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Vigilance, flock size and domain of danger size in the White-fronted Goose

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This paper investigates two hypotheses associated with the proposal that flocking in birds reduces the individual's risk of predation. Gregariousness might function in this way by making the predator's search and detection problem more difficult, by providing earlier warning of predatory approach and by reducing the risk of capture should an encounter with a predator occur (e.g. Hamilton 1971; Vine 1971, 1973; Lazarus 1972; Treisman 1975a, b). Empirical support for these proposals has been provided by Powell (1974), Siegfried & Underhill (1975) and Page & Whitacre (1975).

The two hypotheses concern the way in which time is allocated by the individual to vigilance for predators and the hypotheses were tested here in wild flocks of the White-fronted Goose *Anser albifrons*.

Geese are admirable subjects for a study of vigilance since their feeding and vigilant postures are readily distinguishable and, being herbivores, these two classes of activity form a major part of their time budget. In addition the variation of flock size in wintering geese is very great and the open habitat of these large birds makes observation relatively easy.

VIGILANCE AND FLOCK SIZE

The first hypothesis to be explored is that if flocking reduces the individual's risk of capture by a predator then the time spent by individuals in vigilance will decline as flock size increases since the benefit to be gained from such vigilance also declines. This is because it becomes increasingly likely that *other* individuals will make the necessary detections and because the risk of capture is reduced. Since other hypotheses have been advanced which make the same prediction about the effect of flock membership on vigilance the extent to which the data provides support for the different hypotheses will be considered.

Methods

The study was carried out between 20th January and 3rd March on the population of White-fronted Geese wintering at the grounds of the Wildfowl Trust, Slimbridge, Gloucestershire, where their feeding ecology has been studied by Owen (1971, 1972a, b, 1973, 1976). The birds were observed from towers and a hide on the fields known as Dumbles, Warth, Tack Piece, Top New Piece and Bottom New Piece using high-power binoculars. The Whitefronts spend a large part of the day grazing in these fields (Figure 1) and from time to time stand or walk in either the 'head up' or 'extreme head up' posture, these two postures being readily distinguishable (Figure 2). Whilst grazing the eyes are very close to the ground and the

Figure 1. Part of a flock of Whitefronts on the study area.

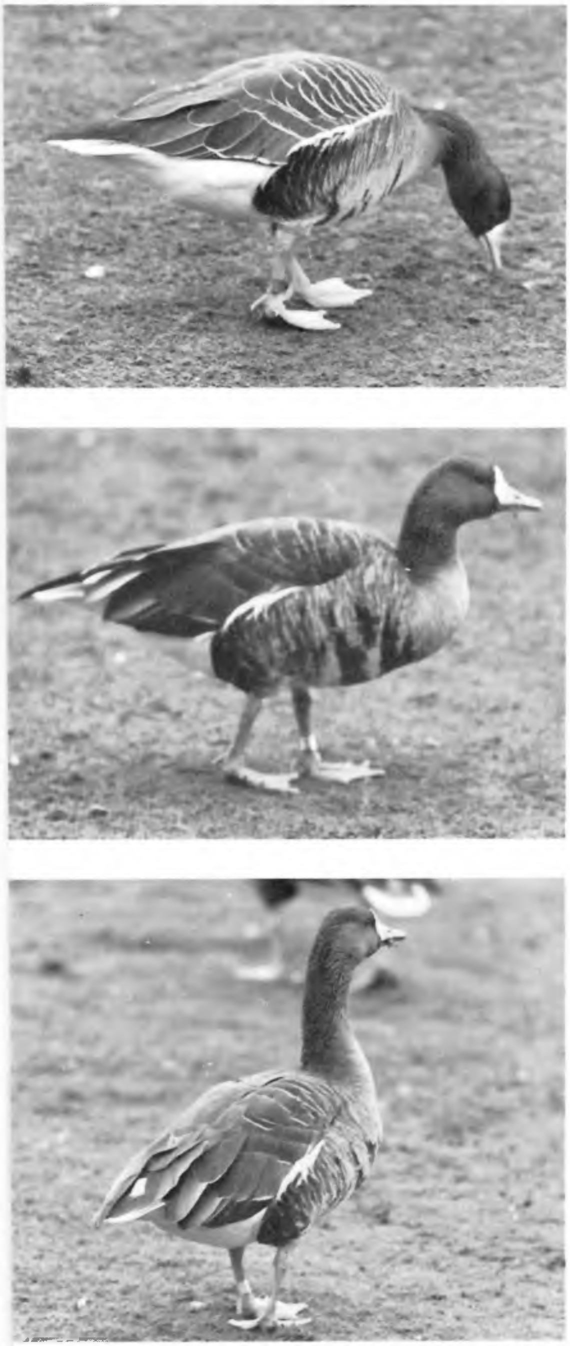

Figure 2. Postures of the White-fronted Goose. From top to bottom the postures are 'graze', 'head up' and 'extreme head up'.

probability of detecting an approaching predator, particularly when surrounded by other geese, must be very low. Other postures (i.e. preen, drink, threat, head low and head on back—see illustrations in Lazarus and Inglis (in press)) must also be associated with low probabilities of detection; in the last two postures the eyes are often closed. In the sense that predator detection seems most likely whilst the bird is either head up or extreme head up these two postures may be labelled as 'vigilant', and indeed there is a greater incidence of these postures in more disturbed situations (Owen 1972a; Owens 1977).

