Territorial behaviour in breeding geese—a re-examination of Ryder's hypothesis

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Following studies on Ross's Geese *Anser rossi*, Ryder (1975) put forward the hypothesis that territorial behaviour in colonially nesting geese had evolved in order to protect the incubating female from attack by males defending neighbouring territories. He further proposed that the male holds a territory which is large enough to provide him with sufficient supplemental food during the nesting season to allow him to stay close to the nest throughout incubation. The size of territory which an individual male defends is determined by the balance between the need to defend a large enough area for feeding purposes and the need to be able to defend it successfully, given that the larger the area the more time and energy would be needed in territorial defence. This led Ryder to the conclusion that territory size was related to the amount of energy reserves carried by the male at the beginning of the nesting period.

Inglis (1976) examined Ryder's hypothesis in the light of studies on Pink-footed Geese *Anser brachyrhynchus* in an Icelandic breeding colony. He disputed Ryder's contention that the prime function of the territory was to defend the female against attacks from close nesting conspecifics since harassment behaviour had no selective advantage for the males involved. Male Pink-footed Geese spent a higher proportion of their time in agonistic encounters during the first six days of the nesting period before the females had begun to incubate. Inglis proposed that the main function of a territory in that species was to ensure a supply of food around the nest, particularly for the female during the early part of the nesting period.

This paper examines data on territorial behaviour in Barnacle Geese *Branta leucopsis*, both in the wild and in captivity, in the light of these conflicting hypotheses on territory function and examines Ryder's hypothesis on the determinants of territory size. Studies on wild geese were conducted on the Nordenskioldkysten 77°53'N, Spitsbergen (Svalbard) in 1977, and those in captivity at Slimbridge, Gloucestershire, between 1975 and 1978.

Methods

Observations on wild geese were made from a canvas hide placed on one of the breeding islands from about the time that most clutches were completed. Eight 24-hour watches were kept, spread throughout the incubation period. All nests were scanned every 10 minutes and the activities of both pair members recorded.

The boundaries of territories (defined as the area defended against conspecifics) of captive geese were mapped during repeat visits throughout the nesting period. Territory boundaries rarely changed once the female had started to incubate. Two males were repeatedly weighed during incubation in 1978 using a spring balance on which the nest was supported (R. Sibley, unpublished).

Results

There were 19 pairs of Barnacle Geese nesting on the island in Spitsbergen, and 10 nests were visible from the hide. For 4 males which were present on all watches, the percentage of time spent in aggressive encounters during incubation and the percentage of time absent from their territories while feeding (almost always on the neighbouring mainland) are shown in Figure 1. The aggressive encounters include those against predators as well as against conspecifics. The main potential predators were Glaucous Gulls *Larus hyperboreus*, which were resident breeders on the nesting island, and Arctic Skuas *Stercorarius parasiticus*, which occasionally flew over the island. Predator activity was relatively constant throughout incubation, and differences in the percentage of time spent in encounters are mainly due to differences in conspecific attacks. Males were more aggressive during the first half of the incubation period (Mann-Whitney U-test $p < 0{\cdot}01$, between the first 5 watches and the last 3). The percentage of time spent off the island by the 2 successful males was low on the last watch (the day of hatching), whereas the unsuccessful males spent a high proportion of time off the island at the end of in-

