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Chapter 5

Body stores in pre-migratory brent geese: the consequence of habitat choice on protein deposition

Jouke Prop and Bernard Spaans

Abstract

Worldwide millions of arctic-breeding geese winter in temperate climate zones. Increasing numbers of geese combined with decreasing availability of natural habitats has resulted in growing numbers becoming reliant on agricultural crops. In spring, when the geese deposit body stores to cover costs of migration, natural habitats seem to be preferred, and agricultural fields function primarily as spill-over areas. We tested the hypothesis that differences in the quality of plants in alternative habitats affected the ability of geese to deposit protein stores. We studied the dark-bellied brent goose Branta bernicla bernicla in the Dutch Wadden Sea during spring staging to investigate the effect of habitat choice on protein deposition, one of the major components of body stores. Study sites were selected from a traditional staging area (a salt marsh) and from a reserve managed to attract geese (an inland pasture). At both sites the deposition rate of protein (or nitrogen) was assessed.

Throughout spring, geese on the salt marsh experienced a decrease in digestibility of nitrogen-compounds (protein) from 85% to 77%. Concurrently food ingestion rates increased, resulting in an absorption rate of nitrogen that increased in April and levelled off in May. After an initial increase, deposition rates of protein stores decreased, and progressively a larger proportion of the food ingested was used to accumulate fat rather than protein. Individuals on the inland pasture digested protein equally well, but they retained less of the protein ingested than birds on the salt marsh, perhaps due to an amino acid deficiency in pasture grasses. The lower retention of protein was consistent with the observation on body mass early in spring that individuals on pastures carried less body stores than those on salt marshes.

Early in spring brent geese moved from pastures (their winter habitat) to salt marshes when it became important to build up protein stores prior to migration. This habitat shift was consistent with the more favourable retention efficiency of protein on salt marshes, which suggested that the timing of the shift was driven by a change in nutrient requirements. The nutritional differences in food plants found in this study may be one of the reasons why brent geese, and possibly other high-arctic goose species, prefer natural vegetation in spring. Maintaining a healthy population of brent geese is therefore more effectively achieved by improving foraging conditions on salt marshes, than by creating inland reserves with intensively managed pastures.

Submitted
Introduction

Pre-migratory birds are well recognized for their ability to deposit large stores of fat and protein (Lindström and Piersma 1993) but relatively little is known about the nutritional demands necessary to produce these stores (Bairlein 1998). In particular the impact of food availability on the timing and rate of protein storage is largely unexplored. This issue is especially relevant to herbivorous migrants who are heavily constrained by the generally low availability of protein in plants (White 1978, Robbins 1993, Sedinger 1997). In addition to the large amount of fat necessary as an energy source, stored protein is required for metabolic processes (Hanson 1962, Jenni and Jenni-Eiermann 1998) and to support the production of eggs (Ankney and McInnes 1978). It is further incorporated in the flight muscles to enhance the power of flight (Lindström and Piersma 1993) or in other parts of the body that are enlarged during periods of hypertrophy (e.g. the heart, Piersma 1998). The idea that protein is in short supply to pre-migratory herbivorous birds is supported by observations in barnacle geese Branta leucopsis. Individuals that deposited much fat but little protein were less successful in subsequent reproduction than individuals that deposited the same amount of fat but more protein (Prop and Black 1998). This gives rise to the question as to whether protein is generally limited available to herbivorous birds preparing for long-distance migration.

There are two major nutritional factors that potentially constrain the deposition of protein stores. First, the availability of protein in the food may be limited because only a portion can be digested and absorbed, which largely depends on the characteristics of the food plants (Van Soest 1982). Secondly, the amino acid composition of proteins in the food must match the composition of the target muscle tissue (Williams et al. 1954). The amino acid profile in the food determines therefore the suitability of that food for conversion into protein tissue. Because there are large differences in amino acid composition among plant species (Thomas and Prevett 1980, Sedinger 1984, Sedinger 1997), plants differ in how suitable they are as a source to build proteins (Fisher 1972).

