Goose Flocks and Food Exploitation: the Importance of Being First

Jouke Prop and Maarten Loonen
Zoological Laboratory, University of Groningen, P.O. Box 14, 9750 AA HAREN, The Netherlands

reprint from: Acta XIX Congressus Internationalis Ornithologici (Ottawa, Canada) 22-29. VI. 1986

Prop, J. & M. Loonen (1989) Goose flocks and food exploitation: the importance of being first. Acta XIX Congr. Int. Orn. (Ottawa): 1878-1887.

Goose Flocks and Food Exploitation: the Importance of Being First

Jouke Prop and Maarten Loonen
Zoological Laboratory, University of Groningen, P.O. Box 14, 9750 AA HAREN, The Netherlands

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 surveillance from an observation tower, complete ciné-film records of all feeding visits by Brant (*Branta 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 first birds in had a higher intake rate and tended to make a different selection from the plants on offer compared with birds farther back in the flock, even within a single visit. Similar depletion effects were found with Barnacle Geese (*Branta leucopsis*) feeding on tundra during the egg stage and Snow Geese (*Anser caerulescens*) utilizing a salt marsh during the gosling stage. In several situations, the differences in intake rate and diet achieved by "early" compared with "late" individuals were correlated with subsequent breeding success. Discussion centers on determinants of individual position within the flock and designing models for optimal flock size.

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 models constructed in optimal-foraging theory to 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 (for review, see Pyke 1984).

In field studies, a change in observed intake rate, or 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 ("resource depression"). A study on food depletion, and how it impinges on habitat use, diet, and time allocation of the consumer, therefore hinges on the ability to monitor the food stock more or less continuously.

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. By choosing a surface-feeding herbivore, we were able to measure the food supply by nondestructive methods and follow the fate of the plant parts that were sampled.

Food Stocks and Flock Visits

Data were collected in 1984 on a salt marsh of the island Schiermonnikoog, The Netherlands, where about 100 ha are used throughout May by a total number of 800 to 1000 Brant (*Branta bernicla*).

Important for the Brant is a pronounced zonation in the distribution pattern of plant species. *Plantago maritima*, one of the food plants for the Brant, is found in belts just above the water level during high tide. Our intensive study area (Fig. 1) was situated across this *Plantago* zone. *Plantago* grows there in distinctive patches, varying in size from a few to several hundred rosettes. *Puccinellia maritima*, the other prominent food plant for the geese, forms a sward covering most of the remaining parts of the study area.

Prins *et al.* (1980) described a cyclic pattern in the exploitation of the feeding grounds by Brant, 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. We received a hint of food depletion in our situation by analyzing the time-allocation pattern of the Brant over different vegetation types. The time spent by the geese in the *Plantago* zone per 7-d period was positively related to the growth rate of *Plantago*.

To unravel the factors responsible for this presumed depletion, more detailed observations were collected. 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.

The observation quadrangle was visited several times by a flock of Brant 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 cm^2 (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., 40–75% of the seed stock was taken by finches; Pulliam and Enders 1971).

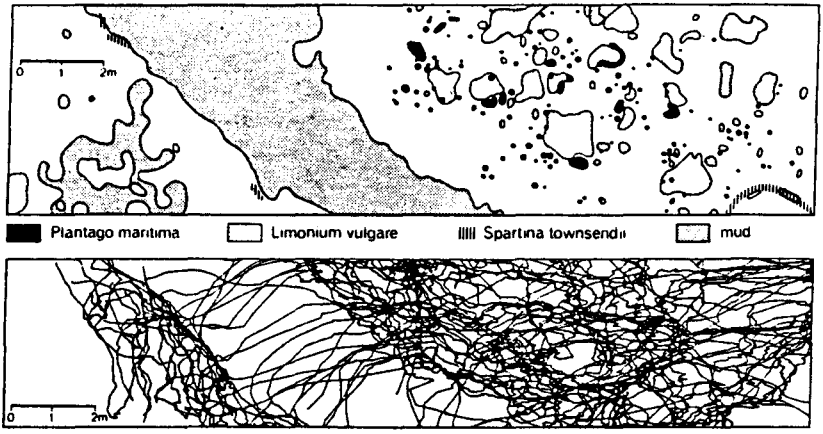

Figure 1. The study area with the most important food plants, patchily distributed *Plantago maritima* and the sward-forming *Puccinellia maritima* (covering the blank area). All tracks of the 67 individual geese that visited the area on 26 May are shown. Time elapsed from first to last goose is 0.5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

