Adjustments to nitrogen metabolism during wing moult in Greylag Geese, *Anser anser*

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Summary

1. This study examined the nitrogen balance of free-living flightless moulting Greylag Geese, *Anser anser*, in relation to food quality, nitrogen absorption, food retention time and nitrogen excretion rates.

2. Food intake rates during moult were the same as those before and after the flightless period, but total daily time spent foraging fell by 58% from 9·45 h to 3·96 h. Dropping production during moult was 43%, and mean dropping mass 42% of that before and after moult, suggesting a considerable increase in food passage time through the gut during moult. Nitrogen absorption increased from 25% prior to moult to 47% during moult.

3. At the same time, excreted dry mass uric acid in faecal material fell by 68%, such that the proportion of nitrogen absorbed and retained in the body as a proportion of the nitrogen ingested in food rose from 16% prior to moult to 42% during moult.

4. Based on these significant increases in nitrogen absorption and decreases in nitrogen excretion, geese were able to compensate for reduced food intake and derive sufficient nitrogen from their diet to re-grow flight feathers.

Key-words: Digestibility, feather growth, protein

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Introduction

Northern Hemisphere goose species undergo a simultaneous wing moult that renders them flightless while flight feathers are regrown (Owen 1980; Hohman, Ankney & Gordon 1992). Feather growth necessitates nutrient supply, particularly protein, over and above that required simply for self-maintenance. Feather is ≈ 90% keratin, fibrous protein characterized by its resilience, strength and resistance to enzymatic digestion (Brush 1978). Northern geese are herbivorous and compared with other nutrients and energy, protein is considered to be of restricted availability in plant tissue (Hohman *et al*. 1992). In particular, the sulphur-rich amino acids typical of feather protein are relatively scarce in green plant material (Hanson 1962; Hohman *et al*. 1992). The capacity of birds to store protein is limited (Blem 1976) and conversion of dietary protein to feather protein is energetically costly (Murphy & King 1984; van der Wal 1992). From his study of captive Canada Geese *Branta canadensis*, Hanson (1962) concluded that moult is a period of nutritional stress (i.e. a period when nutrient demand exceeds nutrient ingestion, resulting in catabolism of body tissue; Ankney 1979). However, analysis of the body composition of geese undergoing moult suggests that geese rely very little on

catabolism of body tissue to meet nutrient demands for feather growth despite the apparent constraints upon the acquisition and conversion of dietary protein into feathers (Ankney 1979; Raveling 1979). Nevertheless, the protein requirement to complete the wing moult cycle successfully is still in excess of normal requirements for repair and maintenance. Moulting geese are unable to fly and are therefore more susceptible to predation, and so remain in close proximity to open water (e.g. Madsen & Mortensen 1987; Fox *et al*. 1995) or show other antipredator responses (e.g. feeding at night; Kahlert, Fox & Ettrup 1996). Such behaviour may further restrict the ability of flightless birds to accumulate adequate protein to complete feather regrowth, given a finite food resource.

In an earlier analysis, we demonstrated that moulting Greylag Geese, *Anser anser*, select for the most protein-rich food available on the Danish island of Saltholm (Fox, Kahlert & Ettrup 1998). However, geese habitually select their food on the basis of high protein content throughout much of the annual cycle (Sedinger 1997). Hence, in the absence of a nitrogen budget for moulting birds, this does not confirm the hypothesis that this mechanism alone enables geese to meet their enhanced protein requirements during

moult. In another analysis, we also demonstrated that flightless moulting Greylag Geese fed for an average of 8·9 h (± 0·1 SE) compared with 16·2 h (± 0·3) among birds capable of flight (Kahlert *et al*. 1996).

Typically, geese feed on relatively low energy food, so must therefore forage for long periods to meet daily energy requirements, maintaining high rates of food passage through the alimentary tract (Ebbinge, Canters & Drent 1975; Summers & Grieve 1982). Nevertheless, there is evidence that birds can modify their alimentary canal structure to meet specific nutritional demands at critical periods of their life cycle (e.g. Barnes & Thomas 1987; Piersma, Koolhaas & Dekinga 1993). Geese possess relatively well-developed caeca (Mattocks 1971), known to play an important role in the nitrogen economy of birds, although the energetic consequences of geese carrying well-developed caeca during their long-distance migrations probably precludes their further development (Sedinger 1997). However, it has been demonstrated that, during critical periods of the life cycle, extended food retention times in Barnacle Geese, *Branta leucopsis*, can enhance absorption of food material (Prop & Vulink 1992). Hence, geese are able to modify their ability to exploit different fractions of their food material. Although it has never been previously demonstrated, it could be that geese can modify their caecal or other internal structures to elevate protein uptake from the diet during periods of high demand.