Our study species, the dark-bellied brent goose Branta bernicla bernicla, deposits large body stores before migrating to its arctic breeding areas (Ebbinge and Spaans 1995). In winter brent geese mainly occur on inland pastures, where the high abundance of food provides an almost unlimited supply of energy. In April, however, when the geese start accumulating body stores, they shift to salt marshes (Ebbinge et al. 1982). Similar abrupt shifts in habitat or food choice are commonly observed in migratory birds (Bairlein and Gwinner 1994). Two non-mutually exclusive hypotheses could explain these shifts. First, the shifts may be due to changes in the availability of food, and birds select the habitat that provides the best food, or where food is most abundant, or where disturbance is least (Boudewijn 1984, Vickery et al. 1995, Prins and Ydenberg 1985). Such a mechanism is a fundamental to theory about how organisms generally are distributed in relation to resource availability (Sutherland 1996). Secondly, migratory birds may shift to another habitat in response to a change in their requirements for particular nutrients when the alternative habitats provide better opportunities to satisfy their needs (McKay et al. 1994).
Since the 1980’s, an increasing proportion of the dark-bellied brent goose population has been using pasture throughout spring staging (Spaans and Postma 2001) instead of shifting to salt marshes. Ebbinge (1992) suggested that this was due to a density dependent regulation of the numbers on salt marshes, birds balancing the costs of increasing densities with the nutritional benefits in the traditional habitat. In this view, the abundance of food in the alternative habitat apparently outweighs the disadvantage of a lower food quality. We tested one aspect of this hypothesis by comparing the digestibility of the food between the two habitats, and, suspecting that the habitats differed in how well geese were able to convert food into protein stores, by comparing the availability and suitability of the protein in the food.

More specifically, we first determined directly the weight gain of individual spring-staging geese in the two habitats of interest to test for any differences in body stores dynamics. We then examined if the deposition of protein stores by brent geese in each of the habitats was limited by the availability or by the suitability of proteins ingested. For this purpose we determined the digestibility of protein through the season as an indicator of availability, and the proportion of protein ingested that was retained in the body (the retention efficiency) as an indicator of suitability. If the size of the protein stores was limited by the intake of protein we expected invariably high retention efficiencies of protein. Otherwise, we expected the efficiencies to be low or variable through time. Actual deposition rates of protein depend on retention efficiencies in combination with the amount of food ingested. To find when most protein stores were deposited, we constructed a nitrogen balance for geese on salt marshes based on the amounts of nitrogen ingested and excreted.

**Methods**

During spring almost the whole population of the dark-bellied brent geese (brent geese hereafter) resides in the Wadden Sea area. The geese rapidly build in numbers in April to peak by the end of this month and in early May (Ebbinge et al. 1999) in preparation for the first leg of a 4000-5000 km migration to the breeding grounds in Siberia. The majority of the birds arrive from the wintering areas in England and France after moving an average of 600 km. Other birds spend most of the winter on inland pastures along the Wadden Sea coast and travel only a short distance to the spring staging grounds. In spring the geese occur on offshore islands and along the mainland coast where both salt marshes and inland pastures are found. Mudflats are also present but are an important foraging habitat only in autumn. We collected observations in two study areas in the Dutch part of the Wadden Sea, one located on the salt marshes of Schiermonnikoog, and one on the pastures of the nature reserve Zeeburg on the island of Texel (Fig. 1). We present additional data collected on the salt marshes of the island of Terschelling. The latter area hosts large flocks of brent geese exclusively feeding on salt marshes (Ebbinge 1992), and we here assume that the geese perform similarly to those in our study site on Schiermonnikoog.
Body stores
To determine the mass of geese in early spring and the rate of change through the season, geese were caught with cannon nets on Texel and on Terschelling. Catching times were at the arrival of peak numbers (the end of April - early May), and close to departure by the geese at the end of May. Birds were weighed to the nearest 10 g, and as measures of structural body size the head length (the distance from the tip of the bill to the back of the head) and the wing length (from the elbow joint to the distal end of the longest primary) were measured to the nearest 1 mm. We used Principal Components Analyses to examine the correlation matrix of wing length and head length, and used the first principal component as our index of structural body size (Reyment et al. 1984). We then indexed body stores by taking the residuals of the regression of body mass against body size (Piersma and Davidson 1991).

