Agonistic behaviour of breeding Pink-footed Geese with reference to Ryder's hypotheses

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Throughout the summer of 1973 an ethological study was made of the breeding behaviour of the Pink-footed Goose *Anser brachyrhynchus* at Thjorsarver (64°35′N, 18°40′W) in central Iceland. The majority of the results of this research will be presented elsewhere. This paper will discuss only those findings of some relevance to the recent proposals of Ryder (1975). He put forward two hypotheses, one concerned with the reasons why Artic breeding geese form territories and the other with the determinants of territory size. He proposed that territories are formed as a result of a gander's defence of his incubating mate from attacks by neighbouring males. The size of the area thus effectively defended was thought to be determined by the balance of two conflicting factors. In order to stay near his mate for as long as possible the male must defend an area around the nest large enough to sustain his food requirements. Yet a larger area might increase the number of contiguous neighbouring territories and thus the number of males from which the female must be adequately defended.

Methods

Observations were made from a small hut situated on the crest of a gravel moraine which overlooked a portion of the nesting area. The study area had been 'gridded' into 100′ (30·5 m) squares, aligned N-S, E-W, before the arrival of the geese. Throughout the nesting period the geese within the study area were not disturbed in any way. They were observed for 10 hours per day, weather permitting. Every 30 minutes the position and activity of every goose was noted. The mean number of such scans per day was 21·97 (SE = 0·95). Additionally some of the more easily visible nests were given detailed monitoring. This consisted of 10 minutes of continuous observation per hour for each nest.

Results and discussion

No gander was seen attempting to attack a neighbouring incubating goose. Indeed the Pink-footed Goose would seem to be one exception to the statement that 'ganders spend a large amount of their time defending an area immediately around the nest' (Delacour 1964). For each of the sixteen ganders with easily visible nests, the percentage of each day's set of scans containing a threat posture was calculated. Figure 1 gives the mean value of all males per day. It can be seen that on the majority of days no threats were recorded in the scan data. Even on days when threat behaviour was recorded it took up only a relatively small amount of the gander's time. Further, this was greater throughout the early days of the nesting period. The peak on 23rd June occurred when a number of pairs with young moved through the study area on their way to the feeding grounds. (No observations were made on the days when the observers' food supplies were collected from base).

The early period of agonistic activity corresponds with the build up of goose numbers (Figure 1). This activity is not simply a function of the number of geese present, for the latter is relatively constant from 26th May until 14th June, yet the number of agonistic encounters falls. For each nesting male the percentage of daily scans containing a threat posture was examined from the first sign of nest building to the day before the nest was abandoned (for whatever cause). Figure 2 gives the mean values derived from the data from all the males. The ganders spent the greatest proportion of their time indulging in agonistic encounters within the first six days. During this period the females were spending a large amount of time feeding in the area around the nest (Figure 3) accompanied by their mates.

These data are not congruent with Ryder's first proposal. If males were indeed continually attempting to harass neighbouring incubating females, then the percentage of their day spent in agonistic encounters should be approximately the same throughout the nesting period and certainly not greatest at the beginning, before the females have completed their clutch and begun intensive incubation. It is difficult in any case to visualize how the proposed harassment behaviour could have evolved in the present context. The harsh climate throughout most of the nesting period together with food shortage at the beginning, would seemingly discourage the evolution of behaviour patterns which use large amounts of energy, unless these patterns had some strong selective advantage. It is important that the males should have food

