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Keeping up with early springs: rapid range expansion in an avian herbivore incurs a mismatch between reproductive timing and food supply

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Abstract

Within three decades, the barnacle goose population wintering on the European mainland has dramatically increased in numbers and extended its breeding range. The expansion has occurred both within the Arctic as well as by the colonization of temperate areas. Studies of performance of individuals in expanding populations provide information on how well species can adapt to novel environments and global warming. We, therefore, studied the availability of high quality food as well as timing of reproduction, wing moult, fledgling production and postfledging survival of individually marked geese in three recently established populations: one Arctic (Barents Sea) and two temperate (Baltic, North Sea). In the Barents Sea population, timing of hatching was synchronized with the peak in food availability and there was strong stabilizing selection. Although birds in the Baltic and North Sea populations bred 6–7 weeks earlier than Arctic birds, timing of hatching was late in relation to the peak in food availability, and there was moderate to strong directional selection for early breeding. In the Baltic, absolute timing of egg laying advanced considerably over the 20-year study period, but advanced little relative to spring phenology, and directional selection on lay date increased over time. Wing moult of adults started only 2–4 weeks earlier in the temperate populations than in the Arctic. Synchronization between fledging of young and end of wing moult decreased in the temperate populations. Arctic-breeding geese may gradually accumulate body stores from the food they encounter during spring migration, which allows them to breed relatively early and their young to use the peak of the Arctic food resources. By contrast, temperate-breeding birds are not able to acquire adequate body stores from local resources early enough, that is before the quality of food for their young starts to decrease. When global temperatures continue to rise, Arctic-breeding barnacle geese might encounter similar problems.

Keywords: adaptation, global change, latitude, migration, range expansion, survival, timing of reproduction

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Introduction

Understanding the mechanisms by which species adapt to shifting climatic zones is crucial to predict the impact of global change. Recent studies mainly emphasized the *inability* of species to adapt sufficiently to rapidly changing environments (Both & Visser, 2001; Visser & Holleman, 2001; Gienapp *et al.*, 2008). Especially long-distance migrant birds seem vulnerable to large-scale

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[1] Rudi Drent deceased on 9 September 2008. Rudi's contribution to modern day ornithology has been exceptional, and he served as a mentor for a large group of young ecologists. Research on arctic geese was his great passion and he played a pivotal role in the studies in arctic Russia that are part of this paper. The work we present here is to a large extent inspired by his enthusiasm.

climatic change, because they rely on a whole series of environments at different times during their annual cycle, and these may change at different rates (Both *et al*., 2006; Sanderson *et al*., 2006; Jonzén *et al*., 2006). However, studies of migratory species that, *in contrast*, have been very successful in spreading into new environments are equally relevant to the study of global change, because such studies provide information on how well species can adapt to different environments, and thus provide information about the limits of their plasticity. Rapid range expansions along a north–south gradient, other than due to climate change, are particularly useful, as these give information on adaptation to different climatic zones, and can therefore serve as natural experiments in which large shifts in climate can be studied in a relatively short time span.

Species ranges have contracted and expanded many times during evolutionary time as a response to shifting environmental conditions. Some species, for example the finches of the genus *Carpodacus* seem more prone to rapid range alterations than other species, most probably as a result of their remarkable capability of rapidly evolving new adaptations to novel environments (Badyaev & Martin, 2000; Badyaev *et al*., 2002). Many historic range alterations also involved major changes in migratory behaviour. In some cases, for example that of the blackcap *Sylvia atricapilla*, the change in migratory behaviour resulted from selection on genetically determined variation (Berthold *et al*., 1992; Pulido *et al*., 2001). Indeed, most passerines seem to have genetically determined migratory behaviour (Van Noordwijk *et al*., 2006). However, in a review of recently documented rapid shifts in migratory behaviour, most cases were confined to species with extended parental care, such as waterfowl, where information on timing and direction of migration is transmitted culturally (Sutherland, 1998). Although changes in breeding range or migratory behaviour have frequently been described, studies in which the performance of individuals in historical vs. newly colonized environments, or of individuals adopting traditional vs. novel migration strategies are rare (Eichhorn *et al*., 2006).

Here, we compare three recently established populations of the barnacle goose *Branta leucopsis*, one of the new Arctic colonies (Barents Sea) and two temperate (Baltic, North Sea), that have all been subject to long-term studies. The species has long been considered a specialist of the high-Arctic, benefiting from the short but productive Arctic summer at the cost of a long migration route and severe environmental conditions. However, it now seems to be rapidly adapting to a wide range of habitats in the temperate zone, thereby considerably shortening the migration route, or even giving up migration altogether. Human impacts must also be included as causes of these range changes (Van der Graaf *et al*., 2006a). These rapid changes raise questions about the limits of plasticity and the possibility of rapid evolutionary change. We compare major life-history characteristics between these populations, focussing on timing of reproduction in relation to food availability. We will show that despite their initial rapid increase and general success, temperate populations of the barnacle goose are currently not completely adapted to their novel environment.

Material and methods

Study populations

In recent decades, the East Atlantic Flyway population of barnacle geese *B. leucopsis* has undergone a dramatic change in numbers (Ganter *et al*., 1999). In the 1960s, the population numbered ca. 25 000 individuals. By 2006, it had increased more then 20-fold to an estimated 550 000 individuals (SOVON, unpublished results). This increase went hand in hand with the colonization of new breeding areas to the west and southwest of the original breeding grounds on Novaya Zemlya and Vaigach in Arctic Russia, including our recently established study colony in the Barents Sea (Filchagov & Leonovich, 1992; Syroechkovsky Jr., 1995). Present numbers along the Western Barents Sea coast, including the island Kolguev, are not well known, but are likely to exceed 60 000 breeding pairs (Y. Anisimov *et al*., unpublished results).

Already in 1971, the first breeding pair in the Baltic was found (Larsson *et al*., 1988), and since then this population has grown at a spectacular rate, numbering 17 000 individuals in 1997 (Larsson & Van der Jeugd, 1998) and approximately 21 000 individuals in 2005 (K. Larsson, unpublished results). More recently, a population was established in the southwest of the Netherlands (Meininger & Van Swelm, 1994; Ouweneel, 2001). Here, the first breeding pair was encountered in 1981, and since then, the North Sea population has been growing rapidly and numbered 25 000 individuals in 2005 (Van der Graaf *et al*., 2006a; Voslamber *et al*., 2007). During the same period, barnacle geese have also appeared as breeding birds in other western European countries. All recently established breeding areas are situated within the flyway, that is they are confined to historical wintering areas and staging grounds of the species.

