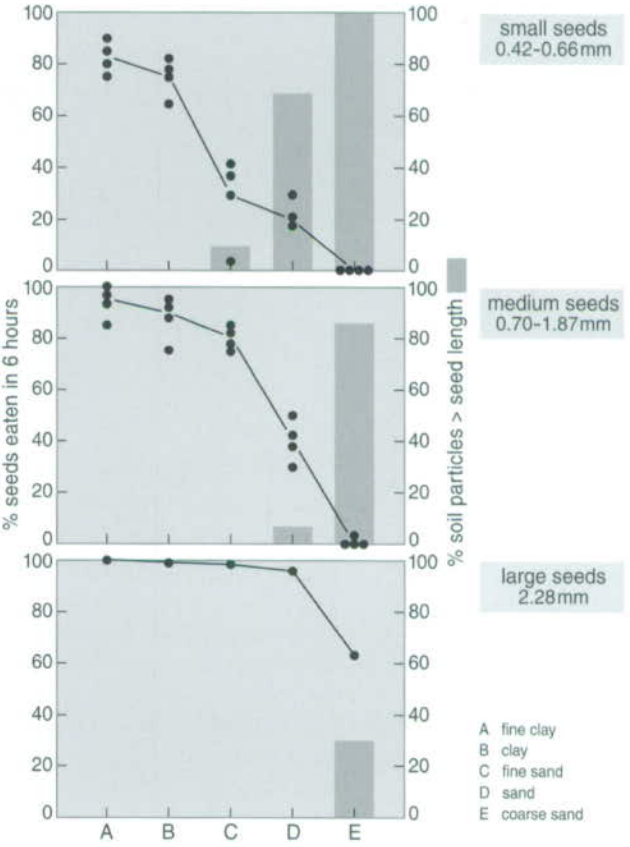

**Figure 5.** Patch harvest levels (% depleted in 6 h) of preferred seeds belonging to three different size classes when offered on different soil substrates. For seed sizes smaller than the average soil particle size, the proportion harvested is strongly suppressed, the effect being already apparent at 5-10% of all soil particles being larger than seed size.
Both soil type and seed mass contributed significantly to the harvest level observed (Friedman two way ANOVA statistic for soil type $\chi_r^2 = 30.32$, $P < 0.0001$, df = 4; for seed mass $\chi_r^2 = 24.77$, $P < 0.005$, df = 9). A stepwise multiple regression entering both variables resulted in $R^2 = 0.38$; ANCOVA, $F = 16.06$, $P < 0.0001$.

fered in the amount of interactions in which they were involved and also in the proportion of quarrels won. The dominant male "yellow" only initiated interactions with the two males ranking just below it, males "blue" and "white". No interactions occurred between "yellow", the low ranking male "green" and the female. Dominance rank was directly related to structural size of the bird, expressed as the multiple of body mass, wing length and tarsus length.

The allocation of foraging time was also linked to dominance position, the top two males only spending time in the most profitable patches. Lower ranking birds foraged also in intermediate and poor patches. Female "red", the most subordinate bird, was effectively restricted to the least favourable patches and compensated by spending twice as much time feeding as the higher ranking males did (Table 2). Dominant Teal thus forced subordinates to patches of lower quality, although all five birds had access to the food tray.

### Patch use and exploitation patterns

When feeding in a patch, Teal experience a continuously decelerating intake rate as a result of food depletion (Fig. 6). Because of the suction pumping foraging method, Teal experience an instantaneous uptake of food items when foraging in a patch. These results fulfil the requirements for a proper test of patch use with resource depletion (Brown 1988, Mitchell 1990, Mitchell & Brown 1990). We used debris as described before to manipulate gain curves per patch. Travel time between patches was considered equal, and patch depletion was monitored by continuous observation and regular counts of

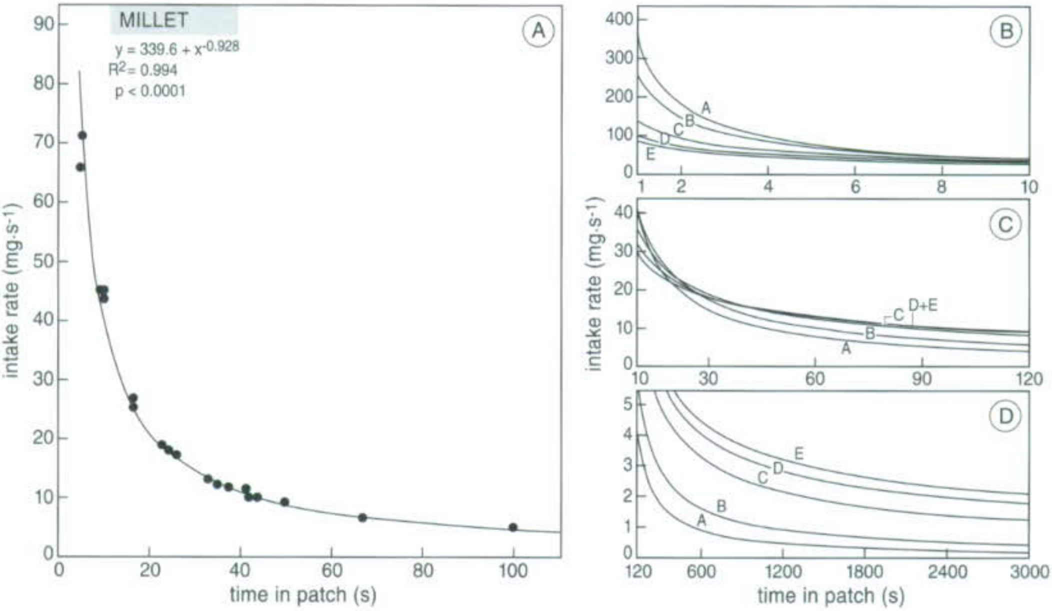

**Figure 6.** (A) Intake rate of Millet for individual Teal in relation to cumulative time in patch. Initial seed mass in patch was 445 mg. The decelerating curve of intake rate resulted from four different trials and is described by $y = 339.6 + x^{-0.928}$, $R^2 = 0.994$, $P < 0.0001$. (B)-(D) Intake rate for different periods of cumulative time in patch, showing shift in rank of profitability between patches. Note the decreased variability of patch quality during the course of the experiment.

seeds left over. Patch residence time (PRT), total foraging time (FT) and giving up density (GUD) were used as determinants of patch exploitation.

First, we considered the initial phase when Teal enter the new patch situation. In two out of four trials, PRT was equal for all patches with the same food density but with different gain curves ($\chi^2 = 1.12$ and 4.48, df = 4, NS). In the other two trials, there was a significant deviation from equality ($\chi^2 = 21.8$, $P < 0.001$ and $\chi^2 = 17.55$, $P < 0.01$, df = 4) and birds spent more time in patches of higher quality. However, when tested against the expected time spent per patch according to harvesting rate experienced, only one trial matched completely ($\chi^2 = 6.12$, df = 4, NS) but the rest differed significantly. This means that time spent per patch tended to be more evenly distributed than expected ($\chi^2 = 17.46$, df = 4, $P < 0.01$; $\chi^2 = 17.39$, $P < 0.01$; $\chi^2 = 13.21$, $P < 0.02$). We conclude that in the early phase of patch exploitation, Teal tended to use a Fixed Time Strategy.

In subsequent phases of depletion, more food was extracted from high quality patches. All patches were used, however, and the initial differences in quality remained during successive phases (Fig. 7A). The poorest patches were exploited to a level related to the average quality of the environment (Fig. 7B). GUD thus shifted downward as habitat quality decreased. From these data we conclude that Teal were Bayesian Foragers during the major part of patch depletion. Bayesian Foragers are assumed to have knowledge of the distribution of patches of different quality in their environment, in our case likely to result from Fixed Time Sampling in the first phase of the experiment, but are unable to assess immediately the quality of an encountered patch. Instead, patch quality (intake rate) is assessed during the harvest process. A Bayesian Foraging Strategy leads to an under-utilisation of rich patches.

Patch residence time tended to be longer in high quality environments and increased in some

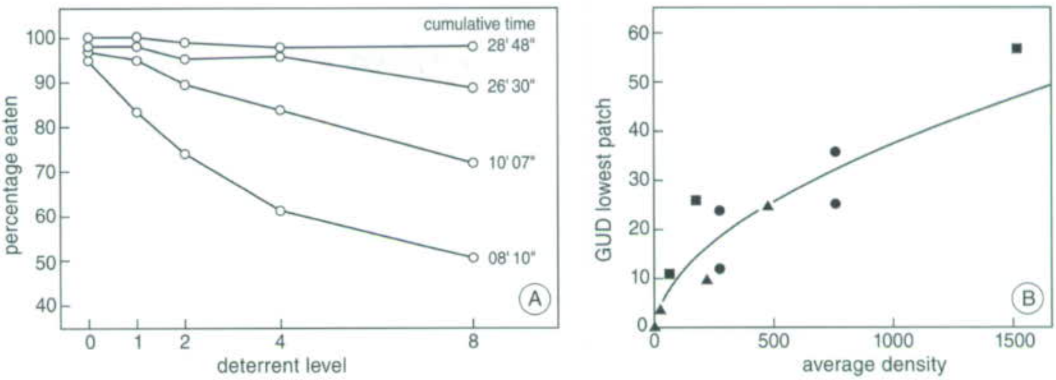

**Figure 7.** (A) Subsequent phases of patch harvest showing the simultaneous record of successive depletion of patches with the highest gain curves (low debris level) followed by patches of lower quality. Note the constant position of the patches of different quality, in relation to each other. (B) Giving up density of lowest patch in relation to the average quality of all the patches. During depletion, GUD shifts downward as average environmental quality decreases. Symbols indicate different trials.

patches as time progressed. Especially the patches with initially the lowest gain curves were better later on, when the best patches had almost entirely been depleted. In this phase the longest PRT's were measured. However, the poor (formerly richest!) patches were also continuously revisited (Fig. 8). When compared to the calculated profitability of each patch prior to each successive trial, the shift in foraging time towards the poor patches is obvious. During the final sequences of this experiment, patches with debris density eight were of superior (although marginal) quality compared to the rest. Patch quality was less variable than during the start of the experiment and differences remained rather constant. This pattern was caused by the different behaviour of individual Teal. The dominant males "yellow" and "blue" (*cf.* Table 2) spent all their time in these patches, leaving the other birds the rest of the tableau of patches. The prolonged stay by the most dominant birds in the (marginally) richest patches during the second part of the experiment led to a relatively over-exploitation of these patches if compared to the poorest patches. In the stable environment at that phase apparently a Rate Assessment rule was applied.

Multiple regression analysis with backward deletion of terms was used to determine variables explaining patch attendance (PRT and total time in patch). As criterion to remove a variable $P_{OUT} = 0.10$ was used by default. Standardised regression coefficients (betas) are given in brackets. During the first five sequences of the experiment, intake rate (0.595, $P = 0.007$), seed density (0.704, $P = 0.027$) and deterrent level (0.865, $P = 0.025$) contributed positively to PRT while total time in patch during last visit was negatively correlated with PRT (-0.951, $P < 0.001$); adjusted $R^2 = 0.552$, $F_{4,20} = 8.402$, $P < 0.001$. During the second phase of the experiment, previous food uptake in patch contributed negatively to actual PRT (-0.541, $P = 0.066$), while average intake for all patches (1.397, $P = 0.081$), sequence number (1.395, $P = 0.075$) and deterrent level (1.193, $P < 0.001$) all contributed positively to the model (adjusted $R^2 = 0.646$, $F_{4,20} = 11.946$, $P < 0.001$).

Total time spent in patch was determined in the first five sequences by average intake for all patches (-1.596, $P = 0.024$), actual intake rate (1.531, $P = 0.011$), and two variables related to previous patch information: total food uptake (2.598, $P = 0.009$) and actual intake rate (-2.281, $P = 0.022$); the model, however, showed a poor fit and was just not significant (adjusted $R^2 = 0.211$, $F_{4,20} = 2.607$, $P = 0.067$). During the second five sequences, when intake rate had dropped to marginal values, food uptake

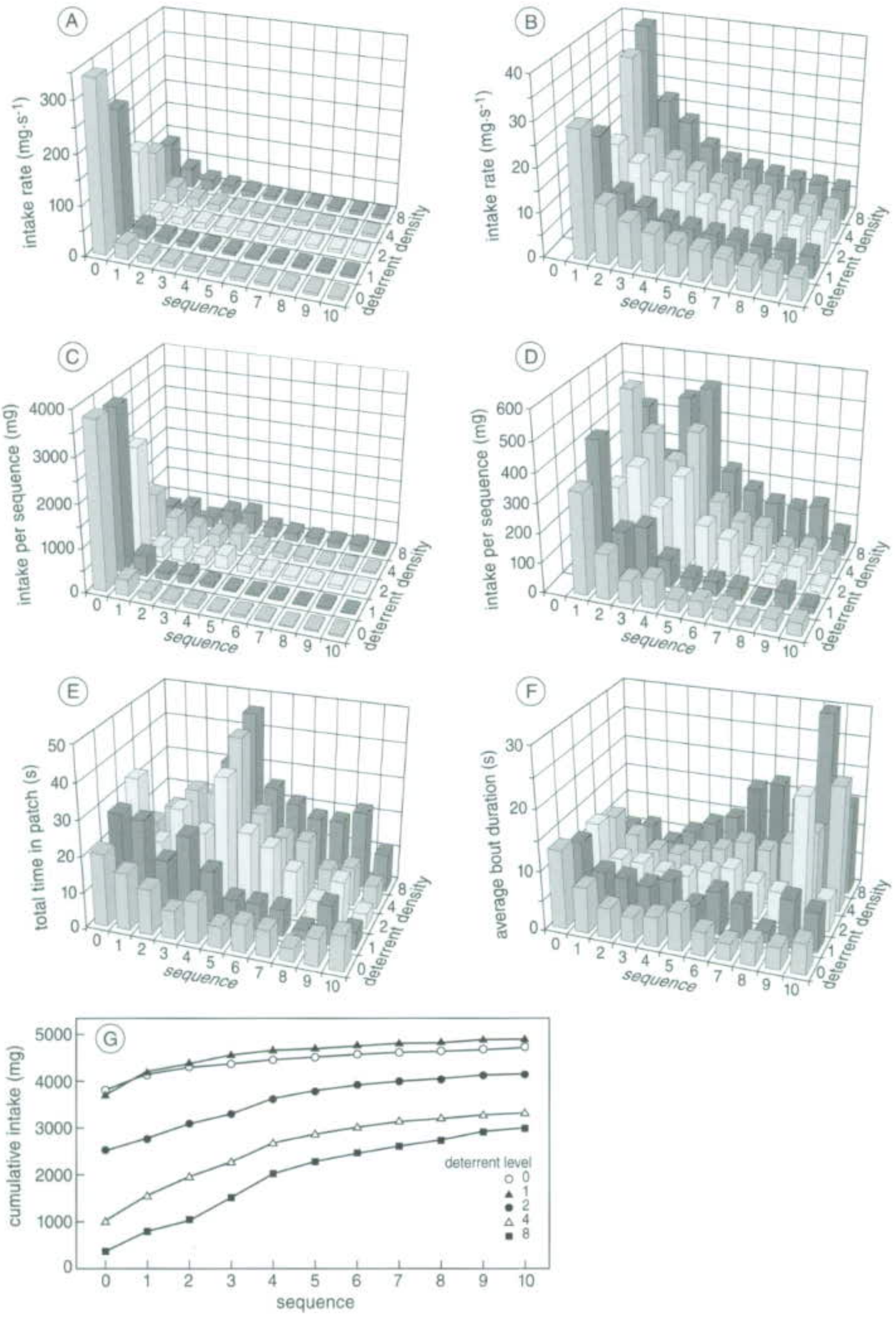

**Figure 8.** Subsequent phases during patch depletion by five Teal in ten subsequent trials. 25 Patches were offered simultaneously, greatly differing in initial quality. Seed density (Millet, 1-5 volume units) and gain functions (0-8 volume units of debris Rapeseed added) varied per patch (G).

(A)-(D) profitability per patch, expressed as the intake rate at the beginning of each sequence, (E) total time spent per patch per sequence and (F) average patch residence time (length of straining bout). Each bar represents the mean of 5 patches.

(2.330, $P = 0.001$) and total time in patch (-1.582, $P = 0.029$) during the previous patch visit were the only determinants. Total fit increased considerably (adjusted $R^2 = 0.649$, $F_{2,22} = 23.18$, $P < 0.001$). Teal thus combined both actual information from the patch under exploitation (especially during the early phase of depletion) as well as prior information from the previous visit.

## Discussion

### Straining mechanics and profitability rules

The anatid bill is highly adapted to perform the sieving of small food particles from a wet habitat. This sieving technique has been described in detail for anatid ducks by Kooloos *et al.* (1989) in a situation without deterring matter. These authors showed the high flexibility in maxillary rotation, gape and pumping speed of the feeding apparatus in adjustment to kernel size. Once inside the bill cavity, seeds may be lost across the sieve of the lamellae. Seed size affects seed retention in a positive way. The species with the highest number of lamellae, Shoveler *Anas clypeata,* was able to retain smaller items than larger species such as Mallard *A. platyrhynchos* and Tufted Duck *A. fuligula*. Compared to these species, Teal performs only slightly less efficiently than Shoveler, taking the number of lamellae into account (Lüttschwager 1955).

We showed that in undisturbed conditions, Teal are able to select seeds on the basis of size and morphology (volume to surface ratio, presence of spines or feather-like structures, hardiness of the seed coat). These variables are not only relevant because they govern the gross intake rate, but the digestibility of seeds was also related to certain morphological features. In natural situations with a mixed seed stock, Teal may therefore use tactile cues to select certain seeds which may be of help in achieving the highest net energy gain.

Teal may effectively keep unwanted particles out of their bill by narrowing down the entrance opening at the tip of the bill. Especially food items smaller than the average debris size can be taken up effectively (Fig. 4C). Intake rate was suppressed to roughly half of that without debris present. It is likely that the reduction of the water flow which is the result of the smaller entrance at the tip of the bill causes this effect. Not exactly understood is the fact that at higher debris densities, the suppressing effect becomes less and a plateau value is reached (Fig. 4B). The relative density of the preferred seeds declines continuously as more and more unwanted particles appear, so it seems that the intake rate would concurrently fall as well. This separating technique was demonstrated to be effective in water, where Teal had no problem in straining very small seeds (< 0.3 mm). On the contrary when offered in soils, seeds larger than the average soil particle were more easily retained. This is caused by a different selection procedure which takes place inside the bill. Teal take both water, soil and food particles in a water flow in their bill and subsequently have to filter the edible parts by means of their lamellae along the sides of their bill.

The two techniques of separation could not be compared directly in terms of intake rate. However, given the different mechanisms involved (keeping debris particles out in water or separating seeds actively in soils) foraging in soil probably negatively affects intake rate, as this procedure involves more material to be handled and expelled actively. Teal are therefore probably better off in inundated situations on fixated soils or vegetation than on mud. Moreover, the different straining mechanisms used in both environments require different objectives to be searched for. Not a single strategy can be used, but, depending on the habitat which is exploited, either small or larger food particles may be optimal.

## Patch exploitation and foraging strategy

### *Methodology*

Teal quickly learned to exploit our multi-patch situation. The dominant birds took the better positions, forcing the subordinates to patches of lower quality. The sight of eating birds stimulated other birds to enter the spot also, thus ensuring that motivation was high in all test situations. This is important as Kooloos *et al.* (1989) have shown that non-motivated captive ducks may cause severe bias in, for example, measuring intake rates. In our experimental set-up, conclusions about patch use and decision making could not be drawn always on the individual level, as foraging theory requires. However, we have chosen the group foraging experiments to resemble the natural situation as closely as possible. At this point, we agree with Mitchell (1990) who points out that lack of patch quality information on the level of a single individual due to the presence of competitors is a common feature of patch use in natural systems. At least this is true for situations where abundant, high quality food is used by flock-feeding predators such as water birds.

By manipulating food intake rate, we could effectively study patch depletion in this species, in a way which has much in common with the natural situation. Unlike many other predatory passerines like titmice *Paridae* and Starlings *Sturnus vulgaris*, Teal meet the requirements of the instantaneous intake rate. The time frame over which information builds up is short and can easily be influenced in an experimental set-up. Experiments with Teal may be worth being followed up in order to refine questions about foraging strategies in birds, especially with respect to the importance of recent information (*cf.* Cuthill *et al.* 1990) and flock foraging (*cf.* Valone & Giraldeau 1993, Alonso *et al.* 1995).

### *Intake rate and social dominance*

We showed that Teal had higher patch harvest rates when seed density was higher and seed size was larger. Both results can be explained as a consequence of the suction pump foraging method. In the water flow that is generated, the total food mass that can be transported is dependent on the particle size and density. Teal can probably manipulate the flow rate and the kinematics of the sieving apparatus as was found in Shoveler and Mallard by Kooloos *et al.* (1989). These authors found a maximal range in flow rate between the smallest (shrimp pulp, 0 - 0.5 mm) and the largest food items (Red Milo, 2.6 - 4.4 mm) by a factor three. However, higher pumping rates can apparently not compensate for the smallest seed sizes and subsequent higher losses over the sieving gear. Both seed size and density had a similar effect on the intake rate in *Dipodomys deserti* a small microtine granivore mammal which extracts seeds from top soil layers (Podolsky & Price 1990).

Mitchell (1990) has addressed the question of re-visitation of patches in a depletable situation. He showed that under the circumstance of exploitative competitors, the optimal strategy for an individual is to expand from being a specialist, feeding at rich patches first, and to become a generalist later, when resource density has decreased. Contrary to this, Teal exploited rich and poor quality patches simultaneously. Patch re-visitation occurred during the entire period for all patches. However, social rank determined access to different patches. Dominant Teal were specialists concentrating on the better areas only, the sub-dominant Teal were forced to devote a relatively large proportion of their time to poor patches. Only after Teal experienced a more or less constant, although marginal gain rate (after depletion of the rich patches), did they show an enormous preference for these initially poorest patches. Again, the dominant birds spent most of their time in the better patches, forcing the lower ranking ducks to the even poorer patches. By sacrificing patch harvest rate, sub-dominant Teal managed to continue foraging in the group (*cf.* Valone & Giraldeau 1993). The dominant birds monopolised by their prolonged stay the future gain in these patches. Although marginally different from the other patches, if the future time of possible seed uptake is taken into account, this behaviour is highly adaptive.

In our experimental situation no alternative set of patches was available. In nature, however, spacing out is more common (Zwarts 1976, pers. obs.) and this will affect the use of the poor patches. In conclusion we state that, also in nature may these social dominance effects determine the degree of utilisation of the poorest patches.

*Decision rules*

Deterrent level, corrected for all other variables, was positively correlated to PRT. This is consistent with foraging theory stating that if foraging effort increases, PRT should increase (Charnov 1976), which occurred. Interestingly, total time spent in patch (multiple visits) did not correlate with deterrent level, which confirms that PRT, which was measured on individual Teal, best recorded individual response.

Concerning foraging strategy, for most of the time of the patch exploitation, Teal behaved as Bayesian Foragers. They spent more time in better quality patches, where they harvested more and in a density dependent way. Recording the sequence of exploitation, Teal underused rich patches in relation to poor, all being hallmarks of this strategy (Iwasa *et al.* 1981, Valone & Brown 1989). Only at the beginning of the experiment, when the patch environment was totally unknown to the birds, a tendency towards a Fixed Time Strategy was observed. The observation that this strategy is linked to uncertainty about patch quality distribution has been theoretically worked out (Iwasa *et al.* 1981, Stewart-Oaten 1982, McNair 1983). In our situation Teal may have used this tactic to sample their environment, before switching to a strategy which requires more information. In a test situation with wild, seed-eating desert rodents and birds, Valone & Brown (1989) found different strategies among the different co-existing species. A Fixed Time Strategy occurred either in species which had general difficulties in assessing patch quality (Mourning Dove *Zenaida macroura* and Gambel's Quail *Callipepla gambelii*) or in low variance environments only (Arizona Pocket Mouse *Perognathus amplus* and Round-tail Ground Squirrel *Spermophilus tereticaudus)*.

The ducks used both actual and previously collected information during patch exploitation. As depletion proceeded to the situation with only slight, but stable differences in profitability between patches, birds responded no longer to actual intake rate (PRT and total time in patch). Instead, they responded more closely to the previously collected information during the last patch visit. Because of the stability of the patches during the second part of the experiment (*cf.* Fig. 8), this prolonged stay can be considered in terms of a timely monopolisation of future gain. Although the gain rate is extremely low compared to the start of the experiment, the ducks thus could take advantage of their position, not allowing others to enter it by re-sampling the environment. Also Valone and Brown (1989) showed that the degree of variation in patch quality affected the forager's ability to equalise GUD and to perform a different strategy, dependent upon this variation. Roche (1996), in line with our data, stresses the difficulty a forager has to assess differences in patch quality between slowly falling gain curves. A tendency to a biased stay in the current patch has been observed more often (Stephens & Krebs 1986, Roche 1996). In our experiment this prolonged stay yielded the best future reward, although only achievable for the dominant birds.

We conclude that decision rules vary, depending on actual variation in patch quality, the rate of change of this variation and the social interaction between flock members.

## Acknowledgements

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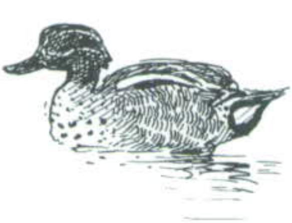

## Chapter 10

# Patch use by Bewick's Swans *Cygnus columbianus bewickii* feeding upon Sago Pondweed *Potamogeton pectinatus* in shallow lakes in the Netherlands: variation in exploitation threshold caused by social, environmental and time dependent factors

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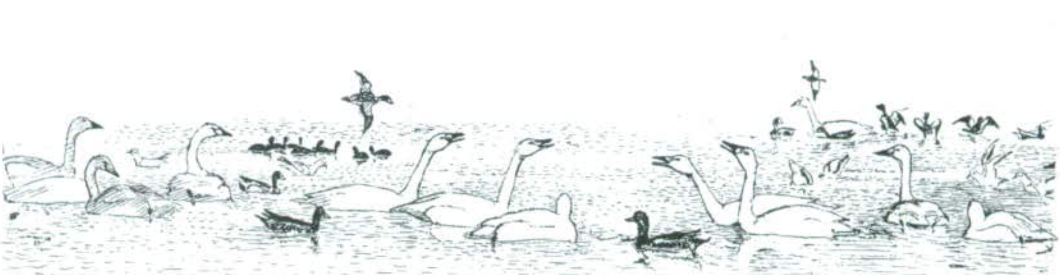


# Patch use by Bewick's Swans *Cygnus columbianus bewickii* feeding upon Sago Pondweed *Potamogeton pectinatus* in shallow lakes in the Netherlands: variation in exploitation threshold caused by social, environmental and time dependent factors

Below ground biomass of the macrophyte Sago Pondweed *Potamogeton pectinatus* is exploited by herbivorous wild swans *Cygnus columbianus bewickii* on their autumn migration. Data from five different lakes in the Netherlands and ten different seasons showed that tuber grazing by large flocks of swans depends upon touch in shallow water (15-60 cm water depth), the limits being set by the foot trampling foraging method. The patchy distribution of tuber density prior to the swans' grazing ended up each year with a general levelling off, representing site dependent threshold levels of 1.8-9.0 gDW $m^{-2}$. The threshold levels were related to the initial stock and corresponded to a 60-90% depletion by mass.

Continued nocturnal foraging at roosts by swans using *Potamogeton* only as supplementary food later in the season, after the shift to agricultural food, demonstrated the existence of a lower, probably physically determined threshold level of 1.6 gDW $m^{-2}$. Water depth (attainability of bottom) and soil type (energetic expense for pit digging) further affected local patch depletion levels.

Although family size determined dominance as measured by supplanting behaviour over food patches, the lower threshold of food density for larger families was apparently higher than that for smaller families and for swans not accompanied by young. It is suggested that the number of cygnets determines the minimum space for each social unit and thus sets the average intake rate required, thus making families more sensitive to depletion effects.

Swans took selectively more large tubers which in general occur deeper in the soil. Tuber selection was strongest between 25 and 55 cm water depth.

Concerning the decision strategy used during patch exploitation, Bewick's Swans were Bayesian Foragers in areas where food density was high but became Rate Assessors in poor environments.

