

# Connecting seas: western Palaearctic continental flyway for water birds in the perspective of changing land use and climate

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## Abstract

The western Palaearctic continental flyway that connects the tundra and taiga belts of Russia with north-west Europe is the major migratory avenue for an estimated 9.3 million herbivorous water birds (swans, geese and ducks). Agricultural practices together with protection measures subsidize the carrying capacity of winter habitats of the birds. Densities of these birds are highest in the Netherlands, where nitrogen (N) inputs to farmland have increased during the last 70 years and became the highest in Europe ( $>250$  kg manure and fertilizer  $\text{ha}^{-1}\text{yr}^{-1}$ ). A comparison of population trends of 13 species of avian herbivores reveals generally expanding populations in the past 50 years, with the greatest increases from 1970 to 1990. Populations of the smallest avian herbivores, such as ducks, are either stable or have peaked and are now in decline, whereas numbers of larger herbivores (geese and swans) continue to increase and barnacle and greylag geese now breed in the Netherlands, in addition to northern sites.

During the northerly spring migration, stop-over sites, mostly in the agricultural regions of eastern Europe and Scandinavia, lie between the 3 and 6 °C mean daily temperature isotherms in April, temperatures at which grasses start to grow, where flooding of riparian wetlands frequently occurs and fertilizers are applied to farmland. However, the restructuring of agricultural practices in an enlarged EU is likely to affect water bird populations and their migration routes. The reduced use of N in the Netherlands is predicted to constrain population growth, especially of the smallest avian herbivores with their high basal metabolic rates, because of the declining food quality of grass leaves. The introduction of large-scale farming of oilseed rape, winter cereals, sugar beet and potatoes at the expense of grassland also will adversely affect these birds, whereas larger species are likely to continue exploiting these crops.

*Keywords:* barnacle goose, carrying capacity, dark-bellied brent, fertilizer use, improved grassland, plant phenology, salt marshes

*Received 15 June 2004; revised version received 24 November 2004; accepted 24 January 2005*

## Introduction

Profound changes have occurred in the European landscape during the 20th century. Intensification of land use has led to a simplification of the trophic structure of many ecosystems, giving man control over

natural variation in managed landscapes (Heath & Evans, 2000). In a deteriorating environment, migratory birds are forced to cope with ever-changing patchy environments, which result from frequent and often radical shifts in land use. Although herbivorous water birds used transient food sources in wetlands long before man transformed these sites into agricultural land, many species have responded by exploiting agricultural crops (Hochbaum, 1955; Scott & Boyd,

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1957). The evidence of these responses to the extension of agriculture comes from records of distributions and the population sizes of different species. Numbers of water birds have been monitored assiduously, spurred by nature conservation as well as hunting interests. These data, together with ring recoveries, enable analyses to be made of the distributions and movements of birds, as well as trends in population numbers along flyways and on the wintering grounds (Madsen *et al.*, 1999). The underlying causes accounting for current trends in waterfowl numbers may be grouped into two main categories, namely those linked to food availability (especially as the result of modern agriculture) and those that result from hunting pressure (Ebbinge, 1991; Van Eerden *et al.*, 1996).

Nutrient requirements of water birds during the course of the year differ; protein is important during spring as a prerequisite to egg laying, whereas carbohydrates provide fuel when food is scarce (autumn, winter), or during migration (Klasing, 1998). In relation to body size, the smaller species of avian herbivore require a diet with relatively more protein, in contrast to the larger species that ingest more biomass per bite at all stages of the annual cycle. The smallest species, therefore, are more sensitive to changes in food quality measured as the nitrogen (N) content of food (Bruinzeel *et al.*, 1997). In addition to the use of agricultural land, the availability of coastal seminatural freshwater and salt marshes (roosting, staging and feeding sites) is important for survival of water birds, as demonstrated for ducks (wigeon, *Anas penelope*, depend on seeds; Van Eerden, 1984), geese (brent, *Branta bernicla*, depend on eelgrass, algae, and salt-marsh species; Bos, 2002; Prop, 2004) and swans (Bewick's swan, *Cygnus bewickii*, depend on pondweed; Beekman *et al.*, 1991).

In this paper we concentrate on the continental western Palaearctic flyway. Our aim is to show the current status of herbivorous water birds in relation to man's activities and to assess possible effects of agricultural and climatic changes. We use data on the ecology and status of brent and barnacle geese in the Netherlands, but we also make multispecies comparisons in order to elucidate important driving forces behind population changes observed in Europe (Drent *et al.*, 2003).

## Methods

Although water birds are counted in January each year, in order to detect trends in numbers and shifts in distribution, counts are often made on a monthly basis in western Europe. Counts of geese and other water birds in the Netherlands have been made by some 1500

observers on a near-monthly basis over the past 40 years, currently coordinated by SOVON (cf. Van Roomen *et al.*, 2004). Over-winter counts (or in the case of brent geese counts in May) from 1960 to the present are given in this paper.

In order to provide a quantitative overview of total food extracted by water birds in the Netherlands, a *consumption index* has been calculated from the census data. For this exercise the total consumption (at 10-year intervals) has been derived from the population count multiplied by the allometric prediction (Bruinzeel *et al.*, 1997) of daily existence energy (DEE) based on the mid-winter body mass of each species (data from Bauer & Glutz von Blotzheim, 1968; Cramp & Simmons, 1977; Van Eerden, 1997). The formula predicting DEE is based on empirical data for 33 species of herbivorous water birds ranging from 0.3 to 6 kg, including 10 species in our census (Bruinzeel *et al.*, 1997). The calculation for 2005 is based on an extrapolation of counts for 2003 and 2004, and that for 1965 on an interpolation for certain species.

Spring weather data along the Baltic–White Sea migratory flyway were obtained from five selected stations (cf. Table 1). The date of onset of spring growth of graminoids was calculated as the date when the cumulative daily mean temperature above 0 °C, calculated from 1 January, exceeds 180 °C. This threshold provides an estimate of the initiation of spring growth in grasses, such as *Festuca rubra*, a major forage species for staging barnacle (*B. leucopsis*) and brent geese. Field measurements during six springs of the standing crop of *F. rubra* using biomass data on Schiermonnikoog (NL) confirm the validity of the  $T_{\text{sum}}$  method (see Klimkowska, 2003). Weather data were supplemented by a broader database from 405 stations collated by Müller (1980), in order to plot the position of daily mean temperature isoclines in spring in western Europe and to link these data to the timing of the onset

**Table 1** Selected weather stations for derivation of onset of spring growth of graminoids along the western Palaearctic flyway (coastal route along Baltic and White Sea)

Site	Location	Period of data analysed
Schiermonnikoog (the Netherlands)	53°28'N, 6°10'E	1972–2003
Gotland (Sweden)	57°30'N, 18°33'E	1970–2002
Vilsandi (Estonia)	58°24'N, 22°29'E	1920–2001
Archangelsk (Russian Federation)	64°50'N, 40°73'E	1881–1999
Nar'yan Mar (Russian Federation)	67°38'N, 52°57'E	1926–1999

of grass growth along the flyway. Data of total amounts of N fertilizer applied to grassland between 1960 and 2000 were compared with changes in bird use of grasslands in the Netherlands (LEI/CBS, for Europe from Eurostat at <http://europa.eu.int/comm/eurostat/>, see also Van Eerden *et al.*, 1996).

