Foraging routines and estimated daily food intake in Barnacle Geese wintering in the northern Netherlands

BARWOLT EBBINGE, KEES CANTERS AND RUDOLF DRENT

Statement of objectives

Investigation of the food intake of unrestrained animals in the field is one of the blind spots of ecology. In grazing animals that process large amounts of vegetation daily, and reject the greater part of it, it has been realized (see Petrusewicz & Macfadyen, 1970) that a 'tedious but possible' method of arriving at the daily food intake is to measure (a) the daily faecal output and (b) the quantitative relation between the food ingested and that rejected in the faeces, expressed as the apparent digestibility or rate of utilization of the food on a weight basis. If a component of the natural food happens to be completely indigestible for the bird in question, the measurement of utilization rate is, theoretically at least, quite straightforward. Quantitative analyses of samples of food and of droppings for the indigestible component yield a measure of food utilization on a weight basis (grams retained as percentage of grams ingested) according to the formula:

$$\% \text{ utilization (dry weight)} = \left(1 - \frac{M_f}{M_d}\right) 100\%$$

where M_f = gm of the marker substance (the indigestible component) per 100 gm food (dry), and M_d = gm of the marker substance per 100 gm droppings (dry). The method has successfully been applied in galliform birds, both in laboratory trials (Bolton, 1954) and in both laboratory and field conditions (Moss & Parkinson, 1972; Moss, 1973).

Recent physiological work (Mattocks, 1970; Marriott & Forbes, 1970) indicates that cellulose digestion, if indeed it occurs at all, is a quantitatively unimportant phenomenon in geese. This means that the relative content of cellulose in the food and in the droppings can be used as an indicator for digestibility (= rate of food utilization) in these birds. Providing that the daily output of droppings could be obtained from field observation, the daily food intake might be arrived at. Owen (1971, 1972a, 1972b) has demonstrated the feasibility of quantifying the foraging routines of wild geese, and thus encouraged we have attempted to apply the 'tedious but possible' approach to estimating food intake in the species most easily observed in our area, the Barnacle Goose *Branta leucopsis.*

Aside from its intrinsic interest, information on the food intake and food utilization of the Barnacle Goose can be expected to have practical implications. The world population of this species has doubled over the past decade, leading to increased conflicts with agricultural interests in the wintering areas, conflicts that can be properly resolved only after the critical habitat requirements of the Barnacle Goose have been defined.

We have sought answers to three related questions: (1) the plant species upon which the bird relies, (2) the quantity of food that the bird must obtain daily, and (3) the carrying capacity of the areas grazed. Preliminary results on the latter two points are presented here; work on selectivity in the feeding of the Barnacle Goose is continuing and will be the subject of a later report. In addition to the indirect estimation of intake via the droppings as outlined above, exclosure experiments of the type common in grazing studies were carried out to obtain an independent measure of the maximal intake of the Barnacle Goose. Basic to this approach was the use of the density of droppings as a measure of goose visitation on the plots. Observations on carrying capacity included direct census and extensive sampling of the density of goose droppings. In short, we rather had the feeling that we were studying droppings rather than wild geese.

World population of the Barnacle Goose in 1972–1973

The world population of the Barnacle Goose is considered to consist of three more or less discrete populations. Total censuses in the 1972–1973 winter season put the world population at approximately 70,000, comprised as follows: (a) the Greenland population wintering in western Ireland and western Scotland totalling 24,000 individuals (Ogilvie & Boyd, 1975); (b) the Spitsbergen population wintering in south-western Scotland totalling 4,400 individuals (Owen & Campbell, 1974); (c) the Barents Sea (more accurately Novaya Zemlya and Vaigach) population wintering in north-western Germany and the Netherlands, totalling approximately 40,000 individuals, as documented in Table 1. The good agreement between the various censuses through the winter 1972–1973 shows what can be

Table 1. Total census of the Barents-Sea population of the Barnacle Goose, winter 1972–1973

Date	Netherlands[1]	Niedersachsen[2]	Schleswig-Holstein[3]	Total
12 November 1972	28,800 (28,800)	3,100	10,000	41,900
2 December 1972	37,500 (30,500)	1,004	75	38,600
14 January 1973	37,200 (21,400)	1,298	1,500	40,000
17 February 1973	25,500 (2,800)	7,373	9,000	41,900

[1] Counts by our group supplemented by T. Lebret, G. Ouweneel, J. Philippona, K. Sikkema, G. Slob, J. Smittenberg, A. Timmerman Azn, and H. G. v. d. Weijden for other parts of the country; in parentheses the total for our study area on that date.
[2] J. Dircksen.
[3] G. Busche.

achieved by a network of observers confronted by a conspicuous and local species.

The Barnacle Goose in the northern Netherlands

Our study area, indicated in Figure 1 accounted for practically 40% of all goose days spent by the Barents Sea population of the Barnacle Goose in its wintering area in the 1972–1973 season (the winter period is here considered to extend from mid-October to mid-March). Early in the season *Salicornia* was taken and from the last week in November foraging was concentrated on pastureland, as is indicated by the counts shown in Figure 2. Most of our observations on foraging geese were made on the island of Schiermonnikoog, where the University has a small field station. Practically all foraging in this area occurred on pastureland utilized in

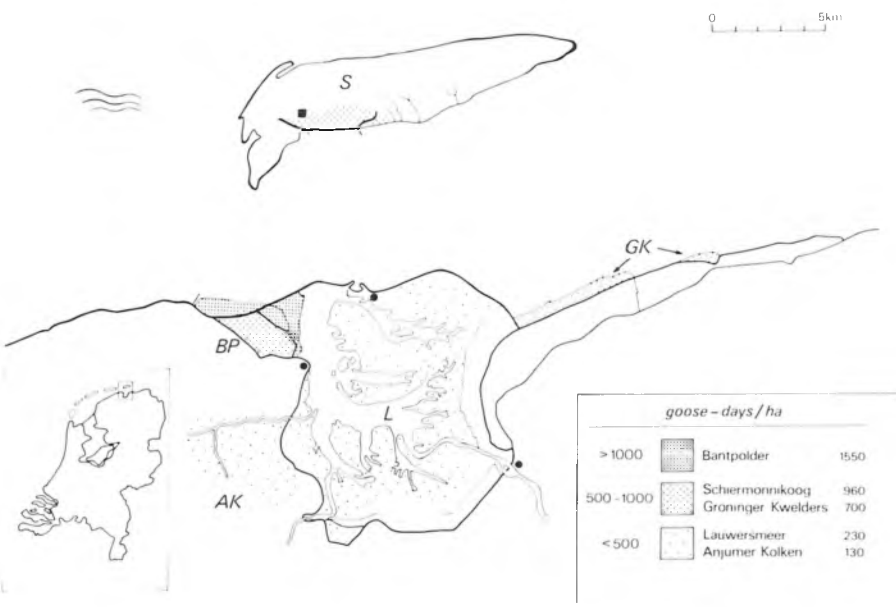

Figure 1. The study area in the northern Netherlands. S = Schiermonnikoog, BP = Bantpolder, AK = Anjumer Kolken, L = Lauwersmeer, GK = Groninger kwelders. Areas visited by Barnacle Geese are stippled; grazing pressures in the 1972–1973 winter being identified in the key.

