EXPLOITATION OF A NEW STAGING AREA IN THE DUTCH WADDEN SEA BY GREYLAG GEESE ANSER ANSER: THE IMPORTANCE OF FOOD-PLANT DYNAMICS

LIESBETH BAKKER, RENÉ VAN DER WAL, PETER ESSELINK & ALMIRA SIEPE


The colonisation by Greylag Geese Anser anser of a new autumn migration staging area was studied on the island of Schiermonnikoog, The Netherlands. Over 500 Greylag Geese first visited the island in 1991. During subsequent years, peak numbers rose to 700-900 birds. The geese most likely originated from the neighbouring staging area on the mainland, the Lauwersmeer, where goose numbers had levelled off since 1985. Because of the time-lag between saturation of the source population and colonisation of the island, changes on the island itself were investigated as a possible trigger for the arrival of the geese. Potential food availability on the island had increased for the geese as a result of vegetation succession. Two food-plants, Sea Club-rush Scirpus maritimus and Common Cord-grass Spartina anglica have increased over the last four decades. Greylag Geese fed mostly on Scirpus tubers and Spartina rhizomes. The soluble-carbohydrate content of the latter two food items did not differ significantly, and was approximately 25% on a dry weight basis. Negative effects of grubbing by Greylag Geese on stands of both Scirpus and Spartina appeared limited during the study period. Although Greylag Geese now spend most of the year in agricultural areas, our study indicates that natural habitats are still of importance for migrating Greylag Geese as staging areas.

Key words: Anser anser - Scirpus maritimus - Spartina anglica - herbivorous birds - colonisation - habitat use - food-plant quality - vegetation succession

INTRODUCTION

The population of Greylag Geese Anser anser in NW-Europe has increased during recent decades from 20 000 around 1970 to 200 000 in the early 1990s (Madsen 1991; Madsen et al. 1996). The increase in population size is explained by a shift in primary foraging habitat from natural to agricultural areas as a response to an increased availabil-
spend on average nine months per year in agricultural habitat, and only three months in natural wetlands (Van Eerden et al. 1996).

The Scandinavian and Baltic breeding Greylag Goose populations migrate through the European lowlands and France to winter mainly in Spain. Greylag Geese stage in The Netherlands normally from September until December, but considerable numbers may also winter there, especially during mild winters. Peak arrival in Spain is in December and January (Amat 1986). Although agricultural habitats have become increasingly important, staging geese still seem to show an affinity for natural habitats. In southern Spain, agricultural land was used only when Scirpus stands were inaccessible or depleted (Amat 1986). In The Netherlands, the most important present staging area for this population is a brackish tidal marsh in the southwest that also has Scirpus stands (Castelijns et al. 1991). Greylag Geese from the Central European flyway are also largely confined to Scirpus marshes while wintering in North Africa. Only in very wet years, when the Scirpus stands were inaccessible to the birds due to increased water depth after flooding, did geese move to adjacent agricultural land (Dick et al. 1991). Besides Sea Club-rush Scirpus maritimus, Greylag Geese also exploit below-ground storage organs from other plants such as Cattail Typha latifolia and Reed Phragmites australis (Dubbeldam 1978), Marsh Arrow-grass Triglochin palustris (Van Eerden et al. 1997), Scirpus littoralis (Amat et al. 1991) and more recently Common Cord-grass Spartina anglica (Esselink et al. 1997).

As the Greylag Goose population continued to increase, new breeding grounds as well as new staging areas have been occupied by the geese (Amat 1986; Koffijberg et al. 1997). In this paper we report on Greylag Geese which have started to use the island of Schiermonnikoog (Wadden Sea area, The Netherlands) as a staging site. We seek to identify what factors may have been responsible for this colonisation, especially whether vegetation changes have occurred which could have been responsible for transforming the island into a suitable staging area. We present data on the changes in abundance of Greylag Geese on the island, seasonal patterns in numbers, and their habitat use. We then assess changes in the abundance of potential food plants from 1960 onwards as a consequence of vegetation succession.

