Bewick's Swans *Cygnus columbianus bewickii* utilising the changing resource of *Potamogeton pectinatus* during autumn in the Netherlands

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Returning from the breeding grounds, Bewick's Swans show a clear preference for Sago Pondweed tubers. For two lakes in the Netherlands, which may hold up to almost half of the entire flyway population, data on timing of arrival, exploitation patterns, and bird numbers in relation to available food stocks are presented. The swans depleted the tuber stocks down to a certain threshold value, below which no grazing occurred. Estimates of daily energy intake were in accordance with field metabolic rate. Quantifying food stocks by means of aerial photography and detailed sampling reveals an adequate estimate of carrying capacity. The importance of the availability of high quality macrophyte food during autumn migration is stressed, and discussed against the background of the apparent scarcity of such food sources along the flyway of this population. We suggest the necessary existence of stopover sites during autumn somewhere in the NE Baltic/White Sea region.

Like many other migratory waterfowl, Bewick's Swans *Cygnus columbianus bewickii* rely heavily on agricultural land for the greater part of the period of wintering in western Europe (Cramp & Simmons 1977, Merne 1972, Dirksen *et al.* 1991). The swans' original foods, however, consist of submerged macrophytes vegetation such as Pondweeds *Potamogeton* spp., *Myriophyllum, Ceratophyllum* and *Zannichellia* (Brouwer & Tinbergen 1939), but also *Phragmites australis* and *Typha latifolia* (Bauer & Glutz 1968, and pers.obs.), typical species for eutrophic fresh water marshes. In brackish tidal basins *Zostera* is also eaten (Brouwer & Tinbergen 1939, Spärck 1957). Often the birds' winter food consists of below ground parts like stolons, tubers or bulbils. The loss of principal aquatic habitats for Bewick's Swans in the Netherlands, and their consequent shift to arable land, has been described by Timmerman (1977) and Poorter (1981). The present distribution and food choice in the Netherlands is described by Dirksen *et al.* (1991).

Table 1. Peak number of Bewick's Swans simultaneously feeding on *Potamogeton* in the Netherlands 1986-88. Population size: 16-17,000 birds (Beekman *et al.* 1985, Dirksen & Beekman 1991).

year	Lauwersmeer	Borderlakes	total
1986	3600	4400	8000
1987	1200	6800	8000
1988	6500	1500	8000

Few studies exist relating bird numbers on the larger scale to available food stocks (*cf.* Newton 1980 for review). In this paper we present evidence for the presence of a limiting food stock which attracts a major part of the entire flyway population to a few lakes in early autumn (Table 1). Quantifying this food stock (consisting of tubers of Sago Pondweed *Potamogeton pectinatus*) revealed data which describe the carrying capacity for the entire site. We argue that detailed measuring of annual variation in available food stocks, combined with data on utilization by the birds, is an important method leading to a better understanding of the birds' requirements and also enabling us to detect possible bottle-necks for survival in their annual cycle. The potential role that *Potamogeton* plays in replenishing energy reserves of Bewick's Swans after the long migration from the breeding grounds is discussed in relation to timing of autumn migration.

Study sites

The two study sites, lake Lauwersmeer and lake Veluwemeer, were formed by the embankment of estuaries (Fig. 1). Lake Lauwersmeer (2100 ha, 53°22'N 06°13'E) was created in 1969 when the Lauwerszee was closed off from the Waddensea. Within two years the water became fresh but the bottom contained salt for a period

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Figure 1 Location of sites where Bewick's Swans feed on*Potamogeton* in the Netherlands. The study areas are indicated on the map. Lake Veluwemeer is part of the border-lakes.

between zero and 20 years (Joenje 1978, de Glopper 1985). The area of shallow water, less than 70 cm deep, is 750 ha. The area is protected and no hunting occurs. Only the deeper parts of the lake are open to boat traffic. The lake serves as a reservoir for superfluous polder water. The water level may rise over one meter when strong (north)westerly winds prevail, and superfluous water can not be sluiced into the Wadden sea.

Lake Veluwemeer (2880 ha, 52° 25'N 05° 45'E) is part of the so called border-lakes which were created after the construction of large polders in the lake IJsselmeer area. This former estuary was closed off from the sea in 1932. Lake Veluwemeer was formed in 1957 in order to avoid the lowering of the water tables on the mainland by the new, lower lying, polder Eastern Flevoland. The area of shallow water, less than 70 cm deep, is 1375 ha. A general description of the border lakes is given by Poorter (1981). In this paper most data will refer to lake Lauwersmeer, with additional data from lake Veluwemeer.