If we hypothesize that moult is a period when selection acts upon geese to modify their physiology in order to regrow flight feathers in the shortest possible period, two potential mechanisms could operate to maximize protein retention in the body. Firstly, geese may enhance protein absorption from food within the alimentary canal. Second, the costs of storage and reallocation of body stores of protein for investment in feather growth may be so high that birds modify their general (i.e. non-moulting) pattern of protein metabolism to maximize the use of dietary protein in re-growth of feathers. In considering the nitrogen budget of moulting Greylag Geese in this paper, we examine two testable predictions to determine if these mechanisms are operating during the flightless period. Firstly, that geese would increase nitrogen retention rates during moult compared with before moult (based on changes in nitrogen levels in the food and faeces controlled for differential absorption rates by comparison with an inert marker substance in the food). Second, we would predict decreases in excretion rates of metabolized protein (measured by the changes in uric acid and ammonium ion concentration in faeces) during moult compared with before moult. In this analysis, we also combine these factors to construct a crude nitrogen budget to see if such modifications can account for the ability of geese to meet their nitrogen demand for feather synthesis from exogenous sources during this period of their life cycle.

Materials and methods

STUDY AREA

Up to 14 000 Greylag Geese moult on the low-lying Danish island of Saltholm, arriving in mid-May (A. D. Fox & J. Kahlert, unpublished data); the vast majority moult highly synchronously and disperse quickly from the island, having regained the powers of flight before the beginning of July (Fox *et al*. 1995). The geese exploit the coastal fringe of Saltholm, feeding on saltmarsh communities dominated by *Puccinellia maritima and Scirpus maritimus* (Fox *et al*. 1998). Detailed study of the geese was carried out in the southeast corner of the island where over 90% of the moulting Greylag Geese were concentrated (see Fox *et al*. 1995; Kahlert *et al*. 1996). Observations were carried out from a hide 6 m above ground level (see Kahlert *et al*. 1996 for details and location map).

MOULT PERIOD DEFINITIONS

During each year of the study since 1993, the degree of moult was assessed on large samples of birds on an almost daily basis. A visual score of the extent of old feather loss and new feather growth was made using a 6-point scale, ranging from 0 (all old feathers lost) to 5 (feathers completely grown; see Fox *et al*. 1995). For the purposes of this analysis, the start of moult is defined as being the date at which 50% of birds have shed their flight feathers (28 May, based on combined data from 1993 to 1997). The end of moult is defined as the date at which 50% of birds have reached moult score 4 (by which date the majority of geese have regained the powers of flight, 23 June). These dates have been used to define the periods 'premoult', 'moult' and 'postmoult'.

GOOSE DIET

During the premoult settlement phase (when geese had yet to shed flight feathers and could still fly) and during the initial moult period (when geese were flightless), more than 94% of the diet comprised the green above-ground parts of *Puccinellia maritima* prior to 18 June (Fox *et al*. 1998). After that date, the content of the diet became varied, but the percentage of *Puccinellia* fell rapidly (Fox *et al*. 1998). For this reason, in discussion of the protein budget of the moulting geese prior to 18 June, we consider *Puccinellia* effectively the only food source utilized at that time.

INTAKE RATES

Peck rates were sampled by timing the number of pecks taken per minute by focal birds chosen at random feeding on *Puccinellia* swards. Because this had to be recorded opportunistically, 95 sampled peck rates were compiled from a total of 13 dates in

1993–95 inclusive and combined on the basis of pre-moult (prior to 28 May), moult (29 May to 23 June) and postmoult (after 24 June). Only peck rates compiled during the period 1830–2100 h were used to minimize any diurnal variation that might occur in this measure. The assumption is made that there is no variation in mean bite size and hence that intake rate of *Puccinellia maritima* is directly proportional to peck rate.

Mean time spent on the feeding areas was calculated by counting the numbers of geese distributed over a defined count area at 15-min intervals on the feeding grounds to estimate the daily arrival and departure of birds. Activity budgets were compiled from the observation tower by following focal individuals on the feeding grounds for a period of exactly 3 min using an event recorder. Data were compiled almost daily throughout the premoult and moult periods. Goose activity was assigned to the following categories: feed, rest and other activities not considered here (see Kahlert *et al*. 1996). Since flightless geese feed at night, a 7×60 mm night-scope with electronic light amplification (range $\approx$ 500 m; on loan from the Danish military) was used during darkness. During moult the effective foraging time was calculated by multiplying the mean percentage of time spent feeding with the mean duration of stay on the feeding grounds corrected for disturbance events where geese escaped on to the water. Before moult, some geese utilized the feeding grounds throughout the 24-h period; however, all departed from the feeding areas each evening, hence it is assumed that they ceased to feed at night, i.e. a period of 6 h. Thus, during premoult, the percentage of time spent feeding was multiplied by 18 h less the period spent by geese on the water to obtain effective foraging time.