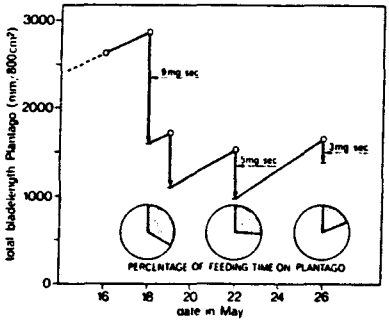

Figure 2. Food stock of *Plantago* (sum of all blade lengths), as measured in five sample plots of 800 cm^2 each. Intake rate for *Plantago* on the three visits is shown together with the importance of *Plantago* feeding (note that time-budget data underestimate the proportion of *Plantago* in the diet).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

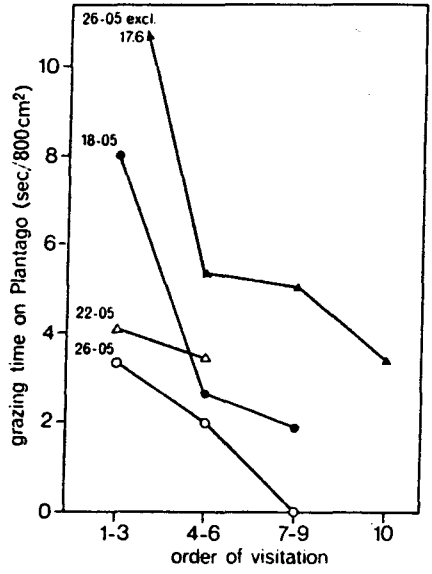

Figure 3. Feeding by Brant in plots in relation to the order of visitation, from film (mean of two to four plots per day). Plots on 26 May accessible to the geese for the first time after having been protected by an exclosure receive an accumulated grazing time comparable to the sum of all 3 d in other (always accessible) plots.

mapped on the coordinate system of the observation quadrangle, to an accuracy within 10 cm (Fig. 1). The position coordinates allowed calculation of the walking speeds and the linearity of the tracks (= quotient of the shortest distance between the positions of a goose at 10-s intervals and the total distance walked in each interval).

(b) Activity of every goose for every 0.1 s: i.e., feeding, interactions, or otherwise, representing 87, 3, and 10%, respectively, of the time spent by all individuals.

(c) Ingested food type during feeding for every goose in the study area: as Brant showed a distinctive head and neck movement during *Plantago* feeding compared with *Puccinellia* feeding, it was possible to discriminate between periods of feeding on each food item.

In comparison of intake rates over 3 d (see Fig. 2), a drastic drop is discernible for the *Plantago* feeders. An inconsistency 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, but it is an interesting example of an effective anti-grazing response by *Plantago*.

Changes in the daily intake rates are accompanied by changes in the proportion of *Plantago* feeding in the observation area (Fig. 2). Highest intake rates coincide with highest proportions of *Plantago* feeding. This relationship gives an indication that geese react to changes in the food availability of a preferred species by shifting to another plant.

To analyze how a decrease in food supply and intake rate affected the feeding behavior of the geese exploiting an area, the next step was to look at shifts in the diet of geese.

Shifts in the Diet

In this analysis, the observation area 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 declines in favor of *Puccinellia*. The same trend exists in less heavily grazed squares, although there the very high early rates of *Plantago* feeding did not occur at all (inset of Fig. 5). So the total grazing pressure per square meter seems to be dependent on the harvestable amount of *Plantago*. This total grazing time per square meter is influenced by the number of geese visiting the area (Fig. 6), but even more strongly by the time an individual goose spends in a square. This is the result of the combination of a lowered

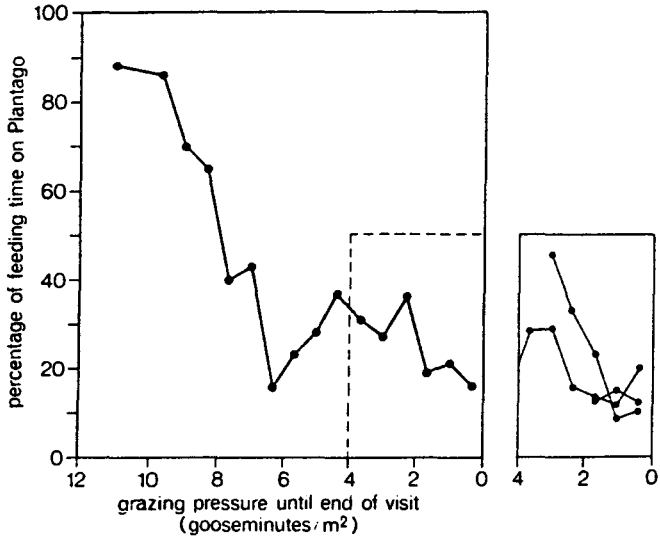

Figure 5. The proportion of *Plantago* feeding in relation to cumulative grazing time per square meter (restricted to cases with more than 5 min grazing time per square meter). The inset shows the trend in the less heavily visited squares (accumulating 2, 3, and 5 goose-minutes).

