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ORIGINAL ARTICLES

Energetics of feeding on winter wheat versus pasture grasses: a window of opportunity for winter range expansion in the pink-footed goose *Anser brachyrhynchus*

Ole R. Therkildsen & Jesper Madsen

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Traditionally, pink-footed geese *Anser brachyrhynchus* wintering in Denmark, the Netherlands and Belgium have used the Danish sites only during mild winters, rapidly moving southwards in case of cold spells. Since the 1980s, an increasing number of geese have remained on the Danish wintering grounds despite cold spells, foraging on pastures and winter wheat *Triticum aestivum* fields. We compare the daily time and energy budgets and the food quality in the two habitats during winter. Winter wheat fields were increasingly used by the geese as temperatures dropped. At temperatures around 0°C, the geese foraged in both habitats, spending on average 83.8% and 74.9% of the daytime foraging in pastures and winter wheat, respectively. The estimated daily energy expenditure was slightly higher on pastures than on winter wheat fields (1,076 vs 1,057 kJ). The estimated daily food intake determined using the 'marker substance' method was 148 and 157 g ash free dry weight (AFDW) in geese feeding on pastures and winter wheat fields, respectively, equivalent to a daily net energy intake of 1,109 kJ and 1,145 kJ. Daily food intake, estimated on the basis of oesophagus contents of collected birds, was 170 g AFDW in pasture feeding geese and varied within 159-229 g AFDW in winter wheat feeding geese. In the mild winter, the protein content in winter wheat and *Poa* did not differ, whereas in the severe winter the protein content remained high in winter wheat but decreased in *Poa*. During the winters of 1994-1996, the abdominal profile index, API, in individually neck-banded geese observed repeatedly, only changed significantly during late January 1996. Neither during cold spells was there any change in API. Since the 1980s, the area covered by winter wheat has increased markedly in Denmark. Because winter wheat represents a reliable and profitable food source even in severe winters, the recent change in agricultural practice has enhanced the development of a new wintering strategy of pink-footed geese, allowing a northward expansion of their winter range. Potentially, this will increase the crop damage conflict and may lead to further population growth.

Key words: body mass, feeding ecology, habitat selection, wintering ecology

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During the 1970s-1990s, the number of geese wintering in western Europe has tripled (Madsen, Fox & Cracknell 1999). Simultaneously, the geese have increasingly shifted from feeding in natural habitats and rough grassland/saltmarshes to cultivated grassland and arable crops. Van Eerden, Zijlstra, van Roomen & Timmerman (1996) hypothesised that this transition enhanced the feeding opportunities especially in winter when food quality and quantity in the traditional habitats deteriorated and that this may have contributed to improved survival and, ultimately, the observed population increases.

Furthermore, in some goose populations winter range expansions have been observed, e.g. in two populations of pink-footed geese *Anser brachyrhynchus* (Gill, Watkinson & Sutherland 1997, Madsen, Kuijken, Meire, Cottaar, Haitjema, Nicolaisen, Bønes & Mehlum 1999), the northwest European population of greylag geese *Anser anser* (Nilsson, Follestad, Koffijberg, Kuijken, Madsen, Mooij, Mouronval, Persson, Schricke & Voslamber 1999) and the Russian population of barnacle geese *Branta leucopsis* (Ganter, Larsson, Syroechkovsky, Litvin, Leito & Madsen 1999). The expansions can be interpreted as a result of either increased competition for resources in the traditional wintering areas as population sizes have grown or an attraction to newly discovered profitable food sources.

During autumn, the Svalbard breeding population of pink-footed geese passes through western Jutland, Denmark, staging there from late September to late October before moving further south to the Netherlands and Belgium. In mild winters, flocks return to Denmark from mid December onwards. Traditionally, the geese foraged on rough pastures and they only stayed as long as temperatures remained above 0°C; after few days with temperatures below 0°C, they emigrated southwards (Madsen 1980). Since the 1980s, the area covered by winter cereals has increased markedly in Denmark (Anon. 1987), and the pink-footed geese have increasingly foraged on these crops during winter. Furthermore, large numbers of geese now remain in western Jutland despite cold spells of weather (Madsen et al. 1999).

To investigate whether this change in wintering strategy and habitat use can be explained by the presence of a more profitable food source (*sensu* Crawley & Krebs 1992), a comparative study of time and energy budgets of pink-footed geese feeding on winter wheat *Triticum aestivum* fields and pastures was carried out in Ballum Enge, the central wintering area in Denmark, during the winters of 1994-1997. Data on habitat use and abdominal profile index (API) of neck-banded geese were analysed to describe body weight changes and possible relations to habitat choice and weather conditions.

