SECTION 5: HABITATS FOOD AND FEEDING

Bewick's Swans *Cygnus columbianus bewickii* in the Netherlands: numbers, distribution and food choice during the wintering season

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Numbers, proportion of cygnets, brood size and food choice of a large proportion of the western population of Bewick's Swans have been established in the whole Netherlands on a bi-weekly basis throughout the winters 1982-83 and 1983-84. From November to March at least 6,000 were present, including a peak of nearly 9,000 in January (55 % of the flyway-population). Patterns in the proportion of cygnets can be explained by families arriving later in autumn, and cygnets departing later in spring. On arriving in autumn the swans prefer feeding on pondweed tubers in aquatic habitats. Having depleted these they switch to arable land (root crops, winter wheat) and grassland. After January only grassland is utilized. The switch from food types with a high carbohydrate content (pondweed tubers, sugar-beet, potato) to protein-rich food (winter wheat, grasses) is discussed. The sequence in food choice through the winter season is compared with the history of food choice of Bewick's Swans in the Netherlands in which major changes have occurred in the last few decades.

Bewick's Swans *Cygnus columbianus bewickii* wintering in Western Europe belong to the western population of the species, which has its main breeding areas in the tundra zone of the northeast European part of the USSR (Cramp & Simmons 1977, Mineyev 1991). The main wintering sites in Western Europe are situated in Ireland, the United Kingdom and the Netherlands. During migration important staging areas are also found in Denmark, West and East Germany and the eastern Baltic (Cramp & Simmons 1977, Beekman *et al.* 1985, Monval & Pirot 1989, Rees 1991, Dirksen & Beekman 1991). In recent years, the west European winter population has been estimated at 16 -17,000 individuals (Dirksen & Beekman 1991).

The Netherlands are of special importance within the wintering range of this population. Large numbers of Bewick's Swans use wetlands and agricultural areas between October and April. In recent years half of the population is present by early November, feeding on aquatic vegetation (Beekman *et al.* 1991). More than half of the total flyway population is counted on Dutch wintering grounds during January-censuses, except for severe winters (Beekman *et al.* 1985, Monval & Pirot 1989, Dirksen & Beekman 1991).

Despite the importance of Dutch wintering sites for the species, there was no complete and recent description of numbers, distribution and food choice of Bewick's Swans in the Netherlands at the beginning of the nineteen-eighties. We therefore started a two-year project (the "Dutch Bewick's Swan project 1982-84") in which numbers, proportion of cygnets and brood size, distribution and food choice were monitored every two weeks throughout the Netherlands. In this paper we present a general review of the background, methods and results of this project. Data will mainly be presented for the country as a whole; results of a more detailed analysis will be published later.

The "Dutch Bewick's Swan project 1982-84"

Background and aims

The general purpose of the project was to describe the present occurrence of the Bewick's Swan in the Netherlands: assessing numbers, areas visited, habitat requirements and food choice throughout the winter season. During the sixties and seventies food and habitat choice of the species changed drastically, due to changes in food availability (Timmerman 1977, Poorter 1981, see section Food choice). The Bewick's Swan had spread out from the principal aquatic habitats to grasslands and arable land, utilising a lot of sites previously not visited.

During the winters of 1975-76 and 1976-77, Mullié & Poorter (1977) organised five counts covering a large proportion of the Dutch sites holding Bewick's Swans. They reported high total numbers, a description of food utilisation, and a striking difference in proportion of cygnets between the north and the south of the country. It was clear that more frequent counts of (nearly) all individuals in the country would not only give a description over the entire winter season, but might also lead to a better understanding of the factors influencing patterns of food choice and distribution.

Juvenile swans are easy to age, and they stay with their parents until at least their first spring. This facilitates the establishment of juvenile proportions and brood sizes within observed groups (e.g. Evans 1979 and Scott 1980a,b). If these data were gathered for most observed groups on a bi-weekly nationwide basis, it would be possible to analyse numbers, distribution and food choice in the course of the winter in relation to status (families vs. adults without cygnets, within families according to number of offspring).