the summer months (April to October) by cattle, and observations could be done easily from nearby roads, the dike serving as a background thus enabling the geese to be approached to within 100–200 metres.

For comparison with descriptions that have been offered for the vegetation utilized by Barnacle Geese for winter foraging elsewhere (Roberts, 1966; Bjärvall & Samuelson, 1970; Owen & Kerbes, 1971) the following can be

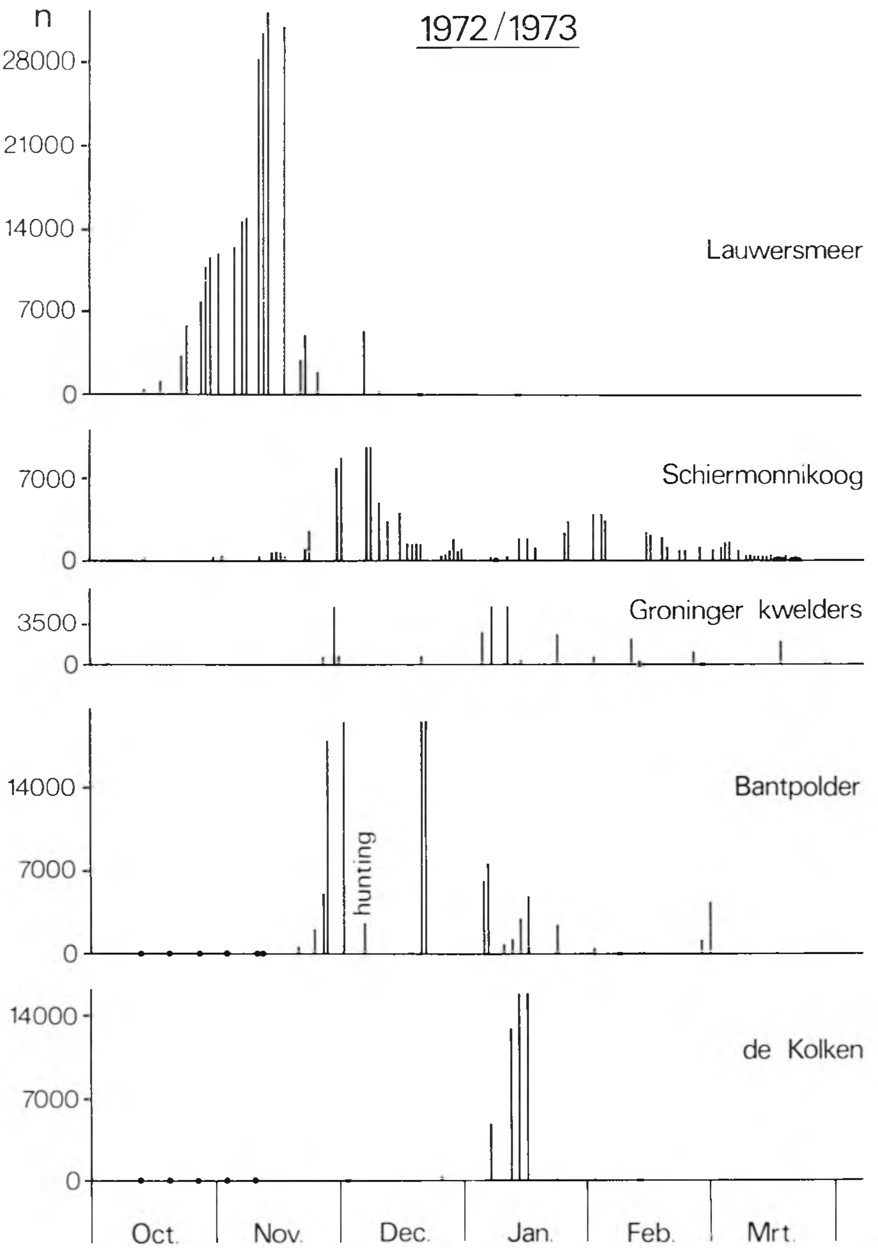

Figure 2. Direct counts of Barnacle Geese in the study area throughout the 1972–1973 winter season. The subareas are identified in Figure 1. Solid dots indicate that no geese were present on the date in question.

said of our study area. Dominant in the diked-in pasturelands are the grasses *Lolium perenne, Poa pratensis* and *P. annua* and the herbs *Taraxacum officinalis* and *Trifolium repens*. The adjacent merseland, completely inundated by the sea several times each winter, has a grass cover composed predominantly of *Festuca rubra* and *Puccinellia maritima* with *Agrostis stolonifera, Poa pratensis* and *Lolium perenne* occurring to a lesser extent, along with the herbs *Trifolium repens, Plantago maritima, Potentilla anserina* and *Armeria maritima*.

Historically, as documented by Timmerman (1962), Loterijman (1972) and Mooser en Zwarts (1968) in this area the Barnacle Goose has principally been observed on merseland or the adjacent pastureland. Aside from its occurrence on the massive *Salicornia* fields that have developed (no doubt temporarily) as a consequence of the closure of the Lauwerszee in 1969 it will be seen (Figure 1) that this pattern is still true today. Elsewhere in the country, concentrations of Barnacle Geese occur in the Hollands Diep–Haringvliet area (in Sw-Netherlands) (see Ouweneel, 1971) and in central and south Friesland (see Philippona and v.d. Meulen, 1969; summary in Mörzer Bruyns, 1966).

