FOOD, FEEDING BEHAVIOUR AND NUTRITIONAL ECOLOGY OF WINTERING GREYLAG GEESE *Anser anser*

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ABSTRACT Just after arrival in early autumn, Greylag Geese *Anser anser* wintering in the Marismas of the Guadalquivir (SW Spain) concentrated on *Scirpus litoralis* areas, but moved to *Scirpus maritimus* areas as soon as these zones were flooded after autumn rains. In both *Scirpus* habitats the diet was dominated by tubers of these plants, but during the late winter there was an increase in the consumption of green parts. The tubers of *Scirpus* have high concentrations of both soluble carbohydrates and fibre, but low concentrations of protein and minerals. Adequate quantities of the essential nutrients seem to be acquired by switching to foraging on pastures. In spite of their relative high protein and low fiber contents, *S. litoralis* tubers were less preferred than those of *S. maritimus*. The reason for this is that geese need more time to forage on *S. litoralis* tubers. In the *S. maritimus* habitat type the geese may spend more time on other activities and vigilance.

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INTRODUCTION

Geese are primarily herbivorous. The nutritive quality of plant food is generally lower than that of animal food. Because geese have a simple digestive system, they are inefficient digesters of their food, and to overcome this physiological constraint they tend to maximise their rate of food intake (Sibly 1981). However, although undigested food can pass the digestive tract in less than one hour (Dorozynska 1962), increasing intake rate is constrained because processing rate is slower than intake rate, thus requiring foraging interruptions so that the gut can be emptied (Sibly 1981, Sedinger & Raveling 1988). Furthermore, there are several plant constituents that may affect plant choice and/or its digestibility by geese, such as structural cell walls and presence of toxic or inhibitory substances (Buchsbaum *et al.* 1984, 1986, Buchsbaum & Valiela 1987). These physiological and nutritional constraints may lead to a high selectivity by geese when choosing both feeding sites and plant parts upon which they feed (Owen 1978/79). Temporal variations in both seasonal availability of plants and energetic requirements, and handling costs may also dictate food choice by geese.

In this contribution we analyse some aspects of the nutritional ecology of a wintering Greylag Goose *Anser anser* population. Although the diet of Greylags has been studied in some parts of their wintering area (Newton & Campbell 1973, Loosjes 1974, Dubbeldam 1978, Middleton & van der Valk 1987), few data have been collected on seasonal variations in the composition of their diet (Newton & Campbell 1973, Middleton & van der Valk 1987) and the basis for observed seasonal feeding preferences.

METHODS

Study area

This three winter study (1981-82 to 1983-84), was conducted in the Biological Reserves of Doñana (RD) and Guadiamar (RG), in the Marismas of the Guadalquivir, SW Spain. The RD marsh is almost completely covered by *Scirpus maritimus*; some parts of RG are covered by *Scirpus litoralis*, and others by *S. maritimus*. Water depth is greater in *S. litoralis* than in *S. maritimus* areas.

On arrival in early autumn, most geese concentrated on *S. litoralis* areas, which were the first to flood; however, the geese moved to *S. maritimus* zones as they were flooded after autumn rains (Amat 1986b). Small flocks also used the pastures found in the levées adjacent to *Scirpus* areas. It was on these three habitat types (*S. litoralis*, *S. maritimus* and pastures) that we made our study. The pattern of use suggests that these pastures are not utilised continuously by the same individuals (J. A. Amat, pers. obs.), as opposed to other natural pastures found in the periphery of the Marismas, whose use has become more prominent in recent years perhaps as a result of a numerical increase of the wintering population (Amat 1986b).

In the *Scirpus* marshlands the geese mainly feed on the tubers of these plants (see below). The root system of *S. maritimus* is made up of scattered tubers interconnected by rhizomes, whereas that of *S. litoralis* is characterised by densely packed tubers that also are interconnected by rhizomes. *Scirpus maritimus* tubers are individually extracted by geese, while those of *S. litoralis* are taken as clusters from which only one of the tubers is normally consumed. See Amat (1986a) for further description of the tubers and their handling by geese.

Analysis of droppings

Faecal samples were collected in each of the three major habitat types each month the geese were recorded feeding on them throughout the winter. Each sample usually constituted 20-30 droppings collected from each site each sampling day. The droppings were dried and preserved in paper bags until analysis.

