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Foraging dynamics in goose flocks: the cost of living on the edge

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Abstract. The effects of flock position on the foraging performance of individual barnacle geese, *Branta leucopsis*, were determined by comparing foraging behaviour, vegetation quality and diet of geese at the edge and centre of feeding flocks. Birds on the edge of flocks fed in a hurried fashion compared with centre positions (shorter bouts of foraging) probably because of the increased amount of vigilant behaviour and aggressive encounters. In energetic terms, however, the costs of grazing and vigilance balanced out, so that it was as 'expensive' to feed in either flock position. Geese appeared to obtain more food when in edge positions because they pecked faster and obtained more food per peck as a result of the higher biomass of grass. A series of calculations, which included measures of energy expenditure, gross intake and energetic quality of the food, showed that the net energetic payoff of birds in edge positions was substantially higher than that of those in the centre. The relative merits of taking positions in the flock edge for single geese, pairs and families are discussed. The finding that dominant families were most often in edge positions and avoided the centre, and the fact that families attacked neighbours more often than did any other geese, suggests that they actively attempt to monopolize the best food resource available to flock members which is usually on the edges of the flock.

When animals are foraging in a flock, a range of behaviour is acted out in relation to, on the one hand, the need to obtain an adequate diet and, on the other, the need to monitor the surroundings for potential competitors and predators. The time devoted to such behaviour can have direct consequences for the fitness of each flock member. Different rates of finding food, competition and predation risk may occur in different flock positions. Presumably the relative costs and benefits to the individual determine where that individual is situated within the flock.

A common feature of flock foraging is that animals on the edge of the flock spend more time scanning the horizon and less time eating than individuals in the centre, a relationship documented in many African ungulates (Lipetz & Bekoff 1982; Underwood 1982), white ibises, *Eudocimus albus* (Petit & Bildstein 1987), woodpigeons, *Columba palumbus* (Murton et al. 1971), starlings, *Sturnus vulgaris* (Jennings & Evans 1980; Keys & Dugatkin 1990), and a variety of goose species (Diamond & Lazarus 1974; Drent & Swierstra 1977; Inglis & Isaacson 1978; Inglis & Lazarus 1981).

Two of these studies are particularly revealing as to the nature of the energetic costs and benefits associated with different flock positions. Murton et al. (1966, 1971) showed that subordinate woodpigeons in the edge positions suffer in terms of lost foraging time. Edge birds obtain fewer fresh clover leaves, take fewer pecks per minute and are substantially lighter than centre birds. They are also more vulnerable to attacks from hawks (Kenward 1978). The white ibis study, on the other hand, showed virtually no difference in foraging costs nor in the relative numbers of prey captures by individuals in edge and centre positions. Ibis feed on live prey that hide when disturbed by outer edge birds (Petit & Bildstein 1987).

Within goose flocks, dominant birds occupy the edge positions and avoid the centre (Teunissen et al. 1985; Black & Owen 1989a). Owing to the pattern of food depletion, edge birds have access to a larger amount of vegetation (Prop & Loonen 1988; Black & Owen 1989a). In addition to showing higher rates of vigilance and having less time to feed, individuals on the edge spend more time in aggressive encounters (Inglis & Isaacson 1978). Based on these

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relationships in goose flocks, Drent et al. hypothesized that, in spite of the increased competition and having less time to graze, the counter-balancing advantage of access to more and better quality food results in dominant geese preferring the edge (Drent & Swiestra 1977; Drent & Van Eerden 1980; Prins et al. 1980). Calculating whether or not animals at the edge actually obtain more and better food has proved difficult (Krebs & Davies 1987, page 123).