The grasslands mentioned as being the principal haunts of the Barnacle Goose in our area (Schiermonnikoog, Bantpolder and Groninger Kwelders) were not visited by other goose species in this period (the Brent Geese *Branta bernicla* not moving to the grasslands until April). We could therefore be certain that all goose droppings counted on our transects were indeed produced by the species we were interested in. In areas visited by other geese as well (up to 1,000 White-fronted Geese *Anser albifrons* in 'De Kolken,' and several hundred Greylags *Anser anser* in both 'De Kolken' and the Lauwersmeer) dropping transects were not carried out, and goose usage assessed by direct counts instead.

Daily activity rhythm

In our area, Barnacle Geese hardly ever sleep on the foraging areas, but withdraw to tidal mudflats or permanent sandbanks to rest. In all cases, these resting areas were less than 10 km from the feeding areas, and a relatively small proportion of the day was devoted to flight. During the dark phase of the moon, the time spent on the foraging area by the Barnacle Goose is restricted to the daylight hours and a very sharply defined daily shift from feeding to resting areas can be discerned (Figure 3a). During moonlight periods however (Figure 3b) feeding also goes on at night and in this period the foraging rhythm can become very complex. When nights are bright a complete reversal of the 24-hour rhythm occurs: feeding occurring exclusively in the night period, and the geese spending the day at rest on the tidal mudflats. As shown in Figure 3 more time is spent on the foraging areas when foraging is possible both by day and by night than when foraging is limited to the daylight hours. This may

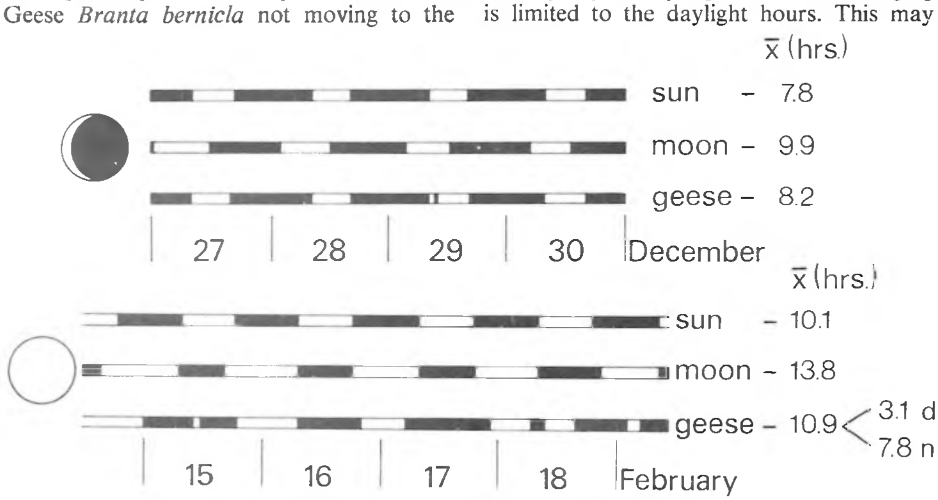

Figure 3. Presence of Barnacle Geese on the foraging grounds (open segments of the bottom bar in each diagram) **in relation to rising and setting of the sun and moon, during the dark phase of the moon** (last quarter on 27th December, top) **and during bright moonlight** (full moon on 16th February, bottom). The geese spent an average of 8·2 hours per 24 hours on the foraging grounds, all of it during daylight, in the dark phase of the moon, and an average of 10·9 hours per 24 hours (3·1 by day, 7·8 by night) on the foraging grounds during the moonlit period.

Table 2. Time budget of Barnacle Geese during the dark phase of the moon

Date	Day-length[1]	Hours spent[2]		Per cent of the time on foraging area devoted to:					
		on foraging area	actively foraging	foraging	drinking	alert	body care	sleep	social interactions
5.11.72[3]	9·4	10·0	8·3	83·2	4·1	10·1	1·9	0·7	0
28.12.72	7·8	8·1	6·2	76·7	0	22·5	0·6	0	0·2
29.12.72	7·8	7·8	6·8	86·3	0	12·9	0·7	0	0·1
30.12.72	7·8	8·7	6·9	78·8	0	20·3	0·6	0	0·3
3.2.73	9·2	7·7	6·5	84·6	0	13·7	0·4	1·2	0·1
4.2.73	9·3	8·6	7·3	85·4	0	11·0	1·0	2·5	0·1

[1] Hours from sunrise to sunset.
[2] Time actually on grassland (i.e. disturbance flights excluded); hours spent actively foraging is the product of (hours on foraging area) × (mean per cent of time devoted to foraging).
[3] The November observations concern geese foraging on the halophyte *Salicornia* in the Lauwersmeer (note time devoted to drinking fresh water), the other dates concern pasture foraging on Schiermonnikoog.

mean that foraging is less efficient at night but we do not have the data to test this supposition. Since the data concerned lie two months apart it is possible that other variables such as height of sward are in fact responsible.

As is typical for most grazing animals, the Barnacle Goose devotes the major part of its day to feeding. Several all-day observation records are collected in Table 2 and show that on average 82·5% of the time at the foraging grounds is actually devoted to feeding. The data were assembled by sweeping across a group of 100–200 geese by telescope every 15 minutes, and classifying each bird seen as feeding, being alert (head up), preening, sleeping, drinking, or engaged in social interactions. In between these activity counts the rate of pecking and walking was determined by clocking the number of seconds required to perform 50 pecks or 25 paces, ten actively grazing birds being observed in each session.

Despite the high level of activity a daily rhythm in time devoted to feeding similar to that found in many other birds (Morton, 1967; Gibb, 1958; Verbeek, 1964; Markgren, 1963; Owen, 1972a) can be discerned, in which a period of intense activity at the start of the day is succeeded by a trough, and the day terminated by a final rise in feeding activity. A parallel is seen in the rate of pecking and walking (Figure 4).

Maximal food intake estimated from exclosure experiments

Standing crop measurements were taken by clipping squares 20 × 20 cm (thus 400 cm²) at regular intervals (approximately every 25 days) both within and outside wire enclosures (1 × 5 m, and 30 cm high) placed on pasture- and merse-land.

In all, 15 enclosures were placed on pastureland, and 11 on merseland, and on each sampling date a square was cut inside each enclosure, and adjacent to it at a distance of about 5 metres. Most samples were cut to soil level using garden shears, but in a separate series samples were also taken to 'goose-grazed height' with scissors. Every fortnight goose droppings were counted and removed from a series of 22 permanent quadrates (2 × 2 m = 4 m²) in the vicinity of the enclosure to serve as an indirect measure of grazing intensity to compare with the observed rate of disappearance of grass from the sward. All samples were taken to the field laboratory in plastic bags, and dried to constant weight in an oven set at 85°C (generally 12 hours or longer).