Prior to examination, the droppings of each sample were thoroughly mixed; this preparation was then soaked overnight in water. These samples were microscopically examined (Baumgartner & Martin 1939, Owen 1975, Holecheck 1982).

Four slides were prepared for each sample using Hertwig's (chloral hydrate) solution to clear cuticule fragments. The Hertwig's solution was boiled off and 25 microscope fields per slide were observed (100x), recording the presence of each dietary item in each microscope field. The relative frequencies of the different food types in 100 microscope fields examined were transformed in relative densities using a table in Fracker & Brischle (1944). Following Reichman (1975), such relative densities were expressed as percentages of the diet.

Chemical analysis of food samples and faeces

Samples of the main foods were collected at the feeding areas for comparison of nutrient and mineral contents with those found in faeces, thus allowing estimates of digestibility. Earlier work suggested that geese do not digest cellulose (Marriott & Forbes 1970, Mattocks 1971), so that this constituent was formerly used as a marker substance to study the amount of food retained during digestion (e.g. Ebbinge *et al.* 1975, Halse 1984). A recent study, however, demonstrated that geese are able to digest some cellulose and hemicellulose (Buchsbaum *et al.* 1986). We therefore calculated "apparent digestibility" by using lignin as an indigestible marker (Buchsbaum *et al.* 1986).

The minimal concentration recommended for using lignin as an indigestible marker is 6% (see Buchsbaum *et al.* 1986). Although the lignin content of our samples was slightly lower than the 6% lignin minimum concentration recommended for a marker, we used it to get some idea of the efficiency of assimilation of different plant constituents by Greylags.

Following Buchsbaum *et al.* (1986), the apparent digestibility of total organic matter (*OM*) was calculated as:

$$\%OM \text{ digested} = 100 \cdot (1 - \%LP/\%LF),$$

in which *LP* and *LF* are the lignin fraction in plants and faeces respectively. The apparent digestibility of specific plant constituents (*A*) was calculated by:

$$\%A \text{ digested} = 100 \cdot (1 - \%LP/\%LF) \cdot (\%AF/\%AP)$$

In which *AP* and *AF* are the specific plant constituents in plants and faeces respectively. The digestibility was only determined for *Scirpus* tubers, because when the geese were feeding on *Scirpus* habitats the diet (and hence the faeces) was almost exclusively composed by these plant parts (see below). As sample sizes are rather small, our estimates must be interpreted with caution, although they may be considered as indicative of the amount of plant constituents assimilated. Details of the analyses may be obtained from B.G.C. and A.G.C.

Abdominal profile of geese

Owen (1981) developed a visually-based, body condition index as a means of assessing fat storage in living geese, and found that abdominal profile index correlated well with body mass. Owen's index has been questioned (Gauthier & Bédard 1985), but we used it because it was the only way we had to get adequate sample sizes of the condition of birds at our study sites throughout the winter. Birds were observed within 50-300 m of the observer using a 20-45x spotting scope. We aimed to record the abdominal profiles of 100 individuals, although samples were sometimes smaller because the marsh vegetation precluded detailed observations of geese, and in other cases most geese were swimming.

Foraging behaviour

We made two types of observation on the feeding behaviour. Firstly, we tried to ascertain whether food type affected the birds' searching and handling behaviour. During one minute observation periods we recorded the time spent by geese with "head down" (searching for or handling food), the number of times the geese raised the head ("head-up" plus "extreme head-up" postures as defined by Lazarus 1978) and the distance moved. We considered that the geese were searching for food when the bill was pointing down. Distances were visually estimated to the nearest metre.

Secondly, we recorded data on extraction and handling times of tubers. Feeding efficiency on tubers was recorded as the proportion of successful attempts to extract tubers during 5 minute observation periods (see Amat 1986a for further details).

In both types of observation we distinguished whether the geese were walking or swimming (feeding by dipping the head underwater at water depth <0.30 m) or by up-ending (at water depth > 0.30 m).

RESULTS

Food

Tubers, and to a lesser extent stems of *S. maritimus* and *S. litoralis*, constituted most of the diet of Greylags in the habitats dominated, respectively, by these plant species (Table 1). This effect lasted throughout the winter season, although from Feb-

Table 1. Food habits of Greylag Geese in three habitat types of the Marismas. Averages for all food items are given by percent (calculated from relative densities of food items in faeces, see text) ± *SD*. Numbers in parentheses are sample sizes.