Collection of food and droppings
Digestibility of food was determined by comparing the composition of droppings and corresponding food plants. Food plants known to be important to the geese (Prop and Deerenberg 1991) were sampled by hand, taking care to collect only the green parts that are grazed by the geese. Samples of 25 droppings were collected regularly throughout the staging period by recording flock movements from an observation tower, and subsequently recovering the fresh droppings produced. Dropping samples were underrepresented early in the season because the brent geese on Schiermonnikoog usually mixed with barnacle geese, so that identifying the droppings by species was difficult. Samples of plants and droppings were oven-dried at 45ºC to constant weight, and subsequently weighed. To determine the diet composition, plant fragments in the dropping samples were microscopically analysed as described by Prop and Deerenberg (1991).
Chemical analyses
Food and droppings were ground through a 1 mm sieve and analysed for total nitrogen (Kjeldahl), cell wall components (neutral detergent fibre NDF, and acid detergent fibre ADF; Goering and Van Soest 1970) and ash. Most of the nitrogen in plants is associated with proteins, and we calculated (crude) protein from total nitrogen using a multiplier of 6.25 (Robbins 1993). Avian droppings contain nitrogen originating from the faeces (mainly undigested proteins) and nitrogen from urinary waste products (mainly uric acid, Robbins 1993, Fox and Kahlert 1999). To distinguish between these two fractions (N and E, respectively, in Fig. 2), we determined the content of the uric nitrogen following Terpstra and De Hart (1974).

![Diagram](image)

Fig. 2. Schematic representation of the pathways of protein. Proteins in the food are digested and assimilated (A), or remain undigested (N). Droppings contain both the excretion products of proteins (E) and undigested proteins (N). The amount of proteins retained in the body (R) can be estimated from the rates of nitrogen assimilated and excreted.

Calculations
The digestibility of organic matter (%) was calculated as:

$$D_{om} = \frac{CF_{om} - (CD_{om} \times R)}{CF_{om}} \times 100,$$

where $CF_{om}$ and $CD_{om}$ are the concentrations of organic matter in the dry mass of food and droppings, respectively, and $R$ is the ratio of the ADF content in the food and droppings, using ADF as a natural marker substance (Prop and Vulink 1992). The chemical composition of the food corresponding to each of the samples of droppings was calculated on the basis of seasonal trends of the chemical components in separate food species, in combination with the diet composition (Prop and Deerenberg 1991).

By distinguishing between the two pathways that proteins follow through the intestinal tract and body (Fig. 2), we were able to calculate (1) the digestibility of protein, and (2) the retention efficiency of protein. The digestibility of protein $D_{protein}$ describes what percentage of protein in the food is absorbed ($A$ divided by $A+N$ in Fig. 2), which we approximated by substituting $CF_{om}$ and $CD_{om}$ of the formula above with the concentration of nitrogen in food and droppings (excluding urinary nitrogen). The retention
efficiency of protein describes what percentage of the protein ingested is retained in the body (R divided by A+N in Fig. 2), which is approximated by substituting the concentrations of nitrogen in food and droppings (excluding urinary nitrogen) in the formula above. The retention efficiency is negative when the amount of nitrogen excreted is larger than the ingested amount (E+N > A+N in Fig. 2). The digestibility of protein defined above is an alias for ‘true assimilation efficiency of nitrogen’ (Karasov 1990), and the retention efficiency of protein is also called ‘apparent assimilation efficiency of nitrogen’.

The ingestion rate of organic matter (g min⁻¹) was calculated from each of the dropping samples as

\[ IR = \left( \frac{W}{I} \right) \times \left( \frac{100}{100 - D_{\text{ash}}} \right) \]

where \( W \) is the average dropping weight (g ash-free), \( I \) is the dropping interval (min) derived from the regression of intervals by date. Dropping intervals were determined by following random individuals using a telescope and recording the timing of two successive droppings. The ingestion rate of nitrogen (g min⁻¹) was calculated as

\[ IR_N = IR \times (CF_N / 100) \]

where \( CF_N \) is the nitrogen content of the food. The absorption rate of nitrogen (g min⁻¹) was calculated as

\[ Abs_N = IR_N \times (D_{\text{protein}} / 100) \]

The excretion rate of urinary nitrogen (g min⁻¹) was calculated as

\[ Exc_N = \left( \frac{W}{I} \right) \times (CD_{\text{uric}} / 100) \]

where \( CD_{\text{uric}} \) is the concentration of the excretion products in the droppings. The retention rate of nitrogen (g min⁻¹) was calculated as

\[ Ret_N = Abs_N - Exc_N \]

All dates are expressed as the number of days since 1 April.

