

Skipping the Baltic: the emergence of a dichotomy of alternative spring migration strategies in Russian barnacle geese

Götz Eichhorn^{1*}, Rudolf H. Drent^{1†}, Julia Stahl², Aivar Leito³ and Thomas Alerstam⁴

¹Animal Ecology Group, Centre for Ecological and Evolutionary Studies, University of Groningen, PO Box 14, 9750 AA Haren, The Netherlands; ²Landscape Ecology Group, University of Oldenburg, 26111 Oldenburg, Germany; ³Institute of Agricultural and Environmental Sciences, Estonian University of Life Sciences, Kreutzwaldi 5, 51014 Tartu, Estonia; and ⁴Department of Animal Ecology, Lund University, 22362 Lund, Sweden

Summary

1. Since the early 1990s, an increasing proportion of barnacle geese, *Branta leucopsis*, bound for breeding sites in the Russian Arctic delay their departure from the wintering quarters in the Wadden Sea by 4 weeks. These late-migrating geese skip spring stopover sites in the Baltic traditionally used by the entire population.
2. Individual geese from an arctic colony tracked by satellite or light-level geolocators during spring migration in 2004 and 2005 predominantly followed the new strategy, but a minority still maintained the traditional pattern. Despite a spread of more than 50 days in departure date from the Wadden Sea, both early and late departing females laid their eggs within the short time-window conferring breeding success.
3. The spread of these new migration routines coincided with a strong increase of overall numbers and the exploitation of new spring staging resources in the Wadden Sea. Counts from Estonia demonstrate that numbers have levelled off recently at the Baltic staging sites, suggesting that the capacity of these staging sites in spring has been reached. Although onset of spring affects migratory timing in barnacle geese, it cannot explain the observed delay in departure from the wintering grounds.
4. We hypothesize that the new migratory strategy has evolved in response to increased competition for food at spring staging sites in the Baltic. According to an analytical model of optimal migration, the geese should skip the Baltic whenever the energy deposition rate falls below 88% of the Wadden Sea value.

Key-words: arctic breeding, geolocation, global change, migratory timing, tracking

Introduction

Geese select forage plants of high quality (in terms of protein content and digestibility) and it has been proposed that they time their spring migration to their arctic breeding grounds to match the spring flush of plant growth along their route (Drent, Weijand & Ebbinge 1978; Van der Graaf *et al.* 2006). Due to their dependence on plant forage, herbivores can be expected to show early and strong responses to climate change, which will alter feeding conditions at staging sites (Bauer, Gienapp & Madsen 2008a; Bauer *et al.* 2008b). The rate of nutrient acquisition and consequently body condition

is known to influence migratory decisions (Weber, Ens & Houston 1998; Drent *et al.* 2003; Prop, Black & Shimmings 2003). Both the timing of migration and body condition at arrival in the breeding grounds are crucial determinants of reproductive prospects (Kokko 1999; Bêty, Gauthier & Giroux 2003). Moreover, body condition as early as in the pre-migratory stage on temperate wintering grounds can be decisive for arctic breeding success (Ebbinge & Spaans 1995). Arctic breeding geese have to deposit resources in excess of what is needed to cover the flight costs. Due to the strong seasonality of the arctic environment, the growth period of offspring needs to be tightly matched with local food peaks (Lepage, Gauthier & Reed 1998; Black, Prop & Larsson 2007). During egg laying and early incubation, local food resources are still scarce. Furthermore, incubation tasks minimize foraging opportunities for the female as daily nest

*Correspondence author. E-mail: g.eichhorn@rug.nl

†R.H. Drent passed away on 9th September 2008



Fig. 1. Map showing spring migratory route of Russian breeding barnacle geese with distances between staging sites and observation points. Dark grey shaded areas indicate wintering/staging grounds in the Wadden Sea and Baltic, and breeding grounds in Russia.

attentiveness is usually above 90% (e.g. Bowler 2005). Therefore, arctic geese arrive at the breeding grounds with a substantial surplus of endogenous nutrient reserves. They are doomed to fly in at least some 'capital' gathered at spring staging sites (Drent *et al.* 2007).

Such a strategy does not minimize the energetic costs of migration, as flight costs increase with extra fuel loads (Pennycuik 1975; Alerstam & Lindström 1990). However, birds may start breeding earlier through overloading at the last staging site as long as the increased costs on flight economy are more than counterbalanced by a higher rate of nutrient deposition at this staging site compared to the breeding site (Gudmundsson, Lindström & Alerstam 1991; Alerstam 2006a). The same condition applies to a time minimizing migrant when by-passing a potential staging site further along the migratory route should be favourable, that is, deposition rates at succeeding stopovers must fall below those at the departure site.

We here examine a 30-year data set on migration of the barnacle goose along the Baltic route and compare these with population counts. Additionally, individual travel schedules were combined with observations of the same birds in the breeding colony allowing us to evaluate possible fitness consequences of migratory strategies. The monitoring of the progress of avian long-distance migration at individual level and its linkage to events in the breeding phase has so far only rarely been achieved (Madsen 2001; Bêty *et al.* 2003; Alerstam 2006b; Drent *et al.* 2007). Thus the main objectives of this study are to: (i) describe the timing of spring migration of barnacle geese over the past decades in perspective of a growing total flyway population as well as changes in the onset of spring, (ii) evaluate under which conditions by-passing of the Baltic may become beneficial for a time-minimizing capital breeder, (iii) present individual spring itineraries and examine if the dichotomy of alternative migration strategies incurs differences in the timing of breeding.