Interannual variation in patch depletion level was observed at the same sub-sites within a lake. After 1989 *Potamogeton* was exploited to a lesser extent than before, which coincided with a better body condition of the swans arriving from further north-east.

We hypothesise the existence of a time window, which would dictate the requirements at a certain stopover site in relation to the situation at other stopover sites. Body condition, which fluctuates because of depletion of fat deposits during migration and recuperation at stopover sites, may be the physiological trigger to adjust the energetic and possibly nutritional needs at a certain site, resulting in a differential use of *Potamogeton* along the migratory pathway.

As a consequence, tuber grazing by Bewick's Swans is considered to have a major although somewhat stochastic impact on the plant's potential to recover next season.

## Introduction

Many studies dealing with vertebrate herbivory focus upon diet composition of the consumer. Often emphasis is laid upon the constraints set by the low energy content of the food plants available to the consumers in spite of the apparent super abundance of their resources. Much attention is also paid to the many defensive mechanisms plants have adopted to avoid over-exploitation (Barker *et al.* 1977, Rosenthal & Janzen 1979, Crawley 1983, 1997 for review). Recent work on herbivorous waterfowl points at the relative simplicity of their diet, with only a few plant species being exploited at any one time (Van Eerden 1984, Drent & Prins 1987, Wilson & Atkinson 1995). This makes these species ideal subjects for analysing questions about the carrying capacity of natural resources (Clausen 1994, Alonso *et al.* 1994).

The development of patch use theory during the past decades has provided a concept of great importance in understanding an animal's decision making with respect to its foraging behaviour (Charnov 1976, Parker & Stuart 1976, Caraco 1980, Tinbergen 1981, McNamara 1982, Stephens & Krebs 1986). Despite an overwhelming series of papers describing purely theoretical foragers, sometimes extended with elegant experiments with captive animals, little information has been gathered hitherto measuring the patch use by wild animals under purely natural circumstances. The complexity of nature at a larger scale and the often mixed diets of the foragers cause unworkable problems in most situations. Recent work on wintering cranes in an agricultural scene with large scale patches (sown cereal fields or stubble after harvest) has provided a test situation for foraging decisions under field conditions (Alonso *et al.* 1994, 1995, Bautista *et al.* 1995).

We present field data on the consumption of a non-renewable, natural resource, the storage organs of the macrophyte Sago Pondweed *Potamogeton pectinatus* by a group forager, the Bewick's Swan *Cygnus columbianus bewickii*. At the time of arrival of the swans from their sub-arctic breeding grounds in Russia in early autumn, all above ground biomass of the vegetation has died off and the birds have to locate their food through consecutive sampling of the mud of the shallow lake margins. Pits are trampled and the food items are sieved from the substrate. The food consists of small (0.5-2.0 cm), but discrete tubers, present in variable densities in the top 25 cm of the soil (Van Wijk 1988, Van Vierssen *et al.* 1994). During autumn no production occurs which facilitates quantifying the grazing pressure.

Upon arrival in the Netherlands, the Bewick's Swans always first consume Sago tubers, before turning to other food sources (Poorter 1981, Beekman *et al.* 1991). Obvious threshold levels, or giving up densities (GUD's, Valone & Brown 1989) have been demonstrated to occur under field situations thus forcing the swans to stop exploitation of Sago tubers and switch to other foods (Beekman *et al.* 1991). By trampling discrete pits and feeding on extremely small food items (50-150 mgDW) compared to the birds' body mass (5.7-6.4 kg: Cramp & Simmons 1977), foraging swans in an area covered by Sago Pondweed will experience the continuous uptake of edible particles as a true gain function as defined by optimal foraging theory, both within and between patches. We consider this species therefore as a suitable target to test predictions about foraging decisions concerning patch use.

In theory a forager possesses complete knowledge about the environment ("the omniscient forager") and it should behave according to the Marginal Value Theorem (MVT: Charnov 1976). All patches should be left at an equal quitting-harvesting rate, rich and poor patches being depleted to equal levels. *MVT Foragers* will spend more time in rich patches compared to poor, which results in a positive density dependent resource harvest. Four major strategies have been defined with respect to actual patch use by a forager (Valone & Brown 1989, Valone 1991). If not all but a considerable amount of patch quality information is available to the forager, the *Prescient Strategy* applies. By means of olfaction, visual or tactile cues, patch quality can partly be assessed other than by sampling alone. Unlike perfect MVT Foragers, the quitting-harvest rate may vary over different patches, but the other assumptions of MVT are met. At the other extreme, if no information about patch quality is present at all, foragers should spend equal time exploiting the different patches in order to optimise the long-term energy gain of the environment (Stewart-Oaten 1982, McNair 1983). Foragers behaving in this way are known to be employing a *Fixed Time Strategy*. In this case, the rich patches are underused compared to the poor, and there is no density dependent resource harvest. As in most natural situations the amount of information will lay between these extremes, two other strategies are imaginable. *Bayesian Foragers* would use a so called "prior distribution", a probability function of patch quality information based on earlier experience, which is constantly up-dated by more recent information while harvesting new patches. The estimator of patch quality, being the mean of the prior distribution, is thus constantly compared with actual information during patch harvest. As the decision to leave a patch is based on this patch estimator and not directly on the absolute quality of the patch under exploitation, rich patches will be underused compared to poor ones. Bayesian Foragers would perform a positive density dependent harvest. The fourth strategy supposes a forager instead to base its decisions purely on the actual information obtained during harvest of the local patch. This so-called *Rate Assessor Strategy* leads to the overuse of rich patches compared to poor, while also a positive density dependent harvest occurs. As pointed out by Valone & Brown (1989), from each of these strategies a unique set of results can be predicted, based on the relative use of rich compared to poor patches and the degree of positive density dependent resource harvest.

One of the issues not covered by foraging theory is the extent to which inter-annual food exploitation varies. Because of the scarcity of the *P. pectinatus* tubers at stopover sites along the flyway in combination with the strong preference by the birds, we might expect area specific, fixed threshold levels to exist each year. A physical constraint of extracting the tubers would, in combination with the specific nutritious demands by the swans in that period of the year, lead to such a pattern. On the other hand, fluctuating thresholds over the years are to be expected, if birds were adjusting their foraging behaviour to the energetic return of the annual stock on offer and in relation to the alternatives available. Then, applying foraging theory on a much wider scale, considering stopover sites as "super patches" along the flyway, GUD in a certain year and site might be variable and related to the average energy gain experienced.

By comparing exploitation patterns in two different lake systems with different soil conditions, we will test the hypothesis that the foraging cost, *i.e.* the cost of trampling a pit in the lake bottom, affects the lower threshold level. The water stream, induced by the paddling birds has to bring soil particles in suspension. Orbital velocity, *i.e.* that current at which resuspension starts, is related to particle size and cohesion (Blom *et al.* 1992). Also, water depth is likely to affect the maximal water stream the birds can achieve, thus resulting in a lower limit of food attainability.

This paper aims to describe long-term patch use by relatively long-lived avian herbivores (see Scott 1988), in a variable but not entirely unpredictable environment. We concentrate on the question of how different scale factors (ranging from a square foot up to a vegetation zone) and time factors (ranging from a foraging season to a series of years (1978-1992)) operate on the exploitation of the patch. We will show that the incorporation of these various scale and time factors into models of foraging theory is necessary in order to interpret the different decisions taken by these migratory herbivores utilising the same food source along a chain of stopover sites (Beekman *et al.* 1996).

(A,B) Sampling tubers of Pondweed *Potamogeton pectinatus*, Lauwersmeer, October 1984.

## Methods

### Study sites

The study was conducted on several freshwater lakes in the Netherlands, lake Lauwersmeer in the north and the so-called Borderlakes, a chain of 5 lakes created as a buffer between the mainland and the new polders of Flevoland (Fig. 1). In the latter region the most important for swans is lake Veluwemeer (52°25′N 5°45′E). Originally this area belonged to the brackish Zuyder Zee, but after the construction

**Figure 1.** Areas along the flyway of Bewick's Swans with important natural aquatic feeding habitat (black dots), most of which is *Potamogeton*. Open dots refer to stopover sites where aquatic feeding is less important. Inset shows lakes in the Netherlands where *Potamogeton* is of importance to Bewick's Swans. Of these, lake Lauwersmeer and lake Veluwemeer held up to 50% of the entire flyway population during several weeks in autumn in the 1980s.

of a barrier dam in 1932, the water became fresh within a few years as a result of the continuous inflow of river water. The embankment of the Eastern Flevopolder in 1957 was the second major change in the environment, which led to the separation of the border lakes from the main lake IJsselmeer. Lake Veluwemeer is 3200 ha, the average water depth is 1.4 m (*cf.* Berger 1984). The lake is very exposed to the prevailing south-westerly winds which give rise to a great turbidity (25-40 cm Secchi depth). In the 1980s, extremely low water transparency was recorded during the summer months (Secchi depths < 20 cm), due to blue green algae bloom *Oscillatoria agardhii*. The bottom is sandy except for the dredged channel (depth 4 m) in the centre of the lakes, which contains recently deposited clay (Berger 1987, Blom *et al.* 1994).

Already during the brackish period prior to 1932 the area was well known for the occurrence of *Potamogeton pectinatus* (Van Goor 1922). Thousands of Bewick's Swans were reported to feed there during autumn and winter (Brouwer & Tinbergen 1939, Poorter 1981, 1991). After the formation of the polder dikes, the water body became more quiet and as a result the total area covered by macrophytes increased to *c.* 1500 ha during the 1960s. Then, in 1970, a sudden decline to 450 ha was reported, probably due to the continuous eutrophication of the water by the effluent of local farms, after which the macrophytes collapsed and an almost persistent bloom of *Oscillatoria agardhii* became evident (Berger 1984, Scheffer *et al.* 1994). Recently carried out purification programmes have led to the recovery of part of the former macrophyte areas in the years after 1985. About 20% of the lake area (650 ha) is now covered with submerged vegetation. The other three lakes vary in size and somewhat in average depth and soil type, but the general appearance is much similar to that of lake Veluwemeer.

The closure of the estuary of the Lauwerszee in 1969 turned a tidal, saltwater area with gullies and exposed mudflats into a freshwater area (1970 ha) with regulated, fixed water tables (Fig. 1). Originating from the streams entering the lake, *Potamogeton* first colonised this area in 1972. The bottom of the lake margins is sandy in the northern part and consists of heavy loam in the south. Bewick's Swans first exploited lake Lauwersmeer (53°22′N 06°13′E) in 1973 (Prop & Van Eerden 1981).

The total area covered by Sago was 1100-2000 ha in these five lakes during the 1980s which represented at that time about 80% of the Netherlands' total as available to the swans (water depth < 65 cm). Table 1 summarises bathimetrical, geomorphological and botanical characteristics.

## Grazing losses and vegetation sampling

Vegetation cover of the entire lake was determined by aerial photographs taken mostly in July or early August when above ground biomass was at maximum. Due to the relationship between above ground

**Table 1.** Characteristics of the five *Potamogeton* lakes under study which were in use as foraging sites by Bewick's Swans during the 1980s. Data refer to Berger (1987), Beekman *et al.* (1991), Doef *et al.* (1994). Area covered by *Potamogeton* expressed as the 75 percentiles for the period 1980-1992. For water depth and soil type (top 25 cm) in Sago areas the 90 percentiles are given. Secchi and water depths refer to summer averages (April-September) for the entire lake. Water depth in winter is *c.* 0.2 m lower for the Borderlakes, for lake Lauwersmeer 0.1 m lower.

| Lake | Area (ha) | Depth (m) | Water depth Sago area (m) | Secchi (m) | Area with Sago (ha) | Soil type Sago area | Lutum content | Samples taken |
|---|---|---|---|---|---|---|---|---|
| Lauwersmeer | 1970 | 2.3 | 0.25-1.30 | 0.40 | 270-450 | Loam-clay | 5-30% | 1750 |
| Vossemeer | 275 | 1.0 | 0.25-0.80 | 0.30 | 0- 50 | Sandy-loam | 5-12% | 120 |
| Drontermeer | 600 | 1.2 | 0.25-1.10 | 0.30 | 150-275 | Sandy-loam | 5-12% | 120 |
| Veluwemeer | 3180 | 1.4 | 0.20-1.30 | 0.35 | 500-650 | Sandy-loam | 5-17% | 613 |
| Wolderwijd | 2550 | 1.7 | 0.30-1.50 | 0.30 | 200-580 | Sand | 3- 8% | 330 |

biomass in summer and tuber biomass in autumn (Van Wijk 1988) integral vegetation mapping of food stocks over larger areas, up to an entire lake, was possible.

Tubers were sampled before and after the swans visited the areas using core samplers with vacuum extraction of the sediment (6.4, 9.6, 14.6 and 15.1 cm diameter, 25 cm deep). Mud was washed over a 1 mm sieve in the field and tubers collected in plastic bags. Samples were taken on three levels, (1) concentrated in "patches" being *c.* 5 $m^2$ marked with a PVC stick or (2) placed in a regular grid, covering *c.* 5000 $m^2$ representing as much as possible one single vegetation class further called "area" and (3) samples in a transect perpendicular to the shoreline, across a vegetation zone to study patch exploitation relative to its immediate environment. Using vegetation cover of the entire lake that same summer, an estimate of food abundance at the highest level, called "site" was obtained.

Exclosures (1 $m^2$) were used to estimate losses not caused by grazing. Two types were used: a floating cone-shaped type sliding along a central pole which was useful in areas with changing water tables (Lauwersmeer) and a standing type consisting of four triangular pieces of concrete wire, put together to construct a stable pyramid (1.5 $m^2$), that was placed gently on the bottom (Borderlakes). The exclosures were located in areas of different vegetation density as shown by aerial photographs. Samples of 20 cm deep (sometimes sub-divided in depth classes) were taken and tubers were collected as described above.

All collected tubers were carefully rinsed with tap water in the laboratory again, after which they were dried for 48 hours at 70 °C. Densities are expressed as number or dry weight (DW) per $dm^2$. Tubers were weighed individually to the nearest 0.1 mg.

In total 2933 core samples were taken and 13 651 tubers measured.

### Swan grazing

Swans were counted bi-weekly during the period of autumn migration, over sub-areas within a lake. The counts allowed the calculation of "swan-days", which can be compared to the extension of the vegetation, mapped by aerial photographs.

Using buoys and islets as marking points, swan groups were mapped over Sago areas in lake Veluwemeer in 1987. Families (grey young) were counted separately, which enabled us to study the behaviour of socially different categories. To assess the dominance relationships between the different social groups, swans were watched while actively foraging. Continuous group scans were made to record agonistic interactions, mostly resulting in supplanting other swans at patches being under exploitation. The use that swans make of an area was further analysed by the reading of individually marked individuals (leg rings, neck-collars).

Body condition of wild swans was estimated in the field according to abdominal profile scores (see Bowler 1994) of swans resting ashore shortly after aquatic foraging had stopped. Fresh droppings from swans feeding on Sago tubers were collected from swans that rested ashore. Ash-free dry mass of droppings was assessed and digestibility of tubers was determined using ADF as marker (Prop & Vulink 1992). Analysis of the most important alternative feeds on agricultural fields such as grass and sugar beets allowed a comparison with Sago tubers as concerned chemical composition and digestibility.

### Analyses and statistics

Samples of the food and the droppings were prepared for analysis by oven-drying at 70 °C to constant weight. Droppings and food samples were finely ground (1 mm sieve). The chemical analyses comprised ash, Kjeldahl-nitrogen and cell wall components (neutral detergent fibre NDF and acid detergent fibre ADF: Van Soest & Wine 1967). Hemicellulose was obtained by the difference between NDF and ADF. Protein content was estimated as 6.25 × Kjeldahl-nitrogen. A constant fat content of 5% was assumed (Owen 1976, Thomas & Prevett 1982, Sedinger & Raveling 1984). Soluble carbohydrate content was calculated as 100%-fat%-protein%-NDF%. Additionally, droppings were analysed for non-precipitable nitrogen (Terpstra & De Hart 1974) to differentiate between nitrogen of urinary and faecal origin.

The digestibility of component *i* in the food was calculated using the following equation:

$$DC_i(\%) = \frac{(Cf_i-(Mf\,/\,Md) \times Cd_i)}{Cf_i} \times 100$$

where *Mf* and *Md* respectively are the percentages of the so called marker in the food and the droppings. $Cf_i$ and $Cd_i$ the percentages of component *i* in the food and the droppings, excluding the matter of urinary origin. ADF was used as a marker because cellulose digestion is unlikely to occur under winter circumstances (Prop & Vulink 1992). All analyses are presented on the basis of ash-free organic matter. Digestibility of fat was estimated at 30%, based on the digestibility of fat by geese (Lichtenbelt 1981, Buchsbaum *et al.* 1986).

The metabolisable energy of a food species ($ME$, kJ $g^{-1}$) was obtained by:

$$ME = \sum_{i=1\text{-}4} (Cf_i \times DC_i \times EC_i)$$

The energy value for food component *i* ($EC_i$) was taken from Schmidt-Nielsen (1975): fat 39.3 kJ $g^{-1}$, protein 17.8 kJ $g^{-1}$, structural and soluble carbohydrates 17.6 kJ $g^{-1}$.

The maximum food intake rates ($IR$, g $hr^{-1}$) on sugar beet, grass and Sago tubers were calculated using the formula:

$$IR = \frac{3600 \times DW \times (Md/Mf)}{DI}$$

where $DW$ = Dropping Dry Weight (g) and $DI$ = Dropping interval (s).

All data were analysed using SPSS 6.0 (Norušis 1993). Where necessary, arcsine or log transformation was applied to achieve normalised data.

One-tailed ANOVA procedures were used to test for differences in tuber stock prior to and after the swans' visit. To analyse the contribution of the different factors and co-variates to the final GUD as measured in the field, a MANOVA procedure was run.

## Results

### Tuber preference, food quality and general patch use

As shown by Beekman *et al.* (1991), Bewick's Swans show an absolute preference for Sago tubers upon arrival in the Netherlands in autumn. Swans grazing on tubers had the highest energetic return per gram of food ingested compared to the alternatives on agricultural land nearby. Moreover, the longer working day (and night) on tubers as compared to agricultural feeds further enlarges the difference (Table 2). Of the agricultural food crops, soluble carbohydrate content of sugarbeet is higher than grass. Grass contained a high level of protein, sugarbeet was low in protein, whereas the tubers had intermediate levels of protein. The digestibility of soluble carbohydrates of all three food types was high. The digestibility of protein was higher in grass and tubers, whereas the digestibility of hemicellulose was

**Table 2.** Chemical composition (% organic matter) and digestibility (%) of Sago tubers in comparison with the most important alternatives in agricultural fields. ME = Metabolisable Energy (kJ $g^{-1}$). On a daily basis $DME_{max}$ combines field estimates of foraging intake (throughput time of food) with observed number of foraging hours and energy gain per gramme of food ingested.

| | | CHEMICAL COMPOSITION | | | DIGESTIBILITY | | | ME | $DME_{max}$ |
|---|---|---|---|---|---|---|---|---|---|
| | ADF | Hemi cellulose | Protein | Soluble carbohydrates | Hemi cellulose | Protein | Soluble carbohydrates | | |
| Sago tuber | 6.7 | 36.5 | 14.8 | 36.9 | 85.6 | 39.7 | 100 | 13.6 | 11 300 |
| Sugarbeet | 5.5 | 5.6 | 6.6 | 77.4 | 6.5 | 75.5 | 94.7 | 14.4 | 7 200 |
| Grass | 16.2 | 31.8 | 33.4 | 13.7 | 55.9 | 41.9 | 100 | 8.6 | 2 700 |

higher in grass and tubers than in sugarbeet. Overall metabolisable energy of grass was considerably lower than that of tubers and sugarbeet. Tubers are different from other food sources as judged by the ratio of crude protein and soluble carbohydrates. This may be an extra factor why this food is preferred in favour of sugarbeet and potato root-crops.

Sago Pondweed is a perennial macrophyte which grows up to 1 m water depth in lake Lauwersmeer and the Borderlakes. After mid July (Borderlakes) or mid August (Lauwersmeer), above ground vegetation deteriorates quickly and only tubers remain. In order to reach the tubers, swans make paddling movements with their feet in shallow water, thus inducing a jet stream which flushes the substrate aside. Pits may cover 1 $m^2$ and be 25 cm deep. Each pit is usually exploited by the swan that excavated it, except when supplanted by dominant birds in aggressive interactions. Tubers are extracted from the soil upon touch by a sieving action of the bill. Before exploiting a patch, swans have no cue of its content. The water is turbid which does not allow visual inspection. Exploited patches are clearly noticeable, but only when birds put their head down under water. This remains the case after some weeks when soft, recently settled mud which has filled up the pit can be distinguished upon touch from the fixed non-exploited soil. Areas covered by Sago are exploited successively as the number of harvested patches increases. In rich areas almost the entire bottom became "plowed", in poor areas only scattered, often clumped groups of pits were found (Fig. 2). Detailed sampling directly in and around exploited pits, after the swans had gone, showed that the lowest tuber densities occurred in the pits, increasing towards the edges and just outside the pit (Fig. 2). Compared to the average of the environment before exploitation a tremendous decrease is visible. If compared to the average for the area (vegetation zone) the heavily exploited area showed no significant difference between the emptied patches and the average for the area. In the poor, partly exploited area tuber density within the pit was higher than the average of the environment. The higher densities at the edge and just outside the pit point to the fact that swans must have initially selected the better areas there.

### Tuber grazing and flock feeding behaviour

In 1987 a detailed mapping of swans over the Sago area in the northern part of lake Veluwemeer showed the typical pattern of use. The first 22 swans arrived in the area on 1 October 1987. Peak numbers were counted late October, the maximum number being 877 on 28 October 1987. In early November, numbers fell considerably and after 13 November only a few swans were present, the rest had spread out over the surrounding polders or had migrated to southern England. Swans visited the tuber banks in a systematic order and the first swans to arrive were already foraging at the zone with the highest tuber density. During late October a number of coherent flocks slowly moved across the area and they were first seen foraging on parts with a lower density between 23 and 28 October 1987. On 1

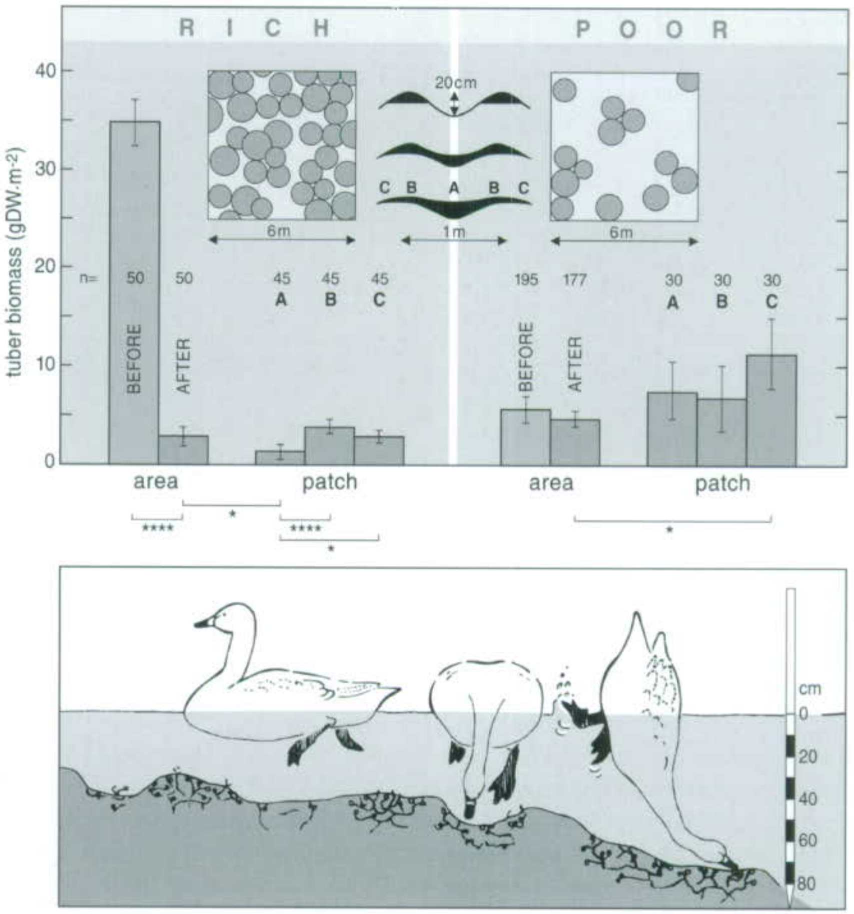


**Figure 2.** Schematic representation of patch occurrence and exploitation by Bewick's Swans (down). The lake bottom is set aside by a jet stream caused by foot trampling (central). The soft, whirled-up mud quickly settles in the pits (shaded dark) which may act as a cue for swans to detect already exploited patches. Detailed sampling in the centre, on the edge and just outside the trampled pits after the swans had left, show that in poor environments swans are able to select the better patches.
* $P < 0.05$, *** $P < 0.0001$.

November a new influx of swans occurred which visited the dense stands, like the first wave of exploitation. From 10 November on, smaller flocks exploited only the margins of the Sago zone, spending most time in areas with either a low or a high variable tuber density (Fig. 3). The few weeks of extensive tuber foraging resulted in the removal of the greater part of the tuber standing crop (see Fig. 4, where the result from the 16 patches has been summarised). Tuber biomass and tuber numbers had been depleted down to 14.1% and 21.6% respectively of values prior to the grazing period. The final level of a certain patch did not correlate with the initial biomass, in this case all patches were being grazed down to about 1.8 gDW $m^{-2}$ or 69 tubers $m^{-2}$. The swans thus exerted a density dependent grazing pressure on the different patches, richer ones losing more tubers than the poor patches. From the lower panel in Figure 4 it can be seen that also the proportion of empty cores increased after grazing. This means that the swans had the ability to remove all tubers in part of the soil. The proportion of

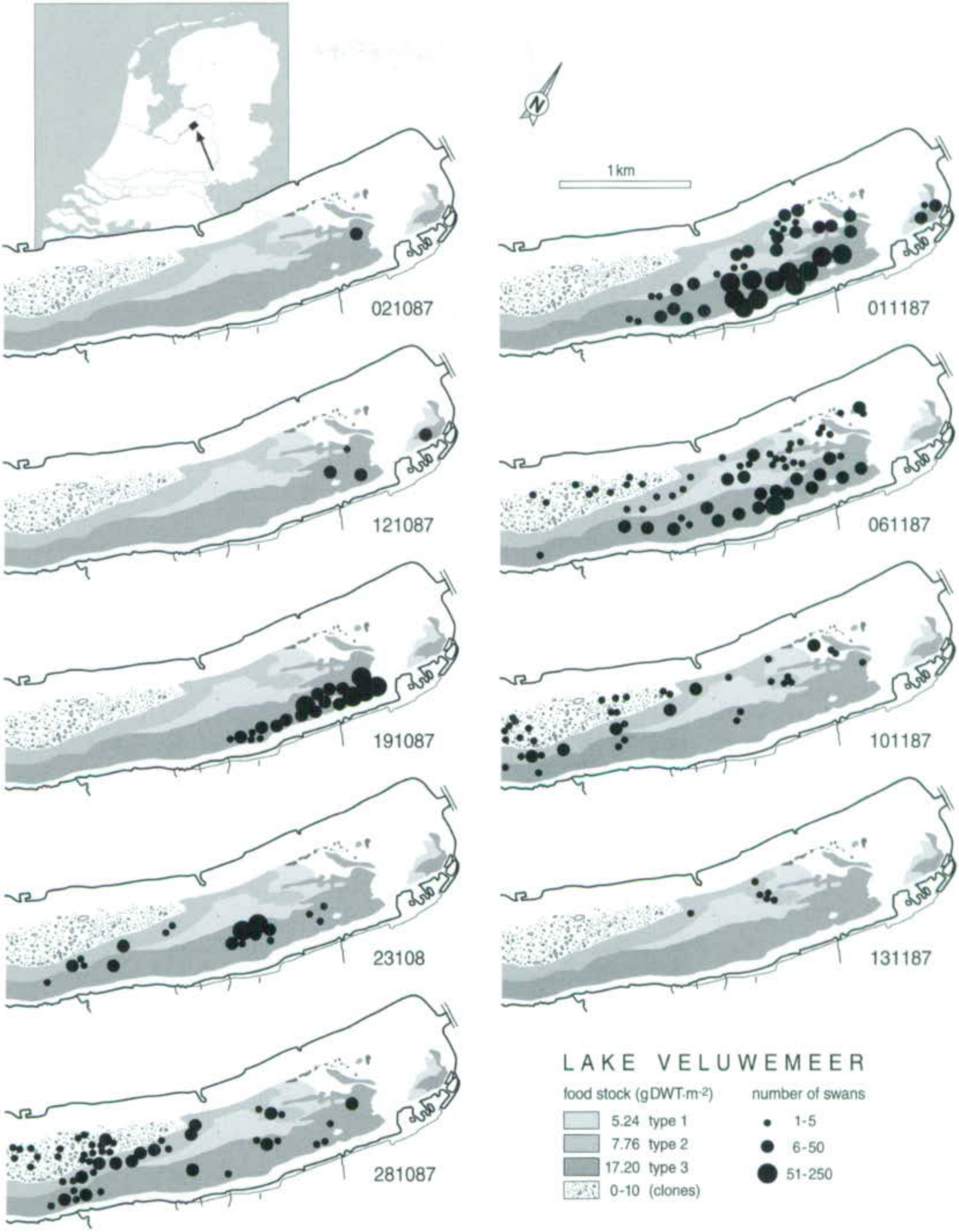


**Figure 3.** Sequential series of maps showing utilisation of tuber-banks in the northern part of lake Veluwemeer in 1987. Note the concentration of flocks in the most densely vegetated parts as well as the exploitation of below-ground parts in two waves. Tuber densities were mapped on this level by means of aerial photographs of peak above ground leaf biomass in July, which are correlated.