## Results

### *Waterbird populations and agricultural practice in the Netherlands and the western Palaearctic*

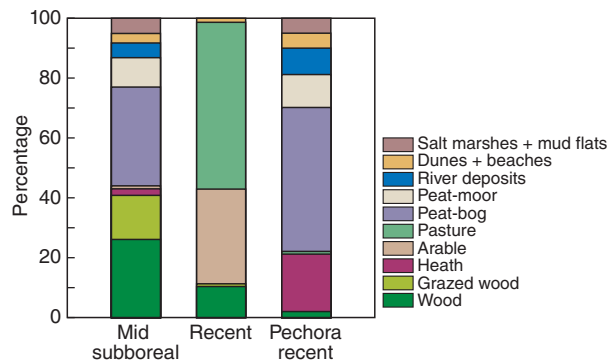
Well over 26 million avian herbivores of 17 species migrate within the western Palaearctic, based on winter counts (Table 2, compiled from Monval & Pirot, 1989; Scott & Rose, 1996; Madsen *et al.*, 1999; Gilissen *et al.*, 2002). In winter geese and swans are concentrated in north-west Europe, including the UK (2.4 million, 61% of total number of 3.9 million), whereas ducks are relatively more abundant in the Mediterranean, Black Sea and Caspian/south-west Asian wetlands (Table 2). Data for populations in the UK and Ireland have been given separately, as several goose and swan populations which breed in Greenland, Iceland and Spitsbergen winter in the British Isles.

In the Netherlands the area of grassland peaked at between 1.1 and 1.4 million hectares in the 20th century, and improvements in quality of forage plants enhanced attractiveness to avian herbivores. The successful switch by geese, ducks and swans from natural foods to exploiting agricultural sources masks the recent disappearance of alternative food sources. Almost 80% of the total flyway population of barnacle geese in north-west Europe rely on agricultural land in the Netherlands in winter (Madsen *et al.*, 1999), compared with 33% of the staging brent and 50% of the Bewick's swan flyway populations (Beekman *et al.*, 1991). Managed habitats now dominate the landscape of the Netherlands, at the expense of the natural ones (Fig. 1). The original diversity of habitat types reconstructed for the Rhine and Meuse delta in its natural state (3700 years ago), resembles the patchwork of habitats still present in the Pechora delta in Arctic Russia where many herbivorous water birds breed (Fig. 1). Original goose habitats consisted of coastal marshes (algae, grasses, sedges), raised bog (dwarf shrubs sedges) and fen habitat (reeds, sedges, submerged macrophytes). Nowadays geese only exploit these habitat types in summer since most have disappeared on the wintering grounds through land reclamation, drainage and cultivation.

**Table 2** Population estimates of herbivorous water birds ( $\times 1000$ ) according to wintering region in the western Palaearctic

Species	Wintering area				
	NW Europe	UK – Scotland, Ireland	S Europe, N,W Africa	C, Europe – Black Sea, NE Africa	Caspian – SW Asia
<i>Cygnus olor</i>	400	35		61	250
<i>C. cygnus</i>	40	16		17	20
<i>C. columbianus</i>	14	3			1
<i>Anser brachyrhynchus</i>	34	225			
<i>A. fabalis</i>	280			100	
<i>A. albifrons</i>	600	30		750	15
<i>A. erythropus</i>				4	20
<i>A. anser</i>	80	105	120	45	100
<i>Branta bernicla</i>	180	100			
<i>B. leucopsis</i>	176	44			
<i>B. ruficollis</i>				40	30
<i>Anas penelope</i>	1000	250	250	560	250
<i>A. strepera</i>	20	10	130	112	130
<i>A. crecca</i>	250	150	1000	1500	1500
<i>A. platyrhynchos</i>	4840	160	1000	2250	800
<i>A. acuta</i>	35	25	1200		700
<i>Fulica atra</i>	1350	150	755	491	1500
Total number ( $\times 1000$ )	9300	1300	4500	5900	5300
% number	35.4	5.0	16.9	22.5	20.2
% ME <sub>eq</sub>	40.5	6.1	13.3	21.1	18.7

Data compiled from Scott & Rose (1996), Monval & Pirot (1989), Madsen *et al.* (1999); feral populations excluded from totals. ME<sub>eq</sub> = adjusted number on the basis of metabolizable energy uptake ( $\text{kg}^{0.68}$ ).



**Fig. 1** Reconstruction of extent of habitats important for waterfowl in the Rhine/Meuse delta in the Netherlands at about 3700 years ago (from Van Eerden, 1997) in comparison with the present situation in the Netherlands and the Pechora Delta (Russia).

Despite the deterioration of their natural habitats many species of herbivorous waterfowl have shown a spectacular increase in numbers. But is modern agriculture the cause of major expansion of these herbivorous birds? To answer this question we have summarized the factors operating on species and populations in Europe. Populations dependent upon agricultural habitats in winter, spring and summer are among the most numerous and show greatest increases. The degree of agricultural exploitation correlates with population size and the populations of Baltic barnacle geese, Russian barnacle geese and greylag geese rank highest in this respect. Protection from hunting does not add significantly to this food quality effect (Table 3).

Only two species of geese are classified as being of vulnerable conservation status in Europe and both have largely failed to exploit high intensity agricultural crops

**Table 3** Description of different flyway populations of western Palaearctic goose species with classification of population status, hunting impact and forage use

Species	Breeding area	Population status	Protection	Agricultural subsidies			Food total score	Food and protection total score
				Winter	Spring	Summer		
Spearman's $r_s$			-0.068ns				0.647**	0.559**
Barnacle goose	Baltic-North Sea	3	5	5	4	3	12	17
Greylag goose	Europe continent	4	3	5	4	3	12	15
Barnacle goose	Russia	4	4	5	3	1	9	13
White-fronted goose	Russia west	4	2	5	3	1	9	11
Bean goose	Russian tundra	4	3	4	3	1	8	11
Pink-footed goose	Spitsbergen	3	3	5	3		8	11
Greylag goose	Europe east	3	3	3	3	2	8	11
White-fronted goose	Siberia east	4	3	3	3	1	7	10
White-fronted goose	Russia east	4	2	3	3	1	7	9
Greylag goose	Iceland	4	3	4	2	1	7	10
Brent goose	Russia	4	4	3	3		6	10
Pink-footed goose	Iceland/Greenland	4	3	4	2		6	9
Bean goose	Russian taiga	3	3	3	3		6	9
Barnacle goose	Greenland	3	5	3	2		5	10
Barnacle goose	Spitsbergen	3	5	3	2		5	10
Red-breasted goose	Russia	3	4	3	2		5	9
Lesser white-fronted goose	Europe	2	3	3	2		5	8
White-fronted goose	Greenland	3	5	2	2		4	9
White-fronted goose	Siberia north	3	3	2	2		4	7
Lesser white-fronted goose	Russia east	3	3	2	2		4	7
Brent goose	Greenland	3	5				0	5
Brent goose	Spitsbergen	2	5				0	5

Classification scheme as follows: population status: 2 = <10 000 birds, 3 = 10 000–100 000, 4 = 100 000–1 000 000. Protection: 5 = completely protected over flyway, 4 = partially hunted, 3 = commonly hunted, 2 = intensively hunted along flyway. Agricultural dependence: 5 = strongly dependent (>90% of food, uses highly improved fields), 4 = 75–90% agricultural food, 3 = 50–75%, less intensive fertilized fields, 2 = 25–50%, hayfields and grazed areas, 1 = 5–25%, idem 0 = <5% idem. Food and protection measures refer to enquiries and published data for 1990s. Species and populations have been ordered according to decreasing use of agricultural fields; Spearman's  $r_s$  correlation with population size: \*\* $P < 0.01$ .

