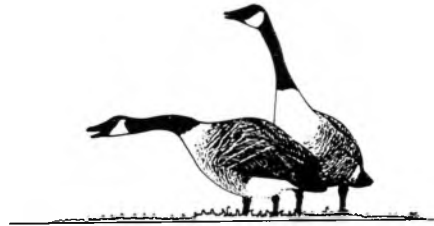


Mate protection in pre-nesting Canada Geese *Branta canadensis*

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Fourteen individually marked pairs of Canada Geese were observed from January to April on their feeding grounds in the south of England. Mated birds associated closely within the flock. Females spent more time feeding than did their mates, while male geese were more vigilant and more frequently involved in aggressive encounters. Increased aggression by males and females at the centre of the flock could be a consequence of the shorter distances between birds at the middle. Male vigilance was higher at the edge.

Male vigilance may protect the mate from potential predators (particularly at the edge of the flock) and possibly from interference by conspecifics. Protection enables females to decrease the time they spend vigilant, and thus increase the time spent feeding, allowing them to gain the reserves of fat and protein needed for successful breeding.

Breeding is energetically stressful for female geese, which rely on reserves of fat and protein for production and incubation of the clutch (e.g. Newton 1977, Raveling 1979, Akesson & Raveling 1981). Incubation is performed solely by female Canada Geese *Branta canadensis*. It is therefore not surprising that females gain condition faster than males prior to breeding in both England and North America (Raveling 1979, Johnson 1986). Since the food in England is grass, which is time-consuming to ingest, much time must be spent feeding, especially by females. However, vigilance is also important, because geese are desirable prey and take off slowly. Present day predation in England is mostly by shooting.

Vigilance is achieved by holding the head high to get an unobstructed view of the surroundings. One cannot, however, infer unambiguously the function of 'head up' behaviour from observation only of its form. Lazarus & Inglis (1978) provide a useful discussion of possible functions during the period of parental care, including watching for predators, looking for food, and looking for conspecifics to avoid interference during feeding. These are all possibilities during the pre-nesting period also. Interference might occur in a dispute over a feeding area or in an attempt by a male to copulate with a female other than his own mate.

Here we investigate the possible functions of the 'head up' behaviour of male and female

Canada Geese in England in the period prior to nesting. This allows us to examine the suggestion that males protect their mates from predators and conspecifics, thus enabling them to obtain more of the resources they need for breeding.

Methods

Observations were made on the behaviour of mated pairs of Canada Geese on their feeding grounds in Hampshire during January to April 1984. The viewing distance varied from less than 100 to a maximum of approximately 600 m, with 200 to 400 m being the usual range. Observations were made from a Landrover or from a portable canvas hide, using a 15-60 X telescope, from between 08.00-18.00 h. Flock size varied between 4 and 350 birds, averaging 180 ± 99 (S.D.).

Individual Canada Geese were identified by the use of black plastic neck collars, each engraved with a unique two-letter code (Johnson & Sibly 1989). Birds had been fitted with collars during an earlier summer moult under licence from the Nature Conservancy Council. Pair relationships were confirmed by subsequent observations of birds at their nests.

Continuous records of focal animals were made over a number of five-minute periods. Pairs were selected for observation at random

with respect to behaviour. In many cases, members of focal pairs were observed in consecutive 5 minute observation periods. A mean of 10.4 ± 2.6 (S.D.) observations was made on each focal bird. Behaviour was classified as feeding, vigilant or other, as defined below.

Feeding: Bill held below base of neck and pointing downward; birds either pecking or uprooting food or remaining in feeding posture, apparently scanning the ground, in between bouts of pecking.

Vigilant: Standing, sitting or walking in 'head up' or 'extreme head up' postures (Lazarus & Inglis 1978). In 'head up' the bill is clearly above the level of the back, but the neck is not stretched. In 'extreme head up' the neck is stretched vertically, so the black neck feathering is all above the level of the back. The body axis is usually tilted towards the vertical. Occasional eye closure may occur in the 'head up' but never in the 'extreme head up' posture.

Other: All other behaviour including preening and sleeping.

The percentages of each observation period for which the focal animal was feeding or was vigilant were calculated. The number of aggressive interactions (threat displays, chases and fights) with other geese was recorded. The distances between the focal animal and its mate ('mate distance') and between the focal animal and its nearest neighbour, other than its mate ('nearest neighbour distance') were estimated in 'goose lengths' at the start of each observation. In addition the focal animal was classified, according to its position at the start of the observation period, as either middle, intermediate or edge of flock. A bird was said to be on the edge of the flock if there were less than five birds closer to the nearest point on the (imaginary) convex polygon enclosing the flock. If there were ten or more birds closer to this point the focal animal was classed as being in the middle of the flock. Geese falling into neither category were classed as intermediate.