walking speed and a decreased linearity of the path of a goose. The better circumstances in the more intensively used parts are reflected by the positive relationship between the feeding intensity (percentage of the time spent feeding) and grazing pressure. Better places thus were more intensively used by the geese, which probably detected the better spots from a distance of several meters. They also showed a feeding behavior response, in that an individual stayed for a longer period on a better spot (the area-restriction effect).

The Individual Faced with a Declining Food Stock

Before the depletion of *Plantago*, resulting in a decline in its importance for the geese (Fig. 5), on average only 100 s were spent per square meter. How is the foraging behavior 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 unfavorable 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 is a very unequal allocation of the food supply between the individual geese, only a minority profiting by the higher return from eating *Plantago*.

To find a rich *Plantago* patch, a goose has to arrive on the spot before, and defend the spot against, other geese. That some geese arrive before the others is suggested in Fig. 8. When an area had not yet been grazed, we observed—

To test the idea that the *Plantago* stock was depleted during the Brant visits, the foraging behavior of the geese was related to changes in the amount of available food. For this purpose, the visits on 18, 22, and 26 May were recorded on 16-mm film (10 frames per second), from an observation tower 4 m high, about 10 m from the observation quadrangle. On a film analyzer, all pegs marking the sampling plots were visible. It was thus possible to reconstruct the usage of the plots by the geese (on the basis of seconds spent in the plot or pecks directed at the plants). In this way, the total amount of material removed on each plot and the total grazing time during each flock passage were known. This allows the calculation of a mean food intake rate per plot.

Plantago Patch Use

On all days, the geese showed a declining "residence time" 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) observed a comparable trend, although without having the opportunity to relate the performance of the geese to the food availability.

Differences in use of the plots (expressed as pecks per individual per plot) can be largely explained by variation in the food supply (Fig. 4). Data were entered in this figure only when relevant data on food availability existed, as with the first geese visiting a plot after following a photo sampling, or when the photo sampling was repeated after departure of the flock. Data sets from different days seem to fit the same line, so we may explain the observed differences in grazing pressure per plot (Fig. 3) by differences in food availability. From Fig. 4 we concluded that no attention is paid to a patch after reaching a level of about 1000 mm per 800 cm^2 (summed blade lengths).

As on each grazed plot the mean food intake rate (see above) 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). It is found that there is a giving-up level for the *Plantago* intake rate of about 3 $mg \cdot s^{-1}$.

Thus, grazing intensity on *Plantago* patches is tuned to the local food supply in the patch. Grazing results in a rapid depletion measurable after passage of the first three geese, with a continually declining intake rate. Grazing per patch ends when intake rates fall below about 3 $mg \cdot s^{-1}$.

Puccinellia Exploitation

For *Puccinellia*-dominated plots, we have no proof of any trend in goose usage during a flock passage or of considerable differences in intake rate between days. We conclude that in the circumstances there is no evidence of depletion of the *Puccinellia* stock. The intake rates for *Puccinellia* were around 2.5 $mg \cdot s^{-1}$ (Fig. 4), a value close to the lowest intake rate for *Plantago* (ca. 3 $mg \cdot s^{-1}$). This point will be reconsidered later.

Intake rates of captive Brant on the same type of vegetation (experiments carried out in 1985 by Charlotte Deerenberg) appeared to be of the same order