DEFAECATION RATES AND DROPPING MASSES

Defaecation rates were estimated by following focal individuals for periods of up to 18 min, and counting ejected droppings. Unfortunately, compilation of adequate samples of dropping rates is difficult in the dense vegetation and broken topography of Saltholm, hence data were sampled opportunistically and are presented here from the years 1993–97. For each date, a minimum pooled sample of 18 min of observation periods was used. Defaecation rates are only presented from observation periods when the geese had been actively feeding for several hours, after which the defaecation rate was assumed to be in equilibrium with food intake. Fresh droppings were collected from standard dropping plots in three different parts of the study area every 6–10 days during 1995, dried at 50 °C for 48–72 h and weighed.

NITROGEN RETENTION

The droppings and food of the geese were analysed for an indigestible marker (acid detergent fibre, ADF)

and total nitrogen (Kjeldahl method). Droppings comprise urinary waste products as well as matter of faecal origin, so the uric acid content of the droppings was determined in order to differentiate these fractions. Nitrogen content of ash-free dry mass of plant fractions (N_f) was determined directly, while that of faecal material (N_d) calculated as total nitrogen content (N_{dt}) minus urinary nitrogen (N_u). Apparent nitrogen digestibility (D_N) was calculated as:

$$D_N = \frac{N_f - (M_f / M_d) \times N_d}{N_f} \quad , \qquad \text{eqn 1}$$

where N and M represent the ash-free dry mass determinations of nitrogen and ADF in food (f) and droppings (d), respectively. ADF was chosen as a relatively inert marker because significant cellulose digestion is considered unlikely (Prop & Deerenberg 1991; Prop & Vulink 1992), and other markers (such as lignin; see Clausen 1994) have proved to exhibit very high determination variance in green plant material.

NITROGEN BUDGET ESTIMATION

The daily output (g) of dry mass faecal material (F) was calculated as:

$$F = G \times d_r \times f_w, \qquad \text{eqn 2}$$

where G is the daily period spent feeding, d_r is the dropping rate (droppings h^{-1}) and f_w is mean dropping mass (g dry mass dropping^{-1}). Since it was not possible to record dropping rates during disturbance events (when geese took to water) or those on the roosts, nitrogen budget calculations presented here represent minimum estimations. Daily total nitrogen output (N_T in g dry mass day^{-1}) in faeces (i.e. the unused fraction of plant material plus excreted nitrogen) was calculated as:

$$N_T = N_{dt} \times F, \qquad \text{eqn 3}$$

where N_{dt} is overall proportional nitrogen content of faeces. From this needs to be subtracted the daily excretory nitrogen (N_E) produced (g dry mass day^{-1}), calculated as:

$$N_E = 0{\cdot}333 \times F \times N_u, \qquad \text{eqn 4}$$

where N_u is the proportional uric acid content of faeces. The constant 0·333 adjusts for the relative atomic mass of nitrogen in the uric acid molecule. In this way, total daily non-excretory nitrogen (N_N) in the faeces (g dry mass day^{-1}) was derived:

$$N_N = N_T - N_E. \qquad \text{eqn 5}$$

Given a nitrogen retention rate (D_N), the daily net nitrogen gain (N_g) to the body was calculated as:

$$N_g = \frac{N_N}{1 - D_N} \qquad \text{eqn 6}$$

and the proportion of daily nitrogen intake excreted as uric acid (N_{ua}) calculated as:

$$N_{ua} = \frac{N_E}{N_g} \ . \qquad\qquad\qquad \text{eqn 7}$$

In addition, the levels of ammonium ions present in faeces was determined, since birds do excrete ammonia as a breakdown product of protein catabolism (comprising 6–30% of total urinary nitrogen recorded in avian faeces, compared with 54–80% excreted as uric acid; Shoemaker 1974). However, it is impossible to develop a full budget for ammonia, given its volatility. Furthermore, its soluble form as ammonium ion is also present in the original food material as well as an excreted metabolic by-product in faeces. Hence, we merely consider the possible significance of changes in the faecal content of nitrogen as ammonium ion in the context of the overall nitrogen balance of moulting geese.