Methods

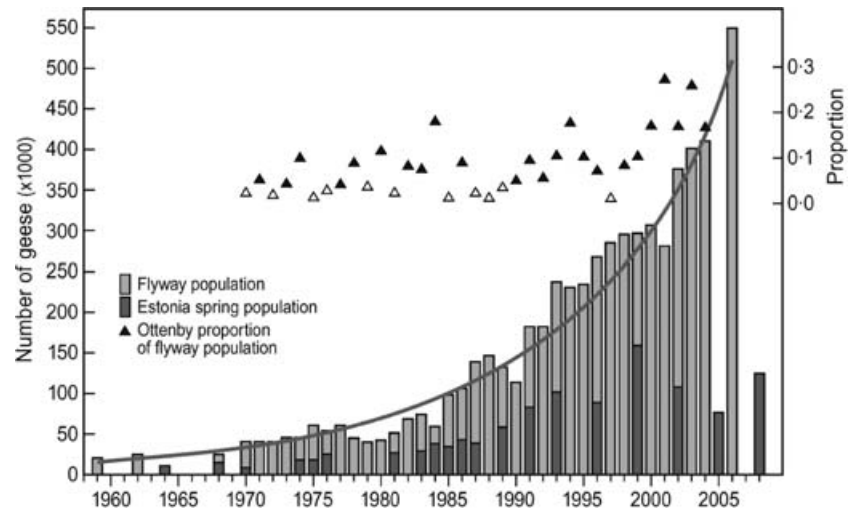
STUDY POPULATION AND STUDY SITES

Barnacle geese wintering along the Wadden Sea coast belong to a population breeding on the Arctic coast of Russia and two, recently established, temperate breeding populations in the Baltic and The Netherlands (Ganter *et al.* 1999). We studied long-distance migrants (3000–3700 km) from the Russian arctic breeding population, which currently represents 90% of the common wintering population of more than 500 000 birds (Black *et al.* 2007). After pre-migratory fattening in the Wadden Sea, the geese migrate via stopovers in the Baltic, most notably in western Estonia and on the Swedish Island of Gotland (Ebbinge, Van Biezen & Van der Voet 1991; Leito, Renno & Kuresoo 1991), and stopovers in the White Sea to their breeding grounds on the Barents Sea coast (Fig. 1). Traditional breeding areas of this population were restricted mainly to the islands of Novaya Zemlya and Vaygach in the eastern Barents Sea. Through expansion since the 1980s, arctic breeding occurs now down to the eastern White Sea coast 650 km westwards (Ganter *et al.* 1999). Barnacle geese feed predominantly on coastal salt marshes and, in temperate regions, adjacent agricultural pastures. Individual migratory itineraries and data on breeding biology were obtained from birds nesting in a colony near the abandoned village of Tobseda (68°35'N, 52°18'E) situated on the Kolokolkova Bay (for details see Van der Jeugd *et al.* 2003).

COUNT AND CLIMATE DATA

Estimates of the total flyway population were based on winter counts in the Wadden Sea from Ganter *et al.* (1999) and updated by SOVON, Dutch Centre for Field Ornithology. Spring staging birds in Estonia were counted by ground surveys in 1964, 1968, 1970 and from 1974 onwards by aerial surveys (in 17 years during 1974–2008). Estonian censuses were conducted in the period 5–15 May using a constant census routine and covered more than 90% of all sites known to regularly support 100 or more geese (Leito 1996). Data on timing of spring mass migration were gathered from three sites along the flyway. (i) Departure dates from the north-eastern Wadden Sea

Fig. 2. Size of flyway population and numbers of spring staging barnacle geese in Estonia are depicted by columns scaled to the left axis. The equation fitted to the flyway population data (grey solid line) is $y = 13\,844e^{0.074x}$, $r^2 = 0.95$, corresponding to a yearly growth-rate of 7.7%. Triangles show the proportion of the total flyway population enumerated on spring passage at Ottenby with values given on the right axis. Open triangles mark years when less than 5% of the flyway population was counted at this observation point.



in Schleswig-Holstein, Germany (54°36'N, 8°52'E), when > 75% of the peak staging population had left the site, were obtained from Stock & Hofeditz (2002) for 1988–97 and updated with dates of mass departure from the same area for 1998–2003 (Koffijberg & Günther 2005) and 2005–06 (K. Koffijberg personal communication). (ii) Arrival in the Baltic area: birds passing the Ottenby bird observatory (56°12'N, 16°24'E) located at the southern tip of Öland, Sweden, were counted yearly in the period April–May. Data for the years 1970–2004 were extracted from the observatory diaries. Ottenby is situated on a main migratory corridor for barnacle geese (Green 1998). We discarded years when < 5% of the flyway population was counted at Ottenby (Fig. 2). Information was updated from online reports of the Swedish Ornithological Society for barnacle geese passing through the southern province of Skania (<http://www.artportalen.se/birds/default.asp>) for 2005–06. The day when ≥ 50% of the season's total passed through Ottenby and Skania, respectively, was taken as estimate for the arrival date in the Baltic. (iii) Mass departure from the Baltic was estimated as median date from days with peak migration over the Gulf of Finland (at Kotka) as reported by the Kymenlaakso Birding Society in their annual reports for the years 1989–2004, and updated for 2005–06 by P. Tolvanen (personal communication).

Daily mean temperatures measured at Baltic and Wadden Sea goose staging sites were gathered from the European Climate Assessment and Dataset (<http://eca.knmi.nl>) for the period 1970–2006 for Vilsandi (58°23'N, 21°49'E) in western Estonia for all years but 1991, covered by data from Gotska Sandön (58°24'N, 19°12'E), and for Leeuwarden (53°12'N, 5°48'E) in The Netherlands covering 1970–71. H. Vugts (personal communication, Free University of Amsterdam) provided data for the Dutch island Schiermonnikoog (53°30'N, 6°10'E) for 1972–2006. From the temperature data sets, we calculated growing degree days (GDD) by summing daily temperatures above a threshold value of 0 °C (following Botta *et al.* 2000) for the period from 1 January until 12 April, the 'traditional' median date of arrival in the Baltic.

OBSERVATIONS ON INDIVIDUAL BIRDS

We employed satellite tracking of platform transmitter terminal (PTT) devices and global location system (GLS) data loggers (light-level geolocators) to track movements of individual barnacle geese breeding in our Russian arctic study site. We found no indication of

impaired behaviour in birds carrying tracking devices (Eichhorn 2005; Eichhorn *et al.* 2006). Accuracy in the timing of movements is within a range of 1 day. We collated individual departures from the wintering grounds together with known laying dates for 21 birds in 2004 (all tracked by GLS), for nine birds in 2005 (one tracked by PTT, eight by GLS) and for seven birds in both years.

Laying date (1st egg) was recorded from direct observations during the laying period or backdated from hatch. For females carrying data loggers, laying date could also be backdated from the start of incubation, which often coincided with laying of the third egg (own observation), and the incubation rhythm detected in the light-level data. Data loggers were retrieved from captures during incubation and/or moult.

CALCULATION OF FUEL REQUIREMENTS

Estimates of fuel requirements were based on flight mechanical theory (Pennycuik 1975) following the principles outlined by Gudmundsson *et al.* (1991) and Alerstam & Hedenström (1998). The distance Y a bird can fly with a certain fuel load can be described by the range equation:

$$Y = c \cdot \left(1 - \frac{1}{\sqrt{1+f}} \right) \quad \text{eqn 1}$$

where f is defined as fuel load relative to the lean body mass of the bird and c is a constant (with same dimension as Y) that depends on factors such as bird morphology, muscle work efficiency, fuel composition and wind conditions. Of fundamental importance here is to note that the potential flight distance is a negatively accelerated function of fuel load, meaning that the marginal gain in flight distance diminishes with increasing fuel levels. Recent empirical work suggests lower additive flight costs of carrying large fuel loads (Kvist *et al.* 2001). However, these results have not been confirmed so far and we consider it premature to adopt them here but realize that our quantitative predictions must be regarded as provisional. Rearranging equation (1) allows the calculation of fuel loads needed to cover flight distances $f(Y)$ between potential stopover sites, depending on migratory strategy:

$$f = \frac{1}{\left(1 - \frac{Y}{c} \right)^2} - 1 \quad \text{eqn 2}$$

We derived an empirical estimate for constant c from data reported by Madsen & Klaassen (2006) for pink-footed geese *Anser brachyrhynchus* flying between Denmark and Vesterålen in northern Norway. For this flight of 1410 km, the authors estimated an average change in abdominal profile index (API) of 2.00 U (for both sexes), corresponding to 371 g and 394 g mass (fuel) loss in female and male geese, respectively (API-body mass relationship given in same paper). Fuel ratios were calculated by dividing these fuel losses by body mass upon arrival in Vesterålen (which was also estimated from API, Madsen and Klaassen personal communication) yielding $f = 0.124$ (females, $N = 18$) and $f = 0.129$ (males, $N = 17$). Inserting these fuel ratios and the flight distance into equation 1 gives $c_{\text{females}} = 24\,765$ km and $c_{\text{males}} = 23\,927$ km and we applied the rounded average (24 300 km) for our calculations.