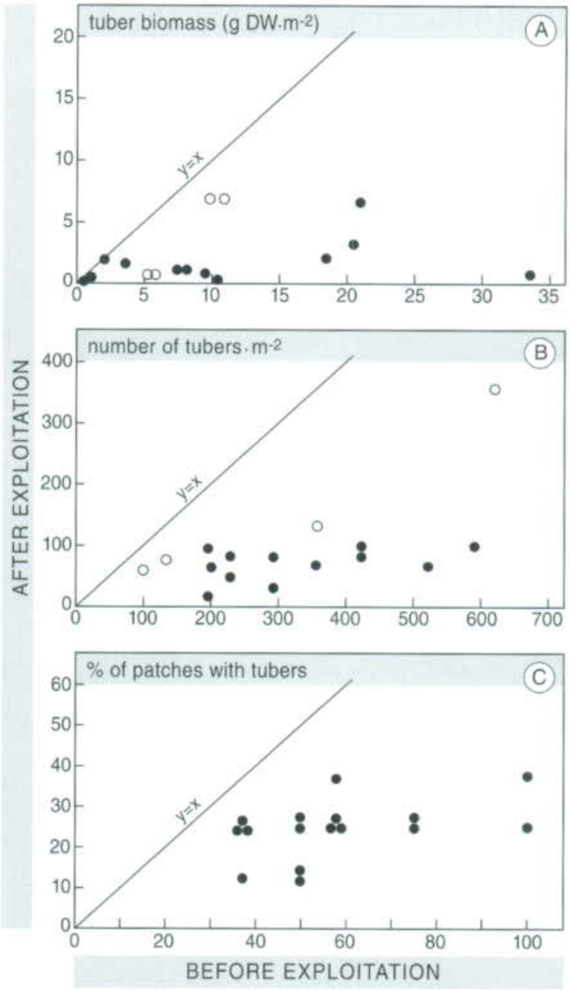


**Figure 4.** Typical example of the relationship between abundance of tubers in patches prior to and after swan grazing in lake Veluwemeer in 1987. (A) based on mass, (B) on numbers and (C) on proportion of empty cores. Open dots refer to patches with more than 500 g marine shell deposits per m$^2$ which hamper tuber extraction.

empty cores did not vary with initial tuber density, however ($\chi^2 = 0.0575$, df = 2, $P = 0.98$).

Some patches ended up at a relatively high tuber level after grazing. These were characterised by marine shell deposits in the upper layer of the lake bottom (Fig. 4). Apparently the attainability of tubers becomes less as the contrast *vis à vis* other items decreases. This supports the view that the patches are being exploited upon touch.

## Body condition

Body condition of arriving swans was variable but generally increased during the period of use of Sago Pondweed (Fig. 5). Only for the years 1984-1986 no significant increase existed. From 1989 on swans were in better condition than in the years before ($F_{1,56} = 36.51$, $P < 0.0001$). Applying multiple

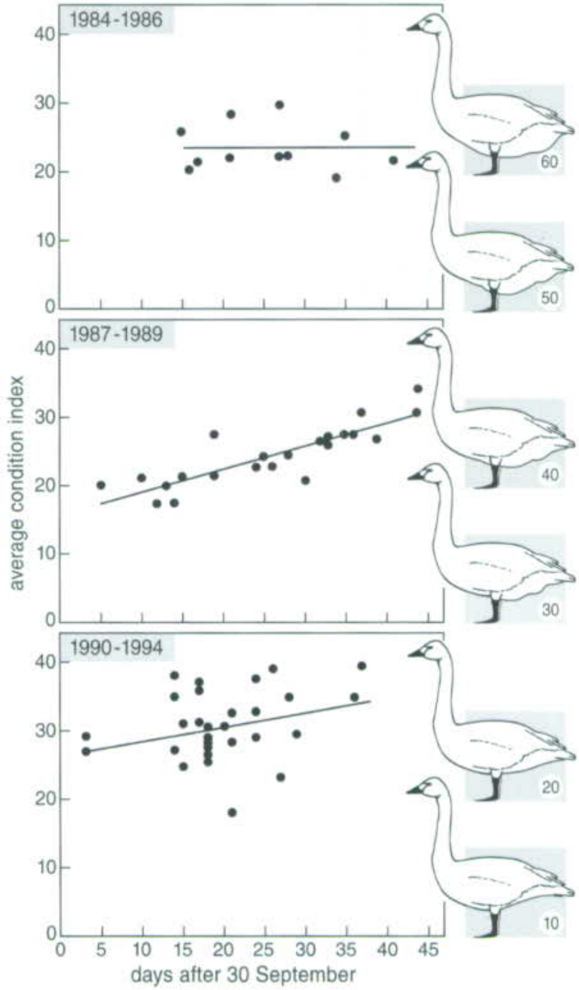


**Figure 5.** Body condition indices in the early autumn, shortly after arrival in the Netherlands. Data for individual swans as recorded by abdominal profiles while in standing position shown separately as group means for three distinct periods of years. Corrected for date, in the period after 1989 the swans were significantly heavier than in the periods before (see text).

regression analysis on the pooled data revealed that day number after 1 October ($P < 0.01$) and year ($P < 0.0001$) both had a significant effect, although the explained variance was rather low (adjusted $R^2 = 0.25$, $F = 11.56$, df = 62, $P < 0.0001$).

### Social status and patch use

As the areas are being successively exploited, more and more pits appear. Swans occur as singles or paired to a partner, and a successful family may consist of 2-4 (1-6) young. As in other monogamous *Anatidae*, families are dominant over paired swans without young, success rate at agonistic encounters being correlated to family size (Fig. 6) whereas single swans rank lowest in the hierarchy as in geese (White-fronted Geese: Boyd 1953, Canada Geese: Raveling 1970, Bar-headed Geese: Lamprecht

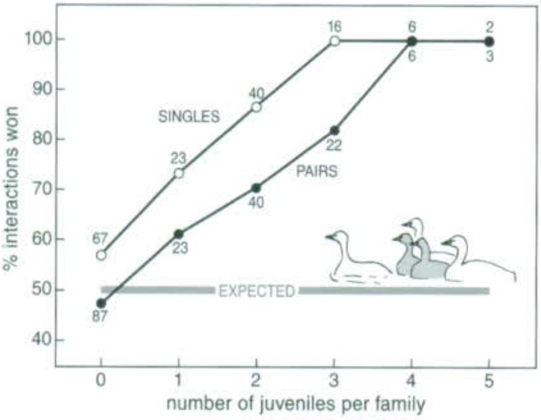


**Figure 6.** Social dominance determined by family size as recorded by interactions during patch exploitation. An interaction won was defined as successful supplanting of opponents. Interactions between families were scarce (see text).

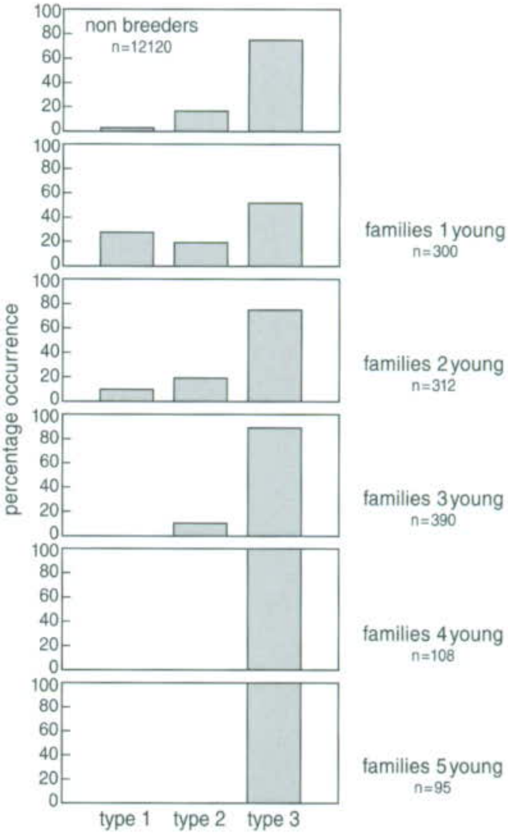


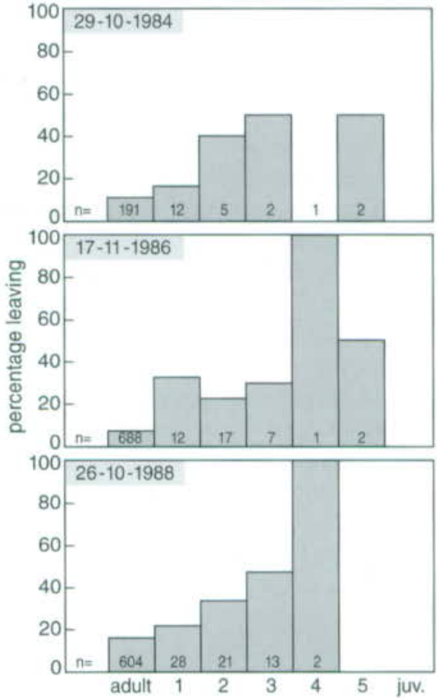
**Figure 7.** Distribution of different social units in relation to the density of the tuber bank in lake Veluwemeer, 1987. Larger families occupied only the best areas (see Fig. 3). →

1986). Families in Bewick's Swans always arrived later than singles and non-breeders (J.H. Beekman & M.R. Van Eerden unpubl.). Compared to swans without young, families were observed to forage almost exclusively in the richer parts of the Sago areas, a tendency which also held among families which, according to the number of young, selected areas with the greatest food density as measured in lake Veluwemeer in 1987 ($\chi^2 = 462.5$, df = 10, $P < 0.0001$). Families of 4 and 5 young were thus observed foraging only in the areas of highest tuber density (Fig. 7). During the course of the exploitation of the Sago tuber stocks, families gave up earlier than unsuccessful pairs and singles (Fig. 8). Correspondingly, within families the number of young per family determined the time of shift, larger families leaving earlier, as was recorded by direct observation at the time of shift during three seasons in lake Lauwersmeer ($\chi^2 = 73.6$, df = 25, $P < 0.0001$). We therefore conclude that the size of the social unit determines the lower threshold level of exploitable tuber density, larger families being more susceptible to depletion effects, albeit their dominant position within the flock.

## Size selection and tuber quality

Tuber size on offer has a clear negatively skewed distribution (Fig. 9). In plots which were strongly grazed by swans, average individual tuber mass on offer was 30.4 mgDW against 23.0 mgDW in slightly grazed plots, which is highly significant ($F_{1,8035} = 75.7$, $P < 0.0001$). After the swans had left, this dropped to 26.2 mgDW for patches with a significant reduction in overall tuber biomass ($F_{1,7629} =$

**Figure 8.** Relationship between social status and giving-up level of exploitation of Sago tubers. For three different seasons the composition of family size of swans leaving lake Lauwersmeer at dusk was compared with counts of the entire population present at the lake earlier that same day. Larger families leave earlier than smaller families and swans without young, indicating that different lower threshold levels operate for individuals belonging to smaller social units.



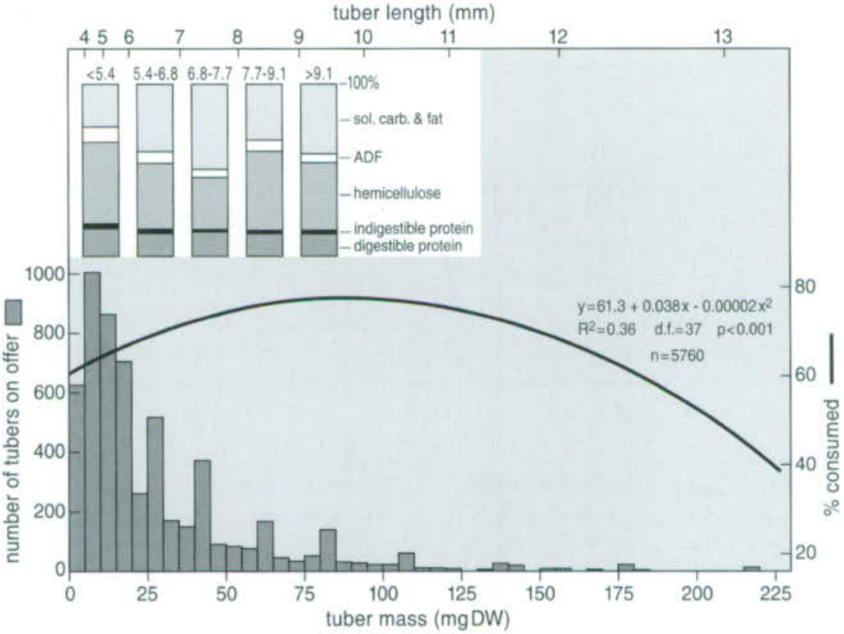


**Figure 9.** Selection of tuber size by Bewick's Swans in all cases where a significant amount of grazing occurred. The frequency distribution of tuber mass (mgDW) on offer is shown together with the proportionate loss due to grazing. Inset shows chemical composition of tubers, based on organic matter, in relation to size, suggesting a slightly better digestibility of larger tubers.

19.9, $P < 0.0001$) and remained constant at 22.7 mgDW ($F_{1,3923} = 0.10$, $P = 0.75$) in patches where no significant grazing could be detected. Although all size classes were consumed, the birds proved to have an overall preference for the larger tubers (Fig. 9: the proportion of tubers eaten is highest at intermediate levels of tuber size). Of all tubers of 50-150 mgDW *c.* 75% has been eaten, decreasing to *c.* 60 % towards the lowest and less than 20% at the highest end of the size range. Within the range of 1-100 mgDW, which comprises 95% of all tubers measured, a significant positive relationship was found between tuber size and (arcsine transformed) proportion consumed (adjusted $R^2 = 0.31$, $F_{1,18} = 9.71$, $P = 0.006$).

Soluble carbohydrate content increased with tuber size and was highest at tuber lengths slightly over 7 mm, tending to decrease somewhat at greater lengths (Fig. 9). Hemicellulose content showed the reverse pattern. Protein contents did not vary with tuber size. By selection of larger tubers the swans thus slightly improved the digestibility of the food.

Comparing sites where swans had removed a significant part of tuber biomass, average tuber size increased with water depth (Table 3), both before and after grazing had occurred. In slightly grazed plots this correlation existed only before the swans arrived. As larger tubers also tend to occur deeper in the substrate (Beekman *et al.* 1991), this suggests that the depth of the trampling pits may limit the level of depletion of the largest size classes. As shown in Table 3 by the ratio of average tuber size before and after grazing, this selection for larger tubers in deeper water indeed was less. However, also in water not deeper than 25 cm on average, fewer large tubers were taken. The swans here took, in fact, preferentially smaller tubers, as the average tuber mass increased after the swans had left. This may also be explained by the limited possibility to trample deeper pits when water depth is less than 25 cm. In areas where no significant reduction in overall tuber biomass occurred, a similar, water depth dependent tuber distribution was found. However, the selection for larger tubers occurred only at lesser depths (Table 3).

To conclude, Bewick's Swans feed on the entire range of tuber sizes available, but tend to remove preferentially the larger tubers. From the swans' point of view, water depths between 25 and 55 cm seem optimal in order to trample pits deep enough to reach the largest tubers.

**Table 3.** Size selection of Sago tubers by Bewick's Swans in relation to water depth and grazing pressure. Size of individual tubers expressed as dry mass, mg ± standard error. In heavily grazed areas tuber size increased with water depth both before and after grazing. $P$ values indicate level of significance for tuber DW before and after swan visit. In case of a significant change in average tuber size, the ratio of average tuber size after and before grazing was calculated to indicate the degree of selection. Spearman $r_s$ correlates individual tuber DW with water depth.

| | Slightly and ungrazed plots | | | | | | Heavily grazed plots | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Water | Before (B) | | After (A) | | | Ratio | Before (B) | | After (A) | | | Ratio |
| depth (cm) | mean | SE | mean | SE | $P$ | (A/B) | mean | SE | mean | SE | $P$ | (A/B) |
| < 25 | 31.23 | 7.88 | 20.69 | 5.95 | 0.44 | - | 12.25 | 0.84 | 20.29 | 2.49 | 0.0001 | 1.66 |
| 26-35 | 23.97 | 1.10 | 25.32 | 1.42 | 0.45 | - | 24.79 | 0.81 | 21.74 | 1.26 | 0.06 | 0.88 |
| 36-45 | 17.90 | 0.71 | 19.56 | 0.85 | 0.13 | - | 33.82 | 1.03 | 25.17 | 1.31 | <.0001 | 0.74 |
| 46-55 | 31.50 | 1.69 | 26.49 | 1.40 | 0.02 | 0.84 | 39.02 | 1.56 | 28.11 | 2.50 | 0.004 | 0.72 |
| >56 | 31.22 | 2.38 | 20.19 | 1.64 | 0.0005 | 0.65 | 38.05 | 1.27 | 35.79 | 2.11 | 0.34 | - |
| Spearman $r_s$ | 0.11 | | 0.03 | | | | 0.25 | | 0.20 | | | |
| $P$ | <.001 | | 0.15 | | | | <.001 | | <.001 | | | |
| $N$ | 2190 | | 1735 | | | | 4963 | | 1537 | | | |

### Variation in lower threshold levels and foraging strategy

The effect of environmental quality on patch exploitation was examined in transects across vegetation zones, sampling adjacent patches by means of a continuous row of cores. Four transects in lake Lauwersmeer in 1984 were selected and as shown in Figure 10, huge differences exist in average density as well as in spatial variation in density between patches. In "Babbelaar 1" a dense tuber stock existed with concentrations in two discrete "super-patches". The swans depleted this area in such a way that two patches of relatively high tuber density remained, but their position shifted away from the original peaks. Also "Oude Robbengat 1 and 2" showed this pattern of shift of relative peaks in tuber density. Dead shells (*Cerastoderma edule,* remainders of the former tidal area) occurred in ridges at a certain distance from the shore, and partly caused these peaks in the "after" distribution. A plot of individual estimates of tuber density before and after the swans' grazing against each other shows the relative use of patches in relation to their environment. In a rich environment, rich patches were underused compared to the poorer patches nearby. When environmental quality decreases, as in "Oude Robbengat 1", all patches were used to an equal GUD, due mainly to an underuse of the poor patches. In an even poorer environment the relationship becomes negative. In this case a relative overuse was made of the "rich" patches compared to the poor in this area. Bewick' Swans thus behaved as *Bayesian Foragers* in rich environments but became *Rate Assessors* in poor environments. Note that the coefficient of determination ($R^2$) describing these relationships was highest in "Oude Robbengat 1" the area with the lowest variance in amount of food originally on offer (Fig. 10).

In 1984 a field experiment was undertaken to enrich the food supply on offer. Extra food (tuber-sized beans, *Phaseola*, 90-100 gDW m$^{-2}$, average seed mass 0.204 gDW) was offered in four Sago areas with a different background density of tubers. Sampling of tubers across a stretch of enriched patches showed no statistical difference in lower threshold level, although all three enriched stretches in a rich environment tended to have a higher GUD as compared to the surrounding areas. This is in line with the Bayesian Strategy described earlier for rich environments (Table 4). In the poor environment, the GUD's tended to be lower, both for beans and tubers suggesting again a Rate Assessor

**Table 4.** Effect of experimentally enriched patches on threshold level of Sago tubers in gDW m$^{-2}$ in lake Lauwersmeer in 1984. Extra food was offered as Beans *Phaseola*. $P$ values (two tailed $t$-test) indicate differences between tuber densities before and after visit by swans (B/A) and densities left over between treated and untreated plots in the same vegetation zone (A/A). $C_v$ = Coefficient of variation of tuber density.

| | BEFORE EXPLOITATION | | | | AFTER EXPLOITATION | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| Plot | beans (g m$^{-2}$) | tubers (g m$^{-2}$) | SD | $C_v$ | beans (g m$^{-2}$) | tubers (g m$^{-2}$) | SD | $C_v$ | $P$ B/A | $P$ A/A |
| Oude Robbengat | | | | | | | | | | |
| I enriched | 96.0 | 20.09 | 16.27 | 80.99 | 4.40 | 8.80 | 0.33 | 3.75 | 0.00003 | 0.0681 |
| I control | | | | | | 5.08 | 5.62 | 110.63 | 0.00021 | |
| II enriched | 96.0 | 16.24 | 13.34 | 82.14 | 6.01 | 7.89 | 0.29 | 3.68 | 0.0005 | 0.4641 |
| II control | | | | | | 5.36 | 8.07 | 150.56 | 0.00008 | |
| Babbelaar | | | | | | | | | | |
| I enriched | 96.0 | 26.24 | 21.91 | 83.49 | 5.21 | 7.07 | 0.46 | 6.51 | 0.0001 | 0.1841 |
| I control | | | | | | 4.35 | 6.05 | 139.08 | 0.00006 | |
| II enriched | 96.0 | 8.64 | 10.45 | 120.95 | 1.05 | 2.18 | 1.33 | 61.01 | 0.0005 | 0.1515 |
| II control | | | | | | 2.31 | 4.22 | 182.68 | 0.0075 | |

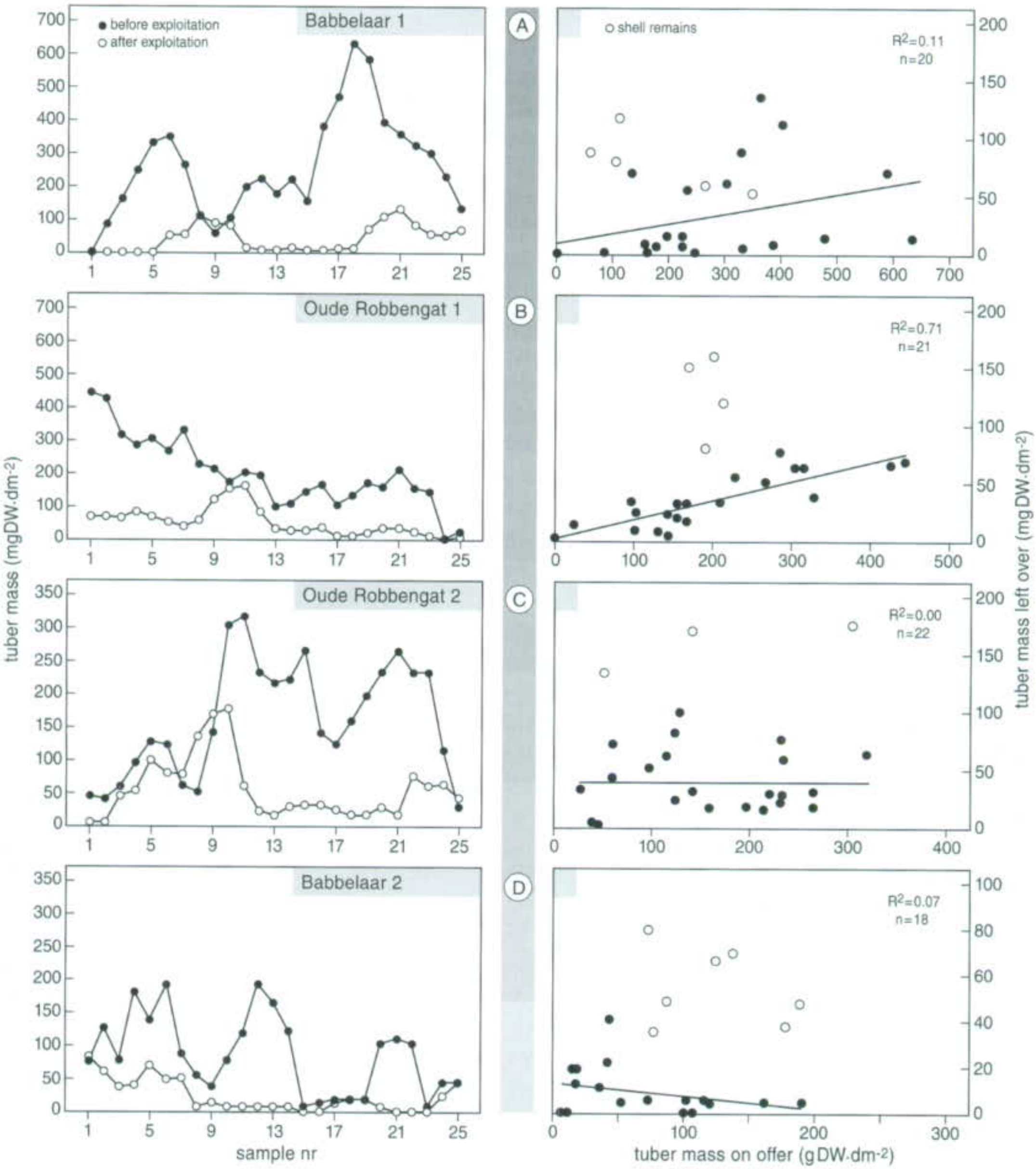


**Figure 10.** Patch depletion in relation to environmental quality. For four transects in lake Lauwersmeer in 1984 the three points running mean of tuber biomass (gDW m$^{-2}$) has been calculated before and after the period of visit by Bewick's Swans. The transects have been arranged from rich (top) to poor (bottom). The richer patches were underused and poor patches overused in a rich environment (A,B) suggesting a *Bayesian Foraging Strategy*. As food density decreased no relationship existed (C) turning into negative relationship as average food density further declined (D) indicating a switch to a *Rate Assessor Strategy*. In all cases a positive density dependent food harvest existed. Patches where tuber extraction was hampered because of dead shells are indicated and were left out in the regression analyses.

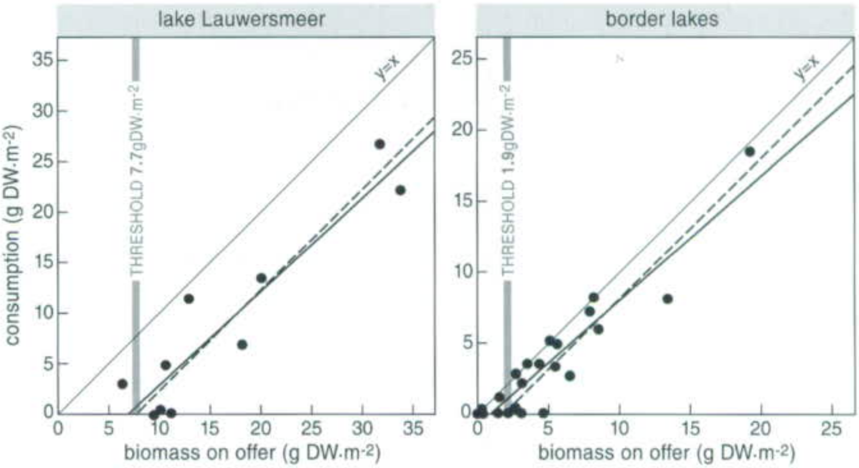


**Figure 11.** Relationships between calculated food stock per patch and consumption by swans for lake Lauwersmeer and the Borderlakes in 1992. The different threshold levels are related to different soil characteristics, the sandier bottoms in the Borderlakes allowing extraction at probably lower costs. Slopes of fitted regression lines (straight lines) do not deviate signification from 1.