Only undisturbed, stable flocks were selected for study. The size of the flock (the mean of a number of counts being taken), its shape (long, oval or circular) and the time were noted. Then the flock was scanned between 1 and 21 times (mean = 5·5) with a minimum inter-scan interval of 30 seconds and the number of individuals head up or extreme head up counted on each scan. The mean of these figures was taken as the number of birds vigilant. Forty-two flocks, ranging in size from 1 to 1,061, were monitored in this way.

Results

The number of vigilant birds in the flock was significantly correlated with flock size ($r = +0{\cdot}874$, $N = 42$, $p = 0{\cdot}00001$, one-tailed; Figure 3). However, the number of individuals vigilant increased more slowly than flock size (see Figure 3) so that the percentage of birds vigilant declined significantly as flock size increased ($r = -0{\cdot}425$, $N = 42$, $p < 0{\cdot}005$, one-tailed), decreasing steeply at first but levelling out at a flock size of 200–300 birds (Figure 4). This relationship remained significant when the two single birds were omitted from the analysis ($r = -0{\cdot}475$, $N = 40$, $p < 0{\cdot}005$, one-tailed). Therefore, on average, individuals in larger flocks spent less time vigilant, as predicted by the hypothesis under test.

Since time both of day and of season are known to affect the time budget of the geese (Owen 1972a), a multiple regression analysis was conducted in which flock size was entered as the last independent variable—after time and date—to provide a conservative estimate of its importance in accounting for the variability in the percentage of birds vigilant, after the influence of time and date had been removed. The analysis showed flock size to have a significant influence on the percentage of birds vigilant

($F_{1,38} = 5{\cdot}28$, $p < 0{\cdot}05$) and to account for 11·4 % of the variance in this measure. Since the relationship between flock size and the percentage of birds vigilant was extremely curvilinear a reanalysis with a $\log_{10}$ transformation of flock size resulted in a more significant influence ($F_{1,38} = 44{\cdot}66$, $p < 0{\cdot}01$) with 50·4% of the variance explained by the transformed variable.

Another potentially confounding variable was the field in which the flock was situated since the five fields employed differed somewhat in disturbance levels. However, neither flock size nor the percentage of birds vigilant in the flock varied significantly with the field ($F_{4,36} = 1{\cdot}39$ and 1·13 respectively, both NS) and when Figure 4 was redrawn for each field separately the same pattern emerged. In addition the values of Owen's (1972b) disturbance index for each field were compared for the points above and below the regression line between flock size and number of birds vigilant (shown in Figure 3). Since the two sets of values did not differ (Mann-Whitney U test, $z = 0{\cdot}19$, NS) it is concluded that disturbance level did not influence this relationship.

A further variable requiring investigation is food density. Krebs (1974) found that the frequency of 'looking' by Great Blue Herons *Ardea herodias* was significantly negatively correlated with flock size, but this relationship disappeared when feeding rate was taken into account. Since rate of food intake was positively correlated with flock size it therefore seemed that 'looking' was a response to a low feeding rate and Krebs suggested that such 'looking' was directed towards herons flying over, to see where they were going to feed. In the present study food density and quality (and thus feeding rate) might vary with the field and the date (and