Results

EMERGENCE OF A NEW MIGRATORY BEHAVIOUR

The barnacle goose population wintering in the Wadden Sea has grown exponentially over the past five decades, increasing at an annual rate of 7.7%, which corresponds to a doubling time of 9.4 years (Fig. 2). Numbers of spring staging barnacle geese in Estonia followed the increase of the flyway population until the mid-1990s but then levelled off.

Figure 3 shows long-term data of the timing of barnacle goose mass movements to and from the Baltic. Observations on departures in the wintering/pre-migratory area and on passage over southern Sweden correlate well ($r = 0.90$, $P < 0.001$, $N = 15$). Both illustrate a distinctive delay of departure from the wintering grounds, starting around the mid-1990s and stabilizing during recent years. In contrast, mass migration along the Finnish coast, the 'exit' of the Baltic, shows a remarkably stable timing over the past 18 years (21 May \pm 3 days, mean \pm SD), indicating that the interval between mass departure from the Wadden Sea and peak passage past Finland has decreased dramatically.

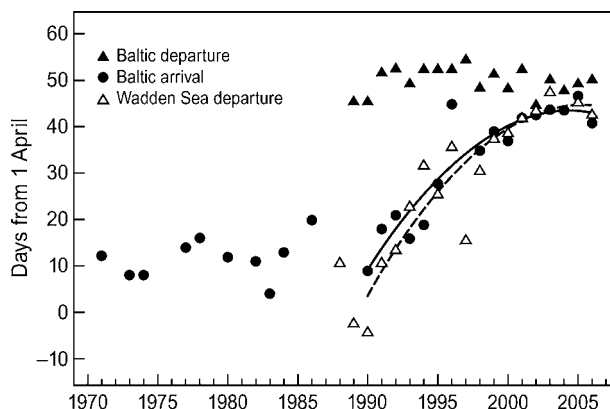


Fig. 3. Passage dates along the migratory pathway: at the Finnish Gulf 1989–2006, over southern Sweden 1971–2006 and mass departures from the German Wadden Sea coast 1988–2006. Curves fitted for the period 1990–2006 (with years renumbered to 1 = 1990 till 17 = 2006) refer to Wadden Sea departure, broken line ($y = -0.175x^2 + 5.729x - 2.051$, $F_{2,13} = 33.16$, $r^2 = 0.84$, $P < 0.0001$) and Baltic arrival, solid line ($y = -0.162x^2 + 5.033x - 4.819$, $F_{2,13} = 42.44$, $r^2 = 0.87$, $P < 0.0001$); the quadratic term significantly improved the fit in both models.

A breakdown of the Ottenby data illustrates the change of the seasonal dynamics of migration into the Baltic (Fig. 4). During the 1970s, more than half of the total number of birds passed Ottenby before 12 April. Delayed mass migrations became obvious from the second half of the 1990s onwards and resulted in an expansion of the migratory window. Beside the traditional mass movements in mid-April, an increasing number of birds delayed their departure well into May. Since 2000 'April migrants' contribute only 20% of the numbers passing Ottenby during April–May, with the majority of the flyway population leaving the Wadden Sea in the first half of May, 4 weeks later compared to before 1990.

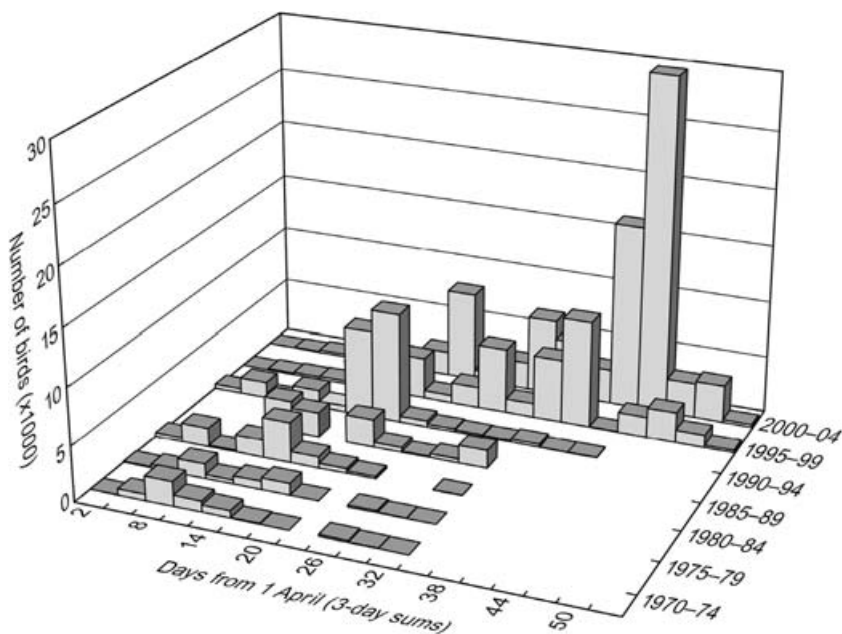


Fig. 4. Development of spring migratory pattern of barnacle geese counted at Ottenby 1971–2004. Census data were first aggregated to 3-day sums for each season (assigned to the central day of the interval) and then averaged over the periods indicated along the right axis (years with counts of $< 5\%$ of flyway population were discarded; see Fig. 2).

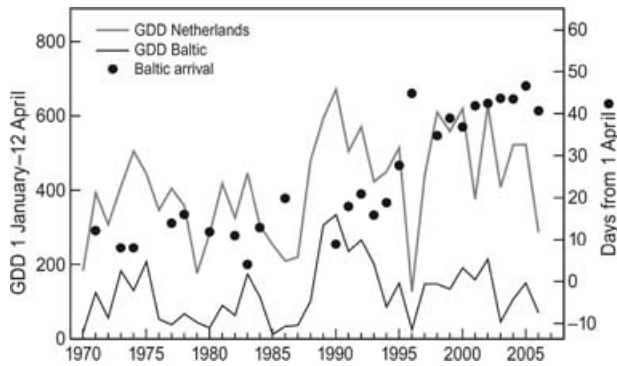


Fig. 5. Annual growing degree days (GDD) accumulated over 1 January–12 April (left *y*-axis) at a Baltic and Dutch staging site, denoted by the lower and upper line, respectively. Linear regression analyses revealed a significant increase of 5.0 GDD/year over the study period for the Dutch site ($F_{1,35} = 6.1$, $P = 0.02$) but not for the Baltic site ($F_{1,35} = 2.3$, $P = 0.14$). Also shown are median arrival dates of barnacle geese in the Baltic as presented in Fig. 3.

ONSET OF SPRING AND MIGRATORY TIMING

Although growing degree days (GDD) measured at the two sites correlate ($r = 0.80$, $P < 0.001$, $N = 37$), springs were substantially warmer since 1990 in the Dutch site compared to the Baltic. The Dutch site also showed a significant increase in GDD over the total study period, whereas the slight increase in Baltic GDD was insignificant (Fig. 5).

