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Chapter

4

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

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Abstract

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 four weeks. These late-migrating geese skip spring stopover sites in the Baltic traditionally used by the entire population. Individual geese tracked by satellite or light-level geolocators during spring migration 2004 and 2005 predominantly followed the new strategy, but a minority still maintained the traditional pattern. Between years six individuals were consistent in their migration strategy but one switched between strategies. 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 nine day time-window conferring breeding success. 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. We hypothesise 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.

Introduction

Small avian herbivores such as 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 as it sprouts along their route (Drent et al. 1978; Van der Graaf et al. 2006b). Due to their direct 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. The rate of nutrient acquisition and consequently body condition is known to influence migratory decisions (Weber et al. 1998; Drent et al. 2003; Prop et al. 2003). Both the timing of migration and body condition at arrival in the breeding grounds are crucial determinants of reproductive prospects (Kokko 1999; Bêty et al. 2003). Moreover, body condition as early as in the premigratory stage, when still on the temperate wintering grounds, can be decisive for success in the arctic breeding grounds (Ebbinge and Spaans 1995), indicating limited possibilities to compensate for deficiencies later on. Arctic breeding geese have to deposit resources in excess of what is needed to cover the flight costs. Strong seasonality of the arctic environment leaves only a narrow time window for successful reproduction. The growth period of the offspring needs to be tightly matched with local peaks of food resources (Lepage et al. 1998; Black et al. 2007). During egg-laying and early incubation local food resources are still scarce. Furthermore, incubation tasks minimize foraging opportunities for the female (Afton and Paulus 1992; Bowler 2005) as daily nest attentiveness is usually above 90%. Therefore, arctic geese arrive at the breeding grounds with a substantial surplus of endogenous nutrient reserves. They are doomed to fly in 'capital' gathered at spring staging sites (Drent et al. 2007).

Such a strategy does not minimise the energetic costs of migration, as flight costs increase inevitably with body mass (Pennycuick 1975). Energy-minimising migrants should travel with minimal loads between subsequent fuelling site (Alerstam and Lindström 1990). However, when time to gain adequate breeding condition is included in the time minimisation argument, overloading is in accord with time selected-migration. 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 et al. 1991; Alerstam 2006b). The same condition applies to a time minimising migrant when by-passing a potential staging site further upstream along the migratory route should be favourable, i.e. deposition rates at succeeding stopovers must fall below those at the departure site.

We here examine a thirty-year data set on migration of the barnacle goose along the Baltic route and compare these with population counts. By means of data on individual geese (tracked in two seasons) we are also able to test if individuals show flexibility of migratory strategies. 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 2006a; Drent et al. 2007). Thus the main objectives of this paper are to: 1) describe the timing of spring migration of barnacle geese over the past decades in perspective of a growing total flyway population as well as differences in the onset of spring, 2) evaluate under which conditions bypassing of the Baltic may become beneficial in the light of optimal migration theory, 3) present individual spring itineraries and their variation between years, and finally 4) examine if the dichotomy of alternative individual spring migration strategies incurs differences in the timing of breeding.

Methods

Study population and study sites

Barnacle geese wintering along the North Sea coast in Germany and The Netherlands belong to a population breeding on the arctic coast of European Russia and two temperate breeding populations in the Baltic and The Netherlands (Ganter et al. 1999). Although the Baltic and Dutch populations have been growing rapidly since their establishment in 1971 and 1981, respectively (Larsson et al. 1988; Meininger and Van Swelm 1994) now together numbering 46 000 individuals, the Russian arctic breeding population is by far the most numerous, currently representing 90% of the common wintering population of more than 500 000 birds (Black et al. 2007). The geese feed predominantly on grasses, sedges and herbs utilising coastal salt marshes and, in temperate regions, adjacent agricultural pastures. On their migration to the breeding sites in the Russian Arctic barnacle geese make use of a number of major staging sites. The North Sea coast from the Netherlands to southern Denmark serves as an important pre-migratory fattening area. Many geese wintering in the western Wadden Sea move short distances to accumulate more body reserves in the north-eastern Wadden Sea prior to their take off to more distant sites in the Baltic, most notably in western Estonia and on the Swedish island of Gotland (Ebbinge et al. 1991; Leito et al. 1991). The longest leap to be made is between the Baltic and pre-breeding sites on the White Sea coast, crossing unsuitable habitat of boreal forests.