Methods

Bird counts and observations

Swans were counted 1-2 times per week. In some years daily observations could be made. The swans were spotted by telescope and counted per flock using tally counters. The number of cygnets (1st calendar year birds) was counted separately, thereby quantifying brood sizes as much as possible. In 1980 and 1987 we mapped the flocks' distribution in greater detail in lake Lauwersmeer and lake Veluwemeer respectively, using emergent vegetation, land-marks, buoys and the presence of exclosures in the shallows. In this way we could correlate the distribution of the swans to the occurrence of the different density-classes of vegetation.

Each count revealed the total number of swans present in the entire area. The number of swan days was used to estimate the level of utilization for a certain year or site.

Observations on the foraging behaviour of the swans were not always entirely comprehensive because of night-time feeding. In one case we used an infra-red telescope (6x magnification) from a 5.5 m high hide placed at the water's edge.

Vegetation mapping and food stock assessment

During summer aerial photographs were taken to map the above ground vegetation, using slides or false colour technique. Aerial surveys were conducted in 1980, 1984, 1986, 1988 and 1989 in lake Lauwersmeer. In lake Veluwemeer this was done in 1987. Mapping above ground vegetation was carried out at times of peak standing crop, between 1 July and 10 August.

During the summer of 1980, a detailed vegetation map of above ground biomass was made by Pot (1981), based on aerial false colour photography and field sampling. Density classes were discriminated using ground cover, ranging from 0-5% to 90-100%, and phenology of the field, i.e. thin, clumped, dense or closed.

The biomass of the below ground storage organs of *Potamogeton pectinatus*, which was the only abundant species, is known to be correlated to the peak biomass of green matter (van Wijk 1988). Standing crop of tubers in a representative *Potamogeton* stand, the so called "Rilveld", was determined in early autumn, well before the Bewick's Swans arrived on the lake, and related to the vegetation classes as given by Pot (1981). For reasons mentioned below, comparisons were made between the so called DENSE vegetation class (closed vegetation stands with >90% cover), and other stands. To determine the loss of tubers from other causes than by waterfowl consumption, four exclosures (6x4.5 m) were used. Immediately after the swans had departed from the lake to feed on nearby arable land, the degree of depletion of the food stock on offer was deter-

Table 2. Dates of arrival (as day-month) and peak numbers of Bewick's Swans feeding on *Potamogeton* in lake Lauwersmeer, 1980-89. Dates in brackets are approximated.

year	first arrival	mass arrival	departure	peak number
1980	28-09	16-10	01-11	692
1981	(04-10)	(22-10)	(30-10)	808
1982	04-10	24-10	13-11	4210
1983	04-10	21-10	25-10	950
1984	03-10	17-10	28-10	2741
1985	15-10	19-10	30-10	2104
1986	04-10	04-11	25-11	3697
1987	03-10	16-10	11-11	1604
1988	03-10	24-10	30-10	6461
1989	04-10	15-10	03-11	2192

mined by resampling. The same method was applied in later years, usually sampling several *Potamogeton* fields.

Samples of tubers were collected using core samplers (7, 10, 15 cm diameter). The samples were taken from the upper 20 cm of the mud at water depths up to 65 cm, which is the lower limit of reach for the Bewick's Swan (Owen & Cadbury 1975). The mud was sieved in the field over a 1 mm sieve, the tubers being collected per sample. Tubers were dried in the laboratory (24 h, 70° C) and data are presented as number or mass (dry weight) per m^2.

Results

Timing of autumn migration and duration of stay

Bewick's Swans, returning from their breeding grounds, usually arrive in large numbers from mid October onwards. The first birds are generally present shortly after 1 October. Table 2 lists timing of tuber exploitation and peak numbers per year for lake Lauwersmeer. Although the peak numbers, number of swan-days and duration of stay vary according to the season, the general timing of arrival is rather fixed. Only in 1986 the swans were considerably late: mass arrival occurred two weeks later than usual. Annual peak number of birds visiting the lake ranged from 700-6,500, whereas the period of foraging on tubers of *Potamogeton* lasts four, sometimes up to eight weeks. The utilization in terms of swan-days varied enormously, from 6,500 to 89,600. The years of intensive usage were 1982, 1986, 1988 and 1989, the level being 5-10 times higher in peak years than in other years.