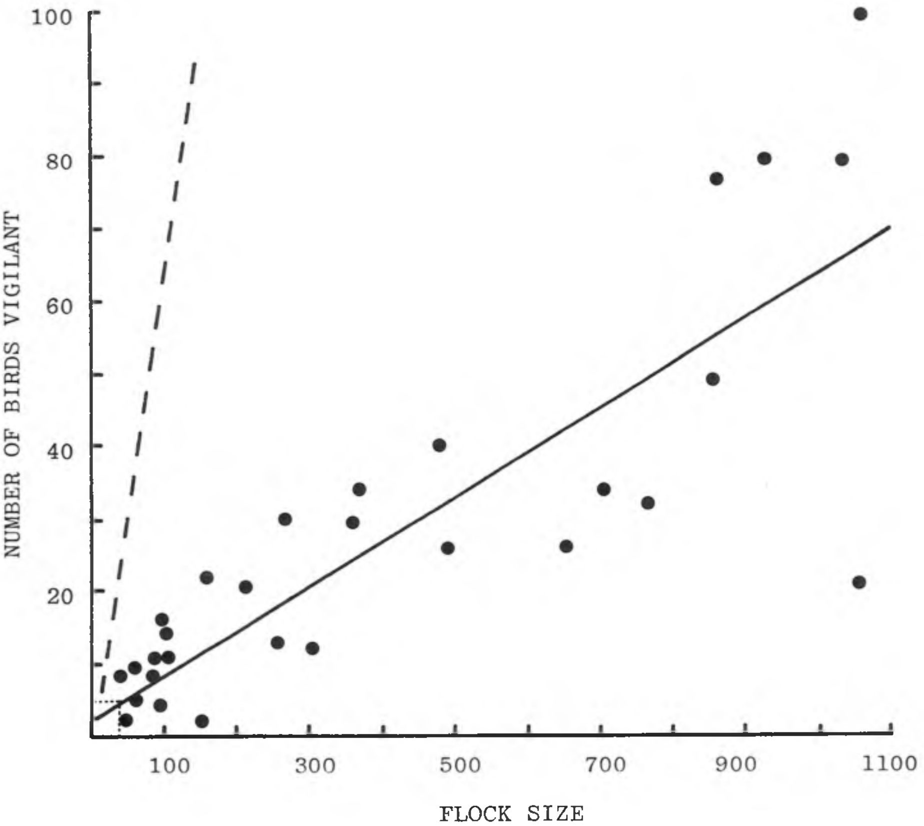

Figure 3. The influence of flock size on the number of birds vigilant (i.e. head up or extreme head up). The area within the dotted line near the origin contains 13 more points. The fitted linear regression line is shown ($Y = 2{\cdot}385 + 0{\cdot}0617X$). The dashed line represents the relationship if the value of the mean number of birds vigilant for a flock of one applied to all flock sizes.

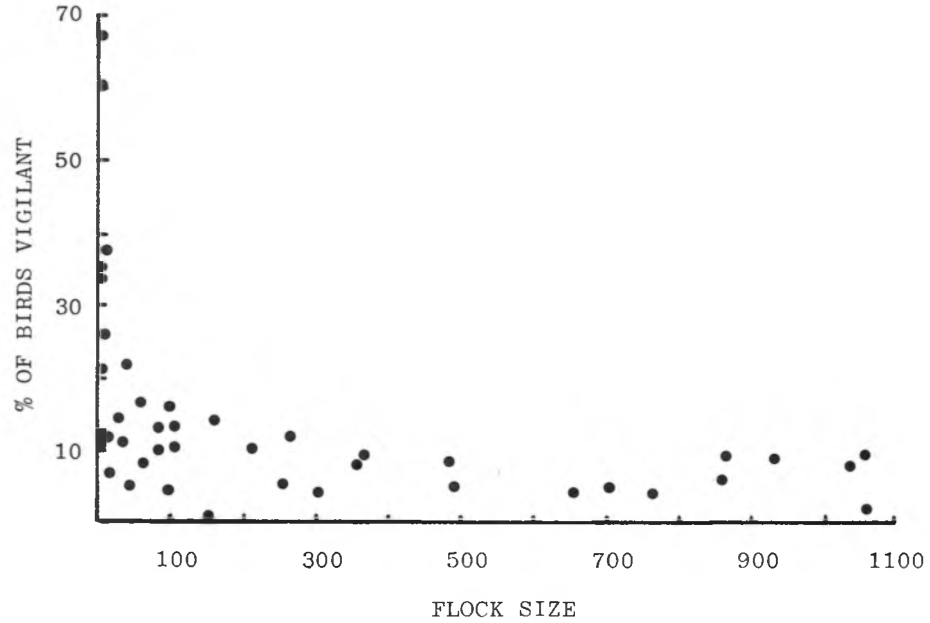

Figure 4. The influence of flock size on the percentage of birds vigilant. The two highest points are for the (only) single birds.

food availability, via ambient light level, perhaps with time of day). As the flock size/vigilance relationship is unaffected by these variables the influence of food density and availability can probably be discounted. The relationship is therefore unlikely to be explicable in terms of feeding rate, but as food quality and the pattern of goose usage also vary through the winter *within* fields (Owen 1971) some doubt must remain.

Finally, although adult Whitefronts spend more time vigilant than juveniles (Owen 1972a) this would not confound the results unless the proportion of juveniles increased in larger flocks, an unlikely situation since flocks are composed of stable family groups (Owen 1972a). In addition juveniles formed only 8% of the population in the year of study (M. Owen, pers. com.).

Discussion

The results are consistent with the hypothesis that individuals in larger flocks spend less time vigilant for predators. Although the relative frequency of head up and extreme head up postures was not determined in this study more recent work on other goose species (Lazarus & Inglis, in press; Inglis & Isaacson, in press) indicates some differentiation in the function (and signal properties) of the two postures.