Traditional breeding areas of this population were restricted mainly to the islands of Novaya Zemlya and Vaygach in the eastern Barents Sea. Through expansion back down the flyway, since the 1980s breeding occurs now down to the eastern White Sea coast, 650 km westwards (Ganter et al. 1999). Figure 4.1 shows areas of wintering, staging and breeding and our study sites along the migratory route. Individual migratory itineraries and data on breeding biology were obtained from birds nesting in a colony near the abandoned village Tobseda (68°35'N, 52°18'E) situated on the Kolokolkova Bay salt marshes on the west coast of the Pechora Delta (for details about this breeding and moulting site see Van der Jeugd et al. 2003).
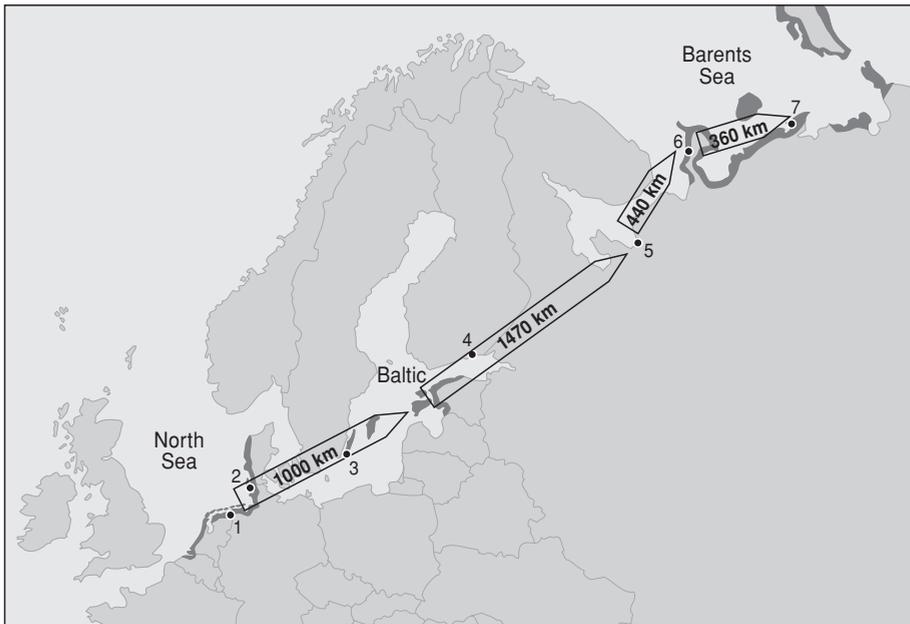
Figure 4.1. Map showing spring migratory route of Russian breeding barnacle geese with distances between staging sites and observation points: 1-Dollard estuary; 2-Wadden Sea; 3-Ottenby; 4-Finland; 5-Dvina delta; 6-Kanin Peninsula; 7-goose breeding colony at Tobseda. Dark grey shaded areas indicate wintering/staging grounds in the Wadden Sea and Baltic, and breeding grounds in the Russian Arctic.

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 16 years during 1974 – 2005; see Fig. 4.2). Censuses were conducted in the period 5–15 May using a constant census area and routine (since 1974) over the years 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. 1) Wadden Sea coast: Departure dates from the north-eastern Wadden Sea in Schleswig-Holstein, Germany (ca. 54°36'N, 8°52'E), when > 75% of the peak staging population had left the site were obtained from Stock & Hofeditz (2002) for 1988-1997 and updated with dates of mass departure from the same area for 1998-2003 (Koffijberg and Günther 2005) and 2005-2006 (Koffijberg pers. comm.). 2) Arrival in the Baltic area: Birds passing by the Ottenby bird observatory (56°12'N, 16°24'E) located at the southern tip of the Swedish island Öland were counted yearly in the period April–May. Data for the years 1970-2004 were extracted from
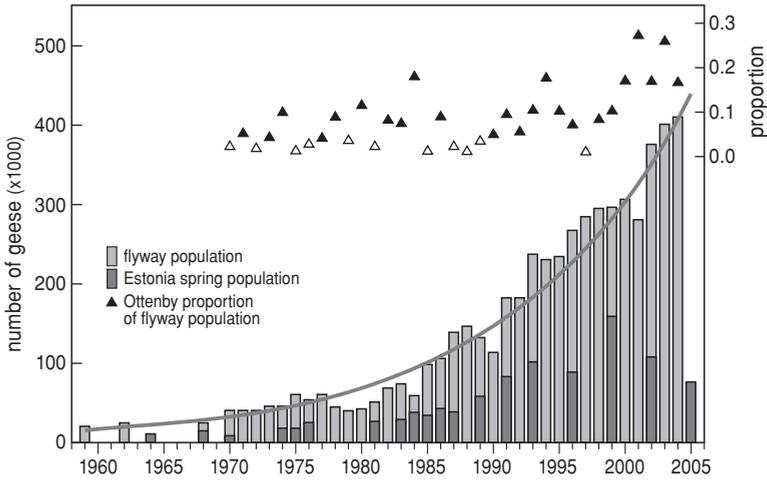
Figure 4.2. Size of flyway population and numbers of spring staging barnacle geese in Estonia depicted by columns scaled to the left axis. The equation fitted to the flyway population data (grey solid line) is $y = 13844e^{0.074x}$, $r^2 = 0.95$, corresponding to a yearly growth-rate of 7.7%. Triangles 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.

the observatory diaries. Ottenby is situated on a main migratory corridor for Barnacle as well as Brent geese *Branta b. bernicla* travelling from the Wadden Sea to Baltic staging sites (Green 1998). To assure a consistent representiveness we discarded years when < 5% of the flyway population was counted at Ottenby (Fig. 4.2). 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 2005-2006. 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. 3) Departure from the Baltic: 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 (Lintukymi) for the years 1989–2004, and updated for 2005-2006 by Tolvanen (pers. comm.). We refrained from using census data recorded at Eemshaven, in the Netherlands, because these likely include substantial short-distance movements within the Wadden Sea.