Strategy. For beans and tubers the swans made a positive density dependent harvest of the food stock on offer. Interestingly, the swans had searched the bottom under the enriched areas more intensively for tubers as judged by the marked decline in the coefficient of variation, $C_v$ in GUD, compared to the initial situation in all four cases (Table 4).

### Physical and ecological thresholds: a multivariate model

Figure 11A, B shows, on the level of individual patches, the linear regression of food consumed on food density for two areas. The Borderlakes and lake Lauwersmeer had a different threshold level, 1.9 and 7.7 gDW $m^{-2}$ respectively. The slopes of the regression lines did not significantly differ from $y = x$, however. Although less prominent before 1990 (see below), this difference was also recorded in other years and corresponded to differences in soil type of the bottom between the two areas (Table 1). The more sandy bottom of the Borderlakes facilitated pit excavating and tuber extraction as compared to the more loamy soils of lake Lauwersmeer, suggesting that GUD (and probably quitting harvest rate) was determined relative to the cost of digging a pit and/or the efficacy of sieving the tubers from the substrate. Consistent with foraging theory, at higher foraging costs the gain curve experienced by the swans was expected to be lower and GUD accordingly higher.

After depleting the Sago food stock, Bewick's Swans leave the area in search for other stopover sites with Sago, or switch to agricultural leftovers such as sugarbeet, potato, stubble or grass. At this time the swans still roost at certain spots on the lake. Sampling one of the main roosts in 1992 showed a significant further reduction of tuber biomass compared to the sites where no swans spent the night (Table 5). This supplementary feeding clearly suggests the existence of two threshold levels: first, an ecologically determined level related to the swans' average intake rate at times of complete dependence upon tubers (8 g $m^{-2}$) and second, the physical lower limit by mechanical constraints (1.6 g $m^{-2}$) setting the lower limit to the detection of tubers from the substrate by the sieving action of the bill or the birds' ability to dig out the perfect pit and collecting all food items. The lowest GUD determined for a roost

**Table 5.** Effect of prolonged feeding of Bewick's Swans at a night roost (JD1) on lower threshold levels compared with two normal plots (OR4 and RL1), (gDW $m^{-2}$) in lake Lauwersmeer in 1992 after the moment at which the swans have shifted to agricultural feeds (threshold 1), $N = 50$ per sample. *t*-tests indicate differences between successive sampling of the same station: *** $P < 0.001$.

| Plot | Initially on offer | | Threshold 1 27 October | | | Threshold 2 5 December | | |
|---|---|---|---|---|---|---|---|---|
| | Mean | SD | Mean | SD | *P* | Mean | SD | *P* |
| JD1 | 113.40 | 116.86 | 5.54 | 7.97 | *** | 1.63 | 2.30 | *** |
| OR4 | 32.69 | 23.69 | 5.55 | 9.20 | *** | 4.70 | 11.33 | NS |
| RL1 | 34.97 | 24.88 | 12.47 | 16.08 | *** | 10.75 | 14.52 | NS |

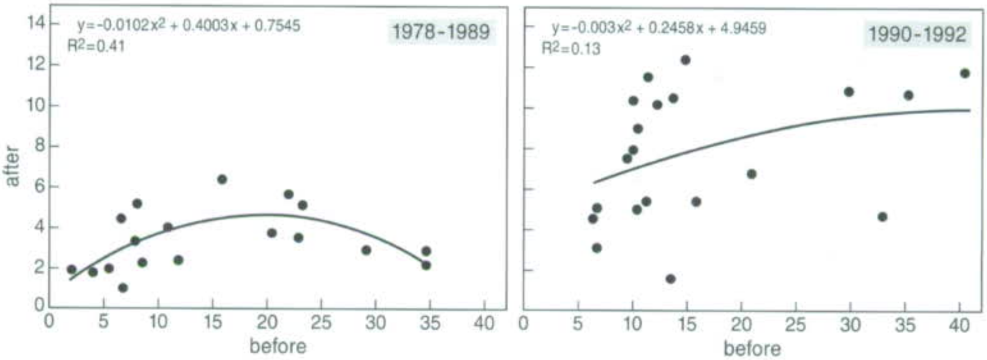


**Figure 12.** Year effect on lower threshold levels of tuber biomass observed in areas of different food density. Prior to 1990 the swans depleted tuber banks further down than afterwards, irrespective of initial tuber mass on offer.

site in lake Lauwersmeer corresponded closely to the average of 1.8 (1987) and 1.7 (1992) gDW $m^{-2}$ in the Borderlakes.

How repeatable are the consumption patterns over the years? Data about initial food density and subsequent patch use by swans was pooled over five lakes and ten different years. Inter-annual changes in consumption existed, before and after 1989. From 1990 onwards the Bewick's Swans took a smaller proportion of the biomass available than in the years before (Fig. 12). At the lower end of the biomass range this reduction in consumption level amounts to a factor three compared to the period before 1990.

MANOVA analysis of the entire data set of 219 cases of lower threshold level showed significant effects of initial tuber mass ($F = 52.7$, $P < 0.001$) and year ($F = 2.61$, $P = 0.012$). No significant effect was found for water depth, soil type and area on this level, nor was there any significant effect of interaction between the variables under consideration. The model explained 48.9% of the overall variation (adjusted $R^2$).

## Discussion

### Foraging strategy and threshold levels

The trampled pit in which the swans search by the sieving action of the bill for tubers is considered the smallest scale at which the birds operate. In terms of optimal foraging theory, the individual behaviour of a bird is determined by the quality of its environment. At the experimental sites where additional food was supplied, no difference could be detected in GUD in comparison with the surrounding, untreated patches. The amount of beans, which represented four times as much food compared to the average for the rich area and more than ten times that of the poor area, was used intensively in all areas, indicating a strong positive density dependent utilisation response. The conclusion from these experiments is that the final lower threshold of tubers was not markedly influenced by the local superabundance of food but still was determined relative to its immediate (tuber) environment. Why did swans start exploiting patches by digging pits after they had discovered so much easily attainable food? We found that the process of equalising variation in patch density had been more effective in the enriched areas. This means that the swans might use the cue of the presence of food in the top few centimeters as an estimator for patch quality. The top few centimeters can be probed by the bill without any trampling movements of the feet. As they were fooled by the super densities in the top layers only, swans must have started digging many patches, stopping shortly thereafter as the expected gain function of food intake was not met with increasing depth. However, in accordance with the results obtained when comparing natural patches, swans tended to leave fewer beans and tubers in the area with a poor tuber stock, indicating a Rate Assessor Strategy which was maintained under the conditions of a rich food supply.

Looking at natural tuber densities, we observed depletion patterns which showed a clear relationship with the patch environment (Fig. 10). Bewick's Swans were Bayesian Foragers in rich environments and became Rate Assessors in poor environments. These results are in line with a field study of patch use patterns by flock-feeding Common Cranes *Grus grus* (Alonso *et al.* 1995). These authors measured intake rate and found that cranes switched foraging strategy from being Bayesian in high quality habitats (mainly cereal fields) to Rate Assessor in poor quality habitats. The switch coincided with a drop in average intake rate below that required for existence metabolic rate. Although we were not able to measure patch residence time and intake rate directly, in concentrating at variation in GUD over areas of different quality, our conclusions about foraging strategy parallel those of the crane study.

With respect to the lower threshold of food density, we concluded that, in fact, three levels exist: (1) to start trampling and digging a pit, (2) to exploit all available tubers from the sediment during the phase of full Sago dependence, and (3) idem but then as additional food only during periods of stay at the night roost. Foraging costs (trampling the pit) were reflected in lower threshold levels in the sandy Borderlakes compared to the loamier lake Lauwersmeer. A similar reasoning exists for water depth; at greater depth GUD was higher and selection (read attainability) of larger tubers was less. Clearly, future work should focus on quantifying the cost factors of tuber exploitation (pit digging and substrate filtering).

How swans detect the food density of a patch remains obscure. Some probing with the bill might detect initial information about patch quality but much is uncertain. In very general terms, swans possess pre-harvest information (Valone & Giraldeau 1993) because of knowledge of the topography of the stopover site from previous years, but this information is insufficient for decision making on the level of the individual patch.

### Public information and flock behaviour affecting patch quality assessment?

We showed that flock behaviour was an important aspect of the individual harvest of patches. This means that our findings about patch exploitation are not necessarily the consequence of individual decisions only. Multi-visits to sub-areas and pits (but not to patches) are probably common, both within an exploitation wave as between them. The entire vegetation zone, consisting of thousands of patches, thus is used by hundreds of birds. The flock habit will be of help to the newly arriving individual to tune into the right spot of exploitation at that moment. Communal sampling of part of a vegetation belt minimises the chance that patches will be overlooked. On the other hand the flock movement will dictate its speed to each individual. The Bayesian Foraging Strategy that Bewick's Swans used in rich environments probably was derived by the trade-off between staying in the flock or moving to another area alone. Swans present in poorer sub-areas thus would continue to exploit patches as their flock mates in the richer sub-area determine patch residence time. Overuse of relatively poor patches can thus be a direct consequence of the prevalence to stay in the flock and sacrifice the individual gain function (Fig. 11A, B). Also the other way round, rich patches may be underused by the flock's movement at the same time. There is evidence that especially in high variance environments the patch equalising ability of the flock is less than could be expected from patch quality alone (compare Fig. 10A, C with 10B).

As pointed out by Clark and Mangel (1984, 1986) and Valone (1989), group foragers might benefit from public information available to all flock members. If patch information is equally shared among all birds, less successful foragers will quit patches at the same time as successful ones (Valone & Giraldeau 1993). The habit to exploit patches in discrete flocks while foraging across vegetation belts (see Fig. 3) might be caused by public, rather than personal information about patch quality. Our data about the use that different social units make of the area are illustrative in this context. We showed that large families occupied the better areas and were dominant over smaller families and swans not accompanied by young. Yet they leave the site earlier than the smaller social units (Figs. 6, 7 & 8). Because of the inexperienced young it is not unlikely that families and especially larger families are less successful on average when exploiting Sago tubers. The fact that they left the site first does not support the prediction made by the public information hypothesis. Apparently, patch-sample and probably to some extent also pre-harvest information are pooled among family members which may decide autonomously to leave the flock (and the site). The other possibility, that families with young would have other nutritious needs and therefore would be likely to shift earlier to other foods cannot be ruled out completely. The fact, however, that at times of abundant stocks of Sago at the 1960s, Bewick's Swans wintered entirely on tubers proves that this resource on its own is well able to sustain the birds' needs in different periods of the year (Poorter 1991). Summing up, there is only indirect evidence that public information could play a role in the patch use pattern within a site. As we see it, public information could play a role during the phase of exploitation when average intake rate is above maintenance requirements, *i.e.* when swans are Bayesian Foragers. However, the decision to leave a site is probably governed by individually collected information about patch quality and average daily food intake, which may be pooled up to the level of a family. Having become Rate Assessors, while more and more birds switch feeding site and leave the area, the remaining swans will again be put under the pressure to either continue foraging in a depleted environment or join the other flock members and switch as well.

## Interannual differences in patch depletion: the time window - body condition hypothesis

One of the unexpected findings of this long-term study is the difference in the annual depletion level that was recorded. Given its preferred status and limited occurrence along the flyway, Sago tubers could be expected to become depleted each year to roughly the same level. However, after 1989 more tubers were left in exploited patches and more patches remained unexploited than in the years before (Fig. 12). Two explanations are likely candidates for this phenomenon. First, the alternatives for Sago in the Netherlands could have improved after 1989. This would make the birds shift earlier to these resources according to the Marginal Value Theorem (Charnov 1976, Stephens & Krebs, 1986). There are no records to support this, all agricultural crop left-overs remained constantly on offer and no large shifts in the management of the cultivated crops occurred since that year (see also Van Eerden *et al.*

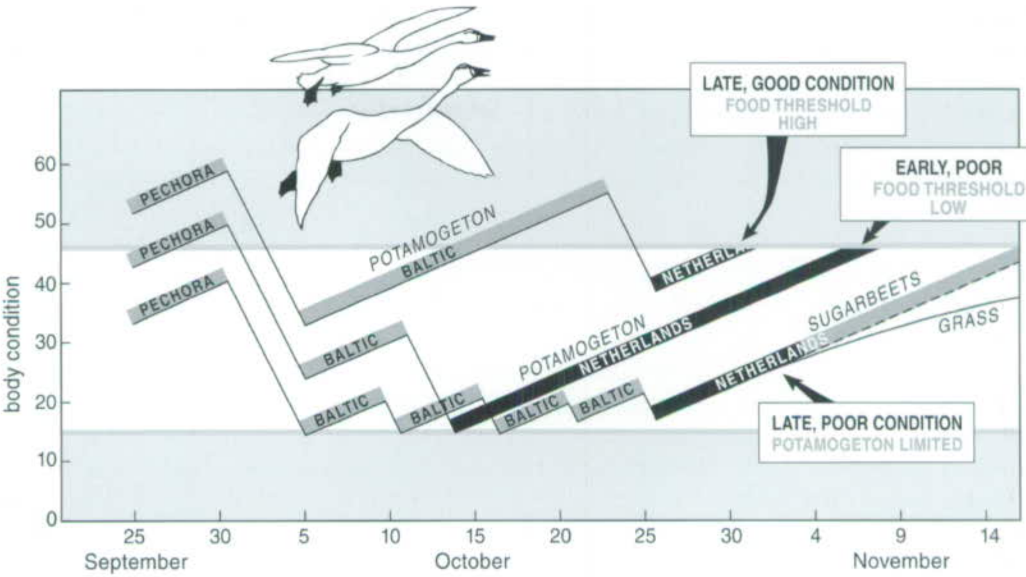


**Figure 13.** Hypothetical time window for tuber exploitation related to body condition of Bewick's Swans (see Bowler 1994 for general methods of field estimation). This model emphasises the role of Sago tubers especially as refuelling food and shows tuber exploitation on different sites along the migratory route (for details see Beekman *et al.* 1991, 1995). Not arrival time, but body condition would set depletion levels of tuber banks to different levels, thus depending upon amount of food on offer at the sites used earlier *en route*. By aiming at reaching a pre-winter peak body condition by the first half of November, as recorded by abdominal profiles recorded in the field, the swans would exploit a given tuber bank to different levels.

1996). Second, the food situation further upstream the postbreeding flyway could have improved, which would result equally well in an underuse of the food stocks in the Netherlands. As the swans that feed on Sago tubers in the Netherlands are presumed to have been feeding on the same food all the time at stopover sites during autumn migration (Beekman *et al.* 1991, 1996), we suggest that the tuber stocks at more eastern sites could have increased. A possible relationship with the political changes that have occurred since 1989 in this part of the world and which, through a decrease in the use of artificial fertilisers and other measures leading to an improved water quality where Sago would have re-colonised, needs further study. This hypothesis is consistent with the observation that the birds arrive in a better condition in the years 1990-1992 than before. There is no indication yet that swans would arrive later, but this can be expected as the food situation further up-stream continues to improve. But why then would the interest in the available resources in the Netherlands be fading? As an explanation for these results we hypothesise the existence of a time window. The limited food stocks at the end of the flyway in the Netherlands would then merely serve to refuel the returning swans. The better the conditions *en route*, the less effort the swans would have to spend to exploit Sago tubers at the down end foraging sites. As shown in Figure 13, arrival time does not necessarily predict body condition. Assuming the rate of body fat increment to be constant for reasons of simplicity, early arriving swans in poor condition thus would deplete Sago down to the lowest level. In years of late arrival of swans in fair condition on the other hand, Sago areas would be left at a high threshold level. The premise for such behaviour is that the fattening goal would be under a time constraint, in our scheme provisionally set at mid November. Such a strategy is probably common in waterfowl wintering on cold water.

Fattening up is done quickly after arrival at the wintering grounds, prior to the period of cold water, which increases thermoregulatory costs in some cases to prohibitive levels (see Chapter 4, De Vries & Van Eerden 1995, De Leeuw & Van Eerden 1995).

With respect to optimal foraging theory, our data clearly show the existence of different levels of geographical and time scale, which are relevant to the birds' decision making, and which have to be incorporated in models predicting the use that birds make of a certain site, area or patch in a certain year.

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Dick Visser took care of drawing the figures. Ineke Touber corrected the English.

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## Chapter 11

# Maximisation of speed of autumn migration and fattening rate by Greylag Geese *Anser anser* cause underuse of natural food supply at a stopover site

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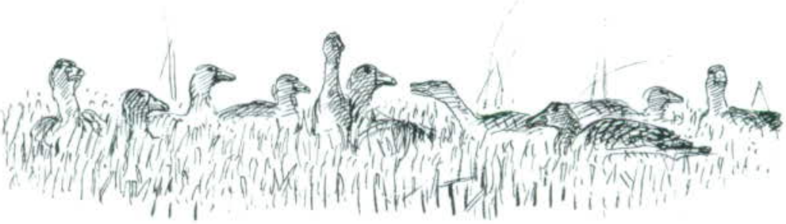

# Maximisation of speed of autumn migration and fattening rate by Greylag Geese *Anser anser* cause underuse of natural food supply at a stopover site

In the past twenty years Greylag Geese (*Anser anser*) from Norway intercalated a stopover site in the Netherlands in early autumn on their way to southern Spain. The geese were originally attracted by the natural vegetarion of the grass *Agrostis stolonifera*. These food plants were the result of natural succession in the ten years after embankment of the Lauwerszee in the northern part of the Netherlands in 1969 and peaked at 1299 ha in 1982. Total seed production in that year amounted to 157 tons DW, of which 38 tons (24%) were eaten by the geese. From the total number of goose days spent in the area, an average food uptake was assessed of 229 gDW goose$^{-1}$ day$^{-1}$. The establishment of a new stopover site was thus governed by the natural event of vegetation development and goose numbers closely followed the expansion of the vegetation. Geese were selective in taking only seeds, switching from *Agrostis* to the (later ripening) halophytes *Salicornia* and *Suaeda*. Negatively selected were leaves of the perennial grass *Agrostis stolonifera*. By selecting seeds geese yielded the highest energy, but not the highest protein return, compared to other food plants available. This selection for an energy rich diet corresponded with the need to build up fat reserves used for migration to the wintering area in Spain. The fat deposition rate was calculated to be approximately 50-55 g day$^{-1}$ at maximum, which is close to the physiological maximum achievable.

Seed density varied among sub-sites and was related to the phase of succession and the elevation above average water level. Geese selected patches with the highest seed density and performed a positive density dependent food harvest. They maximised the gross intake rate (the product of bite frequency and bite size) over costs (number of paces). The goose diet consisted almost entirely of *Agrostis* seeds (95-100%) and when a lower threshold of 5.8 gDW m$^{-2}$ was reached, geese took other food items as well. This dietary shift, however, was only performed by a minority of the geese, as most Greylags had migrated further south by that time.

Experiments with captive Greylags on natural vegetation showed the same sequence of food plant selection but, contrary to the wild geese, captive birds had a lower food threshold for *Agrostis* seeds (4.3 gDW m$^{-2}$) and took, at the expense of longer foraging time, more food items of lower quality.

We conclude that, because of the migratory timetable, wild geese exploited the natural vegetation on this stopover site within the constraint of a fixed time frame. Food selection was thus governed by the short-term foraging goal of gaining fat at the highest possible rate instead of exploiting the vegetation down to levels which no longer could provide energy for maintenance. Greylags thus balanced the proximate goal of local income with the ultimate goal of reaching the wintering area in time. Considerations about the foraging strategy used and the resulting carrying capacity of a stopover site therefore have to be judged in relation to these alternatives.

## Introduction

Migratory birds often use stopover sites during their journey between breeding and wintering area. Depending on species' size and degree of specialisation, these sites may lay far apart or form a chain of similar habitats offering a common resource. Small-sized specialist feeders such as Knot *Calidris canutus* feeding on small mollusc prey in tidal habitats may use stopover sites 1000-4500 km apart (Drent & Piersma 1990). Others, such as Bluethroat *Luscinia svecica*, a reed dwelling insectivorous songbird, travel smaller distances between suitable wetlands (Lindström & Alerstam 1992). Fat load economics are considered crucial with respect to speed of migration and maximal distance to be bridged (Gudmundsson *et al.* 1991, Lindström 1991, Lindström & Alerstam 1992). Birds therefore are forced to select sites suitable to fulfil their energetic demands which may lead to maximum daily fat deposition rates of 1-7% of lean body mass (Alerstam & Lindström 1990). Ecological studies on stopover sites have been undertaken from the view point of timing, energy requirements and safety. Generally, high densities of migratory birds halt together at stopover sites in the temperate regions, where food depletion and competition for a common resource has been reported many times (Goss-Custard 1980, Zwarts & Wanink 1984, Chapter 8, Van Eerden 1984, Piersma 1994).

Stopover ecology and the concept of carrying capacity are linked, although few attempts have been made to study the quantitative use of a site on the level of an entire (sub-) population of migrants. Alonso *et al.* (1994) were among the first to demonstrate the quantitative relationships on a larger scale in the field. They found that the size of the wintering population of Cranes *Grus grus* in Spain was determined by the low mid-winter availability of cereal seeds left over after harvest and partial ploughing of fields. Contrastingly, large numbers of Cranes passing through the area in autumn were not correlated to the (super abundant) biomass available then.

Foraging theory has developed patch use models (see Stephens & Krebs 1986). These models predict the use of a food patch in relation to alternatives in the same region, often within the same habitat. Patch use models form the basis of the supposed quantitative relationship between food abundance at a site and bird numbers, but the habit of migration often complicates the interpretation of the relationship between food on offer and resource exploitation (Newton 1980).

Two hypotheses exist concerning the timing and the extent of bird migration. The first (obligate migration) states that birds perform a fixed, goal-oriented migration using well-defined timetables (Berthold 1975, Gwinnen 1986). The second hypothesis (facultative migration) states that environmental conditions, such as food abundance, would determine the route and timing of the migratory journey. Birds performing facultative migration are therefore more likely to be influenced by the carrying capacity of stopover sites than obligatory migrants are. Birds on migration may judge stopover sites as "super patches" which either can be used or ignored, depending on the migration strategy used on "patch quality". Subsequently, the extension of foraging theory to patch use on this level may be of help in interpreting the role of habitat quality and food abundance on stopover or wintering sites.

In recent years, Greylag Goose migration and use of stopover sites in northern and central Europe has been intensively studied by means of neck collar programmes (Norway: A. Follestad, Sweden: Nilsson & Persson 1991, Germany: Rutschke 1987). Geese from Norway (1200 km north) pass through the Netherlands on their way to the wintering areas in central and southern Spain (Calderón *et al.* 1991, Van Eerden *et al.* 1991). Van Eerden *et al.* (1991) showed that individual Greylag Geese from Norway tended to leave a stopover site in Flevoland in September or October not before a certain body condition had been reached. As only a few flocks were observed in France and northern Spain, the migration from the Netherlands to the two wintering sites in Spain is performed in a single flight of 1550 km (Villafáfila, Zamora) and 2025 km (Marismas del Guadalquivir, Sevilla) respectively.

In this study we concentrate on the post-breeding and early autumn phase when Norwegian geese use the Lauwersmeer as a stopover site on their way to Spain. Foraging by geese was studied over a long period (1969-1995), in relation with changes in the vegetation. We will test one hypothesis which arises directly from foraging theory (1) and two additional ones (2 & 3), which are formulated to test whether the extension of decision rules occurs beyond the scale of the actual habitat under use:

1. Greylag Geese respond to differences in food availability, both on the level of the food plant (patch harvest) as well as on the level of the entire stopover site (carrying capacity).
2. Geese which use a stopover site in between long-distance flights in order to refuel body reserves will choose a diet based on metabolisable energy rather than nutrients.
3. Foraging decisions in a migratory bird are not only based on food availability at the stopover site, but are also affected by higher order goals dictated by the circannual rhythm of the species.

## Methods

### Study area and vegetation

By closing off of the estuary of the Lauwerszee (53°22′N 06°13′E) in 1969 a tidal, saltwater area with gullies and exposed mudflats (9100 ha) was turned into a freshwater area (1970 ha) with regulated, fixed water tables, called the Lauwersmeer. In the first two years, natural succession of the vegetation could take place in the entire area. Some 3000 ha of former sandflats remained undisturbed with respect to drainage, recreation and hunting practices (Joenje 1978). From 1977 onwards an increasing part of the area has been grazed by sheep, cattle and horses (total 1340 ha of which 855 ha from 1982 onwards). The bottom of the lake margins are sandy in the northern part and consist of heavy loam in the south.

Creeping Bent *Agrostis stolonifera* is a perennial grass species which reproduces either asexually by means of stolons and tillers, or by seed. Asexually reproducing stands are found in closed swards in both inland and saltmarsh vegetations. The high vegetative capacity is linked to high levels of polyploidy (Ellis Davies 1953, Aston 1962) and was confirmed by transplantation experiments (Kik 1987). On the other hand, generative reproduction occurs mainly in habitats where competition is reduced, such as sand dune areas and newly emerged sites where colonisation by means of seeds is more effective than by clonal expansion. Kik (1987) found less variation in cytotypes of the Lauwersmeer population, tetraploidy being most common in these sexually reproducing plants.

### Vegetation mapping and sampling seed density

Large-scale vegetation mapping by means of false colour photography was carried out in 1972, 1975, 1980, 1984 and 1989. Ground surveys were carried out in order to identify the different vegetation zones by means of fixed quadrates. Data were computerised using GIS to calculate surface areas and differences in vegetation succession between census years. Additional data were collected using oblique pictures from low flying aircraft and inspection of the area in the field (1994).

Inflorescences were counted using small wire frames of 0.25 $m^2$ which were placed at random in different vegetation zones, just after seeds had ripened. The total production of ears was calculated using weighted means of different zones per sub-area (50-150 ha), visible in the photographs. Seed mass was determined by stripping off husked seeds from the central stalk of the inflorescence and dried for one day at 70 °C. Large exclosures were used to monitor seed loss during the season because of wind effects.

(A) Large scale natural grass vegetation of *Agrostis stolonifera*, Lauwersmeer, August 1982. (B) Greylag Goose *Anser anser* stripping seeds of *Agrostis*.

### Goose counts, habitat use and diet assessment

Integral bird counts in the area were held 13 times a year (at least 6 times between July and November). Waterfowl were counted during specific counts in between. For most years 8-12 complete counts were available during fall migration. Depending on the season, three to fifteen people were involved in counting, covering the sandflats on foot, most of the times assisted by counters from a ship. Each count was performed in about 4 h time, and most of the waterfowl were counted simultaneously in order to avoid double counts of moving groups. Geese were categorised using either natural or agricultural habitat. Within these main categories, subdivisions could be made in many cases to the level of vegetation type.

Goose diet was assessed by direct observation using telescopes. Seed stripping, leaf eating and grubbing for stolons and bulbs could be easily identified. Droppings of Greylag Geese were collected in areas where flocks were seen grazing or identified by their appearance. Dropping size varies significantly between Greylag Goose (1,067 gDW) and the only other co-occurring goose species, the Barnacle Goose *Branta leucopsis* (0,710 gDW, $F_{1,81} = 118{,}3$, $P < 0.001$). Remains of plants ingested were identified by microscopical analysis of their cellular characteristics (Owen 1976), comparing the samples with a reference collection.

In the field, grazing impact by geese was analysed after reconstruction of the removed part of the inflorescences, taking average weight of intact and grazed ears as estimators for local patch harvest.

Detailed observations on geese were made from a fixed hide (6 m above ground level), which was positioned in a part of the area which could be reached without being spotted by the geese. Goose behaviour was observed from day-to-day during the entire season of 1982, centred in the period of most intensive use of *Agrostis*. In later years, additional observations were made from small tents and from a car.

### Trials with captive birds

Two captive adult Greylag Geese, which were caught under license a year before the experiment started, were kept outdoors in a large semi-free penned meadow. Beside grasses, the geese could take cereal seeds and maize which was supplied daily. The two geese formed a pair which facilitated handling and allowed us to place them together in one of the 9 experimental pens in the field. These experimental pens (51-83 $m^2$) were fenced by nylon nets using bamboo sticks, and were set up in natural vegetations in the Lauwersmeer not yet grazed by wild geese. Water and grit were supplied *ad libitum*, but no additional food was offered. A small hide was situated at 20 m distance from the pen to allow observations to be made. The geese were observed in each pen during 4-6 complete days in order to record grazing behaviour, food uptake and impact on the vegetation. The geese were moved to a new pen every other day to avoid too strong depletion effects at once, and to assure a gradual change in the vegetation on offer. Two weeks prior to the experiment and during the nights in between the experimental days, the geese were kept in a large collecting pen over natural vegetation. Diet was assessed using both direct observations as well as dropping analyses. Vegetation was sampled in the pens using a grid of 0.25 $m^2$ squares in which total cover per plant part was determined. Samples of plants taken from adjacent areas provided the conversion from cover to dry mass.