Thus, within the East Atlantic Flyway, three breeding populations of barnacle geese are now recognized (Fig. 1), the Barents Sea, Baltic and North Sea populations, with the Barents Sea population greatly outnumbering the other two. Birds from these populations

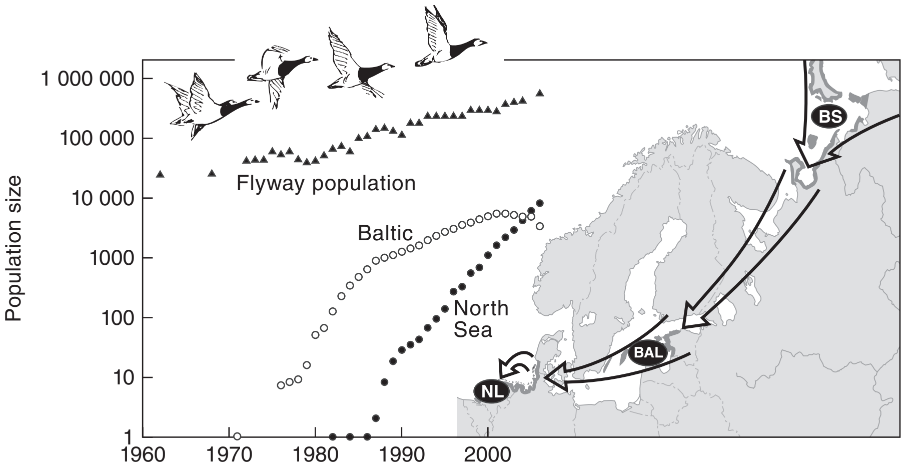

Fig. 1 Number of breeding pairs for two recently established temperate barnacle goose populations (Baltic and North Sea, open and closed circles), and the total number of barnacle geese of the east Atlantic Flyway (closed squares). Letters in the map indicate the position of the study sites: BS, Barents Sea; BAL, Baltic and NL, North Sea. Arrows indicate the migration route Arctic and Baltic birds follow to their wintering grounds. Birds from the North Sea population are sedentary.

share the same wintering grounds, but habitat choice on a smaller scale differs (Van der Jeugd *et al*., 2001). Observations of colour-ringed birds with known origin indicate that there exists some exchange of, predominantly male, individuals between populations, and a limited amount of gene-flow between the different populations along the east-Atlantic Flyway is therefore likely to occur (Van der Jeugd & Litvin, 2006).

Long-term studies have been initiated within each of the three populations (Fig. 1). In the Baltic, birds breeding in the oldest and largest breeding colony situated at Laus holmar (57°17′N; 18°45′E) off the east coast of the island of Gotland, Sweden have been studied from 1984 to 2007 (Larsson *et al*., 1988, 1998; Larsson & Forslund, 1994; Black *et al*., 2007). During the 20-year study period, this colony increased from 450 to a maximum of 2450 breeding pairs. A more detailed description of the study area can be found in Larsson *et al*. (1988) and Van der Graaf *et al*. (2006a, 2007a, b).

In the Barents Sea population, a colony on the northwest coast of Kolokolkova Bay, near the abandoned settlement of Tobseda, Malozemelskaya Tundra, northern Russia (68°35′N, 52°20′E), has been studied annually between 2002 and 2006 (Van der Jeugd *et al*., 2003; Van der Graaf *et al*., 2004; Eichhorn *et al*., 2006). The colony comprised between 1200 and 2000 breeding pairs during our study. Barnacle geese have bred in the study area since at least 1994 (Syroechkovsky Jr., 1995).

In the North Sea population, barnacle geese were studied between 2004 and 2006 at Hellegatsplaten (51°42′N, 4°20′E), one of the largest colonies in the Delta area in the southwest Netherlands. This colony consists of several breeding sites, mostly situated on islands. The total number of nests varied between 518 and 537 during the 3 study years (own observations) (Pouw *et al*., 2005; Van der Jeugd *et al*., 2006).

Capturing, marking and measurement techniques

In each of the three study populations, moulting flocks of breeding and nonbreeding adult and juvenile barnacle geese were captured annually at moulting localities in July (Baltic and North Sea) and August (Barents Sea) using a rounding-up technique (Ogilvie, 1978). In addition to moult catches, a small number of females was captured with clap nets during incubation. Captured birds were ringed with engraved coloured plastic leg rings and with metal rings. Approximately 5500 individual birds were colour-ringed in the Baltic between 1984 and 2000 (after 2000, no new colour rings were applied during moult catches), 1400 in the Barents Sea between 2002 and 2005, and 420 in the North Sea population in 2004 and 2005 (no new colour rings applied in 2006). Sex was determined by cloacal inspection (Owen, 1980). Captured birds were aged as juveniles or adults that were 1 or more years old. Juvenile birds were measured and weighed upon ringing when they were between 3 and 8 weeks old.

The ninth primary feather, counted descendently, of moulting adult birds and wing length of juvenile and adult birds were measured following Larsson (1996) and Van der Jeugd *et al*. (2003). In the Barents Sea and Baltic populations, ninth primary feathers of moulting adult birds that were captured twice within the same year grew on average 6.98 mm day^{-1} in females ($\mathrm{SE} = 0.13$, $N = 163$; males) and 7.44 mm day^{-1} in males

Table 1 Growth rate of juvenile wings based on regression of wing length on age (age × sex: $F_{1,1020} = 3.76$, $P = 0.05$; age × population: $F_{2,1020} = 63.64$, $P < 0.0001$)

	Females			Males		
	mm day^{-1}	SE	N (R^2)	mm day^{-1}	SE	N (R^2)
Barents Sea^a	8.74	0.64	88 (0.69)	10.03	0.91	87 (0.59)
Baltic^b	8.63	0.40	425 (0.53)	9.10	0.38	405 (0.58)
North Sea^b	7.25	1.56	9 (0.76)	9.55	0.93	14 (0.90)

Letters denote which populations differ significantly from each other.