Using regression analysis, we further investigated the effects of GDD, year and year² on barnacle goose median arrival date in the Baltic for two periods separately, before the delay became prominent (i.e. before 1990) and after (from 1990 onwards). Higher (lower) GDD measured at both sites triggered to a significant extent advanced (delayed) arrival in the Baltic during the first period before 1990 ($N = 10$) while there was no effect of year ($F_{1,9} \text{ GDD}_{\text{Wadden Sea}} = 11.14$, $P < 0.05$, $r^2 = 0.58$; $F_{1,9} \text{ GDD}_{\text{Baltic}} = 12.22$, $P < 0.01$, $r^2 = 0.60$). However, 87% of the variation was explained by a (quadratic) year effect in the recent period from 1990 onwards ($F_{2,13} = 42.44$, $P < 0.0001$). At the same time, the effect of GDD disappeared ($F_{1,15} \text{ GDD}_{\text{Wadden Sea}} = 2.64$, NS; $F_{1,15} \text{ GDD}_{\text{Baltic}} = 0.75$, NS). Alternatively, we calculated GDD values accumulated until the actual median departure date for each year, revealing small fluctuations around 366 ± 68 (mean \pm SD, $N = 10$) and 94 ± 49 at the Dutch and Baltic site, respectively, before 1990. Thereafter GDD at departure increased considerably up to average values of 803 ± 139 (Dutch site) and 369 ± 87 (Baltic) for the years 2000–06 ($N = 7$).

INDIVIDUAL MIGRATORY SCHEDULES

Individual female barnacle geese tracked in 2004 and 2005 confirm the two migratory strategies existing side by side (Fig. 6). Median number of days staging in the Baltic was four and three in 2004 and 2005, respectively. Departure from the Baltic (influx into the White Sea) of the tracked birds took place 14–27 May (median 17.5) in 2004 and 18–20 May

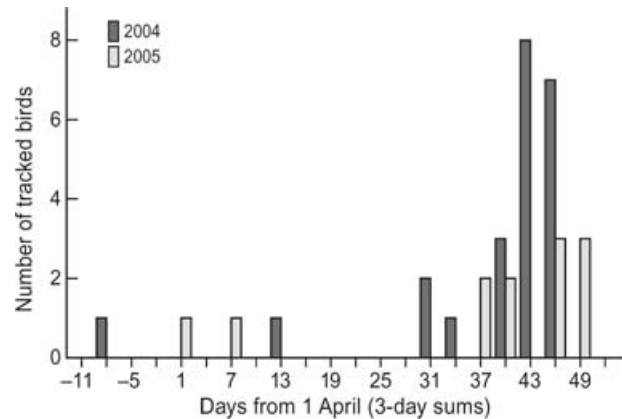


Fig. 6. Timing of individual movements into the Baltic for birds tracked in 2004 (black bars, $N = 23$) and 2005 (grey bars, $N = 12$). Values were summed over 3-day periods and assigned to the central day of the interval.

(median 19.5) in 2005, which was virtually identical to the peak dates of barnacle goose passage observed in southern Finland in these 2 years, that is, 18 and 19 May. Some of the individuals had staged in the Baltic (having left the Wadden Sea as early as 23 March) according to the traditional strategy, others reached the White Sea virtually directly from the Wadden Sea (one individual covering 2250 km in 2 days). These individuals, although nesting close together, did not winter or migrate together, but most converged on a staging site on the lower Dvina River near Archangelsk when they entered the White Sea (staging there about 6 days before moving on to the colony). As already shown for mass movements in Fig. 3, a delay in departure from the wintering grounds does not translate into a delayed departure from the Baltic staging sites. Instead, birds reduce their stay in the Baltic.

Both timing of geese observed during passage at Ottenby and of individually tracked birds from the same breeding colony imply that most geese prefer either an early (April) or a late (May) departure from the Wadden Sea but avoid the period in between (Figs 4 and 6). Thus, recently we encounter two major spring migratory strategies within one flyway population, which exhibit a difference of about 1 month in the timing of departure from the wintering grounds.

Although our sample is small, individual geese followed more than one season were usually consistent in their use of spring staging site. Of the seven geese tracked in both years, five were 'Wadden Sea stagers' in both seasons, one was consistently 'Baltic stager', and one switched from Baltic to Wadden Sea staging.

BY-PASSING THE BALTIC IN VIEW OF OPTIMAL MIGRATION THEORY

Differential energetic costs, expressed as (extra) fuel loads, for the two strategies (i.e. by-passing the Baltic or not) and for two scenarios depending on whether the next stopover beyond the Baltic is at the Dvina river or in the Kanin

Table 1. Flight distances (Y) and calculated fuel loads (f) using equation (2) (see methods) for migratory strategies depending on whether the Baltic is by-passed or not and whether the Dvina River or Kanin Peninsula is chosen as next fuelling site. The costs of by-passing the Baltic are expressed as additional fuel load and as percentage extra fuel needed relative to not by-passing the Baltic assuming that the geese leave for their next target site as soon as fuel loads permit to fly there. See Fig. 1 for locations of stopover sites

Flight	$Y(\text{km})$	$f(Y)$	Extra f	Extra f (percentage)
Wadden Sea–Baltic	1000	0.09		
Baltic–Dvina	1470	0.13		
Baltic–Kanin	1910	0.18		
Wadden Sea–Dvina	2470	0.24	0.02	8.4
Wadden Sea–Kanin	2910	0.29	0.03	9.4

Peninsula are shown in Table 1. The outcome of these calculations indicates that it costs approximately 8–10% extra fuel to pay the additional overload when the Baltic is skipped for fuelling en route to the arctic pre-breeding staging sites.

Another avenue to explore the current change in migratory behaviour is to ask to what extent the fuelling rate in the Baltic must have dropped compared to the Wadden Sea to achieve an equal speed of migration by skipping the Baltic. Using equation 1, we substitute f by $k \cdot t$, the product of the rate of fuel deposition (k) and time spent on deposition (t). Expressing equation 1 now as a function of fuel deposition time $Y(t)$ a bird putting on fuel may be regarded as increasing its potential flight range with time. This instantaneous speed of migration (S) is found by differentiation yielding:

$$S = \frac{dY}{dt} = \frac{c}{2} \cdot k \cdot \frac{1}{(1+f)^{3/2}} \quad \text{eqn 3}$$

By inserting $f(Y)$ from equation 2 into equation 3 S can be given as function of the potential flight range:

$$S = \frac{dY}{dt} = \frac{c}{2} \cdot k \cdot \left(1 - \frac{Y}{c}\right)^3 \quad \text{eqn 4}$$

The instantaneous speed of migration thus depends on the local fuel deposition rate but is devaluated by a factor (< 1) reflecting the transport costs for the distance (Y) to the next stopover. With $Y = 1000$ km (i.e. the flight distance between Wadden Sea and Baltic) this deflation factor $(1 - Y/c)^3$ yields 0.88, indicating that at a deposition rate of 88% or higher in the Baltic compared to the Wadden Sea the birds should stopover there.