The moment of arrival at different sites in western Europe is rather similar (Fig. 2). Birds

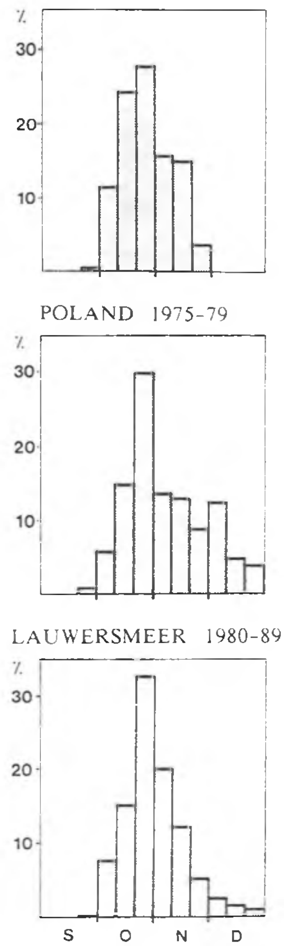

Figure 2 Timing of autumn migration and arrival of Bewick's Swans per 10 day period, in Sweden, Poland and lake Lauwersmeer, the Netherlands, expressed as percentage of the total number of swans. Data from Poland modified after Górski & Jesionowski (1983), data from Sweden by courtesy of the Ottenby Ringing Station, Öland.

passing Poland, Sweden and the GDR, and arriving in the Netherlands and Denmark, show up at the same time of year, indicating simultaneous departure from the breeding grounds or from an identical stop-over site. Stop-over sites between the breeding grounds and the wintering grounds are unknown at present, but due to the fact that there is about one month discrepancy between mass departure from the arctic tundra (Mineyev 1991) and arrival in western Europe, we infer that the swans do not fly directly to the wintering grounds.

As an example, Figure 3 depicts the arrival of

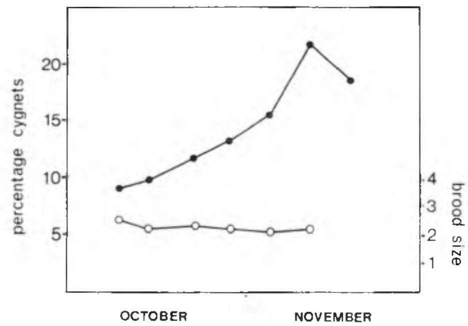

Figure 3 Arrival of successful Bewick's Swans breeders and their offspring in lake Lauwersmeer, 1989. Percentage of cygnets in total numbers counted (●) and average brood sizes (○). Number of swans checked for proportion of cygnets was 700-3,363; range of sample sizes for broods 43-227.

Bewick's Swan families in lake Lauwersmeer in the autumn of 1989. Usually, successful breeders return from the breeding grounds somewhat later than non-breeding birds, but there is no difference between successful breeders according to brood size. Although breeding success, expressed as cygnet proportion and brood sizes, may vary between years, the general pattern is consistent over the 10 year study period.

Site tenacity

Based on observations of birds ringed in England with individually engraved darvic tarsus rings, we have some information about site faithfulness. Out of 43 birds sighted in lake Lauwersmeer in 1986, 19 (44%) were sighted in more than one year (up to five years). Figure 4 gives an example of site tenacity for a few selected individuals visiting lake Lauwersmeer in more than three seasons. Some birds do indeed visit the lake in several subsequent years. Others however, may come to feed on *Potamogeton* only in some years, while visiting other lakes in other years, or simply arrive after the stock has already been depleted, and move on.

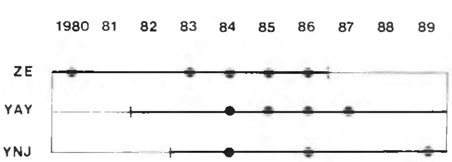

Figure 4 Site tenacity of individual Bewick's Swans sighted in lake Lauwersmeer, illustrated by a few individuals (indicated by ring inscription) recorded in more than two years. Each dot represents at least one sighting of the bird in the year along the horizontal axis. The thick lines show the period that the birds were ringed and alive.

Interpretation of the sightings remains difficult however. Due to difficulties with reading codes on tarsus rings of birds feeding on water, the available information is certainly incomplete. The fact however that the two *Potamogeton* lakes may hold up to 50% of the entire flyway population at the same time (Table 1) implies site tenacity to occur regularly.

Habitat choice and aquatic feeding

Food preference

After arrival the swans always start exploiting the tubers of *Potamogeton pectinatus,* although other food is available as well. After feeding on tubers the birds switch to field feeding. Here they consume crop wastes of sugar beets and potatoes which are, just like tubers, rich in carbohydrates and energy. Figure 5 depicts fluctuations in numbers for different seasons in lake Lauwersmeer, in relation to aquatic or terrestrial feeding. Only when the water level rises such that water depth prevents the swans from feeding on tubers, (as in 1984), will the birds shift to nearby arable land; they will immediately resume aquatic feeding as soon as the water level drops. The preference for tubers was noticed in all ten years of observations