METHODS

The study was conducted on the island of Schiermonnikoog (Fig. 1AB). The eastern half of the island is a dune ridge and a back-barrier salt marsh. The salt marsh became more protected from the sea after coastal-defence authorities strengthened the natural dunes with an artificial dune ridge in 1959. Storm tides made breaches in this ridge, however, and maintenance of the eastern part of the artificial dune ridge was abandoned by 1972. The most north-western part of the salt marsh remained in the lee of the artificial dune ridge and developed from a bare sandy plain in 1959 into a 155 ha brackish marsh with stands of Scirpus maritimus and Phragmites australis in the early 1990s (Van der Veen et al. 1997). This marsh is waterlogged during autumn and winter and contains some areas with open brackish water during this part of the year. Spartina anglica was introduced in the Wadden Sea in the 1920s for coastal protection and land reclamation (Van Eerde 1942; Reise 1994). Nowadays it is a common salt marsh species of the pioneer zone, often in dense monospecific stands. On Schiermonnikoog, Spartina has a limited distribution in the salt marsh. It is mainly restricted to a 28 ha area in the pioneer zone and the lower salt marsh (Fig. 1B). The Spartina marsh becomes wetter during autumn due to a combination of rainfall and higher flooding frequency, and shallow natural depressions may become waterlogged.

Goose counts

The maximum number of Greylag Geese staging each year was obtained from bird counts covering the whole island. Counts were performed several times per year from 1960-1998. Only
counts carried out between September and January were used in the analysis to obtain the maximum number of staging geese during autumn or winter. In 1994 and 1995, additional goose counts were performed weekly between early October and late December, which were focused on the roosting area of the Greylag Geese (Scirpus marsh). From a high dune, geese leaving the roost were counted from dawn till approximately three hours later. After each count, the roost was checked for birds that possibly did stay in the Scirpus marsh.

In 1994 and 1995 the whole island was surveyed once a month from September until February, to assess the distribution of the geese over the agricultural and salt-marsh habitats on the island. The time spent in the Scirpus and Spartina marsh by geese was estimated by recording the time when the geese left the roost in the Scirpus marsh for the lower salt marsh and the time when they returned. The number of geese flying in or out was recorded every minute from one hour before until three hours after sunrise and from three hours before until one hour after sunset. Up to one hour after sunset, arriving flocks were heard but not all returning geese could be counted because of the growing darkness towards the end of the counts. This missing number of incoming geese was obtained indirectly by comparing the number from the evening count with the number counted
next morning. The extra birds counted in the morning were assumed to have arrived in the dark the previous evening. The counts were performed on six days, equally spread over October, November and December 1995.

Vegetation changes
Changes in the incidence of *Scirpus* and *Spartina* could be reconstructed on the basis of vegetation maps. We measured the surface area covered by the *Spartina* community from a vegetation map from 1958 (B. Van Tooren pers. comm.). The cover of *Spartina* within this community was at least 5%. In 1996, stands of *Spartina* were delineated in the relatively small part of the salt marsh where this species formed dense stands. Other parts of the marsh, where the incidence of *Spartina* was very low, were excluded from the analysis.

Vegetation maps of the *Scirpus* marsh were available from 1958, 1970, 1976, 1978 and 1994 (Van der Veen *et al.* 1997). On these maps, areas with \( \geq 25\% \) *Scirpus* cover were shown. Additional data on the incidence of *Scirpus* were available from 12 transects, from which data were recorded between 1973 and 1997 (Olff *et al.* 1993; B. Van Tooren pers. comm.). The transects were located on a gradient from a low (plain) to a high elevation (dunes), along each of which the presence of *Scirpus* was recorded in 20 plots of 1 m x 0.4 m. The distance between transects was 1 m which together formed a grid. Only low-lying plots in the plain \( (n = 132) \) were relevant for *Scirpus*. *Scirpus* abundance over the years was expressed as the percentage of plots in which the species was present. Transects were positioned in one of the most suitable habitats for *Scirpus*, i.e. in the centre of its current distribution (Fig. 1B).