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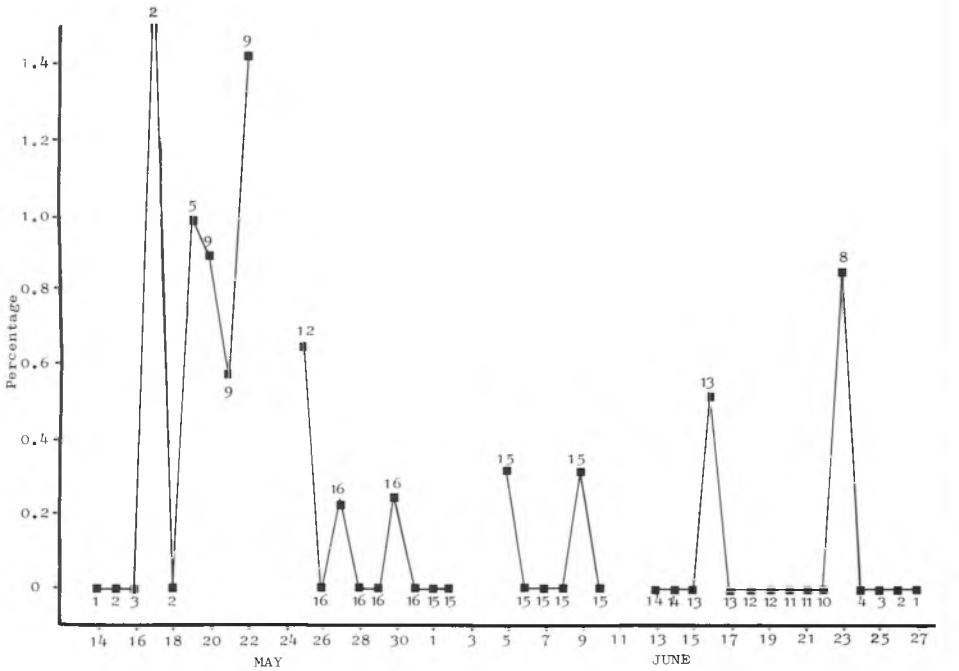

Figure 1. Mean percentage of time spent in agonistic interactions by males in relation to date. The numbers indicate the number of breeding males whose data was included in the mean shown.

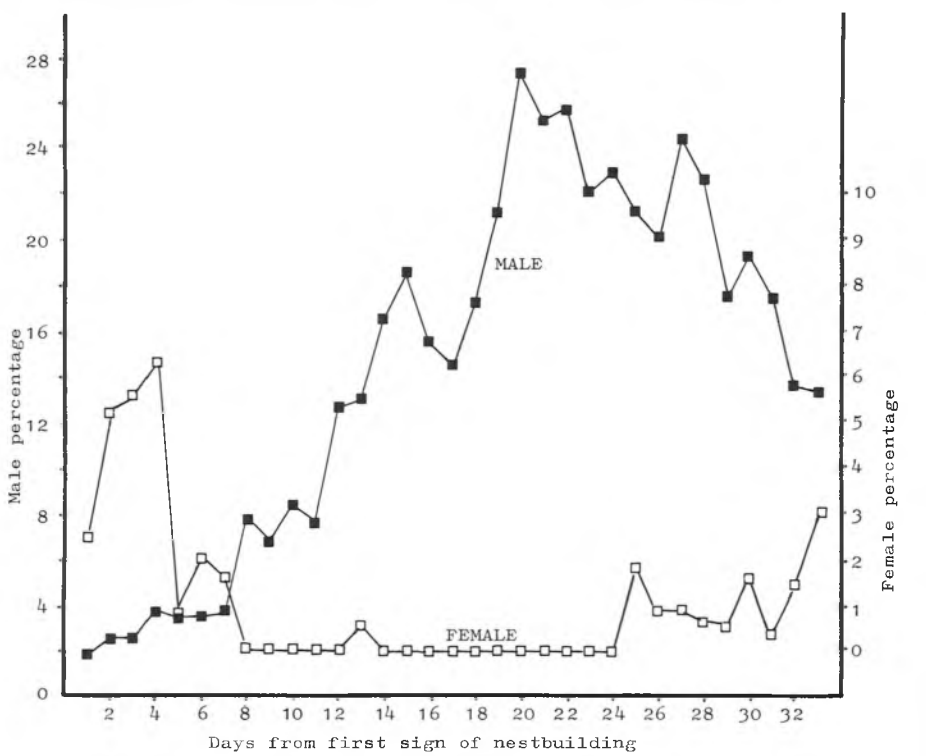

Figure 2. Mean percentage of time spent in agonistic interactions by males in relation to onset of nest building.