Results

EFFECTIVE FORAGING TIMES DURING PREMOULT AND MOULT PERIODS

Greylag Geese spent 65·5% of the daylight period (0400–2200 h inclusive) during the premoult period on land (based on 18 daily observations). Of this total, 80·2% of time was spent feeding (based on 61 observation periods) resulting in an effective foraging time of 9·45 h. Prior to moulting flight feathers, birds do not forage during the night, as they were seen resting and swimming offshore at dusk, and swam in at dawn, and were rarely seen feeding in darkness (using night-sight equipment) in other years. During the moult, geese spent 49·3% of the 24-h period on land (mostly during the night, dawn and dusk, based on 8 daily observations), of which 33·5% (based on 49 observations) was spent feeding, giving an effective foraging time of 3·96 h.
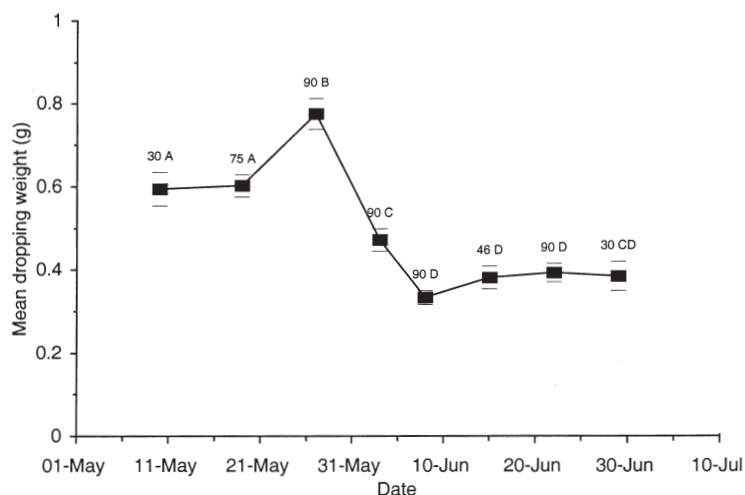

Fig. 1. Mean dry mass of collected fresh Greylag Goose droppings from areas heavily used by geese during the premoult, moult and postmoult period on Saltholm in 1995. Digits indicate sample sizes for each mean value for each date ($\pm$ SE). Common letters indicate no significant difference between means, based on Tukey HSD tests.

INTAKE RATES

There was no significant difference between mean peck rate during the premoult period (73·2 pecks min^{-1}) and during moult (75·3 pecks min^{-1}, $t_{26} = 0.01$, $P = 0.50$), nor between the moult and postmoult period (69·4 pecks min^{-1}, $t_{47} = 1.11$, $P = 0.14$). Hence, geese did not compensate for the reduced period spent feeding by conspicuously increased peck rate during moult.

DROPPING MASSES AND DEFAECATION RATES

Dropping masses fell after the onset of moult in all three areas where fresh droppings were collected in 1995. Analysis of covariance (ANCOVA, using site as a covariate) showed that there were no significant differences between dropping masses from the three different collection sites ($F_{2,514} = 2.12$, $P = 0.12$), nor any interaction between site and date ($F_{2,514} = 2.83$, $P = 0.07$), so the masses were combined for each collection date. One-way ANOVA showed there to be significant differences between masses sampled on different dates: there were no differences between the first two sample dates and the last four sample dates (Fig. 1), but droppings collected on 27 May were heavier than at any other sampling date. The samples from 3 June were not significantly different from those of 29 June. Hence, mean dropping masses during the flightless period (0·397 g dry mass $\pm$ 0·013 SE) were significantly lighter than during the period before feather loss (0·682 g dry mass $\pm$ 0·022 SE), a reduction of 42%.

Defaecation rates were lowest during the middle part of the flightless period, being higher before and after the main moult (Fig. 2). By combining rates before and after moult (9·08 droppings h^{-1}), and comparing these with rates during the moult (3·93 droppings h^{-1}), dropping rate was reduced by 43% during the moult period.

NITROGEN/ADF CONTENT OF FOOD PLANT AND FAECES

Nitrogen content of *Puccinellia maritima* declined from the premoult to the postmoult period (Fig. 3), but the ADF content remained relatively constant throughout (Fig. 4). The nitrogen content of faecal material declined in parallel with that of *Puccinellia*, increasing in the postmoult period when geese switched to other dietary items (Fig. 3). Uric acid nitrogen content of faeces was significantly less in the moult period than either during the pre- or postmoult periods (one-way ANOVA $F_{7,15} = 57.4$, $P < 0.001$; Fig. 5). Overall uric acid content decreased from 2·51% dry mass (before and after moult combined) to 1·05% dry mass during moult. Ammonium nitrogen content of faeces was significantly less in the moult period than during the

premoult period (one-way ANOVA $F_{1,13} = 9.58$, $P = 0.009$; Fig. 5), although contamination of one sample on 3 June resulted in only one sample on that date.