Habitat selection in the salt marsh
In November 1995, a four-meter-high observation tower was erected in the salt marsh close to an extensive *Spartina* stand. From the tower, goose visitation was recorded in an area of 33.3 ha which comprised four plant communities dominated by Common Cord-grass *Spartina anglica*, Red Fescue *Festuca rubra*, Sea Couch *Elymus athericus* and Sea-purslane *Atriplex portulacoides*, respectively (Fig. 1C). Nomenclature of plant species follows Van der Meijden *et al.* (1990). To analyse goose preference, the number of geese were recorded every 30 min in each of the four communities. It was sometimes difficult to assess the number of geese accurately, especially in the *Spartina* and *Atriplex* communities, because the vegetation was too tall. It was not possible therefore to calculate the number of goose hours for each of the four communities. Instead, the maximum number of Greylag Geese observed in a plant community each day was used to express the relative importance of the different communities for the geese. Observations were performed with a 20-60x telescope on 7 days during the second half of November 1995, for 5-8 hours per day.

Soluble-carbohydrate content of food plants
From October 1995 until January 1996, three samples of *Spartina* and *Scirpus* plants were harvested every month to determine non-structural-carbohydrate content (subsequently referred to as soluble carbohydrates), a measure of plant quality as winter food for Greylag Geese (Amat *et al.* 1991). From *Spartina*, above- and below-ground parts were collected and these were subdivided into green leaves, upper and lower stem part, stem base, rhizomes and roots. From *Scirpus*, only below-ground tubers were collected. All samples were washed and dried for 24 hours at 70°C. Soluble-carbohydrate content was analysed with anthrone reagens following Allen (1989). Measurements using this method should also include starch. Based on reference samples (potato), recovery of starch proved, however, to be incomplete (22.7 %). Therefore, soluble carbohydrates and starch were determined separately in three *Scirpus* samples from December. The samples were treated with the enzyme amyloglucosidase to break down the starch into monosaccharides. The ratio between starch and soluble carbohydrates in these *Scirpus* tubers was 11:1. However, when adding up the amount of soluble carbohy-
drates and starch measured, the sum was only a factor 1.35 higher than in the initial analyses, indicating that starch had been partially measured in the first analysis. The data presented for *Scirpus* were corrected for the incomplete recovery of starch by multiplying the initial soluble-carbohydrate value by a factor 1.35. The data presented on *Scirpus*, therefore, include an estimate for starch, while for *Spartina* starch was ignored because content in *Spartina* was expected to be very low (e.g. 4% in *Spartina alterniflora* according to Lytle & Hull 1980).

**Exploitation of the *Spartina* vegetation**

In the *Spartina* marsh, a grid of 180 m x 850 m from the high marsh on to the intertidal flats was established (Fig. 1B). The grid was subdivided in 10 m x 10 m plots in which the cover of *Spartina* was estimated in autumn 1994/95. In the grid, grubbing marks of Greylag Geese were counted twice in November and once in December 1995. A grubbing mark was defined as a hole in the marsh bed accompanied by fresh uprooted *Spartina* or remnants of its roots and rhizomes. During each count, marks were recorded along six parallel lines running north-south through the grid with a width of 10 m each. Hence in total, one third of the grid surface was surveyed. In the first week of November 1995, individual *Spartina* plants were marked (*n* = 196) to study which plants were taken by the geese. Three classes of plants were distinguished: shoots of solitary plants in small clumps of up to 5 shoots, shoots at the outer edge of larger *Spartina* clones, and shoots in the centre of larger clones. The shoots were marked with a small piece of tape on the stem and by a small plastic stick placed at about 50 cm distance from the plant. The marked shoots were checked twice a week from 4 November until 19 December 1995.