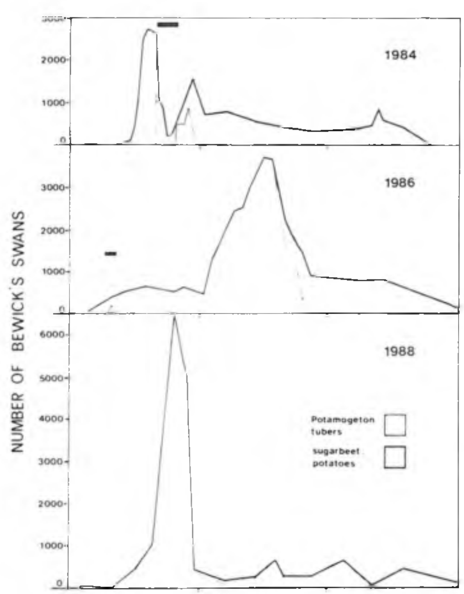

Figure 5 Bewick's Swan numbers in lake Lauwersmeer in relation to *Potamogeton* feeding and feeding on waste root crops. Horizontal bars indicate contemporary periods of high water levels, when *Potamogeton* tubers could not be reached by the swans.

in lake Lauwersmeer (1980-89) and is in accordance with the findings of Poorter (1981), and personal observations for lake Veluwemeer (1980-89). In the latter case the swans also switched to grasslands.

Feeding behaviour

The swans find their food by touch. No visual cues can be used to select the areas rich in tubers. Above ground biomass dies off in the second half of August and early September, the decaying leaves and stems being washed away by the water. The swans dig up their food by foot trampling after which the head and neck are dipped under water to sieve the tubers from the substrate (see also Brouwer & Tinbergen 1939). Often birds can be seen with a slightly opened bill just after returning from below water. Often some clay is visible on the base of the mandibles and occasionally birds with real "muddy heads" show up as a result of the sieving and probing of the bottom.

In this way the birds plough up the entire lake bottom within their reach. The resulting holes could be studied in detail at times of low water levels. The size of the holes can be up to 1.50 m diameter, the average depth was 25 (10-30) cm.

Diurnal activity patterns

Shortly after arrival the birds are active both day and night. Later on, foraging activity concentrates more and more towards the night-time period, and any additional feeding occurs only during early morning and late afternoon. During the day, the swans roost on undisturbed parts of the lake in very shallow water (< 20 cm), and fly or swim to their feeding grounds at dusk. The extended allocation of foraging time early in the season, with abundant food available, may indicate that the swans try to rapidly replenish energy losses from migration.

Exploitation patterns by flocks

During the period of tuber exploitation, the swans visit different stands of vegetation in lake Lauwersmeer in a rather systematic sequence, which is fixed from year to year. The swans first tend to visit the northern part of the lake, with sandy soils, before shifting gradually to the southern parts which have more clayey soils containing old sea shells, a.o. *Cardium* and *Mya*. The swans are thought to sieve tubers more effectively out of coarser sandy soils, which would explain the observed pattern.

Generally speaking the site is subdivided into foraging units, each of which contain several flocks. In the beginning of the season this pattern is more clear than later on, when the flocks tend to disintegrate and bird numbers fall. Figure 6 shows the systematic way in which a flock exploits a field during a period of consecutive days. During the course of several nights the flock visited the same field and moved gradually over the areas of high tuber biomass, hence skipping parts of low tuber biomass. This flock movement is very prominent, and probably contributes greatly to the effective depletion of the available stocks.

Quantifying food stocks and consumption

Spatial distribution of tubers before exploitation.

To understand the way swans exploit the food stocks, and how they maximize intake rates, an

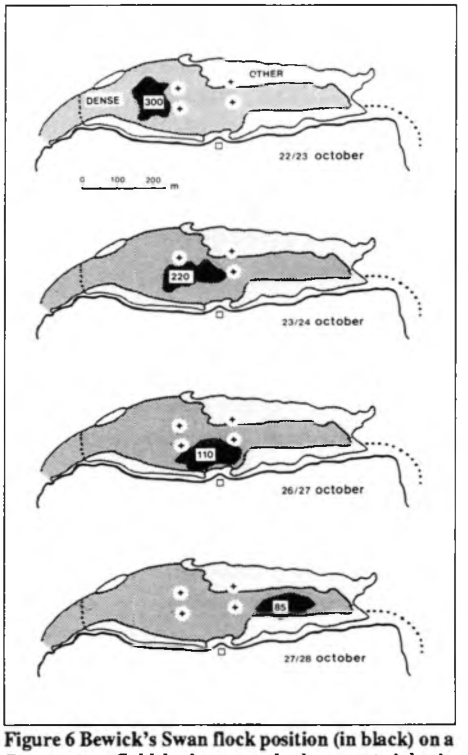

Figure 6 Bewick's Swan flock position (in black) on a *Potamogeton* field during several subsequent nights in the period of exploitation. Dates and flock sizes are indicated, as well as the area with high tuber biomass (DENSE). Positions of exclosures (+) and the observation hide (□) are marked. Rilveld, lake Lauwersmeer, 1980.

