Factors affecting vigilance in Greater White-fronted Geese *Anser albifrons*

T. Shimada[1] & K. Shimada[2]

[1]The Miyagi Prefectural Izunuma-Uchinuma Environmental Foundation,
17-2 Shikimi, Wakayanagi, Miyagi 989-5504, Japan.
Email: tshimada@axel.ocn.ne.jp.
[2]Japanese Association for Wild Geese Protection,
16 Minamimachi, Wakayanagi, Miyagi 989-5502, Japan.

To maximise nutrient intake, an individual may have to trade time spent feeding against time spent being vigilant for predators. Flock formation is one strategy in which individuals can benefit from the vigilance of other flock members to reduce their own level of investment in vigilance. Several authors have reported that vigilance investment by an individual within a flock differs according to social class and location for *Branta* spp. geese. Factors affecting vigilance were examined in an *Anser* sp. goose, the Greater White-fronted Goose *A. albifrons*, in relation to social class and location (edge and centre) in flocks observed in rice fields around Lake Izunuma-Uchinuma, northern Japan. The geese on the edge spent significantly more time than those in the centre on being vigilant. The percentage of juveniles on the edge of the flock was significantly higher than that in the centre. Among families on the edge, there were significant differences among social classes in adults' vigilance and feeding; the vigilance of parents increased with the number of offspring, and parents with three offspring were the most vigilant. Conversely, the proportion of adults feeding significantly decreased with the number of offspring. Juveniles devote most time to feeding in any social class. Parents make a trade-off between vigilance and feeding in relation to the number of their offspring.

Key Words: ***Anser albifrons*, flock, social class, trade-off, vigilance**

Two evolutionary forces are thought to shape an individual's behaviour in order to maximise survival during winter: risk of starvation and risk of predation (Grubb & Pravosudov 1994). To reduce the risk of starvation, an animal must maximise its rate of nutrient and energy intake, but to reduce the risk of predation it must maximise its vigilance (Pravosudov & Grubb 1999). Hence, to maximise nutrient intake an individual may have to trade-off time spent feeding against time spent watching for predators. Flock formation is one strategy from which individuals can benefit from the vigilance of other flock members to reduce their own level of investment in vigilance (Lazarus 1978). Elgar (1989) found a negative relationship between vigilance and group size amongst a range of different mammal and bird species. Geese feed mainly at sites with high food densities (eg stubble fields, Shimada 2002) where the benefits of high intake rates balance interference, and birds gain from shared vigilance.

Several authors have also reported that vigilance investment by an individual within a flock differs according to location and social class. For example, individuals at the edge of a flock would be predicted to be more vigilant because of the greater risk of predation and higher probability of predator detection in these areas (Drent & Swierstra 1977; Inglis & Isaacson 1978). Dominant geese occupy the edge positions and avoid the centre of the flocks (Teunissen *et al.* 1985; Black & Owen 1989). Their rank is ordered according to the number of individual birds (Boyd 1953; Raveling 1970). This research has concentrated mainly on *Branta* spp., eg Barnacle Geese *B. leucopsis*, which forage primarily on grassland (eg Black *et al.* 1992). A few studies have been conducted on *Anser* spp. that forage on grains in rice fields (Lazarus 1978).

Over 80% (60,000 geese) of the Japanese population of the Greater White-fronted Goose *A. albifrons* winter around Lake Izunuma-Uchinuma, northern Japan (Shimada 2002). After the harvest, large compact flocks frequently forage on spilt grain in the rice fields. This allowed a comparison of the levels of vigilance between individuals at the flock edge with those in the centre. In addition, because the flocks comprise family groups and non-breeders (Ely 1993), it was possible to contrast vigilance levels between units of different sizes.

Methods

The study was conducted in rice fields around Lake Izunuma-Uchinuma (38°43'N, 141°07'E), northern Japan, from October to February 1998/99 and October to December 2001 (for detailed information on the wintering geese of this area see Shimada 2002). Greater White-fronted Geese have been protected from hunting since 1971 in Japan (Kato 1984), however some shooting areas, for example for pheasants and ducks, are scattered in goose

foraging areas within 12km of their roosts (Shimada 2003).

The geese fed from sunrise to 1000h and from 1400h to sunset, resting between 1100h and 1300h (Shimada 2002). Undisturbed, stable, circular flocks were observed during the feeding periods. The density of the rice grains, the main food of the geese (Shimada *et al.* 2002), varied between harvesting methods: the density left on the fields after harvesting by combine harvesters was 8.7 times greater than that left by reaping machines (which cut only the stems, Shimada 1999). To eliminate the influence of food abundance on goose behaviour, flocks were sampled only from rice stubbles cut by combine harvesters.