**RESULTS**

**Numerical trends**

During the 1960s, Greylag Geese were observed only occasionally on the island of Schiermonnikoog. Most of the observations were from spring, and rarely exceeded 100 birds on a single day (Mooser 1973). Between 1960 and 1990 only few Greylag Geese visited the island during autumn. From 1991 onwards, however, numbers of Greylag Geese observed on the island during autumn and winter increased sharply to a maximum of just over 900 birds (Fig. 2). Goose arrival on the island and peak abundance differed considerably between the 1994/95 and 1995/96 seasons (Fig. 3). In 1994, goose numbers started to increase in November, peaked in December, and dropped during the second half of January 1995. In the autumn of 1995, geese arrived as early as September and high numbers were present early in October. Thereafter, the number of geese declined gradually to 300 birds in January 1996. The 1995/96 winter was more severe than the preceding winter of 1994/95. In January 1995, temp-

![Fig. 2.](image.png)
Fig. 3. Number (average ± SE) of Greylag Geese on the island of Schiermonnikoog during autumn and winter 1994/95 and 1995/96.

temperatures below 0°C were recorded on only six days, whereas January 1996 had 24 days of frost. Although in the winter 1995/96 Scirpus tubers and Spartina rhizomes were out of reach due to the frozen marsh bed in December, most geese did not leave the island until a second period of frost in the first week of January 1996. The total number of goose days spent on the island was 40 175 in 1994/95 and 59 868 and 1995/96.

Habitat use
Based on island surveys during daytime, Greylag Geese were mainly observed in the Spartina marsh (73% of the 3 485 birds counted) and in the Scirpus marsh (17%). The remaining 10% of the birds were observed elsewhere in the salt marsh, mostly close to the Spartina marsh. Remarkably, not a single Greylag was observed in the extensive agricultural grasslands on the western part of the island. Almost all Greylag Geese spent the night in the Scirpus marsh, where they also foraged for part of the time. Here, geese took not only Scirpus tubers, but also to a lesser extent grazed on grasses, mainly Festuca rubra. During the morning, most geese left the Scirpus marsh for the salt marsh. Some birds, however, flew directly to the mainland and apparently used the island only to roost. Some geese prolonged their stay in the Scirpus marsh, leaving for the salt marsh only later during the day. Geese left the Scirpus marsh on average one hour after sunrise and returned to the roost around sunset. Based on the data of in- and out-flying birds, geese spent on average 8 out of the 9 hours of daylight in the salt marsh.

Habitat selection in the salt marsh, vegetation changes and soluble-carbohydrate content
The plant communities in the salt marsh were not visited by Greylag Geese proportionally to their surface area ($\chi^2 = 11.6, P < 0.01$; Fig. 4). Greylag Geese grazed in the Festuca, Elymus and Spartina communities, but were never observed in the community dominated by Atriplex. Geese had a preference for the Spartina community where they exploited Spartina rhizomes. They grubbed for rhizomes and discarded the stems and leaves, which usually remained on the marsh surface.

The occurrence of two potential food plants for Greylag Geese, Scirpus and Spartina, changed considerably over the years. Scirpus did not occur on the eastern part of the island in 1959, but by
1994 the plant community with >25% cover of *Scirpus* covered 16.7 ha of the brackish marsh (Fig. 5). In this marsh, the number of permanent plots with *Scirpus* increased from 12% in 1973 to 80% in 1989. The surface area of the plant community with *Spartina* (cover >5%) increased from 9.7 ha in 1958 to 27.9 ha in 1996 (Fig. 5).

Rhizomes had the highest soluble-carbohydrate content of the different parts of *Spartina* (Table 1). Below-ground parts contained significantly more soluble carbohydrates than above-ground parts (averages 20.6% and 9.5%, respectively; \( F_{1,19} = 87.97, P < 0.001 \)). Soluble-carbohydrate content of *Spartina* rhizomes increased during autumn, but that of *Scirpus* tubers was more or less constant over time (Fig. 6). During the period that geese exploited the below-ground resources (Oct-Jan), the soluble-carbohydrate content of *Scirpus* tubers did not differ significantly from that of *Spartina* rhizomes (averages 24.9% and 23.5%, respectively; \( F_{1,19} = 0.69, P = 0.42 \)).