Prop et al. (1984) painstakingly quantified the feeding success of successive barnacle geese, *Branta leucopsis*, as they visited patches of tundra vegetation. By counting the number of seed heads and flowers before and after the goose visits, they found that the first goose removed 32% of the food items and visited 63% of the *Saxifraga* plants present. On the wintering grounds, Prop & Loonen (1988) watched a flock of 67 brent geese, *Branta bernicla bernicla*, pass through a patch of salt marsh, and quantified the depletion rate of *Plantago* plants. The first eight geese removed 50% of available leaves. The last leaves were removed by the 59th goose, leaving none for the last eight birds. Clearly, front edge birds are at an advantage, at least in terms of getting first pick of the available food items (also see Prop & Deerenberg 1991). However, it has not yet been determined whether or not this 'food finding' advantage is substantial enough to outweigh the increased costs of being on the edge, i.e. the increased vigilance and competition.

In this paper we present a selection of results from an ongoing study of barnacle geese, in relation to foraging performance in different flock positions. Barnacle geese are herbivores and generally spend the non-breeding season in flocks of 1000 or more individuals (Ebbinge et al. 1975; Black & Owen 1988). Revisiting areas at frequent intervals reduces the biomass and changes the composition of the vegetation (Owen 1972; Prins et al. 1980; Black & Owen 1989a). There are several types of social units within goose flocks. Their dominance rank is ordered according to the number within the unit; families beat pairs and pairs beat singles (Boyd 1953; Raveling 1970). Pairs and family groups work as a team where the males protect females and parents protect offspring from nearest neighbours and potential predators while they feed (Black & Owen 1989a, b). Single birds have a greater competitive burden (Black & Owen 1984). The breeding performance of pairs depends on the females' fat reserves (Ankney & MacInnes 1978; Ebbinge 1989) which are related to their foraging success, which itself depends on their mates' ability to protect their foraging paths (Teunissen et al. 1985; Lamprecht 1989). Similarly, we believe that the survival of offspring depends on parental protection in the first year (Scott 1980a; Black & Owen 1984, 1987, 1989b).

We examine the trade-off between feeding performance and 'protection' behaviour (vigilance and defensive efforts), of 'protectors' (males in pairs and parents), the 'dependants' (females in pairs and offspring) and singles (orphan juveniles and unpaired adults) in different situations within foraging flocks. We test the hypothesis that the geese foraging on the edge obtain a higher energetic payoff than centre birds in spite of the increased demands of non-foraging activities. In the remainder of the paper 'paired' birds refer to birds that are not parents while the subject of study. 'Parent' birds were accompanied by young when the observations were made. Three specific questions are addressed. (1) Is it energetically more expensive to be on the edge? (2) What is the net benefit of edge and centre positions? (3) How do the costs and benefits of flock foraging differ between the social units?

METHODS

During autumn and winter, the geese visit fields in front of permanent hides at the Wildfowl & Wetlands Trust Centre on the Solway Firth in south-west Scotland; the population (11 400 individuals in 1987) spend 50% of the wintering period at or near this managed site (Owen et al. 1987). The data presented in this paper were collected between 1976 and 1987. Between 22 and 30% of the birds were marked with engraved colour leg-bands readable at 250 m. The observations were made while the birds foraged over 10 fields, each between 5 and 15 ha. The vegetation consisted mainly of *Lolium perenne*, with smaller amounts of other grasses and clover, *Trifolium repens*.

Time Budgets and Energy Expenditure

Goose flocks varied in size depending on the number of birds present, but generally the edge birds were 10–100 m from the centre of the flock. The edge of the flock was defined as the outermost band of geese, not more than 5 m from the outermost birds. This incuded the birds that were first to exploit available vegetation, e.g. leading and side edges of an outwardly moving flock. Trailing edge birds were not considered. Centre birds were chosen from the main bulk of the flock, at least 15 m from the periphery. These birds followed the edge birds over the same ground. Flocks of fewer than 400 birds were excluded; smaller flocks behave differently (Inglis & Lazarus 1981). Time budgets of focal birds were recorded as a commentary into a cassette recorder. These were later transferred through an event recorder to a computer for analysis. Individually banded focal birds were watched for as long as possible (usually 10 min). All head-up postures (head raised above the top of the bird's back) while standing still represented vigilance time (Lazarus & Inglis 1978). Feeding time comprised a head-down posture while the bird was rapidly grazing. Aggressive encounters were associated with defending or maintaining a foraging pathway as the geese were continually walking while grazing. The outcome of an encounter was determined by which bird changed direction after the encounter. Walking bouts (when head-up) in between foraging and aggressive bouts were recorded. Since we predicted that time budgets would be more costly in edge positions (see above) the rejection region for testing time budget data was one-tailed (Siegel 1956). All other tests are two-tailed.

