Assessment of food intake rates in pink-footed geese Anser brachyrhynchus based on examination of oesophagus contents

Authors: Therkildsen, Ole R., and Madsen, Jesper

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Assessment of food intake rates in pink-footed geese *Anser brachyrhynchus* based on examination of oesophagus contents

Ole R. Therkildsen & Jesper Madsen

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An alternative to the so-called 'marker substance' method used to estimate daily food intake in geese is presented. Based on the assumption that a grazing bird takes one leaf per peck, the daily food intake rate can be calculated by multiplying mean bite weight, peck rate and total daily foraging time. Wintering pink-footed geese *Anser brachyrhynchus* feeding on pastures and winter wheat fields were collected and samples of leaves in the oesophagus were measured, dried and weighed individually. We measured leaf lengths in unexploited areas of the same fields upon which geese had been feeding. Peck rates of winter wheat feeding geese were measured. Daily foraging time was obtained from observations of activity budgets of flocks of geese. Daily food intake of winter wheat feeding geese was estimated at 159-229 g ash free dry weight (AFDW) during late winter and at 188-212 g AFDW in early spring. For geese feeding on pastures in early spring food intake was estimated at 170 g AFDW. Averages were generally in accordance with estimates derived by the 'marker substance' method. Bite length was positively related to primary leaf length of winter wheat, suggesting that geese adjust bite size to available leaf lengths. There was a negative relationship between peck rate and length of all leaf types, but the relationship was only significant for primary leaves. Based on the assumption that bite length was identical to primary leaf length and the relationship between primary leaf length and peck rate, a quadratic relation between primary leaf length and instantaneous intake rates was derived, yielding a peak intake rate of 0.62 g AFDW min^{-1} at a primary leaf length of 8.4 cm. In the beginning of the winter, bite lengths were close to this optimal leaf length, but decreased during winter.

Key words: Anser brachyrhynchus, feeding energetics, food intake, geese, herbivory, pink-footed goose

Ole R. Therkildsen & Jesper Madsen, National Environmental Research Institute, Department of Coastal Zone Ecology, Kalø, Grenaavej 12, DK-8410 Rønde, Denmark - e-mail: jm@dmu.dk

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Traditionally, daily food intake in geese has been assessed by use of the so-called 'marker substance' method developed on red grouse *Lagopus lagopus scoticus* (Moss & Parkinson 1972) and geese (Ebbinge, Canters & Drent 1975, Drent, Ebbinge & Weijand 1978/79). The method relies on the fact that certain food components which are not digested during gut passage will be concentrated in the droppings. Based on the ratio of this marker in food items and faecal material, the retention rate can be calculated and the daily food intake can be estimated if the daily production of droppings is known Hence, the method relies heavily on estimates of defaecation rates, which may be biased and/or imprecise (Bédard & Gauthier 1986) and on retention rates, which may be subject to diurnal variation as a result of variation in throughput time (Prop & Vulink 1992).

Recently, Rowcliffe, Sutherland & Watkinson (1999) imitated goose grazing on green algae using an artificial brent goose *Branta bernicla bernicla* bill to measure bite size (weight) used for calculations of intake rates. However, since pink-footed geese *Anser brachyrhynchus* are highly selective feeders showing preference for particular plant parts (Fox 1993, Therkildsen & Madsen 1999) this method is not applicable to graminoid feeding geese.

We present an alternative more direct method than the 'marker substance' method for estimating daily food intake, using oesophagus contents of food material, peck rates and feeding duration. In contrast to current approaches, this new method may be used on specific individuals on a short-term basis due to its instantaneous nature. Our study is based upon pink-footed geese feeding on pastures and winter wheat fields during winter. Based on the assumption that a grazing goose takes one leaf per peck, the daily food intake can be calculated by multiplication of mean bite weight, peck rate and total daily foraging time. Since geese feeding on winter wheat and *Poa* sp. in the area were found to positively select for the most profitable leaves (Therkildsen & Madsen 1999) it seems reasonable to assume that only one leave is taken per peck.

The extent to which available leaf length affects bite length and peck rate employed by the geese was investigated to assess any effect on instantaneous intake rates. Furthermore, the relationship between leaf length and time of the wintering period was examined.