Plant	Habitat type		
	S. litoralis (14)	*S. maritimus* (26)	Pastures (8)
Gramineae	3.8 ± 14.0	1.1 ± 2.4	28.0 ± 39.4
Eleocharis palustris (stems)	-	1.2 ± 6.2	7.8 ± 20.2
Scirpus maritimus (tubers)	-	86.6 ± 24.0	61.3 ± 42.7
Scirpus maritimus (stems)	-	11.0 ± 23.7	0.7 ± 1.9
Scirpus litoralis (tubers)	89.6 ± 18.2	-	2.2 ± 4.8
Scirpus litoralis (stems)	5.6 ± 12.3	t	-
Others	0.8 ± 1.8	t	t
Not identified	0.3 ± 0.5	0.1 ± 0.4	0.1 ± 0.2

t: Traces (<0.1%)

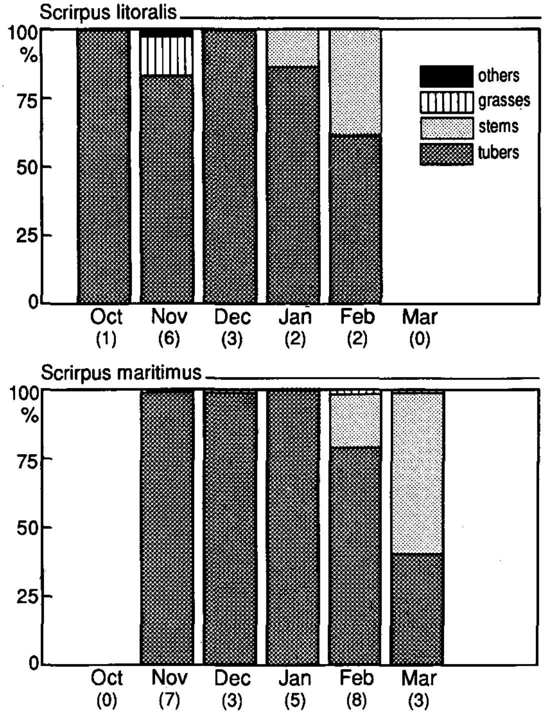

Fig. 1. Food habits of Greylag Geese in *Scirpus*-dominated areas of the Marismas throughout the wintering season. Percentages were calculated from relative densities of food items in faeces (see text). Numbers in parentheses are sample sizes.

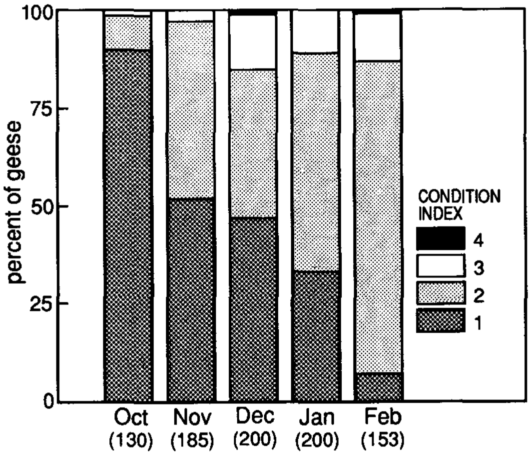

Fig. 2. Monthly variations, for the 1981-82 and 1982-83 seasons, of the percentage of Greylag Geese allocated to four categories of Owen's (1975) abdominal index (1-4, indicating increasing degree of fat deposition). The number of geese indexed each month is indicated above the bars.

ruary onwards there was an increase in the consumption of overground vegetative parts (Fig. 1).

In pastures, the faeces were dominated by *S. maritimus* tubers (61%) and grasses (28%); tubers of *S. litoralis* were also found in the faeces collected on this habitat type (Table 1). This indicates that geese use the pastures after having spent time feeding in the *Scirpus*-dominated habitats.

Table 2. Nutrient concentration in food and faeces of Greylag Geese in the Marismas. Averages are given by percent dry matter ± *SD*. Sample sizes in parentheses.