MIGRATORY STRATEGIES AND TIMING OF BREEDING

Figure 7 shows individual case histories of departure date from the nonbreeding ground and laying date collected over two seasons at the colony. It will be noted that the majority of birds following the new ‘Wadden Sea stagers’ strategy laid their eggs in the period conferring good prospects. Furthermore, no trend towards later laying as result of delayed

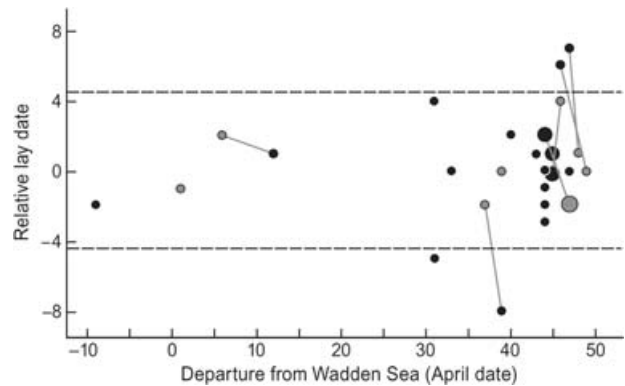


Fig. 7. Lay date relative to the colony's median lay date (13 June 2004, $N = 385$; 6 June 2005, $N = 413$) versus departure date from the wintering grounds plotted for 21 females in 2004 (black dots) and 9 in 2005 (grey dots); size indicates sample size, small dot = 1, large dot = 2; lines connect individuals followed in both years. The two dashed lines include the time-window of laid eggs producing 90% of all fledged young in the colony (Eichhorn 2008).

departure can be identified (2004: $N = 21$, $r = 0.21$, NS; 2005: $N = 9$, $r = -0.06$, NS). Apparently, both strategies are successful with respect to laying eggs ‘on time’.

Discussion

Both observations of departing geese in the north-eastern Wadden Sea and spring counts of geese passing over southern Sweden show that the majority of barnacle geese have delayed their departure from the nonbreeding grounds by a full month. Moreover, this drastic shift evolved over a remarkably short period of 5 to 10 years starting in the first half of the 1990s. Combining these findings with a stable peak migration date in Finland over the same period, we conclude that Baltic stopover, formerly spanning a period of more than 5 weeks, has been reduced to less than 7 days for a sizeable proportion of the flyway population.

WHAT CAUSED THE CHANGE IN MIGRATORY SCHEDULES?

Recent shifts in migration patterns of many bird species have been reported in north-western Europe, and credible relationships with climatic variables such as temperature and the North Atlantic Oscillation (NAO) have been established (e.g. Møller, Fiedler & Berthold 2004; Stervander *et al.* 2005). Our analysis of temperature data suggests a stronger advancement of the growing season over the past decades for the Wadden Sea area compared to the Baltic. This finding is supported by the regional pattern of normalized difference vegetation index (NDVI) derived changes in onset of spring. For the period 1982–98, an advance in the onset of spring of four or more weeks was observed for most of the Wadden Sea area but only about 2 weeks for the eastern Baltic (Høgda, Karlsen & Solheim 2001; Høgda, Karlsen & Tømmervik 2007). Pronounced effects of the onset of spring on migration

schedules and fitness of arctic geese have been demonstrated by Bauer *et al.* (2008b) for the pink-footed goose. This species has discovered a new staging site in mid-Norway and increasingly use it in response to a warming climate (Fox *et al.* 2005). Furthermore, Pistorius, Follestad & Taylor (2006) suggested that increasingly warmer temperatures during spring staging in The Netherlands may have driven a more than 2-week advancement over the past three decades in arrival of greylag geese *Anser anser* breeding on the Norwegian coast. Also, our findings suggest that onset of spring has a potential effect on migratory timing in barnacle geese. However, it cannot explain the observed delay in departure from the wintering grounds followed by an increasing share of the population.

Instead, we propose a capacity problem in the Baltic as key for the emergence of the strategy of delayed departure from wintering grounds in the Wadden Sea and reduced or omitted Baltic staging. Support for this claim comes from several sources. First, numbers of spring staging barnacle geese in Estonia followed the increase of the flyway population until mid-1990s but then levelled off (Fig. 2). Second, Van der Graaf *et al.* (2006) compared nutrient biomass during spring staging in the Wadden Sea and on Gotland in 2003–04 and noted higher values for the Wadden Sea site. High grazing pressure caused heavily reduced food availability in the Baltic, as was indicated by enclosure experiments. This is surprising, as for arctic geese gain rates usually accelerate along the spring migratory route (Prop 2004; Klaassen *et al.* 2006; Madsen & Klaassen 2006) due to increasing food quality and feeding time. Barnacle geese were foraging for 12.8, 16.2 and 20.8 h per day during staging in The Netherlands (53°15'N) in April, in Norway (65°45'N) in May and in the Kanin Peninsula, Russia, in early June (67°55'N), respectively (J. Prop, personal communication and own observation). Only when at or very close to their breeding sites, geese are forced to get ahead of the 'green wave' of high food quality in order to match hatching of offspring with the local crest in food quality. Thus, theoretically, for 'Baltic stagers' one would expect not only reduced flight costs but also potentially higher fuel gain rates. However, according to the optimal migration model, by-passing the Baltic will be favoured by the geese if the fuelling rate in the Baltic falls below 88% of that in the Wadden Sea. That is, below 10 g d⁻¹ nowadays and would mean that the formerly high gain rate in the Baltic of 21 g d⁻¹ has decreased by 52% (Eichhorn 2008).

Confronted with increasing costs of competition (Rowcliffe, Pettifor & Carbone 2004) at the Baltic sites and constrained by the inaccessibility of sites further north along the route (which are still snow bound at that time), the geese concentrate on pre-migratory sites. It is important to note that most of the Wadden Sea sites where barnacle geese nowadays concentrate in spring have only come in use since the early 1990s, for example the Dollard estuary (Fig. 1) at the Dutch–German border (Aerts, Esselink & Helder 1996). In other words, the new delayed strategy involves exploitation of new spring staging resources in the Wadden Sea as well as a change in timing.

Mortality risk due to predation is another factor determining site quality and may play an important role in the development of migratory strategies (Alerstam & Lindström 1990; Lank *et al.* 2003). White-tailed eagles *Haliaeetus albicilla* enjoyed a dramatic increase in numbers in the Baltic over the past decades, in contrast to the Wadden Sea where the species is still uncommon. The Estonian white-tailed eagle population recovered from a low of ca. 16 pairs in 1970s and numbered 110–120 pairs in early 2000s (Randla 1976; Elts *et al.* 2003). Beside the risk of being predated, the geese suffer enhanced energy costs and a loss of feeding time due to eagles' hunting efforts. Such additional costs of a relative change in quality of Baltic and Wadden Sea staging sites may have further facilitated the observed change in goose migratory strategy.

Finally, there is evidence that increasing carbon dioxide increases the amount of plant secondary compounds and decreases the protein content of plant forage (Ayres 1993), which may affect nutrient utilization by geese (McWilliams & Leafloor 2005). Although elevated carbon dioxide is a large-scale phenomenon, negative effects on food quality may be relatively stronger in natural feeding habitats (salt marshes) and further away from the wintering grounds compared to heavily fertilized feeding habitat like pastureland in Western and Central Europe.