Since the flock size/vigilance relationship found here was first briefly reported (Lazarus 1972) the same relationship has been documented in three other goose species (Drent & Swierstra 1977; Lazarus & Inglis in press; Inglis & Isaacson, in press), in captive Starlings *Sturnus vulgaris* (Powell 1974) and in prairie dogs (Hoogland 1977). In a number of other studies which dealt only with the difference between flock and solitary individuals the latter were again found to be more vigilant (Murton 1968; Murton, Isaacson & Westwood, 1971; Smith & Evans 1973; Dimond & Lazarus 1974; Feare, Dunnett & Patterson 1974; Siegfried & Underhill 1975; Wright 1975). Individuals in larger flocks will also be safer simply because at any moment there are more vigilant individuals (Figure 3).

The mechanism implicit in the hypothesis tested here is that individuals estimate the size of their flock and regulate their time budget accordingly. However, there is an alternative mechanism. Individuals on the flock periphery are at a greater risk of capture since they will be encountered first by an approaching ground predator and if attacked from the air they may be selected because of their relative isolation. Evidence for this effect in flocks, colonially breeding birds and other animals is in Rudebeck (1950–1951), Patterson (1965), Hamilton (1971), Tenaza (1967), and Buckley & Buckley (1977). As a result of this 'peripheral predation' phenomenon individuals on the edge would be expected to be more vigilant (and have a higher escape tendency). Evidence for such an effect comes from studies of colonially breeding Adélie Penguins *Pygoscelis adeliae* (Tenaza 1971) and prairie dogs (Sciuridae) (Hoogland 1977) and, anecdotally, from ungulate herds (Altmann 1958) and Rook *Corvus frugilegus* flocks (Feare, Dunnett & Patterson 1974). Then if birds in some peripheral zone of the flock were more vigilant the proportion of birds vigilant would decline as flock size increased since the number of birds in this zone would represent a diminishing proportion of the whole flock. This argument has also been given by Drent & Swierstra (1977) but they did not suggest *why* peripheral individuals might be more vigilant.

The argument can be developed more rigorously as follows. Assume that flocks are circular, with radius r, and that bird density is constant throughout the flock and for all flock sizes. Let birds in a peripheral zone of constant width x spend a proportion Q of their time vigilant, let more central individuals be vigilant for a proportion q of the time and let $Q \gg \beta$. Then the proportion, P, of birds in this peripheral zone is, by simple geometry:

$$P = 1 - [(r - x)^2/r^2]$$

and the proportion of birds vigilant in the flock, V, is equal to:

$$V = QP + q\,(1-P)$$

Figure 5 shows the relationship between V and flock size (which is proportional to flock area) for flocks in the range r = 1 to 32 for x = 1 and various values of Q and q. When Q is maximally greater than q the curve is

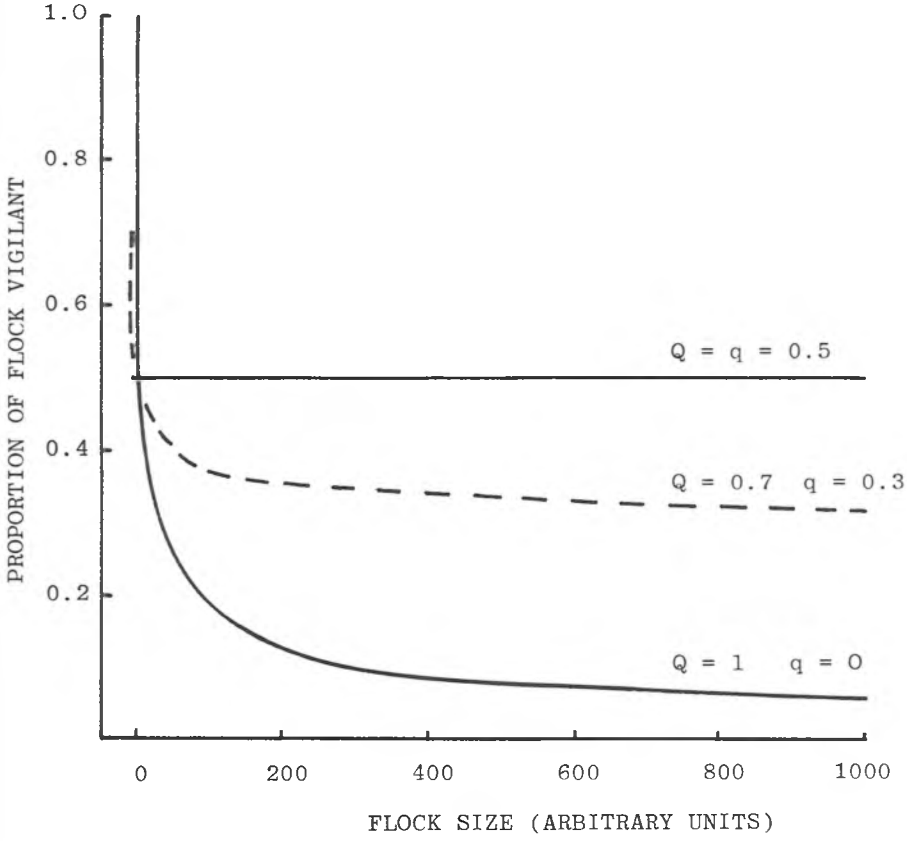

Figure 5. The theoretical influence of flock size on the proportion of the flock vigilant when peripheral birds are more vigilant than central birds. See text for further explanation.