### Chemical analyses of food plants

Samples of food plants were collected in the field, taking only fresh material without dead biomass. Green mass was dried for three days at 70 °C and passed through a 1 mm sieve. Husked seeds of *Agrostis* were crushed by hand in a mortar. Kjeldahl nitrogen was determined and multiplied by 6.25 to arrive at crude protein. Ash, neutral detergent fibre (NDF) and acid detergent fibre (ADF) were determined for plant species which occurred almost singly in the diet. As indigestible marker, ADF was used assuming no digestion of cellulose (Marriot & Forbes 1970, Mattocks 1971, see Prop & Vulink (1992) for detailed description of methods). In most cases, however, the mixed diets of the geese invalidated the use of this method. *In vitro* digestibility of fresh material was determined instead (Van Soest 1982), using ox-rumen fluid at an incubation period of 6 h, which was calibrated to be the period long enough to be compared to true digestion.

## Results

### Vegetation succession and habitat use by geese

After embankment of the Lauwerszee estuary in May 1969, natural succession on the former sea bottom caused the vegetation to change from a halophyte community dominated by annuals, towards a natural grass vegetation consisting of perennials (Joenje 1978). The former sea gullies became filled with stagnant freshwater and water tables were regulated by sluices in the barrier dam. Many species of waterfowl profited from the rich seed supply of Glasswort *Salicornia brachystachya* and *S. dolichostachya* (Prop & Van Eerden 1981, Van Eerden 1984, Van Eerden & Drent in prep.). Because of a slow, but consistent desalinisation of the soil, this vegetation became successively replaced by perennial grasses such as *Puccinellia maritima* and *P. distans*, perennial dicots such as *Aster tripolium*, followed by the grass *Agrostis stolonifera* (Table 1). *Agrostis* first colonised this new territory in 1972, from seeds produced by plants on the saltmarshes on the fringe of the estuary. *Agrostis*, which was of special interest to the Greylag Geese, rapidly invaded the *Puccinellia* swards from 1978 onwards, and already in 1980 a total of 807 ha was covered by this species. This development of a natural grassland vegetation originated from seeds which were present on the former saltmarshes bordering the estuary. Only on the higher soils, desalinisation occurred so quickly that tall grasses such as *Elytrygia repens* and *Calamagrostis epigejos* could become established. In undisturbed lower areas, Reed *Phragmites australis* expanded and caused the grass swards to disappear (Muis 1985). Also scattered willows *Salix* spp. could germinate in these areas. However, because of the introduction of grazing management, the overall aspect of the area was in 1996, seventeen years after the start of colonisation, still very open (Vulink & Van Eerden 1998).

**Table 1.** Area of natural grass vegetations in the Lauwersmeer as determined by aerial photography and ground surveys. By a GIS the vegetation maps provided the area of recently changed vegetations, which are especially productive in seeds. In brackets zone numbers.

| Year | Saline grassland (type 1) | Brackish grassland 1-3 years (type 2) | Brackish grassland > 3 years (type 3) | Desalinated grassland (type 4) | Vegetative grassland |
|---|---|---|---|---|---|
| 1969 | 27 | - | - | - | - |
| 1972 | - | - | - | - | - |
| 1975 | 92 | 580 | - | - | - |
| 1980 | 165 | 350 | 364 | 217 | 14 |
| 1984 | 71 | 287 | 326 | 205 | 37 |
| 1989 | 78 | 313 | 269 | 130 | 44 |
| 1994 | 60 | 340 | 200 | 59 | 75 |

Key-species beside *Agrostis* are for type 1: *Salicornia brachystachya, Puccinellia maritima*; type 2: *Puccinellia maritima, Odontites verna*; type 3: *Aster tripolium, Triglochin palustris*; type 4: *Phragmiles australis, Leontodon autumnalis.*

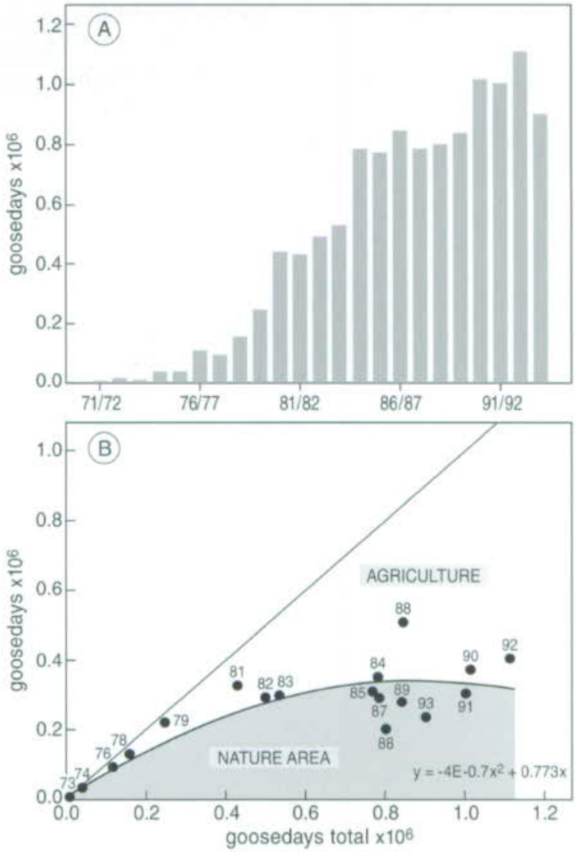

**Figure 1.** (A) Goosedays per season (July-June) for Greylag Geese in the Lauwersmeer area. (B) Limited capacity of natural vegetation at increasing goose numbers. The surplus is being taken up by agricultural grounds.

Greylag Geese were seen on migration in the area from 1969 onwards. Small numbers (up to 300) occurred in the estuarine situation before 1969. However, not until the season of 1971/72 were geese back in the new territory in small numbers (Prop & Van Eerden 1981). Thereafter, numbers rose each autumn and particularly in 1980 a marked increase was noticed with peak numbers of 4000 geese on natural vegetation (Fig. 1). Again in 1984 and 1990, numbers went up sharply, but the overall trend shows a stabilisation of the number of goosedays in autumn. As numbers went up, an increasing part of the geese moved towards agricultural areas in the surroundings, leaving the use of natural areas by geese rather constant. Greylags thus did not react strongly to the abundant seed production by *Salicornia* spp. as did Barnacle Geese *Branta leucopsis* and Wigeon *Anas penelope* (Van Eerden 1984), but only started to use the site in large numbers after the establishment of perennial grasses typical for a brackish environment, especially *Agrostis stolonifera*. This species occurred in clearly distinct zones, differing in height and production of inflorescences. The zones are linked to desalinisation of the soil (Table 2).

**Table 2.** Salinity of soil layers of different depth in the Lauwersmeer in 1982 for different zones of *Agrostis*. Data shown as g NaCl per 100 g dry soil (SD). Zone numbers correspond to Table 1.

| Zone | 0-0.2 cm | 0.2-5.0 cm | 5.1-20.0 cm | 0-20 cm ¹) |
|---|---|---|---|---|
| 1 | 1.039 (0.03) | 0.693 (0.03) | 1.660 (0.22) | 1.422 |
| 1-2 | 0.193 (0.05) | 0.166 (0.03) | 0.952 (0.43) | 0.756 |
| 2 | 0.165 (0.03) | 0.161 (0.01) | 0.781 (0.10) | 0.626 |
| 2-3 | 0.102 (0.02) | 0.109 (0.02) | 0.598 (0.14) | 0.476 |
| 3 | 0.163 (0.02) | 0.153 (0.02) | 0.436 (0.11) | 0.740 |
| 4 | 0.070 (0.00) | 0.046 (0.01) | 0.213 (0.03) | 0.171 |

¹) weighted mean

## Diet and patch use

### *Wild geese*

In the first years of use of the new stopover site in the Lauwersmeer, Greylag Geese were seen foraging on seeds of *Puccinellia distans* and *Salicornia dolichostachya*. Only flocks of up to 30 geese were seen together exploiting these plants in the saltmarsh vegetation (1972-1975). Also *Suaeda maritima* was selected and geese were seen stripping the seeds off the florescences of this halophyte. Seed stripping of *Agrostis stolonifera* was first observed in 1977, when about 200 Greylag Geese switched to this food source for three weeks in September. Each year thereafter, more and more geese responded to this rapidly increasing resource. Geese concentrated their foraging efforts in the most dense stands. The relationship between patch quality, expressed as florescence density, and patch harvest shows a strong positive correlation. For *Suaeda* a slight curvilinear regression provided the best fit to the data without any threshold density (Fig. 2A). For *Agrostis* a sigmoid regression (Fig. 2B) was calculated to give the best fit. In the latter case, a clear threshold (25 ears $dm^{-2}$) existed below which Greylags hardly exploited the vegetation on the smallest patch level. Between 30-40 ears $dm^{-2}$ the highest proportion of seeds was harvested (70-75% on average). The foraging rate by Greylags was negatively affected by the spacing of individual *Agrostis* tussocks and within-tussock density of ears. When plotted against step frequency, as a measure of patch dispersion, the intake rate decreased linearly (Fig. 2C). Observations of wild geese showed preference for vegetations with the highest density of rich patches (Table 3). Combination of bite frequency and dry mass per seed-head shows that intake rate was highest in type 2 *Agrostis* (0.816 gDW $min^{-1}$). Other types showed lower intake rates, being the lowest in type 4

**Table 3.** Use of four different zones of *Agrostis* by wild Greylag Geese as continuously watched from an observation tower in late summer and autumn 1982. Goose hours refer to the period of seed stripping (*Agrostis*) and the period later on when the geese had shifted to other food plants as *Aster*, *Salicornia* and *Puccinellia*.

| Zone | Area ($m^2$) | (%) | Goose hours *Agrostis* | (%) | Goose hours other | (%) |
|---|---|---|---|---|---|---|
| 1 | 2850 | 5.3 | 199 | 11.3 | 205 | 34.5 |
| 2 | 17850 | 33.1 | 1018 | 57.8 | 231 | 38.9 |
| 3 | 23600 | 43.8 | 538 | 30.5 | 153 | 25.8 |
| 4 | 9625 | 17.8 | 6 | 0.4 | 4 | 0.8 |

Geese were selectively foraging more in the younger stages of succession, for *Agrostis* $\chi^2 = 791$, $P < 0.0001$, df = 3; for other food plants $\chi^2 = 1045$, $P < 0.0001$, df = 3.

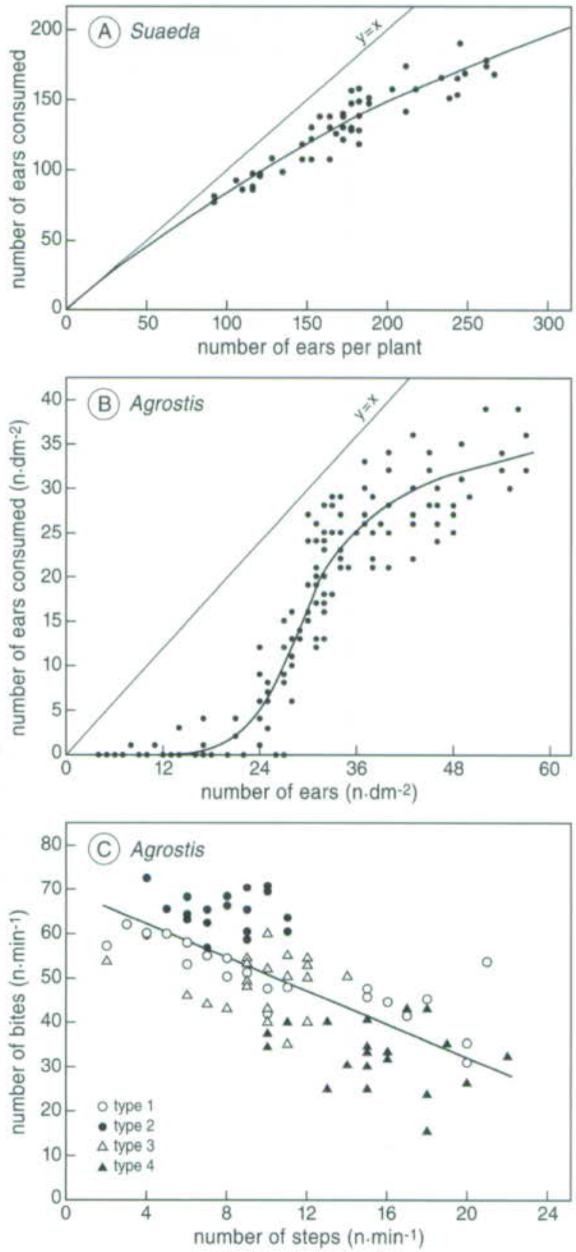

**Figure 2**. Functional response of wild Greylag Geese foraging on seeds of *Suaeda maritima* (A) and *Agrostis stolonifera* (B), showing the relationship between patch quality and patch harvest level. (C) Relationship between step frequency and intake rate for *Agrostis* in different vegetation zones. Pooled data show a significant negative regression (adjusted $R^2 = 0.58$, $F_{3,80} = 58.08$, $P < 0.0001$). The different sub-zones (1-4, in order of progressive succession) differ with respect to the bite/step ratio ANOVA $F_{3,80} = 7.85$, $P < 0.0001$).

**Table 4.** Intake rate for different zones of *Agrostis stolonifera* stands as determined by direct observation (peck rate and bite size) and production of droppings, combined with a 45% digestibility of organic matter.

| Type | Direct observation | | Indirect observation | | |
|---|---|---|---|---|---|
| | Bites $min^{-1}$ | **Intake rate** gDW $min^{-1}$ | Dropping mass gDW(SE) | Dropping production gDW $min^{-1}$ | **Intake rate** gDW $min^{-1}$ |
| 1 | 45 | 0.565-0.735 | 1.250 (0.122) | 0.338 | 0.751 |
| 2 | 65 | 0.856-1.537 | 1.386 (0.097) | 0.375 | 0.832 |
| 3 | 50 | 0.628-0.850 | 1.165 (0.088) | 0.282 | 0.626 |
| 4 | 35 | 0.440-0.600 | 1.062 (0.104) | no data | no data |

(0.440 gDW $min^{-1}$). Dropping production and dropping mass also differed according to vegetation type; in combination with an organic dry matter digestibility of 45% (see below), through-put rates can be calculated. The two independent methods of intake rate compare well (Table 4), although intake rates as observed directly were generally somewhat higher.

The diet of the wild Greylags consisted of *Agrostis* seeds from the end of July until the last days of September (Fig. 3A). On the basis of the vegetation zone, a food threshold of 5.3-5.8 g $m^{-2}$ existed for *Agrostis* seeds. No trend in the time devoted to foraging was apparent when geese were observed in the vegetation. For the 21 days of continuous observation between 19 September and 13 October, the foraging percentage remained constant at 71%. Only a few times during the total daylight period could a flock of wild geese be watched without interference. Time spent foraging was 8.1 h (SE = 0.96 h, $N = 4$) when >70% of the diet consisted of *Agrostis* seeds and 11.0 h (SE = 0.14 h, $N = 6$) for *Agrostis* leaves, the difference being significant ($t = 12.73$, $P < 0.0001$).

*Captive geese*

Trials with captive geese on natural vegetation provided the best data on food selection, because the composition of the patchy vegetation available to these geese was exactly known. During all first days in the 9 enclosed lots of vegetation, the geese preferred seeds of *Agrostis* (98-100% in trial 1-3 decreasing to 35-62% in trial 7-9, Fig. 4A-C). The density of *Agrostis* seeds in the vegetation determined the proportion of seeds taken in the diet. At densities over 4.5 g $m^{-2}$, more than 90% of the food ingested consisted of seeds, while the proportion of seeds in the diet was sharply falling when the density of seeds came below this threshold (Fig. 4D). Leaves of *Aster tripolium* and *Salicornia brachystachya* were taken second to grass seeds, but still occurred in a higher percentage in the diet than in the vegetation. During the second and third day, these plants were still important, but from day 3-6 onwards they were replaced by *Agrostis* and *Puccinellia* leaves (Fig. 3B). The successive use of different food plants coincided with an increase in total foraging time, from 5.0 h at day one to 8.75 h at day six.

**Seed production and use by geese**

Seed availability varied between vegetation zones and during the season (Fig. 5). Seed density varied over the different vegetation zones and average density was much lower than described for individual patches (Table 3). According to paired *t*-tests, both saline zone 1 and the desalinated, reed-invaded zone 4 showed a constant and significant lower seed density than zone 2 (young *Agrostis*, $P < 0.0001$, $P = 0.0006$ resp.) and zone 3 (older *Agrostis*, $P = 0.0003$, $P = 0.0007$ resp.). No difference existed between the two most productive zones: 2 and 3 ($P = 0.49$). Although we suspected a tendency of a

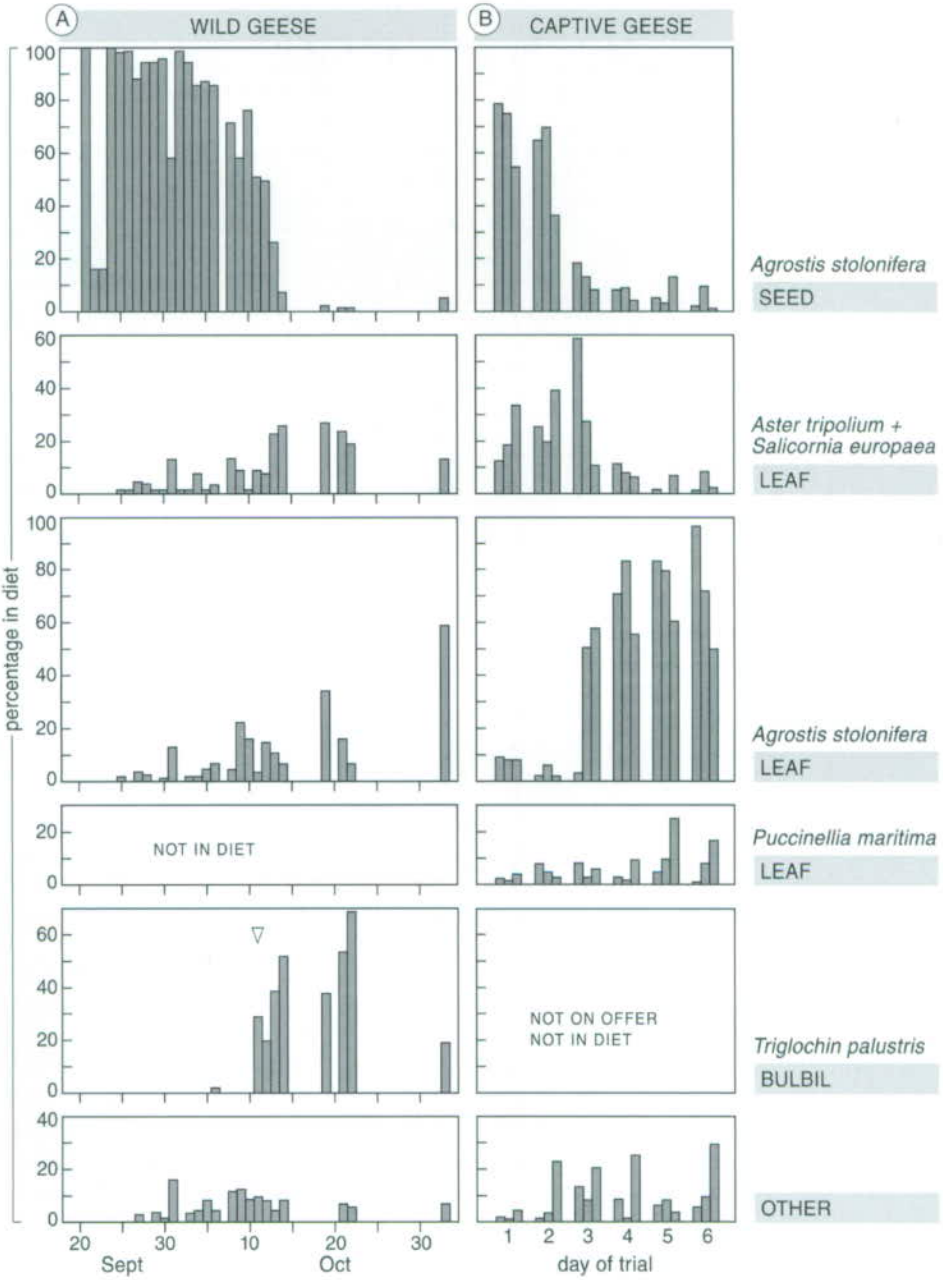

**Figure 3.** Diet in the course of the season as determined by analysis of droppings for (A) wild geese and (B) captive geese. Note the similar sequence of food items taken between wild and captive geese, but the higher proportion of leaf material taken by the captive geese. Arrow indicates the moment of flooding of the top-soil, allowing wild geese to start exploiting the below-ground bulbils of *Triglochin palustris*.

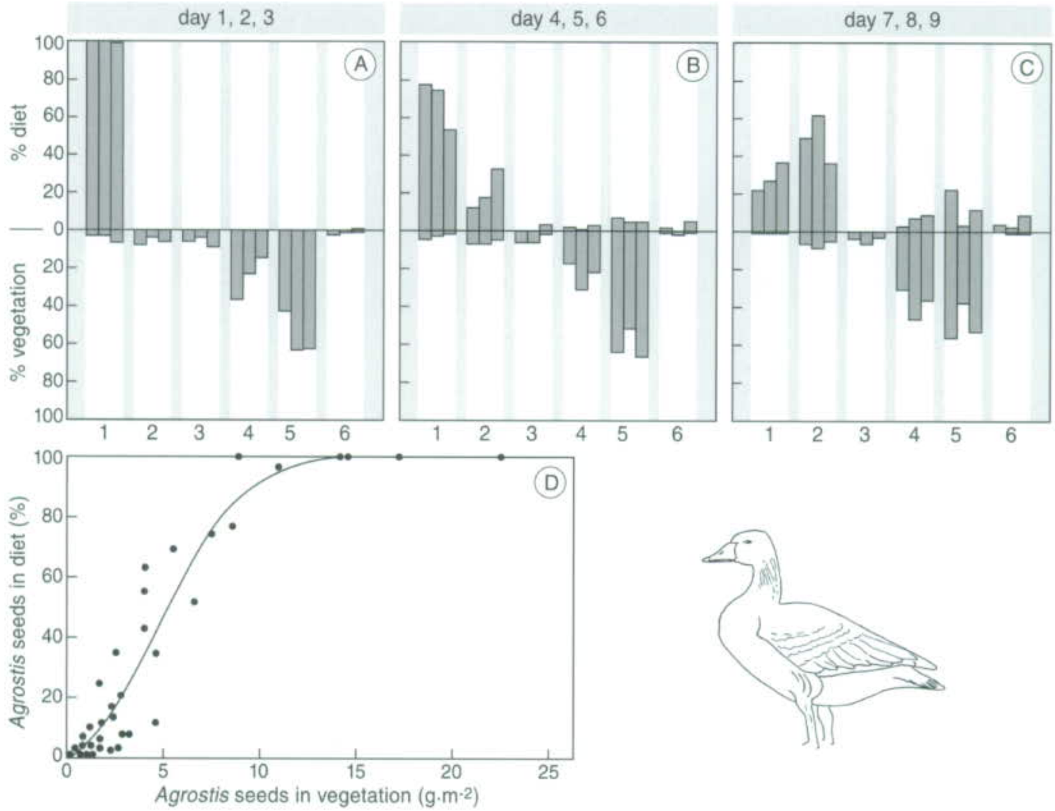

**Figure 4.** (A)-(C) Trials with captive geese on natural vegetation showing degree of food selection. Only data for 9 first days in different, ungrazed areas are shown. (D) Seed density at the beginning of 38 trial days with captive Greylags for all 9 vegetation lots in relation to the proportion of *Agrostis* in the diet of that particular day. Food density expressed as gDW of seeds $m^{-2}$ available for one goose.

1 = *Agrostis* seeds, 2 = *Aster* and *Salicornia*, 3 = *Aster* leaves, 4 = *Puccinellia* leaves, 5 = *Agrostis* leaves, 6 = other.

later ripening of seeds in the more saline parts, this could not be confirmed statistically ($\chi^2$ tests). Geese were predominantly seen foraging at zone 1, 2 and 3, being the younger stages in the succession. Soon after arrival of the first geese in July and early August, seed stripping started in zone 1 and 2, although seeds were not yet ripe. Geese spent significantly more time in zone 2 than 3 (Table 3). A clear seasonal shift in use of the different zones occurred (Kruskal-Wallis statistic 16.63, $P = 0.01$), zones in the younger stages being visited earlier.

On an larger scale, goose density (goosedays $ha^{-1}$) was correlated with the seed production for different vegetation units (10-100 ha) for which both seed stock and goose numbers were available. In a multiple regression model with backward deletion of non-significant terms, three variables were significantly contributing (adjusted $R^2 = 0.339$): seed density ($t = 2.42$, $P = 0.018$), day number ($t = 2.69$, $P = 0.009$) and distance to the roost ($t = -2.96$, $P = 0.004$). The presence of cattle had no effect, neither contributed interactions of terms significantly to the model. Distance to the roost correlated negatively which indicates that geese preferred foraging grounds with the lowest costs for transport.

Greylags were not able to consume all seeds available to them. From data shown in Figure 5 a

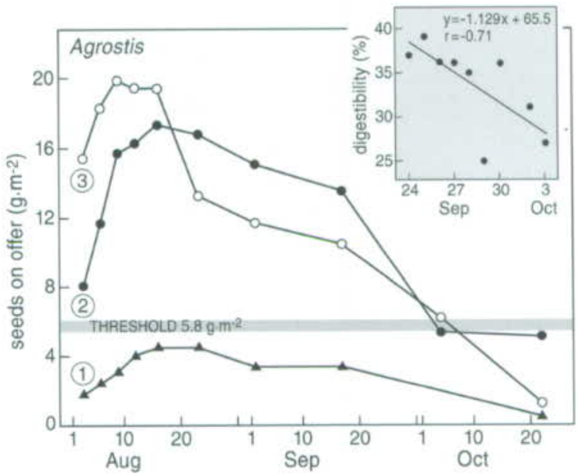

**Figure 5.** Availability of ripe *Agrostis stolonifera* ears (gDW $m^{-2}$) for 3 vegetation zones during the season. Indicated is a density threshold corresponding to > 90% resp. < 5% occurrence of *Agrostis* seeds in the diet of the geese. Inset shows decrease in organic matter digestibility of *Agrostis* seeds during the season.

threshold value of 5.8 g $m^{-2}$ (average for vegetation) was determined for wild geese using *Agrostis* as a single food item (> 90% in diet). After 4 October the percentage occurrence in the diet quickly fell, and after 15 October hardly any *Agrostis* was taken (< 5% in diet, corresponding to 2.6 g $m^{-2}$ on offer).