Results

Body stores in two habitats

Geese on salt marshes were on average 1.3% larger than individuals on pastures (first principal component \( F_{1,527} = 38.97, P < 0.0005 \)). Body mass corrected for structural size did not differ between males and females (Table 1), and data were pooled in further analysis. The geese increased in body mass through May at a rate of on average 11.8 g day⁻¹ (Fig. 3). The significant interaction term between date and habitat (Table 1) modulated the general pattern as follows: birds on pastures had the lowest initial body stores, subsequently they showed the largest rate of increase, and at the end of May the body stores of geese on pastures were larger in comparison with geese on salt marshes.

Table 1. Analysis of variance of body stores (residuals of the regression of body mass on structural size). The non-significant parameter is not included in the final model. Habitat= pasture or salt marsh.

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</table>
Protein stores in brent geese

Fig. 3. Body stores (residuals of the regression of body mass on structural size, average±SE) from the end of April onwards for geese foraging on salt marshes or on pastures. Data are adjusted for differences among years based on the model in Table 1. The slopes of the regressions estimate the daily increase in body mass, 8.9 (SE 0.6, n=300) and 14.6 (SE 1.04, n=230) g day⁻¹ for salt marshes and pastures, respectively. The 95% confidence intervals of the regressions are given.

Fig. 4. A. Digestibility of organic matter through spring for brent geese on salt marshes (closed circles) and on pastures (open circles) (for the pooled data y=44.87-0.25x, F₁,₅₃=20.56, P<0.0005).
B. Digestibility of organic matter in relation to the NDF content of the food (y=85.80-1.02x, F₁,₅₃=13.47, P<0.001, with similar slopes for salt marsh and pastures, F₁,₅₁=0.97, N.S.).
Use of protein in two habitats

The digestibility of organic matter decreased over time (Fig. 4A). There was a tendency for geese to digest salt-marsh plants better than pasture grasses ($F_{1,52}=2.09$, $P=0.15$). The variation of organic matter digestibility, both in time and between habitats, was correlated with the proportion of cell wall components in the food (Fig. 4B).

Similarly, the digestibility of protein specifically decreased through spring (Fig. 5A, $F_{1,52}=25.12$, $P<0.0005$), which was associated with a decrease in protein concentrations in salt-marsh plants, though not in pasture plants (Fig. 6). Geese on pastures tended to digest protein better than those on salt marshes ($F_{1,52}=3.61$, $P=0.06$).

In early April, birds foraging on pastures experienced a lower retention efficiency of protein than birds on salt marshes (Fig. 5B; the intercepts of the regressions of retention by date differed between the habitats, $F_{1,51}=6.23$, $P<0.05$). The retention efficiency of protein dropped rapidly through spring, and the decrease was stronger on salt marshes than on pastures (given the significant interaction term of date by habitat, $F_{1,51}=4.03$, $P=0.05$). As a consequence, the initial difference in retention efficiency between the habitats disappeared in May.

Fig. 5. Digestibility of protein (A) and retention efficiency of protein (B) throughout the staging period. The means (±SE) for brent geese on salt marshes and on pastures are given. The majority of the birds arrive mid-April and depart 20-25 May.
Nitrogen balance on salt marshes

On salt marshes the ingestion rate of food increased through spring \( (y = 0.200 + 0.0173x \text{ g min}^{-1}, F_{1,45} = 10.74, n = 47, P = 0.002) \), which was associated with an increase in dropping weights \( (y = 0.760 + 0.0066x \text{ g}, F_{1,45} = 18.31, n = 47, P < 0.0005) \), and almost constant dropping intervals \( (y = 4.03 + 0.0054x \text{ min}, F_{1,95} = 0.85, n = 96, \text{ N.S.}) \). The absorption rate of nitrogen showed a quadratic relationship with date (Fig. 7A) with highest values during the first ten days of May. The excretion rate of urinary nitrogen was positively related to the absorption rate \( (y = 3.76 + 0.379x, F_{1,45} = 15.7, P < 0.0005) \). The residuals of this relationship showed a strong increase through time (Fig. 7B). This means that at a same absorption rate of nitrogen, geese progressively excreted a larger amount of nitrogen. As a consequence of the increase of nitrogen excretion rate, the nitrogen retention rate dropped from an average of 4 mg of nitrogen per min in April to values close to 0 at the end of the staging period (Fig. 7C). The peak in retention rates in late April - early May was therefore much earlier than the period of highest absorption, and most protein stores were therefore deposited during the early part of the staging period.