There were some indications that such differences might exist. In the Lauwersmeer area (Fig. 1) juvenile proportions increased from 3 to 12 % with increasing total numbers in October-November 1980 (Beekman *et al.* 1981, see Beekman *et al.* 1991 for a more recent example). Mullié & Poorter (1977) found a striking difference in juvenile proportions between the northern and the southern part of the country for all five counts they published: the proportion in the southern part averaged 5.5 % higher (range of difference: 4.0 - 6.9 %). In the Onnerpolder (Fig. 1), a grassland area, the proportion of cygnets increased rapidly during March-April in most years while total numbers decreased because of birds leaving on spring migration (Dirksen & Beekman 1982).

Figure 1. Map of the Netherlands, indicating regions and sites mentioned in the text. Abbreviations: g Groningen, f Friesland, d Drenthe, o Overijssel, fl Flevoland, gld Gelderland, nh Noord-Holland, zh Zuid-Holland, u Utrecht, z Zeeland, nb Noord-Brabant, l Limburg, 1 Lauwersmeer (53°22′ N, 6°13′ E), 2 Onnerpolder (53°10′ N, 6°40′ E), 3 Lake IJsselmeer, 4 Noordoostpolder (52°45′ N, 5°40′ E), 5 Border-lakes (52°25′ N, 5°45′ E), 6 branches of river Rhine, 7 river IJssel, 8 river Meuse, 9 Delta region

Due to the efforts of the Wildfowl Trust in England (Evans 1982) there was a reasonable proportion of individually marked Bewick's Swans in the population (ca. 1.5 %, own estimate) at the start of our project. Reading their engraved darvic leg-rings in combination with the counts would enhance the interpretation of the data set: changes in numbers and distribution throughout the season can more easily be understood when supported by data on movements of individual birds.

At the start of the project there was no consensus on the size of the population wintering in Europe (Atkinson-Willes 1975, 1981, Mullié & Poorter 1977, Scott 1980, Poorter 1981). To assess the importance of Dutch staging sites on a population level we needed a good population size estimate. Two international censuses were organised in cooperation with IWRB and national contacts in all the countries involved. The January 1984 census achieved particularly good coverage of the population. It resulted in an estimate of 16,500 for this population; this figure was confirmed in other recent censuses (Beekman *et al.* 1985, Monval & Pirot 1989, Dirksen & Beekman 1991).

Design and methods

During the period Bewick's Swans were known to be present in the country a counting scheme with a bi-weekly frequency was set up. Because of coordination with existing waterfowl counting schemes, which at most were on a monthly basis, some gaps of three weeks between counts were inevitable. Through national and regional organisations and personal contacts, counters were asked to take responsibility for a certain site to be covered. At least 300 observers were involved in the project directly. Their activities and data-reporting were coordinated regionally.

The following data were requested for each group of swans when visiting a site: total number, number of juveniles, brood sizes, food type if feeding, sightings of engraved leg-rings. These data were collected on standard-forms. Each count was a three day period: Friday till Sunday, to enable professionals as well as amateurs to put in their efforts. Finally data from the next Monday were included if no data from the preceding three days were available.

Information about the sites covered (land-use, infrastructure and other relevant data) was gathered by asking the observers to answer a written questionnaire.

In general the coverage and quality of the data improved from the first to the second project year. This was partly because the project was better known the second year, and attracted more observers. Newsletters with preliminary results stimulated observers to put more energy into recording juvenile proportions, brood sizes, food types and reading rings.

Results

Numbers, percentage of cygnets and brood size

Total numbers, proportion of cygnets and mean brood size for the bi-weekly counts in 1982-83 and 1983-84 are given in Fig. 2. Due to incomplete coverage in the first project-year the totals of the counts at the end/beginning of the month in 1982-83 are probably too low compared to the mid-month censuses. (see Design and methods). This causes the irregularity in the pattern of the successive totals. The total numbers for several regions and important sites are given in Table 1.

In 1982-83 the first Bewick's Swans arrived in the beginning of October. At the end of October a total of more than 6,000 swans was counted. During November numbers remained fairly stable. In December numbers increased again and in mid-January a maximum count of nearly 9,000 birds was made. After this peak, numbers declined slowly during February, and rapidly in the beginning of March. The last Bewick's Swans left the Netherlands in early April.