Material and methods

Study area

Ballum Enge (55°07'N, 08°40'E) is a 12-km^2 polder area positioned on the coast of the Danish Wadden Sea. It consists of a mosaic of pastures, dominated by *Poa* spp. and with *Festuca pratensis*, *Alopecurus* spp. and *Phleum pratense*, and winter cereal fields, mainly with winter wheat. Ballum Enge is an important win-

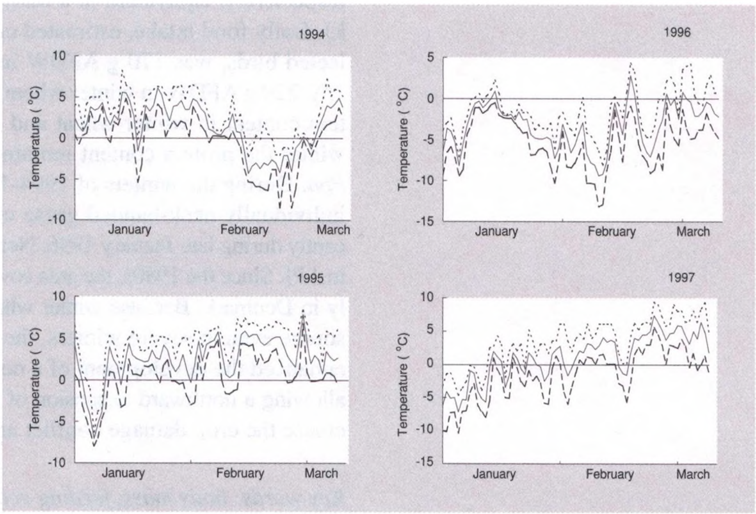

Figure 1. Daily variation in maximum (---), mean (—) and minimum (- –) temperatures during the winters of 1994-1997. (Sources: Rømø, Skrydstrup and Esbjerg weather stations, Danish Meteorological Institute).

Table 1. Minimum, maximum and mean daily temperatures (°C) during January - early March 1994-1997 at Ballum in the southern part of the Danish Wadden Sea. (Sources: Rømø, Skrydstrup and Esbjerg weather stations; Danish Meteorological Institute)

	January			February			1-10 March		
Year	Min.	Max.	Mean	Min.	Max.	Mean	Min.	Max.	Mean
1994	-5.4	8.2	3.2	-8.5	6.2	-0.7	-2.2	4.9	3.8
1995	-8.0	6.5	1.1	-2.7	7.4	3.9	-0.6	8.4	3.2
1996	-10.3	2.2	-3.3	-13.2	4.3	-4.0	-4.9	4.2	-1.0
1997	-10.4	6.1	-1.7	-5.7	9.4	2.7	-1.4	9.3	4.6
Long term	-	-	0.9	-	-	1.0	-	-	1.3

tering area for the Svalbard population of pink-footed geese, which arrive in the area during late December. Peak numbers are reached in January-February, and the geese leave the site during March. Goose numbers have increased from an average of 5,000 in February 1980-1983 (Madsen 1986) to 20,000 in the early 1990s (Madsen et al. 1999). During 1994-1997, the total Svalbard population was estimated at 32,000-34,000 individuals (Madsen et al. 1999). At night the geese roost on the intertidal mud flats or salt marshes outside the sea dikes.

Weather conditions

Daily temperatures for January - early March 1994-1997 (Fig. 1) were obtained from the nearby weather station of Rømø (Danish Meteorological Institute). In a few cases information was missing and data from the nearby weather stations of Esbjerg or Skrydstrup were used. Monthly temperature ranges and average mean daily temperatures are given in Table 1.

Below, the winters of 1994 and 1997 are referred to as 'average' winters, whereas the winters of 1995 and 1996 are referred to as 'mild' and 'severe', respectively, compared to the long-term mean. Unfortunately, no reliable data on snow cover were available, except for 1996, when 30-60 mm of snow covered the ground during 18-26 February. In the other winters, extensive snow cover was observed but it lasted for a few days only.

Field work

Field work took place from early January to early March in 1994-1996, and from late January to early March in 1997. Additional collection of data was carried out in January-February 1998.

Habitat use and scoring of abdominal profiles

Pink-footed geese have been neck-banded since 1990. During the study period, approximately 1% of the population carried blue neckbands with three-digit white codes engraved. During the winters of 1994, 1995 and 1996 the study area was visited daily and searched for goose flocks. In all flocks encountered attempts were made to read all neckbands using a telescope. The habitat used by each marked individual was registered. Based on days with more than 10 different neckband resightings we calculated the daily relative distribution of neck-banded geese observed on winter wheat fields and pastures, respectively. If possible, the abdominal profile (API) was scored using seven categories as described by Madsen, Hansen, Kristensen & Boyd 1997. The development of APIs of individual geese registered at least twice in Ballum Enge was calculated as the daily change between two consecutive observations assuming that the goose stayed in the area during the interim. The midpoint between the two consecutive observations was used as observation date. Because the index is a categorical variable starting with index 1, the rate of change was only calculated for individuals which were >1 on the first observation day. Average daily change of all registered individuals was calculated for 10-day periods. The majority of the scoring of APIs was carried out by one observer (F. Hansen), supplemented by Jesper Madsen. The scoring by the observers was regularly intercalibrated and found not to differ between observers (J. Madsen, unpubl. data). A preliminary analysis shows that there is a significant linear relationship between APIs and body weight (based on birds which were caught, marked and weighed, and subsequently observed in the field within the following two days; J. Madsen, unpubl. data).

Forage quality

During January - early March 1995 and 1996 samples of *Poa* and winter wheat were collected, dried at 50°C for 24 hours and analysed for protein content using the Kjeldahl method at the National Agricultural Sciences Laboratory in Foulum, Denmark.

Energy expenditure

To obtain daily activity budgets, goose flocks of 100-500 individuals were regularly observed from a car using a 30-60x zoom telescope during late January - late February 1997. In each habitat, flocks were scanned every 10 minutes from their arrival at the feeding grounds at dawn until their departure for the roost at dusk. Since geese were only observed roosting on the feeding grounds on one occasion, it can be assumed that flocks returned to the roost each night, restricting feeding to daylight hours.