Daily mean temperatures measured at Baltic and North Sea goose staging sites were gathered from the European Climate Assessment and Dataset (Klein Tank et al. 2002) 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 Sandon (58°24'N, 19°12'E) and for Leeuwarden in The Netherlands covering 1970-1971. H. Vugts (pers. comm., 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 over the period from 1 January until 12 April, the 'traditional' date of median arrival in the Baltic. GDD calculated with this threshold value is a good predictor for the onset of vegetation growth in temperate and cool biomes (Botta et al. 2000).

Observations on individual birds

We employed satellite tracking and Global Location System (GLS) data loggers (also called light-level geolocators) to track movements of individual barnacle geese breeding in our Russian arctic study site. We found no indication of impaired behaviour and/or condition in birds carrying tracking devices (for details see Eichhorn 2005; Eichhorn et al. 2006). Accuracy in the timing of movements is within a range of one day. We collated individual departures from the wintering grounds together with known laying dates for 21 birds in 2004 (all tracked by GLS) and nine birds in 2005 (one tracked by PTT, eight by GLS). For seven individuals spring migratory schedules could be recorded during 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 obs.), and the incubation rhythm detected in the light-level data. Data loggers were retrieved from captures during incubation and during moult. Median laying date for all monitored nests in the colony was 13 June in 2004 (n = 385) and 6 June in 2005 (n = 413). These dates were related to individual laying dates to calculate relative laying dates.

Results

Documenting the emergence of a new migratory behaviour

The barnacle goose population wintering in the international Wadden Sea has grown exponentially since a low in the early 1950s (Ganter et al. 1999), increasing at an annual rate of 7.7%, corresponding to a doubling time of 9.4 years (Fig. 4.2). Numbers of spring staging barnacle geese in Estonia followed the increase of the flyway population until the mid 1990s but then levelled off and are now decreasing.

   Figure 4.3 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) and both illustrate a distinctive delay of departure from the wintering grounds, starting around the mid 1990s and stabilising 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 ± 3 days, mean ± SD), indicating that the interval between mass departure from the Wadden Sea and peak passage past Finland has decreased dramatically.
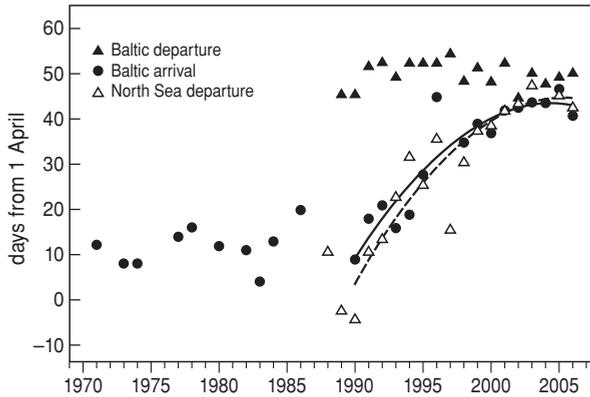
Figure 4.3. Passage dates along the migratory pathway: at the Finnish Gulf 1989-2006, over southern Sweden 1971-2006 and mass departures from the German North Sea coast 1988-2006. Curves fitted for the period 1990–2006 (with years renumbered to 1=1990 till 17=2006) refer to North Sea departure, broken 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.

Figure 4.4 presents a break-down of the Ottenby data illustrating the change of the seasonal dynamics of migration into the Baltic. During the earliest periods (1971-1984) 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 total flyway population leaving the Wadden Sea in the first half of May (peak close to mid May), four weeks later compared to before 1990.

Individual migratory schedules
To interpret the patterns illustrated so far, it is essential to investigate individual choices in the migratory schedule and their consequences. This is especially revealing for birds breeding in the same colony which share exogenous parameters like migratory distance, feeding conditions in the breeding grounds and optimal time of egg-laying. Employing both GLS and satellite telemetry, individual female barnacle geese tracked during spring migration of 2004 (n = 23) and 2005 (n = 12) confirm the two migratory strategies existing side by side (Fig. 4.5). 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 (median 19.5) in 2005,
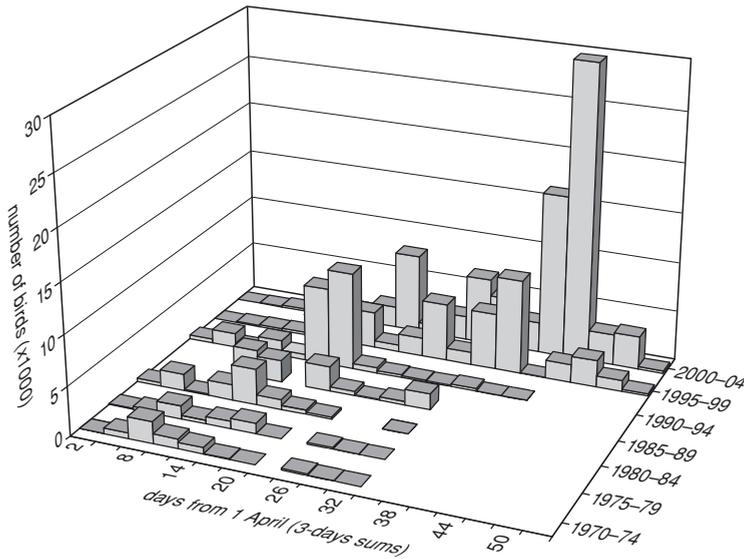
Figure 4.4. Development of spring migratory pattern of barnacle geese counted at Ottenby 1971-2004. Census data were first aggregated to three-day sums for each season (assigned to the central day of the interval) and then averaged over the periods indicated along the right axis (years with counts of < 5% of flyway population were discarded; see Fig. 4.2).