In 1983-84 the pattern was similar, although some differences can be seen. Mass arrival in autumn was 2-3 weeks later, numbers increasing to nearly 8,000 in December. Again the peak number was counted in mid-January (8,800). Possibly part of the difference between this count and the preceding and following one was caused by the extra efforts made in relation to the international census. The swans are scattered maximally in this period, and some addi-

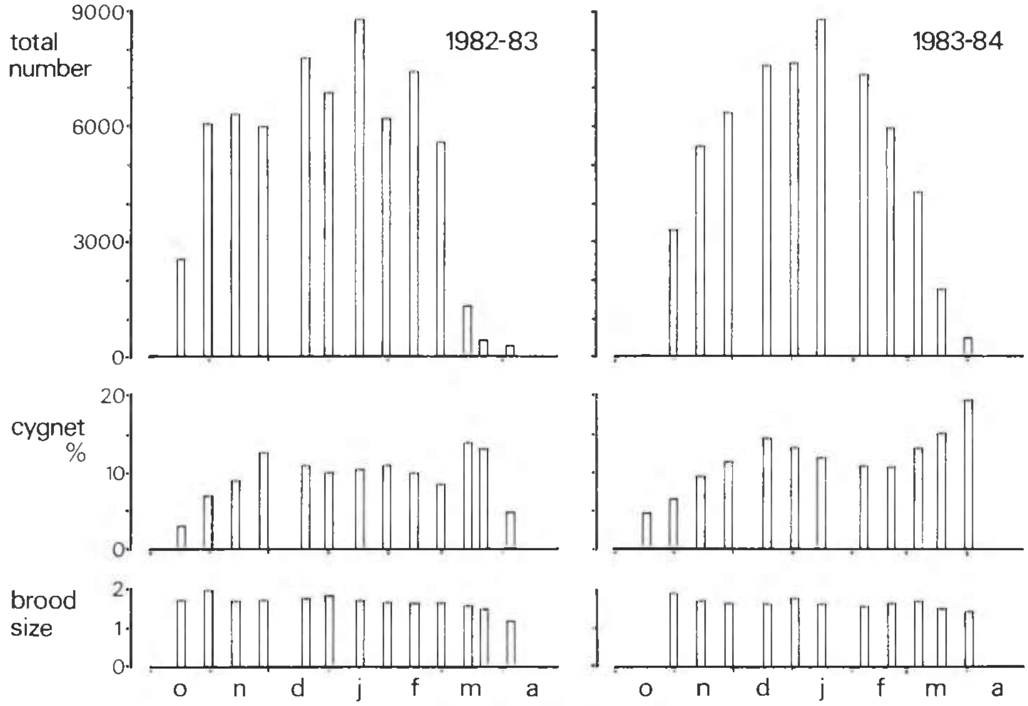

Figure 2. Total numbers, juvenile proportions and brood sizes of Bewick's Swans in the Netherlands, for the bi-weekly counts in 1982-83 (left) and 1983-84 (right). In 1982-83 the mean proportion of swans aged per count was 77 % (sd = 14.7, n = 13), three counts having less than 70 % aged. The number of reported brood sizes varied between 5 and 317, three counts having less than 50 broods recorded. In 1983-84 the mean proportion of swans aged per count was 90 % (sd = 8.7, n = 12), three counts having less than 85 % aged. The number of reported brood sizes varied between 48 and 491, only one count had less than 50 broods recorded.

Table 1. Total numbers of Bewick's Swans in the Netherlands during 1982- 83 and 1983-84.
Regions (letters of provinces refer to Figure 1):
A Lauwersmeer (incl. surrounding agricultural area).
B northern Netherlands: provinces G, F, D, O and NH except region A.
C border-lakes.
D areas along rivers Rhine, Meuse, IJssel.
E middle Netherlands: provinces Fl, Gld and U except regions C and D.
F southwestern Netherlands: provinces ZH, Z and western part of NB.