The number of geese engaged in different activities was recorded for each scan as described by Altmann (1974). Seven activities were defined: feeding, resting (including standing and preening), walking, alert behaviour, flying and social interactions.

We converted the time budget data into daily energy expenditure by summation of the cost of each activity, calculated on the basis of the basal metabolic rate (BMR). BMR was calculated according to the equation given by Aschoff & Pohl (1970) for non-passerines at night: $BMR = 307W^{0.734}$, where W is the body weight in kilograms. The average weight of an adult goose (average for both sexes) during the study period is 2.73 ± 0.26 kg (SE) (N = 20; J. Madsen, unpubl. data), and thus BMR was established at 641.6 kJ/day.

Costs of activities, expressed as multiples of BMR, were obtained from Owen, Wells & Black (1992). As discussed by Gauthier, Bédard & Bédard (1984) such data are rough estimates, but when the same procedure is applied to geese using both habitats, the method seems reasonable.

To assess foraging profitability, pecking rates and walking speeds during uninterrupted feeding bouts on pastures and winter wheat fields were timed on a stopwatch as the time it took to make 25 pecks and 25 paces, respectively.

Daily energy intake rates assessed by the 'marker substance' method

On account of their regularly produced and easily collected droppings, daily energy intake in grazing wildfowl is measured by estimating the daily defaecation and converting this into food intake using digestive efficiency rates. Retention rates are calculated based on the net concentration of an indigestible marker substance in the droppings compared to the food plants (Moss & Parkinson 1972). The assimilation of energy is then obtained from the energy content of food and droppings.

Hand-plucked grass and winter wheat shoots were collected from several recently grazed fields and sorted by hand to include only green parts. Fresh droppings were collected from fields on which the geese had been feeding for several hours. Paired samples were dried at 50°C and analysed for acid detergent fibre (ADF), lignin, ash and energy content at the National Agricultural Sciences Laboratory in Foulum, Denmark. Ash content of plants and droppings was determined after removal of the silica fraction.

The defaecation rate during the day was obtained by observing the abdomen of individual birds as long as possible. Defaecation intervals were estimated by the 'hourly block' method (following the method described by Bédard & Gauthier 1986). A throughput time of 45 minutes was used (Madsen 1985) and, hence, observations were only carried out after one hour of foraging after the geese arrived at the fields from the roost (to allow the gut to be filled). Observations were evenly distributed over the day and throughout the period. We did not attempt to determine the defaecation rate at night, but Ebbinge, Canters & Drent (1975) estimated the ratio between droppings produced during daytime and on the roost to be 135:25 by counting droppings on roosting areas for barnacle geese *Branta leucopsis* wintering in the Netherlands. If this ratio is assumed to be equal for the two species, the nightly defaecation can be estimated.

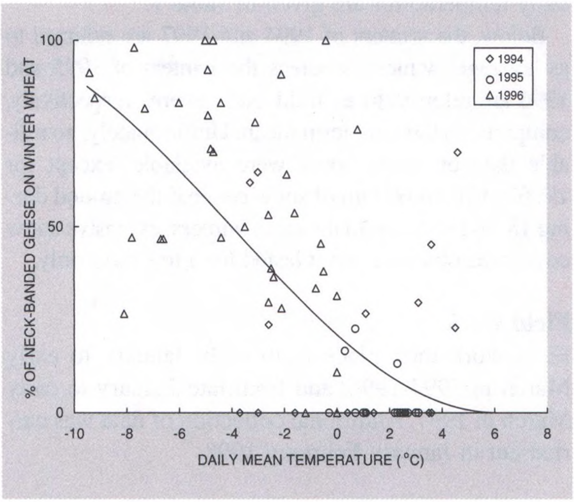

Figure 2. Relationship between daily mean temperature and percentage of neck-banded geese observed on winter wheat fields during the winters of 1994-1996. The regression line was fitted to arcsine transformed data after the formula: $y = 0.475 - 0.078x$ ($R^2 = 0.44$, df = 91) and backtransformed. The relationship is negative and highly significant ($P < 0.0001$). Each data point represents one day with habitat distribution of at least 10 individuals (range: 10-99).