The rationale behind the method is as follows. From the moment an enclosure is placed in a homogeneous field, any difference in standing crop determinations inside and outside are attributed to the activities of herbivores excluded from the enclosures (in our situation principally hares, Wigeon, and Barnacle Geese in ascending order of importance). The amount presumed to have been eaten can be related to the daily ration of the Barnacle Goose by comparing the density of droppings accumulated during the sampling period with the daily output of droppings, as shown in Table 3. Unfortunately, the measurements on the merseland did not lead

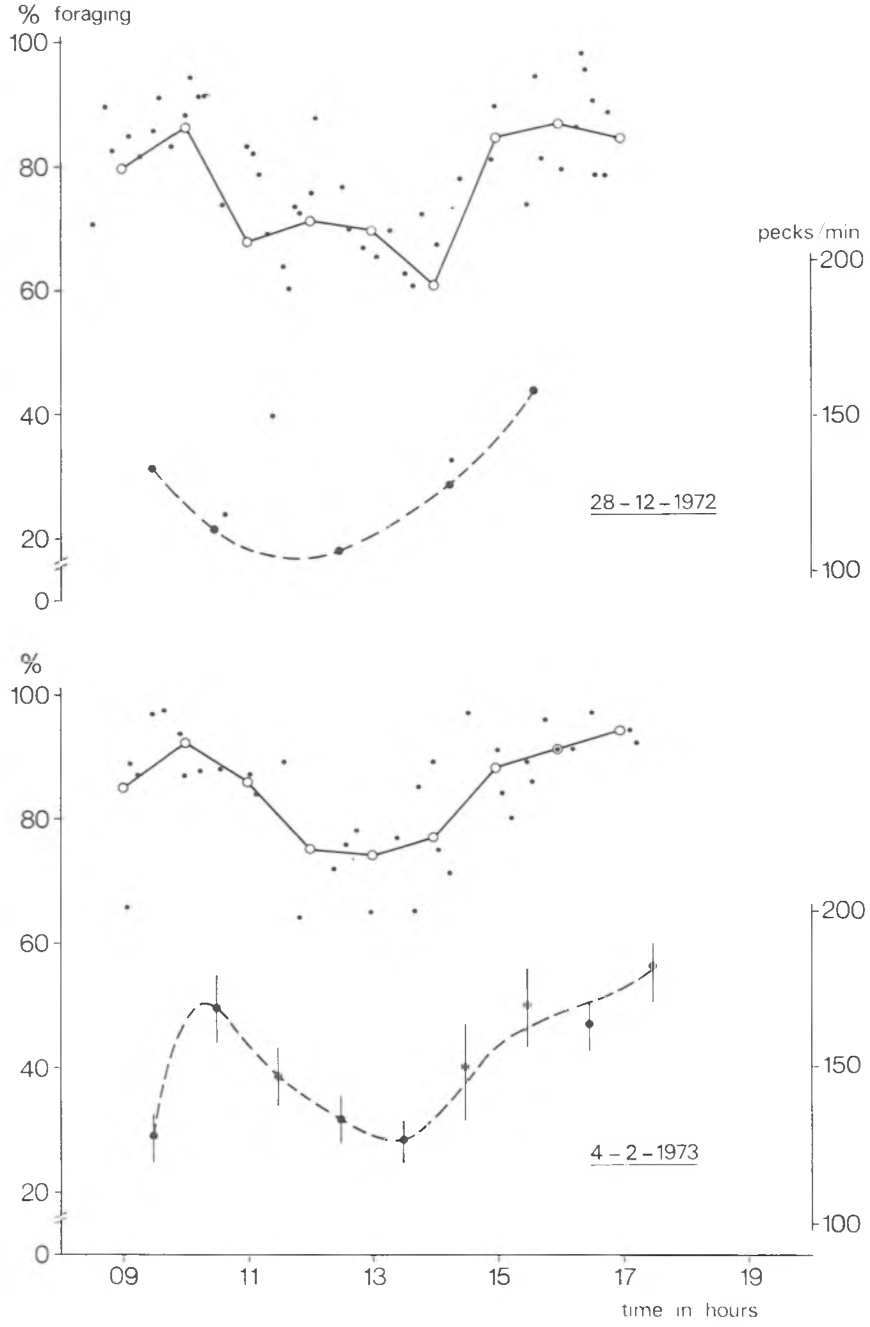

Figure 4. Time devoted to active foraging (open circles, axis on left) **and peck frequency** (solid circles, axis on right) **in the course of the day on two dates in the dark phase of the moon.**

Table 3. Maximal food intake from exclosure data (weights of oven-dried samples)

		Period I 27.12 to 22.1	Period II 16.2 to 13.3
a.	difference between grazed/ungrazed	155 gm/m^2	29 gm/m^2
b.	enclosure cropped to 'goose-grazed height'	110 gm/m^2	58 gm/m^2
c.	mean of estimates a and b	132·5 gm/m^2	43·5 gm/m^2
d.	accumulated droppings during period	53/m^2	23/m^2
	c ÷ d, grass per dropping (mean)	2·50 gm	1·89 gm
	grass per day (on the basis of 135 droppings per day)	338 gm	255 gm

to reproducible results due to the very uneven nature of the sward. We are left then, with two sets of estimates, (a) the difference between total standing crop inside and outside the cages, (b) the amount cut inside the cages when the grass level is adjusted to the level attained by grazing outside the cages.

As can be seen from the table, the daily ration on this basis works out at 255–340 gm dry weight. As we do not have quantitative knowledge of the intensity of grazing by other species, we are not in a position to make adjustments, and must accept the figure as giving a maximum or ceiling value.

Food uptake estimated from production and composition of droppings

The production of droppings by the Barnacle Goose both on the foraging terrain and at the roost totals approximately 160 per 24 hr. This figure was arrived at by a variety of techniques, utilizing both observations on wild Barnacle Geese and observations made on two tame Barnacle Geese kept in a pen (25 × 25 m) on the same fields utilized by the wild individuals.

The number of droppings produced daily on the foraging grounds was determined following three independent methods as follows.