Date	A	B	C	D	E	F	Total
1982-83							
2-4 Oct	0	0	18	0	0	0	18
16-18 Oct	1857	20	706	0	0	2	2585
30 Oct-1 Nov	4019	320	1551	1	150	24	6065
13-15 Nov	1196	922	1853	181	1566	584	6302
27-29 Nov	156	1599	82	160	3121	883	6001
18-20 Dec	411	2352	0	1791	2028	1219	7801
30 Dec-2 Jan	187	1590	40	2252	1813	1002	6884
15-17 Jan	158	2284	0	3414	1786	1155	8797
29-31 Jan	175	1714	35	1609	1885	777	6195
12-14 Feb	21	1628	49	2571	2211	946	7426
26-28 Feb	0	1473	132	612	2883	498	5598
12-14 Mar	0	561	0	173	464	165	1363
19-21 Mar	0	150	0	7	150	142	449
2-4 Apr	0	191	0	0	150	0	341
16-18 Apr	0	0	0	0	0	0	0
1983-84							
1-3 Oct	0	0	0	0	0	0	0
15-17 Oct	37	0	46	0	8	0	91
29-31 Oct	251	175	2619	6	214	44	3309
12-13 Nov	808	1514	1201	107	1421	427	5478
26-28 Nov	513	2372	86	217	2594	585	6367
17-19 Dec	64	2575	23	1045	2860	1033	7600
31 Dec-2 Jan	151	2246	0	1541	2541	1166	7645
13-15 Jan	195	2621	8	2215	2297	1465	8801
4-6 Feb	147	1554	0	2665	2162	819	7347
18-20 Feb	30	864	2	3269	1183	605	5953
3-5 Mar	5	414	0	1494	2212	177	4302
17-19 Mar	0	488	42	142	1080	20	1772
31 Mar-2 Apr	0	241	0	1	248	0	490
14-16 Apr	0	0	0	0	0	0	0

tional small flocks were found in mid-January. Spring departure seems to be gradual and slow during both February and March, in contrast to the spring of 1983 which showed a mass departure in the beginning of March.

The data on proportions of cygnets show some clear patterns. In both winters the proportion increases from 3-5 % in mid-October to 11-13 % at the end of November. In January of both years the proportion of cygnets in the population as a whole was estimated at about 11 %. The same figure was established in the population as a whole in January 1984 (Beekman *et al.* 1985). After the increase in autumn, there was a decrease from the second half of December onwards until February in 1983-84. This decrease is present in 1982-83 as well. In spring, with decreasing total numbers, the proportion of cygnets quickly rises. Especially in 1983-84, the year with the slow and gradual spring-departures, the proportion of cygnets shows a gradual increase from 11 % in February to 19 % in the end of March in the country as a whole.

Mean brood sizes varied between 1.2 and 2.0 (1982-83) and 1.4 and 1.9 (1983-84) respectively. A small increase can be seen during October 1983, possibly indicating a later arrival of larger broods. After that, there seems to be a decrease in brood size over the rest of the winter.

Food choice

A short review of changes since 1930

Thanks to the early work of Brouwer & Tinbergen (1939), a more recent review of

Timmerman (1977) and information of Mullié & Poorter (1977) and Poorter (1978, 1981) the changes in food choice and distribution of Bewick's Swans in The Netherlands are, at least qualitatively, known since approximately 1900. Based on these papers a short review will be given in this section.

In the beginning of this century the Netherlands were already considered as an important wintering area for Bewick's Swans. In the years until 1932 the Zuiderzee estuary was the only area where the species was seen regularly and in large numbers. The distribution of the swans was restricted to two parts of the eastern coast of the estuary, where they were feeding on Eelgrass (*Zostera marina*) and pondweeds (*Potamogeton pectinatus* and, to a lesser extent, *P. perfoliatus*) respectively. From both food types the roots are dug out and eaten. From the pondweeds the tubers that are formed in late summer before the decaying of the above-ground vegetation are the main part of the plant eaten by the swans. Information on numbers is scarce: the swans were 'numerous'.

After the Zuiderzee estuary was closed, and named lake IJsselmeer, by the building of a 32 km long dike in the north, the area changed essentially. The water became fresh, which triggered changes in the submerged vegetation. The Eelgrass disappeared, but in about ten years the pondweeds spread out over almost all shallow parts along the eastern and southern coast. A large area became available for the swans, as at some places the shallow parts extended to 1,250 metres from the coast. Consequently, large numbers of swans were present. There are some counts from the mid thirties, carried out by Brouwer & Tinbergen on several consecutive days along most of the coastline. The totals were 2,000 to 3,200, probably being a large proportion of the population at that time. The swans were present throughout the winter. The first groups arrived in October, numbers increasing over the next month towards a maximum level during January. The birds left during ice-periods, but returned afterwards and continued to feed on aquatic vegetation. The northeastward departures took place in February/ March.