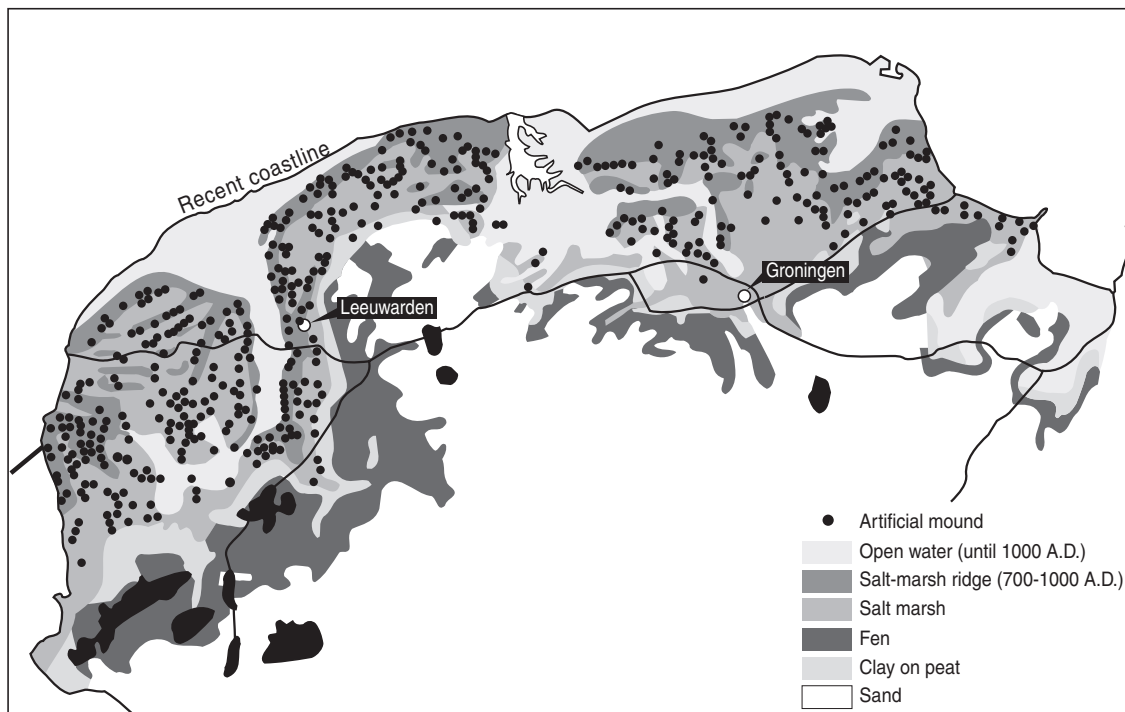


Fig. 2 Pattern of early human settlement of the Dutch Wadden Sea coastline deduced from inhabited mounds projected on the underlying soil type (from Rijksdienst voor Oudheidkundig Bodemonderzoek ROB).

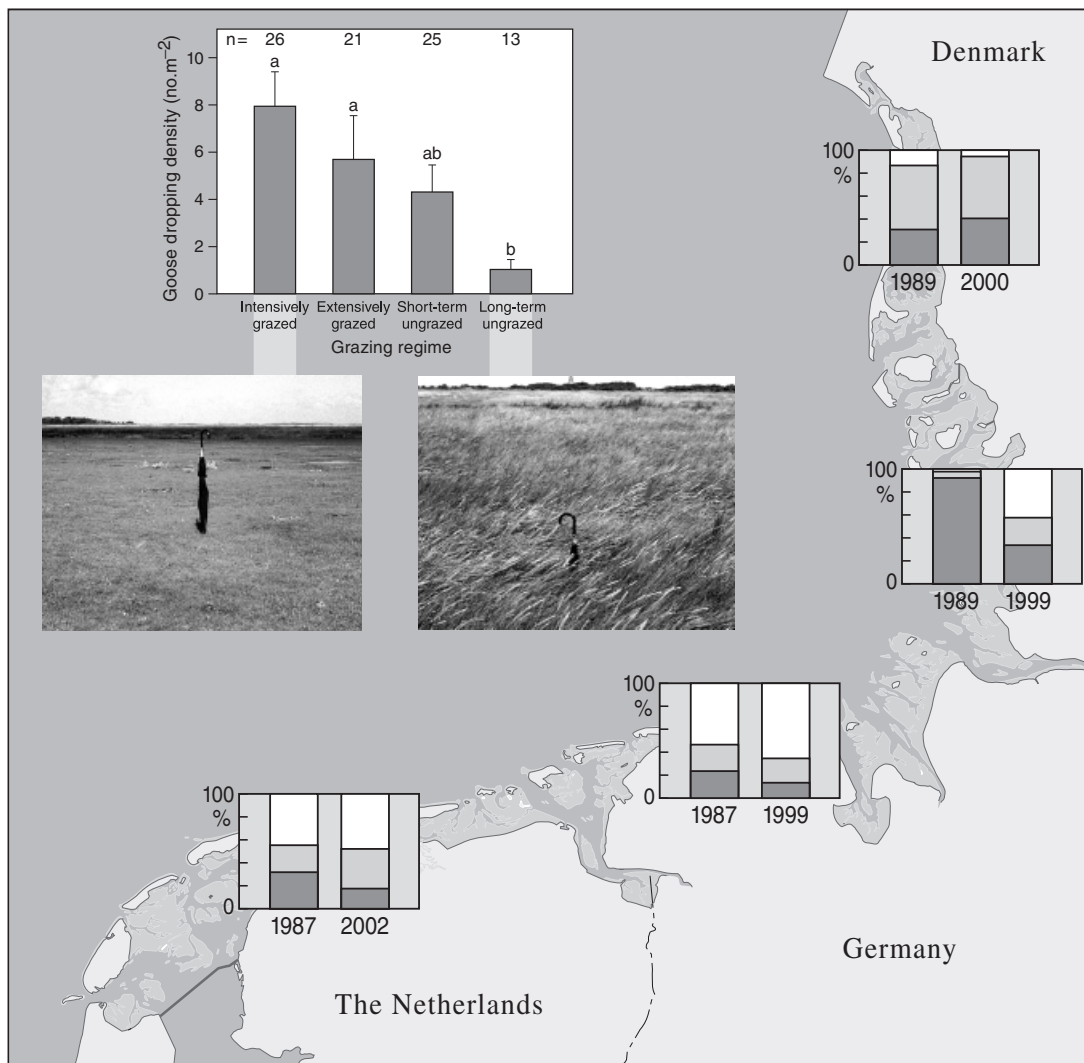
on the wintering grounds. The boreal breeding lesser white-fronted goose, *Anser erythropus*, and the Arctic red-breasted goose, *B. ruficollis*, are also hunted and their traditional wintering and staging wetland sites have been modified or destroyed (Madsen *et al.*, 1999).

