Chapter 8

Goose flocks and food exploitation: the importance of being first

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Abstract
Flocking is a compromise between costs and benefits, and we argue that the degree of benefit depends on individual position within the flock. By continuous observations from a tower, complete film records of all feeding visits by brent geese Branta bernicla bernicla to selected plots during the spring staging season were obtained. Analysis of these films coupled with before-and-after stereo photos of the vegetation confirmed that the vegetation was rapidly depleted, resulting in less than 10 individuals using patches of 800 cm$^2$ covered by the initially preferred food plant Plantago maritima. The lower level of acceptance appeared related to the intake rate of the alternative food species Puccinellia maritima. The first birds that visited the plots had a higher intake rate and tended to make a different selection from the plants on offer compared with birds at the rear end of the flock. The diet composition appeared a good predictor of the birds’ foraging success. The large asymmetries in resource allocation became evident from the use of Plantago; only 12% of the individuals took 50% of the total crop. The film analyses suggested that successful Plantago feeders, which spent long times in rich patches, lost their front position in the flock. To catch-up with the front birds they walked fast while temporarily feeding on Puccinellia. The herbivores studied faced similar problems as many predators do, i.e. their food was distributed in a patchy way and stocks were rapidly depleted. Optimal foraging theory developed for predators is therefore an appropriate tool to understand foraging decisions in herbivores.

Introduction

Food depletion is a common phenomenon in nature. It will be familiar to anyone who has read about insect plagues, impressive both by scale and by impact. It has taken far longer to appreciate that, under other circumstances, food depletion is the rule rather than the exception. In optimal foraging models that explain the time spent by a predator in a habitat patch, the depleting influence of the predator itself on its food supply is a central assumption (‘resource depression’, Charnov et al. 1976). In field studies, a change in observed intake rate, or a decline in residence time in a patch, or some combination of these parameters, is often the only evidence obtained relating to depletion. In such cases, it is not clear whether the consumer has captured so many prey as to deplete the local supply, or whether the actions of the predator have reduced prey availability at least locally and temporarily (Pyke 1984). A study on food depletion, and how it affects habitat use, diet, and time allocation of the consumer, therefore depends on the ability to monitor the food stock more or less continuously.

We studied the dark-bellied brent goose *Branta bernicla bernicla*, which is an herbivorous bird that for much of the year lives in large flocks. By choosing a surface-feeding herbivore, we were able to measure the food supply by non-destructive methods and to follow the fate of the plant parts that were sampled. Prins et al. (1980) described a cyclic pattern in brent geese exploiting the feeding grounds, postulating that the food supply was depleted during peak grazing and that the geese during each revisit were relying on the regrowth of their food plants. Our aim is to demonstrate the reality of food depletion by a flocking species, document the time scale on which it operates, examine the influence of depletion on food choice, and finally relate those changes to the fitness of the individuals comprising the flock.

Methods

Data were collected in 1984 on a salt marsh of the island Schiermonnikoog, The Netherlands, where about 100 ha were used throughout May by a total number of 800 to 1000 brent geese. Important for the brent geese was a pronounced zonation in the distribution of plant species. *Plantago maritima*, one of the food plants for the brent geese, was found in zones just above the water level during high tide. Our intensive study area (Fig. 1) was situated across this *Plantago* zone. *Plantago* occurred there in distinctive patches, varying in size from a few to several hundred rosettes. *Puccinellia maritima*, the other prominent food plant for the geese, formed a sward covering most of the remaining parts of the study area.

To quantify the food stock, the vegetation in the study area was sampled repeatedly by stereophotographs of marked plots (40 × 20 cm). The photographs were used to measure all *Plantago* blades present in each plot, and, by comparing photographs on subsequent days, we assessed the growth or the quantity of *Plantago* and *Puccinellia* removed by geese.
To test the idea that the *Plantago* stock was depleted during the brent goose visits, the foraging behaviour of the geese was related to changes in the amount of available food. For this purpose, the visits on three days in May were recorded on 16-mm film (10 frames per second), from an observation tower 4 m high and about 10 m from the observation quadrangle. On a film analyser, all pegs marking the sampling plots were visible. In this way, the use of the plots by individual geese was assessed as the number of pecks directed to the plot, and as the number of sec spent grazing in the plot. Thus, the total amount of material removed from each plot and the total grazing time during each flock passage were known. This allowed us to calculate a mean food intake rate per plot.

To test if changes in intake rates affected food choice by the geese, the following analyses were carried out using the films.

- To reconstruct the tracks of the geese during their passage through the study area, the position of every goose on the film was plotted for every second with a digitiser. The tracks of the geese could be mapped on the coordinate system of the observation quadrangle (Fig. 1). Tests with dummy geese showed the accuracy of the plotted locations to be within 10 cm. The position coordinates enabled us to calculate the walking speeds and the linearity of the tracks (the shortest distance between the positions of a goose at 10-s intervals divided by the total distance walked in each interval).

- The activity of every goose was determined for every 0.1 s. Activities distinguished were feeding, agonistic interactions, and otherwise. Most of the time was spent feeding (87%), averaged over all individuals.

