

The mixed blessings of compulsory group living

Goose flocks impose
their own rules

Anyone who has spent much time watching wild geese wonders what's wrong when a solitary goose is spotted, so rarely do geese stray from their flock. Goslings are born into a complex social order and will normally spend their entire lives as part of a group. How can an individual balance out its personal costs and benefits in such a competitive lifestyle? Let's take a look at two experiments that examined the pros and cons of flock living, one on the spring staging sites in the Netherlands, the other on the breeding grounds in Spitsbergen.

In winter and early spring, brent geese (*Branta bernicla*) and in some sites barnacle geese (*B. leucopsis*) heavily graze cultivated pastureland on the Dutch Wadden Sea islands. At peak times on Schiermonnikoog in the eastern Dutch Wadden Sea around 6,000 barnacle and 3,000 brent geese can be found foraging on a 290-hectare area of reclaimed grassland (polder) managed for dairy cows. Spring growth on these fertilised pastures is obvious as early as February and you might expect the flocks of geese to remain on the farmland while the cows are kept indoors until May. But the number of geese on the pastures has usually decreased dramatically by March, with most of the geese moving to the adjoining salt marsh while the remaining birds cluster together in a small area. This contradictory trend (decreasing use by the geese as grass production increases) started to make sense when we realised that although the grass biomass was increasing, its quality (nitrogen content) was decreasing.

Experiments with captive brent geese

helped us solve this paradox (Bos et al. 2004). We presented captive geese at the Schiermonnikoog field station with grass sods then measured their intake rate. We found that the intake rate of the geese actually declined when confronted with a taller sward (Fig. 34-2A) and from a nutritional point of view this problem was accentuated by the lower quality of the taller shoots (Fig. 34-2B). Unless the grass was kept to 8 centimetres or less, the small bills of brent and barnacle geese effectively took them out of the picture as they were unable to manage the taller shoots. On some Wadden Sea islands (Ameland and Texel) sheep graze the pastures keeping the sward at around 6 centimetres and geese continue to graze these areas until May. Were the geese being forced out of the Schiermonnikoog polders because they were unable to keep the sward short enough on their own?



The flock as a co-operative mowing machine

A large-scale experiment designed to manipulate goose usage confirmed our suspicions (Bos & Stahl 2003). In 2000 and 2001 the authorities in co-operation with the farmers instituted a ‘disturbance-free’ regime (no deliberate goose scaring and agricultural fields were ‘out of bounds’ to the locals taking part in the traditional hunt for lapwing eggs until after 4.30 p.m.). The idea was to minimise losses to the farming community by allowing the geese to concentrate in a portion of the polder (Fig. 34-1), rather than by trying to drive the geese off with flares, flags, scarecrows, or even people on bicycles, as had been the practice.

We counted the number of geese on the polder and the salt marsh every fortnight and then compared this to the number of geese that had been present at these sites in the previous three springs, when the geese had been disturbed (Fig. 34-3). Counting the geese on both the polder and the salt marsh allowed us

Figure 34-1
Flock of brent geese in the polder on Schiermonnikoog.

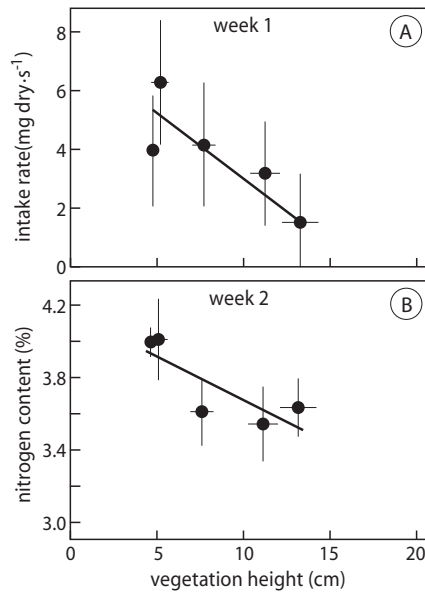


Figure 34-2
(A) The intake rate of captive brent geese (mg dry matter per second feeding time) measured on grass sods of various canopy height declines when confronted by longer shoots. (B) The more mature swards are less nutritious (percent nitrogen content) so do not compensate for the lower intake rate (from Bos et al. 2004).