In north-west Europe salt marshes have been grazed by livestock since they emerged about 2500 years BP (Fig. 2). Since AD 1200 seawalls were established along Wadden Sea coasts for protection and the subsequent embankment of salt marshes has gained new agricultural land with a net decrease in the area of salt marshes along Dutch mainland coasts since AD 1600. At the end of the 20th century, the Wadden Sea supported about 20 000 ha of clay-based mainland salt marshes, 10 000 ha of sandy clay salt marshes on the Frisian Islands and 5000 ha of summer polders (embanked meadows with winter flooding by the sea) (Kempf *et al.*, 1987). The present marshes are retained for coastal protection and nature conservation. However, existing marshes are squeezed between the seawall and the intertidal flats, and hence the pioneer zone, so vital to water birds for feeding, has been transformed into mature salt marsh (Bakker *et al.*, 2002). This aging process has been reinforced by the cessation of livestock grazing, as the marshes have lost their agricultural function and become nature reserves. These trends in land use are of direct relevance to the carrying capacity of salt marshes for waterfowl and their switch into agricultur-

al land. In the absence of livestock grazing a tall canopy replaces a short turf in these marshes (Bos *et al.*, 2002; Bakker *et al.*, 2003). An assessment of goose use at 164 coastal sites around the Wadden Sea indicates a negative relationship between goose usage and canopy height and a positive relationship with livestock density (Fig. 3; Bos, 2002; Bos *et al.*, 2002, 2004b; Bakker *et al.*, 2003).

Although arable fields and improved grasslands make up the reclaimed agricultural polders which are heavily used by waterfowl in winter, geese traditionally switch to the salt marshes during spring prior to migration, particularly those marshes where sheep grazing still persists (e.g. the Dutch island of Ameland). Experiments with captive geese indicate that if the grass becomes too long in the absence of sheep facilitation, it is no longer attractive to geese (Van der Graaf *et al.*, 2002). However, migrating birds may show a behavioural response to tall grass or rapid growth and graze intensively in a few selected salt-marsh pastures, so that the turf is kept short, at least during the staging period (Bos & Stahl, 2003).

The total amount of N applied as manure and artificial fertilizer to grassland in the Netherlands exceeds  $250 \text{ kg ha}^{-1} \text{ yr}^{-1}$  (Fig. 4) (Stanners & Bourdeau, 1995). Aerial deposition of N adds at least another  $15\text{--}20 \text{ kg ha}^{-1} \text{ yr}^{-1}$  (mainly precipitated as ammonium  $\text{NH}_4^+$ ) and is strongly linked to the intensified dairy



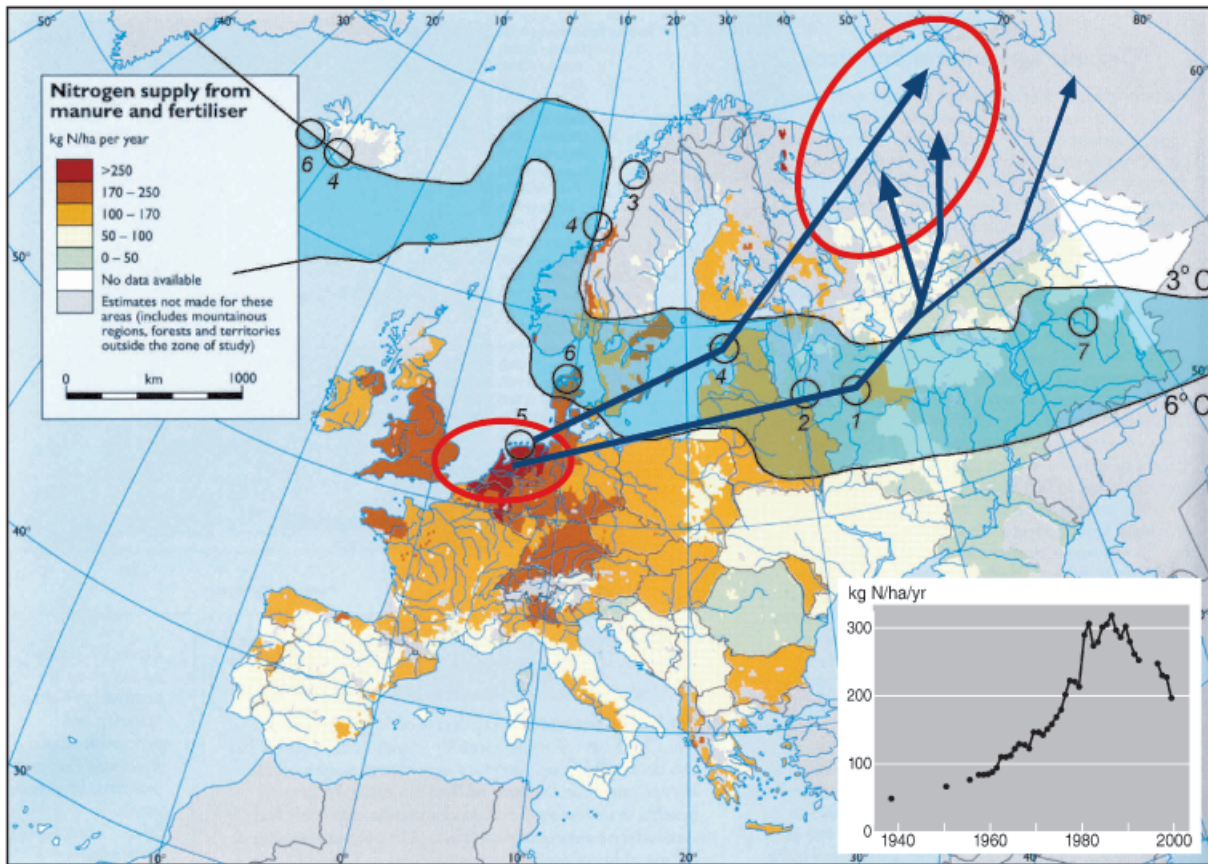
**Fig. 3** Spring habitat use by barnacle and dark-bellied brent geese in the Wadden Sea shows a preference for short swards of *Agrostis*, *Festuca* and *Puccinellia* grazed by livestock (from Bos *et al.*, 2004b). The insets show the decline in grazing in four subregions along the Wadden Sea foreshore over the past 15 years. Dark shading indicates intensively grazed marshes, light shading indicates moderately grazed marshes, white indicates ungrazed areas.

cattle industry. The highest deposition rates in Europe are in the Netherlands, Denmark, parts of UK, as well as Ukraine (Schaug, 1994; Stanners & Bourdeau, 1995). However, the average level of N fertilizer applied to pastures in the western and northern parts of the Netherlands (where most waterbirds occur) has declined from peak values of  $320 \text{ kg ha}^{-1} \text{ yr}^{-1}$  in 1985 to about  $200 \text{ kg ha}^{-1} \text{ yr}^{-1}$  in 2000 (inset in Fig. 4).

#### *Food shift and numerical responses of Anatidae in the Netherlands since 1945*

As indicated above, species of low body mass are expected to be sensitive to shifts in forage quality. In

those Dutch polders used for dairy cattle farming, forage quality on grasslands improved greatly after 1945. Since 1985, the crude protein content of grass leaves in winter has not fallen below 25% of the dry weight (Van Eerden *et al.*, 1996). First the mute swan (*C. olor*), followed by the Bewick's swan and then the greylag goose (*A. anser*) shifted to improved grassland as their main winter food source during the 1950s and 1960s. Smaller geese, such as white-fronted (*A. albifrons*) and barnacle goose followed in the 1970s, and wigeon fed in grasslands after 1985. Figure 5 shows schematically this release from nutritional bottle necks, first of food quantity (green biomass) for the larger birds, later food quality (crude protein content) for smaller birds.