Method (a), *defaecation frequency*

By keeping an individual Barnacle Goose in view through the telescope as long as possible we succeeded in timing the interval between successive droppings 23 times. The mean interval (± 95% conf. int. of the mean) was 3·32 ± 0·59 minutes. An indirect measure of defaecation frequency was obtained when a flock of 181 Barnacle Geese that had been grazing for several hours moved to a field not visited earlier, and was kept under observation until it departed 34 minutes later. At the end of this period we found a total of 1,702 fresh droppings in the field, giving a mean defaecation interval of 3·62 minutes. Provisionally we accept the mean of these two approaches, namely 3·5 minutes, as giving a reliable estimate of the defaecation frequency for actively feeding Barnacle Geese.

The second fact we need to know is over how many hours this mean frequency is maintained. On five occasions we observed flocks of geese that had just arrived from the sleeping areas in the early morning and watched until we noticed the first dropping being formed. Several observers kept continuous watch, each watching a segment of the flock, and on average the first dropping was observed after 57 minutes of foraging. Similar values were obtained for our two tame geese so that we assumed that regular defaecation gets underway after approximately 50 minutes of feeding. For three dates in December therefore we now have the mean starting point for defaecation, the mean rate of defaecation (3·5 minutes) and the mean period of time spent at the foraging grounds. Taking these facts together the mean number of droppings produced per day on the foraging ground would have been 126, 121, and 137 for a mean of 128. The supposition of a set lag time followed by a steady rate of defaecation throughout the remainder of the foraging period on which these figures are based, is borne out by observations reported for other geese. Marriot & Forbes (1970) and Mattocks (1970) indicate a lag time of approximately one hour at the start of the feeding day in the species they worked with, and Dorozynska (1962) gives detailed data for the domestic goose from which it can be inferred that after an initial period of approximately one hour during which the near-empty gut is being filled, defaecation rate remains constant throughout the feeding day, independent of variations in food intake.

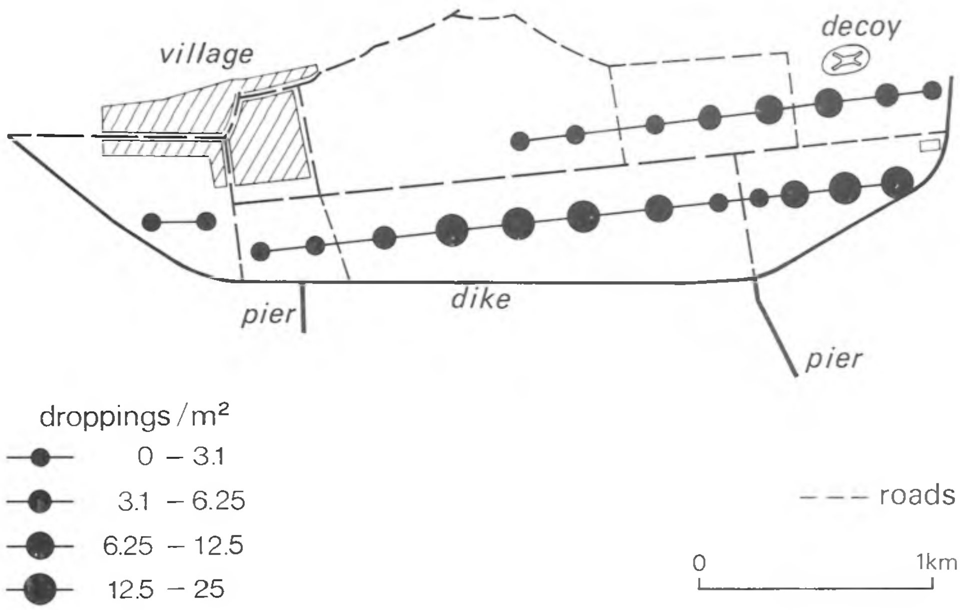

Figure 5. Distribution of Barnacle Goose droppings on pastureland at Schiermonnikoog accumulated up to the end of December 1972. Each point on the figure is the mean derived from 12 plots, each 4 m². The situation of the pastureland depicted will become clear by referring to Figure 1.

Method (b), *total number of droppings divided by goose-days.*

At the close of December we sampled dropping densities over the entire pasture area of the island Schiermonnikoog (four 4 m² quadrates every 100 metres, summarized in Figure 5) and by extrapolation from the 264 sample points arrived at a total of ca. 23,310,000 droppings. From our frequent counts of Barnacle Geese we knew that these droppings had been produced in the course of 155,000 goose-days so that a Barnacle Goose on average would have produced 150 droppings per day according to this approach.

In the foraging areas on the western shore of the Lauwersmeer (Bantpolder) similar data were collected. Again we had a large number of counts allowing us to specify the number of goose-days spent in these areas and the totals over a two month period give 108,000,000 droppings produced during 816,000 goose-days for an average of 132 droppings per day left behind on the foraging areas.

Method (c), *direct observation of tame individuals*

In the period 19th–26th March our two tame Barnacle Geese produced on average 135 droppings during the foraging day (128 fibrous droppings and 7 of the pasty variety termed 'splodge' by Mattocks and identified by that writer as the expulsion of the contents of the caeca).

We now have three independent estimates of the number of droppings produced during the day on the foraging grounds: Method a, 128, method b, 150 and 132 for a mean of 141, method c, 135. The mean of this series (135) is undoubtedly close to the true number.

Droppings produced during the resting phase.

The next problem was to determine how many droppings were produced during the resting period on the mudflats. On 30th December we discovered a sleeping spot on the mudflats that had not yet been reached by the tidal waters. Most of the droppings here lay in discrete piles on the average consisting of 12 droppings. In total over the entire sleeping area 20,600 droppings were found. A photograph taken of the geese foraging in the fields on the following morning gave an accurate count of 846 Barnacle Geese involved. On the average, therefore, 24·4 droppings were produced per goose during the night period, a figure in perfect agreement with the maximum number found in any one pile (25, observed twice). This estimate for the production of droppings in the non-foraging period is reasonably close to the mean of 33 droppings for our tame Barnacle Geese (mean total for

24-hours 168, mean for active foraging period 135, hence by subtraction 33 for the non-foraging period).

Output of droppings in gm/day

As detailed above, our observations indicate that 159–168 droppings are produced by the Barnacle Goose every 24 hours, and we have rounded this figure off to 160 in further computations. On three occasions fresh droppings were collected and dried in an oven until a constant weight was reached. The droppings were weighed individually, and as summarized in Table 4, show a mean dry weight of 0·66 gm. Since 160 droppings are produced daily, the Barnacle Goose thus has an output of 105·6 gm (dry weight) in droppings daily when foraging on pastureland.