which was virtually identical to the peak dates of barnacle goose passage observed in southern Finland in these two years, i.e. 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 two days, with hardly any opportunity for feeding along the way). 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 six days before moving on in short hops to the colony). As already shown for mass movements in Fig. 4.3, 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 4.4 and 4.5). Thus, recently we encounter two major spring migratory strategies within one flyway population, which exhibit a difference of about one month in the timing of departure from the wintering grounds.

Although our sample is small, individual geese followed over several seasons were either consistently traditional 'Baltic stagers' or 'skipped' the Baltic following
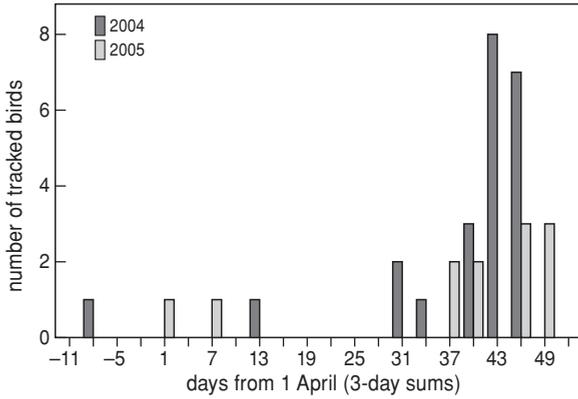
Figure 4.5. Timing of individual movements into the Baltic for birds tracked in 2004 (black bars, n = 23) and 2005 (grey bars, n = 12). Values were summed over three-day periods and assigned to the central day of the interval.

the new 'Wadden Sea stagers' strategy (Fig. 4.6, Table 4.1). However, switching may occur as was shown by one individual (M=W6) which adopted the new strategy in 2005. Because of the strong influence of a single bird in a relatively small sample we present results from repeatability analyses (Lessells and Boag 1987) for both the total sample and excluding bird M=W6 (Table 4.1). Despite the huge annual difference in departure date from the non-breeding grounds, the date of arrival at the breeding site (based on first observations in the colony) for this particular individual was remarkably similar in 2004 (7 June) and 2005 (8 June). The time window for arrival dates in the Baltic covered 58 days in these seven birds tracked over two years, whereas dates of departure from the Baltic fell into a period covering 13 days only (Fig. 4.6).

**By-passing the baltic in view of optimal migration theory**
The following exercise aims at estimating the differential energetic costs of the two migratory strategies and to evaluate conditions for an optimal spacing of migratory stopovers for a time-minimising capital breeder. We base our estimates on flight mechanical theory (Pennycuick 1975) and follow 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:

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

or

$$Y = \frac{c}{2} \ln(1+f) \qquad \text{(eqn 1b)}$$

where f is defined as fuel load relative to the lean body mass of the bird and c is a
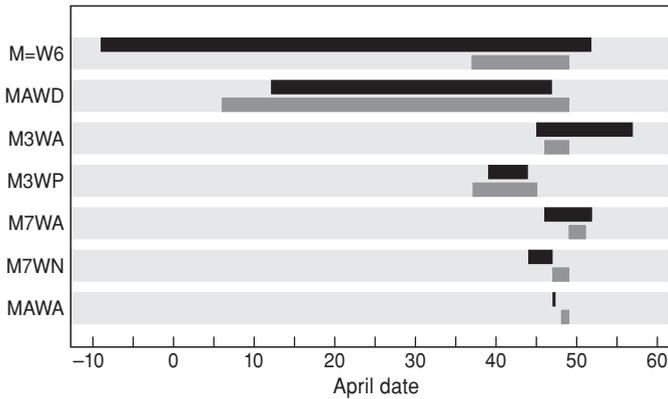
Figure 4.6. Timing and duration of staging in the Baltic for seven individuals tracked in two consecutive spring seasons, 2004 (black) and 2005 (grey bars). Labels given on the y-axis refer to individual colour-ring codes of the birds.