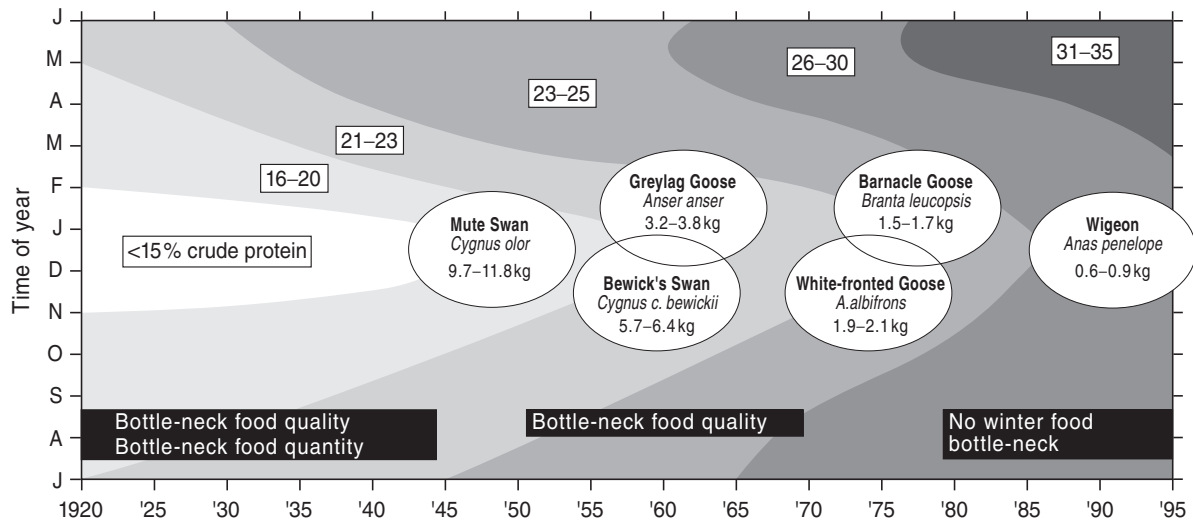
**Fig. 4** Goose flyways in Europe connected to the High Arctic via spring staging sites for each species or population (1, greater white-fronted goose; 2, tundra bean goose; 3, pink-footed goose; 4, barnacle goose; 5, dark-bellied brent goose; 6, light-bellied brent goose; 7, red-breasted goose). The spring staging sites (late April–May) are based on ringing recoveries and observations and generally fall within the 3–6 °C isotherms for April defining the advent of graminoid growth (from Prop, 2004). The continental flyways for barnacle and brent following the coast of the Baltic and White Sea as well as that for the inland migrating greater white-fronted and tundra bean geese are shown. Note the large differences in amounts of nitrogen added to farmland in Europe, the position of the staging sites in winter in the Netherlands as a core area for geese, as well as the stop-over sites in spring. Inset shows nitrogen supplied to grassland in the Netherlands in  $\text{kg ha}^{-1} \text{yr}^{-1}$  for the period of 1940–2000.

Counts of herbivorous water birds in the Netherlands (Fig. 6) reveal three classes of response: (1) a decline from peak numbers in the late 1970s for mallard (*A. platyrhynchos*), teal (*A. crecca*) and coot (*Fulica atra*); (2) little change in values for bean geese, wigeon, brent geese and pintail (*A. acuta*) during the past two decades and for white-fronted geese since the early 1990s and (3) a continuing increase in numbers of barnacle, greylag geese, gadwall (*A. strepera*) and mute swans. However, numbers of Bewick's swan have declined since the mid-1990s, and the population has failed to show a continued positive response to the increase of more intensively managed grasslands and arable crops. In addition, the continued rise in the gadwall population to 20 000 birds is not easily understood in the context of agricultural change.

In order to clarify the overall response of the different species to improved grassland quality a *consumption*

*index* has been compiled (see lower panel in Fig. 6), based on 10-year intervals. The total consumption of vegetation by herbivorous waterfowl on grassland (chiefly improved pasture maintained for dairy cattle) has risen sharply with the largest relative increase from 1965 to 1985 (cf. Van Eerden *et al.*, 1996). However, this rate of increase has not been maintained, especially with respect to the *Anas* species and the coot, *F. atra*. Numbers of these relatively small-bodied species have fallen since the mid-1980s and are predicted to fall further as forage quality decreases because of reductions in fertilizer application. Heavier water birds, such as geese, are less susceptible to changes in forage quality (Bruinzeel *et al.*, 1997).

The population of brent geese in the Netherlands has now reached its carrying capacity at 100 000 individuals, based on the counts in May (Bos *et al.*, 2004a).



**Fig. 5** Approximated long-term changes in food quality of grasslands on dairy farms in the Netherlands 1920–present. The shaded regions enclose zones of crude protein (% dry matter) depicted in a generalized annual cycle, the quality trough falls in mid-winter but has improved during the century. Projected on this matrix is the approximate timing when the most abundant herbivore waterfowl began their phase of full reliance on improved grassland during winter.

The authors concluded that coastal salt marshes and grasslands are fully utilized, and that further expansion of brent geese into estuarine areas is precluded by competition from barnacle geese. Recently, the latter species has extended its spring staging period in the Wadden Sea marshes well into May, which overlaps with the major staging period of brent geese. Brent only exploit agricultural polders intensively in late spring (May) when human disturbance is absent (Bos & Stahl, 2003). There may be some reserve carrying capacity in salt marshes along portions of the German and Danish coasts (Bos *et al.*, 2004a), especially where these are grazed by livestock (Van der Wal *et al.*, 2000), but feeding conditions during spring staging may already be limiting *B. b. bernicla* numbers, as the entire population is concentrated on the Wadden Sea coast at this time (Madsen *et al.*, 1999).