Table 3 Tuber size distribution in relation to soil depth, based on 71 core samples. Length classes 0-4 and 4-8 mm are over represented in soil layer 10-20 cm, 8-12 and 12-16 mm are over represented in soil layer 10-20 cm (P<0.05, Habermann analysis in Everitt (1977).

	Tubers per length class									
	0-4 mm		4-8 mm		8-12 mm		12-16 mm		total	
Soil depth	*n*	%	*n*	%	*n*	%	*n*	%	*n*	%
0-10 cm	14	6.9	129	63.5	58	28.6	2	1.0	203	100
10-20 cm	3	2.1	51	37.0	73	52.9	11	8.0	138	100

analysis of tuber distribution in both horizontal and vertical directions (different soil layers, 0-10 cm and 10-20 cm) direction was made in 1980. Tuber sizes ranged from 1-20 mm (maximum length excluding sprout).

A comparison was made for distribution of tuber length classes between the DENSE vegetation stand and other stands, for each soil layer (0-10 cm, 10-20 cm) and total soil column. None of the three options gave significant differences (χ^2_3 respectively 3.66, 1.12 and 4.27, N.S.), so that we conclude that tuber size distribution is not correlated with tuber density.

However, tuber size distribution does relate to soil depth (χ^2_3=37.85, P<0.0005). Larger tubers of 8-16 mm were under-represented in the 0-10 cm soil layer, and smaller tubers of 1-8 mm were under-represented in the 10-20 cm layer (Table 3). This analysis was repeated for the DENSE and other stands, and gave similar, significant, results. So, large tubers are found deeper in the soil than small tubers, independent of tuber density. By digging craters of about 25 cm the swans reach the largest tubers.

Biomass depletion and lower threshold density

The question to what extent the swans utilize the tubers can be judged from the sampling data. The Lauwersmeer 1980 data are presented here in greater detail to describe the general pattern. Table 4 shows total biomass, in grams dry weight m^{-2}, for the DENSE vegetation class as compared to others, before and after the swans visited the Rilveld. The DENSE class had over

Table 4 *Potamogeton* tuber densities, in g dwt*m^{-2} (average ± 95% confidence limits). Rilveld, lake Lauwersmeer, 1980.

	before exploitation	after exploitation
DENSE (*n*=41)	22.5 ± 6.2	7.2 ± 3.4
OTHER (*n*=30)	6.7 ±4.4	5.4 ± 3.1

threefold the biomass of other classes before exploitation, whereas after exploitation the difference was virtually leveled off. Reduction of biomass in the DENSE class was 68%, in other classes only 20%. The latter was similar to biomass reduction as measured in the exclosures, where biomass reduction amounted to 25%, (Sign-test, P<0.0125), which was mainly caused by decomposition of tubers. Large (8-16 mm) tubers were selected for by the swans, whereas a relatively high proportion of small (1-8 mm) tubers suffered from deterioration (rotting processes). From direct observations on position of the flock (see also Fig. 6), plus the fact that the swans depleted the DENSE vegetation to a level similar to that in other vegetation *before* exploitation, we conclude that no, or almost no grazing occurred except in the DENSE stand. The level of 7.2 g dwt m^{-2} is considered a threshold level, below which the swans apparently did not forage.

Consumption per swan per day

The total area of DENSE vegetation in the sampled stand amounted to 4.6 ha. The total stock of tubers on offer was 1,035 kg dwt, of which 331 kg dwt was left after exploitation. Taking into account that 25% of the tubers disappeared in the exclosures, which was not caused by consumption, and assuming that this occurred outside the exclosures too, 446.2±19.5 kg dwt (average ±95% confidence limits) were consumed by swans. Regular counts of the swans feeding on the Rilveld during each night that the swans were present, revealed 1,574 swan-nights (1,464-1,682). Except for some single Pochards *Aythya ferina* and Coot *Fuligula atra*, no other waterfowl were observed exploiting the *Potamogeton* tubers. Hence, average consumption can be calculated as 283 (254-318) g dwt swan^{-1} night^{-1}. Analysis of the caloric contents of tubers gave 17 kJ*g dwt^{-1}, so that total energy intake is 4810 kJswan^{-1}night^{-1}. Assuming the weight of an average bird to be 5.5 kg, and substracting 35% energy loss through rejecta (i.e. faeces etc.), we arrive at 2.9*BMR (basal metabolic rate: 307.6W$^{0.734}$, where W is body mass in

Table 5 The distribution of Bewick's Swans over *Potamogeton* fields of different vegetation cover in lake Veluwemeer in 1987. Vegetation classes 1-3 represent stands of >90 %, 50-90 % and <50 % cover during summer respectively. The observed number of swan-days in the lowest density class is lower than expected (χ^2_2=57.86, P<0.001).

vegetation class	size ha	tubers gdwt*m^{2}	swan-days per ha	swan-days total	swan-days %	tubers on offer kg dwt	tubers on offer %
1	103	17.20	100.6	10,388	74.6	17,716	74.5
2	47	7.76	49.8	2,341	16.8	3,647	15.3
3	44	5.50	27.1	1,191	8.6	2,418	10.2

kg and BMR expressed in kJ, Aschoff & Pohl, 1970) as an estimate of field energy demands for Bewick's Swans during autumn.

