THE POSSIBLE IMPORTANCE OF NUTRITIONAL REQUIREMENTS FOR DARK-BELLIED BRENT GEESE IN THE SEASONAL SHIFT FROM WINTER CEREALS TO PASTURE

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ABSTRACT The use by Brent Geese of five pairs of winter cereal and pasture fields at Pagham Harbour, West Sussex, England was measured from November 1991 through the end of March 1992. A switch from winter cereals to pasture was observed between November and December. Monthly vegetation samples were analysed for quantitative and qualitative changes which may have affected feeding by the geese. Depletion of winter cereal biomass or percentage live matter, or changes in sward height did not appear to be responsible for the shift from cereals to pasture. Nor was there evidence that geese responded to relative changes in nutrient quality. Additionally, human disturbance did not prompt the switch. One possible explanation is that Brent Geese maximize dietary protein early in the winter, perhaps to replace that lost during migration; thereafter water soluble carbohydrates are maximized.

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INTRODUCTION

Half the world population of over 200 000 Dark-bellied Brent Geese (*Branta bernicla bernicla*) begin to arrive on British shores in late September to feed on mudflats and salt-marsh. They soon leave these traditional feeding grounds, however, and fly inland to graze on agricultural fields. This habitat switch can occur earlier in years when there is a high percentage of juveniles in the population (Tubbs & Tubbs 1982). Autumn-sown wheat, barley and oilseed rape provide the bulk of the early winter diet, though if winter crops are not yet established, the birds will first feed on pasture (McKay mimeogr. rep.). A second habitat switch has also been documented later in the season, this time from cereals to pasture (Summers & Critchley 1990, Vickery & Summers 1992), which is the subject of this paper.

There are several reasons why Brent Geese might make an early winter shift from a diet of cereals to pasture:

(1) Geese may deplete the cereal fields to a level where feeding is no longer profitable.
(2) The geese may be tracking changes in the relative nutritional value of the two vegetation types.
(3) The nutritional requirements of the geese may change through the season, being satisfied by cereals in late autumn and by pasture in winter and spring.
(4) Factors such as scaring, disturbance or changes in day length may be more important to the geese than nutrient content of the diet.

Depletion rates

Depletion of resources (decline due to natural die-back or grazing) has been proposed as the main cause of the autumn shift from intertidal to inland habitats by Brent Geese in North Norfolk, England (Summers 1990a, Summers *et al.* 1993).

If depletion is similarly responsible for the shift from cereals to pasture, we would expect to observe a decline in biomass, percentage live matter or sward height in cereal fields before the

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shift, either in absolute terms or relative to pasture levels. Summers (1990b) showed that Brent Goose-grazed winter wheat plots declined in biomass over the winter relative to ungrazed plots. Drent & Van Eerden (1980) found Brent Geese could deplete green biomass of pasture below a threshold of 50 g dry weight m^{-2}. Above this threshold, increased visitation by geese had no effect on green biomass. When biomass fell below 18 g dry weight m^{-2} the geese could not exploit the vegetation.

Changes in the nutritional value of the vegetation

Geese have relatively short food retention times of a few hours (Prop & Vulink 1992). Because food is not in the gut for long, only easily digestible components are absorbed. Large volumes of food are therefore ejected resulting in a high frequency of defecation (one dropping every 3.5 minutes; Drent *et al.* 1978/79). This fast through-put, low digestive efficiency system appears to be a strategy designed to allow high ingestion rates of food (Karasov 1990) without a large body size.

Digestibility, and hence metabolizable energy, appears therefore to depend mainly on food chemistry. Cell contents (water soluble carbohydrates and non-structural proteins) tend to be completely digested but are in low concentrations. Fibre and cell wall polysaccharides take longer to digest but are in much higher concentrations (Buchsbaum *et al.* 1986). As protein digestion occurs rapidly, optimizing protein intake (by high turnover rates of food) is probably more important to geese than increasing the efficiency of carbohydrate digestion (by retaining foods for longer periods of time) (Buchsbaum *et al.* 1986).

Fibre content has been shown to be inversely related to digestibility (Drent *et al.* 1978/79, Prop & Vulink 1992). Karasov (1990) calculated that an important determinant of the value of a food to a herbivore ('utilization efficiency') is the proportion (*Ri*) of the food that is refractory to chemical digestion. He reported that increasing *Ri* in the diet caused herbivores to increase their daily food intake (and this was accompanied by an increase in gut length). *Ri* is difficult to measure (Karasov 1990) and in this study it is taken to be proportional to neutral detergent fibre and ash.