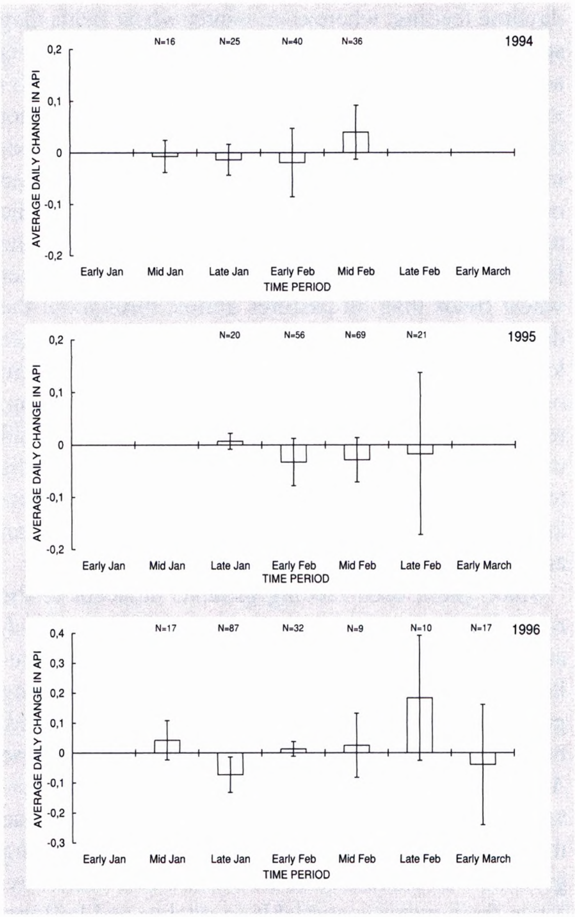

Figure 3. Average daily change in abdominal profile index (API; ± 95% confidence limits) of individual pink-footed geese calculated for 10-day periods during winter 1994-1996.

Daily intake rates assessed on the basis of oesophagus contents and pecking rates

Assuming that the geese take one leaf per peck, the daily intake rate can be calculated by multiplication of mean bite length, pecking rate and total daily foraging time (Therkildsen & Madsen in press). On 2 and 10 February and 1, 5 and 7 March, 1996 a total of 11 geese feeding on winter wheat fields were collected by rifle shooting. On 5 and 7 March 1996, a total of four geese were shot while feeding on pastures. On 3 and 16 February 1998, an additional five geese were shot while feeding on winter wheat fields. Samples of oesophagus contents, i.e. pieces of grass or winter wheat, were taken from each individual. Leaf lengths were measured, and leaves were dried at 80°C for 24 hours and weighed individually.

Table 2. Protein content (mean ± SE) in winter wheat and *Poa* spp. during winter 1995 and 1996.

	1995	1996
Winter wheat (N = 3)	29.46 ± 1.84	30.56 ± 0.72
Poa, primary/secondary leaves (N = 10)	29.68 ± 1.78	23.96 ± 2.27

Results

Habitat use

Regression analysis showed a significant decrease in the proportion of neck-banded geese observed on winter wheat fields (as opposed to geese observed on pastures) with increasing daily mean temperatures (Fig. 2). In 1994, the geese made use of both pastures and winter wheat fields. In 1995, the geese almost exclusively used pastures, whereas in 1996, the geese increasingly used winter wheat fields as temperatures dropped below 0°C.

Development of abdominal profiles

There were on average 8.3 ± 7.8 days (± SE, N = 455) between consecutive observations of individual geese, and the abdominal profile index ranged within 1-3. The proportion of geese observed more than twice in the area was 59, 50 and 41% in 1994, 1995 and 1996, respectively. The geese staging in the area in early February had an average API of 2.0 ± 0.3, 2.2 ± 0.5 and 1.9 ± 0.5 (± SE) during the winters of 1994-1996, respectively. The average API differed significantly between years (Kruskal-Wallis test: $\chi^2 = 17.8$, df = 2, $P < 0.001$). The daily change in API during the winters of 1994-1996 is shown in Figure 3. During one 10-day period, viz. late January 1996, there was a change in API significantly different from zero (t-test, $t = -2.42$, $P < 0.05$), whereas in all other cases the change did not differ significantly from zero (t-tests, $P > 0.05$).

Table 3. Time budgets (mean ± SE) of pink-footed geese during a feeding day on pastures (N = 233 scans) and winter wheat fields (N = 298 scans) during February 1997.

	Time expenditure (%)					
Habitat	Feeding	Walking	Resting	Alert	Social interaction	Flying
Pastures	83.8 ± 2.2	4.1 ± 0.4	4.4 ± 2.2	7.2 ± 2.2	0.3 ± 0.1	0.1 ± 0.3
Winter wheat	74.9 ± 6.0	4.1 ± 0.9	13.7 ± 6.7	7.1 ± 2.0	0.2 ± 0.1	0.1 ± 0.1

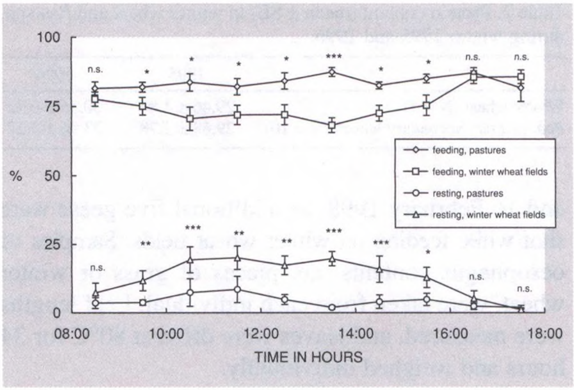

Figure 4. Feeding and resting activity of pink-footed geese feeding on pastures and winter wheat fields, respectively. Means (± SE) are given for the whole study period. *: $P < 0.05$; **: $P < 0.01$; ***: $P < 0.001$; n.s.: not significant.

Food quality

In 1995, the protein content in winter wheat and *Poa* did not differ ($F_{1,12} = 0.04$, $P > 0.85$), whereas in 1996 the protein content was significantly higher in winter wheat than in *Poa* ($F_{1,12} = 63.3$, $P < 0.001$; Table 2).

Time and energy budgets

Since time budget data could not be assumed to be normally distributed (Wilk-Shapiro tests for $N \leq 2000$), the non-parametric Kruskal-Wallis test (χ^2-approximation) was used on untransformed data to test for differences between habitats. To calculate means and standard errors data were arcsine transformed.