Plant species Item analysed	Constituent Lignin	 Cellulose	 Hemi-cellulose	 Protein	 Soluble carbohydrates
Scirpus maritimus					
Tubers (5)	4.4 ± 1.6	13.5 ± 4.7	26.5 ± 5.0	8.1 ± 1.0	42.6 ± 7.3
Faeces (tubers) (3)	11.1 ± 1.8	23.5 ± 3.7	23.0 ± 2.3	6.5 ± 0.7	16.9 ± 3.0
Stems (1)	3.7	24.5	19.3	11.3	30.3
Scirpus litoralis					
Tubers (7)	4.8 ± 3.4	12.2 ± 6.7	15.0 ± 6.2	10.2 ± 1.3	52.1 ± 8.3
Faeces (tubers) (1)	9.5	20.1	12.9	8.0	20.0
Stems (2)	2.5 ± 0.3	23.2 ± 2.3	22.3 ± 4.5	14.7 ± 3.2	24.8 ± 1.9
Pastures (1)	3.7	14.5	15.6	16.6	28.1

Table 3. Ash (% dry matter) and mineral (µg/g for Fe, Mn, Zn and Cu; % dry matter for all others) concentration in plant foods of Greylag Geese in the Marismas. Data are mean ± *SD*. Sample sizes in parentheses.

	Scirpus litoralis		*Scirpus maritimus*		Pastures
Constituent	Stems (2)	Tubers (6)	Stems (1)	Tubers (4)	Stems (1)
Ash	12.5 ± 1.6	4.6 ± 1.3	11.0	3.9 ± 0.9	21.6
P	0.34 ± 0.08	0.19 ± 0.02	0.30	0.17 ± 0.03	0.47
K	2.25 ± 0.04	0.34 ± 0.03	1.80	0.39 ± 0.01	2.50
Ca	0.33 ± 0.11	0.13 ± 0.06	0.65	0.09 ± 0.04	1.27
Mg	0.20 ± 0.07	0.08 ± 0.02	0.14	0.06 ± 0.02	0.40
Na	1.24 ± 0.20	0.13 ± 0.06	0.92	0.27 ± 0.11	1.47
Fe	186.5 ± 228.4	340.2 ± 131.5	490	291.5 ± 66.8	930
Mn	418.0 ± 75.0	49.8 ± 13.4	264	29.5 ± 8.1	110
Zn	31.8 ± 12.0	12.5 ± 2.6	47.8	10.1 ± 2.4	20.3
Cu	8.8 ± 4.4	6.0 ± 3.3	15.0	4.8 ± 1.6	12.5

Chemical composition and digestibility of food

Tubers of both *Scirpus* are high in soluble carbohydrates, but contain high fibre levels (Table 2). Neutral detergent fibre content (≈ cellulose, hemicellulose and lignin) was higher in *S. maritimus* than in *S. litoralis* tubers ($t = 3.78$, $p < 0.01$). The tubers of *S. litoralis* contained more protein than those of *S. maritimus* ($t = 2.70$, $p < 0.05$). Green material (from pastures and *Scirpus* stems) contained more protein, but less soluble carbohydrate than the subterranean parts of plants (Table 2). The mineral content of tubers and stems of *Scirpus* was lower than that of the pastures (Table 3).

The apparent digestibility of soluble carbohydrates of *Scirpus* tubers was higher than that of other constituents (Table 4). The digestibility of protein may be a conservative estimate, as the faeces might have been contaminated with some urine. The apparent digestibility of both hemicellulose and cellulose was rather high (Table 4).

Condition of geese

The abdominal profile index increased during the late wintering season ($G = 87.2$, $df = 4$, $p < 0.001$) although some annual differences may have been attributable to the prevailing hydrological conditions (Fig. 2). In 1981-82 and 1982-83 water levels were low (see Amat 1986ab), and this may explain why the increase in the abdominal index represented in Fig. 2 was not very sharp. In contrast, 1983-84 was a winter with high water levels and better feeding conditions (Amat 1986b), and in January 1984, 62% of 21 individuals was allocated to category 3 of the abdominal index (cf. Fig. 2).

Table 4. Apparent digestibility by Greylag Geese (%) of various constituents of *Scirpus* tubers.

	Constituent				
Scirpus species	Organic matter	Cellulose	Hemi-cellulose	Protein	Soluble carbohydrates
S. maritimus	60.3	31.0	65.7	68.2	84.3
S. litoralis	49.9	17.1	56.8	60.7	80.8

Table 5. Time (s) spent by Greylag Geese with head down (THD), number of times the geese raised the head (NHR) and distance (DIS) (m) moved while foraging, according to habitat type and foraging behaviour. Values are mean ± *SD* for 1 min. observation periods. Sample sizes in parentheses.