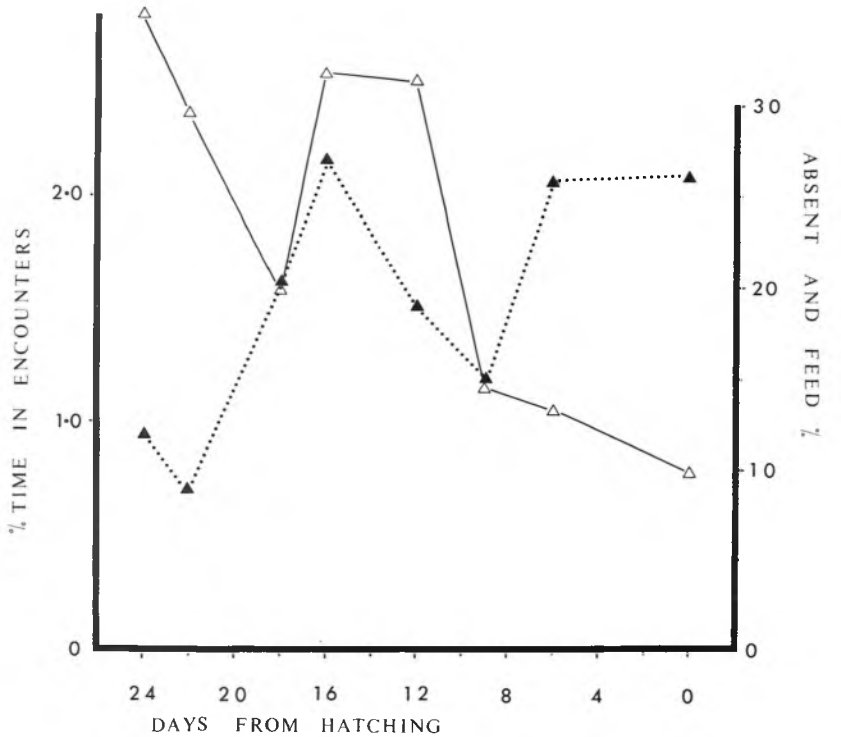

Figure 1. The percentage of time spent by 4 males present throughout incubation in aggressive encounters (solid lines) and absent from the island feeding (dotted lines) during 8 watches.

cubation and their nests were predated on the last day. The activity of successful and unsuccessful males was otherwise similar.

The boundaries of territories held by 25 males in the Wildfowl Trust grounds at Slimbridge in 1976 are shown in Figure 2. Most males defended an area of water as well as land immediately surrounding the nest. Where nests were situated near ground cover territories usually followed the cover boundaries. Nests in open ground tended to be in the centres of territories, and boundaries were roughly equidistant from adjacent nests although the geese nested in prepared sites put out before the breeding season. The territories around nests protected by ground cover were usually smaller than those around nests in the open and their boundaries did not appear to be any more distant on the open side than for wholly open ones. Males holding the 4 largest territories were significantly heavier when caught in moult than those from 11 small territories (means 2300 gm and 2100 gm, Mann-Whitney U-test (1-tailed) $P < 0{\cdot}025$).

Figure 3 shows the body weights of two males during incubation in 1978. Male A held a territory outside the main breeding colony where few pairs were prospecting for nests whereas male B's territory was in the main breeding area. Both territories had two contiguous defended areas. Male B was continually chasing away intruders from his territory during the early nesting period whereas A had little interference. Both lost weight during incubation, and weight losses were greatest during the first 8 days. Both males began feeding (A on and B away from the territory) in the latter part of incubation.

Total weight losses for A were 200 gm (9% of original weight) and for B 360 gm (15%). The difference was attributable to the degree of intrusion into the territory by conspecifics, often pairs prospecting for nest sites, rather than any difference in aggression towards neighbouring territory holders. The latter in both cases were often threatened, but fights or chases were not seen.

In 1975, at Slimbridge, two pairs of Barnacle Geese nested on an island. At the beginning of incubation the island and

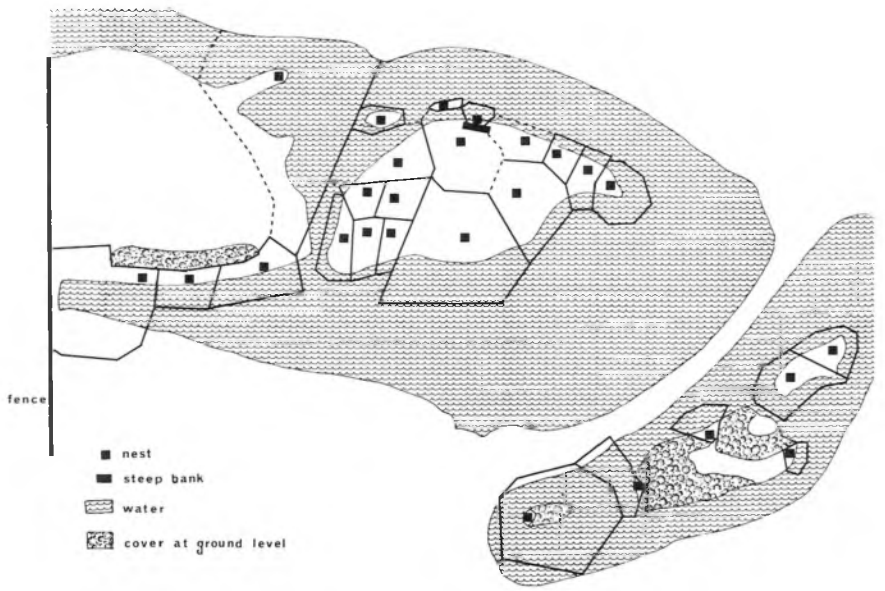

Figure 2. Territory boundaries (solid lines or dotted where exact position is uncertain) of 25 male Barnacle Geese at Slimbridge in 1978.