The expansion of pondweed vegetation after the 1932 closing continued until after 1940. Between 1940 and 1968 two independent factors are of major influence on the submerged vegetation. From the end of the 1930's the consecutive reclamation of three large polders in the eastern and southern part of lake IJsselmeer was started. The first one was a direct extension from the mainland, thus leading to a loss of habitat with submerged vegetation. Between the other polders and the mainland long-drawn lakes were made, the so-called Border-lakes (Fig. 1). In these lakes, which were created between 1950 and 1960, the pondweeds could survive and even increase in area and density. On the other hand, eutrophication with nitrates and phosphates caused severe algal bloom (mainly *Oscillatoria agardhii*), and consequently the disappearance of submerged vegetation. Areas in the eastern part of lake IJsselmeer lost their pondweeds first. The structure of the Border-lakes apparently gave some protection against the pollution, which was partly brought in through the river IJssel (a branch of the river Rhine). This only caused a delay, and during the 1960's the Border-lakes gradually lost their pondweeds as well.

After 1960 Bewick's Swans were observed outside the lake IJsselmeer region more regularly and in larger numbers than before. Especially in the forelands of the large rivers (branches of the river Rhine, and the river Meuse) and in the southwestern Delta-region (Fig. 1) numbers increased.

In 1968 there was a sudden change. In autumn, after only a few weeks of foraging on pondweeds in the Border-lakes, all Bewick's Swans left the aquatic vegetation and started to feed in neighbouring grassland areas. The submerged vegetation had disappeared almost completely. Therefore, in the following years, the food choice and distribution pattern of Bewick's Swans in the Netherlands became completely different. Many new sites were used by the swans, where they were feeding on grass and agricultural crops (waste potatoes and sugar-beet as well as winter wheat). Between 1968 and 1975 the aquatic foraging was of negligible importance.

From 1975 onwards the situation in the Border-lakes slowly improved. The swans returned there for some weeks of foraging in autumn. Furthermore, the recently embanked Lake Lauwersmeer was slowly colonized by pondweeds (mainly *P. pectinatus*). The Bewick's Swans started to feed on these in autumn as well. The food choice pattern in these years is described by Mullié & Poorter (1977). After depletion of the pondweed stocks in the lakes the swans switched to waste crops as well as grass. During winter the proportion of swans on arable land, both waste crops and winter wheat, decreased. In spring all Bewick's Swans were feeding in grassland areas.