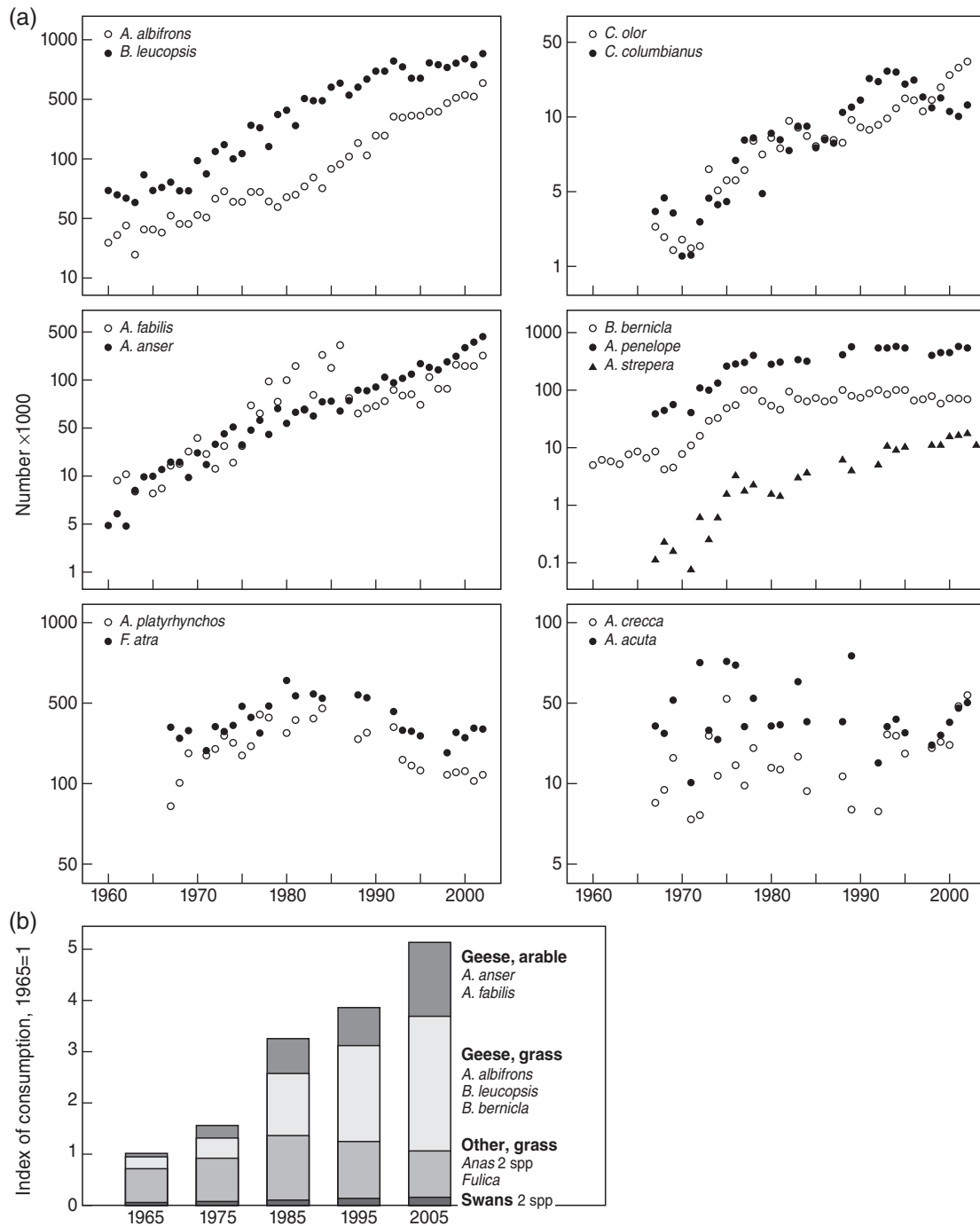
Within the Netherlands, the dark-bellied brent was predominantly restricted to salt marshes and intertidal flats at the periods of peak occurrence (October–November and again in May) in the mid-1970s with 85–95% of the total population of birds present in these habitats. By 1995–2002 the use of these traditional sites had fallen to 50–60% and the remainder fed on improved grassland when free of human disturbance (Van Roomen *et al.*, 2004). Numbers of barnacle geese also have increasingly utilized improved grasslands during the past 20 years, often at some distance from the coast. This expansion has occurred in parallel with the doubling of the wintering population, but numbers in the traditional coastal zone have remained constant,

hence less than 10% are found in the Wadden Sea sector today (Koffijberg & Günther, 2004). However, the coastal marshes in the northern Netherlands that provide spring staging sites during April for up to 150 000 birds (40% of the flyway population) are apparently ‘saturated’ as this number has not increased markedly since 1985 (Van Roomen *et al.*, 2004). Several new coastal staging areas have been ‘colonized’ in recent years to take the overflow (e.g. west Jutland). It is not clear to what extent improved grassland away from the coast that is exploited in winter can provide a fully adequate alternative food source in spring compared with coastal salt marshes.

#### *Land-use patterns, different pathways of migration and range extension*

The continental migration routes across Europe show two distinct avenues: (1) dark-bellied brent geese and barnacle geese fly a narrow corridor both in spring and autumn between the Netherlands, the Baltic/White Sea and the Russian coastal breeding colonies. Staging is concentrated at a few stopover sites; (2) greater white-front and bean geese (*A. fabalis*) migrate over a wide front from the Netherlands to eastern Europe and then north to the Russian taiga and tundra belts where they have many and scattered nesting sites. The positions of spring staging sites in late April and May for seven populations of six species are indicated in Fig. 4. These sites and those of populations of other species breeding in Greenland, Iceland, Spitsbergen and Arctic Russia fall





**Fig. 6** (a) Changes in peak numbers of waterfowl in the Netherlands from 1960 to present, (Van Eerden *et al.*, 1996; Van Roomen *et al.*, 2004; note logarithmic scale). Counts of ducks and coot for severe winters have been omitted. The species have been combined in ecological categories (see text). (b) The trends in total herbivore consumption, that distinguishes geese on grassland, geese on arable land, ducks, and swans (see text for derivation of the consumption index) are shown.

between the positions of the 3–6 °C isotherms in April. In addition, the spring growth of vegetation is enhanced by agricultural fertilizer, which has probably influenced the selection or modification of migratory routes. This timing aspect will be elaborated in the next section.

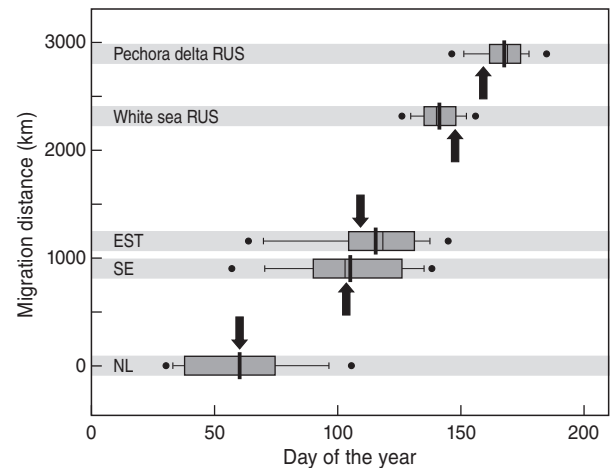
There has been a dramatic change in the breeding sites of some populations during the past two decades. Barnacle geese traditionally bred on Novaya Zemlya and Vaygach but during the past two decades have expanded their breeding range to Gotland, Öland

(Larsson *et al.*, 1988) and Saaremaa in Estonia (Leito, 1996), which were, and still are, used as migratory stopover sites in spring. The geese feed in improved grasslands (Gotland, Saaremaa) or on cereals (Saaremaa). During the 1990s, the Russian population has also expanded to many new breeding sites on the Yugorskiy Peninsula, Kolguyev, Kolokolkova Bay, Sengeyskiy Bay and Kanin (Filchagov & Leonovich, 1992; Madsen *et al.*, 1999; Van der Jeugd *et al.*, 2003). Most of these new colonies are situated in flat coastal marshes, earlier the sites of small human settlements with some livestock, but recently abandoned. Extension of breeding areas of barnacle geese continues also at the other end of the flyway, in Zeeland in the south-west Netherlands. In this wintering area barnacle geese started nesting in 1984 (Meininger & Van Swelm, 1994). In 2003 almost 3000 breeding pairs (H. P. Van der Jeugd, personal communication) were known to nest here.

Greylag geese have extended their breeding range as well. Unlike the barnacle goose it is not a colonial species, hence a range extension is less easy to detect. Detailed mapping of breeding pairs in the Netherlands shows that, although greylags have bred here regularly since 1965, their numbers increased greatly from the mid-1970s with 150 pairs in 41 breeding squares (national 5 km × 5 km grid) occupied in 1977, to 8900 pairs and 545 squares occupied in 2000 (Teixeira, 1979; Hustings & Vergeer, 2002). Greylags breed in protected reed beds and marsh vegetation in enriched wetlands but also feed in improved agricultural land. They have established a major new moulting site in Oostvaardersplassen, where birds from central and northern Europe aggregate with 20 000–30 000 nonbreeders (maximum 60 000 birds) (Zijlstra *et al.*, 1991).