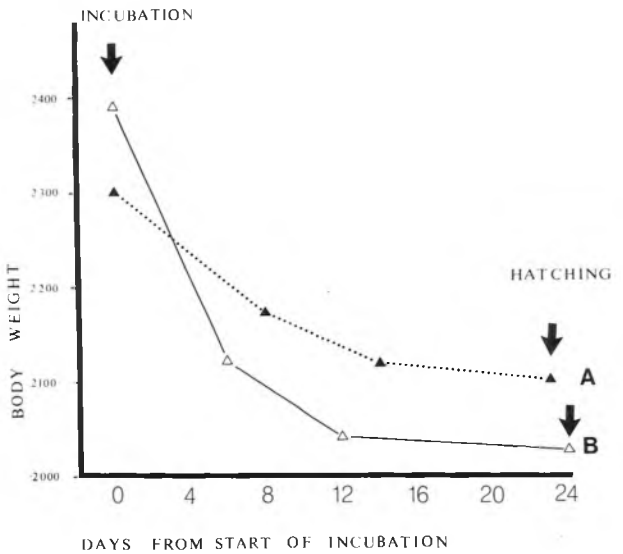

Figure 3. Weights of two males at 4 stages during incubation in 1978. Vertical arrows indicate the beginning and end of incubation.

Figure 4. An intruding female (centre) is attempting to lay in the nest of a female (right) whose mate has died. The neighbouring territorial male (left) attempts to dislodge the intruder.

Figure 5. The male's attack is not vigorous enough to discourage the intruder (right) which eventually lays in the nest.

surrounding water was split between the two males but one then died. The other male then defended the whole island and both nests. Figure 4 shows an intruding female (centre) sitting on the nest together with the widowed incubating female. The surviving male is attempting to dislodge her but his attacks are not vigorous enough and the intruder eventually lays an egg in the nest (Figure 5). Collias and Jahn (1959) reported the loss of a mate by an incubating Canada Goose, which was so harassed by ". . . other pairs as well as unpaired males" that she left the nest for long periods and the eggs failed to hatch.

Discussion

Barnacle Geese in the wild nest on cliff ledges, buttresses on steep hillsides or rocky offshore islands (Dementiev and Gladkov 1952; Norderhaug 1970; Ferns and Green 1975). Although a small amount of grazing does occur on the territories on island sites (Dittami *et al* 1977) the geese have evolved in a situation where the provision of food for either sex could not have been an important function of the territory.

It is common observation in captivity that nesting geese are more aggressive towards conspecifics than to other goose species. Fabricius *et al* (1974) further found that free-living Canada Geese *Branta canadensis* attacked other Canada Geese at a mean distance of 30·6 m but the sympatric Greylag Geese *Anser anser* only at 15·6 m. If providing a supply of food for either sex was the function of territorial defence, other goose species would pose as much of a threat as conspecifics, since the diet of most geese is similar in the breeding season. Dittami *et al* (1977), working on the same island as this study in Spitsbergen, though in a climatologically 'earlier' season, stated that neighbouring territorial male Barnacle Geese were sometimes tolerated while grazing inside a defended area, whereas other intruders were vigorously repelled.

While arguing that the provision of a feeding area is not the main function of territory in geese we agree with Inglis (1976) that there seems no selective advantage for the harassment behaviour described by Ryder.

Recent work on Lesser Snow Geese *Anser c. caerulescens* (Mineau and Cooke 1979) indicates that such harassment is common in that species because territorial males are intent on raping incubating females other than their mates. Although the chances of successful fertilisation were small (most females had completed laying) Mineau and Cooke suggested that rape was a part of the normal breeding strategy of the Snow Goose rather than a behavioural carry-over from copulation. They concluded that the function of territorial defence was to forestall rape attempts as well as to defend the nest against being parasitised.