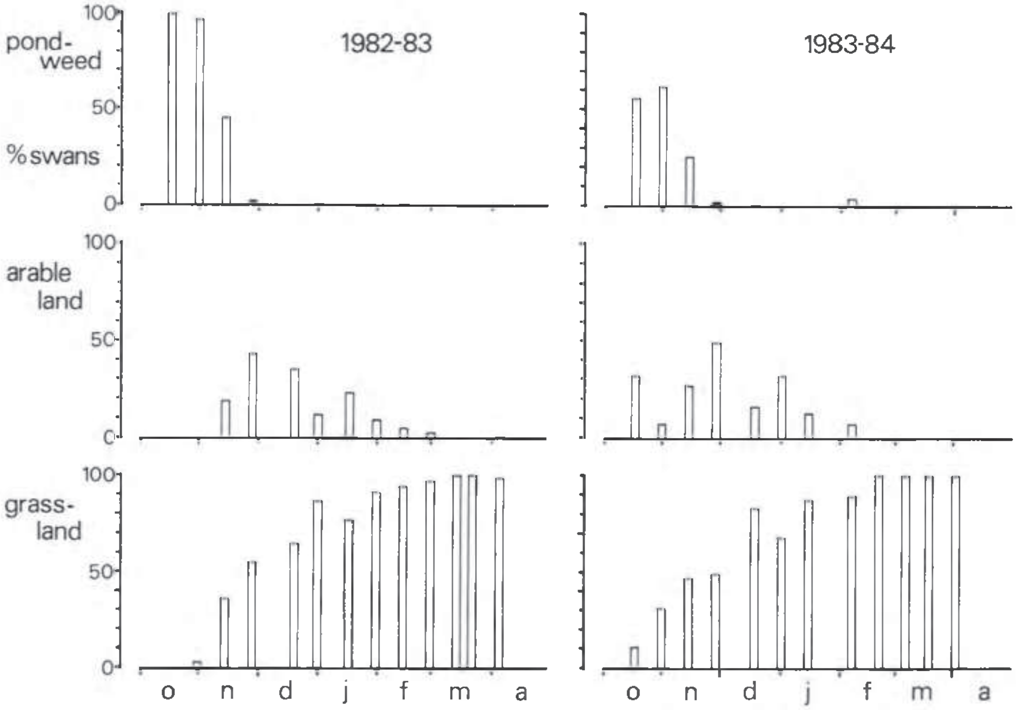

Figure 3. The proportion of Bewick's Swans utilizing the three feeding categories - aquatic vegetation, arable land and grassland - for the bi-weekly counts in 1982-83 (left) and 1983-84 (right).

1982-84

The feeding of Bewick's Swans was divided into three major categories. Aquatic feeding was almost entirely aimed at pondweed tubers, but some groups feeding on algae *Ulva* spp. on brackish lakes are also included in this category. Feeding on arable land included all agricultural crops taken. On grasslands a variety of plant species is taken. For each of the bi-weekly counts the percentage of swans feeding in these three categories was calculated. These percentages are depicted in Fig. 3 for the two consecutive winters of the project.

In 1982-83 almost all Bewick's Swans arriving in October started feeding on pondweeds. The first ones arrived in the Lauwersmeer, where a peak number of 4,210 was reached at 25 October. Numbers on the Border-lakes reached a peak of 1,853 swans on 13-15 November. In November the first groups feeding on arable land (Lauwersmeer, Noordoostpolder; Fig. 1) and grasslands (polders on the mainland south of Border-lakes, Fig. 1) were observed. At the end of the month the pondweed vegetations were completely abandoned by the Bewick's Swans. The proportion of swans feeding on arable land reached a peak in November and December, but small numbers of swans continued to use arable land throughout the winter until the end of February. The importance of grasslands rapidly increased during November and December. From February onwards more than 90 % of all Bewick's Swans in the Netherlands were feeding on grasslands. In mid-winter and early spring the sites along the rivers held large numbers (Fig. 1, Table 1).

In 1983-84 the pattern was the same, with one major difference: already immediately after arrival in October a large proportion of the Bewick's Swans was feeding on arable land or grassland. Only around 60 % of the birds were feeding on pondweeds in October. Peak numbers in the Lauwersmeer (950 on 23 October) were much lower as well. In the Border-lakes a maximum of 2,619 was reached on 29-31 October. From November onwards the pattern is almost identical with the preceding winter.

It should be stressed that grasslands in relatively wet areas seem to be favoured especially. The areas along the rivers attract high numbers of swans in periods of irregular floods. Beside these areas that are wet because of flooding, we have the strong impression that the distribution of swans on grasslands is correlated with the occurrence of seeping water in low-lying areas with peat soils.

In order to assess the relative importance of the three categories of feeding throughout the winter the number of swan-days spent on each

Table 2. Calculated percentage of swan days spent by Bewick's Swans in The Netherlands per food type in 1982-83 and 1983-84.
The percentage given is the percentage of swans observed on the food type concerned during the bi- weekly counts. Thus, the figure is weighted for the total number of swans in the different counts.

	1982-83	1983-84
aquatic vegetation, %	19	7
arable land, %	16	17
grassland, %	65	76
total swans with food type recorded, *n* (%)	59,974 (91)	54,073 (91)
total swans observed, n	65,807	59,145
bi-weekly counts yielding swans, *n*	14	12

food type was calculated (Table 2). The proportion of swan-days on pondweeds was reduced by almost a factor of three in the second winter. The proportion of arable land feeding is equal for both winters. The proportion on grasslands was higher in the second winter, apparently as a consequence of reduced foraging on pondweeds.

Table 3. Calculated percentage of swan days spent by Bewick's Swans in The Netherlands on different food types on arable land in 1982-83 and 1983-84.
The percentage given is the percentage of swans observed on the food type concerned during the bi-weekly counts. Thus, the figure is weighted for the total number of swans in the different counts. 'Other' food types eaten are: carrots, rapeseed and leaves of bean-plants.