Individual geese generally moved very slowly relative to the rest of the flock and bird - bird distances and position in the flock did not vary greatly from start to end of each observation period. Position records at start and end were available in 68 cases, in 59 of which position had not changed, the change being to an adjacent category in the remaining nine cases. Since pair members associated closely within the flock (see below) the position within the flock (i.e. middle, intermediate or edge) is almost always the same for both members of a pair. When pairs of geese walked to new areas be-

tween feeding bouts the sex of the leading bird was recorded.

Data were also obtained on the behaviour of solitary pairs of geese. In total, four such pairs were observed, and the behaviour (vigilant or not vigilant) of both members of each solitary pair recorded simultaneously every 30 seconds throughout the period of observation.

Results

Fourteen pairs of Canada Geese were observed regularly during the study period and 291 five-minute observations were made. Data were obtained from 20 of the 28 individuals on mate and nearest neighbour distances in the middle and on the edge of the flock.

Paired geese associated closely within the flock, and a bird's nearest neighbour was usually its mate. Thus there were no differences between mate distance and nearest-neighbour distance either in the middle or on the edge of the flock (Wilcoxon tests, $T = 81$, $n = 19$, N.S. and $T = 65.5$, $n = 19$, N.S. respectively). However birds were closer together in the middle of the flock, nearest-neighbour distance being 2.2 ± 0.25 (S.E.) goose lengths compared with 5.0 ± 1.00 (S.E.) on the edge of the flock (Wilcoxon test $T = 26.5$, $n = 18$, $P < 0.01$). The corresponding mate distances were 2.0 ± 0.16 (S.E.) and 3.3 ± 0.42 (S.E.) goose lengths (Wilcoxon test $T = 29.5$, $n = 19$, $P < 0.01$).

Females were putting on weight faster than males during the period in which the observations were made (Johnson 1986 and see above), and spent longer feeding (a median of 55% of their time, compared with 44% for males (Wilcoxon test, $T = 22$, $n = 14$, $0.05 < P < 0.10$)).

Female feeding behaviour did not vary significantly with position in the flock (Fig. 1a), but males fed less when on the edge of the flock than when in intermediate or central positions (Wilcoxon test, $T = 10$, $n = 11$, $P < 0.05$ and $T = 14$, $n = 12$, $P < 0.10$, respectively).

Overall males were more vigilant than their mates (44% v 36% (medians), Wilcoxon test, $T = 6$, $n = 14$, $P < 0.01$). Male vigilance tended to be higher on the edge of the flock than in the middle (Fig. 1b, Wilcoxon test, $T = 16$, $n = 12$, $0.05 < P < 0.10$), but there was no corresponding increase in female vigilance on the edge of the flock.

Aggressive interactions involving focal birds were relatively rare, being recorded in only 13% (37/294) of observation periods. Males were more aggressive than females (25/150 male

observations revealed aggression compared with 12/144 for females, $\chi^2 = 3.91$, 1 df, $P < 0.05$). More aggression occurred in the middle of the flock than on the edge (23/115 v 4/77, $\chi^2 = 8.3$, 1 df, $P < 0.01$). This was particularly evident in focal females (Fisher Exact Test, $P = 0.024$) but focal males showed the same trend ($\chi^2 = 3.3$, 1 df, $0.05 < P < 0.10$).

Observations on solitary pairs of geese revealed that on over 98% of occasions (300/305) at least one member of the pair was in a vigilant posture. The distribution of occasions when neither, one or both members of a solitary pair were vigilant was significantly different from that predicted if the birds behaved independently of one another (Table I, $\chi^2 = 47.9$, 1 df, $P < 0.001$). Thus high combined vigilance was achieved by male and female alternating their behaviour.

Discussion

In this study females fed 11% more than their mates. That this only achieved borderline statistical significance ($0.05 < P < 0.10$) is probably a result of the imprecision of individual measurements, which were obtained by 5 minute focal animal study. The time spent feeding in the pre-nesting period must be important to females, since they need to acquire reserves not only for the production of the eggs, but also to sustain themselves through incubation, which is performed solely by the female and therefore allows very limited opportunity for feeding. Fat, protein reserves and belly profile are known to increase in pre-nesting female geese faster than in males (Raveling 1979, Johnson 1986).

Any increase in the time spent feeding is likely to mean less time is available for vigilance, since feeding and vigilance together oc-

cupy nearly all a female's time, especially in intermediate positions or on the edge of the flock.