**Effects of grubbing on Spartina**

Solitary plants had a significantly higher risk of being taken by Greylag Geese than shoots from the fringe or the centre of clones (Table 2; \( \chi^2_{2} = 19.6, P < 0.005 \)). During a six-week period in November and December 1995, 22% of the marked

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**Table 1.** Soluble-carbohydrate content of separate parts of *Spartina anglica*. Figures are average values from October to January (\( n = 4 \)).

<table>
<thead>
<tr>
<th>Plant part</th>
<th>Soluble carbohydrates (%)</th>
<th>Mean</th>
<th>SE</th>
</tr>
</thead>
<tbody>
<tr>
<td>Above-ground</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>leaf</td>
<td>7.0</td>
<td>1.5</td>
<td></td>
</tr>
<tr>
<td>upper 1/3 stem</td>
<td>8.1</td>
<td>1.0</td>
<td></td>
</tr>
<tr>
<td>lower 1/3 stem</td>
<td>13.1</td>
<td>1.6</td>
<td></td>
</tr>
<tr>
<td>Below-ground</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>stem base</td>
<td>18.2</td>
<td>2.0</td>
<td></td>
</tr>
<tr>
<td>root</td>
<td>20.2</td>
<td>3.0</td>
<td></td>
</tr>
<tr>
<td>rhizome</td>
<td>23.5</td>
<td>2.7</td>
<td></td>
</tr>
</tbody>
</table>

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**Fig. 5.** Development of the incidence of *Scirpus maritimus* and *Spartina anglica* communities on Schiermonnikoog from 1958-1996. The *Scirpus* is from the *Scirpus* marsh and represent the area with >25% *Scirpus* cover. The vegetation was mapped in 1958, when no areas with >25% *Scirpus* cover occurred. In 1970 the area of *Scirpus* was very small, but just visible in Fig. 5. The *Spartina* data are from the main *Spartina* area and show the area with >5% *Spartina* cover. The development of the *Scirpus* abundance from 1972 to 1989 was measured in 12 permanent transects in the *Scirpus* marsh. The abundance of *Scirpus* is expressed as the percentage of subplots in which *Scirpus* was present.

**Fig. 6.** Soluble-carbohydrate content (average ± SE, \( n = 3 \)) of *Spartina* rhizomes and *Scirpus* tubers from late summer in winter. The values for *Scirpus* were corrected with an estimate for starch content (see Methods).
Table 2. Number of marked *Spartina* plants per category and the number of plants that disappeared due to Greylag grubbing. $\chi^2 = 19.6, P < 0.005$.

<table>
<thead>
<tr>
<th>Position</th>
<th>$n =$</th>
<th>grazed</th>
</tr>
</thead>
<tbody>
<tr>
<td>Solitary</td>
<td>72</td>
<td>16</td>
</tr>
<tr>
<td>Edge of clone</td>
<td>68</td>
<td>0</td>
</tr>
<tr>
<td>Inside clone</td>
<td>56</td>
<td>0</td>
</tr>
</tbody>
</table>

Fig. 7. *Spartina* cover and grubbing marks in the *Spartina* transect. On the x-axis the distance (in meters) from the dunes (north) to the mudflat (south, starting at 800 m from the dunes) is indicated. The values of *Spartina* cover and grubbing marks are averaged over the transect-width ($n = 18$ and $n = 6$ respectively). Grubbing-mark values are explained in the text.