Discussion

Use of proteins

Animals with simple digestive systems are able to digest proteins well (Karasov 1990) and the invariably high digestibility in brent geese (>75%) was therefore expected. The proportion of protein that was retained in the body was similarly high, though much more variable through time. Comparisons with other studies suggest that spring staging brent geese are leading edge of what these birds can achieve in retaining 40% of the protein ingested into body tissue (Fig. 5). For example, even though pre-fledging waterfowl...
can be assumed to develop body tissue at maximal efficiencies (Fisher 1972), they nevertheless retained food protein with an average efficiency of only 40.3% (Sedinger 1992, selecting studies based on carcass analysis from his Table 4-2). Similarly, the efficiency of protein retention in growing chickens feeding on different kinds of vegetable food was 41.5% (Fisher 1972). Adult greylag geese retained 37.6% of the protein ingested during the wing moult when the birds were in nutritional stress (Fox and Kahlert 1999). The maximal values of the retention efficiency and the digestibility of protein in

Fig. 7. The use of nitrogen by brent geese on salt marshes through spring. A. Nitrogen absorption rate ($y=5.47+0.27x -0.0036x^2, F_{2,44}=3.70, P<0.05$). B. Residuals from the regression of nitrogen excretion rates against the absorption rates of nitrogen ($F_{1,45}=39.85, P<0.0005$). C. Nitrogen retention rates ($y=1.50+0.155x -0.0033x^2, F_{2,44}=7.28, P=0.002$).
early April (50% and 85%, respectively) indicate that $50/0.85 = 59\%$ of the absorbed protein was actually retained, which is also close to maximal values observed in young, growing birds (maximally 68%, Sedinger 1984).

During the second half of the staging period the retention efficiency of protein decreased steeply, while the amount of nitrogen excreted progressively increased. By comparing Fig. 5A and 5B we conclude that a lower digestibility of protein attributed only little to the decline in retention efficiency. Similarly it is unlikely that the decline in retention efficiency was caused by a lowered suitability of proteins ingested because the diet composition through the season was relatively constant (Prop and Deerenberg 1991) and the composition of amino acids within plant species is stable (Sedinger 1984). In birds generally, protein ingested in excess of the nitrogen requirements is catalyzed, the overload of nitrogen is excreted and the remaining carbon chains are used as an energy source (Mitchell 1962, Fisher 1972) or as a substrate for fatty acid synthesis (Klasing 1998). We suspect brent geese followed the same pathway. In conclusion, during the early part of spring staging, brent geese retained protein at maximal efficiencies, whereas later in May the geese progressively used proteins ingested for other metabolic processes as discussed below.

**Deposition of protein stores through spring**

Early in spring the geese were ineffective in depositing body stores (Fig. 8), mainly due to a low intake rate as a result of low food availability (Prop and Deerenberg 1991). Deposition rates of body stores (fat and protein together) peak in early May, and from then onwards, rates stabilize or slightly decrease (Ebbinga 1989, Prop and Deerenberg 1991). By comparing the pattern of deposition of total body stores with the deposition of protein we conclude that arriving brent geese start depositing protein stores on the salt marshes, whereas during the second half of the staging period, they preponderantly deposit fat (Fig. 7). Indeed most birds arrive when conditions to deposit protein stores are improving. We interpret this finding as evidence that the geese adjust their migration schedule to the local food conditions (the ‘Green wave hypothesis’, Drent *et al.* 1978).