Flocks of over 1,000 geese were selected for observation because the boundary between centre and edge was less well defined in small flocks. Edge birds were sampled at not more than 5m from the outermost band of geese and central birds within 30m of the flock centre. Total flock size was recorded for each set of observations, and for each 100 geese selected randomly from the centre and edge of a flock, the number of vigilant or non-vigilant individuals and adults or juveniles was recorded. Numbers for birds showing 'head up' or 'extreme head up' posture were combined and defined as showing vigilant behaviour (Lazarus 1978). The dark brown to black blotches and bars on the breasts of the adults distinguished them from the uniform breasts of juveniles (Bellrose 1980). These two vigilant postures and two age groups were distinguishable in the field. Vigilant geese were counted in three random locations at the edge and centre of each sample and the proportion of juveniles calculated.

The behaviour of each family member on the edge of the flock was observed, regardless of flock size. When all members of a subgroup, including the two adults, moved in the same direction or attacked another group, the group was defined as a family. Based on the numbers of juveniles present, the geese were divided into five social classes: lone pairs and two parents with one, two, three or four offspring.

The behaviours were classified as follows: feeding, vigilance, locomotion (eg walking), comfort (eg preening and bathing), resting (eg sleeping and loafing), social (eg ceremony) and agonistic behaviour (eg threat and fighting, Ely & Dzubin 1994). The behaviours of each individual were recorded every 30 seconds for 10 minutes, and the percentage of time given to each behaviour was calculated. All field observations were conducted from a car using 10x binoculars, 30x spotting scopes and several hand-held counters.

The relationship between vigilance rate and flock size was tested by Kendall's rank correlation (τ), using data from the edge and centre of different-sized flocks. If the relationship was not significant (n.s.), the data were combined from edge and centre

observations and the Wilcoxson signed-ranks test was used to determine significant differences between the percentages of vigilant geese and individual geese in samples at the edge and in the centre. One-way ANOVA was used to determine differences in the percentage of behaviours of adults or juveniles among social classes. When ANOVA revealed significant differences among the classes (n.s.), post-hoc differences were assessed by Scheffe F. Values presented are means±S.E.

Results

The mean flock size was 2,493±415 geese (n=16 flocks, range 1,000-6,790 geese). There were no significant correlations between vigilance rate and flock size at either the edge or the centre (edge:τ=-0.09, centre:τ=-0.14, both: n.s.).

Greater White-fronted Geese on the edge of the flock spent significantly more time than those in the centre on being vigilant (edge: 28.8±1.7%, centre: 11.6±1.1%, Z=-3.52, n=16, P<0.001, **Figure 1a**). The percentage of juveniles on the edge (21.5±2.2%) was significantly higher than that in the centre (5.9±0.9%, Z=-3.52, n=16, P<0.001, **Figure 1b**).

There were significant differences in the time that adults devoted to vigilance ($F_{4,136}$=25.1, P<0.0001) and feeding ($F_{4,136}$=11.8, P<0.0001) among the social classes (**Table 1**). However, there was no difference in the time allocated to other behaviours (n.s.). Adults without juveniles were the least vigilant (7.2±1.4%). The vigilance of parents increased with the number of offspring, and parents with three offspring were the most vigilant (47.9±5.5%). Contrastingly, the proportion of time spent feeding decreased significantly

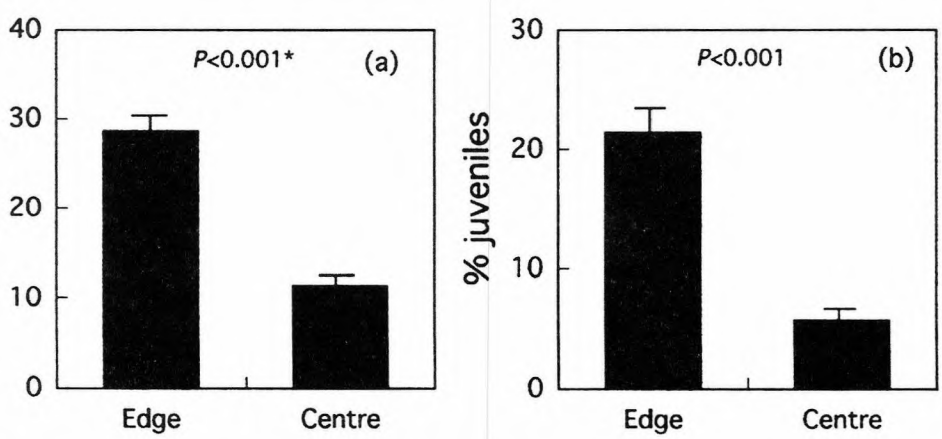

Figure 1. The percentage of vigilant geese (a) and juveniles (b) in a sample of 100 geese at the edges and centre of flocks with more than 1,000 individuals at rice fields around Lake Izunuma-Uchinuma, northern Japan (*: Wilcoxson signed-ranked test).