### Digestibility and metabolisable energy

In vitro digestibility of organic matter was negatively correlated with the fraction of cell wall material of food plants (44 samples, arcsine transformed, $R^2 = 0.60$, $P < 0.0001$). Within one food type, stripped ears of *Agrostis* and organic matter digestibility showed a linear positive relationship with the digestion of cell wall material ($R^2 = 0.77$, $P < 0.0001$). Except for the seed heads of *Agrostis*, the preference for different food items was correlated with the in vitro digestibility of cell walls. The dicots *Aster* (leaves) and *Salicornia* (leaves and seeds) ranked highest (53.9%) followed by *Suaeda* (leaves and seeds)

**Table 5.** Selectivity, digestibility and chemical composition of different food plants available to captive geese in grazing trials on natural vegetation. (l) = leaf, (s) = seed head, (f) = flower. Due to difficulties in identification of *Aster* and *Salicornia* leaves in droppings these food plants have been taken together. S = selectivity coefficient based on availability of food item *i* in the vegetation and presence in the droppings (based on dry matter). $DCWC_i$ = *in vitro* digestibility as determined by incubation in ox-rumen fluid.

| Food plant | S | $DCWC_i$ total | Cell wall components | Hemi cellulose | Lignine | Cutine | Crude protein |
|---|---|---|---|---|---|---|---|
| *Agrostis* (s) | 24.5 | 45.2 | 69.8 | 36.5 | 17.9 | 15.4 | 9.5 |
| *Aster* (l) and *Salicornia* (l) | 3.8 | 53.9 | 28.2 | 7.6 | 8.9 | 11.7 | 10.2 |
| *Suaeda* (s) | 1.0 | 41.2 | 44.2 | 23.6 | 7.6 | 13.0 | 10.1 |
| *Puccinellia* (l) | 0.23 | 36.7 | 48.1 | 25.8 | 12.5 | 9.8 | 9.5 |
| *Aster* (f) | 0.21 | 28.7 | 32.1 | 11.5 | 12.7 | 7.9 | 12.3 |
| *Agrostis* (l) | 0.11 | 18.0 | 51.4 | 32.1 | 14.9 | 6.0 | 18.1 |

41.2% digestibility (Table 5). Grass leaves of *Puccinellia* (36.7%), and *Agrostis* (18.0%) had the lowest digestibility. They were taken during the last days of the trials by the captive geese, but never by the wild geese. Stripped *Agrostis* seeds had an apparent digestibility of only 0.9% when passed through a 1 mm sieve. When squashed in a mortar to a particle size equal to fragments of seeds found in the droppings of wild geese as shown by microscopical examination, the *in vitro* digestibility of organic matter rose to 45%, which is close to the value derived for *Suaeda*. We used the latter value in a comparison between food preference and apparent digestibility as determined in the experimental grazing trials with captive Greylags. A strong, almost perfect relationship existed between the share of a food species in the diet and its apparent digestibility ($r_s = 0.98$, $P < 0.01$, $N = 6$). The geese did not, however, show any preference with respect to protein content.

In Table 6 the energy balance of geese feeding on *Agrostis* seeds is compared to that of geese feeding on *Agrostis* leaves, being the most and the least preferred food species, respectively. In order to do so, at first the metabolisable energy (ME) was calculated for these two extremes. In this calculation, the individual bite size was determined by the ratio of total food uptake (faecal output and digestibility of organic matter) and the total number of bites (average bite frequency and total foraging time per day). From Table 6 it is clear that Greylag Geese, by selecting *Agrostis* seed heads over leaves, could almost double their energy uptake. In combination with the total time spent foraging, 8.1 h in wild geese, the daily metabolisable energy (DME) amounted to 4131 kJ day$^{-1}$ for seed heads and to 2970 kJ day$^{-1}$ for leaves. Reconstruction of total energy expenditure from time budget data (see Goldstein 1988, Wooley & Owen 1978) shows that daily energy expenditure (DEE) for seed head stripping geese would arrive at 1059 kJ day$^{-1}$. This equals 1.9 × BMR, a rather low value if compared to other species, many of which fall between 2.5-3.0 × BMR (Drent & Daan 1980, Kirkwood 1983). This low value is caused by hardly any flight costs (0.1 h) during this period. However, as BMR is likely to be somewhat elevated as a result of (body) feather synthesis (measurements M. Loonen), we prefer instead to use the range of 2-2.5 × BMR as the best estimate. Using this range the DEE for foraging on seeds would vary between 1343 and 1622 kJ, and for foraging on leafs between 1460 and 1768 kJ. So, for seeds as well as for leaves, DME is considerably higher than DEE, allowing the deposition of fat reserves by the geese.

We conclude that, while foraging on seeds of *Agrostis*, Greylags were in a definite positive energy balance. This was also the case, although to a lesser extent, while foraging on leaves of *Agrostis*. However, these leaves were not taken at all by the wild geese.

**Table 6.** Metabolisable energy (ME) for *Agrostis* seed heads and leaves in trials with captive geese on natural vegetation. Daily ME (DME) expressed as multiples of basal metabolic rate (BMR) according to the formula of Aschoff & Pohl (1970)[1]. DME was calculated using total time spent foraging of wild geese for two food types, bite frequency and bite size, corrected for digestibility. Fat deposition rate (FDR) was calculated according to Kersten and Piersma (1987)[2] using time budget data and activity specific energy expenditure to calculate DEE (Goldstein 1988, Wooley & Owen 1978) added with the costs of feather synthesis[3].

| | ME | Bite size | ME, kJ min$^{-1}$ | | DME, kJ day$^{-1}$ | | DEE | $FDR_{max}$ |
|---|---|---|---|---|---|---|---|---|
| | kJ g$^{-1}$ | mg | ♂ | ♀ | total | × BMR | kJ day$^{-1}$ | g day$^{-1}$ |
| Seed heads | 8.8 | 16.5 | 8.1 | 8.9 | 4131 | 7.4 | 1343-1622 | 50-56 |
| Leaves | 6.3 | 13.2 | 4.1 | 4.9 | 2970 | 5.3 | 1460-1768 | 24-31 |

[1] $BMR = 307.6 \times BW^{0.734}$ assuming a body mass at arrival of 2.5 kg (♂, 603 kJ day$^{-1}$) and 2.0 kg (♀, 512 kJ day$^{-1}$).

[2] FDR = DME-DEE taking 39.3 kJ g$^{-1}$ as the energetic value of fat at a transformation rate of 0.88 (Kersten & Piersma 1987). $FDR_{max}$ assumes a 90% storage of surplus energy into fat.

[3] costs for body feather moult (114 kJ g$^{-1}$ feather, at 2 g day$^{-1}$ (data M. Loonen & R. Van der Wal).

## Discussion

### Patch exploitation and carrying capacity

*Agrostis* in the Lauwersmeer was very productive in seeds compared to stands in well established grasslands (Kik 1987). Lack of competition caused great plasticity in growth forms during the very first years of colonisation. We showed that Greylags were closely linked to *Agrostis* both between and within years. Total seed consumption amounted to 38 117 kg in 1982. Out of a total production of 157 000 kg, the geese only took 24%. Part of the production occurred in vegetations below the threshold of 5.8 g m$^{-2}$ and geese were shown to select zones of high seed density. Patch quality on the lowest level distinguished (100 cm$^2$) determined the use that geese made of it. The intake rate (yield) in relation to the number of steps (effort) probably provided a quick measure for the geese locating the richest patches. Especially the younger stages were used to a greater extent than the older, more closed stands. Both the lower seed density and the limited possibility to walk through the older stages of the natural grassland may have been responsible for this. The longer grass, interspersed with emergent reed vegetation caused a less open landscape where birds may have had greater problems in detecting predators such as Fox *Vulpes vulpes* (after 1984 increased numbers).

Comparing seed density in relation to consumption, the geese showed a positive density dependent patch harvest. Being able to assess patch quality by visual observation, the geese could be expected to

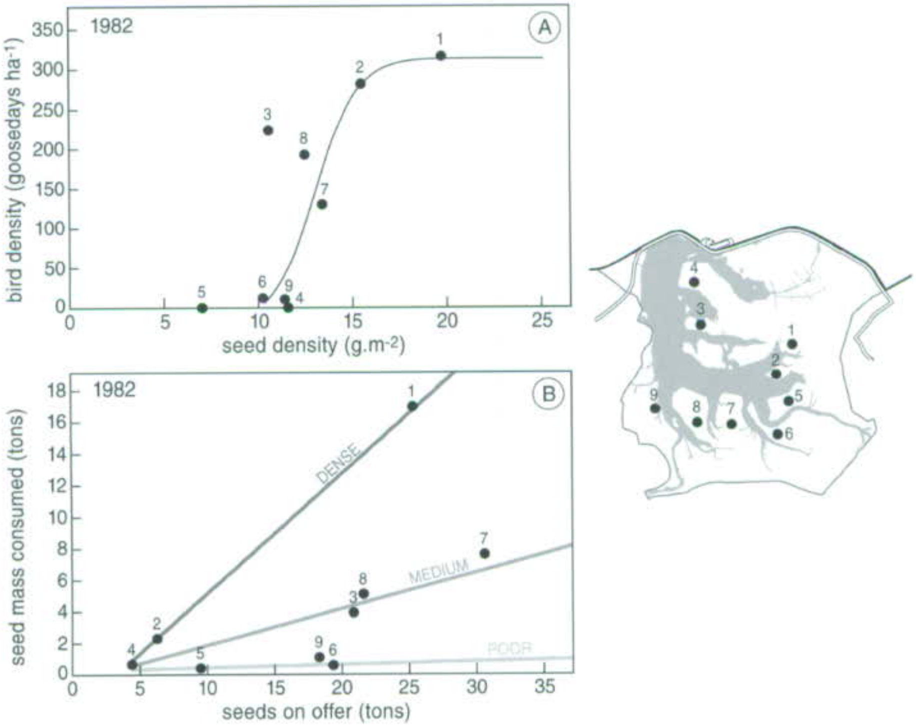

**Figure 6.** (A) Relationship between seed density of *Agrostis* and goose density for different sub-sites in the Lauwersmeer area in 1982. Wild Greylag Geese respond with increasing density above a threshold of *c.* 10 gDW m$^{-2}$. (B) Corresponding use of seed crop for the same sites showing the importance of seed density instead of total biomass in determining goose numbers. Site 3 is a peninsula serving as a resting place for geese disturbed elsewhere.

obey a Prescient Foraging Strategy. Rich and poor patches are exploited at equal rate in this case (Valone & Brown 1989). However, it was found that in *Suaeda* the larger plants were relatively underused compared to the smaller ones. Similarly, also the most dense patches of *Agrostis* were less used as judged by the levelling off of the response curve in the upper region of patch density (Fig. 2). These observations are in line with a Bayesian Foraging Strategy (Iwasa *et al.* 1981, Valone & Brown 1989). In this case a forager matches a prior distribution of patch quality, based on the average encountered in the environment, with a posterior distribution based on actual information from the patch under exploitation. At first hand it is difficult to see why underutilisation of rich patches would occur. Only a higher gain rate at higher seed density could explain such a pattern. Although we have no data about intake rate on the actual patch level, this seems not unlikely. Gain rate may be higher because of the possibility to take several seed heads in one stripping movement. As shown in Table 4, based on differences in patch quality, actual (short term) intake rate may be higher than average (long term) intake rate. Another point to explain is the sigmoid form of the response curve of *Agrostis*. As long as the rate of digestion is lower than actual uptake, it pays a consumer to increase intake rate. The observed cut off point in the response curve therefore is considered the lower threshold of acceptable intake rate. Can we scale-up the patch use pattern of a $dm^2$ to the entire stopover area? Figure 6 shows that goose density responded closely to the average seed density for different sub-sites. Again a threshold of *c.* 12 g $m^{-2}$ appears. The consequence is that not total biomass on offer but biomass above the threshold value is exploitable (panel B).

Natural foods formed the basis for the geese to chose the Lauwersmeer as a stopover site. The carrying capacity of *Agrostis* at this new stopover site changed in the course of time. First, a steady improvement occurred, followed by increasing numbers of geese, later a decline was seen, caused by

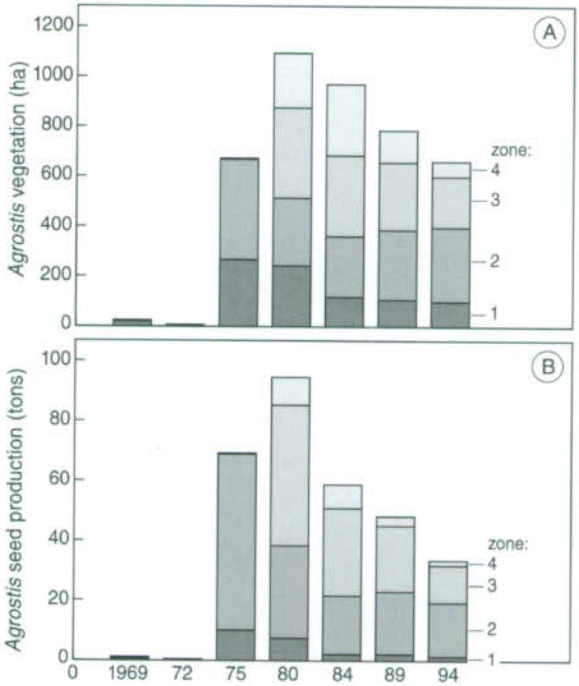

**Figure 7.** Vegetation succession and seed production of *Agrostis stolonifera*. (A) Surface areas of different vegetation zones as determined by aerial photography *cf.* Figure 2, (B) seed stock on offer for the entire stopover site.

natural succession (Fig. 7). Greylags remained faithful to the stopover site and continued to increase in numbers, but they switched more and more to arable land where they took cereal grains, left over after harvesting (Fig. 8). However, the number of birds on the natural vegetation remained high, despite the decrease in supplies of natural seeds (Fig. 7). This is caused by another shift within the natural vegeta-

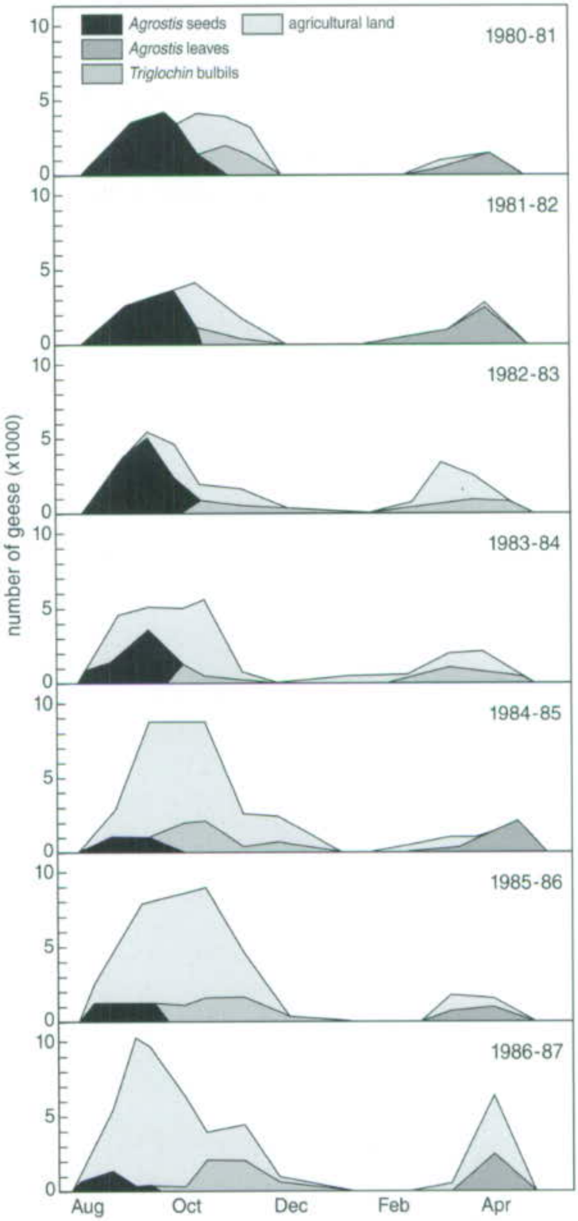

**Figure 8.** Use of natural and agricultural land by Greylag Geese in the Lauwersmeer area during the non-breeding season. Note the declining use of *Agrostis* seed stock in relation to the timing of use of agricultural land (subsequently cereal stubble, sugar beet leftovers and grassland). In spring only leaves are eaten.

tion towards the highly palatable bulbs of *Triglochin palustris*. If we correct for birds feeding on this food source, the decline in use of *Agrostis* ears was even greater than the decline in the availability of this food stock. This can be explained because stubble feeding was more profitable than foraging on *Agrostis* seeds (Chapter 6). The fact that, in the first years of usage of the new stopover site, all geese profited from *Agrostis* ears sheds light on the importance of natural vegetations in building up migration traditions. Cereal fields were present well before 1969, but were not used, probably because of the lack of experience with the area. After the geese had started the exploitation of natural feeds, also the cereal fields were discovered and subsequently used. In building up migration traditions the timing of visiting the different stopover sites is important as well. For instance, the development of the vast seed supplies by pioneers such as *Salicornia* which do not ripen before October, did not attract any Greylags. Both the timing of food availability and safety (no predators) were important triggers to chose the Lauwersmeer as a new stopover site. Once the tradition to stage in this site was established the geese could assess the area in more detail, and switches in food choice could take place.

### Time window and speed of migration

Wild geese concentrated only in the areas of highest seed density. Concerning the total vegetation on offer, they only superficially used the vegetation and could have prolonged their stay with at least two months as judged by the trials with captive geese and the food supply on offer. Are there reasons to believe that the fast migration to the south parallels the minimisation of a cost factor linked to time? Two candidate hypotheses seem likely in this respect: (1) minimisation of time devoted to migration and (2) minimisation of cost of transport. Is there a need to be early at the southern wintering site? Early arrival after an energy consuming flight means a quick recovery and a good condition may be of help to defend the richer sites in the marsh. Amat (1986) and Amat *et al.* (1991) have studied the winter ecology of Greylag Geese in the delta of the Guadalquivir in SW Spain (80-120 000 winterers). Geese were selecting energy-rich food consisting of the tubers of *Scirpus maritimus* and *S. littoralis*. Greylags depleted their food supply in the marshes. The Norwegian Greylags (recognisable by neck collars) were found more frequently on the edges of the marsh and were observed to forage more on grasses than the geese from Sweden and central Europe (H. Persson, B. Voslamber, MRE pers. obs.). Also Villafáfila in northern Spain (15-35 000 winterers of which many Norwegian) has both *Scirpus* tubers on offer in the brackish marshes, as well as leaves of cereals on the neighbouring fields (MRE pers. obs.). Whether intraspecific competition with the (structurally larger) Swedish and central European geese plays a role in this within-site differentiation of habitat use remains uncertain (A. Follestad, B. Voslamber pers. comm.). A fact is that the Norwegian geese do feed on *Scirpus* tubers, and that early arrival, given the limited availability of marsh plants, together with the possibility of arriving in a dry winter, sets a premium for the geese. A large number of geese, in combination with drought of the early 1990s, caused thousands of geese to starve or become victim of hunters on the adjacent arable fields (L. Nilsson, B. Voslamber pers. comm.). There must be therefore a strong selective pressure to be ready in time to build up fat reserves in order to perform the second part of the autumn migration to Spain. In Flevoland, another important stopover site for Norwegian geese in autumn (Dubbeldam & Zijlstra 1996), Greylags were indeed observed delaying migrating south until a certain body condition was reached (Van Eerden *et al.* 1991). In accordance with this, we showed for the Lauwersmeer in this study that geese selected only food with a high energy content and "ignored" the majority of plant biomass, both in terms of species and parts of food plants. By means of the chemical analyses of these food plants and the trials with the captive geese which did not need to perform a long migratory journey, we have shown that other food items could be taken as well. However, as a consequence of lower quality, the foraging time increased markedly but this could not prevent Greylags from experiencing a marked drop in DME. As a consequence, they faced a reduced (but still considerable!) rate to store body fat from these items. Instead of awaiting the deteriorating situation these Greylags migrated south.

In a recent study on Cranes feeding on cereal seeds after harvest in agricultural fields in Gallocanta (northern Spain), Alonso *et al.* (1994) observed a comparable pattern as was described in this study. Cranes "overflew" the area in autumn although food was super abundant. No correlation existed between crane numbers and food supply in this period. The number of winterers, however, correlated well to the then much lower seed abundance. As for our geese, the winter situation was definitely far less favourable compared to the conditions when birds pass by during autumn. Alonso *et al.* (1994) suggest the existence of a feed-back mechanism in which the cranes assess actual patch quality and respond to a decrease in food abundance by a fortnightly period of delay. We think, however, not denying this feedback mechanism, that also the knowledge of other (predictable) food sources further to the south (*e.g.* the Holm Oak *Quercus rotundifolia* acorns in Extremadura) might have caused this pattern. Birds leaving Gallocanta then need not to do so (only) because of a deteriorating local food supply, but (also) because of the missed opportunity costs of staying longer at a site where they are not able to winter anyhow and reaching the main wintering site too late. The question, comparable to that of the geese, is by what proportion of the total number of cranes attending the site, this stopover site is used just for fattening up in order to reach the wintering site, and to what extent cranes are really intending to winter at the site. The meaning of the concept of facultative migration is rather limited if, as we state, well-defined ecological goals exist behind the time horizon of exploitation of the available foods present at the stopover site. Caution has to be taken before interpreting site specific foraging patterns or applying foraging theory to local field situations, without taking these choices of higher order into account.

### Fat deposition rates and maximum range of flight

The fat deposition rate in seed stripping geese was probably close to the upper limit achievable by a species of that size. According to Lindström (1991), the maximum fat deposition rates in birds are related to body weight as described by:

$$\mathrm{FDR}_{\max} = 2.80 \times \mathrm{M}^{-0.27}.$$

$\mathrm{FDR}_{\max}$ is expressed as a percentage of lean body mass. For a 2.5 kg Greylag Goose this would amount to a 2.19% increase per day or 55 g of fat, which closely corresponds to our estimate in Table 6.

In conclusion, we state that the goose's strategy is to migrate fast, by maximisation of the fat deposition rate while selecting only high energy foods. The fact that wild Greylags did not forage on leaves of *Agrostis* corroborates this conclusion, although geese were shown to be able to put on fat as well from this food type.

Gauthier *et al.* (1984) found for Greater Snow Geese *Anser caerulescens atlantica* that 41-85% of the total body mass increase was due to fat, the rest being protein and water. Also in the smaller Brent Geese *Branta bernicla* 67% fat was found (Korte 1988), compared to 77% in White-fronted Geese *A. albifrons* (Ely & Raveling 1989). Larger Sandhill Cranes *Grus canadensis* stored 40-68% as fat maximally (Krapu *et al.* 1985), whereas this was 47-61% in the Giant Canada Goose *Branta canadensis maxima* (McLandress & Raveling 1981). As was pointed out by Lindström and Piersma (1993), all these studies were carried out during spring migration. They argue that during spring the proportion fat may be lower due to the necessity to use non-fat energy stores to enhance breeding performance. If we use a conservative estimate of 60-80% fat in Greylags during autumn migration, a 56 g daily increase in fat level would mean a 70-93 g $\mathrm{day}^{-1}$ increase in total body mass. A stay of 20 days at the stopover site Lauwersmeer would thus imply an overall mass gain ranging from $20 \times 70 = 1400$ g to $20 \times 93 = 1860$g.

A male goose of 2500 g upon arrival would thus increase to 3900-4360 g, which corresponds to actual peak body mass recorded in the species (4200-4560 g, Cramp & Simmons 1977, M.R. Van Eerden & M. Zijlstra unpubl. data).

The second line of arguing in order to explain the fast migration and connecting fattening rate is derived from the cost of transport. In a relatively heavy species as the Greylag Goose, the cost of active flight achieving maximum range $P_{mr}$ is estimated from allometric parameters according to Rayner (1988, 1990) by the formula:

$$P_{mr}\ (\text{Watt}) = 27.21 \times M^{1.590} \times B^{-1.818} \times S^{0.275}$$

For a goose with a fresh body mass $M = 3.5$ kg, a wingspan of $B = 1.60$ m and a wing area of $S = 0.307$ $m^2$, the required power amounts to 61.3 Watt. From empirical data, Rayner (1990) also estimated the maximum flight range r, taking into account a reduction of flight costs as body mass progressively declines over the flight-path:

$$r\ (\text{km}) = 82430 \times e \times m^{-0.177} \times B^{1.265} \times S^{-0.370} \times (1 - f^{-0.177})$$

In this formula we used a power efficiency of $e = 0.15$, and a lean fresh mass of $m = 2.2$ kg. As we know the distance to be travelled, 1550 km to Villafáfila (Zamora) and 2025 km to the Marismas del Guadalquivir (Sevilla), we can derive f = ratio between maximum fresh weight and lean mass and thus the peak body mass required to overcome the distance under still air conditions. A peak body mass of 3500 g is thus able to carry the goose down to 2377 km, good enough for a non-stop flight to southern Spain. By contrast, a Greylag Goose of 3000 g is just able to reach the stopover site Villafáfila within its range of 1611 km. It is clear from this exercise that only body weights over 3500 g enable birds to reach the final destination. Overweights of 4000 g and more that were calculated, result in either a better condition upon arrival, which may be used either during the phase of exploration of the new area or as a buffer against headwind which may confront the geese on their long journey. Maximum range would be extended to well over 3000 km, or stated otherwise, would provide extra energy to overcome a headwind of 40 km $h^{-1}$ for 25 h in duration. Overloads are well-known to occur in arctic breeding waders during spring migration (see review by Gudmundsson *et al.* 1991).

Saving energy in choosing tailwind may therefore be an important strategy to minimise the risk of getting stranded between the stopover sites. Ebbinge (1989) showed for Brent Geese a significant correlation of tailwind assistance in the Baltic and breeding success, mediated through body condition upon arrival. Greylags often use the days around the full moon to migrate from the Netherlands southward during autumn (M. Overbeeke & M. Zijlstra unpubl. data). As tailwind and moonlit nights rarely coincide during each lunar cycle, the birds can only profit from good flight conditions when the required body condition has been achieved. Whether or not the chance of having tailwind along different parts of the migratory pathway shows a seasonal dependence as well is unknown. Future study may shed light on this aspect which, if it exists, would only further narrow down the time window that the birds can use. Maximisation of the fattening rate at the stopover site is thus of prime importance in order to be able to respond most adequately to weather conditions which permit migration.

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## Chapter 12

# Moulting Greylag Geese *Anser anser* defoliating a reed marsh *Phragmites australis*: seasonal constraints *versus* long-term commensalism between plants and herbivores

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# Moulting Greylag Geese *Anser anser* defoliating a reed marsh *Phragmites australis*: seasonal constraints *versus* long-term commensalism between plants and herbivores

Greylag Geese *Anser anser* (> 60 000) exert a strong grazing pressure (foraging zone 300-700 ha) while flightless for 40 days during wing moult in the Oostvaardersplassen, a recently established freshwater reed marsh in the Netherlands.

The annual event of mass defoliation (max. 70%) of the new growth of reed by the avian herbivores is considered a strong selective force leading to a substantial change in plant phenotype (decreasing seed production, height and stem diameter, increasing shoot density) and thus leading to a spatial differentiation of the previously homogeneous reed beds.

Leaves of reed stands that had been heavily grazed over many years had a higher protein content than leaves from ungrazed stands. Geese selected leaves which gave the highest energetic return and neglected stems, which were less profitable. Overall, the food was only poorly digestible (13-35% of organic matter), sharply decreasing during the period of wing moult. At the same time an increasing proportion of cell wall components was digested (hemicellulose 21-34%). However, this physiological adaptation by the geese and the higher yield due to changes in the plant's morphology, which was the result of mass feeding over many years, could not prevent an energy shortfall of less than 50% of the estimated daily energy requirements because of intraspecific competition. Due to increasing bird numbers and the sudden decrease of habitat because of lowered water tables, DME decreased to even 22% of DEE on average in 1988, the rest was mobilised from the fat reserves (upper limit of 27 g day$^{-1}$). This peak demand on body reserves coincided with the observation of reverse migration of 7-15 000 geese in the years 1988-1990 which had arrived in the area but left again and moulted elsewhere. Also, the body condition of geese returning from the reeds in this period was poorer than before.

It is concluded that the area of flooded reed limited the number of moulting Greylags after a period of 15 years with increasing numbers. Apparently geese are able to determine their food supply needed to overcome the period of flightlessness (38 days) and we suggest that the pre-moult body condition may be used as an extra estimator for the decision to remain or depart.

Detailed records of the grazing process, both on the scale of individual leaves and on the scale of the entire marsh, provided evidence for the long-term benefit for both geese (increased carrying capacity) and the heavily exploited vegetation (a slowing down of the rate of succession).

## Introduction

Common Reed *Phragmites australis* often forms a major component of freshwater marshes in both the northern as well as the southern hemispheres. In the temperate regions, its perennial life form is

(A) Aerial view of grazed and ungrazed Reed *Phragmites australis* vegetation by moulting Greylag Geese *Anser anser*. (B) Close-up of Geese and Reed, showing turned head at breaking of stems, Oostvaardersplassen, July 1985.