Table 4. Weights of Barnacle Goose droppings (grams)

Date	Sample Size	Fresh weight	Dry weight
12.12.72	9	3·65	0·65
16.2.73	90	5·57 ± 0·22	0·66 ± 0·02
6.3.73	100	4·87 ± 0·22	0·66 ± 0·02

Means ±95% confidence interval.

This figure is unexpectedly close to the 120 gm dry weight estimated for the daily production of droppings in the White-fronted Goose by Owen (1972a). Bearing in mind the difference in body weight (Barnacle Goose 1·55 kg, Whitefront 2·3 kg) we had expected the figures to diverge more. (The weights were taken just before release of individuals held during the night following capture (Eygenraam, in Bauer & Glutz (1968); with a full gut the birds might weigh some 10% more.) Three domestic geese studied by Dorozynska (1962, 1969) at weights of 1·08, 2·14 and 2·60 kg had daily outputs of 81, 140 and 197 gm (dry weight) in feeding trials with green grass. Extrapolation from these data would yield an estimate of 122 gm for the Barnacle Goose.

Estimate of daily food intake

Samples of droppings and fresh grass cut to goose grazing height in the field from which the droppings were collected, were submitted to two laboratories for cellulose analysis, and caloric values determined for subsamples using a ballistic bomb calorimeter. All of the data are collected in Table 5. Assuming that our geese did not digest cellulose in appreciable quantities, the ratio of percentage cellulose content in droppings and in the food is a measure of the retention rate (see the formula presented in the introduction). In terms of dry weight, our tame Barnacle Geese kept in a small enclosure retained 33·2% of their food primarily *Lolium perenne*, wild Barnacle Geese feeding on the adjacent fields earlier in the winter 21·7%. This difference is in the direction expected on the basis of the crude fibre content of the grass available. As Nehring & Nerge (1966) have demonstrated in laboratory trials with *Anser anser*, an increase in crude fibre content lowers the digestibility of the feed (presumably because the cell walls are more resistent to mechanical breakdown) as has also been established in other herbivores (McDonald *et al.* 1968). For comparison, Greylag Geese feeding on *Lolium* retained 34·6% of their food (dry weight, computed from Dorozynska, 1969), and feeding on *Puccinellia* 32–40% (Wijngaarden, 1970), whereas Cape Barren Geese *Cereopsis novaehollandiae* feeding on Lucerne *Medicago sativa* with a relatively high crude fibre content of 34%, retained only 25·8% (dry weight).

Table 5. Analysis of grass and droppings

	Wild geese		Tame geese	
	grass	droppings	grass	droppings
% water content of fresh material	74·0%	87·4%	—	—
% cellulose by dry weight[1]	17·2%	21·2%	—	—
% crude fibre by dry weight[2]	21·0%	27·8%	13·1%	19·6%
kcal per gram dry weight	—	—	4·46	4·38
% food retention by dry weight	21·7%		33·2%	
apparent digestibility (caloric basis)	—		34%	

[1] Laboratory for Veterinary Biochemistry, Utrecht.
[2] Agriculture Experiment Station, Maastricht.

As we do not at present know which of the conversion rates is the more representative for the entire winter period, it seems the safest procedure to compute two estimates. The 105·6 gm dry weight in droppings produced daily would then correspond to 134·9 gm (21·7% retention) or 157·6 gm (33·2% retention) intake. The caloric value of the grass (*Lolium perenne* with a small admixture of *Poa pratensis*) was determined at 4·46 kcal/gm, so that gross intake can be estimated at 602–703 kcal/day.

Adequate figures on apparent digestibility (kcal retained divided by kcal ingested) were obtained only for the two tame individuals, an overall figure of 34% being obtained. Applying this to the gross intake estimate gives us a net daily intake of 205–239 kcal for the wild geese.

It is generally accepted that the net caloric intake (equivalent to energy metabolized) should vary with respect to body weight in much the same fashion as does basal metabolism, in other words by an exponential function proportional to approximately the three quarter power of body weight (King & Farner, 1961; Kleiber, 1961; Kendeigh, 1970). In fact this relationship has been demonstrated for birds held in caged conditions but as far as we know there is no generally accepted level or multiple of the basal metabolism valid for unrestrained birds in the wild state. Estimates we have found in the literature are collected in Table 6 and when plotted on a double logarithmic scale (see Figure 6) indicate that a linear relation with body weight is a reasonable approximation of the data through the weight range from 100 grams to 3 kilos. Metabolizable energy for most wild birds appears to be in the neighbourhood of two to four times the basal metabolic rate. It should be kept in mind that the gross intake, the ecologically relevant parameter when considering the impact of a bird on its food resources, will not vary in a predictable relationship with the basal metabolic rate since the digestibility varies so enormously (from above 90% in fish eating birds to as low as 34% in our geese).

The most elegant study to date of energy expenditure (here taken as equal to metabolizable energy) in an unrestrained bird has been carried out on a passerine, the Purple Martin *Progne subis* by Utter & Lefebvre (1970, 1973). It is reassuring to find that here, too, the daily energy expenditure averages 2·2 times the basal metabolic rate.

An alternative approach for arriving at an energy expenditure estimate is to obtain a detailed time budget for the species in question and measure the energy expenditure of the various types of activity. In the case of our Barnacle Geese in December for example, our observations indicate that in a typical 24 hour period the birds walked a distance of 1–1½ km during foraging, and flew approximately 30 km in the half hour devoted daily to flight (chiefly commuting between sleeping and foraging areas). Making use of the formula developed by Tucker (1972) the metabolic cost of these activities (walking + flight) can be estimated at a total of 70 kcal/day. Heat loss, another important avenue of energy expenditure, can be estimated with reference to the experimental work of Irving, Krog & Monson (1955) on the Pacific Brent Goose *Branta bernicla orientalis* to constitute approximately 120 kcal/day and is therefore within the range of standard metabolic rate. Taking into account energy required for active grazing all that could be said on the basis of this as yet incomplete budget is that the daily net caloric intake would have to total at least 200 kcal. Another approach has been taken by Lefebvre and Raveling (1967) in what they termed thermal modelling. On the basis of their computations for the Canada Goose, scaled down to the mean body weight of the Barnacle Goose (1·55 kg) the expected net caloric intake would be in the neighbourhood of 250 kcal/day.