DISCUSSION

Patterns of colonisation

Colonisation of new areas by geese has previously been documented, and there seem to be two main causes. The first is that population growth may cause interference among birds in a traditionally exploited area to such a level that for some birds it becomes energetically more profitable to exploit a nearby new area that was initially of lower value for geese (cf. Milinski & Parker 1991). Ebbing (1992), who showed an increase in Dark-bellied Brent Geese *Branta bernicla* numbers on the island of Texel (Wadden Sea area, The Netherlands) after other areas had become saturated, described this 'overflow' principle. Second, vegetation and land-use changes may induce colonisation of new areas, either because traditional areas become unsuitable for foraging, or new areas become more profitable. A traditional area may become unsuitable due to over-exploitation, as has been described for exploitation by Greylag Geese of intertidal *Scirpus* marshes (Zwarts 1972; Esselink et al. 1997), and for exploitation by Lesser Snow Geese *Anser c. caerulescens* of subarctic salt marshes in Canada (Iacobelli & Jefferies 1991; Srivastava & Jefferies 1996). A traditional area may also become unsuitable because preferred food plants dwindle and non-food plants predominate during vegetation succession. Succession may, however, also lead to the development of new feeding resources. The latter two situations have been simultaneously observed in Dark-bellied Brent Geese on Schiermonnikoog. These geese gave up traditional feeding grounds in older parts of the salt marsh, while newly formed salt marshes were immediately exploited (Drent & Van der Wal 1999). At the same time, several herbivorous waterfowl species started to exploit agricultural habitats instead of their natural habitats as a response to an increased availability of high-quality agricultural food sources (Van Eerden et al. 1996).

Colonisation of Schiermonnikoog by Greylag Geese was abrupt, from occasional flocks in the late 1980s to 700-900 birds in the 1990s. Two im-
important staging areas lie close to the island: the Dollard estuary (65 km distant) and Lauwersmeer area (10 km). Up to 10 000 Greylag Geese stage during autumn in the Dollard (Esselink et al. 1997) and similar numbers use the Lauwersmeer (Koffijberg et al. 1997). It is most likely that geese staging on Schiermonnikoog have spilled over from the Lauwersmeer area. Like the majority of the Greylag Geese in the Lauwersmeer area (Vos­lamber et al. 1993), all three neck-banded birds identified on the island were of Norwegian origin. During geese counts at the roost in the Scirpus marsh in 1995, up to 300 geese were observed to originate from the Lauwersmeer area, flying in late and leaving very early in the morning, using the island only as a roosting place. Schiermonnikoog might offer a safe site, because of an almost complete lack of predation, whereas in the Lauwersmeer area, the density of Red Fox Vulpus vulpus has become high since the area was colonised during the 1980s (Dijkstra & Zijlstra 1997).

Other goose species have colonised the island earlier. Barnacle Goose Branta leucopsis arrived on Schiermonnikoog in 1962 (Mooser & Zwarts 1968), and their number increased gradually. Today, more than 5000 birds winter on the island (Koffijberg et al. 1997). This pattern of colonisation is in contrast with the sudden exploitation as observed in the Greylag Goose. A possible explanation for the abrupt colonisation by Greylag Geese could be that the carrying capacity of nearby staging areas was reached and therefore geese moved to other areas including Schiermonnikoog. The number of staging Greylag Geese in the natural habitats in the Lauwersmeer and the Dollard have been relatively constant since 1985 (Fig. 8; Koffijberg et al. 1997; Esselink et al. 1997). The natural habitat of the Lauwersmeer seems to have been at carrying capacity since the early 1980s (Van Eerden et al. 1997). The number of Greylag Geese staging in the vicinity of the Lauwersmeer has increased since then, although these numbers seem to stabilise. Greylag Geese now forage mainly on pastures and arable fields in close vicinity of the Lauwersmeer (Van Eerden et al. 1997). For the Lauwersmeer area as a whole the overflow principle seems to be operating, possibly in combination with improved feeding conditions in the agricultural habitat. The colonisation of Schiermonnikoog may not, however, be a direct result of this overflow. Observations of Greylag Geese on the island from 1985 onwards indicate geese knew of its existence, but numbers remained low until colonisation in 1991. Thus there was a time-lag of at least six years between saturation of the habitat in the Lauwersmeer and the colonisation of Schiermonnikoog.