**Table 1**. Maximum aboveground biomass of *Phragmites australis* (gDW m$^{-2}$) for different countries in the western Palearctic. Trophic level of marsh is indicated, h: hypertrophic, e: eutrophic, m: mesotrophic, o: oligotrophic *cf.* Vollenweider & Kerekes (1982). Tetra = tetraploid races included in countries in eastern Europe.

| Author | Max. Biomass (gDW m$^{-2}$) | Trophic level | Country | Remarks |
|---|---|---|---|---|
| Korelyakova 1971 | 74 - 9 339 | e | European Russia | Tetra |
| Dykyjová 1970 | 3 700 - 8 560 | e/h | Czech Republic | Tetra |
| this study | 539 - 4 400 | e | the Netherlands | |
| Ho 1981 | 3 975 | h | United Kingdom | |
| Gorham & Pearsall 1956 | 500 - 2 500 | o/e | United Kingdom | 9 sites |
| Kvêt 1971 | 943 - 2 428 | e | Czech Republic | |
| Van der Toorn 1972 | 952 - 2 075 | o/e | the Netherlands | |
| Krisch *et al.* 1979 | 1 100 - 1 800 | e | Germany | |
| Hübl 1966 | 1 350 - 1 550 | e | Germany | |
| Mook & Van der Toorn 1974 | 540 - 1 549 | e | the Netherlands | |
| Kvêt 1973 | 824 - 1 510 | e | Czech Republic | 17 stands |
| McLeod 1981 | 1 300 - 1 400 | e | United Kingdom | |
| Van der Linden 1990 | 1 360 | e | the Netherlands | |
| Ho 1981 | 669 - 1 351 | m/e | United Kingdom | |
| Best *et al.* 1981 | 286 - 1 247 | m | the Netherlands | |
| Mason & Bryant 1975 | 524 - 942 | e | United Kingdom | |
| Meulemans 1989 | 714 - 906 | o/m | the Netherlands | |
| Kowalczewska & Wasilewski 1966 | 502 - 820 | o/m | Poland | 4 sites |

most prominent during summer, when peak biomass is variable but may amount to well over 2500 gDW m$^{-2}$ (Table 1). Reed ecology is comparatively well studied (Björk 1967, Haslam 1969a, b, c, 1970b, Van der Toorn 1972, Dykyjová & Kvêt 1978). Several forms or ecotypes have been described (Bakker 1958, Conert 1961, Haslam 1970a, Jansen 1951), differing in production and structural characteristics (stem density, diameter, shoot length and number of inflorescences). According to Van der Toorn (1972), these different types are best adapted to their specific environment (edaphic and microclimatic). Part of the variation could be attributed to differences in chromosome idiograms (Björk 1967, Dykyjová 1971, 1978).

During winter the dead stems with panicles constitute an important structural factor in the marsh, where many other plant species occur only below ground. Reed is well-known for its protective effect on soil erosion as it gives protection from wind and waves. Many species of marsh birds nest in extensive reed stands, and others find sufficient shelter to moult (a.o. Hudec & Štastný 1978). However, the substantial reed production leads to an expansion which may cause rapid overgrowth of shallow water. The accumulation of litter, on the ground as well as in standing dead shoots, may eventually cause reed to disappear in terrestrial stands because of the invasion of other plant competitors (Graneli 1989).

Wetlands are typically detritus based ecosystems (Odum 1971). The largest part of the yearly production within stands of *Phragmites* goes directly to the decomposers (Imhof 1973, Mason & Bryant 1975, Úlehlová 1978). Direct attacks on green biomass during the growing season occur by means of fungi (*Puccinea phragmites*, *P. magnusiana: cf.* Sessink 1988), insects and acarids (a.o. the moths *Archanara geminipuncta* HW *(Lepidoptera, Noctuidae)*, the flies of the genus *Lipara (Diptera, Chloropidae)* and the acarid *Steneotarsonemus phragmitidis:* Skuhravy 1978), birds (Coot *Fulica atra:* Krauss 1979, Greylag Goose *Anser anser*: Kvêt & Hudec 1971) and introduced mammals (Coypus

*Myocastor coypus:* Mason & Bryant 1975, Boorman & Fuller 1981, Muskrat *Ondatra zibethicus:* Pelikán 1978, cattle: Van Deursen & Drost 1990). Man often harvests reed during winter and the cutting and removal of biomass is known to support the maintenance of a vital stand (Van der Toorn & Mook 1982, Husák 1978).

The natural event of mass grazing on reed vegetation by Greylag Geese *Anser anser* during wing moult in June was studied in order to unravel the mutual effects of herbivory on both plants and consumers. The extreme defoliation of the reed vegetation seemingly contradicts the short-term goal of plant growth and survival, but is, as we will show, definitely beneficial to both herbivore and plant in the long-term.

## Study area and methods

### Study area

This study was conducted in the Oostvaardersplassen, a freshwater marsh in the Netherlands (5600 ha, 52°26′N 5°19′E). The area has been able to develop with a minimum of management measures since 1968, when the polder Zuid Flevoland was reclaimed from lake IJsselmeer. Reed sowing from aeroplanes was commonly practised as the first step of polder development (Bakker *et al.* 1960, Van der Toorn & Hemminga 1994).

A 2600 ha reed marsh on clayey soil forms the wet part of the reserve together with an area of 1060 ha of shallow water and pools, a further 2300 ha consists of wet meadows, extensively grazed fields with some bushes and small woodlots on drier soils. The Oostvaardersplassen nature reserve has become one of the most important freshwater marshes for water birds in western Europe (Vulink & Van Eerden 1998). The area is the key moulting site for Greylag Geese in Europe with a yearly maximum of over 60 000 birds in recent years (Zijlstra *et al.* 1991 and unpubl. data).

The water table management in the reserve is set by a controlled system of a pumping station and an outlet. The maximum fluctuation in water tables in the wet part was between -3.65 m NAP (Dutch ordnance level) during both winter and spring and -4.25 m NAP during summer. In 1987, water tables were lowered in the western part of the marsh in order to re-extend the vegetated part of the marsh. In the eastern part, water tables were kept at the original high spring level. The drawdown in the western part lasted until 1991 when water tables were reset stepwise by keeping the precipitation surplus in order to reach the original level within three years. This gave us the opportunity to study the large scale effects of the water table management on the behaviour of the geese and the performance of the reed.

### Vegetation patterns and goose numbers

Aerial photography (perpendicular false colour 1:5000) provided data on the distribution and density of reed vegetation. Marsh-wide surveys were available for 1975, 1980, 1985 and 1988. Partial surveys existed for 1983 and 1991. After identifying the different vegetation patterns in the pictures, the vegetation was described in the field in permanent quadrates. The following structural parameters were measured: total cover, shoot density, shoot length, stem diameter and the number of panicles per shoot (as determined in August when growth was completed). Reed samples were taken to determine the dry weight of leaves and stems. Prior to the actual moult (bi-weekly), geese were counted in the fields surrounding the wet part of the marsh. Identification of individually coded neck-collars assisted in determining the turnover rate of bird numbers present on the fields (*cf.* Zijlstra *et al.* 1991). Aerial counts at the time of peak numbers in the marsh and a registration of geese seen migrating to and from the Oostvaardersplassen provided additional information about the actual number of moulters.

### Production and consumption

Standing crop was estimated by clipping of green material, or by means of a calculation from repeated measurements of stem height and density per zone (see review of method by Ondok & Kvêt 1978). The growth pattern was determined in a non-destructive way by following the condition of individually marked shoots. Losses of biomass were calculated by taking note of grazing by geese and/or insects as well as of natural mortality of leaf and shoot material. The measurements were conducted in different zones, which could be detected in aerial pictures. Production was thus calculated on a larger scale than the result of consumption, dead-loss and re-growth after grazing.

The diet of the geese was determined by identifying the grazed plants in the moulting area and by microscopical analysis of the droppings (Owen 1975).

Areas grazed by geese were determined through aerial surveys by taking oblique colour slides from a high-winged Cessna 172. Grazing by geese turns the vegetation from bright-green into a distinct yellowish-brown. In the field, consumption was quantified just after the geese had left the area. The breaking and snapping of stems and subsequent stripping of leaves could be well reconstructed from the remaining material. A comparison was made with ungrazed parts (naturally or in exclosures). Detailed records of marked shoots provided information on a small scale *e.g.* about the timing of grazing, the preference for individual leaves and the amount of material spilled. The distribution of vegetation and areas grazed by geese were entered into a GIS, allowing for a detailed calculation of areas and an assessment of relationships with water tables.

To assess food quality and usage by the geese, chemical analyses of food plants and fresh droppings were carried out (*cf.* Van Soest 1982). Neutral detergent fibre (NDF), acid detergent fibre (ADF), hemicellulose (NDF-ADF), Kjeldahl N and ash on vegetation and fresh droppings of wild birds (collected on introduced small wooden plateaus used by resting geese) provided information on digestibility and protein content (6.25 × N-Kjeldahl) of the food plant. Unprecipitable nitrogen was determined in droppings according to the method of Terpstra & De Hart (1974) to allow a distinction between faecal and urinary N. Using ADF as an internal marker (no cellulose digestion), the digestibility of component $i$ in the food was calculated according to the equation given by Prop and Deerenberg (1991):

$$DC_i(\%) = \frac{[Cf_i\text{-}(Mf/Md) \times Cd_i]}{Cf_i} \times 100$$

where $Cf_i$ and $Cd_i$ = percentage of component $i$ in the food and droppings; $Mf$ and $Md$ = percentage of the marker in the food and the droppings.

Some observations on foraging wild geese could be carried out from hides in the area. Gross food intake rate was calculated for leaves of different position at the shoot, expressed as average leaf mass per height class. Handling time and the time needed to tear off and swallow a leaf, added to the time needed for snapping of the stem, was measured in order to quantify the intake rate. The snapping power in relation to stem width was determined by taking freshly collected shoots into the laboratory and putting weight perpendicularly until breakage occurred.

### Reed growth and recovery from grazing

Enclosures were used for the short-term assessment of plant growth and food quality during the season. In addition, enclosures were set up around individual patches of reed to study the effects of undisturbed growth over a period of five years (1986-1990). During the moulting period in 1989, four captive Greylags (originating from the wild population several years before) were introduced in a series of 100 m$^2$ large plots of penned reed vegetation. The birds were kept in the pen fenced with nylon netting for several days in succession. At a known grazing pressure the effects of grazing could be quantified more precisely, also at times different from grazing by the wild geese. A small hide was installed to watch the geese from nearby.

After the drawdown of the water table in the western part of the Oostvaardersplassen in June 1987, only a few centimetres of water remained on the surface of the reed marsh during the growing season. The large-scale effects of the reduced grazing pressure on the vegetation could thus be studied, using the same sample sites as when the water tables were high.

## Results

### Goose grazing

The diet of the moulting geese consisted for almost a 100% of the leaves of reed. Accidently taken were *Typha latifolia, Urtica dioica, Lycopus europaeus* and *Salix viminalis,* together representing less than 1% of the diet of the geese. Few other plants occurred in the moulting area. Definitely avoided were *Senecio congestus, Mentha aquatica* and *Rumex hydrolapathum* which never showed any sign of having been grazed.

The geese entered the marsh between 27 April and 15 June. The majority performed wing moult from 25 May until the first days of July and were flightless for a period of 38 days (Loonen *et al.* 1991, Zijlstra *et al.* 1991). Goose numbers have increased from a few hundred in the early seventies to over 60 000 in 1992 (Fig. 1). Grazing always occurred in dense flocks. In the early seventies, the geese concentrated their grazing on a few spots only, extending considerably as their number increased (Fig. 1).

Each year, the geese started defoliating the reed plants from the centre of the marsh. They reopened the marsh from pools or open places with scattered vegetation and grazed in a systematic way towards the edges. This annual movement occurred in more or less the same sequence as was observed during the original extension of the exploited area over the years. Water proved to be an essential factor for grazing. Only reeds standing in water were grazed, a knife-edged border limiting the area of exploited and totally unaffected reeds. The drawdown of the water table that occurred in part of the marsh from 1987 on caused the geese to retreat into the wet part entirely (Fig. 1).

The geese operated in dense flocks and were observed working shoulder to shoulder through the jungle of reed. They grazed during the day and sometimes also during the night, but quantitative data are insufficient to provide a complete time budget. The geese used two techniques for leaf ingestion. First, they opened the "runways" of the previous season re-colonised by solitary thick shoots. They did so by grazing while swimming ("swim-graze") just feeding on the green parts within easy reach. By reaching slightly above their heads, the new shoots and the lower leaves on older shoots were torn off. Second, the geese returned for a second and sometimes a third time to exploit the denser part of the vegetation by "snap-grazing". Shoots were vigorously snapped on average 32.8 cm (SD = 11.3 cm, $N = 78$) above the water's surface and subsequently geese bit and tore off the leaves. The leaves were observed to be swallowed whole, during which the geese drank frequently.

During the snapping phase, the birds concentrated their grazing on the heavier leaves of the middle part of the shoot. Because of the larger size of the fully emerged, higher ranking leaves on the growing stems, leaf mass ingestion increased when the geese started snap-grazing instead of swim-grazing (Fig. 2A, B). The uppermost leaves were little grazed, despite their high mass. Foraging on the highest ranking leaves on the stem was hampered because of the greater distance to the twisting point, which made them less easy to tear off. The intake rate was significantly lower for high and low ranking leaves compared to the preferred central leaves (Fig. 2C). The longer shoots often appeared to have been snapped

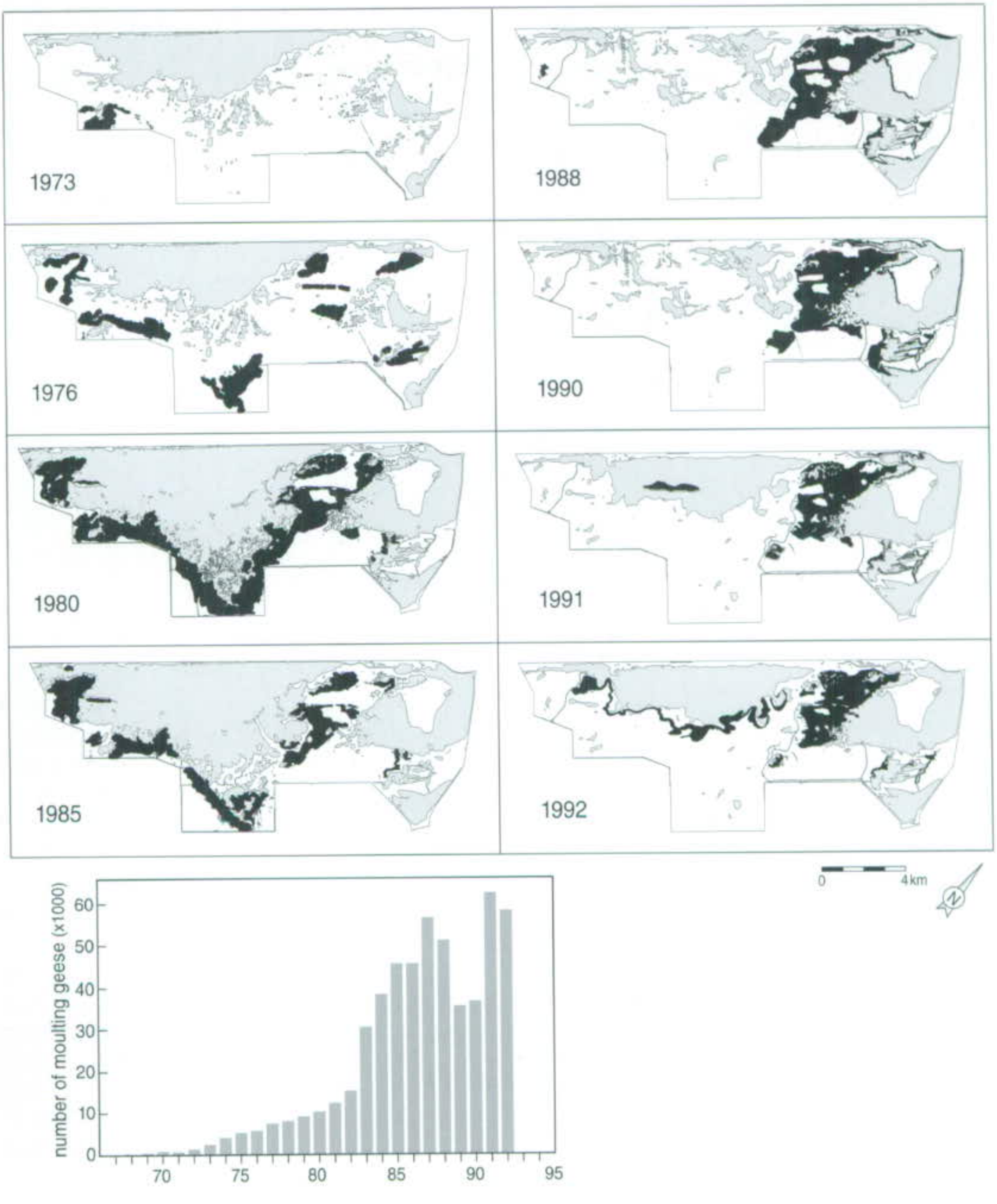

**Figure 1.** Moulting areas in the Oostvaardersplassen (black) in eight different years in relation to the number of Greylag Geese (below). Indicated are only areas intensively used by geese. Note the extension of the moulting area along with increasing numbers of geese and the concentrated start of usage of new areas from pools. In 1988 the SW part of the marsh was set in the dry phase, resulting in a complete abandonment by the moulters. Re-flooding in 1991 and 1992 led to the return of the geese in the western part.

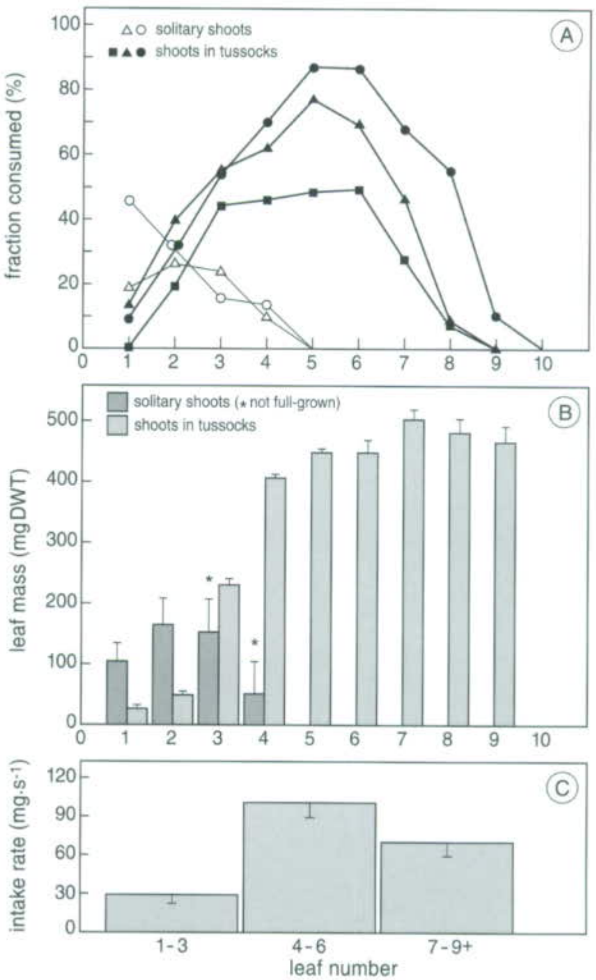

**Figure 2.** (A) Seasonal grazing sequence of a stand of type 3 reed. At first the heavier leaves from solitary shoots are grazed by which the runway system is re-established, followed by leaves of the tussocks themselves. Data presented as fraction of leaves consumed per interval. Geese preferentially took the leaves from the central part of the shoot leaving the lower ranking (smaller) and highest ranking leaves (beyond reach) underrepresented. (B) Average mass per leaf in relation to leaf number and shoot type. (C) Intake rates by wild geese for three categories of leaves in tussocks calculated over total foraging time observed per category. Bars indicate SD in (B), 99% CL in (C). Leaves number from bottom up.

up to four times. About 15-20% of the total biomass eaten is grazed directly while swimming, the rest is taken by the snapping method. A comparison between the material floating around and that disappearing in total from the vegetation gave an estimated spilling rate of 5% of all leaves, 15 - 30% of the stem base of newly emerged shoots outside the tussocks and 50 - 70% of the top ends of snapped shoots from tussocks.

## Vegetation patterns

The continuous grazing of the marsh during spring growth year after year resulted in an alteration of

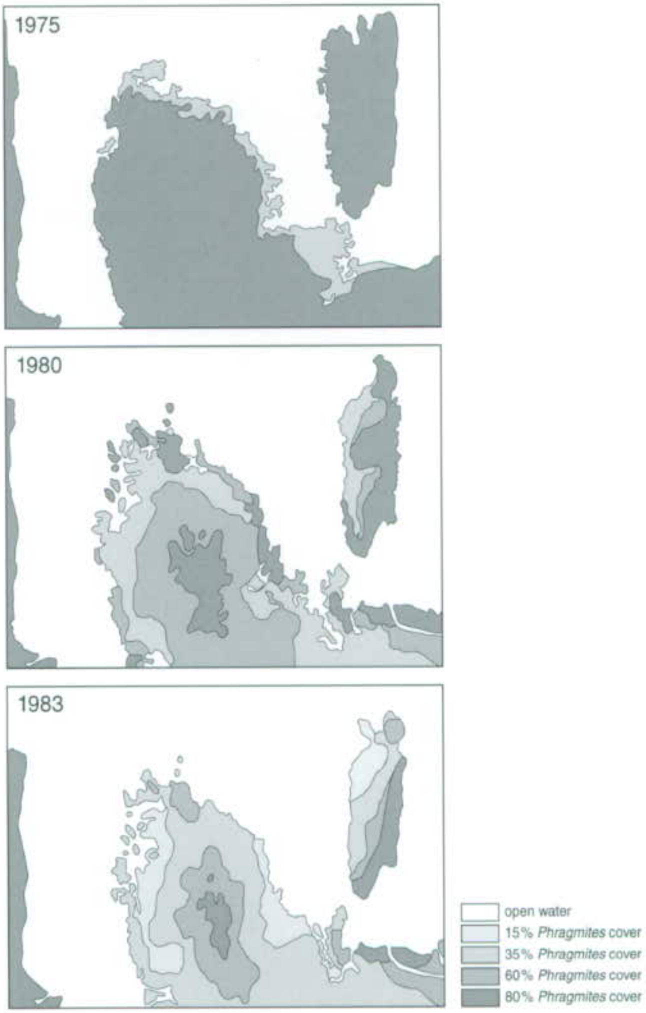

**Figure 3.** Long-term effect of grazing of an originally closed stand of reed. Vegetation maps deduced from aerial photographs show the percentage cover in the Willemsvaart area. From 1983-1987 no major changes occurred, in 1990 the fourth year of the drawdown of the water table, the ban of goose grazing resulted in the situation comparable to that as shown for 1975.

the habitus of *Phragmites*. Figure 3 shows the process of opening up the formerly closed stand of reed over a period of eight years. The geese started moulting in this area in 1973, exploiting only the margins. In later years more and more of the centre of that bed was used. After 1983, *i.e.* after ten years of successive grazing, a stabilisation occurred in this process. Although the total vegetation cover declined over ten years, the boundaries of the original vital field remained almost unaffected. This finding is verified by a marsh-wide comparison between digitised aerial photographs (H.J. Drost pers. comm.).

From the photographs, five different zones of vegetation cover could be distinguished. Measurements were taken in the field and revealed significant differences among the various parameters of the vegetation structure (Table 2). Type 1 represented the most heavily grazed reed belt over the years. After grazing, the geese had completely bitten off the shoots, leaving partly dead, broom-shaped bundles of straw. Only some green leaf material was apparently hidden in the tussocks. Type 2, 3 and 4 consisted of gradually taller and thicker shoots, occurring in tussocks of increasing diameter (type 2 and 3), or in large patches of reed transected by paths only (type 4). Type 5 consisted of ungrazed reed. The grazing by geese over many years during late May, June and early July thus resulted in the gradual development of a structurally finer type of reed with a dense stand of slender stems and relatively narrow leaves.

### Production and consumption

The reconstruction of the green material removed by grazing geese led to an estimation of consumption per zone. Consumption, loss through senescence and recovery after grazing until the end of the growing season in early September, gave an estimation of the total production (Table 2). Considering

**Table 2.** Various parameters of performance of *Phragmites* as distinguished in the field by five different types (1 = most heavily grazed, 5 = ungrazed by geese).

Consumption by geese, leaf mass and production expressed for vegetated area (veg) and average per zone (zone) including uncovered areas. Leaf mass refers to the situation in June prior to the start of grazing. Production includes grazing losses and regrowth after moult. All mass data expressed as dry weight. Spearman $r_s$ correlates average values for different parameters with long-term grazing pressure for each type.

| | Vegetation type | | | | | | |
|---|---|---|---|---|---|---|---|
| *Phragmites australis* | 1 | 2 | 3 | 4 | 5 | $r_s$ | *P* |
| Vegetation cover, per cent | 8 | 15 | 35 | 60 | 80 | -1.0 | 0.01 |
| Shoot length, cm | 62.9 | 80.7 | 85.4 | 160.7 | 221.4 | -1.0 | 0.01 |
| Stem diameter, mm | 3.1 | 3.5 | 3.1 | 4.6 | 5.9 | -0.9 | 0.05 |
| Shoots $m^{-2}$ | 1180 | 1560 | 1325 | 625 | 250 | +0.9 | 0.05 |
| Leaves $m^{-2}$ | 3068 | 2964 | 2120 | 1938 | 1525 | +1.0 | 0.01 |
| Leaves per shoot | 2.6 | 1.9 | 1.6 | 3.1 | 6.1 | -0.6 | NS |
| Secondary stems, per cent | 31 | 44 | 58 | 57 | 0 | +0.1 | NS |
| Panicles per 100 shoots | 0.03 | 4.49 | 14.73 | 82.66 | 46.88 | -0.9 | 0.05 |
| Leaf mass, mgDW | 143 | 244 | 153 | 236 | 412 | -0.7 | NS |
| Leaf mass, g $m^{-2}$ (veg) | 437 | 724 | 323 | 458 | 628 | +0.5 | NS |
| Leaf mass, g $m^{-2}$ (zone) | 35 | 109 | 113 | 275 | 502 | +1.0 | 0.01 |
| Consumption, g $m^{-2}$ (veg) | 307 | 32 | 113 | 91 | 0 | +0.9 | 0.05 |
| Consumption, g $m^{-2}$ (zone) | 25 | 49 | 40 | 55 | 0 | +0.1 | NS |
| Consumption, per cent (biomass June) | 70 | 45 | 35 | 20 | 0 | +1.0 | 0.01 |
| Production, leaves g $m^{-2}$ $year^{-1}$ (veg) | 2890 | 3340 | 1400 | 1810 | 1300 | +0.8 | NS |
| Production, stems g $m^{-2}$ $year^{-1}$ (veg) | 3850 | 5650 | 3000 | 4200 | 4200 | +0.2 | NS |
| Production, leaves g $m^{-2}$ $year^{-1}$ (zone) | 231 | 497 | 490 | 1086 | 1040 | +0.8 | NS |
| Production, stems g $m^{-2}$ $year^{-1}$(zone) | 308 | 848 | 1050 | 2520 | 3360 | +1.0 | 0.01 |
| Production, total g $m^{-2}$ $year^{-1}$(zone) | 539 | 1345 | 1540 | 3606 | 4400 | +1.0 | 0.01 |

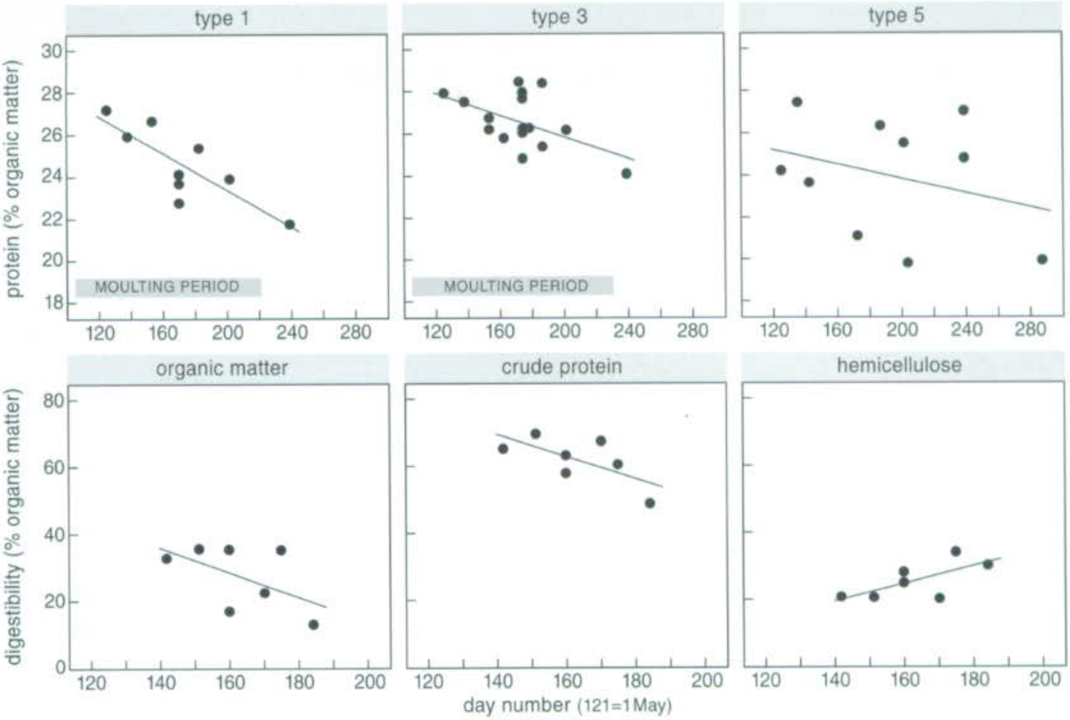

**Figure 4.** (A) Crude protein content for leaves of three types, corresponding to the level of grazing pressure in the years before (see Table 2). (B) Digestibility of leaves of *Phragmites* for three components during the course of the year as measured by chemical analysis of droppings of wild geese.

only the vegetated parts of the areas, the total production was 4400 gDW $m^{-2}$ in the moderately grazed area (type 3). In the slightly grazed or ungrazed areas, the total production was higher, ranging from between 5500 and 6010 gDW $m^{-2}$, while the highest values were recorded at the most intensively grazed parts with an average net above ground production between 6740 and 8990 gDW $m^{-2}$ vegetated area. Over the entire zone, including the uncovered parts, these values become lower: then the highest production occurred in the ungrazed parts (4400 gDW $m^{-2}$, type 5) and the lowest in the most heavily grazed parts (539 gDW $m^{-2}$, type 1).