- As brent geese showed a distinctive head and neck movement during *Plantago* feeding compared to *Puccinellia* feeding, it was possible to discriminate between periods of feeding on each of the food plants. This was done for each of the individuals visiting the observation area.

Fig. 1. The study area with the most important food plants, patchily distributed *Plantago maritima* and the sward-forming *Puccinellia maritima* (covering the blank area). All tracks of the 67 individual geese that visited the area on 26 May are shown. Time elapsed from first to last goose is 0.5 h.
Results and discussion

Food stocks and flock visits
The observation quadrangle was visited several times by a flock of brent geese in the second half of May. The grazing resulted in a decrease in the standing crop of Plantago to a level of about 1000 mm per 800 cm² (sum of all blade lengths) (Fig. 2). The visit on 18 May was ended by a disturbance before the whole flock had moved through the quadrangle, and the passage the next day can be seen as a continuation. In contrast, the new growth of Plantago seems responsible for the flock visits on 22 and 26 May. Overall, about 65% of the above-ground Plantago production was consumed by the geese before their departure at the end of May. This rate of utilization is in the upper end of the range reported elsewhere for herbivores (e.g., 50-80% of Salicornia stocks were grazed by Wigeon Anas penelope, Van Eerden 1984; 40-70% of the seed stock was taken by finches, Pulliam and Enders 1971).

![Food stock of Plantago](image)

Fig. 2. Food stock of Plantago (sum of all blade lengths), as measured in five sample plots of 800 cm² each. Intake rate for Plantago on the three visits is shown together with the importance of Plantago feeding (note that time-budget data underestimate the proportion of Plantago in the diet). The threshold level for goose exploitation is derived in Fig. 4.

Plantago patch use
On all days, the geese showed a declining ‘residence time’ (Krebs 1978) in the plots: the more predecessors a goose had in a plot, the shorter the time it spent there (Fig. 3). Drent and Van Eerden (1980) observing patches of undefined size found a comparable trend, although without having the opportunity to relate the performance of the geese to the food availability. In most cases, our plots were visited by less than 10 individuals, which underlines the high rate of food depletion within a single patch.

As a following step, the use of the plot can be related to the food available. For this purpose, observations were used only when relevant data on food availability existed,
as with the first geese visiting a plot immediately after a photo sampling, or when the photo sampling was immediately repeated after departure of the flock. Use of the plots was closely related to variation in the food supply (Fig. 4). Data sets from different days seem to fit the same line, and we explain therefore the observed differences in grazing pressure per plot (Fig. 3) by differences in food availability. From Fig. 4 we conclude that patches were ignored after reaching a level of approximately 1000 mm per 800 cm² (sum of all blade lengths), which we interpret as a lower level of acceptance.

As on each grazed plot the mean food intake rate and the mean food availability (average of the food present before and after the grazing episode) were known, we reconstructed the relationship between food intake rate and food availability (Fig. 4). This shows that the lower level of acceptance for Plantago occurs at an intake rate of approximately 3 mg sec⁻¹.

**Puccinellia exploitation**
For Puccinellia-dominated plots, we obtained no proof of any trend in goose usage during a flock passage; nor we found any considerable differences in intake rate between days. We conclude that in these circumstances there is no evidence of depletion of the Puccinellia stock. The intake rates for Puccinellia were on average 2.5 mg s⁻¹ (SD= 0.59, n=15, Fig. 4), a value close to the lowest intake rate for Plantago (ca. 3 mg sec⁻¹). This point will be reconsidered later.

**Intake rates and food choice**
When comparing intake rates during three successive visits to the observation quadrangle (see Fig. 2), a drastic drop is discernible for the Plantago feeders. An inconsistency

![Fig. 3. Feeding by brent geese in plots in relation to the order of visitation, from film (mean of two to four plots per day). Plots on 26 May accessible to the geese for the first time after having been protected by an exclosure receive an accumulated grazing time comparable to the sum of all 3 d in other always accessible plots.](image-url)
appears when comparing trends in the Plantago supply and Plantago intake rate: a restoration in the amount of Plantago available between 22 and 26 May was followed by a further decline in the intake rate. We think this can be explained by a change in the growth form of the Plantago plants after the first grazing: in contrast to the original vertically directed blades (easily cropped by the geese), the new growth consisted of horizontal, prostrate blades. This might confuse the relationship between food supply (as measured by photographs) and the intake rate, although it is an interesting example of an effective anti-grazing response by Plantago. Changes in the daily intake rates were accompanied by changes in the proportion of Plantago feeding in the observation area (Fig. 2), and highest intake rates coincided with highest proportions of Plantago feeding. This relationship indicates that changes through the season in the availability of a preferred food species result in a diet shift to other plants.