The alternative hypothesis concerns vegetation change, either in the source or in the sink area. Feeding conditions in the Lauwersmeer were subject to considerable change due to vegetation succession after the area was embanked in 1969. The steep increase in the number of Greylag Geese around 1980 coincided with the sudden expansion of Creeping Bent Agrostis stolonifera, whose seeds formed an important part of the diet of the Greylag Geese (Van Eerden et al. 1997). After 1980 the availability of Agrostis seeds gradually declined, and in 1994 seed stock was reduced to about one third of the initial amount. Rather than a decline in number of Greylag Geese using natural habitat, numbers remained constant due to a switch of feeding onto the bulbils of Triglochin
It is unlikely, therefore, that vegetation change in the source area was the trigger for Greylag Geese to colonize Schiermonnikoog. Vegetation on the island itself, however, has changed considerably over the last decades. *Spartina* extended its distribution in the salt marsh, and *Scirpus* increased sharply, especially during the second half of the 1980s (Fig. 5). Most likely, it is the combination of high goose numbers in the Lauwersmeer area, and changes in the vegetation on the island, that triggered the colonisation of Schiermonnikoog by Greylag Geese.

**Habitat choice and food-plant quality**

Our study shows that Greylag Geese readily exploit natural habitat when it becomes suitable for feeding, in this case due to natural vegetation succession. This is in line with the findings of Van Eerden *et al.* (1997) for Greylag Geese utilizing the Lauwersmeer area. A similar pattern is observed in Bewick’s Swans *Cygnus bewickii* in The Netherlands. On arrival in autumn, these swans feed on tubers of Fennel Pondweed *Potamogeton pectinatus*. After reaching an exploitation threshold, the swans then switch to harvest leftovers on agricultural fields (Beekman *et al.* 1991; Van Eerden *et al.* 1997). Since food intake and energy return are high when geese forage on harvest leftovers on arable fields (Van Eerden *et al.* 1997), the reason why geese prefer natural feeding habitats is not obvious. Herbivorous waterfowl might be attracted to natural habitats for reasons other than food availability. The need for a safe roost is one of the likely reasons for Greylag Geese and Bewick’s Swans to stay in close vicinity of their original natural staging habitat. Moreover, human disturbance in agricultural areas may represent an energetic penalty in the form of both enhanced flight costs and less time available to feed.

After the breeding season, Greylag Geese feed mainly on plant organs, which are high in soluble carbohydrates (Table 3). On average, natural food sources contain much less of these compounds than harvest leftovers, such as sugar-beet and potato on arable fields which have a soluble-carbohydrate content of 80-90%. Although in most other studies *Scirpus* tubers had a much higher soluble-carbohydrate content than *Spartina* rhizomes, we found values of approximately 25% for both food items. Carbohydrate storage in plants is sensitive to environmental conditions, such as light and nutrient availability (Heilmeier & Monson 1994). Seeds of *Scirpus*, collected at the study site, sown in potted soil, and grown in a greenhouse in April, produced plants with 64.6 ± 2.0% (mean ± SE; n = 3) soluble carbohydrates in their tubers in December of the same year (H. Olff pers. comm.). Vegetative material from the

### Table 3. Soluble-carbohydrate content of food plants of Greylag Geese and Greater Snow Geese (with respect to *Spartina alterniflora*).

<table>
<thead>
<tr>
<th>Species</th>
<th>Records of % soluble carbohydrates</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Spartina anglica</em></td>
<td>22</td>
<td>Briens &amp; Lahrer 1982</td>
</tr>
<tr>
<td></td>
<td>24</td>
<td>this study</td>
</tr>
<tr>
<td><em>Spartina alterniflora</em></td>
<td>22</td>
<td>Lytle &amp; Hull 1980</td>
</tr>
<tr>
<td><em>Scirpus maritimus</em></td>
<td>43</td>
<td>Amat <em>et al.</em> 1991</td>
</tr>
<tr>
<td></td>
<td>52</td>
<td>Clevering <em>et al.</em> 1995</td>
</tr>
<tr>
<td></td>
<td>22</td>
<td>Olff unpubl.</td>
</tr>
<tr>
<td></td>
<td>25</td>
<td>This study</td>
</tr>
<tr>
<td>Sugar-beet</td>
<td>77</td>
<td>Van Eerden <em>et al.</em> 1997</td>
</tr>
<tr>
<td>Potato</td>
<td>90</td>
<td>this study</td>
</tr>
<tr>
<td></td>
<td></td>
<td>AVEBE pers. comm.</td>
</tr>
</tbody>
</table>
site which was grown in a greenhouse reached 48.7 ± 1.6% \((n = 3)\) in the tubers. Tubers collected in August from the study site had, however, a soluble-carbohydrate content of only 22.1 ± 3.2% \((n = 5)\), comparable to our values (see Fig. 6). A difference in environmental conditions most likely explains the discrepancy between the greenhouse and field values of carbohydrate storage in the *Scirpus* tubers.