We converted time budgets to energy expenditure per h in different flock positions using the formula

$$\text{energy consumed (kJ/h)} = (\text{cost of the activity} \times \text{basal metabolic rate}) \times \text{proportion of time (min/h)}$$

Based on Wooley & Owen's (1978) measurements on black duck, *Anas rubripes*, we estimated the values for the cost of goose activities (as multiples of the basal metabolic rate) at 2·1 for vigilance, 2·0 for feeding while periodically stepping, and 1·7 for active walking. We assumed that aggressive encounters cost a goose 6·4 times the basal metabolic rate which is 31% of the difference between the values for wing-flapping (3) and flying (14 after Koplin et al. 1980)+3; 31% of aggressive encounters involved physical contact or chases while other encounters involved more subtle threat movements ($N = 2056$ encounters in Black & Owen 1988). Basal metabolic rate for an average female barnacle goose weighing 1650 g during the winter is 4·5 kJ/h (calculated from the equation in Lasiewski & Dawson 1967). Similar values were estimated for single and family goslings (1575 g for males/females = 4·3 kJ/h, single adults (1760 g for males/females = 4·8 kJ/h), paired males and parent males (1875 g = 5·1 kJ/h) and paired and parent females (1650 g = 4·5 kJ/h). All weights were measured during mid-winter (November/December).

Individual foraging performance of females attended by a mate and no offspring was monitored more intensively. Peck and step rate were timed (time for 100 pecks and for 20 steps). Only individually ringed females were chosen; sex was determined cloacally at banding (Owen 1980). The intervals between successive droppings were also timed with a stopwatch (Owen 1975). These data were collected in pairs, alternately between the edge and centre positions. Vegetation height was measured in the evening after each observation session with a light cardboard disk fitted over a smooth rod marked in centimetres. An inconspicuous grid of 20 × 20 m was marked with stakes in three fields so the grass height near the focal birds could be determined, as a mean of 20 measurements.

Intake Rates and Energy Gained

We estimated digestive efficiency by assessing the relative amounts of grass consumed and present in droppings using the marker-substance method (Ebbinge et al. 1975; Drent et al. 1979). Fresh grass and droppings were collected periodically through the season from fields where the geese had been feeding for 4 h or more. Samples were dried overnight at 90°C. Using the methods described by Allen et al. (1974) the crude fibre content of the grass and droppings was determined.

The apparent (dry matter) digestive efficiency was calculated using the formula

$$\% \text{ digested} = \left(1 - \frac{\text{proportion of crude fibre in grass}}{\text{proportion of fibre in droppings}}\right) \times 100$$

and the net energetic intake was estimated by the formula

$$\text{net energetic intake (kJ/h)} = (\text{food intake} \times \text{energy value of food}) - (\text{throughput of food} \times \text{energy value of droppings}) - (\text{energy expended})$$

Diet and Digestibility Index Assessments

Droppings were collected using the grid to map the location of centre and edge birds. Sets of 30 edge and centre droppings were collected and the