#### *Spring migration along the Baltic–White Sea flyway follows the green wave*

The onset of spring growth of grasses in the Netherlands can be reliably predicted from the 180 °C cumulative temperature for each year based on the average daily temperature above 0 °C (Lantinga, 1985). We were able to confirm this prediction based on a temperature survey over six seasons at our field site on the island of Schiermonnikoog (Klimkowska, 2003). The onset of spring growth along the coastal flyway is in close accord with the migratory timing of the barnacle goose based on direct observations from 1990 to 2003 (Fig. 7). The geese arrive at each staging site when grasses are at their peak nutritional quality and digestibility, as demonstrated in feeding trials with captive barnacle geese (Prop, 2004; Prop *et al.*, 2004). Detailed data on intake rates and retention of nutrients (barnacle geese in northern Norway, Prop *et al.*, 1998,



**Fig. 7** Spring migration schedule of the Russian barnacle goose in relation to phenology of the major food plants (graminoids and sedges) along the route (NL, salt-marsh habitat Netherlands, SE = Sweden, EST = Estonia, via the White Sea to the breeding area in the Pechora delta, Russia). The box diagrams enclose the central 75% of the predicted dates of onset of graminoid growth at each locality, derived from temperature records (see text, minimally 20 years) with heavy bar marking the mean, light bar the median and dots at the extremes. Arrows indicate mean arrival date of barnacle geese during migration.

brent geese in the Netherlands, Prop, 2004) indicate that the staging period at each site corresponds closely with the phase of positive protein accumulation by the birds. At the first three sites (Wadden Sea, Gotland, Estonian coast) on the migration route, the barnacle geese utilize grasslands generally grazed by livestock in summer. In the White Sea area the geese feed on coastal swards until they reach the breeding areas at Kanin and further NE.

The contrast between the staging and migratory pattern of the barnacle goose just described with that of the dark-bellied brent utilizing the same flyway is illuminating. Brent geese normally remain longer in the Wadden Sea where they exploit the last phase of the flush of spring growth in the salt marshes (Prop & Deerenberg, 1991). Subsequently, they 'leap-frog' over the barnacle geese in the Baltic area to fly nonstop to the White Sea (Green *et al.*, 2002). The arrival time of brent in the White Sea (last week in May, approximately day 142) coincides with the break-up of coastal ice in brackish waters, thus making available *Zostera* shoots growing beneath the ice. This food resource is not exploited by barnacle geese that have a less well-developed nasal gland to remove excess salt from the diet (Stahl *et al.*, 2002). This contrast in itinerary underlines the primary role of food resources in setting the migratory agenda. The brent are still primarily dependent on natural foods during their spring

movements, as is true for other populations of this species (see Ward *et al.*, this issue) whereas the barnacle goose (Prop & Black, 1998) relies to an increasing extent on agricultural foods.

*The interior route used by 'grey' geese in spring: the role of spring cereals and grasslands in flooded riparian wetland systems*

Grey geese (*Anser* species), such as the bean goose and the greater white-fronted goose, follow an interior, eastward route through continental Europe before turning north to the northernmost taiga and tundra areas in Russia. These species normally leave the Netherlands in February and early March, well before departure of the *Branta* species. The flooding regime of the larger rivers sets the migratory timetable; stopover sites occur in the eastern parts of Germany and Poland, where birds concentrate in riverine areas of the Elbe, Oder, Varta and Wisla. Spring flooding usually peaks here in March and April. After mid-April and early May these species move further east into Belarus and the south-western part of European Russia. In Belarus the vast area of the Pripyat River system (upper Dnepr catchment) floods in early May and forms the route to the major staging sites (Heath & Evans, 2000). Further to the east, in Russia the staging sites comprise similar habitat in the floodplains of rivers such as the Iput, Desna, Oka, Kostroma, Moksha and Vorona (Volga catchment, Heath & Evans, 2000), but this becomes slightly later available. These areas have large-scale flooded meadows, oxbow lakes in the vicinity of improved grasslands and some fertilized arable land (spring cereals). Seed of spring barley is an important carbohydrate source. In addition, raised bogs and transitional mires provide natural food sources, such as stolons of *Eriophorum*, *Trisetum* and *Rhynchospora* (M. R. Van Eerden, unpublished results). Spring staging areas in grey geese are much more scattered than those utilized by *Branta* species. The mapped (average) staging areas for different populations in Fig. 4 fail to convey the fact that these grey geese utilize a much larger staging area.

As early as mid-May, bean and white-fronted geese appear in natural habitats along the coasts of Kanin, Kolguyev and at Pechora Bay, whereas other birds of the same species are still 1500 km to the south at spring staging areas in a semiagricultural environment. Bean geese follow a somewhat straighter (closer to the Baltic–White Sea) course than that used by white-fronted geese (Bauer & Glutz von Blotzheim, 1968). Whether any 'leap-frogging' by white-fronted geese, the smaller species, occurs like that described for the black-bellied brent goose remains unknown. None of the *Anser*

species is restricted to 'natural habitats' during spring staging and the main concentrations coincide with areas with a combination of flooded meadows, grain crops and improved grasslands. At some sites, natural vegetation, either in peat bogs or in wetlands along the river provides additional food as well.

## Discussion

*Effects of changes in land use in the breeding areas and along the flyways*

The Pechora is the last remaining river system in Europe that has maintained its natural heterogeneity and contrasts strongly with the highly modified landscape in the Netherlands. However, the Pechora is not devoid of impact by man, and the traditional forms of reindeer management, in particular, must have modified the tundra system on a large scale. Reindeer grazing is believed to be a key process in making the vegetation attractive to the smaller herbivores, not only through selective removal of lichens, but by providing a nutrient pulse via the faeces for grass and sedge growth (Van der Wal *et al.*, 2004). Avian herbivores rely on rhizomes (spring) or leaves (summer) of grasses and sedges, berries and seed heads in late summer. Ducks and swans depend on algae and macrophytes (system analysis in Van Eerden, 2000). Over the past decade reindeer numbers in the western sector of the Pechora have declined by one-third as herding is currently not profitable and there is some concern regarding long-term impacts on the system (A. Glotov, personal communication). The Dutch landscape offers the other extreme with no large native herbivores of quantitative importance and maximum control by man.

Grazing effects on pasture swards by cattle, horses and sheep allow grazing by geese and swans along the entire flyway. Hayfields and riverine grasslands grazed by livestock in summer are currently the preferred spring staging habitats for geese and swans. The decline in animal husbandry, particularly dairy farming, in the Dvina delta on the southern margin of the White Sea is already having a deleterious impact on the number of visits in spring in the past decade by barnacle and white-fronted geese (V. A. Andreev, personal communication). The loss of human settlements along the north coast of Russia has led to a decline in haymaking, grazing by livestock, and the hunting of Arctic fox, *Alopex lagopus*. The effective removal of the principal predators (fox and man) may account for the range expansion of the barnacle goose in northern Russia (K. Litvin in Madsen *et al.*, 1999).

The only goose population relying mainly on natural foods during spring migration on this flyway is the

dark-bellied brent, and although peak spring numbers in the Netherlands are still high the population has declined recently for reasons that are unclear (Ebbinge *et al.*, 2002). There is a parallel here with the situation in North America, where the related black brant are still coast-bound foragers and have failed to show the response to the agricultural bonanza that has led to the explosion of most other goose populations on that continent.