In the mornings, geese arrived at the feeding grounds around dawn and stayed in the fields until the return flight to the roost around dusk. This gives an average of 570 minutes day^{-1} spent on the feeding grounds in the study period.

On pastures, geese spent on average 83.8% of the daytime feeding, whereas on winter wheat fields they spent 74.9% (Table 3). In both habitats the feeding activity varied during the day (Fig. 4). Feeding activity peaked during morning and evening and did not differ significantly between habitats, whereas the feeding activity was significantly higher on pastures than on winter wheat fields during the middle part of the day. The daily variation in resting activity reflects the feeding activity with more geese resting on winter wheat fields than on pastures almost throughout the day (Kruskal-Wallis tests; see Figure 4 for significance levels). Geese on winter wheat fields and pastures spent on average 13.7% and 4.4% of the daytime resting, respectively. The time devoted to other activities did not differ between the two habitats (Kruskal-Wallis tests: $P > 0.05$), except for social interactions (Kruskal-Wallis test: $\chi^2 = 7.0$, df = 1, $P < 0.01$), possibly an artefact due to the low frequency of this behaviour.

Since geese used feeding grounds adjacent to the roost first and then gradually moved further inland, an average flight distance of 4 km was used to calculate the time spent flying between roost and feeding grounds. The flight speed could not be determined, but Mooij (1992) found that for white-fronted geese *Anser albifrons* and bean geese *Anser fabalis*, the average roost flight speed was 44 km h^{-1}. Using this value the average flight time between the roost and feeding grounds was calculated to be 5.5 minutes each way. Since fresh water is available in ditches and hollows on most fields no drink flight is made during the day.

There was no marked difference in daily energy expenditure between geese feeding on pastures versus winter wheat (Table 4). The calculated daily energy expenditure was slightly higher on pastures than on winter wheat fields, which was primarily a result of the longer time spent feeding and less time spent resting.

Table 4. Estimates of the 24-hour time and energy expenditure for a pink-footed goose feeding on pastures and winter wheat fields, respectively, expressed as mean values for the period late January - late February 1997. It is assumed that the goose roosts throughout the night. BMR and multiples of BMR: see text.

		Pastures		Winter wheat fields	
Activity	Cost of activity (x BMR)	Time spent (min)	Energy consumed (kJ)	Time spent (min)	Energy consumed (kJ)
Feeding	2.0	477.4	425.4	427.0	380.5
Resting	1.3	25.2	14.5	78.1	45.2
Walking	2.3	23.6	24.1	23.4	23.9
Alert	2.1	41.1	38.5	40.2	37.7
Social interactions	2.3	1.9	2.0	1.0	1.0
Flying	14.0	11.8	73.6	11.3	70.6
Roosting	1.3	859.0	497.6	859.0	497.6
Daily energy expenditure			1075.8		1056.5

Table 5. Estimates of the time spent on the feeding grounds, of the daily production of droppings, of the food intake and the net energy intake of pink-footed geese feeding on pastures and winter wheat fields during mid-February 1997.

	Pastures	Winter wheat fields
Time on feeding ground (min)	570	570
Defaecation period during daytime (min)	525	525
Defaecation interval (s)	280.8[a]	298.5[b]
Dropping production on feeding ground	112.2	105.5
Dropping production on roost	20.8	19.5
Total daily dropping production	132.9	125.1
Dry weight of dropping (g)	0.85[c]	1.15[d]
Organic contents (g)	0.76	0.94
Daily defaecation (g AFDW)	101.1	117.8
Retention rate (%)	31.7	25.0
Daily intake (g AFDW)	148.0	157.2
Energy content of food (kJ/g AFDW)	19.73	19.95
Energy content of faeces (kJ/g AFDW)	17.91	16.89
Net energy intake (kJ/day)	1109.2	1145.0
Assimilation of energy (%)	38.0	36.5

[a] N = 352 min, SE = 39.7
[b] N = 281 min, SE = 54.9
[c] N = 447, SE = 0.19
[d] N = 78, SE = 0.27

Daily food and energy intake based on the 'marker substance' method

Defaecation intervals did not differ significantly between habitats ($Z = 1.02$, $P > 0.05$; Table 5). There was a reasonable accordance between retention rates based on ADF and ash, whereas the values based on lignin differed (Table 6). The retention rates used for calculations are means for ADF and ash after exclusion of lignin. Because of the discrepancies, the values must be regarded as crude estimates, giving approximately similar retention rates for geese on pastures and on winter wheat fields during the study period. The estimated intake rates of 148 and 157 g ash free dry weight (AFDW) d^{-1} when feeding on pastures and winter wheat fields, respectively, correspond to 740 g fresh weight grass d^{-1} and 786 g fresh weight winter wheat d^{-1} during the study period, respectively, if a water content of 80% of fresh weight is assumed.

Feeding profitability

Geese feeding on pastures pecked faster ($F_{1,478} = 46.48$, $P < 0.0001$), but walked more slowly ($F_{1,40} = 100.05$, $P < 0.0001$, for unequal variances) than geese feeding on winter wheat (Table 7). Vegetation on pastures is patchy (O. Therkildsen, pers. obs.) and, presumably, geese seek out areas with high densities of the principal grasses, i.e. *Poa*, and graze these with a high pecking rate while walking slowly through the area. On winter wheat fields, the vegetation is evenly distributed, but with a longer distance between shoots, resulting in a higher walking speed but a slower pecking rate. Converted into net energy intake per peck, geese on winter wheat had a 25% higher net energy intake than geese foraging on pasture grasses.