Table 4.1. Repeatabilities (r_i) of Baltic arrival, stopover duration and departure times of barnacle geese tracked in 2004-2005. Analyses were performed on the total sample of seven birds and again but excluding bird M=W6; see Fig. 4.6 for reference

Variable	Total sample			Excluding bird M=W6		
	r_i	F (*df*)	P	r_i	F (*df*)	P
Arrival Baltic	0.57	3.67 (6,7)	0.06	0.98	90.4 (5,6)	< 0.001
Stopover Baltic	0.59	3.82 (6,7)	0.05	0.93	29.1 (5,6)	< 0.001
Departure Baltic	0.39	2.27 (6,7)	0.15	0.47	2.79 (5,6)	0.12

constant (with same dimension as Y) that depends on factors such as bird morphology, muscle work efficiency, fuel composition and wind conditions. The difference between the two equations is whether one assumes that fuel load increases both induced and parasite drag of a flying bird (1a) or only the former component (1b) (see also Alerstam & Lindström (1990). The occurrence of parasite drag is expected due to an increased body frontal area when fuel is added (note the bulging abdomen of fat geese in flight). Therefore, we will proceed with equation (1a). We derived an empirical estimate for c from data reported by Madsen & Klaassen (2006) for pink-footed *Anser brachyrhynchus* geese flying between Denmark and Vesterålen (Norway). For this flight of 1410 km the authors estimated an average change in API (abdominal profile index) of 2.00 units (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 & Klaassen pers. comm.) yielding $f = 0.124$ (females, n = 18) and $f = 0.129$ (males, n = 17). Inserting these fuel ratios and the flight distance into equation (1a) gives $c_{females} = 24765$ km and $c_{males} = 23927$ km. We applied the rounded average of these values, $c = 24300$ km, as estimate for our further calculations.

Of fundamental importance here is to note that the potential flight distance is not a linear but a negatively accelerated function of fuel load, meaning that the marginal gain in flight distance diminishes with increasing fuel levels. Thus, over-loading, which includes fuel in excess of what is needed to reach the next stopover site, must produce extra flight costs. Recent empirical information suggest possibly 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 realise that our quantitative predictions must be regarded as provisional. Rearranging equation (1a) to express fuel load as a function of potential flight distance $f(Y)$ gives:

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

From this equation we calculated the fuel loads needed to cover flight distances between stopovers 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 Peninsula (Fig.4.1, Table 4.2). 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.

Overloading and by-passing can become optimal in time selected-migrants, when deposition rates at succeeding stopovers fall below that at the departure site. Thus, another avenue to explore the current phenomenon 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. We start again from the range equation and substitute f by $k \cdot t$, the product of the rate of fuel deposition (k) and time spent on deposition (t). Expressing equation (1a) 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:

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

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

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

The instantaneous speed of migration thus depends on the local fuel deposition rate but is devalued 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, $\left(1-\dfrac{Y}{c}\right)^3$, 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. This also means that if the deposition rate in the Baltic falls below 88% of that in the Wadden Sea, continued energy deposition at the latter site and a postponed departure from the Wadden Sea without stopover in the Baltic will be favoured.

Table 4.2. Flight distances (Y) and calculated fuel loads (f) using equation (2) and c = 24,300 km 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 under the assumption that the birds leave for their next target site as soon as fuel loads permit to fly there. The geographical locations of the stopover sites are illustrated in Fig. 4.1

Flight	Y (km)	f (Y)	extra f	extra f (%)
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

What are the Fitness Consequences of the New Strategy?
Since extra costs are involved in by-passing the Baltic staging site, the question arises if individuals following this strategy encounter certain fitness consequences. Our data on the reproductive output of tracked birds is too incomplete to be used for this purpose, as egg loss and nest desertion due to stochastic factors like predation, flooding events and human disturbance reduced the potential sample size substantially. However, we know the time of egg-laying for most of the birds (recall that for 'logger birds' incubation rhythm and start of egg-laying could be inferred from the light logger data, hence not necessitating direct observation of the breeding bird). We can use this parameter to assess potential penalties of the new strategy, because laying date is a good predictor of reproductive prospects in arctic geese. In our study colony 90% of fledged young derive from eggs laid over period of nine days (ch. 6 this thesis). Figure 4.7 shows individual case histories of departure date from the non-breeding ground and laying date collected over two seasons at the colony. It will be noted that the majority of birds following the new 'Wadden
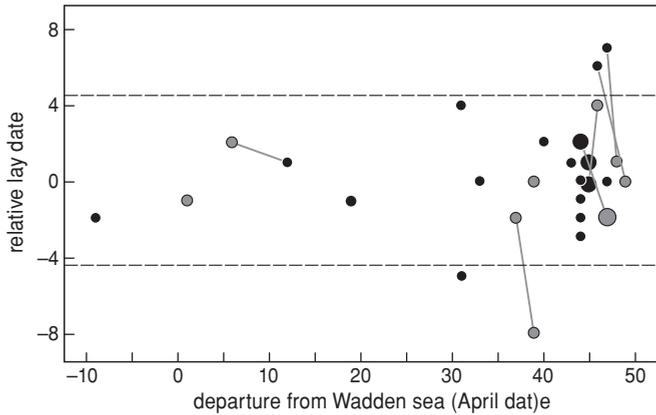
Figure 4.7. Lay date relative to the colony's median lay date versus departure date from the wintering grounds plotted for 21 females in 2004 (black dots) and 9 in 2005 (grey dots); size indicates sample size, small dot=1, large dot=2; lines connect individuals followed in both years. The two dashed lines include the time window of laid eggs producing 90% of all fledged young in the colony.