Clearly further refinements are called for before any one of these alternative methods will yield an explicit result, but so far as the figures go it would appear that our field estimate is at least of the right order of magnitude.

Grazing pressures and carrying capacity

On the basis of repeated census throughout the study area the number of goose-days can be calculated. In Table 7 the number of goose-days has been specified for each of five sub-areas, and with the total area utilized by geese known, total goose-days for the season per hectare can be computed. As can be seen in the table, values in our study varied between 700–1,550 goose-days/ha for the grassland areas most frequently visited. Recently Owen & Campbell (1974) have presented data on winter feeding of Barnacle Geese at Caerlaverock, Scotland, and indicate that 1,900 goose-days per hectare accumulated on the grazed merse where clover stolons accounted for about half of the food. Grazing pressures for other species of geese have been reported for several other areas. In England Owen (1972b) recorded grazing pressures

Table 6. Estimates of net caloric intake (ME = energy metabolized daily) in wild non-passerine birds

Species	Body weight (gm)	ME (kcal)	Authority
Saw-whet Owl *Aegolius acadicus*	90	59	Graber, 1962
Mourning Dove *Zenaidura macroura*	115	53	Schmid, 1965
Sparrow Hawk *Accipiter nisus* (female)	246	105	Tinbergen, 1946
Long-eared Owl *Asio otus*	285	92	Wijnandts, pers. com.
Long-eared Owl *Asio otus*	299	159	Graber, 1962
Blue-winged Teal *Anas discors*[1]	320	62	Owen, R. B., 1969, 1970
Short-eared Owl *Asio flammeus*	360	188	Graber, 1962
White-tailed Ptarmigan *Lagopus leucurus*	360	105	Moss, 1973
Cattle Egret *Ardeola ibis*	383	150	Siegfried, 1969
Rock Ptarmigan *Lagopus mutus*	420	100	Moss, 1973
Willow Ptarmigan *Lagopus lagopus*	500	140	Moss, 1973
Barnacle Goose *Branta leucopsis*	1550	205–239	this study
Snowy Owl *Nyctea scandiaca*	2086	272	Gessaman, 1972
Cormorant *Phalacrocorax carbo*	2130	400	van Dobben, 1952
Wood Stork *Mycteria americana*	2500	450	Kahl, 1964

[1] Estimate for non-flight conditions, hence the arrow in Figure 6.

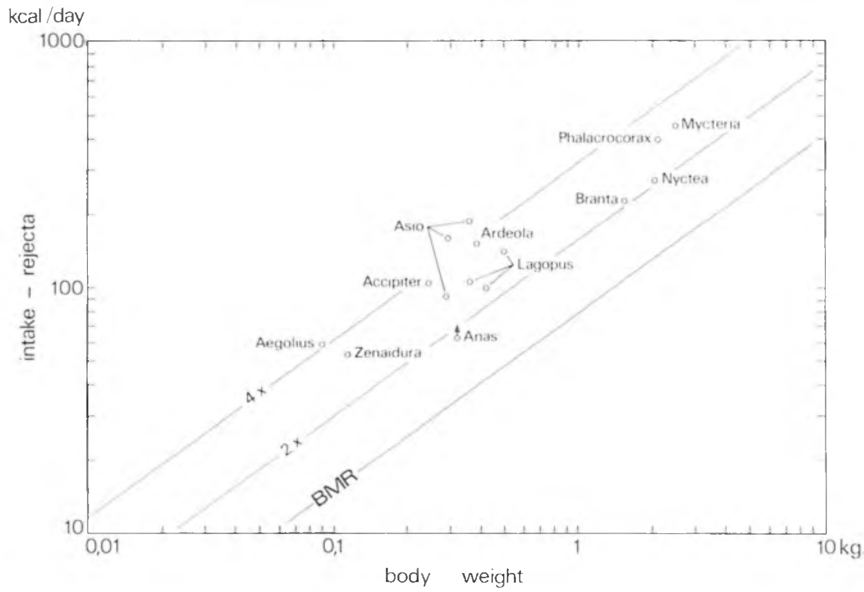

Figure 6. Energy metabolized daily (= total intake minus the rejecta) **in free-living non-passerine birds, plotted in relation to body weight.** Both scales are logarithmic, such that exponential functions become straight lines. The relation between BMR (Basal Metabolic Rate) and body weight is thus depicted by a straight line, and together with twice the BMR, and four times the BMR as predicted for non-passerines (computed from Kendeigh 1970) is shown in the figure. The original data are listed in Table 6.

Table 7. Barnacle Goose grazing pressures, winter 1972–1973

Locality and period utilized by geese		Goose-days (season total in thousands)	Area (ha)	Goose-days/ha (a) overall	(b) ceiling
Lauwersmeer	14.10–11.12	743	3300	230	
Groninger kwelders	27.11–18.3	200	280	700	
Bantpolder	25.6–7.4	820	490	1550	2500 p
De Kolken	26.7–12.2	184	1400	130	
Schiermonnikoog	2.10–4.4	287	306	960	2800 p 3300 m

Areas concerned are identified in Figure 1; p = diked-in pastureland, m = merseland.
Ceiling values for grazing pressures computed from droppings transects of kilometre length, see text.

which yield season averages of 630–780 goose-days/ha for the White-fronted Goose at the New Grounds, Slimbridge, when computed over the total refuge area of 506 ha. Certain parts of the refuge attracted grazing pressures far in excess of this mean value, the heaviest used areas reaching 1,730 goose-days/ha. In Scotland, Newton & Campbell (1973) working with Greylag and Pink-footed Geese *Anser brachyrhynchus* recorded averages of 78–120 goose-days/ha as measured over the entire study area. Their computations for individual fields are more relevant in this connection, the figures for grassland ranging from 640–1,350 goose-days/ha. Finally Kuyken (1969) working in Belgium has recorded mean grazing pressures ranging from 741–876 goose-days/ha for an area visited by White-fronted and Pink-footed Geese (areas of heaviest usage surpassing 1,000 goose-days/ha). Certainly the values reported for our study area are within the range of observations elsewhere.