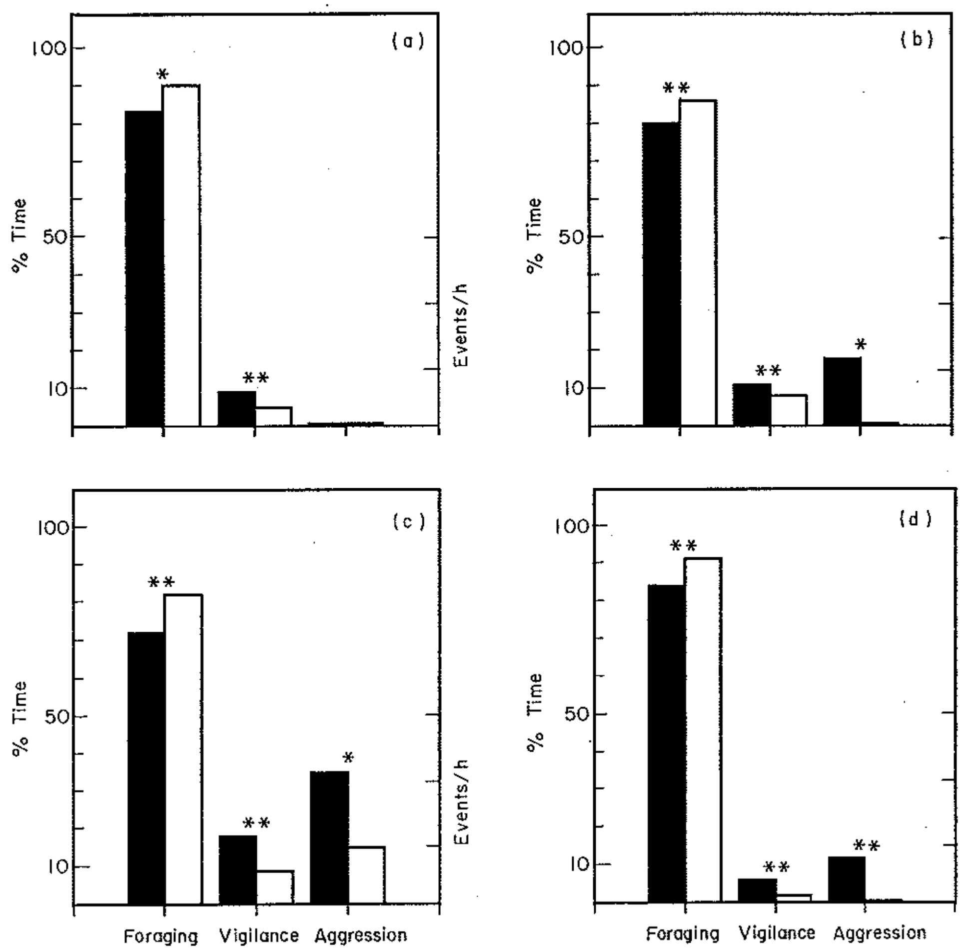

Figure 1. Relative effort put into foraging, vigilance and aggressive encounters in the edge (■) and centre (□) positions for (a) paired males (edge and centre $N=32$, 33) (b) parent females (162, 44) (c) parent males (169, 43) and (d) family goslings (168, 52). $^*P<0.01$; $^{**}P<0.001$; one-tailed Mann–Whitney U- tests (Siegel 1956).

proportion of different grass types was assessed through the identification of 50 cell wall fragments using a gridded lens (Owen 1975). An index of nutrient availability from ingested plants was assessed as the proportion of fragments appearing in droppings with the leaf fractured so that the two surfaces had been separated (the fragmentation index of Owen 1976).

RESULTS

Time and Energy Expenditure

Feeding, vigilance and walking

The most obvious theme that emerged from the comparison between edge and centre behaviour was that the protector classes (paired males and parents) spent significantly more time in a head-up scanning posture and less time feeding in the edge positions (Fig. 1). The time budget of single goslings, single adults and paired females showed no significant differences between edge and centre. Family juveniles, thought of as dependants, were an exception in that they spent significantly more time head-up and less time feeding on the edge than in the centre. All classes walked similar amounts in both flock positions.

Encounter rates

While in the edge position all family members defended their positions significantly more than in

Table I. Estimates of hourly energy expenditure for different classes of geese that were foraging within the edge and centre of a flock

	Energy expenditure (kJ/h)	
Bird class	Edge of flock	Centre of flock
Single goslings	33·08	32·95
Single adults	37·64	36·59
Paired female	36·80	36·26
Paired males	40·32*	41·07
Parent females	36·76	36·05
Parent males	40·78	40·07
Family offspring	33·29	33·87

The time spent in agonistic encounters were multiples of the median number of bouts per hour where encounter duration ranged between a mean of 2 and 6 s (from Black & Owen 1989a) depending on the goose class that was involved.