(SE = 0.15, $N = 124$). There was no difference in growth rate between the populations ($F_{1,184} = 0.01$, $P = 0.97$), but females tended to grow their primaries slightly slower than males ($F_{1,184} = 3.09$, $P < 0.1$). We calculated the start and end dates of the adult wing moult in all three populations by using the length of the ninth primary upon capture and the sex-specific growing rates reported above [see also Larsson (1996)]. Fledging dates of juveniles were calculated using linear regressions of wing length on age (date of capture minus hatch date). Female juveniles grew their wings slower than males, and growth rate of juvenile wings decreased significantly from north to south (Table 1). We assumed that birds were capable of flying slightly before reaching their full-grown wing length (adult males: 420 mm, adult females: 395 mm; juvenile males: 405 mm, juvenile females: 380 mm; own observations).

Reproductive success in relation to lay date

Hatch dates of broods of marked pairs were determined either by direct observations of pairs with young leaving their nests, by estimating the age of newly hatched young on nearby grazing grounds and then backdating (Larsson & Forslund, 1991), or during repeated nest checks during the hatching periods when many chicks were webtagged (North Sea and Barents Sea populations only). When caught as fledglings later during round-ups, hatch dates of these individuals were known. Fledglings without webtags that were colour-marked during round-ups and seen in the company of marked parents during observations made after capture were assigned the hatch date of their parents nest. For some juveniles caught as fledglings, hatch dates could not be assigned using one of these methods. In those cases, we estimated hatch dates using the regression of age on wing length for each sex and population separately for juveniles with known hatch dates (Table 1). In the Barents Sea and North Sea populations, we actively searched for new nests once every 2 or 3 days. In the Baltic, regular nest checks were only performed in 2003 and 2004, but not in other years. Lay date was defined as the day at which the first egg was laid. For incomplete clutches found during egg laying, lay date was estimated as follows: 1 egg, day of discovery; 2 eggs, day of discovery minus 1; 3 eggs, day of discovery minus 3, 4 eggs, day of discovery minus 4; 5 eggs, day of discovery minus 6). This method differs slightly from the one used by Lepage *et al*. (1999) in that we subtracted 1 day more for clutches of three and five eggs.

The median interval between lay- and hatch date for nests where both dates were recorded averaged 30 days without any difference between populations ($F_{2,405} = 0.69$, $P = 0.51$). Although the interval increased with clutch size (0.5 days per egg, $P < 0.0001$), controlling for clutch size did not alter subsequent results because of the large variation in clutch size compared with its seasonal decline, and was therefore ignored. To be able to express reproductive output as a function of lay date, we simply calculated lay date as hatch date minus 30 days in all cases where hatch date was known, but lay date was not known from direct observations (this was done in 129/347 breeding attempts in the Barents Sea, 3224/3423 breeding attempts in the Baltic and 29/136 breeding attempts in the North Sea populations).

Number of fledged young per breeding attempt was defined as the number of young in families with at least one marked parent observed on the day closest to 10 July (within ± 14 days) in the North Sea population, on the day closest to 20 July (within ± 14 days) in the Baltic population, and on the day closest to 14 August (within ± 4 days) in the Barents Sea population. These dates represent the period between 1 and 3 weeks before fledging for most individuals. Breeding attempts that failed at an earlier stage due to predation of eggs or chicks or nest abandonment were assigned zero fledged young. Intraspecific nest parasitism as well as brood mixing after hatching occurred in all populations. In the Baltic, it was found that about 17% of the fledged young are not the true offspring of the adults guarding them (Forslund & Larsson, 1995; Larsson *et al*., 1995). There are currently no data that can confirm these figures for the North Sea and Barents Sea populations. Brood sizes were not adjusted for intraspecific nest parasitism or brood mixing after hatching.

Postfledging survival in relation to lay date

Postfledging survival of individual young was estimated using mark–resighting analyses of observations of marked juveniles on the wintering grounds gathered by a network of nearly 1000 volunteer ring readers. In total, 105, 956 and 608 individuals from two (2004, 2005), 16 (1985–2000) and three (2003–2005) cohorts were available for survival analyses in the North Sea, Baltic and Barents Sea populations, respectively. As the number of cohorts differed between populations and partially referred to different years, birds from each population were analysed separately, using Program MARK (White & Burnham, 1999). All analyses started from a two age-class model with time-dependence, model $\phi_{a \times t}$, $P_{a \times t}$. The first age-class (a1) spanned the period between marking and arrival on the wintering grounds in October–November (Van der Jeugd & Larsson, 1998) and, hence, measured postfledging survival. The second age-class (a2) spanned all subsequent years and measured adult survival after the first winter. Within both age-classes, survival estimates for different years were identified separately. Model selection was based on a modified Akaike's Information Criterion (AICc, (Anderson *et al*., 2000). In addition to AIC, we used the ANODEV procedure in MARK to test for the effect of lay date on postfledging survival. Goodness of fit to the Cormack–Jolly–Seber model was tested using a bootstrap procedure provided in MARK. No adjustments to deviance and AIC were made, as the bootstraps yielded scale parameters ($\hat{c}$) that were less then 1 for each population, indicating a good fit. After resighting rate had been modelled, a number of models for survival was tested to specifically investigate the effect of lay date on postfledging survival (Lebreton *et al*., 1992). This was done by first running a model where survival in the first age-class, that is postfledging survival, was held constant among years, and second, adding individual lay date as a covariate to explain variation in postfledging survival in this model. The ANODEV test including these two models and the global model ($\phi_{a \times t}$, $P_{a \times t}$) specifically tests for the presence of a significant effect of lay date on postfledging survival (Skalski *et al*., 1993). Some additional models were run to check the robustness of the results.

We then calculated the number of young that arrived at the wintering grounds by multiplying the number of young observed *per nesting female* around fledging at the breeding grounds by the predicted postfledging survival probability that corresponded to the particular lay date of those young (if significant relationships with lay date were found). The relationship between lay date and number of fledged young per female was subsequently analysed using separate multiple regressions for each population. Before analyses, lay date was standardized to control for differences in mean lay date among years. We tested for quadratic relationships by including both lay date and (lay date)^2 as explanatory variables.