very like that obtained for the Whitefronts (see Figure 4) but as Q and q become more equal V varies less extremely with flock size. When Q = q, V is naturally constant (= Q). A more elaborate model, with vigilance declining gradually towards the flock centre, and with different flock shapes, would not materially alter these conclusions. (If the width of the zone is a constant *proportion* (= 1/k) of the flock's radius, then by simple geometry:

$$P = 1 - [(k - 1)^2/k^2]$$

and both P and V are independent of r and therefore of flock size.)

It is therefore possible that the flock size/vigilance relationship is a result of individuals regulating their behaviour not to flock size but to their distance from the flock periphery. It is also possible, of course, that both effects are at work.

One piece of indirect evidence is inconsistent with this 'peripheral vigilance' effect. It can be shown that a greater proportion of the flock will be vigilant the more it departs from a circular plan (this follows from the classical isoperimetric problem; see, for example, Pars 1962). Therefore it would be expected that for a given flock size long flocks would have the highest number of birds vigilant and circular flocks the smallest, with oval flocks intermediate (assuming that density was constant throughout the flock and the same for all flock shapes). However, regressions of the number vigilant on flock size gave the highest value for circular flocks and the lowest for oval flocks over most of the flock size range (Figure 6). However, the above assumptions concerning flock density are of unknown validity, so this evidence is insufficient to dismiss the peripheral vigilance effect which must remain as a possible alternative, or supplement, to the regulation of vigilance directly by flock size.

A complicating factor in testing this

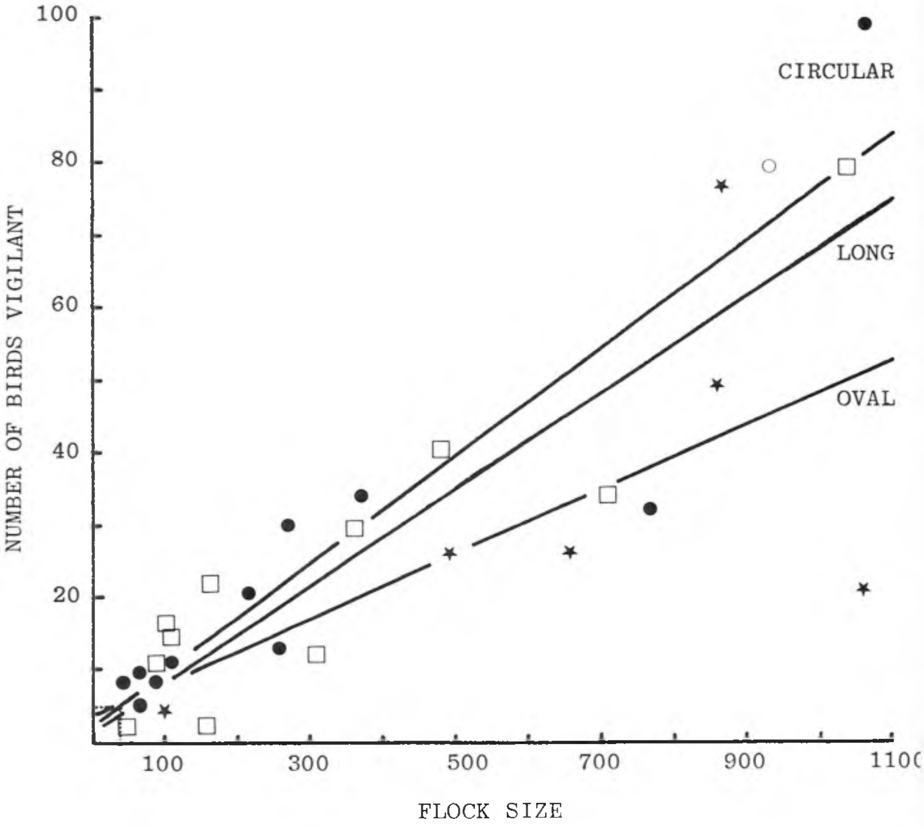

Figure 6. The influence of flock size on the number of birds vigilant in circular (●), long (□) and oval (✶) flocks. Fitted linear regression lines are shown. The area within the dotted line near the origin contains 13 more points. ○ = shape of flock not determined.

peripheral vigilance hypothesis will be that families tend to occur at the edge of Whitefront flocks (Owen 1972a, 1976). Since parental adults spend more time vigilant, and juveniles less time vigilant, than adults without young (Owen 1972a; and see Lazarus & Inglis (in press) on the Pink-footed Goose *Anser brachyrhynchus*) the social status of birds will have to be taken into account.