Is the lower vigilance shown by females disadvantageous? Before answering this question we consider in detail the functions of the behaviours here called vigilant, i.e. 'head up' and 'extreme head up'. Three possible functions have been suggested for these behaviours: 1) Watching for predators; 2) Watching for conspecifics (to avoid interference); 3) Looking for food (see above). Since males showed head up and extreme head up behaviour more than their mates, but did not usually lead movements between feeding areas in six out of seven pairs observed, 3) is less likely than 1) or 2).

Watching for predators is extremely important on the edge of a flock, since edge birds are more vulnerable to predation than birds within the flock (e.g. Hamilton 1971, Drent & Sweirstra 1977, Lazarus 1978, Krebs & Davies 1987). In accordance with this idea, males were some 10% more vigilant when on the edge of the flock than when in the centre (Fig. 1b). Females on the edge of the flock were no more vigilant than when they were within the flock (Fig. 1b), but since they were close to their mates it seems plausible that edge females relied on their mates for predator detection. Our results refer to changes in behaviour within individual geese according to their position within the flock and so indicate actual effects of position on individuals acting as their own controls. Similar results for vigilant behaviour in Greenland White-fronted Geese *Anser albifrons flavirostris* were obtained by Fox & Madsen 1981. They compared solitary pairs with pairs in flocks and found male vigilance was lower in flocks, whereas female vigilance did not vary between the two situations.

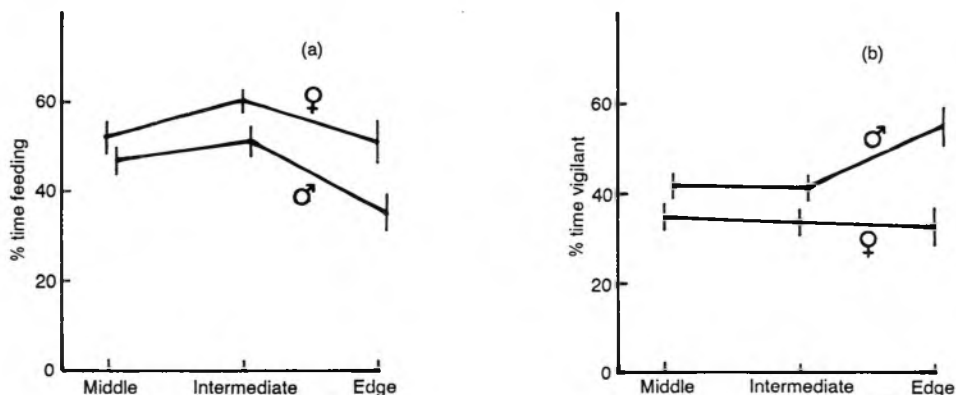


Figure 1 a. Time feeding in different parts of the Canada Goose flock. b. Time vigilant in different parts of the Canada Goose flock.

Table I: Vigilant behaviour of solitary pairs of Canada Geese. * Expected numbers were calculated on the basis of no co-ordination between birds.

	Birds vigilant <i>n</i>		
	0	1	2
Observed	5	211	89
Expected*	32.6	155.9	116.5

The importance of vigilance on the edge of the flock is indicated by the results of observations on solitary pairs. (Being a solitary pair is effectively an extreme example of being on the edge of a flock.) It was found that for over 98% of observations at least one member of such pairs was vigilant (Table I). Since no other geese were present and since movements to new feeding areas occurred only rarely during these observations, the high level of vigilance is likely to be a consequence of the need to watch out for predators. These observations also indicate that geese rely on their mates' ability to detect predators, since the high level of vigilance was achieved by male and female modifying their behaviour according to that of their partner.

Protecting the female from other geese would be less important for edge males than for central males, because nearest neighbour distances were greater on the edge and aggressive interactions were less frequent there. None of the interactions that were seen on the edge of the flock involved

focal females, although the sex of non-focal birds interacting with focal males was not known. It seems likely that the higher rate of aggression in the centre of the flock was a consequence of the shorter distances between central birds.

In most cases it was not possible to determine the cause of aggressive behaviour. However, on a small number of occasions the focal female was observed to be threatened or attacked by another bird. The focal animal's mate then attacked the aggressor. No copulations were observed on the feeding grounds, so mates were not attempting to prevent extra-pair copulations. Almost invariably the bird which initiated an aggressive encounter would win that encounter (i.e. would displace its opponent). The only occasion when this was not the case occurred when a focal male attacked another individual which had threatened his mate.

We conclude that while on the edge of the flock the increased vigilance of the male protects his mate from the possibility of predation. Within the flock male and female vigilance is probably largely concerned with observation of other geese, since aggressive interactions are more frequent in these more crowded positions. Some observations of aggression indicate that males attempt to defend their mates from other geese in the flock. These behaviours of the males allow their mates to reduce their level of vigilance from what would otherwise be required and, therefore, to increase the time spent feeding which is especially important during the pre-nesting period.

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