Food quality

The quality of forage biomass was determined by taking samples of leaf tips of the main forage species Red Fescue *Festuca rubra*, common salt-marsh grass *Puccinellia maritima* and creeping bent grass *Agrostis stolinifera* in the Netherlands and the Baltic region, creeping salt-marsh grass *Puccinellia phryganodes* and Hoppner's sedge *Carex subspathacea* in the Barents Sea region (Van der Graaf *et al*., 2006b). Samples were taken at roughly 10-day intervals throughout the entire breeding season in 2003 in the Barents Sea, in 2003 and 2004 in the Baltic, and in 2004 in the North Sea population. At the same time, samples were also taken at a major spring staging site in the Netherlands (Schiermonnikoog; Van der Graaf *et al*., 2006b). Samples were dried at 60 °C for 48 h and analysed for nitrogen (N) content using an automated CHNS-analyser (Interscience EA 1110, New York, New York, USA).

Statistics

All statistics were performed using SAS version 8.2 (SAS Institute, Cary, North Carolina, USA) and SPSS version 12.0.1 (SPSS Inc., Chicago, Illinois, USA). All data presented include mean ± SE. The relationships between date and N content, and standardized lay date and fledgling production were analysed using multiple regressions including linear as well as quadratic terms. Quadratic terms were removed when not significant.

Selection differentials were constructed for each population by calculating the difference between the population mean lay date and the mean lay date of all breeding attempts that were successful, weighted for the number of young produced and their postfledging survival. Selection differentials were standardized by dividing by the standard deviation of lay date in each population (Falconer, 1989).

Results

Timing of reproduction and moult

There were large differences in the timing of reproduction and moult between the populations. On average, eggs hatched on 11 July in the Barents Sea, on 29 May in the Baltic and on 25 May in the North Sea populations.

Thus, whereas there is only a small difference between the two temperate populations, hatching in these populations takes place ca. 6 weeks earlier compared with the Barents Sea population (Fig. 2). Also, the range of lay and hatch dates increased from north to south. In the Barents Sea population, 90% of all nests were initiated within a period of 12 days, compared with 15 days in the Baltic and 36 days in the North Sea population.

Timing of wing moult did not differ as much as hatch date did. In the Barents Sea population, nonbreeders started their wing moult on average on 15 July, whereas families leading broods started ca. 2 weeks later at 27 July (Fig. 2). The bimodal pattern in the start of wing moult is absent in the Baltic and also in the North Sea population (Fig. 2), although both breeders and nonbreeders were present in the samples. In these populations, wing moult started on average around 1 July, 2–4 weeks earlier than in the Barents Sea population.

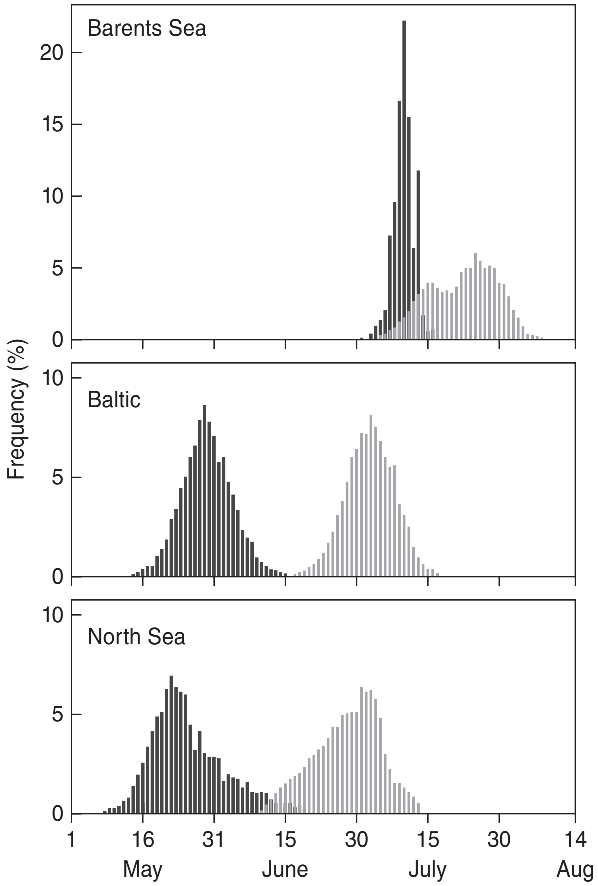

Fig. 2 Timing of hatching (black bars) and start of wing moult (grey bars). Note the bimodal pattern in the start of wing moult in the Barents Sea population caused by breeders moulting later than nonbreeders (see text).

Juvenile birds grew their wings slightly more slowly in temperate populations compared with the Barents Sea population (Table 1). However, because of the much longer time span between hatching and start of wing moult, juveniles fledged on average 2 weeks earlier relative to the moment their parents regained flight ability in temperate populations. Hence, the synchronizations of wing moult of adults and fledging of young that was observed in the Arctic disappeared (Table 2).

Food quality

In the Barents Sea population, N content of food plants showed a peak around 20 June, ca. 2–3 weeks before hatching (N content $=-29.040+0.3767\times\text{date}-0.0011\times\text{date}^2$; date: $F_{1,76}=22.40$, $P<0.0001$; date^2: $F_{1,76}=26.08$, $P<0.0001$). In the Baltic, N content was highest around 20 April, ca. 5 weeks before hatching, although the peak was less pronounced compared with the Barents Sea population (N content $=-0.850+0.0625\times\text{date}-0.0003\times\text{date}^2$; date: $F_{1,148}=9.61$, $P=0.002$; date^2: $F_{1,148}=13.15$, $P<0.001$). There was no effect of year on N content ($F_{1,146}=0.96$, $P=0.33$; year × date: $F_{1,146}=0.42$, $P=0.52$). In the North Sea population, no peak in N content was apparent, and N content declined throughout the season (breeding site: N content $=6.073-0.0214\times\text{date}$; date: $F_{1,37}=22.49$, $P<0.0001$, date^2: $F_{1,36}=0.28$, $P=0.60$; Staging site: N content $=5.535-0.0233\times\text{date}$; date: $F_{1,69}=72.18$, $P<0.0001$, date^2: $F_{1,68}=1.20$, $P=0.28$,). Presumably, N content already had reached its highest value before measurements started in March, at least 2 months before hatching. N content was higher at feeding sites in the study colony compared with a staging site in the North of the Netherlands, where barnacle geese do not breed (Fig. 3).

Table 2 Calculated median dates (see text) at which juveniles fledged and parents regained flight ability in three populations of barnacle geese *Branta leucopsis*

	Fledging	End of moult	Difference	*N*	*Z*	*P*
Barents Sea	31 Aug	28 August	+ 3 days	861, 924	6.8359	< 0.0001
Baltic	29 July	8 August	−10 days	3777, 10 493	−45.4520	< 0.0001
North Sea	23 July	3 August	−11 days	131, 214	−7.9625	< 0.0001

Statistical significance based on median two-sample tests. *N* refers to the number of juvenile and adult birds, respectively, for which fledging date and end of wing moult could be calculated.