Methods

Our field work was carried out in Ballum Enge (55° 07'N, 08°40'E), a polder area situated on the coast of the Danish Wadden Sea. It consists of a mosaic of pastures, dominated by *Poa* ssp. interspersed with *Festuca pratensis*, *Alopecurus* ssp. and *Phleum pratense*, and winter cereal fields, sown mainly with winter wheat *Triticum aestivum*. Ballum Enge is an important wintering area for the Svalbard population of pink-footed geese. Geese arrive during late December and peak numbers are reached in January-February when 20,000 geese overwinter in the area (Madsen, Kuijken, Meire, Cottaar, Haitjema, Nicolaisen, Bønes & Mehlum 1999). The geese leave the area during March. At night the geese roost on the intertidal mud flats or salt marshes outside the sea dikes.

Below the individual leaves of winter wheat are referred to as primary, secondary and tertiary, respectively. The primary leaf is the youngest, erect leaf, whereas the older, subtending secondary and tertiary leaves are ascendent, but not erect. The geese included in this study were collected for carcass analysis and other purposes of which the results are yet to be published (J. Madsen, unpubl. data). On 20 January, 2 and 10 February, 1, 5 and 7 March 1996, a total of 12 geese were shot with rifle while feeding on winter wheat fields. On 20 January, 2 February and 1 March 1996, primary (the youngest) leaf lengths of 15-20 ungrazed shoots were measured in unexploited areas of the fields where geese were collected. On 5 and 7 March 1996, a total of four geese were shot while feeding on pastures. On 3 and 16 February 1998, five additional geese were shot while feeding on winter wheat fields. Primary leaf lengths were measured as described above.

Oesophagus contents consisting of pieces of grass or winter wheat were removed from each collected individual and a sample was taken with a pincer and all leaves were lined up and selected at random to avoid bias to large leaves (N = 21-125, see Table 1). In a few cases, i.e. when the oesophagus contents were small, all leaves were included. Leaf lengths were measured and leaves were dried at 80°C for 24 hours and weighed individually to obtain estimates of bite weights. Since the fraction of dead leaves in the oesophagus contents of six geese shot in January - February 1996 on winter wheat fields was remarkably high, additional samples (N = 14-50) were taken from the five individuals shot in February. The dead leaf length was measured and compared to the total leaf length. The dead leaf fraction was negligible for geese feeding on pastures in 1996 and on winter wheat in March 1996 and February 1998. The inorganic fraction was assumed to be 1.525% (O.R. Therkildsen & J. Madsen, unpubl. data).

Since no data on peck rates in 1996 were available, data from 1997 (Therkildsen & Madsen 2000, O.R. Therkildsen, unpubl. data) and 1998 were used in the calculations leading to two estimates of the daily food intake. Time budget data were obtained from Therkildsen & Madsen (2000) who found that the geese spent 84 and 75% of the daytime feeding on pastures and winter wheat fields, respectively. Daylength was determined as the period from 15 minutes before sunrise till 15 minutes after sunset.

Variance and mean of bite weights, pecking rate, dead leaf and inorganic fractions were estimated by means of bootstrapping (resampling, with replacement, from the observed sample). Hence, 5,000 numbers were regenerated for each parameter and the daily intake was estimated by randomly selecting 1,000 numbers from the distributions and multiplying these accordingly. Monthly averages were calculated using these estimates.

During February 1998, peck rates of geese feeding on 13 different winter wheat fields were timed using a stopwatch, and expressed as the time it took to make 25 pecks (N = 21-40). Later, when the flocks of geese had left the fields, 15-20 ungrazed winter wheat shoots were collected in unexploited areas of the fields and primary, secondary and tertiary leaf lengths were measured. The relative contribution of individual leaf types to the total variation in peck reate was determined using stepwise regression.

Statistical analyses were performed using SAS/STAT® (SAS Institute 1989) and S-PLUS® 2000 (MathSoft 1999). All tests were two-tailed. Percentages were arcsine transformed before analysis.

Results

Bite lengths, bite weights and feeding parameters used in the calculations are presented in Table 1. In February 1996, the dead leaf fraction did not differ between individuals feeding on winter wheat (ANOVA, $F_{4,142}$ = 0.479, P > 0.05) and was calculated to be 23.0 ± 0.4% (mean ± SE).