**Shifts in the diet**

To analyse diet choice in relation to food availability in more detail, the observation quadrangle was divided into squares of 1×1 m, which were considered as entities exploited by the geese. For our purpose, only that part of the study plot where both food plants occurred is taken into account, i.e., the right part in Fig. 1. Having the choice between two food species, the first geese exploiting the area consumed mainly Plantago
(Fig. 5). With an increasing grazing pressure, the importance of *Plantago* in the diet declined in favour of *Puccinellia*. The same trend existed in less heavily grazed squares, although these lacked the high initial rates of *Plantago* feeding (inset of Fig. 5). This suggests that the total grazing pressure per square meter was dependent on the harvestable amount of *Plantago*. The total grazing time per square meter was affected by the number of geese visiting the area (Fig. 6), but even more strongly by the foraging behaviour of the individual geese visiting the squares. Individuals spent more time in squares receiving a high grazing pressure, and this was the result of the combination of a lowered walking speed and a decreased linearity of the path of a goose (the area-restriction effect, Smith 1974). The better foraging conditions in the more intensively used parts are also reflected by the positive relationship between the percentage of the time spent feeding and grazing pressure (Fig. 6). Better places thus were more intensively used by the geese, that we suspect detected the better spots from a distance of several meters.

![Graph showing the proportion of *Plantago* feeding in relation to cumulative grazing time per square meter](image)

**Fig. 5.** The proportion of *Plantago* feeding in relation to cumulative grazing time per square meter (restricted to cases with more than 5 min grazing time per square meter). The inset shows the trend in the less heavily visited squares (accumulating 2, 3, and 5 goose-minutes).

**The individual faced with a declining food stock**

Before the depletion of *Plantago*, when this plant became unimportant to the geese (Fig. 5), on average only 100 sec were spent per square meter. How was the foraging behaviour of the individual affected by this rapid depletion and the resulting need to shift to another food plant? Summed over all squares, nearly 50% of all goose-seconds were spent in the last unfavourable 2 min of foraging in a square. In fact, 50% of all time spent feeding on *Plantago* involved only 12% of the individuals (Fig. 7), and 27% of all geese crossing the observation area did not ingest *Plantago* at all. Clearly there was an unequal allocation of the food supply among the individual geese, and only a minority was able to benefit from the high return from taking *Plantago*. 
Fig. 6. The feeding intensity, number of visiting geese, and mean residence time in relation to the grazing pressure on the basis of values for different square meters in the observation area. Squared correlation coefficients are 0.104 ($P=0.05$), 0.244 ($P<0.02$), and 0.840 ($P<0.001$), respectively.

Fig. 7. Rank of individuals according to cumulative feeding time on *Plantago*. Half the total *Plantago* feeding time (as estimated from the head stance during pecking; see inset) is accounted for by a minor portion of the geese. Note that 27% of the birds obtained no *Plantago* at all.
To exploit a rich *Plantago* patch, a goose should - apart from defending the patch against other individuals in the flock (Boyd 1953) - arrive on the spot before other geese. Being earlier than other individuals requires fast walking, and from our film records we suggest that some of the geese were attempting to achieve a leading position. When a flock entered the observation quadrangle, we observed - besides the geese that were eating *Plantago* - geese that passed the area walking much faster than the others, and taking mainly *Puccinellia* (Fig. 8). We suggest that those individuals were trying to secure better feeding positions in the flock, for the short term ignoring better feeding spots and obviously accepting a temporary low intake by feeding *Puccinellia*. For geese passing later, the difference in intake rates between *Plantago* and *Puccinellia* was less marked, and so the advantage to stay before other geese also declined. We suggest that this gradient of decreasing food availability was reflected by the declining difference in walking speed between the *Plantago* and *Puccinellia* feeders.

![Graph](image)

Fig. 8. Trends in the walking speed for geese that fed predominantly on *Plantago* or on *Puccinellia*. Only square meters with a grazing pressure of at least 5 min have been used in the analysis. Every symbol represents the average walking speed per successive 40-s periods for all squares; the regression lines have been calculated on the basis of the ungrouped data.

On the longer term, the aim of this study is to relate the foraging behaviour of an individual to its fitness, or more directly to its gain in condition. Those relationships are being tested in the population under study, as outlined by Teunissen et al. (1985). Their work showed that geese in the rear end of a flock had the lowest chance to return with offspring the next autumn, compared with geese more in the front, which is consistent with our observations. In our data, differences in individual performance might be partly due to the short time scale considered. There may be compensation, and a goose that achieves a low intake rate during a brief period might do better later. To place our observations in the context of a whole day’s foraging, we feel the need to follow individuals for longer times at a stretch (Prop and Deerenberg 1991).
Chapter 8

Acknowledgments

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Film shot of a brent goose flock.
Stereo photographs are a powerful tool to assess food available to herbivores, and to determine the amount of forage removed by grazers. Stereoscopic view allows distinction of the finest details of food selection. These pictures of stereo-pairs were taken on the same day (16 May) before and after passage of a brent goose flock. All rosettes of *Plantago maritima* in the plot (20×20 cm) were grazed, whereas only the largest tillers of the grass *Puccinellia maritima* were removed.
A peregrine falcon defends its two nestlings, thus protecting the red-breasted geese nesting in the close proximity of the eyrie.