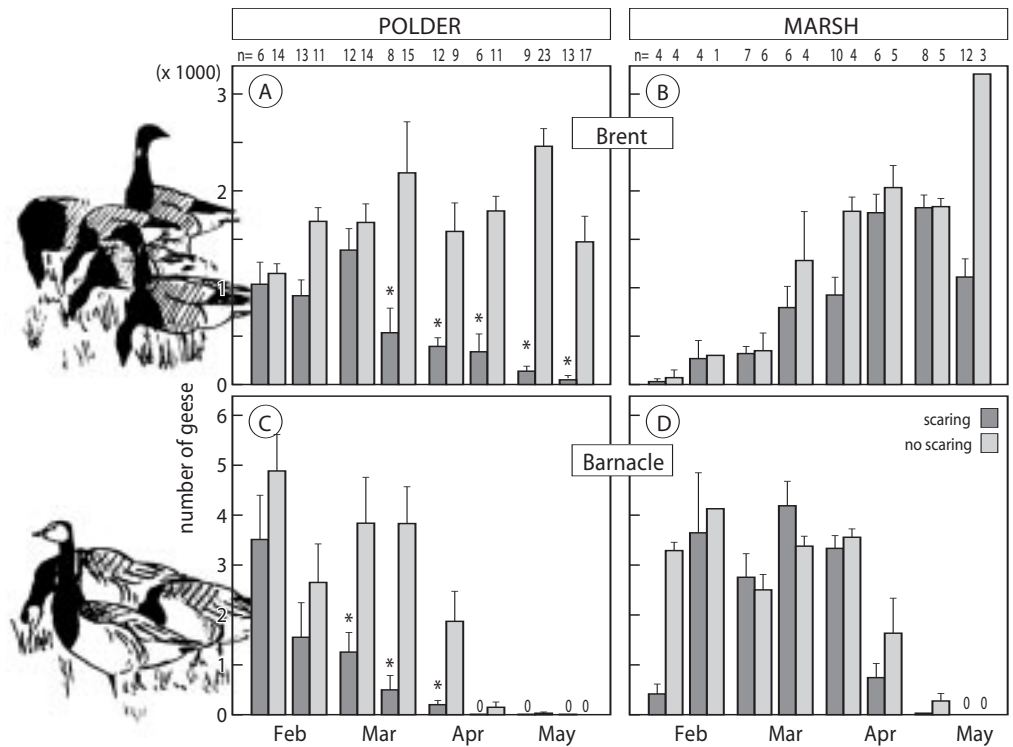


Figure 34-3
Fortnightly counts of brent (A and B) and barnacle geese (C and D) on Schiermonnikoog in spring in the polder (left) and on the salt marsh (right). In three seasons the geese were deliberately disturbed (scaring), while in two seasons the geese were protected from human disturbance (no scaring; from Bos & Stahl 2003).

to assess changes in goose visitation to the island as a whole. The barnacle geese kept using the agricultural fields for a much longer period when they weren't disturbed and the counts showed that the total number of geese staging on Schiermonnikoog in March practically doubled in the disturbance-free years. There is considerable interchange with the adjacent mainland and it appeared that the undisturbed grassland was acting as a goose-magnet! Results for the brent geese were even more spectacular. Large numbers continued to graze the pastureland right until departure for the Arctic in late May without affecting the numbers using the salt marsh. The total staging population on Schiermonnikoog had doubled during the disturbance-free years!

In a disturbance-free season the geese concentrated their foraging in the best corner

of the polder as spring progressed – in March these were mixed flocks of barnacle and brent but by April only brent geese remained (Fig. 34-3). This corner was the area near our field station with the least disturbance, nearest to drinking water, and where grass growth commenced relatively late in the season. It should be noted that the higher goose densities were due to the consistent presence of the geese (observed on 80 percent of the counts) rather than ever-increasing numbers. When we measured the grass height in the goose 'hot spot' it turned out that the geese had managed to keep the grass in this area below 5 centimetres throughout May, in sharp contrast to the fields that they had abandoned where the grass was already 15 centimetres high. So when they were free of disturbance the brent geese were capable of concentrating their grazing in one part of the polder, thus keeping the grass at the growth stage best suited to their own grazing abilities.

Whether even more geese could have been accommodated given tighter control

over human interference remains unanswered, but this experiment successfully demonstrated just how effective flocks of geese can be as a mowing machine when left undisturbed. This form of self-management is only feasible in a flocking species where the ‘mowing machine’ can be implemented at an appropriate scale while the many eyes of the flock watch for disturbances with minimal time costs overall. The larger the flock, the lower the time each individual flock member needs to spend on the alert, and in this sense being the lookout is a shared cost, while keeping the sward short (and the grass in an active growth phase) is a shared benefit.