*This does not account for the fact that paired males were displaced from their foraging path by dominant neighbours significantly more while in edge than in centre positions; the median value was 0.

the centre (Fig. 1). All other classes had similar rates of supplanting neighbours. Paired males were supplanted more often when feeding on the edge than in the centre (Mann–Whitney *U*-test $z=0{\cdot}174$, one-tailed test, $P<0{\cdot}05$).

Energy expenditure

Despite significant differences in percentage time spent feeding, being vigilant and in aggressive encounters in several of the social classes, overall energy expenditures were similar in both edge and centre positions (Table I); in all cases differences in costs were less than 3%, amounting to 1·05 kJ/h.

Type and Quality of Diet

We categorized 2009 cell wall fragments into five classes: *Lolium perenne*, *Trifolium* sp., *Phleum* sp., grass sheath and a few unidentified grasses. Although *Lolium* was the predominant food for both edge (89%) and centre (92%) birds, their overall diets were significantly different ($\chi^2=23{\cdot}98$, $df=4$, $P<0{\cdot}001$). The largest contribution to the test statistic was clover (5% in edge and 2% in centre samples) and sheath (0·1% in edge and 2% in centre samples). Clover is the most nutritious plant available to the geese at this study site (Owen & Kerbes 1971) and the sheath (the part of the leaf enclosing emerging shoots) is a skeletal structure, low in cell contents and of low nutritive value (Boudewijn 1984).

We compared 55 samples from the edge of the field and 57 from the centre with regard to the fragmentation index. A significantly higher proportion of the fragments in the edge samples was fractured ($\bar{X}\pm\mathrm{SE}=55\pm2\%$) than were those from centre samples ($48\pm2\%$; Mann–Whitney *U*-test $z=2{\cdot}2$, $P=0{\cdot}02$).

Dry weights of droppings from the edge and centre were similar (edge droppings: $\bar{X}\pm\mathrm{SE}=0{\cdot}68\pm0{\cdot}03$ g, $N=143$; centre: $0{\cdot}67\pm0{\cdot}03$ g, $N=131$).

Foraging Performance

Based on the edge and centre observations of paired females with no offspring ($N=29$), we found no significant differences in the mean pecking rate (edge: $\bar{X}\pm\mathrm{SE}=137\pm4$ pecks per min; centre: 130 ± 4), stepping rate (edge: $\bar{X}\pm\mathrm{SE}=11{\cdot}0\pm0{\cdot}6$ steps per min; centre: $10{\cdot}7\pm0{\cdot}6$) or dropping interval (edge: $\bar{X}\pm\mathrm{SE}=263\pm10$ s; centre: 269 ± 10 s). It appears that observations that were made in similar or overlapping grass heights confounded the pairwise comparisons; grass height did not differ significantly between edge and centre observation locations (edge: $\bar{X}\pm\mathrm{SE}=3{\cdot}75\pm0{\cdot}23$ cm; centre: $3{\cdot}26$ cm $\pm0{\cdot}17$ cm; *t*-test $=1{\cdot}71$, $df=38$, NS).

A two-way analysis of variance between grass height and flock position revealed that each of the feeding parameters varied significantly with grass height and that there was no difference between edge and centre positions (Fig. 2). Although differences were not significant the trend in each case was for edge birds to take more bites, walk faster and obtain more food particularly in the highest vegetation; longer dropping intervals indicate a higher intake and better food quality (Teunissen et al. 1985; Prop & Vulink, in press). It appears that geese on the edge graze faster because, except for single adults, they have significantly shorter bouts of uninterrupted feeding time (Table II).