Production of fledged young and selection on timing of breeding

In the North Sea and Barents Sea populations, one common resighting probability could be used for all years whereas in the Baltic, resighting probabilities were year-specific (Table 3). In the North Sea population, postfledging survival was very high, on average 97% (± 1.90%), and was not related to lay date (ANODEV $P = 0.41$; Table 3; Fig. 4). In the Baltic and Barents Sea populations, postfledging survival significantly declined with lay date (ANODEV, $P = 0.006$ and 0.005, respectively; Table 3; Fig. 4). Including annual variation in survival in the first age-class in addition to the effect of lay date in the Baltic yielded an even better model (ΔAICc: −17), but the decline in postfledging survival with lay date was virtually identical (−0.75 vs. −0.73,

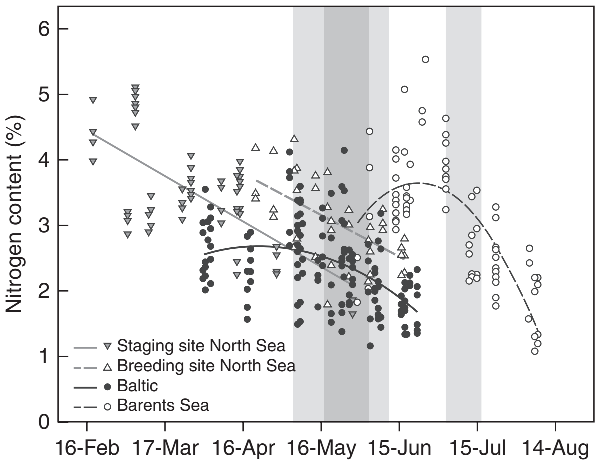

Fig. 3 Food quality (N content) at staging and breeding sites of the three populations of barnacle goose *Branta leucopsis* [grey dots (staging site) and grey squares (breeding site) and dashed lines: North Sea; black dots and solid line: Baltic; white dots and stippled line: Barents Sea]. Shaded boxes indicate the periods during which 90% of eggs hatch in the three populations. Note that the hatching period of the Baltic population (BAL) falls within that of the North Sea (NL) population.

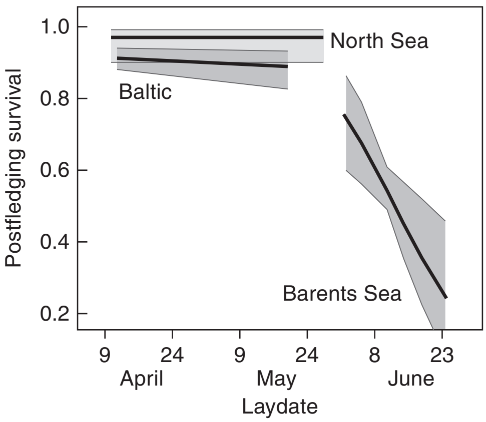

Fig. 4 Postfledging survival in three populations of barnacle geese *Branta leucopsis* in relation to lay date. Bold lines indicate postfledging survival, shaded areas represent 95% confidence limits. Lines are based on the analyses presented in Table 3. The slopes of the relationships (β-values) are Barents Sea: −9.90 (± 2.74); Baltic: −0.73 (± 0.22); North Sea: no relationship found (see text).

Table 3 Modelling postfledging survival in three populations of barnacle geese *Branta leucopsis* using capture–resighting analyses in Program MARK (see text)

Model name	ΔAICc	Likelihood	N.P.	Deviance
Barents Sea (608 individuals, three cohorts)				
Φ(*a* × *t*),P(*a* × *t*)	10.2767	0.0042	11	1994.23
Φ(*a* × *t*),P(..)	4.2845	0.0833	7	1996.40
Z(*a*;a1 = laydate,a2 = constant),P(..)	0.0000	1.0000	4	1998.19
Φ(*a*),P(..)	13.0456	0.0015	3	2013.25
Baltic (956 individuals, 13 cohorts)				
Φ(*a* × *t*),P(*a* × *t*)	1.1090	0.5744	71	11 622.73
Φ(*a* × *t*),P(..)	424.4903	0.0000	38	12 113.67
Z(*a*;a1 = laydate,a2 = *t*),P(*a* × *t*)	0.0000	1.0000	57	11 650.39
Φ(*a*;a1 = constant,a2 = *t*),P(*a* × *t*)	18.4930	0.0000	56	11 670.94
North Sea (105 individuals, two cohorts)				
Φ(*a* × *t*),P(*a* × *t*)	6.1809	0.1368	7	190.71
Φ(*a* × *t*),P(..)	3.9490	0.4617	5	192.70
Φ(*a*;a1 = laydate,a2 = constant),P(..)	1.7944	0.3114	4	192.63
Z(*a*),P(..)	0.0000	1.0000	3	192.91

Φ denotes survival, P resighting rate, *a* age (two age classes, a1 = fledging to first winter, a2 = after first winter), and *t* time (year). ΔAICc: difference in the corrected Akaike's Information Criterion between models. N.P., number of parameters. For each population, the best model is given in bold.

Fig. 4), illustrating the robustness of these results. In the Baltic, postfledging survival averaged just over 90% (± 1.24%). In the Barents Sea, postfledging survival was much lower than in the two temperate populations, averaging 55% (± 2.65%) (Fig. 4).

We calculated the number of young *per nesting attempt* that arrived at the wintering grounds as outlined in the methods, combining the significant relationships derived from the survival analyses (Table 3; Fig. 4) with data on the production of fledged young from the breeding grounds. In the North Sea and Baltic populations, the number of fledged young arriving at the wintering grounds declined linearly with standardized lay date, whereas the relationship between standardized lay date and number of fledged young was quadratic in the Barents Sea population (*despite* the strong decline of postfledging survival with lay date), with most surviving young being produced at intermediate lay dates (Fig. 5, Table 4). In the North Sea and Baltic populations, most birds started egg laying at the moment when reproductive prospects had already declined, whereas the median date at which birds in the Barents Sea population laid their eggs corresponded well with the date that yielded the highest number of surviving young (Fig. 5). In the Baltic, the majority of lay dates were estimated from hatch dates. However, as complete clutch predation in the Baltic is low and there was no quadratic relationship between lay date and nest success (number hatched young = 3.86−0.063 young × lay date, lay date: $F_{1,112} = 4.81$, $P = 0.03$; lay date^2: $F_{1,111} = 0.01$, $P = 0.92$), this cannot influence the results.