Table 6. Retention rates of pasture grasses and winter wheat calculated using the 'marker substance' method.

	ADF	Ash	Lignin
Pasture grasses	38.7	24.7	54.7
Winter wheat	31.2	18.9	59.2

Table 7. Feeding parameters and profitability of feeding on pastures and winter wheat fields.

	Pastures	Winter wheat fields
Pecking rate (seconds/25 pecks)	11.9[a]	13.2[b]
Walking speed (seconds/25 paces)	59.4[c]	32.8[d]
Net energy intake (kJ/day)	1109.2	1145.0
Total number of pecks/day	60170	48393
Energy intake (J/peck)	18.4	23.7

[a] N = 365, SE = 1.78
[b] N = 114, SE = 1.97
[c] N = 32, SE = 14.04
[d] N = 57, SE = 7.22

Daily food intake based on bite lengths

The fraction of dead leaves in the oesophagus contents was negligible in geese feeding on pastures in 1996 and on winter wheat in 1998, whereas the fraction made up 23.0 ± 0.4% in geese foraging on winter wheat in February 1996.

The daily food intake (Table 8), calculated from bite lengths and weights, activity budget data and pecking rates, was estimated at 170 g AFDW for pasture feeding geese and varied between 159 and 229 g AFDW for winter wheat feeding geese (see Table 8).

Table 8. Estimates of daily food intake obtained by examining oesophagus contents of pink-footed geese feeding on winter wheat fields and pastures, respectively. N = number of collected individuals.

Food	Time period	Intake/day ± SE (g AFDW)[d]	N
Winter wheat	Feb. 1996	229 ± 116[a,e]/203 ± 104[b,e]	5
Winter wheat	Mar. 1996	212 ± 32[a]/188 ± 29[b]	6
Winter wheat	Feb. 1998	159 ± 22[b]	5
Pasture grass	Mar. 1996	170 ± 81[c]	4

[a] Peck rate, Feb. 1997
[b] Peck rate, Feb. 1998
[c] Peck rate, late Feb. 1997
[d] Corrected for 1.525% inorganic constituents (O. Therkildsen & J. Madsen, unpubl. data)
[e] Corrected for dead material

Discussion

Habitat choice

According to optimal foraging theory the net rate of energy gain while foraging, i.e. profitability, is the key criterion to compare alternative values of the decision variable, i.e. where to feed (Crawley & Krebs 1992). In this study, winter wheat fields proved to be the most profitable food source when profitability is expressed as energy intake per peck. An alternative currency for foraging models is the time spent feeding; an optimal forager may be regarded as a time minimiser (Crawley & Krebs 1992). The geese feeding on winter wheat fields evidently maximised intake rates and minimised foraging time by feeding on winter wheat rather than on grass.

At lower temperatures the protein content of winter wheat was higher than the protein content of *Poa* and evidently geese preferred winter wheat in this period. At higher temperatures the geese showed a preference for pastures, despite the fact that there was no difference in protein content between *Poa* and winter wheat. However, as found by Therkildsen & Madsen (1999), protein contents of food plants alone may not provide the full explanation for feeding preferences since other factors, i.e. leaf length, can determine the availability of resources. In mild winters there may still be a net growth in *Poa* (J. Madsen, unpubl. data), increasing the potential bite length, hence, making this resource the most profitable. However, during periods with subzero temperatures, *Poa* stops growing and the quality deteriorates.

Time and energy budgets

The observed diurnal variation in feeding activity on pastures is similar to the general pattern found by for instance Ebbinge et al. (1975) for barnacle geese wintering in the Netherlands, and by Mooij (1992) for bean geese and white-fronted geese wintering in northern Germany. No comparable data are available for feeding activity on winter wheat fields.

The calculated daily energy expenditure averaged approximately 1.6 x BMR. This is lower than the 1.8 x BMR reported by Madsen (1985) for pink-footed geese feeding on pastures in late March. The difference is mainly due to prolonged daylength which enables longer periods of activity.

In both habitats the daily energy intake exceeded energy expenditure, i.e. 33 kJ on pastures and 89 kJ on winter wheat fields. This surplus may be used to compensate for energy deficits caused by migration, bad weather conditions and disturbance, or it can be deposited as fat (Mooij 1992). Thus, in mild and average winters as in 1997, when the energy expenditure for thermoregulation is considered to be small and food quality is relatively high, there is a potential for gaining weight during late winter. If the energy budget holds for the whole study period and assuming that the geese spend the same amount of time in the two habitats, it can be calculated that the geese made a surplus of 2,133 kJ during the five-week study period. This is equivalent to a build-up of 38 grams of lipid when fat is assumed to yield 42 kJ g^{-1} and a conversion efficiency of 75% is used (Owen et al. 1992, Drent, Ebbinge & Weijand 1979). However, since the thermoregulatory cost will probably increase during cold spells, this surplus may well be smaller in a cold winter.