	Habitat type					
	Scirpus maritimus			*Scirpus litoralis*		
Foraging behaviour	THD	NHR	DIS	THD	NHR	DIS
Walking	52.9 ± 9.4 (208)	1.7 ± 1.8	1.4 ± 1.5	54.8 ± 8.3 (254)	1.4 ± 1.6	1.1 ± 1.7
Swimming:						
Head submerged	47.8 ± 8.1 (75)	7.2 ± 2.5	1.1 ± 1.6	53.0 ± 7.6 (4)	6.5 ± 2.6	0.0 ± 0.0
Up-ending	41.1 ± 10.4 (47)	5.6 ± 1.7	1.2 ± 1.5	-	-	-
	Pastures					
Walking	56.1 ± 6.9 (60)	1.1 ± 1.4	1.7 ± 1.4			

Foraging behaviour

When Greylags foraged by walking, the time spent with head down on *S. maritimus* habitat was shorter than when they foraged either on *S. litoralis* ($t = 2.28, p < 0.05$) or on the pastures ($t = 2.90, p < 0.01$) (Table 5). There were no differences in the time spent with head down between *S. litoralis* stands and the pastures ($t = 1.26, p > 0.05$). The number of times the geese raised the head was similar on both *Scirpus* habitats ($t = 1.87, p > 0.05$), and also on *S. litoralis* and the pastures ($t = 1.45, p > 0.05$); however, Greylags raised a greater number of times the head when they fed on *S. maritimus* than on the pastures ($t = 2.73, p < 0.01$).

The geese moved shorter distances when they foraged on *S. litoralis* than either on *S. maritimus* ($t = 2.01, p < 0.05$) or on the pastures ($t = 2.86, p < 0.01$); distances moved on the latter habitat types were similar (Table 5).

On *S. maritimus*, Greylags adopted different feeding methods depending on water levels. When they foraged by walking, they spent more time with head down than when they foraged either by dipping the head underwater ($t = 4.47, p < 0.001$) or

Table 6. Mean number ± *SD* of *Scirpus litoralis* clusters and *S. maritimus* tubers attempted to extract by geese, and successfully extracted, according to foraging behaviour, during 5 min. observation periods (number of periods in parentheses).

	S. maritimus			*S. litoralis*		
Foraging behaviour	Number attempts	Number extracted	Percentage foraging success	Number attempts	Number extracted	Percentage foraging success
Walking	12.7 ± 3.8 (30)	9.3 ± 4.1	73	5.4 ± 4.2 (70)	1.9 ± 1.6	35
Swimming						
Head submerged	19.9 ± 6.5 (16)	15.9 ± 7.5	80	-	-	-
Up-ending	17.9 ± 4.6 (8)	10.6 ± 3.1	59	-	-	-

Table 7. Extraction and handling times (s) of *Scirpus maritimus* tubers and *S. litoralis* clusters by Greylag Geese according to foraging behaviour. Values are mean ± *SD*. Sample sizes in parentheses.

Foraging behaviour	*S. maritimus*		*S. litoralis*	
	Extraction	Handling	Extraction	Handling
Walking	9.5 ± 7.4 (45)	13.7 ± 10.3	17.2 ± 17.4 (60)	62.3 ± 93.0
Swimming				
Head submerged	8.2 ± 5.8 (42)	7.3 ± 8.3	-	-
Up-ending	5.7 ± 3.5 (8)	4.8 ± 3.7	-	-

up-ending ($t = 7.15, p < 0.001$) (Table 5). The time spent with head down when dipping the head underwater was longer than that spent when foraging by up-ending ($t = 3.76, p < 0.001$). Also, the number of times that Greylags raised the head when foraging by walking was greater than when foraging by either dipping the head underwater ($t = 17.49$, $p < 0.001$) or up-ending ($t = 14.05$, $p < 0.001$) (Table 5); the geese raised the head more when they dipped head underwater than when up-ending ($t = 4.20, p < 0.001$). Distances moved when searching for food on *S. maritimus* habitat were not related to foraging method (Table 5).

The rate of extraction of *S. litoralis* tubers was lower than that for *S. maritimus* (Table 6). Also, the geese took longer in both extracting and handling *S. litoralis* than *S. maritimus* tubers (Table 7). Perhaps because the foraging efficiency of Greylags was higher when they feed on *S. maritimus* than on *S. litoralis* tubers (Table 6), the time spent foraging throughout the day was shorter in the former habitat type ($G = 13.6$, $df = 1$. $p < 0.001$) (Fig. 3).