Ash is almost certainly less digestible than fibre, and has been used successfully as a natural indigestible marker for Brent Geese (Drent *et al.* 1978/79, Boorman & Ranwell 1977).

If changes in relative nutrient levels through the season are responsible for the shift from cereals to pasture we would expect to be able to measure a decline in protein or carbohydrates and an increase in fibre or ash in cereals with respect to pasture.

Seasonally changing nutritional requirements

Migratory geese generally replenish protein reserves lost during migration before building up their fat reserves (Gauthier *et al.* 1992, Owen *et al.* 1992). Alisauskas & Ankney (1992) argue that stored fat rather than protein is the more efficient source of energy because protein must be deaminated. The changing diet of Snow Geese as they migrate northwards from the United States to Canada has been attributed to changing nutritional requirements from protein to carbohydrates (Alisauskas & Ankney 1992).

If this is true for Brent Geese overwintering in England, we would expect to observe higher levels of protein in cereals than in pasture before the shift, and higher levels of carbohydrates in pasture than in cereals after the shift.

Other factors

Farmers scare geese off cereal fields and this may reduce feeding time to unacceptable levels. Feeding time is also affected by changing day length. Longer days may allow the geese to alter their feeding strategy from one of high intake rate to one of longer retention time of food in the gut. The relative nutritional value of dietary components may therefore change from an emphasis on easily digestible proteins on short days to the less digestible carbohydrates on longer days. For example, Barnacle Geese *Branta* *leucopsis* retain food in the gut for longer in the summer than in the winter, and this enables them to feed on mosses of low digestibility in the summer (Prop & Vulink 1992).

If disturbance is responsible for the shift, we would expect it to be greater on cereals than on pasture. If changing day length is important, we would expect geese to concentrate on high protein foods on short days and high carbohydrate food on long days.

METHODS

The study was carried out in the winter of 1991-92 in the area around Pagham Harbour Local Nature Reserve in West Sussex on the south coast of England. Pagham Harbour is of national importance for Brent Geese with a yearly average annual maximum of 3000 birds (1983-1987); it is a European Community Special Protection Area and a Ramsar Site (Grimmett & Jones 1989). The area has extensive salt-marsh dominated by *Spartina* sp. and *Halimione portulacoides* with shingle banks and islands in the harbour. No sailing, fishing or wildfowling take place within the estuary.

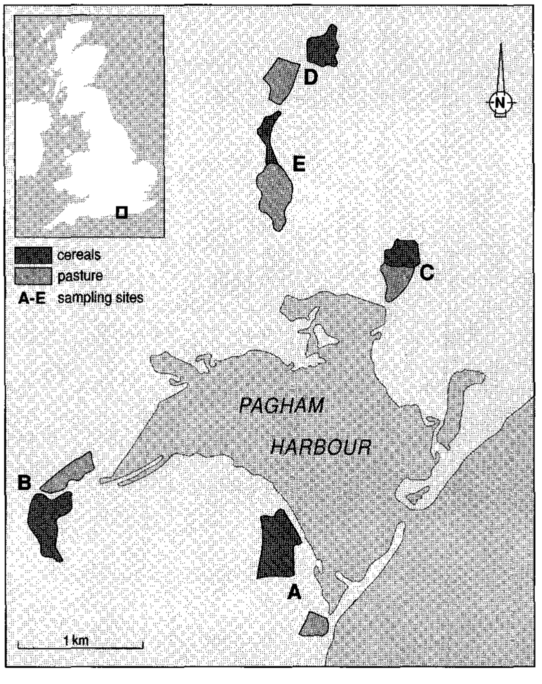

Fig.1. Map of the study area around Pagham Harbour showing the five sites (A to E).

In order to study the switch from cereals to pasture, a sample of fields were chosen which were unlikely to differ in factors important in the selection of fields by Brent Geese, other than in the crop grown. Previous work has shown that field width and distance from the sea are important in determining whether fields are used by geese (McKay mimeogr. rep.). Bearing this in mind, pairs of pasture and winter cereal fields were chosen at five sites in September 1991 (A to E on Figure 1) where geese were known to graze in previous years (from survey data and information from farmers).