COSTS AND CONSEQUENCES OF THE NEW STRATEGY

A crucial question when dealing with expanding populations is whether individuals are being forced into less favourable habitats, that is, entailing fitness consequences. Such a 'buffer effect' has been demonstrated, for instance, for the Icelandic population of the black-tailed godwit *Limosa limosa islandica* at wintering as well as breeding sites (Gunnarsson *et al.* 2005). We are aware that subtle effects on survival and reproductive success are associated with changing stopover patterns during spring migration in the pink-footed goose of the Svalbard population (Madsen 2001) despite its relatively modest size. However, for the Russian barnacle goose population, we have so far found no tangible signs of fitness costs associated with the saturation of the Baltic sites thus penalizing the recently evolved alternative strategy of delayed departure from the Wadden Sea. Timing of egg laying, a strong predictor of potential breeding success (Lepage, Gauthier & Menu 2000), was the same for 'Wadden Sea-stagers' and 'Baltic-stagers', and while the proportion of 'Wadden Sea-stagers' increased, the overall population showed an unbroken geometric growth.

Apparently, by their large-scale change in site and habitat use the geese have managed to spread optimally over the total of resources available to them in the Wadden Sea–Baltic region during spring thereby escaping negative effects of density dependence. Van Eerden *et al.* (2005) have argued convincingly that this was largely facilitated by the acquisition of new resources in improved grassland, where forage quality is enhanced due to intensive agricultural fertilization during the past 20 years. Aggregation and extended grazing of the geese helps to maintain and prolong the profitable

phase of the vegetation in the Wadden Sea in spring (Bos, Van der Koppel & Weissing 2004; Van der Graaf, Stahl & Bakker 2005). Reduced prosecution through the positive effect of human abandonment of the Russian coastline and enhanced protection along the entire flyway have been regarded the other major drivers for the impressive growth of the barnacle goose population (Ebbinge 1991; Syroechkovsky 1995).

Finally, conditions encountered after the Baltic stopover may have improved to compensate for the loss of the Baltic fuelling site. The 1990s marked a period of substantial expansion of barnacle goose breeding area towards south-west along the Russian coast (Syroechkovsky 1995). Geese may have benefited from breeding at these new sites by more benign climatic conditions allowing higher plant productivity over a longer season and by a shortened migratory distance.

FLEXIBILITY OF MIGRATORY SCHEDULES

Whether the recently observed rapid advance of spring arrival of long-distance passerine migrants throughout Europe reflects an evolutionary response or a phenotypic reaction to changed environmental conditions is matter of current debate (Both 2007; Jonzén *et al.* 2007). The barnacle goose is a long-lived species. Ebbinge *et al.* (1991) estimated a mean annual adult survival rate of 90% corresponding to a mean life expectancy of 9 years (Seber 1982), and life spans of more than 20 years have been frequently recorded for marked birds from the Russian population (Ebbinge, personal communication). Given the short time span over which the shift in migratory timing in the population occurred, it is evident that this process must have involved individually altered behaviour. This conclusion is reinforced by our observation of one tracked individual departing from the Wadden Sea 44 days later in 2005 compared to the previous year. Nevertheless, individual consistency usually prevails after the adoption of a migratory schedule (six of seven cases in our study).

In birds, the timing of events through the annual cycle has been shown to be regulated by the interaction of internal and environmental cues, of which daily photoperiod is the most important one (Gwinner 1996). Studying free-ranging Bewick's Swans, Rees (1989) suggested individual response thresholds to photoperiod triggering spring departure. However, the strong and rapid shift in departure time of individual barnacle geese does not support this hypothesis. We expect photoperiod to be primarily relevant for the timing of physiological responses accompanying migratory preparation, mainly related to the deposition of body stores (Bairlein & Gwinner 1994), rather than triggering actual migration (but see Helm & Gwinner 2005).

In geese, migratory routes are transmitted culturally, where young benefit from the experience of their parents, helping them to optimize own future decisions (Sutherland 1998). Social information transfer likely boosts speed and extent of adjustments to new environmental conditions (Helm, Piersma & Van der Jeugd 2006). Cultural transmission need not be restricted to parent-offspring relationships. Social learning can involve more members of the flock and lead to concerted

group behaviour further enhancing speed of phenotypic reactions (e.g. Conradt & Roper 2005). Moreover, learning from their own experience represents effective means for optimal adjustments. If short-living blue tits *Cyanistes caeruleus* are able to exploit previous experience to adjust seasonal schedules a year later (Grieco, Van Noordwijk & Visser 2002), there is reason to assume ample scope for such capacity in long-lived geese. Indeed, Madsen (2001) showed how pink-footed geese explored alternative spring migratory strategies and switched among them depending on the repercussions on breeding success. For the same species, Klaassen and co-workers (2006) highlighted the importance of learning in order to cope with rapidly altered conditions along the spring flyway. Their modelling exercises predicted dramatic differences in fitness consequences between omniscient and naïve geese. The authors emphasize that time is a crucial factor to allow the birds to experience, learn and re-adjust migratory strategies in an adaptive fashion. The remarkable phenotypic plasticity demonstrated by the barnacle goose will enhance its ability to cope with current and future environmental changes including climate change.

Acknowledgements

We thank all collaborators of the Dutch-Russian expeditions to Tobseda, and Konstantin Litvin in particular for his unflagging efforts at capturing geese. Mennobart van Eerden played an important role in the organization of these expeditions. Support by the Institute of Biology in Syktyvkar, by the Nenets Autonomous District and the State Nature reserve Nenetskiy, and by the Russian Hunters Association is gratefully acknowledged. Petteri Tolvanen and Anders Hedenström helped to retrieve data on goose passage over Finland and Ottenby, respectively. GLS loggers were developed at the British Antarctic Survey and we thank Vsevolod Afanasyev in particular. Financial assistance came from the Dutch Institute RIZA, the Schure-Beijerink-Popping Fonds, the University of Groningen, the Deutsche Forschungsgemeinschaft and The Netherlands Arctic Programme of NWO. GE was supported by ESF travel grants and scholarships from the Marianne und Dr. Fritz Walter-Fischer Stiftung, Germany, and the Ubbo Emmius Programme of Groningen University. Helpful comments by Jesper Madsen and one anonymous referee improved the manuscript.