When the data were lumped together the grass height effect became clearer. Pecking and stepping rates were negatively correlated with grass height, although r^2-values were rather small (pecks/min $r^2=0{\cdot}24$, $df=37$, $P<0{\cdot}01$; step rate $r^2=0{\cdot}14$, $df=37$, $P<0{\cdot}02$). Dropping interval was positively correlated with height of the grass being grazed by the focal birds; birds produced fewer droppings in taller grass ($r^2=0{\cdot}43$, $df=15$, $P<0{\cdot}01$).

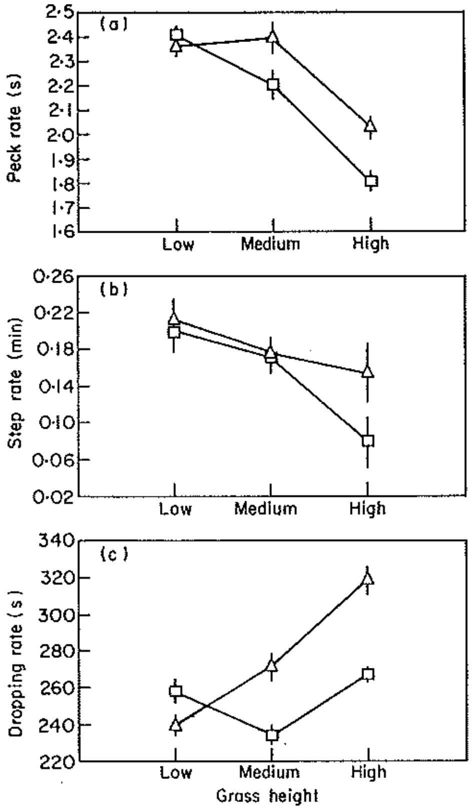

Figure 2. Foraging performance of paired females in different grass heights: low (2·1–3·3 cm), medium (3·4–4·4 cm) and tall (4·5–5·8 cm) for edge birds (△) and centre birds (□). (a) Pecks/s $N=38$, ANOVA Position F-ratio $=$ 0·92 NS, Grass height F-ratio $=4·79$, $P<0·02$; (b) steps/min $N=37$, ANOVA Position F-ratio $=1·96$ NS, Grass height F-ratio $=4·50$, $P<0·02$; (c) droppings/s $N=15$, ANOVA Position F-ratio $=1·06$ NS, Grass height F-ratio $=1·11$ NS. The vertical bars show standard errors.

Estimating Gross and Net Energetic Payoff

Table III lists the variables necessary to estimate energetic payoff for paired females in mid-winter (November and December). The most striking suggestion from this exercise is that, even though the overall energy expenditure was virtually the same for edge and centre females, the combined effect of several subtle variables involving the quality of food and intake rates in edge positions (where grass was taller and of better quality) did amount to a substantial difference in net energetic intake rate. The final calculation suggests that females in edge positions gained about 27% more energy per foraging-hour than females remaining in the centre.

We were unable to detect a difference in intake between edge and centre paired samples, perhaps because the mean grass heights between the two sets of observations were not substantially different (only 0·5 cm). We believe, however, that the average difference in grass heights where edge and centre birds forage will eventually amount to a significant difference in the quantity of food that edge and centre birds obtain. By comparing the means in pecks/min at the three grass heights in Fig. 2, we estimated that edge birds took on average 6·6 pecks/min more than centre birds. This amounts to 394 bites/h more than birds in the centre.

DISCUSSION

Flock Position and Energy Expenditure

Four of the seven social unit types spent significantly more time being vigilant and less time grazing on the edge than in the centre. All family classes attacked neighbours more and paired males were themselves attacked more when in the edge position. However, the difference in the estimated energy expenditure in the two flock positions was negligible for all social units (2·7% variation was the extreme); for five of the seven unit types it was slightly more costly to live on the edge. It appears that the trade-off between the costs of foraging and the costs of vigilance compensate for each other, assuming as we did that foraging and vigilance costs were very similar at 2·0 and 2·1 times basal metabolic rate, respectively.