The density of droppings is a measure of the amount of goose grazing (Patterson 1991). However, the total area of fields monitored in this study was too great for this method to be used satisfactorily. Field use was therefore quantified by counting the numbers of geese on a survey route covering all ten fields, in the morning and again in the afternoon. Additionally, a dawn-to-dusk search was undertaken, starting at the roost in Pagham Harbour. Geese were observed as they flew inland in small groups to feed on fields. The small groups would join birds already feeding, resulting in larger flocks building up. When most of the birds had left the roost a vehicle was used to search the area shown in Figure 1 for the rest of the day, and all observed birds were counted. On occasion birds would leave the area covered by Figure 1; this often coincided with extreme weather conditions. Both sorts of observations were carried out weekly between October and April, alternately at high and low tides. Both methods were undertaken because the survey is likely to be more accurate in assessing the relative intensity of grazing on the fields, whereas the dawn-to-dusk search is more likely to identify low levels of grazing of individual fields.

In order to monitor changes over the winter in the quantity and quality of food available to the geese in the two habitats, vegetation samples were taken monthly (chemical changes during spring growth, in contrast, can be much more rapid; Prins & Ydenberg 1985). Ten points per field were chosen using random number tables. At each point the height of the sward was measured using a 'sward stick' (a polystyrene disc on a graduated stick; Summers & Critchley 1990). A 0.5 m x 0.5 m area was then clipped to ground level using hand shears and stored in a sealed plastic bag for laboratory analyses.

At the laboratory, total wet weight of each sample was determined and a 10 g sub-sample removed and hand sorted into live and dead material. Both were dried overnight in an oven at 50°C and percentage live matter (dry weight) and biomass (total dry weight live matter) calculated, the latter by extrapolation from the sub-sample. The percentage live matter and biomass comprised the variables used to monitor depletion rates. The live matter for each field was then bulked and analysed for Kjeldahl nitrogen, digestible crude protein, water-soluble carbohydrates, ash, (MAFF 1986) and neutral detergent fibre (Van Soest & Wine 1967). These measures enabled us to track changes over the winter in dietary components.

Spearman's Rank correlation coefficients (r_s) were calculated between the different dietary components and between those components and indices of goose use. Coefficients quoted are all significant at the $P < 0.01$ level.

RESULTS

The maximum number of geese observed on each field during the four week period after vegetation sampling was log transformed and used as an index of intensity of usage by the geese. In addition, the proportion of observation days on which birds were seen feeding on each field was calculated. When this proportion was analysed using logistic regression (Aitkin *et al.* 1989), there was no significant difference due to the method used (survey or dawn-to-dusk search, logistic regression $\chi^2_1 = 0.14$, $P > 0.05$) so results were pooled, and these are shown in Figure 2.

Winter cereal fields at sites D and E were not used by geese at any time during the season. Winter cereal fields at the other three sites were used in November and all five pasture fields were used in January and often later in the season. In general, both the maximum number of geese and the proportion of days geese were seen, were greater for pasture than cereals.

The proportions of observation days on which geese were seen on each field were analysed using logistic regression. The resulting model involved a significant interaction between type of vegetation (pasture or cereal) and month, indicating a significant change over time (logistic regression $\chi^2_4 = 34.4$, $P < 0.005$). The predicted mean proportions with estimated standard errors for the logistic regression model are shown in Table 1. These show a large decrease in the use of cereals, and an increase in the use of pasture, between November and December.

Figure 3 shows the quantitative changes in pasture and winter cereals over the season (depletion rates) which could be due to goose graz-

Table 1. Predicted values from a logistic regression model incorporating an interaction between type of vegetation (pasture or cereal) and month, indicating a significant change over time ($\chi^2_4 = 34.4$, $P < 0.005$). *Prop* is the predicted mean proportion of observation days geese are seen on pasture and cereal fields in each month.