NITROGEN RETENTION RATES

Nitrogen retention rate, as measured by the difference between nitrogen content of the faeces and food material of the geese adjusted for the differences in indigestible marker, increased during the moult period (mean 46·7%) compared with the premoult period (mean 25·3%, one-tailed *t*-test for equal variances after arc sine square root transformation, $t_4 = 5.18$, $P = 0.003$, Fig. 6).
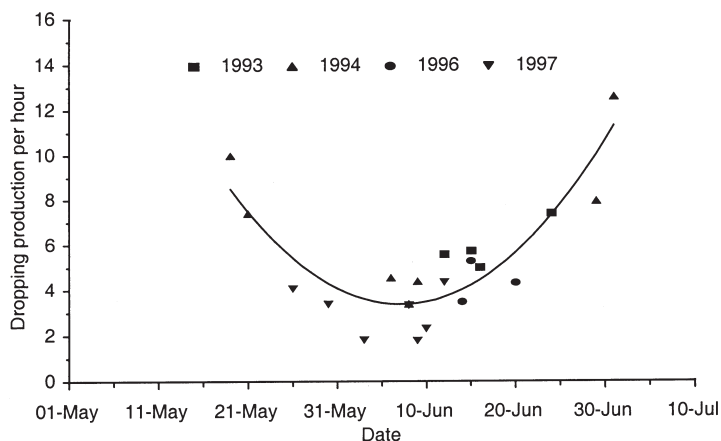
Fig. 2. Mean dropping rate per hour (*D*) of Greylag Geese during the premoult, moult and postmoult period on Saltholm in 1995. Each value represents at least 18 min of observations for each date. Best least-square fitted regression is the quadratic $D = 23.8 - 1.07t + 0.017t^2$ ($r = 0.88$, $F_{2,12} = 29.7$, $P < 0.001$), where t = time in days from 1 May.
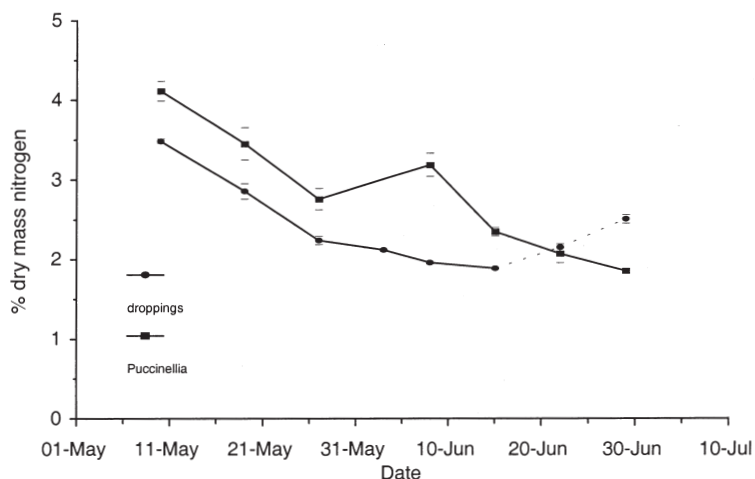

Fig. 3. Percentage dry mass nitrogen content of Greylag Goose droppings and aboveground material clipped from grazed *Puccinellia maritima* swards in areas heavily used by geese during the moult period on Saltholm in 1995. Each mean value represents five replicates for each date (± SE). Note that after 18 June 1995, the diet of geese becomes more varied, and hence protein content of faecal material is no longer related to that of *Puccinellia*.

NITROGEN BUDGET COMPILATION

The calculation of the overall nitrogen budget was carried out for each sampling interval during 1995, and is summarized in Table 1. Since the geese began to feed on a diversity of plant foods after 18 June, retention rates could not be calculated after this time.

The proportion of available nitrogen absorbed by Greylags increased from 25% to 47% and the proportion of daily intake excreted as uric acid fell significantly from a mean of 35% prior to moult to 11% during moult (one-tailed *t*-test for unequal variances after arc sine square root transformation, $t_4 = 4.46$, $P = 0.006$). These two mechanisms enabled geese to significantly increase the proportion of nitrogen absorbed and retained in the body as a proportion of the amount in the food ingested from an average of 16% prior to moult to 42% during moult (Table 2; one-tailed *t*-test for unequal variances after arc sine square root transformation, $t_4 = 4.93$, $P = 0.004$).