Thanks to Bart Ebbinge’s goose ringing scheme (Chapter 38), observations of ringed geese on the polder gave us some idea of where the ‘extra geese’ were coming from in the disturbance-free years. There was also an observation tower on the salt marsh that was manned daily allowing us to compare the history of the salt marsh and pasture birds. As in previous years, the salt marsh brent were mainly ‘old hands’ that we had regularly observed in the same place before (25 of the 32 ringed birds identified, almost 80 percent). An average of 74 percent of the ringed salt marsh geese were resighted the next year, indicating a high degree of site faithfulness. In contrast, 16 of the 28 individuals spotted on the pasture had never been seen on the island before. Eight of these ‘immigrants’ had been seen staging on the adjacent mainland shore in previous years, and other Wadden Sea islands accounted for three more (one goose each from Texel, Terschelling and Ameland). A staging history was lacking for the remaining five ‘new’ birds. None of the individuals recorded at our salt marsh site was observed on the pasture in May during our study (1997–2001). The information provided by the ring reading supports our conclusions from the goose counts that the extra pasture birds in 2000 and 2001 were immigrants, new to the island. Apparently there is a ‘floating contingent’ of geese that shop around for a better staging site than that used in the previous year, and our undisturbed pastureland suited their requirements.

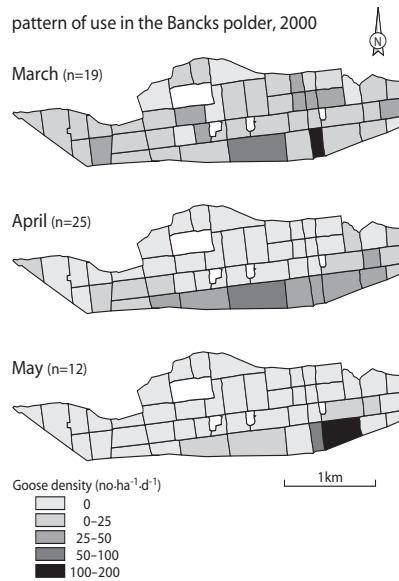


Figure 34-4 Maps of the average density of geese (both brent and barnacle geese in March, only brent in April and May) on the polders of Schiermonnikoog in spring 2000 (a disturbance-free year). The number of counts each month is shown (from Bos et al. 2004).

We would never have made these discoveries without the ‘disturbance-free’ experiment, and we consider ourselves lucky to have been working on Schiermonnikoog at that time.

The social ladder

Dominance relationships develop in goose groups, just as they do in other groups of long-lived social animals. If individuals are recognisable (as the geese that wear inscribed leg rings are) you quickly realize that some birds consistently win and others do less well when feeding together. We assume that the geese themselves recognise one another by their calls and facial characteristics. By keeping track of conflicts you can assign a ‘dominance score’ to each marked bird (the percentage of interactions won by the focal bird when divided by the total number of conflicts in which the bird participated, regardless of whether the opponent was marked or not).



Figure 34-5

Barnacle geese in their moulting habitat on Spitsbergen: the flock has withdrawn to the safety of the tundra lake after a disturbance (possibly a fox raid).



Figure 34-6.

The set-up with the enriched vegetation plots on Spitsbergen showing the temporary fencing.

During the annual moult on the Arctic tundra, geese are extremely vulnerable to predation because they drop their primaries (the flight feathers) simultaneously and temporarily lose the ability to fly (Fig. 34-5). Throughout this time, unrelated geese flock together in very restricted areas and face intense competition when foraging. We concentrated on one such flock of barnacle geese at Ny Ålesund (Spitsbergen) during their moult and tried to relate the observed dominance scores to the individuals' characteristics as determined when caught in the moult roundups (Chapter 7). There had already been annual roundups in this area for many years and, as both goslings and yearlings can be distinguished from adults in the catches, we had quite a few ringed birds of known age in the flock (all the way up to 13 years old).

As you might expect, high-ranking geese were generally paired, large, old and heavy. Since body mass and age are statistically impossible to separate in our data, the simplest formulation is to emphasise status (being paired as opposed to single) and age as the main contributors to high dominance. We wanted to find out if these high-ranking geese were heavier because of their ability to

'corner' the food supplies, and if so, why the less dominant individuals remained in this particular group. Why not go off on their own?