	Nov	Dec	Jan	Feb	Mar
pasture					
Prop	0.00	0.30	0.38	0.40	0.16
SE	0.00	0.04	0.07	0.05	0.05
cereals					
Prop	0.18	0.04	0.00	0.03	0.02
SE	0.07	0.03	0.00	0.02	0.02

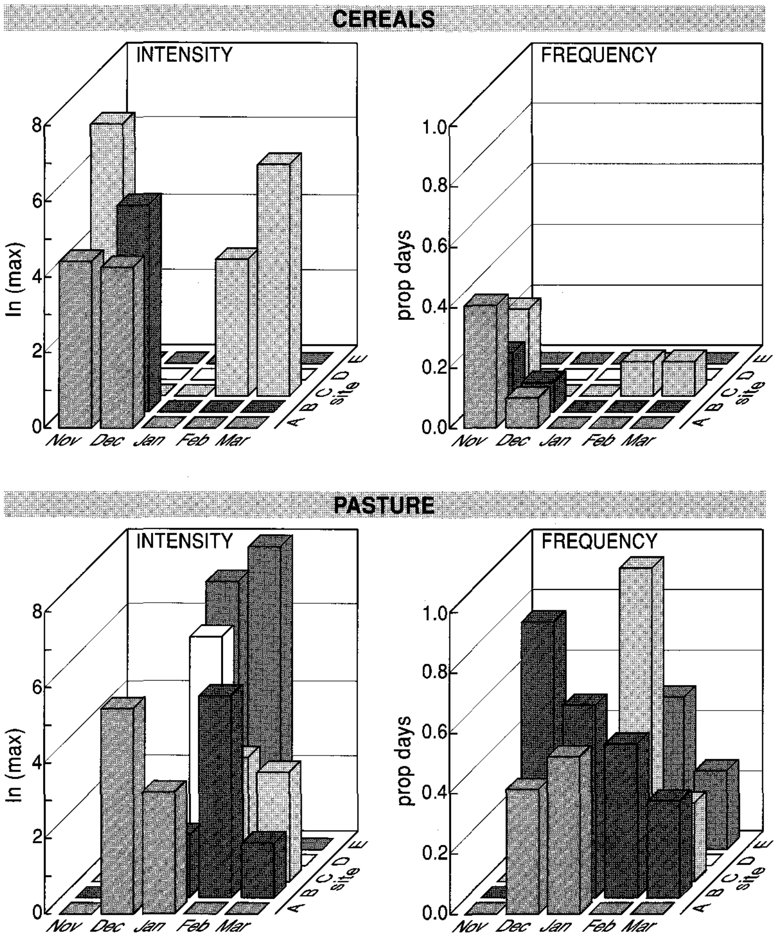

Fig. 2. The intensity and frequency of use by Brent Geese of winter cereal and pasture fields at the five sites (A to E) during winter 1991-92.
The values plotted are: the natural logarithm of the maximum number of geese observed on each field, ln(*max*) and the proportion of observation days on which geese were seen feeding on the field, *prop days*. Both values were calculated for the four week period following vegetation sampling for that month.

ing or natural die-back. In November pasture had a greater biomass than cereals but this declined to lower levels by December and then there was little difference over the rest of the season. Biomass tended to correlate with sward height (r_s = 0.67). Pasture and cereal swards were of similar height throughout the winter until March when cereals overtook pasture. The greatest difference between pasture and cereals was in percentage live matter. This remained just under 100% in cereals throughout the season whereas in pasture it remained below 60%.

Figure 4 shows the changes in chemical factors related to digestibility in pasture and winter cereals, ie. qualitative changes. Crude protein (6.25 x total nitrogen) was highly correlated with digestible protein (r_s = 0.99) so only the former is discussed. Crude protein was found to correlate positively with water (r_s = 0.73) and percentage live matter (r_s = 0.64) and negatively with water

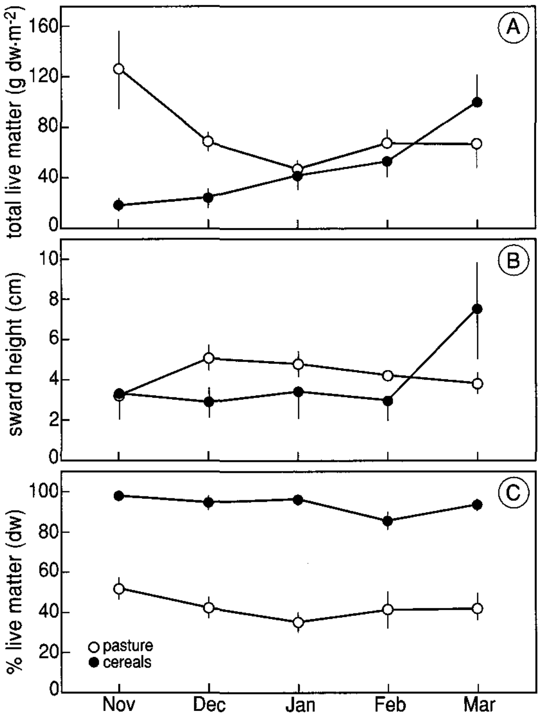

Fig. 3. Quantitative changes in five winter cereal and five pasture fields from November 1991 to March 1992: (a) biomass (total dry weight live matter), (b) sward height and (c) percentage live matter (dry weight). Bars indicate standard errors (*SE*).