Depletion of the total area

Of the total lake shallows (750 ha), 269 ha were covered by *Potamogeton* in 1980. The DENSE stands covered 44 ha in the entire lake. The Rilveld had 4.6 ha DENSE vegetation, and was depleted after 1,574 (1,464-1,682) swan-nights. Thus, the entire lake was calculated to have supplies for 15,000 (14,000-16,100) swan-nights. This was in striking accordance with a total of 14,800 Bewicks' Swan nights actually spent on the lake, based on regular counts of aquatic feeding swans over the entire area.

Relating bird numbers to fluctuating food stocks

The swans are well able to concentrate in the areas of highest tuber densities. This is shown by detailed observations on flock movements collected in lake Veluwemeer in 1987. Table 5 compares the number of swan-days spent on the lake, to the size of the vegetation belt as well as to the total amount of tuber biomass. The swans' distribution pattern is a close fit to the distribution of total tuber biomass, with the exception of the lowest density class. Here fewer swans occurred than would be expected (χ^2_2=57.86, P<0.001)). Thus, utilization by swans of the food stocks, within a given season, is strictly dependent on the tuber biomass available in different patches.

So far, we have shown the small-scale relationship between bird usage and vegetation density within a year. The large differences between years remain to be resolved. The use that the birds make of lake Lauwersmeer varies enormously between years (Fig. 7). Following embankment in 1969, it took only a few years before the swans started using this site. *Potamogeton* had already colonized the lake by 1972 (Joenje 1978) and the first Bewick's Swans were seen foraging on tubers in 1973 (Prop & van Eerden

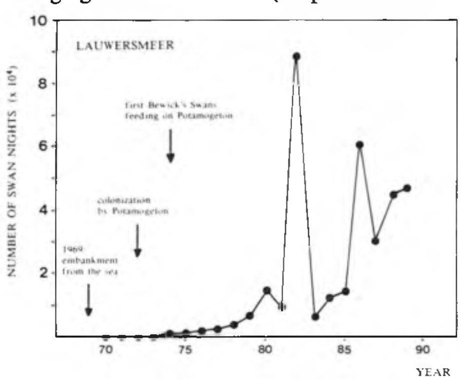

Figure 7 Development of utilization of lake Lauwersmeer by Bewick's Swans feeding on *Potamogeton* tubers, after embankment from the Wadden Sea in 1969. Data 1969-78 according to Prop & Van Eerden (1981).

1981). From then, with the expansion of the vegetation, numbers increased rapidly from year to year. From 1980 onwards, the swans used the lake intensively, but large fluctuations occurred. Table 6 shows that large annual fluctuations in the stands of *Potamogeton* also occur. The total

Table 6 Vegetation of *Potamogeton pectinatus* in lake Lauwersmeer in different years, and utilization by Bewick's Swans. Size of area in ha, measured from aerial photographs. DENSE = >90 % cover.

	area DENSE cover	area OTHER cover	total veget. cover	swan days	swan-days per ha^{-1}	swan-days per ha^{-1} DENSE
1980	44	225	269	14,800	336	55
1984	8	64	72	12,600	1,575	175
1986	228	188	416	61,500	270	148
1989	52	273	325	47,300	910	146

area covered by macrophytes varied between 72 ha in 1984 and 416 ha in 1986. The size of the area with a DENSE (>90% cover) vegetation shows even more variation: 8 ha in 1984 and 228 ha in 1986. For the years with vegetation data, the number of swan-days ranged from 12,600 in 1984 to 61,500 in 1986. However, when expressing utilization as swan-days per hectare vegetation cover (either total cover or DENSE cover only), we see no clear relationship. Hence, vegetation cover alone does not explain differences in utilization sufficiently.

Within the same field of DENSE vegetation, tuber biomass per m² before and after exploitation also varied between years (Table 7), as did the calculated consumption. In 1982, a peak year for Bewick's Swans, tuber consumption per m² was three times higher than in 1980. We are convinced that vegetation density and tuber biomass dictate to a large extent the usage the birds can make of the lake in a given year. Of course for a full understanding of the differences found between years, data about tuber density, tuber mass, length-frequency distribution and threshold levels will also have to be taken into account.