References

- Aerts, B.A., Esselink, P. & Helder, G.J.F. (1996) Habitat selection and diet composition of greylag geese *Anser anser* and barnacle geese *Branta leucopsis* during fall and spring staging in relation to management in the tidal marshes of the Dollard. *Zeitschrift für Ökologie und Naturschutz*, **5**, 65–75.
- Alerstam, T. (2006a) Strategies for the transition to breeding in time-selected bird migration. *Ardea*, **94**, 347–357.
- Alerstam, T. (2006b) Conflicting evidence about long-distance animal navigation. *Science*, **313**, 791–794.
- Alerstam, T. & Hedenström, A. (1998) The development of bird migration theory. *Journal of Avian Biology*, **29**, 343–369.
- Alerstam, T. & Lindström, Å. (1990) Optimal bird migration: the relative importance of time, energy, and safety. *Bird Migration: Physiology and Ecology* (ed. E. Gwinner), pp. 331–351. Springer-Verlag, Berlin, Germany.
- Ayres, M.P. (1993) Plant defense, herbivory, and climate change. *Biotic Interactions and Global Change* (eds P.M. Kareiva, J.G. Kingsolver & R.B. Huey), pp. 75–94. Sinauer & Associates, Sunderland, Massachusetts.
- Bairlein, F. & Gwinner, E. (1994) Nutritional mechanisms and temporal control of migratory energy accumulation in birds. *Annual Review of Nutrition*, **14**, 187–215.
- Bauer, S., Gienapp, P. & Madsen, J. (2008a) The relevance of environmental conditions for departure decision changes en route in migrating geese. *Ecology*, **89**, 1953–1960.
- Bauer, S., Van Dinther, M., Høgda, K.A., Klaassen, M. & Madsen, J. (2008b) The consequences of climate-driven stop-over sites changes on migration

- schedules and fitness of Arctic geese. *Journal of Animal Ecology*, **77**, 654–660.
- Bêty, J., Gauthier, G. & Giroux, J.F. (2003) Body condition, migration, and timing of reproduction in snow geese: a test of the condition-dependent model of optimal clutch size. *American Naturalist*, **162**, 110–121.
- Black, J.M., Prop, J. & Larsson, K. (2007) *Wild Goose Dilemmas*. Branta Press, Groningen, The Netherlands.
- Bos, D., Van der Koppel, J. & Weissing, F.J. (2004) Dark-bellied Brent geese aggregate to cope with increased levels of primary production. *Oikos*, **107**, 485–496.
- Both, C. (2007) Comment on 'Rapid advance of spring arrival dates in long-distance migratory birds'. *Science*, **315**, 598b.
- Botta, A., Viovy, N., Ciais, P., Friedlingstein, P. & Monfray, P. (2000) A global prognostic scheme of leaf onset using satellite data. *Global Change Biology*, **6**, 709–725.
- Bowler, J. (2005) Breeding strategies and biology. *Ducks, Geese and Swans* (ed. J. Kear), pp. 68–111. Oxford University Press, Oxford, UK.
- Conradt, L. & Roper, T.J. (2005) Consensus decision making in animals. *Trends in Ecology & Evolution*, **20**, 449–456.
- Drent, R.H., Weijand, B. & Ebbinge, B. (1978) Balancing the energy budgets of arctic-breeding geese throughout the annual cycle: a progress report. *Verhandlungen der Ornithologischen Gesellschaft in Bayern*, **23**, 239–264.
- Drent, R.H., Both, C., Green, M., Madsen, J. & Piersma, T. (2003) Pay-offs and penalties of competing migratory schedules. *Oikos*, **103**, 274–292.
- Drent, R.H., Eichhorn, G., Flagstad, A., Van der Graaf, A.J., Litvin, K.E. & Stahl, J. (2007) Migratory connectivity in Arctic geese: spring stopovers are the weak links in meeting targets for breeding. *Journal of Ornithology*, **148**, S501–S514.
- Ebbinge, B.S. (1991) The impact of hunting on mortality rates and spatial distribution of geese wintering in the western Palearctic. *Ardea*, **79**, 197–209.
- Ebbinge, B.S. & Spaans, B. (1995) The importance of body reserves accumulated in spring staging areas in the temperate zone for breeding in dark-bellied brent geese *Branta b. bernicla* in the high Arctic. *Journal of Avian Biology*, **26**, 105–113.
- Ebbinge, B.S., van Biezen, J.B. & van der Voet, H. (1991) Estimation of annual adult survival rates of barnacle geese *Branta leucopsis* using multiple resightings of marked individuals. *Ardea*, **79**, 73–112.
- Eichhorn, G. (2005) Northward bound: fat for flight. How barnacle geese budget their spring travels. *Seeking Nature's Limits* (eds R.H. Drent, J.M. Tinbergen, J.P. Bakker & T. Piersma), pp. 102–113. KNNV Publishing, Utrecht, The Netherlands.
- Eichhorn, G. (2008) *Travels in a changing world: flexibility and constraints in migration and breeding of the barnacle goose*. PhD thesis. University of Groningen, Groningen, The Netherlands.
- Eichhorn, G., Afanasyev, V., Drent, R.H. & Van der Jeugd, H.P. (2006) Spring stopover routines in Russian barnacle geese *Branta leucopsis* tracked by resightings and geolocation. *Ardea*, **94**, 667–678.
- Elts, J., Kuresoo, A., Leibak, E., Leito, A., Lilleleht, V., Luigujõe, L., Lõhmus, A., Mägi, E. & Ots, M. (2003) Status and numbers of Estonian birds, 1998–2002. *Hirundo*, **16**, 58–83.
- Fox, A.D., Madsen, J., Boyd, H., Kuijken, E., Norriss, D.W., Tombre, I.M. & Stroud, D.A. (2005) Effects of agricultural change on abundance, fitness components and distribution of two arctic-nesting goose populations. *Global Change Biology*, **11**, 881–893.
- Ganter, B., Larsson, K., Syroechkovsky, E.V., Litvin, K.E., Leito, A. & Madsen, J. (1999) Barnacle geese *Branta leucopsis*: Russian and Baltic populations. *Goose Populations of the Western Palearctic: A Review of Status and Distribution* (eds J. Madsen, A.D. Fox & J. Cracknell), pp. 270–283. Wetlands International, Wageningen, The Netherlands.
- Green, M. (1998) Spring migration of barnacle goose *Branta leucopsis* and dark-bellied brent goose *B. bernicla bernicla* over Sweden. *Ornis Svecica*, **8**, 103–123.
- Grieco, F., Van Noordwijk, A.J. & Visser, M.E. (2002) Evidence for the effect of learning on timing of reproduction in blue tits. *Science*, **296**, 136–138.
- Gudmundsson, G.A., Lindström, Å. & Alerstam, T. (1991) Optimal fat loads and long-distance flights by migrating knots *Calidris canutus*, sanderlings *C. alba* and turnstones *Arenaria interpres*. *Ibis*, **133**, 140–152.
- Gunnarsson, T.G., Gill, J.A., Petersen, A., Appleton, G.F. & Sutherland, W.J. (2005) A double buffer effect in a migratory shorebird population. *Journal of Animal Ecology*, **74**, 965–971.
- Gwinner, E. (1996) Circannual clocks in avian reproduction and migration. *Ibis*, **138**, 47–63.
- Helm, B. & Gwinner, E. (2005) Carry-over effects of day length during spring migration. *Journal of Ornithology*, **146**, 348–354.
- Helm, B., Piersma, T. & Van der Jeugd, H. (2006) Sociable schedules: interplay between avian seasonal and social behaviour. *Animal Behaviour*, **72**, 245–262.
- Høgda, K.A., Karlsen, S.R. & Solheim, I. (2001) *Climate Change Impact on Growing Season in Fennoscandia Studied by a Time Series of NOAA AVHRR NDVI Data*. Proceedings IGARSS 2001, 9–13 July 2001, Sydney, Australia.
- Høgda, K.A., Karlsen, S.R. & Tommervik, H. (2007) Changes in growing season in Fennoscandia 1982–1999. *Arctic Alpine Ecosystems and People in a Changing Environment* (eds J.B. Ørbæk, R. Kallenborn, I. Tombre, E.N. Hegseth, S. Falk-Petersen & A.H. Hoel), pp. 71–84. Springer-Verlag, Berlin, Germany.
- Jonzén, N., Lindén, A., Ergon, T., Knudsen, E., Vik, J.O., Rubolini, D., Piacentini, D., Brinck, C., Spina, F., Karlsson, L., Stervander, M., Andersson, A., Waldenström, J., Lehikoinen, A., Edvardsen, E., Solvang, R. & Stenseth, N.C. (2007) Response to comment on 'Rapid advance of spring arrival dates in long-distance migratory birds'. *Science*, **315**, 598c.
- Klaassen, M., Bauer, S., Madsen, J. & Tombre, I. (2006) Modelling behavioural and fitness consequences of disturbance for geese along their spring flyway. *Journal of Applied Ecology*, **43**, 92–100.
- Koffijberg, K. & Günther, K. (2005) Recent population dynamics and habitat use of barnacle geese and dark-bellied brent geese in the Wadden Sea. *Migratory Waterbirds in the Wadden Sea 1980–2000. Wadden Sea Ecosystem No. 20* (eds J. Blew & P. Südbeck), pp. 149–170. Common Wadden Sea Secretariat, Wilhelmshaven, Germany.
- Kokko, H. (1999) Competition for early arrival in migratory birds. *Journal of Animal Ecology*, **68**, 940–950.
- Kvist, A., Lindström, Å., Green, M., Piersma, T. & Visser, G.H. (2001) Carrying large fuel loads during sustained bird flight is cheaper than expected. *Nature*, **413**, 730–732.
- Lank, D.B., Butler, R.W., Ireland, J. & Ydenberg, R.C. (2003) Effects of predation danger on migration strategies of sandpipers. *Oikos*, **103**, 303–319.
- Leito, A. (1996) The barnacle goose in Estonia. *Estonia Maritima*, **1**, 1–103.
- Leito, A., Renno, O. & Kuresoo, A. (1991) Spring numbers and distribution of barnacle goose *Branta leucopsis* staging in Estonia. *Wildfowl*, **42**, 37–41.
- Lepage, D., Gauthier, G. & Reed, A. (1998) Seasonal variation in growth of greater snow goose goslings: the role of food supply. *Oecologia*, **114**, 226–235.
- Lepage, D., Gauthier, G. & Menu, S. (2000) Reproductive consequences of egg-laying decisions in snow geese. *Journal of Animal Ecology*, **69**, 414–427.
- Madsen, J. (2001) Spring migration strategies in pink-footed geese *Anser brachyrhynchus* and consequences for spring fattening and fecundity. *Ardea*, **89**, 43–55.
- Madsen, J. & Klaassen, M. (2006) Assessing body condition and energy budget components by scoring abdominal profiles in free-ranging pink-footed geese *Anser brachyrhynchus*. *Journal of Avian Biology*, **37**, 283–287.
- McWilliams, S.R. & Leafloor, J.O. (2005) Effects of elevated CO₂ on keystone herbivores in Arctic ecosystems. *A History of Atmospheric CO₂ and its Effects on Plants, Animals, and Ecosystems* (eds J. Ehleringer, T. Cerling & D. Dearing), pp. 369–393. Springer, Berlin, Germany.
- Møller, A.P., Fiedler, W. & Berthold, P. (eds) (2004) Birds and climate change. *Advances in Ecological Research*, **35**, 1–251.
- Pennycuik, C.J. (1975) Mechanics of flight. *Avian Biology* (eds D.S. Farner & J.R. King), pp. 1–75. Academic Press, London.
- Pistorius, P.A., Follstad, A. & Taylor, F.E. (2006) Temporal changes in spring migration phenology in the Norwegian greylag goose *Anser anser*, 1971–2004. *Wildfowl*, **56**, 23–36.
- Prop, J. (2004) *Food finding – on the trail to successful reproduction in migratory geese*. PhD Thesis, University of Groningen, Groningen, The Netherlands.
- Prop, J., Black, J.M. & Shimmings, P. (2003) Travel schedules to the high Arctic: barnacle geese trade-off the timing of migration with accumulation of fat deposits. *Oikos*, **103**, 403–414.
- Randla, T. (1976) *Estonian Birds of Prey*. Valgus Press, Tallinn.
- Rees, E.C. (1989) Consistency in the timing of migration for individual Bewick's swans. *Animal Behaviour*, **38**, 384–393.
- Rowcliffe, J.M., Pettifor, R.A. & Carbone, C. (2004) Foraging inequalities in large groups: quantifying depletion experienced by individuals in goose flocks. *Journal of Animal Ecology*, **73**, 97–108.
- Seber, G.A.F. (1982) *The Estimation of Animal Abundance and Related Parameters*. Griffin, London.
- Stervander, M., Lindström, Å., Jonzén, N. & Andersson, A. (2005) Timing of spring migration in birds: long-term trends, North Atlantic Oscillation and the significance of different migration routes. *Journal of Avian Biology*, **36**, 210–221.
- Stock, M. & Hofeditz, F. (2002) Einfluss des Salzwiesen-Managements auf Habitatnutzung und Bestandsentwicklung von Nonnengänsen *Branta leucopsis* im Wattenmeer. *Vogelwelt*, **123**, 265–282.
- Sutherland, W.J. (1998) Evidence for flexibility and constraint in migration systems. *Journal of Avian Biology*, **29**, 441–446.