soluble carbohydrates (r_s = -0.67). Neutral detergent fibre correlated negatively with both percentage live matter (r_s = -0.67) and ash (r_s = -0.54). Cereals have higher levels of crude protein than pasture, although pasture increases in crude protein through the season. In contrast, water soluble carbohydrates were always greater in pasture than cereals, though they declined over the winter in pasture. Neutral

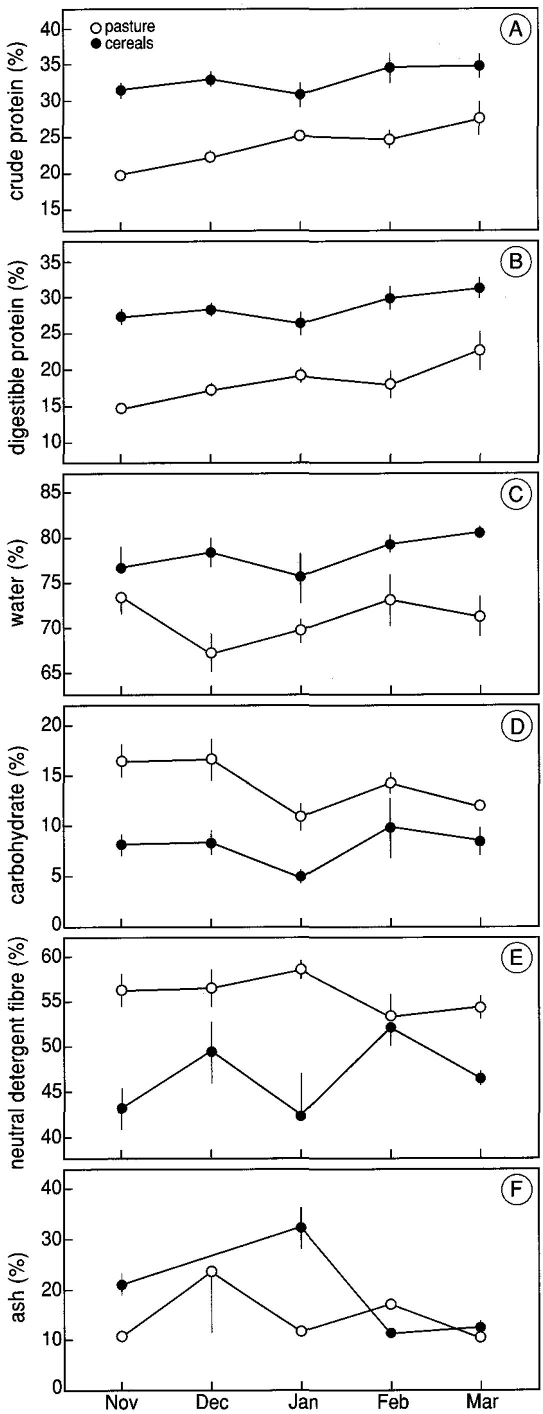

Fig. 4.

Fig. 4. Qualitative changes in dietary components of five winter cereal and five pasture fields from November 1991 to March 1992; (a) crude protein (b) digestible protein (c) water (d) water-soluble carbohydrates (e) neutral detergent fibre (f) ash. Bars indicate standard errors (*SE*).

Table 2. Percentage crude protein in pasture fields at the five monitored sites from November to March, in relation to the month at which geese were first observed to graze (*).

Site	Nov	Dec	Jan	Feb	Mar
A	19.0	19.4*	24.0	20.4	20.9
B	17.3	20.0*	22.8	22.1	22.9
C	19.3	21.0*	24.9	25.0	27.6
D	21.7	23.6	25.4*	27.2	31.5
E	18.1	22.6	26.2*	25.9	32.8

detergent fibre was greater in pasture and water content was greater in cereals, throughout the season.