Consequently, the standardized selection differential (see 'Material and methods') was close to zero (0.035) in the Barents Sea population, indicating weak or no (directional) selection on lay date. In the Baltic, and especially the North Sea population, however, there was considerable selection for earlier breeding with standardized selection differentials of −0.305 and −0.663, respectively.

Advancement of timing of breeding in the Baltic

In the Baltic, population mean hatch date advanced between 1985 and 2004 (Fig. 6a; $r = -0.47$, $P < 0.05$). We calculated 'growing degree days' (GDD), a frequently used measure in studies of spring phenology (Botta *et al.*, 2000), based on daily temperature data from the Baltic from January through April, taken from Klein-Tank (2002). GDD explained over 80% of the variation in lay date (Fig. 6b; $r = -0.90$, $P < 0.0001$), and GDD increased over time ($r = 0.45$, $P < 0.05$). After correcting for this increase, the remaining advancement in lay date was reduced to 3 days (Fig. 6c; $r = -0.58$, $P = 0.01$). During the same period, directional selection on lay date increased (Fig. 6d; $r = -0.60$, $P = 0.01$).

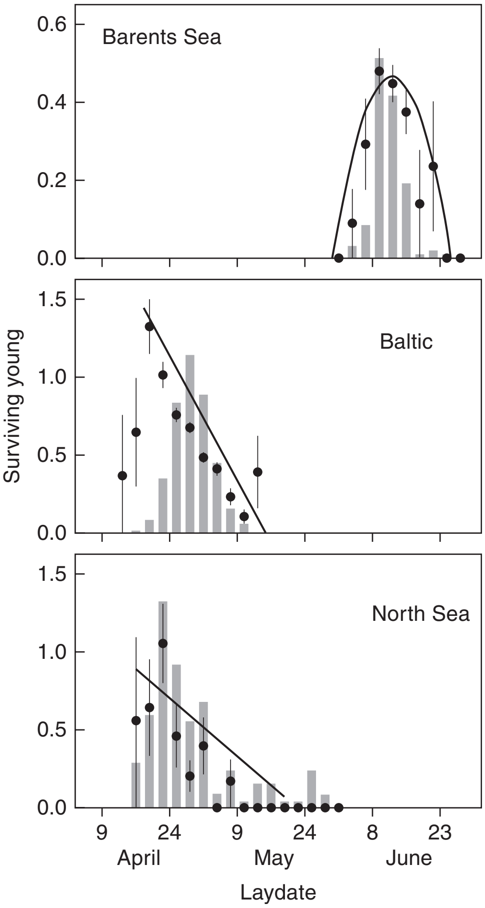

Fig. 5 Timing of reproduction in relation to fitness in three populations of barnacle geese *Branta leucopsis*. Black dots indicate the number of fledged young per nesting attempt surviving to arrival on the wintering grounds in their first winter (means for 3-day intervals), bars denote standard error. Regression lines are based on the analyses presented in Table 4. Grey bars indicate the frequency of lay dates observed in each population.

Discussion

Why do temperate-breeding birds breed too late?

We found that recently established temperate populations of barnacle geese have advanced their reproductive season considerably compared with their Arctic-breeding conspecifics. However, the advancement of lay and hatch dates was not enough to fully exploit the peak in food quality, which occurs much earlier in the season, and is generally lower, at lower latitudes. On average, food quality was highest between 1 and 2 months before hatching, and newly hatched chicks in the Baltic were confronted with a food supply

Table 4 Effect of lay date on the number of young per nesting attempt arriving at the wintering grounds, using linear regression

	Lay date			(Lay date)^2			
	Estimate	t	P	Estimate	t	P	N
Barents Sea	0.380	2.50	0.01	−0.003	−2.56	0.01	347
Baltic	−0.053	−11.52	$<$0.0001	0.000	0.72	NS	3423
North Sea	−0.025	−2.77	0.006	0.000	0.39	NS	136

When (laydate)^2 was not significant, it was removed from the model, and the remaining linear relationship indicates directional selection on lay date. Where (laydate)^2 is significant, the relationship is quadratic, indicating stabilizing selection on lay date.

that was ca. 40% lower in quality compared with the food of chicks hatched in the Arctic, where hatching closely approaches the peak in food quality (Fig. 3). Food quality during hatching in the North Sea population, although already declining from the spring peak, was comparable with that in the Arctic. However, the N contents of food plants at our study site were unusually high due to the management features of this reclaimed area, and are not typical for more representative sites at this latitude (e.g. compare the staging site in Fig. 3). Food quality, measured as the N content of forage plants, is an important determinant of gosling growth and survival (Cooch *et al*., 1991; Larsson & Forslund, 1991; Larsson *et al*., 1998) and N content of forage plants can serve as an index of the high-quality food needed for gosling growth.

Postfledging survival of individual goslings (Fig. 4) declined steeply with lay date in the Barents Sea population. However, the decline was only moderate in the Baltic, and absent in the North Sea population. The compound effect of nesting success and survival of goslings until fledging, modulated by postfledging survival is assembled in Fig. 5 and is our crown witness regarding these lay date effects on fitness. Despite the steep decline in postfledging survival, the mean number of surviving young per nest was at its maximum around the median standardized lay date in the Barents Sea population because both hatching success and prefledging survival showed highest values at intermediate lay dates, as was also found in other Arctic geese and other waterfowl (Findlay & Cooke, 1982; Brinkhof *et al*., 1993; Lepage *et al*., 2000). In contrast to the close match in the Barents Sea population, the median standardized lay date for both temperate populations (Baltic and North Sea) occurs at the time well beyond the point where the mean number of surviving young per nest was at its maximum. As a result of these effects, selection on lay date was stabilizing in the Arctic, whereas there was strong directional selection for earlier breeding in the Baltic and North Sea populations.