Our study agrees with previous work on geese and waders which suggested that premigratory birds first deposit protein and later mainly fat (McLandress and Raveling 1981b, Korte 1988, Alisauskas and Ankney 1992, Gauthier *et al.* 1992, Battley and Piersma 1997). In some other species protein deposition seems to be extended for a longer part of the staging period (Piersma and Jukema 1990, Clausen *et al.* 2003) but this may be an artefact of the method followed (Lindström and Piersma 1993). Most of the previous studies were based on carcass analyses, and determined protein deposition from time series of fat-free body mass of samples of birds collected through time. Our approach of constructing a nutrient balance has the advantage that it avoids the pitfalls associated with the carcass-collection-method (Lindström and Piersma 1993), and that no specimens of the study species have to be collected.

We can speculate why birds preparing for a long distance migration should aim to deposit fat and protein at different times, rather than depositing both in a fixed proportion.
For herbivores generally, it might be more efficient to deposit protein stores when the food contains most protein, i.e. early in the season, but this is unlikely to be a full explanation because waders, which depend on protein-rich food throughout the pre-migration period, exhibit the same pattern of deposition of body stores. Much of the protein deposited by geese is invested in breast and leg muscles (Gauthier et al. 1992), and promotes therefore both walking (essential for foraging) and flying. Carrying large fat deposits is known to enhance the risk of predation (Lima 1986), and building stronger flight muscles might therefore be anticipatory to the large fat stores deposited later in the season.

Habitat shift by changing requirements?
Assuming geese select the habitat that provides them with the best opportunities for foraging, the decision to move from pastures to salt marshes must result from balancing food quality (Boudewijn 1984) and food availability (Vickery et al. 1995) in the two habitats. However it seems unlikely that these factors alone were responsible for the shift observed because 1) the trends in food quality ran parallel in the two habitats (Fig. 6), and 2) food available was constant or increased only slightly on salt marshes (Prop and Deerenberg 1991) but increased rapidly on pastures (unpublished JP, Spaans and
Protein stores in brent geese

Postma 2001). Instead we suggest that the shift in habitat was driven by a change in needs for nutrients because the shift coincided with the onset of deposition of protein stores. From a post-winter energy limited metabolism, which in waterfowl in general is best satisfied by foraging on agricultural pastures (Bruinzeel et al. 1997), the deposition of stores urged the birds to change foraging goal by maximizing protein retention. Shifts in habitat or diet resulting from changes in nutrient requirements are common in passerine birds (Bairlein and Gwinner 1994) but are much less recognized in waterfowl species (but McKay et al. 1994). A change in nutrient needs as a main factor to explain the habitat shift in brent geese is also consistent with a similar shift in habitat by barnacle geese in our study area (Prins and Ydenberg 1985). Barnacle geese shift 6 weeks earlier than brent, and their migration is similarly earlier. Assuming the two species are affected in the same way by human disturbance, this also disqualifies disturbance (Bos and Stahl 2002) as a main cause for the habitat shift.

Our study provides evidence that it is necessary to account for differences in suitability of proteins when explaining habitat preference in waterfowl; although the protein content in pasture grasses was invariably higher than in salt marsh plants (39 and 31% in April, respectively), the actual percentage of protein retained per g food ingested was considerably higher on salt marshes than on pastures (averaged at 12 and 8% in April, respectively).

**Geese on pastures deposit less protein stores**

Brent geese that did not shift to salt marshes but continued foraging on pastures experienced a lower retention efficiency of protein compared to individuals that did make this shift (Fig. 5). In theory, the lower retention efficiency in pasture birds in April could have resulted from a lower requirement for protein if these birds had already deposited protein earlier in the season. However, foraging activities in brent geese in March are low and coincide with a decline in body mass (Ebbinge 1989), which indicates that brent geese do not start depositing body stores before April. Moreover, our data on body stores in early May indicate that birds on pastures were lighter than birds on salt marshes (Fig. 3). Although it was not possible to discriminate between stores of fat and of protein on the basis of body mass alone, the data clearly suggest that pasture birds were less advanced in depositing body stores than individuals on salt marshes.