Sea stagers' strategy laid their eggs in the period conferring good prospects. Furthermore, no trend towards later laying as result of delayed 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 non-breeding grounds by a full month. Moreover, this drastic shift evolved over a remarkably short period of five to ten 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 five weeks, has been reduced to less than seven days for a sizeable proportion of the flyway population.

Driving forces behind the emergence of a new migratory strategy
We propose that a capacity problem in the Baltic is the key for the emergence of the strategy of delayed departure from wintering grounds in the North 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 and are decreasing over recent years (Fig. 4.2). Second, Van der Graaf et al. (2006b) compared nutrient bio-

mass (product of forage biomass and protein content) during spring staging in the Wadden Sea and on Gotland in 2003–2004 and noted higher values for the Wadden Sea site. High grazing pressure caused heavily reduced food availability, as was indicated by exclosure experiments. Confronted with increasing costs of competition (Moore et al. 2003) 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 premigratory 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, e.g. the Dollard estuary (Fig. 4.1) at the Dutch-German border (Aerts et al. 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.

The two strategies do not represent two ends of a continuum. Migrants appeared to prefer either an early (Baltic) strategy or a late (Wadden Sea) option while few movements occurred in between (Figs 4.4 and 4.5). Various factors may shape an individual's choice for the one or other strategy, such as individual competitive ability (Moore et al. 2003), strategy of parents or mate, experience and learning.

Further triggers of migratory schedules

In birds the timing of events through the annual cycle, including migration, has been shown to be regulated by the interaction of an internal circannual clock 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 (see next section) does not support this hypothesis. We expect photoperiod as Zeitgeber to be primarily relevant for the timing of physiological responses accompanying migratory preparation, mainly related to the deposition of body stores (Bairlein and Gwinner 1994), rather than triggering actual migration (but see Helm and Gwinner 2005).

Recently, shifts in migration patterns of many bird species have been reported in NW Europe, and credible relationships with climatic variables such as temperature and the North Atlantic Oscillation (NAO) have been established (e.g. Møller et al. 2004; Stervander et al. 2005). Among waterfowl studies Pistorius et al. (2006) suggested that increasingly warmer spring temperatures in The Netherlands may have driven temporal changes in arrival and nesting of greylag geese *Anser anser* breeding on the Helgeland coast in central Norway. This population uses Dutch spring staging sites on their migration from Spanish wintering grounds. Arrival and nesting of the geese in Norway has been advanced by more than two weeks over the past three decades.

The seasonal progress of vegetation development in temperate regions, notably the onset of leaf growth, is closely related to growing degree days (GDD), i.e. the sum of daily mean temperatures above a defined threshold accumulated over a certain period (Botta et al. 2000). Using 'onset of spring' (defined as a GDD value of
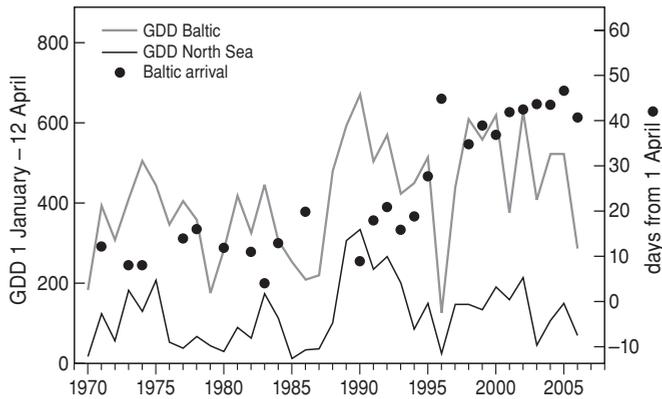
Figure 4.8. Annual Growing Degree Days (GDD) accumulated over 1 January–12 April (left y-axis) at a Baltic and Dutch staging site, denoted by the lower and upper line, respectively. Linear regression analyses revealed a significant increase of 5.0 GDD/year over the study period for the Dutch site ($F_{1,35} = 6.1$, $P = 0.02$) 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. 4.3.

180 accumulated above a threshold of 0°C) Van Eerden et al. (2005) compiled data on the timing of spring migration of barnacle geese from the Russian flyway population along the whole route and concluded that their measure of onset of spring was in close accord with the timing of geese (observations 1990–2003). We analysed our data on the timing of yearly mass movements of barnacle geese into the Baltic together with annual GDD values (see methods) at a Baltic and Dutch staging site (Fig. 4.8). Although 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. 4.8). These findings are supported by the regional pattern of NDVI (Normalized Difference Vegetation Index) derived changes in onset of spring observed by Høgda et al. (2001). For the period 1982–1998 these authors report an advance in the onset of spring of four or more weeks for most of the Wadden Sea area but only about two weeks for the eastern Baltic.