	1982-83	1983-84
sugar-beet, %	75.1	63.4
potatoes, %	1.1	11.2
winter wheat, %	14.9	18.6
other, %	0.3	1.1
not specified, %	8.7	5.7
total swans feeding on arable land, *n*	9,566	9,094
bi-weekly counts yielding swans, *n*	14	12

The category arable land is comprised of different agricultural food sources: sugar-beet (both roots and leaves are eaten), potatoes and winter wheat are the main food types taken. Carrots, rapeseed and leaves of bean-plants are taken in smaller amounts. In Table 3 the percentages of swan-days for the main food crops are given separately. In both winters sugar-beet attracts the largest numbers of swans. The heads and leaves of sugar-beet are available every year, although some farmers may collect the green in some years as food for cattle. The availability of potatoes is much more variable between years, as the timing and efficiency of the harvest is dependant on the weather. In 1984, increased feeding on potatoes by swans was a consequence of extremely wet weather in autumn, which prevented harvesting.

Proportion of cygnets in groups on different food types

In the first half of the winter different food types are utilized, but after January nearly all birds were feeding on grassland (Fig. 3). For October-January 1982-83 the proportion of cygnets are separated per food type for each count (Table 4). The proportions of cygnets in flocks feeding on pondweeds are lowest, generally followed by grassland, sugar-beet, potato and winter wheat in ascending order. This trend was found in both years.

In evaluating the importance of the different food types for families and non-families the absolute number of cygnets per food type is important as well. These figures are calculated from the proportion of cygnets on each food type and the proportion of swans utilizing that food type during the count concerned (Table 5). Although the proportion on winter wheat is relatively high, its importance in absolute numbers is low. Already from the end of November onwards the majority of cygnets feeds on grassland.

Discussion and conclusions

Bewick's Swans are present in the Netherlands from October to March. At least 6,000 were counted from November to February inclusive in 1982-83 and 1983-84, including a peak of almost 9,000 in January. Both winters were normal to mild. In more severe winters numbers are much lower (Dirksen & Beekman 1991). The January maximum represents 55 % of the estimated total population size. During January-censuses in recent years 93 % (1984, Beekman *et al.* 1985) and 99 % (1987, Dirksen & Beekman 1991) of all Bewick's Swans were found in or to the west and south of the Netherlands. Many of the birds wintering on the British Isles are known to use Dutch sites on migration, known from sightings of individually ringed birds (Evans 1982, pers. obs.). Therefore we agree with Osieck (1986) in supposing that most individuals in the population use Dutch sites each winter for either overwintering or staging during migration.

The bi-weekly censuses yielded some interesting differences in timing of migration between families and adults without cygnets. In the

Table 4. Juvenile proportion on the different food types, October-January 1982-83.
Proportions are given only for food-types with at least 100 swans aged in the count concerned. N of total may be larger than the sum of n of all the food types, due to food type other or not specified (Table 3).

Date	Pondweed		Sugar-beet		Winter-wheat		Grassland		Total	
	%	*n*	%	*n*	%	*n*	%	*n*	%	*n*
16-18 Oct	2.8	2067							2.7	2089
30 Oct-1 Nov	7.2	3938					13.3	166	7.3	4399
13-15 Nov	4.1	2127	13.5	1076			9.8	1898	8.8	5362
27-29 Nov	6.3	112	13.7	2014	15.9	302	11.0	2300	12.9	5078
18-20 Dec			11.9	2094	9.6	531	11.4	3084	11.3	5851
30 Dec-2 Jan			12.4	672			10.1	4454	10.2	6276
15-17 Jan			10.8	965	13.3	278	10.3	3389	10.6	5426
29-31 Jan							10.8	4634	11.3	5437

Netherlands, the proportion of cygnets increases until the end of November. On leaving the breeding grounds, families are 2-4 weeks behind adults without cygnets (Mineyev 1991): they leave in the second half of September. Apparently this difference in timing persists until they reach the wintering grounds. In spring juvenile proportions increased with decreasing total numbers (1984). On average adults apparently leave northeastward earlier than juveniles do. Since brood sizes decreased as well, this probably reflects the breaking up of the families.