The consumption by moulting Greylags was highest in type 1 and 2 with a removal of up to 307 and 326 gDW $m^{-2}$ in the vegetated areas in recent years (70 and 45% respectively of available biomass, 1991). Goose grazing has thus resulted in a highly productive stand which, however, through the concurrent losses of overall coverage has led to an overall decline of production.

Green leaves of *Phragmites* are of poor quality as forage. Organic matter digestibility for wild geese varied between 13 and 35%, the leaves at the end of May being more than twice as digestible as the older leaves later in July (Fig. 4). Crude protein content averaged 24.3% ($SD = 1.24$, $N = 14$) for leaves and 13.1% ($SD = 3.37$, $N = 6$) for stems (type 3), which is in accordance with the almost absolute preference of the geese for leaves. These values are low compared to reported values of 38-54% organic matter digestibility for graminoid leaves digested by Barnacle Geese and a crude protein content between 18 and 35% on the basis of dry weight reported in graminoid feeds of various species of geese

**Table 3.** Size of moulting area and reed biomass consumed per zone in the Oostvaardersplassen for six different years. In the course of the years geese concentrate their grazing more on the densely covered type 3 and 4 instead of on the open types 1 and 2. In the course of the years total yield per zone increases but average daily consumption per goose decreases as the number of geese increases. Biomass data per zone adjusted for yearly differences in weather condition.

| | 1976 | 1980 | 1983 | 1986 | 1988 | 1991 |
|---|---|---|---|---|---|---|
| Area used by geese (ha) | 280 | 674 | 461 | 452 | 387 | 309 |
| *Phragmites* 1 | 9.8 | 6.2 | 3.8 | 5.1 | 8.0 | 3.7 |
| consumed 2 | 50.1 | 48.0 | 61.2 | 19.3 | 17.5 | 22.6 |
| per zone 3 | 33.5 | 32.9 | 20.2 | 47.6 | 25.4 | 25.3 |
| (per cent) 4 | 6.6 | 11.9 | 14.8 | 28.0 | 50.5 | 48.5 |
| Total (kgDW) | 31 544 | 74 967 | 73 546 | 108 624 | 133 792 | 143 831 |
| Number of goosedays | $1.90 \times 10^5$ | $3.42 \times 10^5$ | $5.70 \times 10^5$ | $11.40 \times 10^5$ | $12.16 \times 10^5$ | $13.7 \times 10^5$ |
| Average consumption per goose per day (gDW reed) | 166 | 219 | 129 | 64 | 63 | 105 |
| Percentage DME from food [a] | 58 | 77 | 45 | 22 | 22 | 26 |
| Required use of body fat (g goose$^{-1}$ day$^{-1}$)[b] | 14.6 | 7.9 | 19.1 | 26.9 | 27.0 | 25.8 |

[a] DEE for a 2600 g goose halfway moult is set at 2 × BMR = 1237 kJ day$^{-1}$.

[b] Body fat yields 39.6 kJ g$^{-1}$ at a 0.9 efficiency rate

(Owen 1980, Prop & Vulink 1992, Chapter 3, Van Eerden *et al.*). As shown in Figure 4, protein content dropped in all three types as the season progressed, but was consistently higher in type 3 than in type 1 and 5 (ANOVA, $F = 20.37$, $P < 0.0005$, Multiple $R^2 = 0.65$ and $F = 8.94$, $P = 0.0004$, Multiple $R^2 = 0.44$ respectively). Grazing by geese thus improved food quality in the long-term. Grazing also tended to minimise the variability in protein content as determined by the coefficients of variation Cv being 0.37, 0.28 and 0.90 for type 1, 3,and 5 respectively. Digestibility of cell wall components tended to increase during the moult period, as shown for hemicellulose in Figure 4. This may be related to a longer retention time of food as the season progresses, possibly caused also by an extension of the food processing time as reported in arctic geese during the northern summer (Prop & Vulink 1992).

The average intake per day could be estimated from data on consumption per vegetation type in relation to the number of geese and the presence and usage of the different types in different years. Over the years the percentage consumption of green leaves increased as bird numbers increased by a factor ten. In 1991 geese cropped type 1 until 4 up to *c.* 70, 45, 35 and 20% respectively of the green biomass in June. Over the years, an apparent shift occurred in the relative importance of the different zones, from type 1 and 2 in 1976, 2 and 3 in 1983 to 3 and 4 in 1986 and later on. The total biomass removed was highest in the most recent years (Table 3). However, in relation to the increasing number of goosedays spent per season, the estimated average intake per goose per day decreased from 219 gDW in 1980 to 64 gDW in 1986 and 63 gDW in 1988. In 1991, the extension of the flooded part of the reed marsh again led to an increase in the average consumption to 105 gDW per goose per day. Over the years the increasing number of geese had apparently been associated with a dramatic fall in average intake. From the abdominal profiles of geese prior to and after wing moult (Fig. 5) it is clear that geese rely on fat reserves during this phase. Fat loads of birds having completed wing moult was in all five years lower than before (Kolmogorov Smirnov, $P < 0.001$). Also, in accordance with the calculations about average intake, geese tended to lose less fat in years where average calculated intake of reed per goose per day was higher (poor years 1988 and 1989 average condition after moult 3.15 and 3.04 *vs.* 3.53 and 3.69 for the better years 1991 and 1992 respectively). All differences between years are significant and body condition after moult increased from 1988 onward ($R^2 = 0.07$, $F_{1,1061} = 86.5$, $P < 0.001$).

### Reed growth and recovery from grazing

A continuous record of enclosed and grazed areas was carried out throughout the season in order to describe growth patterns. Data for the three main reed types are presented in Figure 6A. Growth rate of primary shoots increased during spring and was highest mid May coinciding with the arrival of the first large flocks of geese in the marsh. Growth rate slowed down for all types during July. The growth rate of individual shoots was associated with the level of grazing pressure previously experienced. It was highest in type 5 (ungrazed) and lowest in type 1 (heavily grazed) with type 3 being intermediate. Stem borers, caterpillars of the moth *Archanara geminipuncta,* caused a significant reduction in growth rate and peak standing crop. Those sites which suffered the least from grazing by Greylags were affected most by *Archanara* due to their larger stem width (*cf.* Table 2 and Mook 1971).

Time for recovery, *i.e.* the start of new growth, was always 20 - 35 days after termination of grazing, irrespective of the time of grazing as shown by the grazing trials with captive geese. Grazing losses

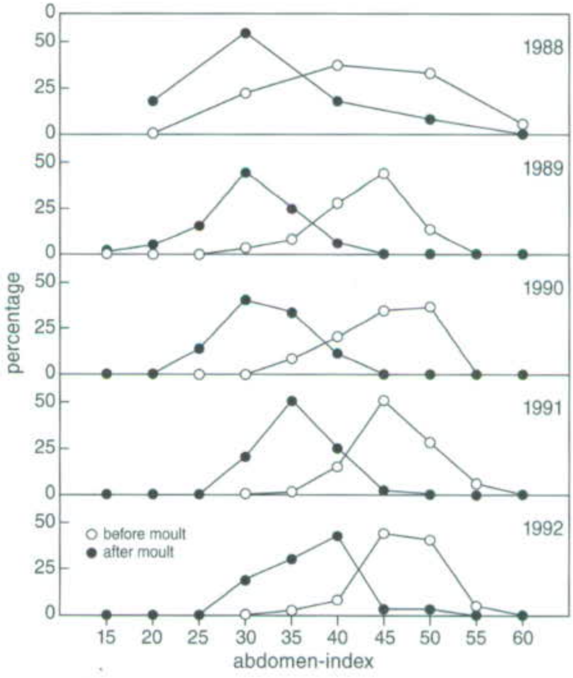

**Figure 5.** Change in body condition prior to and after wing moult in the Oostvaardersplassen as measured by abdominal profiles. The differences in rate of decrease of body condition between years coincide with the estimated average daily uptake (see Table 3).

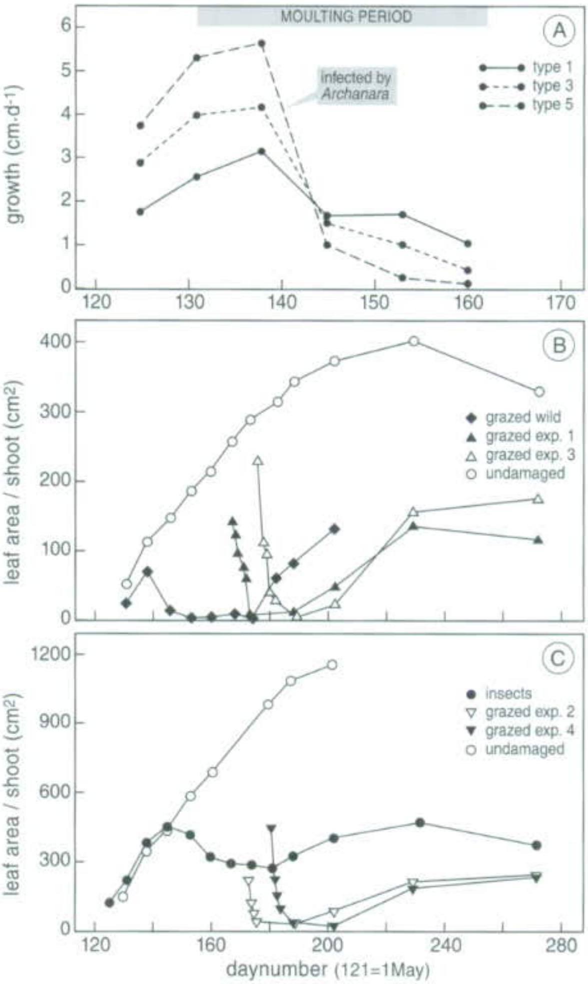

**Figure 6.** (A) Differences in growth rate of shoots of *Phragmites* from three types of enclosed reed and the differential degree of attack by caterpillars of the stem boring moth *Archanara geminipuncta*. Types 1 and 3, which usually receive a heavy grazing pressure by geese, suffer least from insect herbivory due to the smaller stem width (*cf.* Table 2). (B), (C) Biomass of two different types of reed in relation to the recovery from grazing by wild and experimentally introduced geese. Note a fixed time for recovery (25 days) irrespective of reed type and time of year.

by birds and insects in May and June were not compensated for by an increased growth rate (Fig. 6B, C). At the time of recovery, the growth rate of damaged shoots was significantly faster for type 1 than that of the undamaged shoots at the same time (Mann-Whitney *U* test, $P < 0.001$). In 1988, the end of the growing season was about three to four weeks longer for stands recovering from grazing, which, however, did not result in a compensation in achieved biomass. This implies that for a given shoot, any loss in shoot biomass due to grazing by geese, insects, or both results in a permanently lowered standing crop over the entire season.

After the drawdown of the water table in 1987, the effects of the absence of goose grazing could be

## Constraints and benefits for plants

It is an interesting question whether differential survival could have acted in such a way as to favour those clones able to cope with the circannual event of stress by grazing during the phase of most rapid growth. Plant cover decreased, associated with increasing grazing pressure (Table 2). Type 1 and 2 were, at the time of the study, the result of a struggle for existence lasting for up to 14 years after the attack of the previously seemingly homogeneous stand of tall reed. In the middle of the range is type 3 with a somewhat ambiguous growth performance. It can be regarded to consist of partly well adapted and partly not adapted clones still present in the population.

What are the overall effects of mass grazing on plant survival and fitness? The ultimate criterion for judging a plant's success or the contribution of any character to that success, is the number of descendants it leaves (Waller 1988). In *Phragmites*, individual performance is to a large extent limited to vegetative growth through clones, and generative reproduction is not very important in established stands (Haslam 1971). However, being a long-lived species (over 100 years: Rudescu *et al.* 1965) *Phragmites* may have only a few bumper years to achieve its entire reproductive output. In dynamic situations where colonisation and succession succeed each other with certainty but at an irregular time scale, the periods of vegetative growth and generative reproduction will succeed each other as well. Two fundamental goals will be pursued by the plants, first the survival of the individual and second the maximisation of the number of fertile offspring over its entire life-span. As we can only speculate about the division of individuals or clones over the different tussocks, the lifetime reproductive output on the individual level is almost impossible to determine. One tussock may comprise one or several individuals, but one clone may also survive in different tussocks.

We have shown that with respect to survival, the territory occupied by *Phragmites* has not changed greatly over the years, but that the actual coverage has (Fig. 3). As stated before, this might well be the result of a grazing-induced mortality of individual plants not well adapted to the mass defoliation in late spring. The tussocky growth pattern probably reduces the degree of defoliation because of the densely packed stems forming a defensive barrier against total depletion. Even in the most intensively visited areas, the total leaf area drops no further than to about 30% (Table 2), assuring a rapid recovery after the geese have left.

With respect to the reproductive output, we demonstrated that the highest seed output occurred in type 4, which was slightly grazed by geese. So, grazing stimulates the formation of panicles when it occurs at a very low level (Table 2). However, within one year after grazing had stopped, seed output was highest in the previously most heavily grazed zones (Table 4). This means that after the reduction of grazing pressure, the surviving plants rapidly claim the new space in between the tussocks by both the production of runners and through the establishment of seedlings. Stress tolerant clones are thus able to expand enormously, and the total seed output in the years following the ban of grazing by geese outnumbers by far the production by undamaged stands. It is clear that the selective force of grazing thus enhances the fitness of at least some, well adapted individuals. It depends, however, on the length of the stress cycle by grazing and the subsequent recovery by the abandoning of the marsh by the geese, whether goose grazing results in an evolutionary stable strategy of increasing plant fitness at the scale of its entire lifetime. Because of the present scarcity of moulting sites for Greylag Geese in Europe, geese will not often switch from one site to another. Under natural conditions it is likely that the period of stress by goose grazing which leads to a reduced reproduction is shorter than the lifetime expectancy of *Phragmites*. This means that the cyclic event of stress and recovery may well lead to an increase in fitness of those individual plants able to survive. Without any grazing, *Phragmites* stands in shallow eutrophic marshes become invaded by other species and are eventually replaced. The accumulation of litter (see Table 4) is a first step in this process. In conclusion, we hypothesise the existence of a grazing induced selection, which would result in grazing resistant ecotypes. This will be tested after the reset of the original water tables in the western part of the reserve from 1992. If right, the expanded stands of *Phragmites* will then resist grazing for a longer time than was the case during the first period of grazing, which started in the early 1970s. Transplantation experiments with the different types, accompanied by research into their genetics are underway to answer this question (Van Eerden & Zijlstra unpubl.).

A point that deserves further study is the way by which the insect and acarid herbivores lead to a counter attack, which is more or less complementary to that by the geese. The types that were heavily grazed by geese proved less vulnerable to the stem borers because of their initial stem diameter of less than 5 mm (see also Mook 1971, Tscharntke 1990). After inclusion of these alternating pathways of response to different herbivores, the earlier suggestion of Owen & Wiegert (1976) and Stenseth (1978) that the overall effect of grazing by herbivores may well lead to an increased fitness of the plants involved, could be tested. In a recent review, Crawley (1997, p. 443), still doubts any proof in favour of this hypothesis.

### Constraints and benefits for herbivores

The peak standing crop of *Phragmites* in the Oostvaardersplassen is among the highest recorded in Europe (Table 1). The young stage of the system and the fertile clayey soil rich in calcium originating from marine shell deposits, together with a favourable water table management (Van der Toorn 1972, Van der Linden 1990), may have caused this rapid growth. It might be one of the reasons that geese have become attracted to the marsh, as they are flying all the way down from their breeding range in southern Scandinavia to Poland (500-1000 km), just in order to moult. Probably the vast majority of the population of non-breeding moulters of Greylags from central Europe attended the site inside the marsh for 38 days (neck-collars, *cf.* Zijlstra *et al.* 1991). This great production together with the early phenological timing of growth of *Phragmites* compared to other helophytes (*cf.* Loonen *et al.* 1991), added to a geographically based 20 days earlier start of growth may have set a premium for the geese to arrive in such huge numbers from more eastern countries. The low metabolisable energy content of the green biomass which is even gradually decreasing during the period of moult (Fig. 4) is an extra reason for individual geese to arrive as early as possible. In the period 1980-1992, the Greylags indeed came to moult some 12 days earlier. The increase in the digestibility of cell wall components (Fig. 4) can be regarded as another adaptation to maximise the use of the food on offer, although the reported values of digestion of organic matter (max. 30%) are still low compared to those found in the arctic breeding Barnacle Goose (max. 48%, Prop & Vulink 1992). In the latter situation (24 h of daylight) also cellulose digestion was found which did not to happen in our situation.

How does the average uptake relate to the daily needs? A goose of 2600 g halfway during wing moult (unpubl. data) is assumed to have a daily energy expenditure between 1.5 and 2.0 BMR or 928 - 1237 kJ (see Chapter 6; BMR according to Aschoff & Pohl 1970). These low values which are close to the value reported for Greylags during cage existence (Gavrilov & Dolnik 1985) are not unrealistic because of low costs for locomotion (no flight, swimming/floating instead of walking/standing) and no apparent costs for thermoregulation (thermoneutrality between 16 and 32 °C). The energetic return for leaves is 18.78 kJ per gDW. Given the organic matter digestibility of 30% halfway through the period of moult (Fig. 4) and an ash content of 7% this means that a goose would need 177 - 236 gDW of reed per day. Compared to the data in Table 3, it is clear that only in 1976 and 1980 geese could rely for the greater part on the energy supplied by the food. In more recent years, they must have utilised an additional source of income in the form of body fat. Using an energy return for fat of 39.6 kJ $g^{-1}$ and an assimilation efficiency of 90% (Ricklefs 1974), we can calculate the daily contribution of fat needed to balance the budget with goose numbers as high as 56 000 in 1988. After the drawdown of 1987, in 1988 some 56 000 moulters had to concentrate budget. As plotted in Figure 7, we suggest

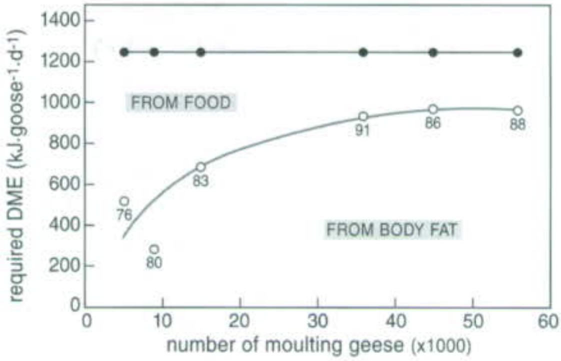

**Figure 7.** Calculated metabolisable energy from reed and fat for geese in the Oostvaardersplassen in different years. As numbers go up, birds rely to an increasing level on the use of body fat reserves. The apparent upper limit of 27 g day$^{-1}$ of fat use for the population as a whole which was reached in 1988 coincided with the reported reversed migration of 11 000 late arriving geese that year. In 1989 *c.* 15 000 geese migrated back and in 1990 *c.* 7000, after which year no more reversed migration took place.

a density dependent use of fat reserves with an upper limit at goose numbers on those areas in the marsh that still contained water (*cf.* Fig. 1). That year, according to the calculations, an average of only 63 gDW per goose per day was taken up, the lowest estimate over the entire range. It was also the year, as well as in 1987 and 1989, that between 7-15 000 Greylags departed in NE direction after having arrived in the area (neck-collars, direct observations *cf.* Loonen *et al.* 1991). The numbers showing reversed migration are higher than previously estimated because they are related to the total number of moulters, which has also been corrected after comparison of aerial counts and daily counts of geese leaving the area after moult. In 1990 and 1991 numbers were considerably lower and no return migration was observed. In 1992 and 1993 re-flooding of the western part of the marsh attracted higher numbers again, over 60 000 geese at maximum and without any reversed migration. It appears that on the level of the entire moulting population, geese may not be able to mobilise more than *c.* 77 % of their metabolisable energy from their fat stores (964/1237 kJ at 2 BMR). Transformed into fat this would be a rate of $964/(39.6 \times 0.90) = 27$ g day$^{-1}$. Over the entire moulting period, a goose would thus need at maximum $38 \times 27 = 1026$ g of fat. This is about the upper range in fat levels found in wild Greylags as determined by Soxhlet extraction of dead birds prior to wing moult (M.R. Van Eerden & M. Zijlstra unpubl.). A. Follestad (pers. comm.) reports a daily 25 g decrease in body mass of moulting Greylags in coastal Norway which corresponds well with our calculations for the Dutch site. Prior to the actual start of wing moult, geese are apparently able to judge the extent of the moulting area and the prospects for future foraging and take the decision whether or not to stay. We observed (by dropping analysis on adjacent pasture land) that geese which are still able to fly already start with the consumption of reed. They probably do this at night when roosting in the marsh. So they may use the information about the actual food situation to assess their future prospects. Interesting in this respect is that this decision making must be based on the capability to foresee the food stock available over a long period of use (38 days flightless) in relation to the density of birds. The decision to leave is not just based on the short term information of achievable daily intake rate during the first days of moult when food is still abundant.

The result of the behavioural response of reversed migration was a reduction in bird numbers. Although we do not have enough data to show that the average decrease in body condition of geese that did actually moult, as measured by abdominal profile scores before and after moult, was related to the estimated daily intake rate *i.e.* related to the degree of crowding in the marsh, the observed tendency of increased body condition after moult at a lowered goose density goes in the direction proposed. During the years of the dry phase in part of the marsh, this density was highest and return migration was observed in exactly the same three years. We suggest therefore that individual birds judge the food availability in relation to their body condition, because both factors determine the level of body condition at which geese return from the marsh. It could be shown that geese arriving relatively late *i.e.* those from Sweden (Zijlstra *et al.* 1991) and/or having a moderate to poor body condition (*i.e.* socially induced or as a result of migration costs) are likely to take part in reversed migration (Loonen *et al.* 1991). It is clear that these factors, added to the fact that the returning geese have to moult later and at second choice sites means a further set back, but it apparently still outweighs the severe risk of starvation.

## A mutual relationship

Grazing by Greylag Geese during wing moult has always been a concentrated event, even at the time of low numbers (*e.g.* 1973, Fig. 1). This concentration and a systematic way of grazing led to the mass defoliation of the food plants which, in the longer term, changed the structure of the marsh. It is clear that in this way the geese provided themselves with a suitable moulting habitat over many years. The opened reed marsh still offers enough protection, while the possibilities to escape from predators are better than in the case of a closed stand. According to data by Šmíd and Pribán (1978), penetration by solar radiation increases as the marsh opens (less foliage cover and less litter), causing higher water temperatures (up to 5 °C on average over 24 h) which may be of help in saving the costs of energy expenditure (direct radiation by the sun, indirect by higher water temperatures thus less cooling). Direct effects of grazing on the food plants consist of the formation of thinner stems growing in a more dense but less high vegetation. The habit of snapping the stems in order to reach the growing leaves high up means an extra cost to the geese. Experimental snapping of stems showed that the effort required increased exponentially with stem diameter. So, by a reduction in stem width, mass grazing

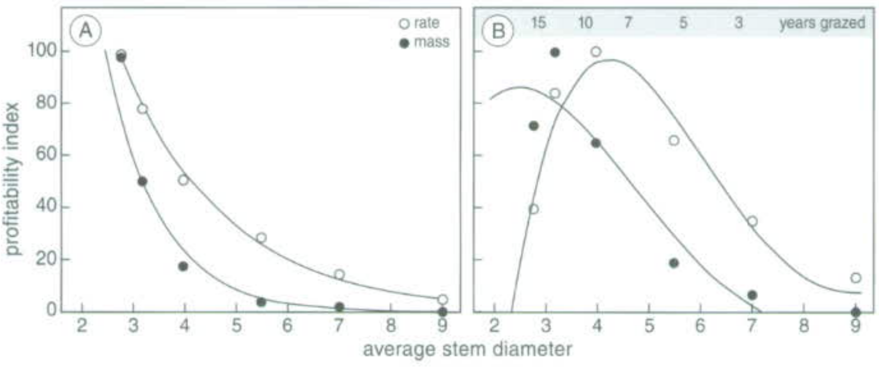

**Figure 8.** Model assessing profitability of *Phragmites* for grazing geese in relation to stem diameter. Experimentally derived values for snapping power of shoots in relation to stem diameter are the main cost factor. Protein content, leaf mass and organic matter digestibility determine yield. Two models are presented (A) based on single shoots and (B) on the biomass typical for a stand of the average stem diameter under consideration. Within each model, two curves refer to ingested digestible mass ("mass") and mass over handling time, *i.e.* time needed to snap a shoot and to swallow the leaves ("rate"). Average size of stem diameter in relation to grazing pressure by geese is indicated also, showing that the highest gain of profitability occurs after some ten years of intensive grazing.

itself has, in the long term, resulted in lower foraging costs. Similarly, the more slender leaves of type 1 and 2 can be torn off and swallowed more easily, whereas the digestibility and protein content of leaves in the grazed areas was shown to be higher. Figure 8 shows the còmbined effect of plant quality and yield for the geese in terms of profitability in relation to stem diameter. Two sets of models have been worked out, one based on individual shoots and the other on a higher vegetation level, taking shoot density and percentage cover into account. Within each model, two profitability curves have been calculated, one based on ingested *mass* and the other on mass and time needed, referred to as *rate*. As can be seen, both sets of models have the highest profitability at the lower end of the range in stem diameter *i.e.* after a period of grazing of at least ten years in succession. Concerning the level of individual shoots, the form of the curve is exponential, with the highest profitability at the lowest stem diameters. This set of curves is relevant to geese which are able to arrive early, and face little competition from other geese. They show no restriction to any lower limit, the main factor being the reduction of the cost to snap the shoots as stem diameter declines. If, on the other hand the vegetation density is being taken into consideration, an optimum profitability exists between 2 - 4.5 mm shoot width. In other words, from an evolutionary point of view, the prolonged grazing pressure over many years has resulted in a continuous process of shaping the plant's phenotype into the direction of the herbivore's benefit. Only because of intraspecific competition amongst the herbivores (which causes an upper limit of carrying capacity), the highest profitability occurs between 2 and 4.5 mm stem width, below which profitability declines because of the low density of plants. The latter model with an upper limit of grazing pressure is the most realistic for the field situation.

By transformation of the reed beds, the geese increased their yield per hectare from a mere 112 kgDW $ha^{-1}$ in 1976 and 1980 to 465 kgDW $ha^{-1}$ in 1991. We may therefore conclude that the geese, by the effect of concentration, both on a European scale as within the marsh, reap several benefits of their own action.

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