It is unlikely that the concentration of families on the flock edge could itself produce a peripheral vigilance effect sufficient to explain the flock size/vigilance relationship found here. This is because the high vigilance level of parents is balanced by the low vigilance level of their offspring. Using Owen's (1972a) data on the duration of vigilant bouts and the intervals between them, the mean proportion of time spent vigilant by parents, by adults without young and by juveniles is 0·0191, 0·0168 and 0·0146 respectively. Then, assuming that all families, but no adults without young, are on the edge of the flock, the average proportion of time spent vigilant for peripheral and non-peripheral birds, and the ratio (the 'edge/centre ratio') between these values, can be calculated for different brood sizes. (It is also assumed that parental vigilance is independent of brood size, which is known to be true for the Pinkfoot (Lazarus & Inglis, in press).) For a mean brood size of 2·1 the vigilance of parents and juveniles exactly counterbalance giving an edge/centre ratio of 1 and no peripheral vigilance effect. For larger broods peripheral vigilance is *less* than that in the rest of the flock. The mean Whitefront brood size at Slimbridge is generally between 2·5 and 3·5 (Wildfowl Trust data, published annually in *Wildfowl*) and taking 3·0 as a mean value gives an edge/centre ratio of 0·98. In the present study mean brood size was unusually low at 2·0 giving an edge/centre ratio of 1·003 and a very small positive peripheral vigilance effect. The smallest possible brood size is of course 1, giving a maximum value for the edge/centre ratio of 1·05 which is still very low (cf. Q/q ratios in Figure 5). Even if family members were differentially distributed on the periphery, with parents on the very perimeter of the flock and their juveniles just inside them, it is unlikely that such a small peripheral vigilance effect could account for the flock size/vigilance relationship found here. To investigate this further, in the manner of Figure 5, one would have to make assumptions about the width of the peripheral zone and the numbers of families in flocks of different sizes.

As well as the two mechanisms for an anti-predator functional interpretation of the present findings, two further hypotheses may be offered. The first is the 'conspecific hypothesis' which asserts that solitary birds spend more time vigilant, searching for conspecifics to join, rather than for predators, in order to benefit from the feeding advantages of flocking (Murton, Isaacson & Westwood 1971; Krebs 1974). The hypothesis could readily be generalized to predict less vigilance in *larger* flocks if the feeding advantages of flocking were to increase with flock size. Lazarus & Inglis (in press) point out that the hypothesis need not rely on the existence of feeding advantages of flocking and could equally well be argued *whatever* the advantages of flocking. The hypothesis is difficult to refute and could explain the present data, although birds on the ground were rarely seen to join others flying over.

The second argument, developed by Lazarus & Inglis (in press), may be called the 'food hypothesis'. It has been proposed that individuals might monitor the food items and feeding efficiency of their neighbours and scan the environment for new food patches in order to obtain information on their profitability (Murton 1971a, b; Murdoch & Oaten 1975; Drent & Swierstra 1977) or might watch where conspecifics are travelling to feed (Krebs 1974). Lazarus & Inglis add to this proposal the argument that there will be a greater pressure on birds of currently low feeding efficiency to acquire such information. Then since flocks often build up where feeding conditions are good (Murton, Isaacson & Westwood 1966; Goss-Custard 1970) individuals in larger flocks would be expected to spend less time monitoring conspecifics and potential feeding sites and more time actually feeding.

Evidence for the food hypothesis in Great Blue Heron flocks (Krebs 1974) has already been discussed and it has been argued that vigilance in the Whitefront is unlikely to be a response to a low feeding rate (unless within-field variations prove to be important). R. Wells (pers. com.) has pointed out that the food hypothesis would predict an increase in vigilance as the winter proceeds and food stocks decline (Owen 1972a); although this might not be so if the *relative* profitability of alternative feeding sites remained stable over the winter. When the effect of flock size is partialled out the correlation between the proportion of birds vigilant and the date is insignificant ($r = -0{\cdot}0005$, $N = 42$, NS). Also the food hypothesis would not explain the flock size/vigilance relationship in the Starling study (Powell 1974) in which food was always provided in superabundance.

In conclusion, while the evidence does not favour either the conspecific or food hypotheses it must be admitted that crucial evidence for the original anti-predator hypothesis is not yet available.

VIGILANCE AND DOMAIN OF DANGER SIZE

Hamilton (1971), in developing a model to explain the evolution of gregariousness in prey animals, introduced the concept of a 'domain of danger' surrounding each prey individual. Such a domain encloses all those points, and only those points, closer to the prey owning it than to any other. Hamilton pointed out that in cases where a predator emerges at an unpredictable site within the prey group individuals with the largest domains will be at the greatest risk of predation (and that consequently natural selection will favour the more gregarious individuals with smaller domains since approaching a neighbour is a ready method of reducing one's domain).