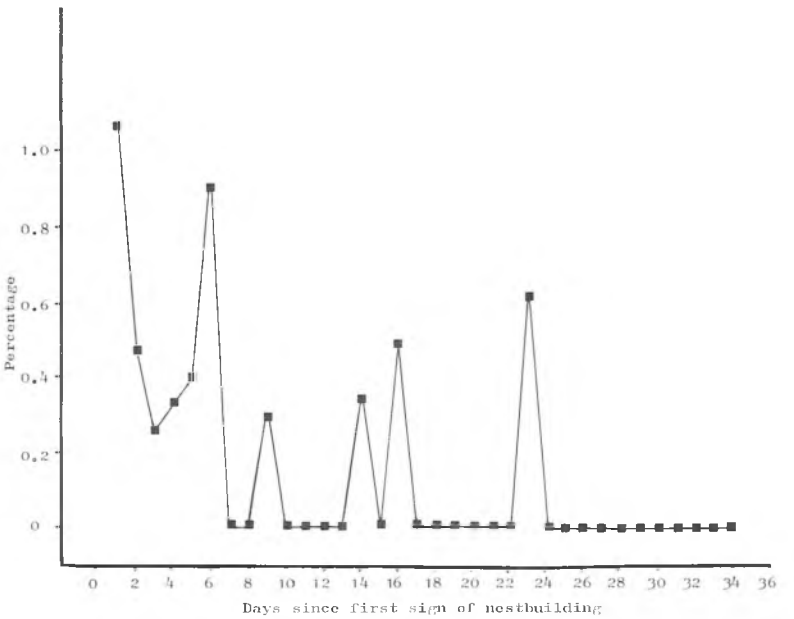

Figure 3. Mean percentage of time spent feeding within 30 feet (9 m) of the nest.

reserves as large as possible at the end of the nesting period for they can then forage relatively little, having almost sole responsibility for the protection of the young. What then could be the advantage of harassment behaviour? It is doubtful whether it would significantly enhance a male's genetic contribution to the next generation. Mating with neighbouring females is unlikely, for the geese arrive in Thjorsarver paired and having already copulated. Obviously by causing the failure of nearby nests a male will be increasing his own genetic contribution but in a population of approximately 11,000 nesting pairs (Kerbes, Ogilvie & Boyd 1971) this advantage would seem to be negligible compared to the disadvantage of the energy loss. Further there are some distinct advantages in having neighbours. A gander's defence of his own nest was often sufficient to drive avian predators from a vicinity of nearby nests as well, and further, the noise of this defence elicited the swift return to their nests of any nearby geese who had been feeding at the time of the attack.

It would appear therefore that harassment can provide no functional explanation of Pinkfeet agonistic behaviour. The second proposal of Ryder (1975) concerning the factors regulating territory size is difficult to assess in the present context not only because body weights of the study birds are not available but also because agonistic behaviour is mainly confined to the beginning of the nesting period. Therefore the territory, if defined as a defended area, is transient. However if a territory is defined as an area of exclusive use then it would appear that territories are persistent, the boundaries being established during the nest extablishment phase, when the peak of agonistic behaviour occurs, and then to a large extent remembered and respected by the nesting geese.

Figure 4 gives territories of ganders whose behaviour was monitored in detail, a territory being taken to be a defended area. The lines demarcating the territory are those joining the furthest position reached by intruding geese before being threatened by the resident male. Although the territories shown are derived from the maximum distances at which geese were threatened, this does not mean that within the area thus specified geese were invariably threatened. Not only were there large individual differences in the distances at which geese were threatened but also individual tolerance of intruders was affected by snow cover. The intruders might be a pair or single birds from adjacent or distant nests.

The boundaries of the exposed substrate at the beginning and end of the nest establishment phase are also shown on Figure 4. These

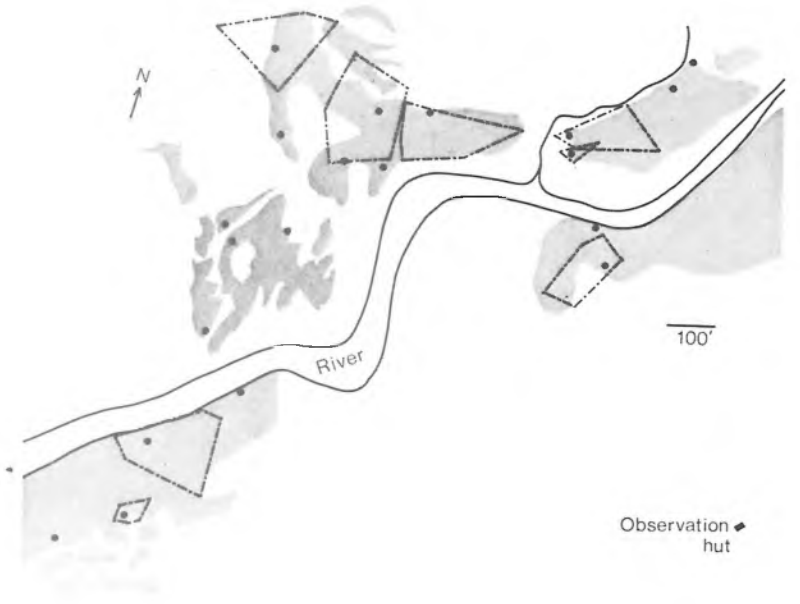

Figure 4. Territories of the eight nests that received detailed monitoring. The lines join the furthes positions of intruding geese when threatened by the resident male. The darker shading is the area o exposed land at the start of the nest establishment period (May 14th), the lighter shading gives the ad ditional land exposed at the end of the period (May 28th).

boundaries can to a large extent explain the asymmetries of the territories. Intruders could walk unthreatened on the snow much closer to nests than if they had been walking on exposed land. The snow-covered areas were therefore in a sense 'neutral' ground.