Using regression analysis we further investigated the effects of GDD, year and year2 on barnacle goose median arrival date in the Baltic for the period before 1990 and for the period from 1990 onwards (GDD measured at the Dutch and Baltic site were each separately tested together with year effects). We analysed these two periods separately, because we were interested in comparing the influence of GDD on migratory timing before and after birds started to delay their departure from the non-breeding grounds. 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 ($F_{1,9}$ GDD$_{North\ Sea}$ = 11.14,

$P < 0.05$, $r^2 = 0.58$; $F_{1,9}$ GDD$_{Baltic}$ = 12.22, $P < 0.01$, $r^2 = 0.60$). However, in the recent period from 1990 onwards (n = 16) considerably more variation was explained by a quadratic year effect (see Fig. 4.3 for statistical tests and calculated parameters). At the same time, the effect of GDD disappeared ($F_{1,15}$ GDD$_{North Sea}$ = 2.64, NS; $F_{1,15}$ GDD$_{Baltic}$ = 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 ± SD, n = 10) and 94 ± 49 at the North Sea and Baltic site, respectively, before 1990. Thereafter GDD increased considerably up to average values of 803 ± 139 (North Sea) and 369 ± 87 (Baltic site) for the years 2000-2006 (n = 7).

Thus, our findings refine the conclusion of Van Eerden et al. (2005, see above) and suggest a temporal change in the relationship between seasonal development of forage plants (GDD used as a proxy) and timing of migration from the Wadden Sea. We conclude that seasonal progress in vegetation development has a potential effect on migratory timing in barnacle geese. However, GDD cannot explain the observed delay in departure from the wintering grounds followed by an increasing share of the population. The modulating effect of spring development on departure decisions has recently been overruled by other factors, of which we regard the capacity problem in the Baltic as the dominant one.

Consistency in individual migratory behaviour
The barnacle goose is a long-lived species. Ebbinge et al. (1991) estimated a mean annual survival rate of adult birds belonging to the 'Russian flyway population' of 90% corresponding to a mean life expectancy of nine years (Seber 1982) and life spans of more than 20 years have been frequently recorded for birds from this population (Ebbinge pers. comm.). 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 the observation of one tracked individual departing from the North Sea 44 days later in 2005 compared to the previous year. Nevertheless, the overall pattern hints at individual consistency after the adoption of a new migratory schedule.

Individual consistency in annual bird migratory schedules has been proven for a number of species and populations. However, most of these studies dealt with timing from or to a single site (e.g. Rees 1989; Møller 2001; Forstmeier 2002; Gunnarsson et al. 2006; Battley 2006). Only few studies included more than one site (Bêty et al. 2004) or the entire migratory route (Berthold et al. 2002; Berthold et al. 2004; Phillips et al. 2005; Alerstam et al. 2006). The osprey *Pandion haliaetus* study of Alerstam et al. (2006) revealed that individual consistency (repeatability as high as $r_i = 0.81$) in timing observed at one site (e.g. departure site) does not necessarily persist throughout the entire migratory route. Temporal patterns at subsequent sites (e.g. arrival site) can differ and furthermore may vary between homeward and outward migration. Bêty et al. (2004) reported a site dependence of annual consistency for female greater snow geese *Anser caerulescens atlanticus* which showed relatively high individual consistency in the arrival date at the breeding site

on Bylot island ($r_i = 0.42$) but not in the departure date from a major staging site at the St. Lawrence river 3,000 km away. For our barnacle geese we found consistent patterns for the timing of arrival and stopover duration in the Baltic (Table 4.1). Increasingly tighter migration schedules as birds get closer to their breeding grounds, as indicated here for geese by their first two major leaps (to and from the Baltic), may be common among long-distance migrants (Battley et al. 2004; Gunnarsson et al. 2006).

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). For the barnacle goose most of the flexibility in migratory schedule must be attributed to phenotypic plasticity. Most barnacle geese do not start breeding before three years of age and breeding success is usually low during the first attempts (Black et al. 2007). The observed response was too rapid to be produced by natural selection, even when strongly directional (note also that 'traditional' schedules seemed not per se to incur fitness penalties). Furthermore, in geese migratory routes are transmitted culturally by the family, where young benefit from the experience of their parents, which helps them to optimise their own future decisions (Sutherland 1998). The barnacle goose is a highly sociable species breeding in colonies and living in flocks for the rest of the year. Scheduling of events is virtually always a sociable process in this species and social information transfer likely boosts speed and extent of adjustments to new environmental conditions (Helm et al. 2006). Cultural transmission need not be restricted to parent-offspring relationships. Social learning and communal decisions can involve more members of the flock and lead to concerted group behaviour further enhancing speed of phenotypic reactions (Galef and Heyes 2004; Couzin et al. 2005; Conradt and 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 et al. 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 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 emphasise that time is a crucial factor to allow the birds to experience, learn and readjust migratory strategies in an adaptive fashion.