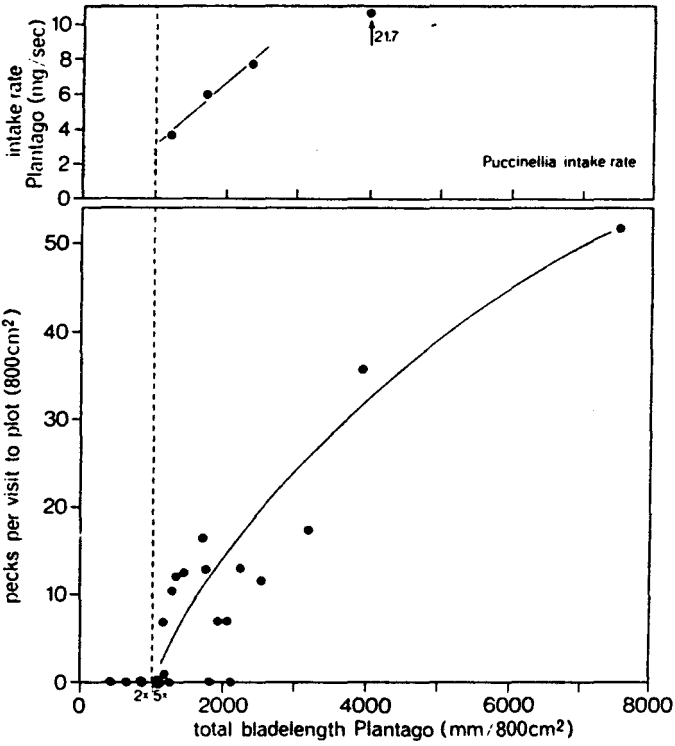

Figure 4. Pecks per goose directed to a plot and the intake rate of geese feeding on *Plantago* related to the amount available. Grazing on *Plantago* stops when the food supply drops below the indicated value. By then, the *Plantago* intake rate approaches the value for *Puccinellia*. The high intake rate (22 $mg \cdot s^{-1}$) refers to the exclosure.

as the values we found in the field, although no difference between *Plantago* and *Puccinellia* was detected. Both food plants offered an intake rate around 4 $mg \cdot s^{-1}$. In the controlled conditions of these experiments, the digestibility of the different food plants was assessed, and it was found that for the same (gross) intake rate the net intake rate of the *Plantago*-feeding goose was 1.4 times the net intake rate of the *Puccinellia* feeder.

Intake Rates and Food Choice

The next step was to look for the effects of changes in intake rates on food choice by the geese acting on a larger scale. Using the 16-mm films, the following analyses were carried out:

(a) Reconstruction of the tracks of the geese during their passage through the study area: by plotting the position of every goose on the film for every second with a Hewlett-Packard Digitizer, the tracks of the geese could be

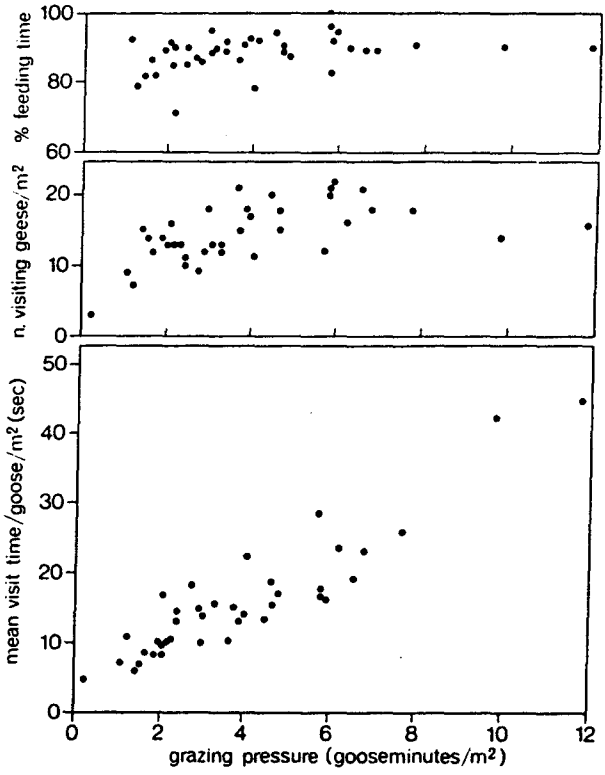

Figure 6. The feeding intensity, number of visiting geese, and mean residence time in relation to the grazing pressure on the basis of values for different square meters in the observation area. Squared correlation coefficients are 0.104 ($P = 0.05$), 0.244 ($P < 0.02$), and 0.840 ($P < 0.001$), respectively.

besides the geese that were eating *Plantago* there—geese that passed the area walking much faster, eating only the *Puccinellia* present everywhere. We suggest that those geese are trying to secure better feeding positions in the flock, for the short term ignoring the better feeding spots. For geese passing later, the difference in intake rates between *Plantago* and *Puccinellia* is less marked, and so is the advantage to stay before the other geese, being reflected in the declining difference in walking speed between the *Plantago* and *Puccinellia* feeders.