As barnacle geese have only recently colonized temperate environments, it is possible that they have not yet been able to adapt fully to the earlier springs at these latitudes, and therefore currently lag behind. Adaptation can occur as a result of phenotypic plasticity or through a microevolutionary response to directional selection on lay date (Visser, 2008). In the Baltic, population mean lay date has indeed advanced between 1985 and 2004. However, during the same period it has become warmer and much of the observed advancement in lay date could be attributed to this. Shifts in lay date have been observed in many other bird species (Crick *et al*., 1997; McCleery & Perrins, 1998), and most likely result from phenotypic plasticity, but do not necessarily mean that birds are perfectly adapting to the warming climate (Visser, 2008). After correcting for the effect of warmer springs, the remaining advancement in lay date of Baltic barnacle geese can easily be explained by the changed age-distribution of the breeding birds (Forslund & Larsson, 1992), and does not have to be the result of an adaptation, by whatever mechanism, to the earlier springs that occur at temperate latitudes compared with those in the Arctic. In fact, directional selection on lay date *increased* over the same period. Hence, the rate of adaptation, if any, in the Baltic population is insufficient to keep up with earlier springs. Similar results have been found for great tits *Parus major* (Visser *et al*., 1998) and pied flycatchers *Ficedula hypoleuca* (Both & Visser, 2001) breeding in the Netherlands.

There are several explanations as to why the majority of individuals in avian populations fail to breed in time. The most relevant one here is the 'constraint hypothesis' (Lack, 1966; Perrins, 1970; Price & Liou, 1989; Nager *et al*., 2000), which revolves around the idea that only a minority of females is able to monopolize the limited amount of food early in spring and can thereby reach a nutritional state that is needed for egg production sufficiently early in the season, whereas most females are constrained and forced to delay their breeding until after the best time for offspring rearing. We believe that a similar reasoning can explain the fact that the recently established southern populations of the barnacle goose breed too late and, as yet, have failed to advance the timing of breeding towards the optimum, while lay date is optimal with respect to parental fitness in the Barents Sea population, as has also been suggested in other high-Arctic nesting geese (Lepage *et al*., 2000; Black *et al*., 2007).

Arctic-breeding geese and other herbivorous waterfowl travel along a climatic gradient during spring migration to their northern breeding sites, thereby

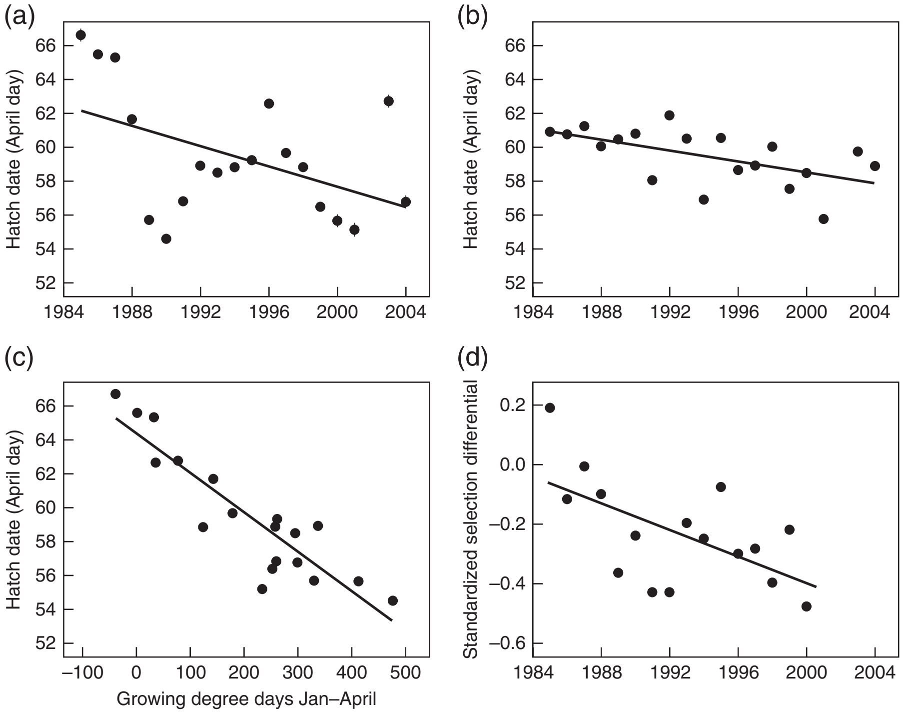

Fig. 6 Annual variation in mean hatch date in the Baltic population of barnacle geese *Branta leucopsis*. (a) Population mean hatch dates (bars denote standard errors) between 1984 and 2004. Hatch date advanced by ca. 6 days during the 20-year study period. (b) Population mean hatch dates as a function of the number of growing degree days (GDD) (see text). Birds lay earlier following warm winter and springs. (c) Population mean hatch dates between 1984 and 2004 corrected for the effect of GDD. Corrected hatch date advanced by ca. 3 days during the 20-year study period. (d) Annual standardized selection differentials (see text) increased indicating increasing selection for earlier breeding during the study period.

taking advantage of the spring flush of forage plants at each stopover site. This idea is formally known as 'the green wave hypothesis' (Drent *et al*., 1978; Owen, 1980; Van der Graaf *et al*., 2006b). It enables the birds to exploit the early spring growth along the flyway and gradually accumulate body stores from the food they encounter at each site (Madsen & Klaassen, 2006). When they finally arrive in their Arctic-breeding grounds, they are ahead of the wave of grass growth and are forced to draw, at least partly, on their capital of stored resources for egg formation, enabling them to breed earlier and allocate more of the local resources to the growth of their young. Studies using stable isotopes indeed showed that Arctic-breeding geese often use a mixed capital/income breeding strategy (Drent *et al*., 2006). Results from tracking studies in six goose species also underline the conclusion that egg formation commences along the flyway before arrival at the nesting colony (Drent *et al*., 2007). Temperate-breeding birds do not have this advantage of exploiting successive waves of spring growth, forcing them to postpone breeding until adequate condition is gained from local resources. For avian herbivores that rely on a seasonal food source, travelling to the Arctic may therefore be an evolutionary escape from the problem that many temperate-breeding birds face: how to time the breeding season in relation to the peak in food supply?

Intriguingly, another goose species, the greylag goose *Anser anser*, of which the historical range has included temperate areas for a much longer period of time (Madsen *et al*., 1999) is capable of breeding sufficiently early. In this species, eggs hatch already in March, when food quality is still high (Kamp & Preuss, 2005). They owe this to a combination of a broader diet, which makes them less dependent on a single food peak (Amat, 1995), and their larger body size, which enables them to produce a full clutch from body stores and thus makes them less dependent on exogenous food sources (Klaassen *et al*., 2006).