An indirect measure of grazing pressure is provided by our counts of the cumulative number of droppings per square metre. Knowing the number of droppings a Barnacle Goose produces per day on the foraging grounds (135) these figures can also be converted to goose-days. In this way a much finer delineation of grazing pressure is possible. Our droppings transects both in Schiermonnikoog (as shown in Figure 5) and in the Bantpolder reveal the influence of the proximity of roads and other sources of disturbance: the central sector of the fields suffer the highest grazing pressures. Similar effects have been noted by Kuyken (1969) and Owen (1972b) in their work on White-fronted and Pink-footed Geese.

It is tempting to derive a measure of carrying capacity from the droppings transects. In our experience, the pattern of utilization followed by the geese is that a relatively small area is visited repeatedly until quite suddenly the birds commence foraging elsewhere; only sporadically will the old area be visited again in that season. From the droppings transects grazing pressures accumulated until the cut-off point can be estimated. In order to obtain a representative figure that could be applied to large areas, we decided to base the computations on entire transects of at least one km in length, with permanent quadrates at every 100 m. In five sub-areas covered by such transects (each represented by at least 11 permanent plots) the grazing pressure computed over all points reached values from 2,200–3,300 goose-days/ha, with a mean of 2,600. We interpret this figure as a measure of carrying capacity because the geese shifted to other areas in the vicinity when this value had been reached. In the Bantpolder for instance, three transects gave values of 2,200, 2,300 and 2,500 goose-days/ha in late December at which point the twenty thousand geese which had been using the area dispersed over other areas in Friesland. No changes in the weather coincided with this shift and geese did not again visit the Bant in numbers (compare Figure 2). Owen (1972b) has presented a provisional estimate of 1,730 goose-days/ha as the carrying capacity for the White-fronted Goose at the New Grounds (confirmed by Owen (1973)). Assuming that food consumption indeed varies in relation to the 0·75 power of body weight (see discussion on p. 14), our empirical limit of 2,600 Barnacle goose-days/ha would be equivalent to 1,900 Whitefront goose-days (respective weight 1·55 and 2·3 kg). In other words, our finding is virtually identical with Owen's estimate. As Owen's research on Barnacle Geese at Caerlaverock continues, more precise comparisons with our situation, where clover stolons form only a minor component of the diet, will become possible.

Some computations on the basis of the estimated food intake of Barnacle Geese yield some credence to the suggestion of the limit of 2600 goose-days just mentioned. According to our estimate of 160 gm dry weight intake/goose/day, this corresponds to a food uptake of approximately 42 gm dry weight/m^2. This figure can be checked against the living grass potentially available by making use of observations as yet unpublished carried out by Van Burg and Postmus in 1971. These workers provide estimates of the mean yield in terms of dry weight of grass/cm grass-length/m^2. In our study area the length of living grass (i.e. sward height) declines by approximately 4 cm throughout the goose season. According to the data of Van Burg and Postmus this decline in length would correspond with a yield of 35 gm/m^2, a figure in astonishingly close agreement with the amount estimated to have been removed by the Barnacle Goose. It should further be pointed out that the geese tended to abandon areas when the height of the sward had declined below approximately 2 cm. Examination of the sward at this point revealed that approximately three-quarters of all grass blades within the effective range of the geese (i.e. higher than 15 mm) had been grazed.

It is unfortunate that our own measurements of standing crop did not take into account a subdivision into living and dead material so that we possess no estimate of the rate of mortality of undisturbed grass during the winter season. A partial reconstruction is, however, possible for the merseland vegetation. In early December, 1972, our measurements indicate that approximately 400gm (dry matter)/m^2 was available when the main mass of Barnacle Geese arrived on Schiermonnikoog. From Ketner's (1972) painstaking work on similar vegetations on nearby Terschelling, it can be estimated that 1/4 of this, or 100 gm/m^2, consisted of living material, and hence was the amount potentially available to the geese. How much of this was low to the ground (less than approximately 13 mm in height) and thus out of reach of the geese we do not know. We have seen that approximately 40 gm (dry matter)/m^2 was removed by the geese before they moved on to other fields, so it is clear that a large proportion of the grass actually available is harvested. Much of this material is doomed to disappear anyway in the course of the winter, however. Alberda made a series of measurements on a merseland vegetation on Schiermonnikoog in the winter of 1968–1969 (see Vervelde, 1970) and showed that the standing crop declined by about half in the period from November to March, irrespective of whether grazing had occurred or not (51% within enclosures, 58% decline in control areas grazed by rabbits) an expression of the mortality and subsequent decomposition in this period.

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Summary

The Barnacle Goose *Branta leucopsis* in winter, according to observations made in the northern Netherlands in the 1972–1973 season, consumes 135–158 gm (dry weight) of grass daily, equivalent to 602–703 kcal, and retains approximately 34% (i.e., metabolized energy = 205–239 kcal). This rough estimate, indicating that wild geese daily expend an amount of energy that can be expressed as twice their basal metabolic rate, was derived from the following information. (a) The Barnacle Goose produces 160 droppings per day, (b) a dropping weighs 0·66 gm dry, (c) analysis of crude fibre and of cellulose in samples of both droppings and the grass the geese were feeding on, with the assumption that these components are undigestible, indicates that 21·7–33·2% (dry weight) of the food ingested is retained, the remainder being rejected as droppings, (d) the caloric value of grass was 4·46, of droppings 4·38 kcal/gm dry weight.

Since our grass samples were clipped samples disregarding the effects of selectivity by the geese (for instance the preference for grass tips which have a lower cellulose content than the plants as a whole) the weak link is likely to be (c), and we expect our value to be an underestimate. Comparison with several theoretical expectations, and with results (most of them equally crude) from studies on other wild birds, does suggest, however, that our estimate is reasonably close to the mark.

In our study area the Barnacle Goose relies heavily on intensely managed pastureland for its winter foraging (66% of all goose-days were spent on grassland grazed by sheep or cattle). In the course of the winter the geese utilized a number of areas in succession, and from transects where the cumulative number of droppings was determined, it was found that the geese tended to abandon an area when approximately 2,600 goose-days had accumulated per hectare. Utilization was, however, not evenly distributed, the least disturbed sectors reaching grazing pressures far in excess of this. Further work will be required to link this empirical figure for carrying capacity, equivalent to a consumption of 40 gm dry matter per square metre, with the amount of living matter available (approximately 100 gm per square metre at the beginning of the winter).

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B. Ebbinge and Dr R. Drent, Zoological Laboratory, University of Groningen, Haren (Gr.), Netherlands.
K. Canters, Plant Ecology Laboratory, University of Groningen, Haren (Gr.), Netherlands.