This proposed relationship between predation risk and the size of the individual's domain can be expected to have similar consequences for prey behaviour to that of the prey risk/flock size relationship: individuals with larger domains, like those in smaller flocks, should be more vigilant. This prediction, not previously proposed or tested, so far as known, is examined here in the White-fronted Goose.

Hamilton's requirement that the predator emerges unpredictably within the prey group is likely to hold only for certain flocking species. Thus, both ground and aerial predators generally attack from outside the flock, although an aerial predator attacking a flock on the ground would fulfil Hamilton's requirement if it selected, at random, an *area* of the flock to be attacked. Then individuals with larger domains would have a greater risk of being selected. If a random selection was made from *individuals*, however, risk would be independent of domain size. In fact neither of these possibilities seems very realistic and it would appear more likely that an aerial predator would select a rather isolated prey (i.e. one with a large domain) since such an individual would be less able to benefit from the alarm responses of neighbours and perhaps from secondary flock defences (i.e. those effective during an encounter between predator and prey; Lazarus (1972)). A ground-feeding species suffering aerial predation therefore seems the most likely to show a positive correlation between domain size and vigilance.

Methods

The population and study period were the same as that in the previous study. An indirect measure of domain size was employed; the number of birds within nine goose lengths (= 6·17 m) of the subject individual. This particular distance was selected to provide a wide range of values (i.e. 0–20).

A bird in the extreme head up posture was selected for observation and when it started to graze the durations of the grazing bout and of the immediately following bout of standing extreme head up were measured with stopwatches. Only observations of an uninterrupted 'extreme head up-graze-standing extreme head up' sequence were used. At the end of the sequence the number of birds within nine goose lengths of the subject was recorded. (In the 30 cases where the numbers were noted at both the beginning and end of the sequence they were identical in 23 cases, greater at the start in 3 and greater at the end in 4.)

Only adult birds in flocks larger than 200 were used since in such flocks the proportion of birds vigilant was uninfluenced by flock size ($r = -0{\cdot}224$, $N = 17$, NS; see Figure 4). Data from 72 individuals in 15 flocks ranging in size from 230 to 1,150 were collected.

Results

The mean length of the grazing bout was 33·7 secs and of the following extreme head up bout 2·6 secs, the two bout lengths not being significantly correlated ($r = -0{\cdot}153$, $N = 72$, NS). Number of neighbours was not related to grazing bout length ($r = +0{\cdot}275$, $N = 17$ [one for each number of neighbours], NS) but was significantly negatively correlated with the duration of the following extreme head up bout ($r = -0{\cdot}430$, $N = 17$, $p < 0{\cdot}05$, one-tailed; Figure 7).

Discussion

The results show that when a bird stops grazing to stand extreme head up the larger its domain the longer will be the duration of this posture, a result conforming with the hypothesis under test.

An alternative explanation of the result is also possible however. An adult that lifts its head from grazing to find itself with a large domain may have to scan for longer to relocate its mate or family or as Hamilton would predict, *any* flock neighbour, before regaining proximity to them. (The results do not reflect the time taken to move closer since they concern only birds that were *standing* extreme head up.) Although further evidence which might allow a choice between these two hypotheses is not available, data from the Pink-footed Goose study by Lazarus & Inglis (in press) provide less am-