The estimates of daily food intake were calculated using peck rates from February 1997 and 1998, respectively. The winter wheat feeding goose shot on 20 January 1996, had an estimated daily food intake of 271 and 241 g ash free dry weight (AFDW). The daily average food intake was estimated at 229 and 203 g AFDW for winter wheat feeding geese in February 1996, at 212 and 188 g AFDW for winter wheat feeding geese in early March 1996, and at 159 g AFDW in February 1998. For geese feeding on pastures in early March 1996 the daily intake was estimated at

Table 1. Feeding parameters, bite lengths, bite weights and calculated intake rates of pink-footed geese collected on winter wheat fields and pastures in Ballum Enge in 1996 and 1998

Date	Food	Foraging time (min)	Peck rate Sec./25 pecks ± SE	Bite length ± SE (mm)	Bite weight ± SE (mg)	Number of bites N	Corr. intake[d] ± SE (AFDW/day)	Monthly average ± SE (AFDW/day)
20.01.96	Winter wheat	362	13.2±0.2[a]/14.9±0.2[b]	7.4 ± 0.7	8.7 ± 1.0	49	271±0.5/241±0.4[e]	(271±0.5/241±0.4)
02.02.96	Winter wheat	399	13.2±0.2[a]/14.9±0.2[b]	4.6 ± 0.3	4.0 ± 0.6	67	139±0.2/123±0.2[e]	229±116/203±104
02.02.96	Winter wheat	399	13.2±0.2[a]/14.9±0.2[b]	6.3 ± 0.5	7.4 ± 0.8	45	253±0.4/225±0.4[e]	
02.02.96	Winter wheat	399	13.2±0.2[a]/14.9±0.2[b]	8.4 ± 0.7	11.8 ± 1.1	62	404±0.6/359±0.5[e]	
02.02.96	Winter wheat	399	13.2±0.2[a]/14.9±0.2[b]	3.5 ± 0.2	3.1 ± 0.3	82	107±0.2/95±0.1[e]	
10.02.96	Winter wheat	424	13.2±0.2[a]/14.9±0.2[b]	5.5 ± 0.7	6.6 ± 0.8	47	242±0.4/215±0.4[e]	
01.03.96	Winter wheat	493	13.2±0.2[a]/14.9±0.2[b]	3.9 ± 0.2	3.4 ± 0.3	59	185±0.3/165±0.2[e]	212±32/188±29
01.03.96	Winter wheat	493	13.2±0.2[a]/14.9±0.2[b]	4.4 ± 0.3	4.8 ± 0.5	53	266±0.4/237±0.3[e]	
05.03.96	Winter wheat	506	13.2±0.2[a]/14.9±0.2[b]	3.0 ± 0.2	3.6 ± 0.2	60	202±0.2/179±0.2[e]	
05.03.96	Winter wheat	506	13.2±0.2[a]/14.9±0.2[b]	3.0 ± 0.3	3.9 ± 0.3	43	218±0.3/194±0.2[e]	
07.03.96	Winter wheat	513	13.2±0.2[a]/14.9±0.2[b]	2.5 ± 0.2	3.1 ± 0.3	46	176±0.3/157±0.2[e]	
07.03.96	Winter wheat	513	13.2±0.2[a]/14.9±0.2[b]	3.2 ± 0.2	3.9 ± 0.3	58	224±0.3/199±0.2[e]	
03.02.98	Winter wheat	403	14.9±0.2[b]	4.4 ± 0.2	4.8 ± 0.3	69	191±0.2	159±22
03.02.98	Winter wheat	403	14.9±0.2[b]	4.6 ± 0.3	3.4 ± 0.3	33	134±0.2	
16.02.98	Winter wheat	445	14.9±0.2[b]	3.4 ± 0.5	3.7 ± 0.2	95	165±0.1	
16.02.98	Winter wheat	445	14.9±0.2[b]	3.0 ± 0.1	3.7 ± 0.1	125	162±0.1	
16.02.98	Winter wheat	445	14.9±0.2[b]	3.0 ± 0.2	3.3 ± 0.2	71	144±0.1	
05.03.96	Pasture grass	566	12.1±0.2[c]	3.8 ± 0.2	3.0 ± 0.2	58	210±0.2	170±81
07.03.96	Pasture grass	574	12.1±0.2[c]	2.8 ± 0.2	1.5 ± 0.2	39	105±0.2	
07.03.96	Pasture grass	574	12.1±0.2[c]	4.2 ± 0.5	3.8 ± 0.7	21	265±0.7	
07.03.96	Pasture grass	574	12.1±0.2[c]	3.0 ± 0.2	1.4 ± 0.1	57	99±0.1	

[a] February 1997 (N = 114); [b] February 1998 (N = 395); [c] Late February 1997 (N = 103);
[d] Inorganic fraction of 1.525% (Therkildsen & Madsen, unpubl. data) excluded;
[e] Dead leaf fraction excluded.