Alternatively, the difference in retention efficiency of protein could be caused by a lower availability of proteins in pasture grasses. The reverse appeared to be the case, however, because the digestibility of protein tended to be higher on pastures than on salt marshes (Fig. 5A). As a most likely explanation for the difference in retention efficiency of protein between the habitats, we suggest that the amino-acid composition in pasture grasses was less balanced relative to the nutritional needs of the geese. Our observations on brent geese are in line with the performance of pre-migratory barnacle geese staging in Norway, in which individuals using pastures exhibited a lower retention efficiency of protein than birds on salt marshes (Prop and Black 1998).

The lower retention efficiency of protein by brent geese on pastures could theoretically have been compensated for by a higher rate of food intake. We did not measure
intake rates on pastures ourselves and to reconstruct the nitrogen balance of geese on pastures we can use ingestion rates collected on captive brent geese on the same pastures of this study by Bos et al. (2002b). These birds achieved maximal ingestion rates of 12.8 mg nitrogen per min (Bos et al. 2002b, intake rates converted into ingestion rates by adjusting for the proportion of time feeding). This is slightly higher than the ingestion rate of 12.0 mg nitrogen per min of birds feeding on salt marshes, as found in this study but probably exaggerates ingestion rates of the wild birds as the experiments were carried out on temporarily ungrazed swards with a high availability of grasses. The comparison suggests little difference in nitrogen ingestion rates between geese on salt marshes and on pastures, and, as a consequence of the lower retention efficiency of protein, we expect that the amount of protein retained was lower in pasture feeding birds. This supports our main conclusion that birds foraging on pasture deposited less protein stores than birds on salt marshes.

Individuals observed on pastures in spring did not differ in subsequent reproductive success from those exploiting salt marshes (Spaans and Postma 2001). Although differences in survival rate or lifetime reproductive success have not been checked for, this suggests that there were no fitness consequences for geese using pastures. Does this mean that the smaller protein store of pasture birds was unimportant for completing a successful migration? Instead we suggest that birds can compensate for smaller protein stores in several ways: (i) by additional feeding on the mudflats, where the birds spend the night, for example on algae which is a potentially important food plant (Ebbing et al. 1999), (ii) by extending the period of depositing protein stores towards the end of the staging period (Fig. 5), (iii) by adopting a different migration strategy and refuelling protein on their way to the breeding grounds (Jenni and Jenni-Eiermann 1998, Green et al. 2002); or (iv) the brent geese could have benefited from the high concentration of metabolizable energy in pasture grasses by depositing a larger amount of fat, as barnacle geese on pastures do (Prop and Black 1998). That brent geese on pastures do benefit from the high metabolizable energy content in their food is supported by the higher deposition rate of the total body stores (Fig. 3).

Management implications
An important suggestion arising from this study is that the difference in nutritional value of the food on pastures and salt marshes has repercussions for the size and composition of body stores that the geese accumulate. On the basis of historical data of goose abundance in different habitats, Ebbing (1992) concluded that spring-staging brent geese preferred salt marshes above pastures. Ebbing suggested that individuals that were out-competed on salt marshes moved to pastures as a second choice habitat. Our observation that geese on pastures are smaller than individuals on salt marshes is consistent with this hypothesis. Although brent geese using pastures may have several mechanisms to compensate for less favourable conditions to accumulate protein stores, we suggest that the nutritional asymmetries between pastures and salt marshes are a potential factor determining the preference by spring-staging brent geese for salt marshes.
Refuge establishment is often advocated to reduce conflicts between geese and agricultural interests (Owen 1990, McKay et al. 2001). Similarly, the Zeeburg reserve on Texel, where we conducted part of our study, was created with this objective in mind (Spaans and Postma 2001). Usually it is more practical to create a refuge inland by providing intensively farmed grassland, because the opportunities to establish new reserves on salt marshes are more restricted. In the case of the brent geese, the creation of reserves becomes urgent as the number of suitable salt marshes has declined during the past few decades due to embanking projects or changes in management which resulted in a vegetation unattractive to geese (Ganter et al. 1997, Prop et al. 1998, Bos et al. 2002a).

Establishing inland refuges may be inappropriate however if the main aim of doing so is to provide pre-migratory brent geese, and possibly other goose species (Prop and Black 1998), with the nutrients they require for accumulating body stores necessary for migration. An important goal in providing suitable refuges along the migration route (Van Nugteren 1997) could therefore be to improve foraging conditions on salt marshes by judicious grazing regimes using domestic herbivores.

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