Mineau (1978) also found that the proportion of time spent by male Snow Geese in the alert posture was highest during laying and declined throughout incubation. This does not correspond to the pattern of rape attempts, 76% of which occur during the victim's incubation. If alert behaviour is largely directed at detecting territorial intrusion the

prevention of rape attempts is not the only, and perhaps not the main, function of territoriality in the Snow Goose, F. Cooke (pers. comm.) states that nests are frequently abandoned early in initiation and suggests that many of these may be due to eviction of the occupants.

There are no other published accounts of rape in wild geese but Mineau (1978) quotes other workers who have observed attempts in Ross's Geese and Lesser Snow Geese in other breeding colonies. Since the chances of successful fertilisation are so low in Snow Geese it seems to us unlikely that this behaviour is adaptive. Mineau argues that males ensure their own parenthood (by waiting until their females have completed laying) before embarking on raping forays but parenthood is not ensured until the goslings fledge. Raping is costly in energy and Ankney (1977) has emphasised the importance of nutrient reserves for males not only during incubation but also after hatching. Raping attempts were largely carried out during the absence of males (often themselves attempting rape) and there must also be a chance that eggs will be damaged during a rape attempt.

During the observations of wild Barnacle Geese several intruding pairs visited the island in the absence of territorial males and harassed incubating females. The females usually managed to repel intruders until their mates returned but in one case the intruding pair lifted a female off the nest with their bills before her mate returned and drove them off.

Mineau (1978) removed two males from territories, one on the third day of incubation. His mate was subsequently 'raped' several times and was finally evicted by non-territorial pairs. The other male was removed late in incubation when the number of non-nesting pairs in the vicinity of the nests was low and his mate successfully hatched the clutch.

We suggest, therefore, that the territory serves to protect the nest from being taken over by intruding birds or from having eggs 'dumped' in it. Egg dumping is fairly common in wildfowl and most studies on geese report clutches too large to have been laid by a single female (e.g. Ryder 1967; Newton and Kerbes 1973). Mineau and Cooke (1979) quote numerous examples of successful 'parasitism' by Snow Geese and argue that the defence of the nest against parasites was a function of territorial behaviour in that species. Pairs which had their clutches increased by dumping might suffer increased gosling mortality in two ways. Lack of synchrony in hatching might cause the pair to wait at the nest site for longer than usual, to the detriment of early hatching goslings, and gosling mortality is higher in very large broods of Canada Geese (K. Lessels, pers. comm.). In situations where there is competition for nests, intruders do pose a threat and in this study, both in the wild and in captivity, nests predated during incubation or vacated after hatching were occupied by other pairs, although such late occupation did not result in breeding. Since most goose species differ slightly in nesting requirements, conspecifics pose the greater threat.

Unfortunately we have no detailed information on the number of intruders on to the nesting island but would predict that this would decline with time. Nest initiation after arrival on the breeding ground is rapid in arctic geese, late nests having little chance of producing fledged young before winter sets in (Barry 1962; Ryder 1967, 1972). Ross's Geese nests were initiated over 8, 8 and 11 days in three different seasons (Ryder 1972), so in each case the last nest was started before the first was a week into incubation. In the same species Ryder (1967) commented that territorial disputes were at a maximum during the egg-laying period and that both sexes combined in driving away intruding geese. Male Lesser Snow Geese also showed a declining level of altertness through incubation (Mineau 1978).

Inglis (1976) states that the number of birds present on his study area remained constant after all nests had been initiated (i.e. pairs were no longer prospecting for nest sites), and that this coincided with a decline in the proportion of time spent by males in aggressive encounters. Inglis also reported that pairs (mainly intruders) were threatened more vigorously and at a greater distance than single birds.

These examples and our own evidence support the hypothesis that the main function of the territory is to defend the nest itself against intruders. In all species studied aggression is most marked during nest establishment because all pairs are then intruders and pose a threat to the nest site.

Although it would be beneficial for both sexes if a territory included a feeding area, we believe this to be of secondary importance, since areas of water are defended as well as land (see Figure 2). Brakhage (1965) similarly reported that Canada Geese nesting in tubs elevated on posts surrounded by water defended territories made up entirely of water. The air above territories is also

defended and on cliff sites most of the territory would presumably be aerial.