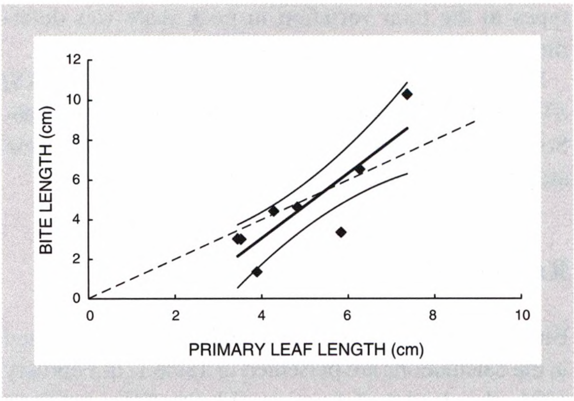

Figure 1. Relationship between bite length of pink-footed geese and primary leaf length of winter wheat. The regression line has been fitted to the formula: $y = 1.64\,x - 3.50$ ($R^2 = 0.72$, df = 6, $P < 0.01$, 95% CL). The broken line illustrates the situation where bite and leaf lengths are identical.

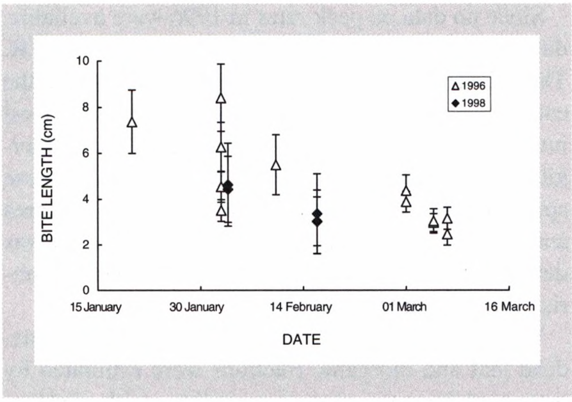

Figure 3. Relationship between bite length for winter wheat feeding pink-footed geese (means ± 95% CL) and time of the wintering period. The relationship is negative and significant ($r_s = -0.78$, $P < 0.001$).

170 g AFDW (using peck rates from late February 1997; see Table 1).

In winter wheat feeding geese bite length was positively related to primary leaf length (Fig. 1). Only primary leaves contributed significantly to explain variation in peck rate ($R^2 = 0.43$, df = 12, F = 8.25, $P < 0.05$) (Fig. 2). Bite length of winter wheat feeding geese decreased throughout the period (Fig. 3).

Instantaneous intake rates were derived from relationships between primary leaf length/peck rate and primary leaf length/bite length assuming that bite length was identical to primary leaf length. To convert bite length to bite weight, the following calibration equation was used: bite weight = 0.001 x bite length + 0.0005 ($R^2 = 0.54$, df = 711, $P < 0.0001$). The resulting theoretical relationship between primary leaf length and instantaneous intake rate is a quadratic curve ($y = -0.008x^2 + 0.13x + 0.08$) with a peak intake rate of 0.62 g AFDW min^{-1} at a primary leaf length of 8.4 cm.

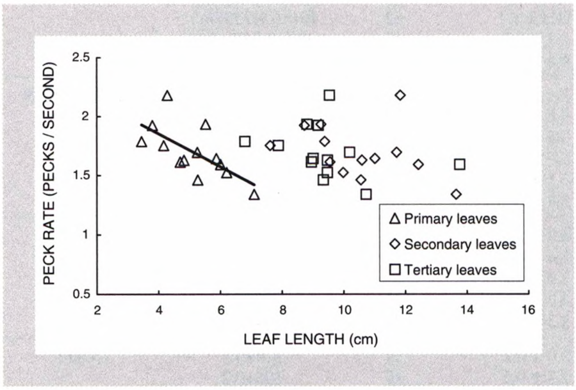

Figure 2. Relationship between leaf length of winter wheat and pecking rate of pink-footed geese. The regression line for primary leaves has been fitted to the formula: $y = -0.14\,x + 2.41$ ($R^2 = 0.43$, df = 11, $P < 0.05$). The relationships between secondary/tertiary leaves and peck rate are negative, but not significant.

Discussion

Interactions between leaf length, bite length and peck rates

The relationship between bite length and primary leaf length shows that bite length is not fixed, but adjustable in relation to availability of leaf lengths.