Discussion

Newton (1980) mentioned the importance of measuring food stocks available to bird populations, as a method to determine limiting factors for population growth. Limiting food stocks may be bottle-necks for survival or even reproductive success at certain times of the annual cycle. Newton also recognized the scarce number of such studies, which is mainly due to the difficulty of measuring most food stocks accurately on a larger scale. Moreover, the amount of food consumed needs to be substantial to allow reliable conclusions. Our study is a case where the carrying capacity of a few lakes, important for a substantial part of the entire population, could be measured. The herbivore-plant relationship is relatively simple here, since we are dealing with very distinct food items and only one main consumer, i.e. the Bewick's Swan. No production occurs during the period of consumption, which further facilitates the measurements. Apart from fairly accurate measurements of the food stock, we were also able to estimate consumption, both for the total area and for the individual bird. Biomass reduction ranged from 68-83%, and stocks were considered as being depleted. In order to judge the impact of depletion on the swans, we need data on the profitability of the *Potamogeton* food stock versus the alternatives available to the birds.

Table 7 Tuber biomass (g dwt*m^{-2}) before and after exploitation in the same DENSE vegetation stand (Riвеld) in different years, and the calculated consumption (g dwt *m^{-2}), assuming 25% disappearance as measured in exclosures in 1980.

year	tuber biomass before	tuber biomass after	swan consumption
1980	22.5	7.2	9.7
1982	50.5	8.5	29.3
1984	29.7	6.7	15.5

Estimating carrying capacity

Measuring food stocks at the scale of an entire stop-over site would not have been possible without aerial photography, vegetation mapping, and tuber sampling. Our field measurements of tuber biomass (22.5-50.5 g dwt*m^{-2}) before exploitation, are within the range given by Van Wijk (1988) for various water bodies in the Netherlands (6.7-60.2 g dwt*m^{-2}). Van Wijk (1988) showed that tuber biomass was related to peak above-ground biomass. When measuring carrying capacity, a complicating factor may be waterfowl consumption of above ground vegetation during summer. In lake Lauwersmeer, Coot, Mallard *Anas platyrhynchos* and Mute Swans *C. olor* moult in significant numbers, and summer concentrations of Gadwall *A. strepera* and Wigeon *A. penelope* are common. These birds are capable of reducing above ground biomass (dry weight) locally to only 17% of the maximum biomass as measured in exclosures. In these exclosures maximum tuber biomass was almost twice as high as in the grazed situation, reaching 109.8 g dwt*m^{-2} (Van Wijk 1988). In this way, Bewick's Swans are faced with indirect competition by other waterfowl which reduce their potential food stocks. The same holds for the negative effect that periods of windy weather in late summer have on the green biomass of the macrophytes. Early storms and waterfowl grazing in late summer both reduce tuber production considerably. Therefore, annual measurements of the actual tuber stock present are needed within well defined density classes of vegetation cover. Aerial photography can be used in a quantitative way only to transform local sampling data to a larger scale, not as an independent estimate by itself.

Estimating daily consumption

When estimating tuber consumption by the

Bewick's Swans, consumption by other waterfowl may also complicate calculations. Very often the swans, when digging for tubers, are accompanied by several Pochards, Coot, Wigeon or Pintail *A.acuta.* These birds benefit from tubers being washed out of the mud, and especially Pochards klepto-parasitize by diving under the swans and stealing tubers. In years of high tuber production, the number of Pochards in lake Lauwersmeer may rise to over 6,000 individuals. In 1980, when we estimated daily consumption by the swans and extrapolated rations to the entire lake, Pochards were not present in any significant numbers.

Our estimate of individual consumption per day of 283 (254-318) g dwt*day^{-1} is comparable with Smit (1988), who estimated a daily consumption of 302 g dwt*day^{-1} in lake Lauwersmeer in 1984, using the same methods. Both 1980 and 1984 were years with small stocks of *Potamogeton* tubers, and as a consequence, a limited number of swan-days. In years with rich stocks, a larger part of the population can benefit from these for a prolonged period, and especially with high tuber biomass per m^{-2}, individual swans might be able to obtain higher food intake rates. The question then is whether the average intake per day would be higher in such years, which would enable the birds to put on fat at a faster rate.

Potamogeton *lakes as refuelling stations?*

Daily estimated energy intake was 2.9 times basal metabolic rate (BMR) in 1980. This is well within the range of other studies on field metabolic rate (*cf.* Drent & Daan 1980, Nagy 1987). If however, at least in some years, the swans would be able to consume tubers in excess of their daily requirements, then they would be able to store the surplus energy as fat reserves for the winter to come, and hence replenish the reserves used during migration. *Potamogeton* tubers are rich in energy, due to a high content of carbohydrates which can easily be converted into fat reserves, and this may explain the absolute preference for this food type by the Bewick's Swans. Kondratyeva (1987) found that *Potamogeton* is also an important food source for eastern Bewick's Swans in the breeding grounds during late summer. However, it is unclear from her paper which parts of the plants are consumed. Tundra Swans *C.c.columbianus* breeding in Alaska are also dependent for part of their food supply on *Potamogeton* (J. Bart & S. Earnst, pers.comm.).