Because crude protein increased over the winter in pasture, it was examined in more detail by tabulating it at each site every month (Table 2). The switch onto individual pasture fields did not appear to occur when crude protein levels reached a particular threshold.

When goose use was compared to the quantitative and qualitative changes in winter cereals and pasture, there were no significant correlations ($P > 0.05$).

Factors which may have affected the relative use of pasture and cereal fields were noted throughout the season. On 25 November twine was strung across the winter cereal fields at sites A and B by the farmer to deter geese. At these sites the geese were shot (under licence from the U.K. Ministry of Agriculture, Fisheries and Food). This did not prevent subsequent use as can be seen from Figure 2. However, the cereal field at site C was unprotected throughout the season and sustained much heavier grazing than the other two grazed cereal fields. Cereal fields at D and E sites were not protected in any way. In addition, all incidents in which feeding geese were disturbed and took to the air were noted and the cause of the disturbance ascertained (Figure 5). Despite scaring by farmers being confined to winter crops, more incidents were observed on pasture, due partly to high levels of amenity use.

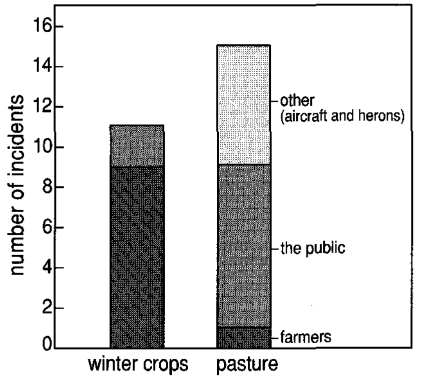

Fig. 5. The frequency of different sources of disturbance (causing feeding flocks of geese to take to the air) at Pagham Harbour during winter 1991-92.

DISCUSSION

The habitat shift from cereals to pasture has particular significance in the conflict between agriculture and the conservation of Brent Geese. If the choice threshold can be manipulated, geese could be persuaded off cereals and on to specially sown and managed grass in alternative feeding areas.

A shift from cereals to pasture between November and December was documented for Brent Geese grazing at five sites at Pagham Harbour. Vegetation samples taken throughout the period revealed higher percentage live matter and higher levels of crude protein in cereals, and higher levels of water soluble carbohydrates and neutral detergent fibre in pasture. Levels and changes over the winter in biomass, crude protein, ash and water-soluble carbohydrates in winter wheat were measured by Summers (1990b) and were broadly consistent with the results presented here. His results suggest that the nutritional quality of wheat is not affected to any real extent by grazing, though biomass can be reduced to about 20 dry g m^{-2}.

The hypothesis that resource depletion explains the shift from cereal to pasture is not supported by our data. Even the most severely grazed cereal field at site C increased in biomass over the season. In contrast, biomass, percentage live matter and sward height decreased from November to January in pasture ie. there was evidence for depletion in pasture but not in cereals. Conversely, differences in sward height do not indicate that cereals were too tall to be acceptable to geese from December onwards.

We also considered whether geese were tracking changes in dietary components. For example, seasonal differences in nitrogen content were measured by Prins & Ydenberg (1985) in salt-marsh relative to pasture (polder) vegetation and were found to explain a spring shift from pasture to salt-marsh by Barnacle Geese. When dietary protein on the salt-marsh reached pasture levels geese shifted from pasture to salt-marsh, which was the preferred habitat due to low levels of disturbance. In our study, cereals remain higher in crude protein and percentage live matter and lower in fibre, relative to pasture, throughout the season. It is likely that digestibility and hence metabolizable energy is always greater in cereals. This is supported by concurrent work on the same population of geese; digestibilities were measured by collecting samples of faeces and vegetation and were found to be higher for cereals (54 - 81%) than pasture (28 - 53%) (McKay mimeogr. rep.). Pasture does, however, increase in crude protein throughout the season, but the data are not consistent with the existence of a threshold below which geese cannot feed.

Changing day length may also be important; short days in November may oblige geese to sacrifice digestive efficiency for energy, which they achieve by maintaining a high intake rate and fast through-put time. In this season it is advantageous for the geese to concentrate on the more easily digestible cereals. When days are longer, retention times can be increased to maximise the efficiency of digestion and high levels of structural carbohydrates can be processed. However, if this was the principal factor determining the switch from cereals to pasture in this study, the geese should have shifted in February (rather than between November and December) when day lengths increase above the autumn level.