The estimated energy expenditures rely on values of energy costs of activity obtained from the literature and should be regarded as rather crude. Furthermore, defaecation rates at night are insufficiently documented. Thermoregulatory costs may be an important part of an energy budget at lower temperatures, but are not easily quantified in a study like this. During the study period ambient temperatures dropped below 0°C during some nights, but seldom did so during the day. Since arctic breeding geese show some metabolic adaptations to cold (West & Norton 1975), it is assumed that body temperature was maintained solely by heat generated during normal activity and that there were no extra thermoregulatory costs. The daily energy expenditure may thus be slightly underestimated.

Daily intake rates

The results obtained using the 'oesophagus contents' method for geese feeding on winter wheat in March 1996 and February 1998 were in accordance with the result achieved using the 'marker substance' method for February 1997. However, the estimate for February 1996 was higher, which may partly be explained by the bite length used in the calculation. In one case, the bite length was on average 8.4 cm and, presumably, by taking such long pieces of leaves, the handling time per bite will be affected, i.e. the time it takes to bite off, manipulate and swallow the leaf. Consequently, this lowers pecking rates, whereas the intake rate may remain unchanged (Therkildsen & Madsen in press). In 1997 and 1998 geese were not observed to take bites of this length (O. Therkildsen, unpubl. data) and their reasons for doing so in 1996 are unknown.

It is likely that leaf lengths encountered when foraging on winter wheat in March 1996 and February 1998 were within the same range as in 1997, resulting in similar pecking rates and, consequently, producing a reasonable fit to the results obtained by the 'marker substance' method. The bite length employed by geese feeding on pastures may not differ significantly between years, since the geese only switch to this habitat when it is energetically favourable, i.e. when leaves have reached an appropriate size to select for. Thus, the higher intake rate in March 1996 than in February 1997 is mainly explained by the more time spent feeding in March.

Body weight implications

The analysis of the change in API during the winters of 1994-1996, supports the results of the analysis of energy budgets carried out in 1997. The geese wintering in the area were capable of maintaining body weights throughout the three winters analysed, except for late January 1996, despite large between-year differences in temperatures. The weight loss during late January 1996 may have been caused by severe cold increasing thermoregulatory costs, since winter wheat food supply is unlikely to be limiting at this time of winter.

Since the geese used only 75% of the time feeding on winter wheat fields there is a potential for an increase in the feeding time and, probably, intake rates, as long as snow cover permits. Similarly, barnacle geese wintering in southwest Scotland both increased pecking rates and feeding effort at the expense of other activities, when food sources declined (Owen et al. 1992). It is unknown whether this is possible for the pink-footed geese because the size of winter wheat leaves may impose digestive constraints forcing the geese to pause when the gut is filled.

It has been hypothesised that endogenous cycles control body mass irrespective of food availability or feeding opportunity (Pienkowski, Lloyd & Minton 1979). Owen et al. (1992) could not entirely exclude this hypothesis, but argued that for barnacle geese wintering in southwest Scotland, the declining food availability caused loss of body weight. In Ballum Enge, pink-footed geese did not increase body weights, even when food resources presumably allowed this as during the mild winter of 1995. This strongly suggests that geese adjust their winter weights to an optimum, based on a trade-off between the need for accumulation of body reserves to meet periods with high energy demands (e.g. during February 1996) and the concomitant increased metabolic cost of maintenance and activities.

Wintering strategy

The increased area of winter wheat, representing a reliable food supply even in severe winters, enables the geese to maintain body mass, when pastures otherwise would have been a poor protein and energy source. This may be part of the explanation for the dramatic change in wintering strategy resulting in both a prolonged wintering and an increase in bird numbers in the Ballum area as well as in other Danish sites (Madsen et al. 1999). However, before the 1990s winter wheat was already widely distributed in the area suggesting that geese have gradually 'learned' that they can survive even severe cold spells on winter wheat, thus showing a lag in response. The speed of the new development shows that this has been a cultural shift of winter strategy. Since winter wheat is widely distributed in Denmark along the migration route northwards, a further extension of the winter range is likely. Actually, recent observations of large numbers (ca 7,000) of pink-footed geese remaining in northwestern Jutland during a cold spell in January 1999 support this (J. Madsen, unpubl. data).

Management implications

In the present case, as well as on a general European-wide scale, increased use of winter cereals may allow goose populations to expand their winter ranges. Potentially, this may allow goose populations to escape limitation by winter food resources and lead to further population growth. The combination of increasing use of winter cereals and population growth is likely to exacerbate the crop damage conflict.

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References

Altmann, J. 1974: Observational study of behaviour: sampling methods. - Behaviour 49: 227-267.

Anonymous 1987: Handlingsplan mod fοrureningen af det danske vandmiljø af næringssalte. - Ministry of Environment, Copenhagen, 20 pp. (In Danish).

Aschoff, J. & Pohl, H. 1970: Der Ruheumsatz von Vögeln als Funktion der Tageszeit und der Körpergrösse. - Journal für Ornithologie 111: 38-47. (In German).

Bédard, J. & Gauthier, G. 1986: Assessment of faecal output in geese. - Journal of Applied Ecology 23: 77-90.

Crawley, M.J. & Krebs, J.R. 1992: Foraging Theory. - In: Crawley, M.J. (Ed.); Natural Enemies. Blackwell Scientific Publications, Oxford, UK, pp. 90-114.