Why do temperate-breeding birds not moult earlier?

Timing of wing moult differed much less between populations compared with timing of reproduction. The lack of advance in the timing of wing moult might be due to a genetic constraint. Photoperiod is the principal environmental cue that is used to time major events in the annual cycle of animals across a wide variety of taxa (Bradshaw & Holzapfel, 2007; Dawson, 2008). Photoperiod is much longer in the original, Arctic-breeding area, and barnacle geese may need to genetically change before being able to moult earlier. Although lay date seems to be more flexible, photoperiod might also be important in explaining the inability of temperate-breeding barnacle geese to breed sufficiently early. Currently, the role of photoperiodism in genetic responses to climate change is not clear (Bradshaw & Holzapfel, 2008).

The smaller difference in the timing of moult between populations might also be the result of relaxed selection on early moulting because of the longer season at lower latitudes, in contrast to the strong selection on early breeding. Postponing moult relatively to the hatching period also increases the time window during which parents can replenish reserves that were lost during incubation. In Arctic-breeding barnacle geese, this time window is only one-third of that of their temperate-breeding counterparts [see also Loonen *et al.* (1997)]. Possibly as a result of this, barnacle geese in the Barents Sea population that were leading young postponed the start of wing moult by ca. 2 weeks compared with nonbreeders whereas in temperate populations, there was no such difference in timing (Fig. 2). Moreover, it might be *more* advantageous to delay moulting in temperate populations compared with Arctic ones due to reduced feeding opportunities before moult. Food quality rapidly declined throughout the season, and was lower at the onset of moult compared with the Arctic (Fig. 3), while feeding time is also reduced due to the shorter day length at southern latitudes.

As a byproduct of wing moult and breeding time changing at different rates, juveniles were able to fly almost 2 weeks before their parents regained flight ability in the North Sea and Baltic populations. In the Barents Sea population, the date at which juveniles and parents could fly was very similar. Hence, the synchronization between wing moult and fledging has decreased in temperate populations. At present, we do not know whether this represents a cost to parents or young, and the whole issue of changes in the timing of moult clearly needs more work.

Explaining the recent range expansion

Barnacle geese expanded their breeding range during a period when the flyway population increased 20-fold. It is likely that the same factors that led to the increase of the population were also responsible for the establishment of temperate breeding colonies. A combination of improved feeding conditions due to changes in agricultural practice in the wintering areas (Van Eerden *et al.*, 1996, 2005; Abraham *et al.*, 2005; Fox *et al.*, 2005; Gauthier *et al.*, 2005) and reduced prosecution which lead to reduced mortality and disturbance (Ebbinge, 1991) are the main factors held responsible for the increase in many populations of waterfowl in the northern hemisphere. At the same time, these changes will have led to a situation where geese now are able to reach adequate breeding conditions earlier in the season that enables them to produce a clutch and incubate it successfully at lower latitudes. Increasing density-dependent effects in the traditional breeding grounds due to the growing population might be an additional factor that triggered birds to seek greener pastures (Van der Graaf *et al.*, 2006a) but can hardly explain the launch of the Baltic breeding population that already took place in 1971. Van der Graaf *et al.* (2006a) could not find any direct indications that changes in land use in the Baltic might explain the establishment of the Baltic population, although breeding in the Netherlands very likely was influenced by such changes. The juxtaposition of rich soils and brackish water in the reclaimed area in the SW Netherlands combined with summer grazing by livestock contribute to the high food quality at our study site (Vulink, 2001). Food quality is considerably lower at a spring staging site in the north of the Netherlands where breeding birds are absent (Fig. 3).

All recently established breeding areas are situated within the barnacle goose flyway, that is they are confined to historical wintering areas and staging grounds of the species. Prior knowledge of potential breeding areas therefore seems to be important for the species. Although the breeding population in the traditional breeding area has extended its range with increasing densities, there seems still ample suitable breeding habitat vacant (Kalyakin, 1986, 2001). Interestingly, no eastward expansion has been reported so far [but see Pokrovskaya & Gavrilo (1998)]. Syroechkovsky Jr. (1995) even speculates that the westward expansion within the Russian Arctic observed during the last two decades could be in fact a recolonization of former breeding sites. Taking this idea further one might also ask whether the temperate sites were in fact part of the species' breeding distribution in historical times, or, even prehistorical times (Ploeger, 1968). Because of the exceptional vulnerability of geese and other waterfowl during the flightless period, they would then have become extinct when the human population increased. Unfortunately, to our knowledge, no information is available to test this idea. As a result of widespread use of pesticides and prosecution, natural predators were still relatively rare during the 1970s and 1980s, when most temperate barnacle goose populations were established. This predator lull might well have facilitated the initial success of these populations.

Conclusions

Temperate-breeding populations of barnacle geese that have been established recently are not completely adapted to the environmental circumstances that prevail at low latitudes, and lay too late to fully exploit the peak in food availability that occurs much earlier at lower latitudes. This is most probably because Arctic-breeding geese gradually accumulate body stores from the food they encounter during spring migration, which allows them to breed earlier and allocate more of the local resources to the growth of their young. Temperate-breeding birds, however, are forced to postpone breeding until adequate condition is gained from local resources. Nevertheless, absolute fitness and, hence, population growth rate in at least the North Sea population is higher than that for the Arctic population as a whole. However, it is not possible to compare absolute fitness between a recently established population and an older one because of strong density-dependent effects (Larsson & Forslund, 1994). Reproductive output and survival of the Baltic population were initially very high, but have now been greatly reduced to levels where the population has become stable or is even declining (K. Larsson, unpublished results).

Although the observed range expansion in barnacle geese is not due to climate change, the observed mismatch between reproduction and food supply in temperate regions is highly relevant in the light of global change. Despite strong selection, Baltic barnacle geese have not shifted their timing of breeding relative to the advancing spring phenology, and adaptation to earlier springs apparently takes a long time in the barnacle goose. Global temperatures are predicted to increase, and the increase is predicted to be most extreme in Arctic areas (IPCC, 2001). This would mean that, in line with our results for temperate populations, barnacle geese as well as other Arctic-breeding geese will be confronted with much earlier springs also within their original breeding range at higher latitudes, and they might not be able to keep up with this shift on the short term.

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