- Syroechkovsky, E.E. Jr. (1995) News in distribution of barnacle goose in Russia. *Casarca*, **1**, 39–46.
- Van der Graaf, A.J., Stahl, J. & Bakker, J.P. (2005) Compensatory growth of *Festuca rubra* after grazing: can migratory herbivores increase their own harvest during staging? *Functional Ecology*, **19**, 961–969.
- Van der Graaf, A.J., Stahl, J., Klimkowska, A., Bakker, J.P. & Drent, R.H. (2006) Surfing on a green wave – how plant growth drives spring migration in the barnacle goose *Branta leucopsis*. *Ardea*, **94**, 567–577.
- Van der Jeugd, H.P., Gurtovaya, E., Eichhorn, G., Litvin, K.Y., Mineev, O.Y. & Van Eerden, M.R. (2003) Breeding barnacle geese in Kolokolkova Bay, Russia: number of breeding pairs, reproductive success and morphology. *Polar Biology*, **26**, 700–706.
- Van Eerden, M.R., Drent, R.H., Stahl, J. & Bakker, J.P. (2005) Connecting seas: western Palaearctic continental flyway for water birds in the perspective of changing land use and climate. *Global Change Biology*, **11**, 894–908.
- Weber, T.P., Ens, B.J. & Houston, A.I. (1998) Optimal avian migration: a dynamic model of fuel stores and site use. *Evolutionary Ecology*, **12**, 377–401.

Received 20 March 2008; accepted 1 September 2008

Handling Associate Editor: Alexandre Roulin