Flock Position and Net Payoffs

Because goose flocks land in the centre of fields and graze towards the edges, the centre of fields are depleted of food sooner than the edges. Birds on the edge of the flocks will, therefore, be first to exploit the higher biomass as the flock moves towards the field edges. Perhaps this is why the dominant social units (e.g. families) invest so much effort in defending their space when they are in edge positions; parent males in particular are involved in most encounters (Black & Owen 1989a).

A goose that forages in edge positions could obtain substantially more food and energy than centre birds, in spite of its reduced feeding time and increased vigilance and competitive demands

Table II. Mean durations of uninterrupted foraging bouts of geese in the edge and centre of the flock

	Foraging bout durations (s)					
	Edge		Centre			
	Mean	(Range)	Mean	(Range)	ANS*	*P*
Single goslings	18·2	(7·9–84·3)	28·7	(11·8–157·5)	2·04	0·021
Single adults	22·5	(15·2–417·4)	37·9	(0·7–327·7)	61†	>0·1
Paired females	27·9	(13·6–159·3)	49·6	(11·6–277·5)	1·61	0·054
Paired males	21·3	(4·8–326·5)	25·6	(12·8–135·2)	1·63	0·052
Parent females	24·2	(2·6–642·5)	40·8	(12·2–308·8)	4·19	<0·001
Parent males	17·9	(1·9–115·1)	25·1	(7·6–100·4)	3·99	<0·001
Family offspring	36·9	(13·2–361·3)	52·4	(12·2–571·0)	2·42	0·008

Sample sizes for edge and centre respectively were single goslings 22, 15; single adults 8, 18; paired females, paired males 32, 33; parent females 162, 44; parent males 169, 43; and family goslings 168, 52.

*ANS: approximate normal statistic from one-tailed Mann–Whitney *U*-tests for large samples (Siegel 1956).

†One-tailed Mann–Whitney *U*-test statistic value for smaller samples (Siegel 1956).

Table III. Estimates of daily dropping production and net energy intake for edge and centre paired females per hour of foraging

	Edge birds	Centre birds
Mean dropping interval (s)	269	263
Dropping production/h	13·28	13·68
Mean dropping weight (g)	0·68	0·67
Droppings (g)	9·10	9·17
Retention rate (%)	27·70	27·70
Adjusted retention for edge birds*	29·60	—
Total intake (g)†	12·93	12·68
Adjusted intake for edge birds (bites/h)‡	394	—
Mean bite size (g)§	0·002057	—
Adjusted total intake (g)	13·74	—
Energestic value of grass (kJ)	18·30	18·30
Total energetic value of grass intake (kJ/g)	251·44	232·04
Energetic value of droppings (kJ)	15·50	15·50
Total energetic value of droppings (kJ/g)	141·05	142·14
Gross energetic intake (kJ/h)**	110·39	89·90
Energy expenditure (kJ/h)	36·80	36·26
Net intake/h of foraging (kJ)††	73·59	53·64

*Edge birds had a 7% higher assimilation rate (from fibre analysis).

†Edge 9·10/(1 – 0·704 retention) = 12·93 g; centre 9·17/(1 – 0·723 retention) = 12·68 g.

‡Edge birds obtained 12 more bites/step than centre birds.

§From Wells (1980).

**Edge 251·44 – 141·05 = 110·39 kJ; centre 232·04 – 142·14 = 89·90 kJ.

††Edge 110·39 – 36·80 = 73·59 kJ; centre 89·90 – 36·26 = 53·64 kJ.

(Table III). The differences might accrue from two subtle disparities between flock positions. First, the diets on the edge consist of plants that are 7% more nutritious in terms of how readily digested they are. This is partly due to the species composition of the diet; edge birds obtain more easily fragmented clover plants and less fibrous sheath. Second, because of the higher demands on edge birds' time budgets they tend to peck slightly faster than centre birds, although not significantly so (Fig. 2a).