On *S. maritimus* the proportion of successful tubers extractions differed according to foraging mode: fewer attempts were made to extract tubers when foraging by walking than when dipping head underwater ($t = 4.63$, $p < 0.001$) or up-ending ($t = 3.19, p < 0.001$) (Table 6). There were no differences in the number of attempts made in extracting tubers when feeding by the last two foraging modes ($t = 0.75, p > 0.05$). The number of extracted tubers only differed when the geese fed by walking and dipping head underwater ($t = 3.77$, $p < 0.001$), in the last case the geese extracting more tubers (Table 7). The feeding efficiency of Greylags when they foraged on *S. maritimus* tubers was higher when dipping head underwater, intermediate when

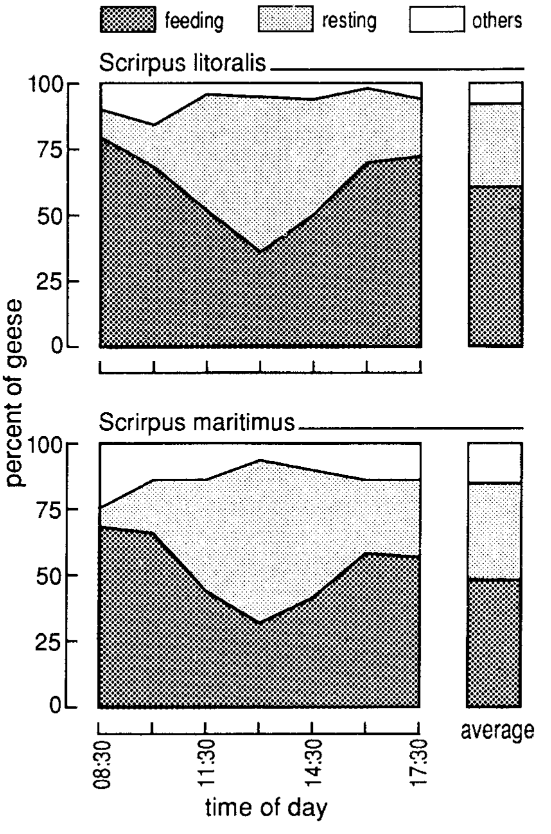

Fig. 3. Diurnal activity of Greylag Geese in *Scirpus litoralis* and *Scirpus maritimus* areas in January 1982. For details on methods see Amat (1986b).

feeding by walking, and lower when up-ending (Table 6).

There where no differences in the time the geese took in extracting individual *S. maritimus* tubers according to foraging mode (Table 7). However, Greylags spent more time handling the tubers after these were extracted by walking than either by dipping head underwater ($t = 3.20, p < 0.01$) or up-ending ($t = 2.37, p < 0.05$). Differences between handling times of tubers extracted after dipping head underwater or up-ending were not significant ($t = 0.82, p > 0.05$).

DISCUSSION

Diet quality and feeding habits

The soluble carbohydrate content of the tubers of *S. litoralis* and *S. maritimus* is lower than that found in the subterranean organs of other plant species on which the geese feed (Thomas & Prevett 1980, Coleman & Boag 1987, Alisauskas *et al.* 1988), and this may be related to the high fibre concentration of *Scirpus* tubers (see Alisauskas *et al.* 1988). The apparent digestibility of the soluble carbohydrates, protein and cellulose of the tubers of such *Scirpus* species is similar to that reported for other geese species feeding on overground plant parts, but the apparent digestibility of the hemicellulose of *Scirpus* tubers was higher than that of overground plant parts (Buchsbaum *et al.* 1986, see also Halse 1984). The tubers probably provide Greylag Geese with their energy requirements throughout most of the winter; however, this type of food should be supplemented with other foods to meet both specific nutrient and more energy demanding requirements during some parts of the wintering season.

Although *Scirpus* tubers are low in protein, they are not, however, very poor compared with other plant parts (see Mattson 1980). The protein content of the tubers could be adequate for maintenance requirements, but it would not be sufficient for storage (Fisher 1972), so that Greylags should rely on other food types (e.g. green vegetation) for this purpose.