Discussion

In a study of captive moulting Greylag Geese, van der Wal (1992) calculated the total mass of the primary, secondary and tertiary wing feathers (i.e. the major flight feathers replaced during the flightless moult period) to be 29·45 g. Of this, 15·2% would be nitrogen (Murphy & King 1984; Wielicki 1986), equating to 4·48 g of nitrogen. Since these flight feather are regrown in ≈ 30 days (van der Wal 1992), this represents an overall mean nitrogen demand of 0·15 g day^{-1}. Since the balance of absorbed over excreted nitrogen equates to a mean of 0·16 g day^{-1} (range 0·14–0·20 in Table 2) geese are just able to meet the demand for protein from the diet during the flightless moult period. This is despite the substantial reduction in foraging time and declining nitrogen content of their food. If, however, the geese were unable to increase their retention rate (D_N) above premoult levels (substituting a mean D_N value of 25·3% in Table 1 for samples during the moult period) the mean nitrogen balance would have been 0·12 g day^{-1}, below the required level. If geese were unable to decrease their uric acid excretion rate (N_u) above premoult levels (substituting a mean N_u value of 2·69% in Table 1 for samples during the moult period) the mean nitrogen balance would be 0·11 g day^{-1}, also below the required level. If neither of these adjustments to nitrogen uptake and metabolism was made (substituting a mean N_u value of 2·69% and a mean D_N value of 25·3% in Table 1 for samples during the moult period), nitrogen balance would equate to 0·08 g day^{-1}, insufficient to meet the demands for the regrowth of flight feathers.

Geese are considered inefficient foragers; their herbivorous feeding strategy and relatively small size restricts their ability to accumulate energy (Demment & van Soest 1985). Their long-distance migratory

nature necessitates high energy from the diet, but the capacity of the alimentary canal to develop to an appropriate size and architecture to more efficiently absorb nutrients is restricted by the need to minimize its mass during long-distance flight (Sedinger 1997). The general model has therefore evolved of geese as superficial digesters of material, characterized by high rates of throughput of selected high-quality food (Owen 1972, 1980; Sibly 1981). However, Prop & Vulink (1992) showed geese could potentially increase the digestibility of their low-quality food on
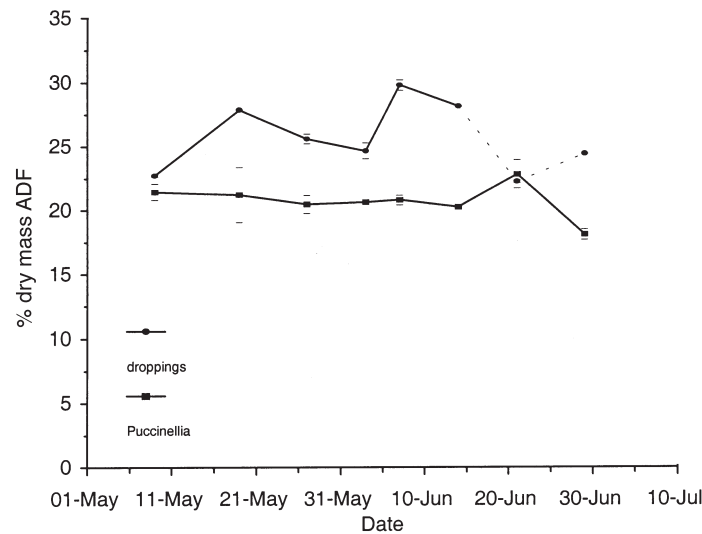

Fig. 4. Percentage dry mass acid detergent fibre (ADF) content of Greylag Goose droppings and above-ground material clipped from grazed *Puccinellia maritima* swards in areas heavily used by geese during the moult period on Saltholm in 1995. Each mean value represents five replicates for each date (± SE). Note that after 18 June 1995, the diet of geese becomes more varied, and hence ADF content of faecal material is no longer related to that of *Puccinellia.*
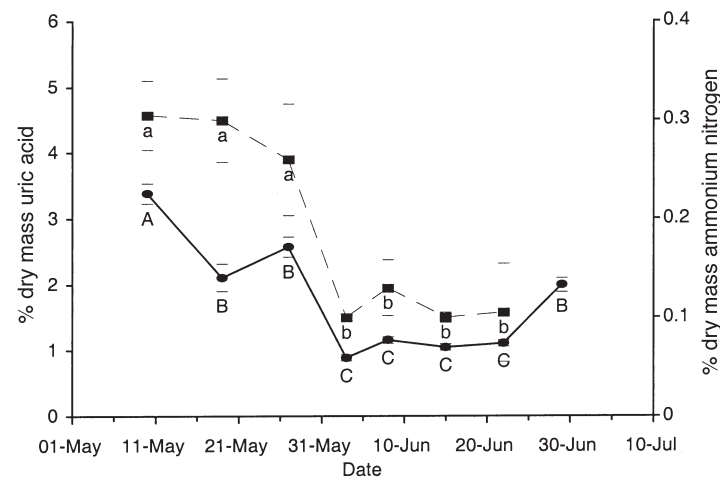

Fig. 5. Percentage dry mass uric acid (●, solid line) and nitrogen as ammonium (■, dashed line) content of Greylag Goose droppings during the moult period on Saltholm in 1995. Each mean value represents two replicates for each date (± SE), except for ammonium on 3 June, when one of the samples was contaminated. Common letters indicate no significant difference between means, based on Tukey HSD tests between means, except for the ammonium value from 3 June, compared using 95% confidence intervals about the determinations on other dates.