Families and adults without cygnets seem to be unevenly distributed over the food types utilized in the first half of the winter (see Black & Salmon 1991 for a comparison with Whooper Swans). The low proportion of cygnets in the groups feeding on pondweeds is puzzling. The possibility that the difference is only caused by the combination of two 'circumstantial' facts (early arriving birds have a lower proportion of cygnets and pondweeds are eaten immediately after arrival of the birds) can be excluded (Table 4). Comparing feeding efficiencies of family members versus paired and single birds, and adult birds versus cygnets, together with their competitive abilities (cf. Scott 1981) on rapidly depleted food stocks, must explain the low cygnet proportions on pondweeds. We have shown changes in food choice throughout the winter. The factors determining these patterns need elucidating because obtaining information about food choice by the swans implies a better insight into the requirements of these birds throughout the year.

The long-term history of food choice, a switch from pondweeds to arable land and grasslands during the end of the 1960's, is nowadays reflected within the pattern of food choice in each winter. On arrival in autumn the Bewick's Swans have a clear preference for pondweed tubers. After depleting these (Beekman *et al.* 1991) the swans feed on root crops, winter wheat and grasses. Tubers and root-crops can be characterized as energy-food: they consist largely of carbohydrates, and have medium protein levels. Winter wheat and grasses are relatively rich in protein. There seems to be a temporal difference in the choice between these two types: energy-food in autumn and proteins in spring. The choice of pondweed tubers in autumn is a real preference above available other food types. Elsewhere we suggest the swans use it as a way of replenishing fat reserves after migration and before cold spells may occur in winter (Beekman *et al.* 1991). There is no indication of a difference in cygnet proportion according to the choice for energy or protein: the proportions on grasslands are comparable to the proportions of the totals, and the lower percentage on

Table 5. Number of cygnets per food type, October-January 1982-83.
Number calculated from: % cygnets F * % swans F * total swans, where F = food type concerned. Data used are in Table 4, Figure 3 and Table 1 respectively.

date	Pondweed	Sugar-beet	Winter wheat	Grassland	Total
16-18 Oct	72				72
30 Oct-1 Nov	424			24	449
13-15 Nov	116	145		222	555
27-29 Nov	8	275	48	363	774
18-20 Dec		251	52	578	882
30 Dec-2 Jan		85		605	702
15-17 Jan		105	35	698	932
29-31 Jan				609	700

pondweeds (see above) is compensated for by a higher percentage on root-crops (Table 4).

Unfortunately, in the present situation it is impossible to decide whether feeding on grasses in winter and early spring is a real preference as well. In all years since 1975 the pondweed tubers are depleted in one or two months and only few root-crops are available after January. Brouwer and Tinbergen (1939) describe how the Bewick's Swans utilized pondweed tubers throughout the winter. This suggests that feeding on grassland could be forced instead of chosen. However, environmental changes in the last few decades provide arguments that the preference in spring may not necessarily be the same as 50 years ago. Human activities have caused major changes in both aquatic and terrestrial ecosystems. The developments in the agricultural sector have been important for Bewick's Swans. Eutrophication, at least partly caused by fertilizer used in agriculture, and consequent algal blooms, made the pondweeds disappear. On the other hand, the same fertilizers improved the quality of grasslands in terms of productivity and grass quality. Especially in spring the growth starts earlier, and protein contents are high. Alongside these changes most agricultural areas have been made much drier by water-table manipulations, while swans favour wet grasslands. The important question is which choice Bewick's Swans would make in spring if they could choose between pondweed tubers and the very protein-rich grass species of present day agriculture.

It is necessary to (further) improve the water quality, in order to give the Bewick's Swans more possibilities to feed on aquatic food sources. The preference for wet or inundated grassland implies that these should be preserved to serve as a foodsource in winter and spring. The latter is equally important since the improvement of aquatic habitats will take many years. Further habitat loss may put a threatening pressure on the small western population of Bewick's Swans.

Nowadays Bewick's Swans staging and wintering in the Netherlands are almost completely dependent on the developments in agriculture, not only on land but also in their aquatic environment. It is not likely this will change in the near future. In combining large scale research with detailed feeding ecology studies the consequences of such developments might be unraveled.

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