As there were more nest-prospecting pairs than single birds on the study area throughout the period of maximum agonistic activity it is perhaps not surprising that more threats were directed against pairs than at solitary geese. However the mean distance at which pairs were threatened was greater than that for single birds (Table 1). Further, if the solitary bird was from an adjacent established nest then the resident male used a mild form of threat. Standing in the threat posture and ruffling his wings at the intruder who would then slowly move away. A chase was rarely involved.

It would appear that agonistic behaviour in this species serves mainly to preserve a supply of food around the nest site particularly for use by the female during the early part of the nesting period. As the eggs are safe from predators for as long as the female is incubating, anything which can increase the time spent on the eggs is important. Food reserves are obviously an important factor. The geese spend some time feeding in the lower coastal regions of Iceland before moving up into Thjorsarver, but it is interesting that subsequently successful females spent more time off their nests feeding during the first six days of the nesting period than did subsequently unsuccessful females. This suggests

Table 1. Mean distances from nest at which single birds or pair were threatened by the males of the eight nests that received detailed monitoring.

Nest number	Mean distances in ft	
	Pairs	Single birds
1	24	18
5	80	47
7	105	45
8	55	80
9	25	–
10	74	62
15	80	30
16	126	37
	$\bar{X} = 71{\cdot}1$	$\bar{X} = 45{\cdot}6$

(Wilcoxon Test, $p < 0{\cdot}05$)

that any extra feeding a female can do on the breeding grounds before her clutch is complete could be an important advantage. During this early period the geese root under the more lightly snow-covered areas, feeding mainly upon *Polygonum viviparum* (Gardarsson and Sigurdsson 1972). As the males usually accompany their foraging mates, if the latter's food can be obtained near the nest then obviously there is a greater chance that predation will also be prevented. A little later in the nesting period the geese begin to feed upon the leaves and buds of dwarf willow e.g. *Salix glauca* (Gardarsson and Sigurdsson 1972) and these bushes are inevitably found surrounding favoured nest sites (Sigurdsson 1974).

The territory (however defined) would seem to be of more importance as a food source to the females than to the males. During the period of maximum agonistic activity the males feed relatively little (Figure 3). Their feeding begins to increase once the female has begun intensive incubation. However, more and more, the males feed amicably together in the 'neutral' areas, previously covered with snow. This tendency produces the decline shown in Figure 3, which gives only the percentage of feeding time spent close to the nest, i.e. within 30′ (9 m). As soon as the last of the snow leaves these low lying areas, sedges begin to grow and from early June start to become the favourite food of the males.

In conclusion it is proposed that agonistic behaviour in Pinkfeet serves to safeguard a supply of food near the nest when overall food is scarce. The males display to each other throughout the nest establishment period to space out the nests but once the nests have been established then they continue to recognise the boundaries created earlier without recourse to further agonistic activity. The 'territories' in any case are by this time becoming of less importance as a food source owing to the rapid growth of new food sources in other areas which are shared by all the males.

The proposals of Ryder (1975) are therefore seemingly inappropriate to this species. Ryder advanced his ideas on the basis of his own work on Ross's Goose *Anser rossii* and of findings from several studies of Canada Geese *Branta canadensis* breeding under both natural and semi-natural conditions. In such studies harassment behaviour was indeed observed. It is however still difficult to see the adaptive significance of such behaviour and Ryder (1975) offers no suggestions on this point.

Summary

The recent proposals of Ryder (1975) are examined in the light of behavioural studies conducted in Iceland on the Pink-footed Goose *Anser brachyrhynchus*. It is concluded that the main function of agonistic behaviour in this species is to safeguard a supply of food, primarily for the female, at the beginning of the nesting period. Ryder's suggestion that the function of the territory is to protect the incubating female from harrassing conspecifics would seem to be inappropriate.

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