Table 1. Breakdown of the elements of the nitrogen budget of moulting Greylag Geese on Saltholm, summer 1995. Given time spent foraging on land by flightless (3·96 h) and flying birds (9·45 h), daily faecal output (F) was calculated based on dropping rate (d_r, estimated from the fitted regression in Fig. 2) and the mean dropping mass (f_w, from Fig. 1). Total nitrogen output (g dry mass day^{-1}) was calculated from overall nitrogen content of the droppings (N_{dt}, as presented in Fig. 3) and F and converted to non-excretory nitrogen output by subtraction of the daily uric acid nitrogen fraction (N_E). The percentage retention rate in the body (D_N, presented in Fig. 6) enables the backward calculation of nitrogen uptake based on the amount of nitrogen present in the total faecal material ejected in 1 day

Date	Daily feeding time (h)	Mean dropping rate (h^{-1})	Mean dropping mass (g dry mass)	Daily dropping output (g dry mass)	% N content of faeces	Daily N loss in faeces	% uric acid content of faeces	Daily uric acid N loss (g)	Daily non-uric acid N loss (g)	% N taken in food retained per day	Daily N gain (g)	% N excreted as uric acid
Pre-moult												
9 May	9·45	15·27	0·59	85·82	3·49	2·99	3·39	0·97	2·03	21·53	2·58	37·44
19 May	9·45	8·51	0·60	48·47	2·86	1·39	2·11	0·34	1·05	26·01	1·41	24·09
27 May	9·45	5·11	0·78	37·49	2·25	0·84	2·58	0·32	0·52	28·41	0·73	44·24
Moult												
3 June	3·96	3·61	4·47	6·76	2·13	0·14	0·89	0·02	0·12	43·56	0·22	9·14
8 June	3·96	3·38	0·33	4·47	1·96	0·09	1·16	0·02	0·07	53·96	0·15	11·28
14 June	3·96	4·03	0·38	6·09	1·89	0·12	1·05	0·02	0·09	42·48	0·16	13·08

breeding areas by increasing the retention time of food by two- to four-fold. In that study, digestion of cell wall carbohydrate material in graminoids was correlated with retention time. Soluble carbohydrates are easily and rapidly absorbed during rapid turnover of food in the alimentary canal, and longer retention rates enable some bacterial breakdown of plant structural carbohydrate (Drent, Ebbinge & Weijand 1980; Buchsbaum, Wilson & Valiela 1986; Prop & Vulink 1992).

In this way, patterns of digestion can be modified by geese as an adaptation to differing energy needs and food availability. The protein requirements of birds differ throughout the annual cycle, and annual changes in protein content of available plant material (generally considered very poor in protein, compared with, for example, invertebrate foods; see Hohman *et al*. 1992) also restricts its availability to herbivores at different times of the year. Furthermore, not all plant protein is available to geese, since a fraction is indigestible (measured in terms of pepsin-insoluble nitrogen; Goering & van Soest 1970), and the proportion of indigestible protein also varies between species and times of year (e.g. Loonen, Zijlstra & van Eerden 1991). It is generally considered that while the soluble fraction of plant protein is relatively efficiently absorbed by the goose gut, the insoluble portion passes out in the faeces largely unabsorbed (e.g. Anderson *et al*. 1997).

This study showed that moulting Greylag Geese on Saltholm made modifications to both nitrogen uptake and nitrogen excretion during this critical period in their life cycle. Whether this enabled the geese to meet their theoretical nitrogen demands from exogenously derived sources for investment in flight feather synthesis depends on a number of assumptions. In this study, it was not possible specifically to measure nitrogen breakdown products excreted by the geese other than uric acid (which is present in negligible amounts in plant tissue; Anderson *et al*. 1997). However, the reduction in the faecal content of nitrogen in the form of ammonium (but which is present in plant material) during the moult period strongly suggests that this too could be an excretory product of protein catabolism which is also much reduced during the moult period. Because of the difficulty in developing a precise ammonium budget for moulting geese, this source of faecal nitrogen was included in the general measure of nitrogen content of faeces, not partitioned between excretory nitrogen and food remnants. In addition, this study will not have accounted for excretory nitrogen deposited as volatile ammonia which would have been lost in transit and during the drying process. However, given the amounts of nitrogen accounted for by ammonium nitrogen, this source of error is considered likely to contribute very little to the overall nitrogen budget of the Greylags considered here. Nevertheless, inclusion of this ion as an excretion product would further enhance the calculated retention rates for nitrogen during moult.