#### *Effects of changes in land use in the wintering areas*

Future developments are viewed from the perspective of the restructuring agricultural practices in Europe. This will lead to a decline in N use in western countries and hence will probably constrain population growth of the smallest avian herbivores. The enlarged EU with 10 new member states in 2004 will cause major changes in crop production. For example, Poland now produces one quarter of the total potato production in the EU. Large-scale farming practices, such as the production of crops like oilseed rape and winter cereals in Denmark, eastern Germany and Poland are likely to increase. Larger geese and swans already feed on these crops. In other countries of the EU it may become less profitable for European farmers to grow certain crops. Moreover, genetic engineering may make these species unpalatable, which has occurred already in Flevoland in the Netherlands in the early 1990s when changes in fatty acid composition led to the abandonment of these crops by geese and swans (M. R. Van Eerden & M. Zijlstra, unpublished results; McKay & Parrott, 2002).

Wetland restoration and the policy of leaving agricultural land for rough grazing are likely to lead to a downward trend in staging and wintering populations of birds in the Netherlands in the absence of high-quality grass leaves. Existing coastal wetland vegetation, such as bulbils, tubers, stolons are already largely eaten so alternative food sources are scarce (Van Eerden, 1997). However, in the past the birds have proven to be highly opportunistic and they will be able adapt to these recent changes as well.

#### *Climate change, staging sites and tundra vegetation*

Recent findings from ringing programmes for different species confirm that few stop-over sites are used by *Branta* geese and Bewick's swans (Beekman *et al.*, 1996). These species may be more sensitive to change than those that feed at many sites on migration. Bewick's swans and grey geese now winter further north which is in line with a rise in winter temperatures at former sites in Ireland, UK, Spain, France and Belgium in recent decades (Monval & Pirot, 1989). In Norway Prop

*et al.* (1998) demonstrated a northward shift of spring staging area of barnacle geese, which they related to improved climatic conditions, mediated through shifts in agricultural practice with an abandonment of sheep grazing at traditional sites.

The belt of potential spring fattening-up sites that lie within the zone bounded by the 3 and 6 °C isotherms in April will tend to move northwards, which is, however, only marginally possible because of fixed positions of islands and low coastal zones as well as the boundary of the taiga zone. Temperature changes of the order of 2–4 °C are to be expected in the next decades (Houghton *et al.*, 2001), so the consequences are at a measurable time scale.

The third area of possible future change lies in the breeding areas. The climate models for Arctic Russia are not equivocal, suggesting positive trends in some areas and negative temperature trends in others. Also the indirect effects on avian herbivores because of rising temperatures are unclear. Thermokarst lakes may disappear leading to the lowering of water tables during summer. If indigenous people continue to abandon their traditional way of living by herding reindeer, grass abundance will decline sharply in tundra habitats (Van der Wal & Brooker, 2004) rendering them less suitable for herbivorous water birds. This makes future developments in this area the most difficult to forecast. Future monitoring of brent, barnacle geese and Bewick's swans is thus of special importance in order to document the impact of these changes.

#### *Monitoring and research needs to safeguard internationally shared waterfowl populations*

The study of the migrant avian herbivores using the western Palaearctic Flyway impinges on several ecological issues of general interest. On account of the sheer numbers involved, and because the rapid transit digestive strategy implies that the bulk of herbage ingested is deposited as droppings, these birds are potentially important agents of nutrient transfer between systems at the landscape level. On the other hand, the transformation of leafy plant matter into droppings also reduces litter accumulation and hence may decrease N mineralization rates in heavily grazed vegetation (Van Wijnen *et al.*, 1999). The daily movements of birds between feeding and roosting areas may cause massive transport of nutrients, especially where grain or other agricultural crops are rapidly ingested and subsequently digested at roosts. Post *et al.* (1998) have quantified this flow in a 50 ha refuge in New Mexico, where waterfowl introduced 40% of N and 75% of P entering the wetland annually. On the seasonal scale, transport of nutrients between sites along the flyway include nutrients stored in the body that are

released when the birds die, as well as the nutrient input from the decomposition of feathers lost during the annual moult, which are deposited at discrete moulting sites. In some circumstances massive predation of eggs or newly hatched goslings by mammalian predators (notably Arctic Foxes and Polar Bears) represent a sizeable input of nutrients some of which are 'flown in' from elsewhere ('capital breeding' strategies). Since foxes cache eggs for use during the lean season, these inputs achieve an extended time frame and can be of great ecological significance to survival of these predators. Waterfowl with their rapid movements over a wide geographical scale combined with concentrations at feeding and resting sites thus have a special significance for the flow of nutrients between habitats or landscapes (see Polis *et al.*, 2004).

A second issue concerns the long-term stability of the systems supporting the herbivores throughout their migratory itinerary. With their strong dependence on agricultural systems in winter, census of the herbivores in relation to habitat use is a viable option in these systems. The 5-year (1998–2003) summary of the swan and goose inventory in atlas format for the Netherlands (Voslamber *et al.*, 2004) demonstrates the fine-scale data now accumulating (monthly counts at 3146 sites with 85% coverage of wintering swans and geese in the country). For four species (white-fronted, greylag, pinkfooted and barnacle geese) where the Netherlands hosts nearly 70% of the flyway population of 1.8 million individuals, an analysis of the 'goose foraging days' summed during the past five winter seasons (September–May) reveals that 72% were accumulated on grasslands (almost all of this on agricultural pastures) and 28% on arable croplands. Monitoring change of waterfowl numbers and their habitat choice is certainly feasible at this fine scale and should be extended to include the neighbouring regions. International coordination is urgent, as change in agricultural practice at the landscape level is imminent. Shrub (2003) rightly describes farming as a catalyst for change rather than acting to preserve the countryside.

At the other end of their annual travels, enumeration of the herbivores is more difficult but remote sensing techniques (such as the current MODIS program) can reveal ecological change at the landscape level (Jano *et al.*, 1998) and if available at the appropriate season may even provide an index of forage quality (Mutanga *et al.*, 2004). Ideally this work should be linked to long-term ecological research sites where experimental exclosures can be maintained to study vegetation change (Callahan, 1984; Jefferies *et al.*, 2003). Geese and swans are particularly promising subjects for enumeration on account of the ongoing marking programmes, allowing the continual updating of

survival estimates (Madsen *et al.*, 2002). In most cases this can be coupled with observation of juvenile ratios in the field to monitor reproductive output. Observations on age ratios when the flocks have reached the wintering grounds thus can provide vital demographic clues of changes in population structure. There is a need to employ telemetric techniques (satellite devices, geo-locators) to discover and quantify the use of stopover sites since our knowledge beyond the areas that humans have settled is still fragmentary. It is not a viable option to attempt intensive study of all waterfowl populations over their entire range of occurrence. Research consortia in Europe are already in place dealing with four representative species (brent, barnacle and pinkfooted goose, and Bewick's swan, and these initiatives deserve strengthening

### Acknowledgements

Agata Klimkowska helped to analyse weather and plant phenology data in relation to the onset of spring. Kostya Litvin, Henk Van der Jeugd and Götz Eichhorn provided information about barnacle geese. Andres Kuresoo provided information on spring staging areas of geese in Estonia as did David Stroud for Iceland. Jouke Prop inspired us to relate the predictions of the onset of spring growth to agricultural practice in Europe. Dick Visser skilfully prepared the figures. The manuscript benefited greatly from the discerning comments by Bob Jefferies and two anonymous referees. Marjolein Munsterman was an indispensable help in editing the text.

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