If the main function of the territory is to defend the nest against intruders, the distance at which intruders are threatened is more important than the area of the territory. In open habitats territory size is proportional to this distance but in protected sites this not the case. Figure 2 shows that the distance at which conspecifics are threatened is no greater on the open side of protected sites than in territories in open ground. Dittami *et al.* (1977) found that Barnacle Goose nests which were out of view of one another, e.g. on opposite sides of rock outcrops, were closer together than those in full view and we suggest that this was because neither male defended an area behind the nest site.

This indicates that topography could influence territory size, and Ryder (1967) found that nesting density was higher in 'mixed' habitat, which gave some protection to nest sites, than in open ground. We suggest that this protection is important in territorial defence as well as in shielding incubating birds from the elements. Sherwood (1968) found that Canada Geese defended entire islands up to 250 feet (77 m) long but that the area of land defended was smaller if islands were smaller. An increase in nesting density was achieved by providing smaller islands and breaking up large ones. Thus water apparently provides some protection for nest sites, and the territories of those Canada Geese were smaller when there was a water barrier between them. The important consideration is therefore in maintaining a safe zone between the nest and intruders.

Territorial defence is costly for males (Figure 3 and Ankney 1977), and as Ryder points out the cost of defending a territory increases with its size. This applies whatever the reason for territorial defence, since large territories have long perimeters and more contacts are likely. We do not believe, however, that territory size is purely a function of energy reserves. If this were the case, territories would be smaller in late seasons when the body reserves of both sexes are depleted because of the delayed start of nesting. However, inter-nest distances for Ross' Geese were similar in three seasons despite differences in laying date (Ryder 1972), and nesting density of Barnacle Geese on the Nordenskioldkysten was similar in 1975 (Ebbinge and Ebbinge 1977), 1977 (Owen *et al.* 1978) and 1978 (A.K.M. St Joseph, pers. comm.), although laying dates were different. In 1977 most males established territories which they later had to leave frequently as their food reserves were depleted. When male and female absences coincided, the nest was predated. Only 16–19% of established nests produced young (Owen *et al.* 1978). This suggests that there may be a lower limit on territory size (or threatening distance).

Large territories, at least in open areas, are more effective than smaller ones and the upper limit of territory size may well be determined by the size of males' body reserves. Large males are able to carry larger amounts of body reserves and should defend larger territories (Ryder 1975) and we have some evidence that this is the case in Barnacle Geese. Where food is present on the territory the significance of size is increased because it allows the male to be continually present.

We suggest, therefore, that territory size is determined by a complex of factors including the nature of the terrain, the size of body reserves and possibly the food supply, but that there is a lower limit. When male reserves are low, they should all be used up in territorial defence rather than the whole breeding effort jeopardised in order to retain some reserves to protect the young.

More work is needed to test the various hypotheses on territory function and size. Our suggestion could be tested by removing males from territories. We would predict that if this were done early in incubation the nest would be taken over by another pair if there were competition for nest sites. The limited amount of evidence from Snow Geese (Mineau 1978) supports this view. We also suggest that territory size and inter-nest distances can be modified by placing obstructions in open habitat to afford some protection to nest sites. The significance of body reserves in determining the size of the area defended is more difficult to investigate but the abdominal profile technique of estimating abdominal reserves (Owen, in press) may be useful in relating territory size to reserves in individual males.

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Summary

The opposing hypotheses of Ryder (1976) and Inglis (1977) on the function of territory in geese are examined in the light of studies on both wild and semi-captive Barnacle Geese *Branta leucopsis*. This species has evolved in a situation where the provision of a feeding area could not be the main function of a territory. It is suggested that its main function is to prevent the nest site from being taken over by intruding pairs of eggs being 'dumped' in it by intruding females. This is consistent with the data of Ryder and Inglis and with other observations on territorial species although the function of the rape behaviour of white geese remains obscure.

Territory size is a function of the ease of defence of the nest site as well as the size of body reserves, proposed by Ryder as the main determinant of size, and it is suggested that there is a lower limit on threatening distance below which males will not go whatever the size of their reserves. Future work should remove males from territories or modify habitat characteristics in an attempt to modify territory size. The size of areas defended by individual males should be studied in relation to the size of their reserves on arrival at the nesting grounds.

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