Costs and consequences of the new strategy

In our attempt to quantify costs of the new strategy we classified it as essentially by-passing the Baltic. It should be noted that the majority of birds included at least

a short visit in the Baltic region, mainly to Estonian sites in the eastern Baltic (Eichhorn et al. 2006). However, settling costs and heavy food depletion at that time (Van der Graaf et al. 2006b) will make significant fuel gain during such short stopover periods unlikely. The results indicate that the marginally higher costs of extra fuel load needed to by-pass the Baltic must be compensated for by overall higher fuel deposition rates in the 'Wadden Sea stagers' if they are to arrive with same reserves and at the same time in the Arctic as the 'Baltic stagers'. The geese should skip the Baltic whenever the energy deposition rate falls below 88% of the Wadden Sea value.

Can this by-passing behaviour be explained by a general latitudinal gradient in stopover site quality along the route? Gudmundsson et al. (1991) hypothesised for arctic waders a decline in deposition rates when moving north, because spring development at higher latitudes lags behind that at more southern latitudes, and from this perspective overloads would be favoured. For arctic geese the situation seems, however, to be largely the opposite. Here gain rates usually accelerate along the spring migratory route (Prop 2004; Madsen and Klaassen 2006; Klaassen et al. 2006). Both food quality (in terms of nutrient content and digestibility) and available feeding time are crucial determinants for the rate of nutrient deposition. Growing grass shows a higher digestibility and concentration of nutrients, and while moving northwards, these herbivorous birds can take advantage of a 'green wave' generated by spring growth at subsequent stopovers (Drent et al. 1978; Owen 1980). Additionally, with latitude they encounter increasing daylength which extends potential feeding time. Only towards the end of spring migration, when at or very close to their destination, geese are forced to get ahead of the green wave in order to match hatching of offspring with the local crest in food quality. Theoretically, for 'Baltic stagers' one would expect not only reduced flight costs but also potentially higher fuel gain rates. That these potential benefits were indeed realised in former times can be inferred from mean body masses of spring staging geese recorded in the Wadden Sea and on Gotland in the period 1979-1989 (Ebbinge et al. 1991). Geese on Gotland showed impressive mass gains after intensive use of this Baltic stopover in those days.

A crucial question when dealing with a strongly expanding population such as our study species is whether some of the birds are being forced into less favourable habitats, i.e. entailing a heightened risk of mortality and/or decreased reproductive success. The Icelandic population of the black-tailed godwit *Limosa limosa islandica* wintering in Britain has increased fourfold since the 1970s, and Gill et al. (2001) demonstrated that this coincided with expansion into heretofore unused estuaries. Godwits wintering in these new sites suffered both a higher mortality and arrived later on the breeding grounds in Iceland presumably leading to a lower breeding success than individuals utilizing the traditional estuaries. Subsequently Gunnarsson et al. (2005) showed that in Iceland the population expansion was associated with an overflow into new breeding habitats conferring lower breeding success, hence this godwit population can be said to experience a double buffer effect (sensu Kluyver and Tinbergen 1953). Since our tracking of barnacle geese was undertaken

primarily with breeding females caught at a specific colony (and not a cross-section of the wintering population as in the godwit) the existence of a buffer effect in our study system remains an open question.

We are aware that subtle effects on survival and reproductive success are associated with changing stop-over 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 a buffer effect associated with the saturation of the Baltic sites thus penalising the recently evolved alternative strategy of delayed departure from the Wadden Sea. Timing of egg-laying (a strong predictor of potential breeding success) was the same for 'Wadden Sea-stagers' and 'Baltic-stagers', and while the proportion of 'Wadden Sea-stagers' increased, the overall population showed a hitherto 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 North 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 form of improved grassland, where forage quality is enhanced due to intensive agricultural fertilization during the past 20 years. At these agricultural sites the geese have yet to face a depletion problem but cope successfully with the very productive vegetation. 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 et al. 2004; Van der Graaf et al. 2005).

Mortality risk due to predation is another factor determining site quality and may play an important role in the development of migratory strategies (Alerstam and Lindström 1990; Lank et al. 2003). Barnacle geese experience predation risk from white-tailed eagle *Haliaeetus albicilla*. This raptor 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). On northern Öland eagles started to breed again in 1994 and reside there now with about ten pairs (own obs.). 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.

No fitness penalties for birds delaying their departure from the Wadden Sea and subsequently 'skipping' the Baltic were revealed by the timing of egg-laying (Fig. 4.7). Furthermore, no signs of retarded growth of the flyway population can be noted so far (Fig. 4.2). Apparently, the enhanced gain rates compensate the 'Wadden Sea stagers' for the loss of an intermediate fuelling site and probably have facilitated the growth of the flyway population in combination with reduced mortality through enhanced protection (Ebbinge 1991). 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.

The remarkable phenotypic plasticity demonstrated by this species will enhance its ability to cope with current and future environmental changes including climate change.

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