The negative relationship between peck rate and length of primary leaves of winter wheat implies that geese select for these high quality leaves. Presumably, as leaf length increases, the handling time per bite, i.e. the time it takes to bite off, manipulate and swallow the leaf, increases accordingly. Consequently, this lowers peck rates at increasing leaf length. Therkildsen & Madsen (1999) found that geese positively selected for both primary and secondary leaves of winter wheat on the basis of protein contents. Supposedly, geese fine-tune peck rates to the length of the erect, apparent primary leaves and subsequent to the removal of these, take the subtending secondary leaves without any effect on the peck rate.

Since primary leaf length is less than 8.4 cm, the instantaneous intake rate is likely to be lower than the calculated optimum if feeding exclusively on this type of leaves. However, when the longer, equally nutritious (Therkildsen & Madsen 1999) secondary leaves are included, the average bite length is increased and intake rates may be closer to the calculated optimum.

Bite length of winter wheat decreased during late winter reflecting gradual resource depletion. In corollary, as leaf tips are depleted, geese are forced to consume the shorter leaf bases by which they cannot maintain instantaneous intake rates even if they increase peck rates.

Daily intake rates

Using the 'marker substance' method with detergent fibre and ash as markers, Therkildsen & Madsen (2000) estimated that in February 1997 the daily food intake for pasture and winter wheat feeding pink-footed geese was 148 and 157 g AFDW. The results obtained by the 'oesophagus content' method for geese feeding on pastures in early March 1996 (170 g AFDW) and on winter wheat in March 1996 (188-212 g AFDW) and February 1998 (159 g AFDW) are in accordance with the 'marker substance' results. The higher intake in March 1996 is partly explained by the longer feeding days (day length in early March is approximately 15% longer than in mid February). Madsen (1985) found that during late March-early April, pasture feeding pink-footed geese had an intake rate of 159 g AFDW (estimated by the 'marker substance' method).

Our results for January and February 1996 are comparatively high, which may partly be explained by the bite lengths used in the calculation. In one case it was 8.4 cm, which inevitably will have repercussions on peck rates, which may have been lower than those used in the calculation. In 1997 and 1998 geese were not observed to take bites of this length (O.R. Therkildsen, pers. obs.). The reasons why geese took longer bites in 1996 are not known, but the severe winter with effective ground temperatures below -20°C (J. Madsen, unpubl. data) may have caused leaf tips to die off, forcing geese to increase bite length to include the basal, more nutritious leaf parts. At temperatures below 0°C, geese are regularly seen feeding while sitting, presumably to reduce heat loss from the legs. In this situation geese graze the surrounding area intensively before moving to another spot. Both phenomena may explain the high fraction of dead material consumed and the extremely long bite lengths taken in January - February 1996.

It is likely that leaf lengths encountered when foraging on winter wheat in March 1996 were within the range as in 1997, resulting in similar peck rates and, consequently, producing a reasonable fit to the results obtained by the 'marker substance' method when longer day lengths are taken into account. The bite length employed by geese feeding on pastures may not differ significantly between years, as the geese only switch to this habitat when pastures become energetically favourable (Therkildsen & Madsen 2000), i.e. when leaves have reached an appropriate size to select for. This may explain why our result for March 1996 obtained using the 'oesophagus content' method (based on peck rates from 1997) is similar to that obtained using the 'marker substance' method in 1997.

Since individual leaf lengths of winter wheat depend on the developmental stage of the shoots, which in turn depends on time of sowing and weather conditions during autumn and winter, the leaf length is likely to vary between years. This may at least be part of the explanation for the discrepancies found when estimating the intake using oesophagus contents and peck rates from different years.

In conclusion, the results show that the 'oesophagus content' method provides reliable estimates of food intake, but that it has to be accompanied by observations of feeding behaviour and measurements of food availability and characteristics to account for differences between habitats and years. Since bite length and peck rate are likely to vary during the day, affecting the instantaneous intake rate, the calculated daily averages must be regarded as rather crude estimates reflecting the intake of individual geese at the time of collection. To obtain reliable estimates of daily food intake rates using the 'oesophagus content' method, larger samples are needed.

Furthermore, understanding the relationship between peck rate and bite length is imperative to achieve reliable estimates of food intake by this method. Once this relationship is established intake rates in geese feeding on graminoids can be obtained in a straightforward way by examination of oesophagus contents using peck rates and activity budgets. However, the disadvantage is that the method is consumptive in that it requires the collection of birds.

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