On Dependants, Protectors and Singles

The relative ability to maintain a chosen flock position will depend on rank. In other words, the larger units, the families, probably find it easier to continue to forage along a particular pathway or in a particular flock position than do pairs or singles. Indeed, we know that families spend most of their time in edge positions and that they spend more time threatening and chasing neighbours than all other classes (Black & Owen 1989a). We also know that in goose families most of the aggression and vigilance involves the parent males (Schindler & Lamprecht 1987; Black & Owen 1989b; Sedinger & Raveling 1990). In addition, when males join the encounters that paired females, parent females and family juveniles are involved in the chances of success are substantially higher (Black & Owen 1989a). The 'dependant' classes therefore have much more time to feed than protectors (Scott 1980a, b; Black & Owen 1989b; Sedinger & Raveling 1990). A field index of how fat the geese are (the abdominal profile index) has revealed that females are fatter than their mates throughout the wintering period (Owen 1981).

A complementary study on brent goose foraging offers an insight into the relationship between dominance and flock position. Teunissen et al. (1985) identified the aggressive status of the first 23 individually marked pairs in a flock that passed in front of the observation post. The males in the first 19 pairs won between 46 and 73% of their encounters whereas the last five birds won only 6%. Teunissen et al. (1985) also showed that females' foraging success is correlated with the males' aggressiveness.

When do the 'protector' males find time to obtain adequate food for themselves? Our calculations show that females can indeed benefit from foraging in the edge position. Presumably, however, a female could not do so if her mate was not there to protect her. Males may not experience the same feeding advantages that females do in the edge positions, although some pairs appear to take turns in protection behaviour (Sedinger & Raveling 1990; J. Black & M. Owen, unpublished data). We suggest that, owing to the increased demand on males when in the edge position, they are unable to obtain enough food and therefore have to seek a more profitable situation from time to time. Males may obtain most of their food during the limited time that they are in the centre of the flocks: very rarely do geese land at the edge of the flock but families that land in the centre soon move to the edge (personal observation). We often witness extremely vigilant fathers foraging rapidly as soon as they walk inside the flock perimeter. Unlike paired females, paired males forage significantly more in the centre than on the edge (Fig. 1). These males would be able to treat the centre position as a refuge, not because their mates lessen their vigilance and competitive burden, but because the risk of predation is smaller and the threat from neighbours is less. Centre birds presumably capitalize on the vigilance of other flock members (Inglis & Lazarus 1981). Paired males would find it least beneficial to take up the edge position where they are more vigilant, feed little and are rebuffed by the more dominant families that are found there. On the other hand, however, they may benefit because their females can then forage the best foods (Lamprecht 1989). Similarly, the overriding payoff that shapes a male parent's behaviour in the flock edges may be the substantially better intake rates of all the members in his family (Black & Owen 1989a).

The relative time budget of family juveniles in different flock positions was similar to that of their parents; they fed less, attacked more and were more vigilant in edge than in centre positions. It appears that goslings spend a proportion of their time helping the family to maintain the position in the edge of the flock. By aiding the parents in this way, benefits are shared by all family members which may increase the gosling's fitness as well as the parents' future reproductive success (Black & Owen 1989b).

Single juveniles and single adults are less than half as vigilant as most other classes and almost never initiate agonistic encounters. They are also displaced more than all other classes (Black & Owen 1984, 1989a). In spite of this, single juveniles spend 52% of their time on the leading edges of the flocks (Black & Owen 1989a) either to obtain the best foods or to try to regain a position within a family (Black & Owen 1984). Because they are often displaced by neighbours, their strategy is apparently one of not fighting back and maximizing foraging time.

We have argued that the social units that occupy edge positions obtain more food than centre birds and are thus better able to meet their daily energy requirements. This is primarily due to the 'first come, first served' situation; edge birds get first choice of foods and feed in areas of higher biomass. Our data on abdominal fatness indicate that feeding in optimal habitats may result in birds departing on migration in better condition (Black et al. 1991; unpublished data) which subsequently increases their chances of survival during migration (Owen & Black 1989) and of breeding successfully in the summer (Ebbinge 1989; Black et al. 1991). Those geese that take advantage of the edges of flocks may also elevate their chances of surviving and reproducing, thus providing a strong selective advantage for flock position in goose flocks.

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