The mineral content of tubers and stems of *Scirpus* was not very high in comparison with that found in other plant parts (see Herrera 1987). In spite of this, it might be adequate for geese, except perhaps for calcium and phosphorus (Fisher 1972, Robbins 1983). However, the amount of these minerals was higher in the pastures.

Sánchez *et al.* (1977) suggested that in the Marismas the tubers of *S. maritimus* made up most of the diet of wintering Greylag Geese. Our data, along with information presented by Amat (1986b) on seasonal variations in habitat use, indicate, however, that throughout the winter the geese first shift from *S. litoralis* to *S. maritimus* tubers, and during the late wintering season from a diet dominated by *Scirpus* tubers to a diet in which green vegetation predominates.

The habitat shift may be considered as a means of maximising food intake. Although *S. litoralis* tubers have a similar amount of soluble carbohydrates, more protein and less fibre than those of *S. maritimus*, this latter species has higher apparent digestibility of the tubers, possibly because of the presence of some inhibitory compound in *S. litoralis*, but also because just after arrival in early autumn, while feeding mainly on *S. litoralis*, the digestive system of geese may have not elongated sufficiently to cope with the high fibre concentration of *Scirpus* tubers (Burton *et al.* 1979). Moreover, the geese took longer in both extracting and handling *S. litoralis* than *S. maritimus* tubers. Also, as water is deeper in *S. litoralis* than in *S. maritimus* habitats, when water levels are high, the geese should feed by upending to reach *S. litoralis* tubers; our results suggest that the foraging efficiency of Greylags decreased when employing this feeding behaviour. As a consequence of all these factors, Greylags should spend more time foraging in *S. litoralis* habitats to meet daily feeding requirements. Therefore, *S. maritimus* tubers seem to be a more profitable food for Greylag Geese than *S. litoralis* tubers in spite of their apparently lower nutritional value.

The utilisation of the pastures adjacent to *Scirpus* habitats might be related to the acquisition of some essential nutrients (e.g. calcium, phosphorus) of which *Scirpus* tubers seem to be deficient (cf. Alisauskas *et al.* 1988). This is suggested by the dominance of *Scirpus* tubers in the faeces collected on the pastures, which indicates that geese shift habitat use, with an unknown frequency, throughout the day.

Late in the wintering season the geese switched from a diet mainly of carbohydrates to a more protein-rich diet. Coincident with this change there was an increase in the time spent foraging throughout the day (see Amat 1986b), and this was associated with accumulation of body reserves. McLandress & Raveling (1981b) and Madsen (1985) found that in both Canada Goose *Branta canadensis* and Pink-footed Goose *Anser brachyrhynchus*, hyperphagia and increased body mass occurred less than one month before starting spring migration.

The change from a diet mainly of carbohydrates to other more diverse and protein-rich foods just prior to spring migration has also been reported for other goose species (McLandress & Raveling 1981a, Boudewijn 1984, Prins & Ydenberg 1985). This switching takes place when the new growing vegetation shows the highest levels of protein and lipids, necessary to gain body mass for the spring migration (McLandress & Raveling 1981a).

To summarise, during the late wintering season there is a change in food priorities, and the geese switch from mainly a time minimisation tactic (sensu Schoener 1971), by which they satisfy minimum energy requirements in the least feeding time, to an energy maximisation tactic, by which they ingest large amounts of lipids and proteins.

Foraging behaviour

Variations in the foraging behaviour of geese were related to food type and environmental conditions. When foraging on the pastures and on *S. litoralis* habitat, Greylag Geese spent proportionally more time with head down than on *S. maritimus* habitat. The difference between the two *Scirpus* habitats may be due to the longer time the geese require in both extracting and handling *S. litoralis* than *S. maritimus* tubers. The difference between *S. maritimus* and the pastures may be due to the need for increasing pecking rate when foraging on food of poorer nutritive quality (cf. Owen 1972, Gauthier *et al.* 1988, Bédard & Gauthier 1989).

On *S. maritimus* habitat, the rate of head-raising was higher than on the pastures. Furthermore, although the rate of head-raising was similar on *S. maritimus* and *S. litoralis* habitats, geese spent more time scanning on the former habitat; probably, lengthening scan-duration may reduce foraging efficiency when feeding on *S. litoralis* because of the longer handling times of its tubers (cf. Metcalfe 1984). Consequently, there is a tradeoff between foraging and vigilance that is dependent on food profitability.