Whilst *Scirpus* is one of the traditional food plants, *Spartina* has only recently been exploited by Greylag Geese (Esselink et al. 1997). It is an exotic species, which was introduced and spread out along the European coast only this century (Gray et al. 1991; Reise 1994). Although changes in the abundance of *Spartina* could have played a role in the colonisation of the island, it might be that the increase in *Scirpus* is of greater importance. In Quebec, Canada, a comparable food situation exists for the Greater Snow Goose *Anser caerulescens atlantica*, which has a foraging ecology similar to the Greylag. In spring, large numbers of Greater Snow Geese stage in a marsh dominated by *Scirpus americanus* (Bédard & Gauthier 1989). Recently, part of the geese started to use a *Spartina alterniflora* marsh, a shift attributed to an increase in population size. Comparison of energy budgets of the geese revealed that *Spartina* was of lower quality than *Scirpus*, mainly because of a lower digestibility of *Spartina* rhizomes.

**Effects of Greylag grubbing**

As has been reported for Lesser Snow Geese in North America, grubbing geese which are supported for a part of the year by agricultural food supplies can cause a trophic cascade leading to destruction of their natural habitat (Srivastava & Jeffries 1996). Greylag Geese have been reported to over-exploit tidal *Scirpus* marshes in The Netherlands (Esselink et al. 1997; Zwarts 1972). However, we expect Greylag numbers on Schiermonnikoog to be too low to have a destructive effect on the *Scirpus* stands. Also wave action, which can potentially enlarge grubbing effects in a tidal *Scirpus* marsh, is very low in this area. At present, *Scirpus* is still spreading, which might lead to a further increase in number of staging Greylag Geese in the coming years.

Severe effects of goose grubbing have been reported in *Spartina* stands (Smith & Odum 1981; Esselink et al. 1997). The effects can be more severe than on *Scirpus*, especially under waterlogged conditions where of *Spartina* is not able to resprout (Braendle & Crawford 1987; pers. observ.). So far, the impact of Greylag Geese on *Spartina* on Schiermonnikoog seems very limited. In one experimental plot, only the fringes of *Spartina* stands and solitary plants were exploited, and the area covered by *Spartina* declined by 2% in a single season (pers. observ.). This is in accordance with our observation on individually marked plants, and resembles the fate of young *Spartina* plants in the study of Esselink et al. (1997).

**ACKNOWLEDGEMENTS**

We thank Ingrid van der Wal, Aaldrik Pot and Julia Stahl for their help during fieldwork. Leo Zwarts kindly provided data on the abundance of Greylag Geese on Schiermonnikoog from 1960 to 1994; Klaas van Dijk and Kees Oosterbeek provided data of the goose counts since 1994. We thank Kees Koffijberg from SOVON for providing data on the abundance of Greylag Geese in the Lauwersmeer since 1980. Han Olff and Bart van Tooren are acknowledged for their data on *Spartina* abundance in the *Spartina* marsh and Han Olff for his unpublished data on carbohydrates in *Scirpus* tubers. The manuscript was improved by comments of Jan Bakker, Rudi Drent, Tony Fox, Maarten Loonen, and Han Olff and an anonymous referee. We are grateful to Natuurmonumenten for their permission to carry out this study. Dick Visser prepared the figures.

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**SAMENVATTING**


Received 24 March 1998, accepted 23 February 1999

Corresponding editor: Theunis Piersma