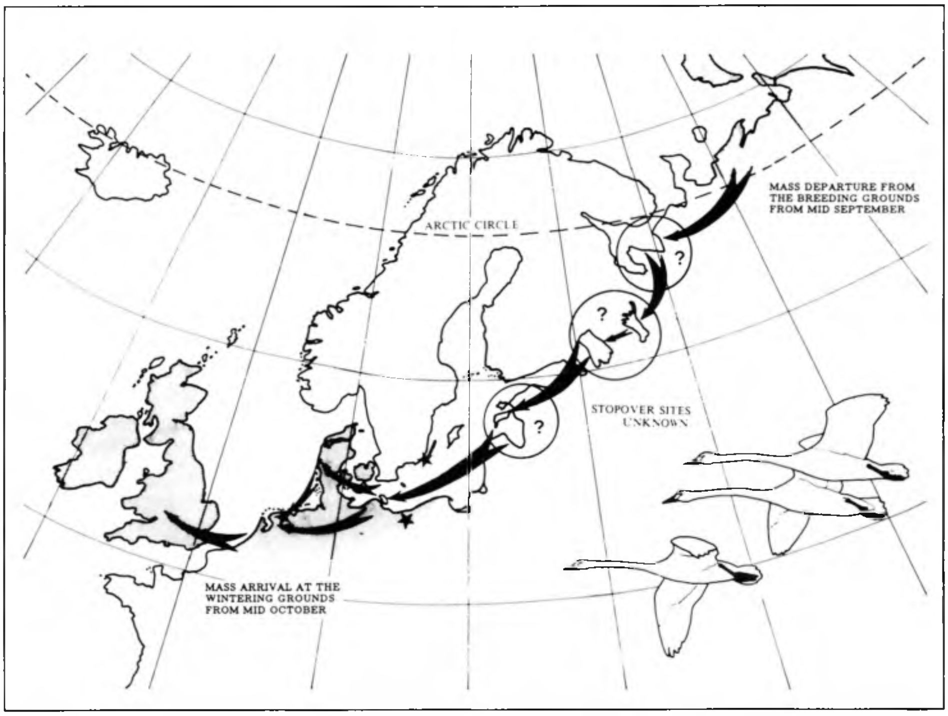

Figure 8 Map of breeding- and wintering grounds of European Bewick's Swans, with hypothetical stop-over sites along the migratory route. The swans do not necessarily migrate in a stepwise manner.

Especially in herbivores efficient digestion of a particular food requires a stable gut flora and gut anatomy. Wood Pigeons *Columba palumbus* take 10-15 days to acclimatise to a change in diet, and are unable to cope with a quick change in diet without loss of body condition (Kenward & Sibly 1978). So it seems likely that swans would maintain their diet as long as possible along their migratory routes. Assuming that western Bewick's Swans also feed on *Potamogeton* in the breeding grounds of northern Russia (as suggested by Mineyev, pers. comm.), and considering that the birds leave the breeding grounds about a month before arriving in western Europe (Mineyev 1991), we may hypothesize that the birds have stop-over sites in between the arctic tundras of northern Russia and the southern Baltic Sea (Fig. 8). At these sites we suggest they should also feed on tubers of submerged vegetation. A.Leito (pers. comm.) mentions about 5,000 birds stopping over in Estonia in autumn, but further details are not available so far. Other possible sites along the migration route would be the coasts of the White Sea, or the lakes Ladoga and Onega in Karelia, USSR. Satellite images (e.g. SPOT TM) might give indications of lakes which are shallow and have a high production of submerged macrophytes, provided that pictures are taken at an appropriate time of the season, i.e. when above ground biomass reaches a maximum at these latitudes.

In conclusion, we have shown that the stock of *Potamogeton* tubers is limited and possibly limiting: in each year of study, after a period of 4-8 weeks, the tuber biomass is depleted by the Bewick's Swans, and consequently the birds have to shift to other food types. Hence, only a part of the population, although substantial, can make use of this stock. It is of great importance to know whether birds feeding on *Potamogeton* tubers have better chances of survival, and how these birds adjust their timing of migration in order to take advantage of this limited, but energy-rich, food source each year. Unfortunately, resightings of individually marked birds are very scarce, although there is some evidence for site tenacity, based on observations of engraved tarsus rings. Marking swans with long lasting neck-collars is a more effective way to obtain data on large scale decision-making and possible differences in survival, which could elucidate the effects of a limited resource on population growth.

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