Water levels affected the feeding behaviour of geese on *S. maritimus* habitat. Under conditions of very shallow water, the rate of head-raising was higher than when water was deeper; this cannot be explained by flock size effects, since during low water levels geese were more concentrated in the feeding areas, and thus would spend less time vigilant. Since the vulnerability of geese to their main diurnal predators in the Marismas (*Aquila adalberti*, *Aquila chrysaëtos*, *Hieraetus fasciatus*) seems to increase with decreasing water levels (M. Ferrer & F. Hiraldo, pers. comm.), geese should scan more frequently under such conditions. However, total scanning time was longer when geese foraged by swimming; therefore, when foraging by walking, probably because of feeding constraints (see below), the geese did not lengthen the duration of each scan, but rather shortened the interval between scans, thus reducing the risk of failing to detect an approaching predator (cf. Metcalfe 1984).

On *S. maritimus* habitat, the time spent with head down was longer when geese foraged by walking than by other modes, because of the longer time needed to handle the tubers; in conditions of very shallow water it is difficult for geese to remove adhering mud and roots from tubers before swallowing them (Burton & Hudson 1978). As a result of the longer handling time of tubers in very shallow water, both the number of attempts and tubers actually extracted were lower when geese foraged by walking than by swimming. In spite of this, the foraging success was lower for geese foraging by up-ending, probably because with increasing water levels geese have more difficulty in grubbing up tubers (Burton & Hudson 1978). Although the feeding efficiency of Greylags decreased when feeding by up-ending, the number of tubers ingested was similar to that eaten when feeding by walking; however, the abdominal profile index was lower during years of low water levels, indicating that the foraging return of Greylags would be lowered because of the lower profitability of the food available under such conditions (Amat 1986b). When water was very shallow, the geese were more concentrated, so that the supply of profitable tubers (i.e. the smallest ones) was depleted (Amat 1986a). If as suggested by MacInnes *et al.* (1974) the condition of geese in spring, upon which they rely during reproduction (Ankney & MacInnes 1978, Thomas 1983), varies depending on the initial state of an individual, poor winter condition could ultimately affect reproductive output (see Ebbinge *et al.* 1982, Vangilder *et al.* 1986).

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SAMENVATTING

Dit artikel geeft details over over het voedsel en het foerageergedrag van Grauwe Ganzen die overwinteren in de Marismas van de Guadalquivir in het zuidwesten van Spanje. Na hun aankomst in het begin van het najaar benutten de ganzen eerst de gebieden met een bepaald soort bies (*Scirpus litoralis*). Zodra de wat hogere gebieden met zeebies (*Scirpus maritimus*) onder water komen te staan door de najaarsregens, verplaatsen de ganzen zich daarheen. Gedurende de hele winter bezoeken zij bovendien de aangrenzende weilanden. Het voedsel van de ganzen bestaat vooral uit de wortelstokken van de twee biezensoorten (Tabel 1). Aan het einde van de winter worden steeds meer bovengrondse delen gegeten (Fig. 1). De conditie van de ganzen wordt beter in de loop van de winter (Fig. 2).

De wortelstokken van de biezen zijn rijk aan koolhydraten en vezels, maar bevatten weinig eiwit en minera-

len (Tabel 2 & 3). Dit belangrijke bestanddeel verkrijgen zij door uitstapjes naar de weilanden, waar het voedsel wel rijk is aan eiwit en mineralen. De verteerbaarheid van koolhydraat, eiwit en vezels uit de wortelstokken van de biezen is tamelijk hoog (Tabel 4).

De ganzen hebben een voorkeur voor de wortelstokken van *S. maritimus*, hoewel die van *S. litoralis* meer eiwit en minder vezels bevatten, maar wel minder goed verteerbaar zijn. De ganzen besteden op *S. maritimus* minder tijd aan grazen en meer tijd aan waakzaamheid dan op *S. litoralis* en op weilanden (Tabel 5). Dat komt omdat er meer tijd nodig is om een wortelstok van *S. litoralis* te bemachtigen in vergelijking met een wortelstok van *S.maritimus* (Tabel 6 & 7). De verschillen in foerageerefficiëntie hebben ook gevolgen voor het tijdsbudget van de ganzen. Aan het foerageren op *S. litoralis* wordt meer tijd besteed dan aan foerageren op *S. maritimus*.