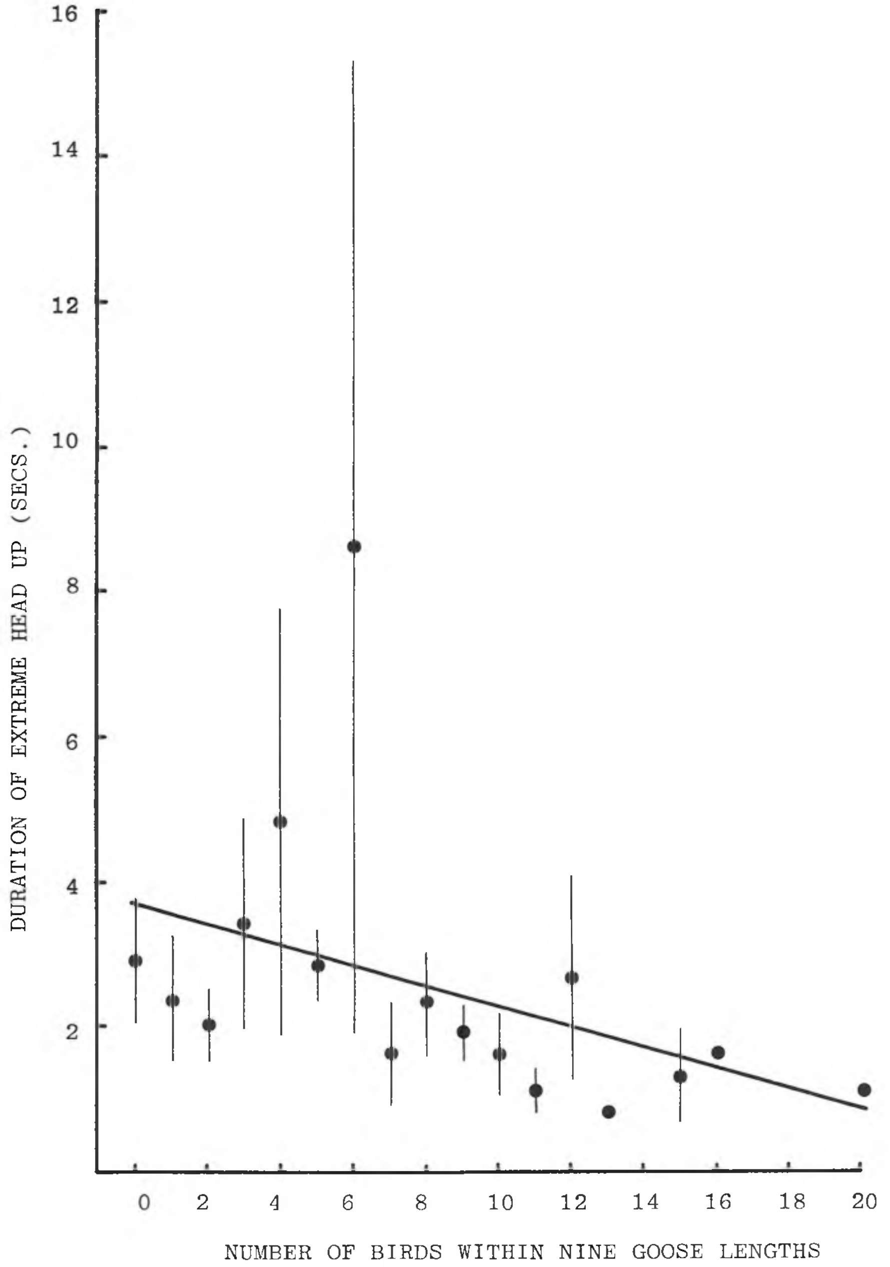

Figure 7. The influence of the number of birds within nine goose lengths on the duration of extreme head up bouts (mean ±S.E.). The fitted linear regression line is shown.

biguous support for the hypothesis being tested. Sitting families of Pinkfeet (i.e. pairs of adults with young) were closer to other geese when the parents were in the 'non-vigilant' head on back or head low postures than when head up or extreme head up (7·8 m compared to 13·6 m; F test from a multiple regression analysis controlling for various potentially confounding variables, $p < 0·01$). In other words parents were more vigilant when domain size was larger.

This finding cannot be explained in terms of scanning for family members since they were sitting in close proximity. Although greater proximity when non-vigilant might be thought to follow automatically from a breakdown of the usual spacing maintained by vigilant birds this would not explain why non-breeding flocks failed to show the same difference. This difference between parents and non-breeders is itself of some interest since it strongly suggests the domain size/vigilance relationship to be functionally a component of parental care rather than of adult survival.

A final question to be considered is the degree to which the two species conform to the rather restrictive predator requirements of an unpredictable attack from within the flock or an aerial attack in which the more isolated flock members are at greater risk.

Since the Whitefronts at Slimbridge are probably in danger only from ground predators approaching from outside the flock (the fox *Vulpes vulpes* and man: Owen 1972b, 1973) they would probably not satisfy these requirements and therefore represent a rather weak test of the hypothesis. The Pinkfeet, however, seem to satisfy the requirements very well. On the breeding grounds they form very large groups (whether these are true flocks is uncertain) composed of widely-spaced families interspersed with a few small non-breeding flocks. These groups (but not the family units or flocks themselves) can be infiltrated by arctic foxes *Alopex lagopus* perhaps unseen by the geese, aided by the greater amount of cover compared to that in the Whitefront winter habitat. Although the adults probably fall prey only to Arctic foxes (and to man in the past) the goslings are additionally vulnerable to a number of aerial predators (Lazarus & Inglis, in press).

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Summary

Two hypotheses concerning the way in which time is allocated to vigilance for predators are investigated in the White-fronted Goose *Anser albifrons*.

The first hypothesis states that if flocking reduces the individual's risk of predation then the time alloted to vigilance for predators will decline as flock size increases. The results were consistent with the hypothesis. Alternative explanations for the same phenomenon are discussed and evaluated.

The second hypothesis concerns Hamilton's (1971) concept of a domain of danger around prey individuals, within which a predator would be closer to the owner of the domain than to any other prey. It is argued that prey with larger domains will be expected to devote more time to predator vigilance. The results were in agreement with the hypothesis but were also explicable on an hypothesis that vigilance was directed towards the detection of conspecifics. Results from a study of the Pink-footed Goose *Anser brachyrhynchus* provide less ambiguous support for the hypothesis.

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Wild Pink-footed Geese *Anser brachyrhynchus* feeding in a stubble field and drinking at a pool at Eastpark Wildfowl Refuge, Caerlaverock, Scotland. (*Philippa Scott*)