On the longer term, the aim of this study is to relate the foraging behavior 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 in a spring staging area had the lowest chance to return with offspring the next autumn, compared with geese more in the front of the flock.

In our data, differences between individuals in their performance during

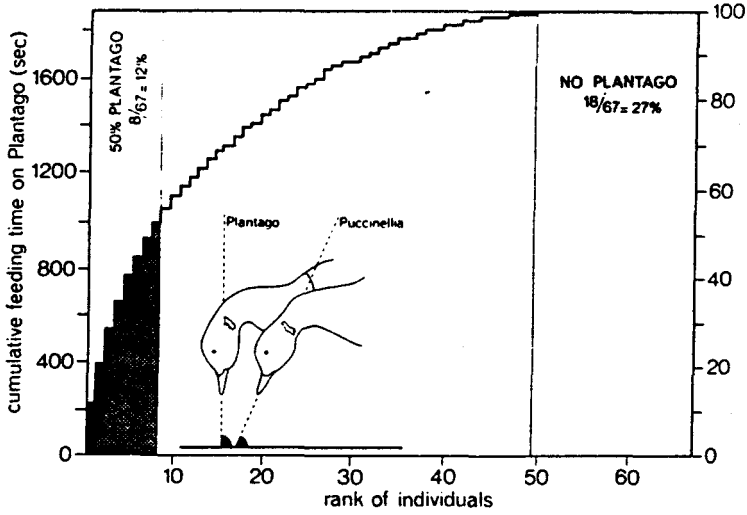

Figure 7. Rank of individuals according to cumulative feeding time on *Plantago*. Half the total *Plantago* feeding time (as estimated from the head stance during pecking; see inset) is accounted for by a minor portion of the geese. Note that 27% of the birds obtained no *Plantago* at all during a visit.

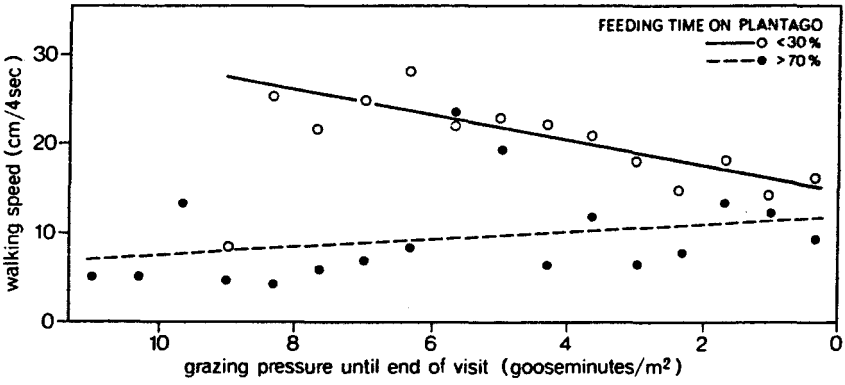

Figure 8. Trends in the walking speed for geese that fed predominantly on *Plantago* or on *Puccinellia*. Only square meters with a grazing pressure of at least 5 min have been used in the analysis. Every symbol represents the average walking speed per successive 40-s periods for all squares; the regression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

their passage might be partly due to the short time scale. There may be compensation in the longer term, as a goose that does not fare very well now 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. This work is being carried out.

Acknowledgments

We thank the Dienst der Domeinen for granting permission to work on the salt marsh of Schiermonnikoog. Addy de Jongh introduced us to the Hewlett-Packard computer. Dick Visser kindly drew the figures. This study is part of a project carried out for the University of Groningen and the Institute for Nature Management (RIN, Leersum), supported by the Foundation for Technical Sciences (STW).

References

DRENT, R.H., and M.R. VAN EERDEN. 1980. Goose flocks and food exploitation: how to have your cake and eat it. Proc. Int. Ornithol. Congr. 17: 800–806.

PRINS, H.H.Th., R.C. YDENDERG, and R.H. DRENT. 1980. The interaction of Brent Geese *Branta bernicla* and Sea Plantain *Plantago maritima* during spring staging: field observations and experiments. Acta Bot. Neerl. **29**: 585–596.

PULLIAM, H.R., and F. ENDERS. 1971. The feeding ecology of five sympatric finch species. Ecology, **52**: 557–566.

PYKE, G.H. 1984. Optimal foraging theory: a critical review. Annu. Rev. Ecol. Syst. **15**: 523–575.

TEUNISSEN, W., B. SPAANS, and R. DRENT. 1985. Breeding success in Brent in relation to individual feeding opportunities during spring staging in the Wadden Sea. Ardea, **73**: 109–120.