Physiological adjustments are being made by the geese that enhance uptake of nitrogen from the food and reduce the amount excreted as uric acid once the flightless period of moult has commenced. The restriction of the birds to feeding at night appears to be linked to the frequency of predator-like stimuli on the moulting areas, rather than diurnal rhythms in food quality (Kahlert *et al*. 1996). Whatever its cause,
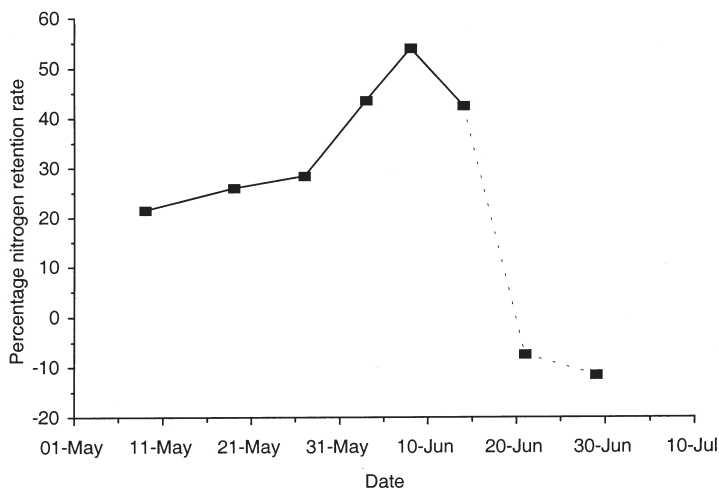

Fig. 6. Percentage nitrogen retention rates of Greylag Goose based on analysis of food and droppings during the premoult and moult periods on Saltholm in 1995. Note that after 18 June 1995, the diet of geese became more varied, and hence retention rates (based on only *Puccinellia* nitrogen content as food material) become invalid.

Table 2. Nitrogen balance compiled for moulting Greylag Geese on Saltholm, summer 1995. Values indicate amount of daily nitrogen ingested, absorbed and excreted, which are then used to calculate a crude nitrogen balance and hence efficiency based on balance achieved as a percentage of nitrogen ingested

Date	Total N ingested (g day^{-1})	Total N absorbed (g day^{-1})	Total N excreted as uric acid (g day^{-1})	N balance (g day^{-1})	% N efficiency
9 May	12·001	2·584	0·967	1·616	13·47
19 May	5·434	1·413	0·341	1·073	19·74
27 May	2·557	0·727	0·322	0·405	15·84
3 June	0·503	0·219	0·020	0·199	39·58
8 June	0·284	0·153	0·017	0·136	47·87
14 June	0·384	0·163	0·021	0·142	36·93

the effect of switching to night-time feeding restricts the foraging time per day by half during the flightless period. Since there is no compensation through increased peck rate, the geese have effectively reduced their opportunity to harvest nitrogen by 50% during the very period when exogenous protein could become an important nitrogen source for feather production. The increased absorption of nitrogen appears to be achieved through enhanced retention rates, since dropping rates reached their lowest levels during the early part of moult and were higher before and after the flightless period. Dropping masses also fell during the moult period, these two measures suggesting longer retention periods in the gut, which has been shown to be an adaptation to enhance carbohydrate uptake in geese (Prop & Vulink 1992). The use of caeca as organs by which to extract dietary nitrogen is well known in geese (Sedinger 1997), and it seems likely that diversion of food into caeca could be involved in this process. Analysis of the size and function of goose caeca during the moult period could provide support for this hypothesis, especially when combined with the experimental monitoring of precise nitrogen budgets of captive geese. The reduction in excreted nitrogen has not previously been reported from geese during moult, but reflects a modification to protein metabolic pathways. This may be the result of a reduction in breakdown products from the 'normal' processes of protein catabolism (e.g. as a potential source of energy), modified to meet the specific protein demands of rapid flight-feather regrowth during the flightless period. The net effect is a reduction in excreted nitrogen breakdown products in ejecta.

In summary, it would appear that these results confirm the flexibility of the goose digestive system to adapt to a period of high nutrient demand, in this case protein demand for feather replacement during the critical flightless moult period. Whatever the precise mechanism, the analysis of ingesta and faecal material shows that selection of high-protein food, increase in retention rate and decrease in the amount of excreted uric acid nitrogen combine to enable flightless moulting Greylag Geese to meet their crude nitrogen demand. This is achieved from exogenous sources during the period when feather re-growth is occurring, despite the change to nocturnal foraging which halved the period available for feeding and an overall decline in nitrogen content of their diet. Since the geese are likely to feed rapidly and fill the gut prior to departure to the roost site, our analysis is likely to underestimate the actual nitrogen intake considerably because it was not possible to recover droppings from these areas. It seems therefore that under these conditions geese are potentially able to meet their nitrogen demand during moult from the diet as suggested by Hohman *et al*. (1992), but only by physiological changes to enhance digestibility and reduce excretion rates.

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