Drent, R., Ebbinge, B. & Weijand, B. 1979: Balancing the energy budgets of arctic breeding geese throughout the annual cycle: a progress report. - Verhandlungen der Ornitologischen Gesellschaft Bayern 23: 239-264.

Ebbinge, B., Canters, K. & Drent, R. 1975: Foraging routines and estimated daily food intake in barnacle geese wintering in the northern Netherlands. - Wildfowl 26: 5-19.

Ganter, B., Larsson, K., Syroechkovsky, E.V., Litvin, K.E., Leito, A. & Madsen, J. 1999: Barnacle Goose Branta leucopsis: Russia/Baltic. - In: Madsen, J., Cracknell, G. & Fox, A.D. (Eds.); Goose populations of the Western Paleartic. A review of status and distribution. Wetlands International Publication No. 48, Wetlands International, Wageningen, The Netherlands. National Environmental Research Institute, Rønde, Denmark, pp. 270-283.

Gauthier, G., Bédard, J. & Bédard, Y. 1984: Comparison of daily energy expenditure of greater snow geese between two habitats. - Canadian Journal of Zoology 62: 1304-1307.

Gill, J.A., Watkinson, A.R. & Sutherland, W.J. 1997: Causes of the redistribution of pink-footed geese Anser brachyrhynchus in Britain. - Ibis 139: 497-503.

Madsen, J. 1980: Forekomst, habitatvalg og overnatning hos kortnæbbet gås Anser brachyrhynchus på Tipperne, 1972-1978. (In Danish with English summary: Occurrence, habitat selection, and roosting of the pink-footed goose at Tipperne, Western Jutland, Denmark, 1972-1978). - Dansk Ornitologisk Forenings Tidsskrift 74: 45-58.

Madsen, J. 1985: Relations between change in spring habitat selection and daily energetics of pink-footed geese Anser brachyrhynchus. - Ornis Scandinavica 16: 222-228.

Madsen, J. 1986: Danske rastepladser for gæs. (In Danish with English summary: Status of the staging goose populations and their haunts in Denmark, 1980-1983). - Miljøministeriet, Fredningsstyrelsen, Denmark. 114 pp.

Madsen, J., Cracknell, G. & Fox, A.D. 1999: Goose populations of the Western Paleartic. A review of status and distribution. - Wetlands International Publication No. 48, Wetlands International, Wageningen, The Netherlands. National Environmental Research Institute, Rønde, Denmark, 344 pp.

Madsen, J., Hansen, F., Kristensen, J.B. & Boyd, H. 1997: Spring migration strategies and stopover ecology of pink-footed geese. Results of field work in Norway, 1996. - National Environmental Research Institute, Denmark, NERI Technical Report No. 204, 31 pp.

Madsen, J., Kuijken, E., Meire, P., Cottaar, F., Haitjema, T., Nicolaisen, P.I., Bønes, T. & Mehlum, F. 1999: Pink-footed Goose Anser brachyrhynchus: Svalbard. - In: Madsen, J., Cracknell, G. & Fox, A.D. (Eds.); Goose populations of the Western Paleartic. A review of status and distribution. Wetlands International Publication No. 48, Wetlands International, Wageningen, The Netherlands. National Environmental Research Institute, Rønde, Denmark, pp. 82-93.

Mooij, J. 1992: Behaviour and energy budgets of wintering geese in the Lower Rhine area of North Rhine-Westphalia, Germany. - Wildfowl 43: 121-138.

Moss, R. & Parkinson, J.A. 1972: The digestion of heather Calluna vulgaris by red grouse Lagopus scoticus. - British Journal of Nutrition 27: 285-298.

Nilsson, L., Follestad, A., Koffijberg, K., Kuijken, E., Madsen, J., Mooij, J., Mouronval, J.B., Persson, H., Schricke, V. & Voslamber, B. 1999: Greylag Goose Anser Anser: Northwest Europe. - In: Madsen, J., Cracknell, G. & Fox, A.D. (Eds.); Goose populations of the Western Paleartic. A review of status and distribution. Wetlands International Publication No. 48, Wetlands International, Wageningen, The Netherlands. National Environmental Research Institute, Rønde, Denmark, pp. 182-201.

Owen, M., Wells, R.L. & Black, J.M. 1992: Energy budgets of wintering barnacle geese: the effect of declining food resources. - Ornis Scandinavica 23: 451-458.

Pienkowski, M.W., Lloyd, C.S. & Minton, C.D.T. 1979: Seasonal and migrational weight changes in dunlins. - Bird Study 26: 134-148.

Therkildsen, O.R. & Madsen, J. 1999: Goose grazing selectivity along a depletion gradient. - Ecography 22: 516-520.

Therkildsen, O.R. & Madsen, J. in press: Assessment of daily food intake in pink-footed geese Anser brachyrhynchus by examination of oesophagus contents. - Wildlife Biology.

van Eerden, M.R., Zijlstra, M., van Roomen, M. & Timmerman, A. 1996: The response of Anatidae to changes in agricultural practice: long-term shifts in the carrying capacity of wintering waterfowl. - Gibier Faune Sauvage, Game and Wildlife 13: 681-706.

West, G.C. & Norton, D.W. 1975: Metabolic adaptations of tundra birds. - In: Vernberg, J. (Ed.); Proceedings of the Ecological Society of America, American Institute of Biological Sciences Symposium. Intertext Press, New York, pp. 301-329.