Time available to feed and energy costs can be adversely affected by disturbance such as scaring (Owens 1977). However, if scaring had been a contributory factor in this study, geese should have avoided cereals in the winter when time available to feed was at a minimum, and returned to them in the spring. Boorman & Ranwell (1977) found that Brent Geese increased the time they spent feeding to a maximum of 95% as the amount of food declined over the winter, which suggests that they are time-limited. We have also shown that geese in this area were more often disturbed on pasture by dog-walkers, bird-watchers, etc. than on cereals by farmers.

Changing nutritional requirements of the geese may best explain the observed shift from cereals to pasture in December. Before the shift geese used fields high in protein and after the shift, fields high in soluble carbohydrates. If this hypothesis is correct, geese should always feed on cereals first, provided the growth of the crop is sufficiently advanced. Dietary protein may be used to replenish protein reserves depleted during migration (Lindström & Piersma 1993) and carbohydrates are probably a more efficient source of energy later in the winter, either for maintenance or as an energy reserve. In addition, *Zostera* sp., the commonly cited traditionally preferred food of Brent Geese, has been found to be high in soluble carbohydrates (Buchsbaum *et al.* 1984). Some studies show a second episode of protein storage in wildfowl before migration to the breeding grounds (Alisauskas & Ankney 1992, Lindström & Piersma 1993) and this may explain the observed return to the cereal field at site C in March in this study (Figure 2).

In this study we have not yet considered the possible role played by dietary lipids, shown by Buchsbaum *et al.* (1986) to be the major source of energy for Brent Geese feeding on *Spartina* spp , or plant anti-feedants (secondary compounds, mycotoxins and silica). Temperate grass species (Gramineae) do not contain condensed or hydrolysable tannins (Barry & Blaney 1987), but they do contain phenolic acids, notably ferulic acid, and alkaloids of fungal origin (mycotoxins). Buchsbaum *et al.* (1984) provide evidence that feeding by Canada Geese, *Branta canadensis*, is negatively influenced by phenolic acids but Gauthier & Bédard (1990) show that phenolic acids are unlikely to affect food choice by Greater Snow Geese (*Chen caerulescens atlantica*). Mycotoxins can cause disease and affect feeding by livestock (Barry & Blaney 1987) and silica has been shown to affect food choice by voles (Gali-Muhtasib *et al.* 1992).

In conclusion the habitat shift from cereals to pasture does not appear to be due to changes in the relative quality or quantity of dietary components. Rather, our data support the hypothesis that habitat shift is prompted by the gooses' nutritional requirements changing over the winter from high levels of protein to high carbohydrates. This hypothesis may partly be tested by investigating:

(a) whether captive birds exhibit an endogenous mid-winter shift in preference from high protein to high carbohydrate and:

(b) whether geese can be induced to avoid winter cereals altogether by increasing nitrogen levels and digestibility of pasture in autumn. If this could be accomplished, then it would have obvious implications for the management of alternative feeding areas of grassland for Brent Geese.

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SAMENVATTING

Dit artikel gaat over de voedselbenutting door Rotganzen in hun winterfourageergebied. Paarsgewijs werden tien percelen wintergraanakker en weiland bij Pagham Harbour in West Sussex (Engeland) onderzocht van november 1991 tot maart 1992. Tussen november en december werd een overschakeling van wintergraanakker naar weiland waargenomen. Maandelijks genomen monsters van de vegetatie werden geanalyseerd op kwantitatieve en kwalitatieve veranderingen die op het vreetgedrag van de ganzen van invloed zouden kunnen zijn.

De afname in biomassa van het wintergraan of het percentage levende stof of veranderingen in de hoogte van de aren bleek niet verantwoordelijk gesteld te kunnen worden voor de overschakeling van graanveld naar weiland. Noch waren er aanwijzingen dat de ganzen reageerden op de relatieve verandering in de voedselkwaliteit. Bovendien was de verstoring door de mens geen aanleiding tot de overschakeling.

Een mogelijke verklaring is dat de Rotganzen het eiwitgehalte in hun dieet maximaliseren in de vroege winter, waarschijnlijk om het verlies tijdens de trek te compenseren; daarna maximaliseren zij het aandeel in water oplosbare koolhydraten in hun dieet.

HWdN