Table 1. Percentage (mean±S.E.) of time budget allocated to different behaviours in adults and juveniles within social classes at rice fields around Lake Izunuma-Uchinuma, northern Japan. Numbers in parenthesis refer to the number of families observed.

	Behaviour of adults[a]						
Social class	Vigilant	Feeding	Locomotion	Comfort	Agonistic	Social	Resting
0 juveniles (58)	7.2±1.4A	83.9±3.0C	0.8±0.4A	5.9±2.1B	0.2±0.1C	0.2±0.1	1.7±0.8D
1 juvenile (23)	24.0±4.2B	70.7±4.4B	1.1±0.4A	2.7±1.2B	1.0±1.2C	-	0.5±0.4D
2 juveniles (32)	28.6±3.2B	66.7±3.5B	1.4±0.5A	1.6±0.7B	0.7±0.4C	-	1.0±0.7D
3 juveniles (19)	47.9±5.5C	47.5±6.0A	0.9±0.6A	3.2±2.0B	0.1±0.1C	-	0.3±0.2D
4 juveniles (9)	39.8±7.8C	51.0±9.2A	2.5±2.2A	6.2±2.8B	0.5±0.4C	-	-
	Behaviour of juveniles[b]						
	Vigilant	Feeding	Locomotion	comfort	Agonistic	Social	Resting
Combined (83)	8.5±1.6	86.4±2.2	1.3±0.4	3.2±0.9	-	-	0.6±0.4

[a] Means within columns with the same letter were not different (n.s.) in behaviour among social classes by Scheffe F.
[b] Combined data of social classes because there were no differences (n.s.) in behaviour among social classes by one-way ANOVA.

with number of offspring (83.9±3.0% to 47.5±6.0%).

There was no significant difference in the behaviours of offspring among the social classes (n.s., **Table 1**), and they devoted most of their time to feeding (86.4±2.2%).

Discussion

Lazarus (1978) showed a negative relationship between vigilance and flock size. However, there was no significant relationship in this study, although flock sizes were considerably larger. Once the flock exceeded 300 geese, the vigilance rate was almost constant - between 5% and 10% - regardless of flock size (Lazarus 1978), therefore there would be no negative relationship between vigilance and flock size in large flocks such as those in the present study.

Vigilance was higher on flock edges than in the centre (**Figure 1a**), as observed by many studies (Drent & Swierstra 1977; Inglis & Isaacson 1978). Juveniles always followed parents (Ely 1993), and hence the higher proportion of juveniles on the edge of the flocks (**Figure 1b**). Shimada (1999) showed that the density of rice grains is higher at the edge of a stubble rice field than in the centre. After goose flocks land in the centre of a field, they spread out and forage towards the edges. The

geese on the edge, therefore, can exploit the higher food abundance as the flock spreads out towards the field edges. A large flock sometimes extends across several stubble fields. The flock expands from one field into another by moving along the edges of the field in which the food is abundant. Families are dominant over lone pairs and singles and win far more aggressive encounters (Boyd 1953; Gregoire & Ankney 1990). Thus, families would occupy the most food-rich areas as a consequence of agonistic interactions.

The foraging behaviour of the geese on snowy days further supported the theory that families dominated rich food patches. When rice fields were covered with snow and ridges were clear of snow (snow depth c.8cm), geese could forage only on the ridges. The ridges were 20-30cm higher than the surface of the fields and were more thinly covered with wind-blown snow. On 8 January 2002, under such conditions, there were 15.6% juveniles amongst geese feeding on ridges compared with 1.5% overall, based on observations from five different rice fields (T. Shimada, unpublished data); ie families dominated the limited foraging areas available.

In Barnacle Geese, which are of similar size to Greater White-fronted Geese, Black *et al.* (1992) revealed that geese that occupied edge positions obtained a greater energy intake than central birds, despite their increased levels of vigilance. The vigilance levels of the parents on the edge increased more than those of the juveniles (Black *et al.* 1992, **Table 1**). Moreover, the present study showed for the first time that the vigilance levels of the parents varied in relation to the number of offspring (**Table 1**). This means that the energy intake of the parents would differ in relation to the number of offspring. Forslund (1993) reported that in Barnacle Geese parents increased their vigilance when brood size increased because young in larger broods face a higher risk of predation. Increased vigilance levels in the parents would secure the safety of their offspring and then heighten the fitness of the parents. Then, many older offspring (eg one or two years old) accompany their birth family to the wintering area before they breed, and these extended families are more dominant and have better access to limited food and safe roost sites (Ely 1993). On the other hand, the decrease in food intake for parents themselves leads to a shortage of nutrient reserves that would subsequently reduce the chances of survival (Black *et al.* 1991) and breeding success (Ankney & MacInnes 1978; Ebbinge 1989). Therefore, the trade-off between vigilance and feeding in relation to the number of offspring would be one of the important wintertime budget decisions for parents in Greater White-fronted Geese.

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