Subordinates lose the plot

To find out what happens when the goose flock entered areas rich in food we created some ourselves. We selected four 2 x 2 metre plots of mossy turf where shoots of the Arctic grass *Poa arctica* (a favoured goose food) protruded, and temporarily kept the birds out by erecting a fence. To enhance the difference between the fenced areas and the surroundings we applied a nitrogen-based commercial fertiliser on the plots then left the enriched patch to grow free of any grazing for a month. At the end of this time we crawled into our nearby hide and as the flock approached we opened the enriched patch by tugging on a rope connected to a sled-like fencing arrangement (Fig. 34-6). The geese accepted these somewhat unorthodox meth-

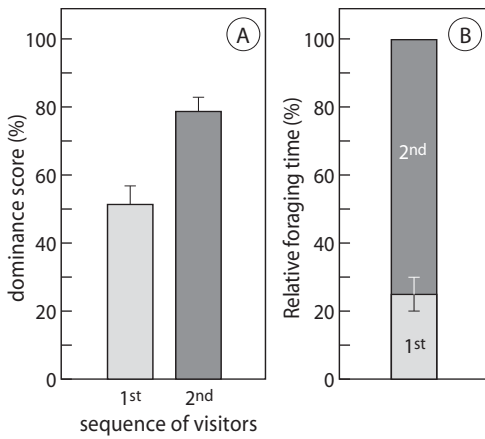


Figure 34-7

Dominance scores (mean \pm SE) of individual barnacle geese entering the experimentally enriched plot on the Spitsbergen tundra in initial (1st) or subsequent (2nd) visits (A), and the share of the total feeding time accumulated by these categories (B; from Stahl et al. 2001).

ods and we could watch the passage of the flock, keeping track of the arrival sequence of the ringed birds, and recording their foraging time within the patch.

We found that the rich patch was quickly identified and conflicts broke out as succeeding geese (or goose pairs) forced each other off the newly discovered riches. So who got there first? It turned out that low-ranking individuals were the first in, quickly followed by more dominant geese that promptly displaced their 'subordinates'. The initial rewards of discovery were usurped by the dominant late arrivals accumulating about 75 percent of the total feeding time (see Fig. 34-7). Due to the small size of the enriched patch only part of the flock could actually profit as they flowed past, and by keeping track of the rings it turned out that individuals who had entered the plot were highly likely (60 percent) to return during a subsequent march past by the flock. In contrast the geese in the vicinity but not on the plot were unlikely to enter it subsequently (less than 20 percent did so). Even one brief exposure thus influenced their feeding routines, and evidence that something subtle was going on emerged when we analysed the dominance

scores determined during earlier flock observations. The 'minority' individuals who 'missed the plot' the first time but visited it later on were characterised by a higher dominance score (62 percent of conflicts won) than the non-returnees (36 percent of conflicts won). Apparently in the goose-world where conflicts are usually resolved in seconds, birds with higher dominance are more successful in jockeying for position.

Our observations also revealed that the detection of new food supplies was the work of subordinates, the 'scouts' who went out ahead of the main flock. The same also applied to spring flocks of brent geese on the salt marsh: the individuals on the front edge of the flock as it flowed into a rich *Festuca* sward had lower dominance scores than those behind the leading edge (and lower breeding success; see Teunissen et al. 1985). By examining the droppings of marked individuals (this sounds straightforward but demands intensive watching and some luck!) it turned out that dominant individuals did indeed obtain a better quality diet on the marsh (Prop & Deerenberg 1991).

So we knew that dominant geese reaped the rewards in the short-term, but was the post-winter return rate to our tundra study area related to summer dominance? Intensive observation the season after our 'plot' experiment revealed that the dominance score of birds that failed to return was markedly lower than that of returning birds. The females that failed to return ($n=12$) had achieved a dominance score of 33 percent the year before, in sharp contrast to the 60-65 percent scores (measured in the previous summer) of the 34 females that did return. This does not mean that all the birds failing to return after the winter had died, but they were certainly lost to the local population. Low-ranking individuals often try to obtain a foothold elsewhere.

This work supports the idea that dominant individuals are heavier because they can monopolise the rich food patches, rather than being more dominant because they are heavier. Age seems a powerful determinant of dominance – and for locally-born individuals



Figure 34-8
Barnacle geese after the moult.

age equates to the number of seasons' experience in the neighbourhood. Geese low in the dominance hierarchy might at first glance appear better off on their own, but the relentless pressure of patrolling Arctic foxes quickly eliminates any individual excluded from the shared vigilance that the flock offers. Presumably the 'underdogs' profit from their exploratory tendency by securing the first bites of new growth without losing contact with the safety of the flock. By gaining a mate a subordinate bird can increase its status, and with every additional season of hard-won experience the pair will inch up towards the

'privileged' category. Unfortunately we do not have observations of these same geese on the wintering grounds, and it remains a tantalizing possibility that much of goose society is under the control of hierarchies that are local or site-bound. What we do know is that at a wintering site where marked barnacle geese originating from differing breeding populations occur together, detailed observations reveal that there is a clear degree of spatial and temporal segregation between them. Something keeps geese from different stocks from mixing, but whether this is the expression of a difference in habitat selection or the outcome of some process of social exclusion is still a mystery (Van der Jeugd et al. 2001).