conditions.

Condition 1 suggests that for an individual to assume a larger than average territory would be detrimental to the pair as it is highly probable that such would lead to a decreased nesting success.

Condition 2 assumes that the gander acquires a territory which is smaller than the surrounding territories. In such a case the number of contiguous territories is reduced and the resident gander is able to effectively defend the smaller area against intrusion by neighbouring territorial pairs. The disadvantage of such a system is that the available food within the smaller territory may be decreased to the point of insufficiency to sustain the male until the young are independent. In such a situation the male would have to leave the territory to acquire food, thus leaving the female potentially susceptible to interruption in her incubation activities by neighbouring males.

Ewaschuk & Boag (1972) found two basic types of Canada Goose territories; larger ones bordering on water and not surrounded by other territories and smaller inland ones, possibly held by younger and less experienced geese, which were surrounded by other territorial pairs. Pairs whose territory bounded on water almost always fed within the territory. Those with smaller territories generally left the areas to feed elsewhere. Ewaschuk & Boag (1972: 1104) state, 'Pair 10 held the smallest territory under observation (221 square yards). On May 16, the gander of this pair left the territory without the goose; whereupon she was immediately attacked by a neighbouring gander. Since the clutch was only about 3 days from hatching, the goose was very attentive and continued her attempts to return to the nest, only to be driven off. The gander returned later that day but took no part in defense of the territory or of the goose, with the result that the goose continued to be harassed by the adjacent ganders until desertion occurred. In this case,

the initial absence of what may have been a subordinate gander with a small territory seems to have been the cause of eventual desertion'. These authors suggest that smaller territories appeared to provide only a nest site and that the resident pairs were forced to obtain food and water elsewhere. They concluded (ibid: 1106), 'the observed absence of ganders from small territories, in which females were unsuccessful, may reflect the necessity of males to feed and drink elsewhere'.

Condition 3 depicts a situation whereby the pair of a colonial nesting species manages to secure a territory of size which provides enough supplementary food for the male and the number of neighbouring territorial males which he can cope with without undue energy utilization during the nesting period. I assert that although this situation may not exist in all colonial goose populations, available data on nest dispersion patterns (see Vermeer, 1970; Ewaschuk & Boag, 1972; and Ryder, 1972) indicate that nests tend to be more uniformly dispersed than clumped or random. The tendency towards a uniform dispersion pattern presupposes *approximately* the same territory size per pair based upon the required within-territory resources and the ability of individuals to protect the area against contiguous neighbouring males.

I hope the thoughts expressed here will lead to studies furnishing conclusive data to support or reject the hypothesis. It is important to understand the relationships between body size, food reserves, territory size and attentiveness of territorial ganders. Similar studies on incubating females have proven extremely interesting in this regard (Ankney & MacInnes, 1973). I predict that when data are available, we will learn territory size is a direct function of the gander's physical condition, as reflected by the amount of food reserves he brings north, his body size, assuming a large bird is able to carry proportionately more food reserves and the number of closest neighbouring territorial conspecifics he can prevent from disturbing the female.

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Summary

Three possible alternatives are presented to explain the evolution of territory size in geese which nest colonially in the Arctic. The author suggests the size of the territory defended by the gander has evolved in relation to food reserves accumulated before the nesting season.

The territory is large enough to provide sufficient supplemental food during the entire nesting season and small enough to enable him to protect the nest site from close-nesting conspecifics. The balance between a large and small territory is realized in the gander spending proportionately more time on the area.

References

Ankney, C. D. & Macinnes, C. D. 1973. An explanation of within-year variation in clutch size of Blue Geese. Unpub. MS. University of Western Ontario, London.

Barry, T. W. 1967. The geese of the Anderson River Delta, N.W.T. Unpub. Ph.D. Thesis, Univ. of Alberta, Edmonton, 212 pp.

Collias, N. W. & Jahn, L. R. 1959. Social behavior and breeding success in Canada Geese *(Branta canadensis)* under semi-natural conditions. *Auk* 76: 478–509.

Cooch, F. G. 1958. The breeding biology and management of the Blue Goose *(Chen caerulescens)*. Unpub. Ph.D. Thesis, Cornell Univ., Ithaca, N.Y. 235 pp.

Delacour, J. 1964. *The Waterfowl of the World.* Vol. IV. London: Country Life.

Elder, W. H. 1946. Age and sex criteria and weights of Canada Geese. *J. Wildl. Mgmt.* 10: 93–111.

Ewaschuk, E. & Boag, D. A. 1972. Factors affecting hatching success of densely nesting Canada Geese. *J. Wildl. Mgmt.* 36: 1097–1106.

Hanson, H. C. 1962. The dynamics of condition factors in Canada geese in relation to seasonal stress. *Arctic Inst. N. Amer. Tech. Paper* 12: 1–68.

Harvey, J. M. 1971. Factors affecting blue goose nesting success. *Can. J. Zool.* 49: 223–34.

Munro, D. A. 1960. Factors affecting reproduction of the Canada Goose. *Int. Ornith. Congr.* 12: 542–56.

Ryder, J. P. 1970. A possible factor in the evolution of clutch size in Ross' Goose. *Wilson Bull.* 82: 5–13.

Ryder, J. P. 1972. Biology of nesting Ross's Geese. *Ardea* 60: 185–215.

Vermeer, K. 1970. A study of Canada Geese *Branta canadensis,* nesting on islands in southeastern Alberta. *Can. J. Zool.* 48: 235–40.

Weigand, J. P., Pollok, M. J. & Petrides, G. A. 1968. Some aspects of reproduction of captive Canada Geese. *J. Wildl. Mgmt.* 32: 894–905.

Wood, J. S. 1964. Normal development and causes of reproductive failure in Canada Geese. *J. Wildl. Mgmt.* 28: 197–208.

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