

Adjustment of the annual cycle to climatic change in a long-lived migratory bird species

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Abstract Climate change has advanced the phenology of many organisms. Migratory animals face particular problems because climate change in the breeding and the wintering range may be asynchronous, preventing rapid response to changing conditions. Advancement in timing of spring migration may have carry-over effects to other parts of the annual cycle, simply because advancement of one event in the annual cycle also advances subsequent events, gradually causing a general shift in the timing of the entire annual cycle. Such a phenotypic shift could generate accumulating effects over the years for individuals, but also across generations. Here we test this novel hypothesis of phenotypic response to climate change by using long-term data on the Arctic tern *Sterna paradisaea*. Mean breeding date advanced by almost three weeks during the last 70 years. Annual arrival date at the breeding grounds during a period of 47 years was predicted by environmental conditions in the winter quarters in the Southern Ocean near the Antarctic and by mean breeding date the previous year. Annual mean breeding date was only marginally determined by timing of arrival the current year, but to a larger extent by arrival date and breeding date the previous year. Learning affected arrival date as shown by a positive correlation between arrival date in year ($i + 1$) relative to breeding date in year (i) and the selective advantage of early breeding in year (i). This provides a mechanism for changes in arrival date being adjusted to changing environmental conditions. This study suggests that adaptation to changing climatic conditions can be achieved through learning from year to year [Current Zoology 55 (2): 92 – 101, 2009].

Key words Arctic tern, Arrival date, Climate change, Migration, Southern Oscillation, *Sterna paradisaea*

Rapidly changing environmental conditions pose special problems for organisms because they are generally assumed to be adapted to prevailing conditions (Møller et al., 2004a; Root et al., 2003; Walther et al., 2002). A case in point is the recent dramatic increase in temperature throughout the world, but mainly in temperate and polar regions during the last century, with particularly large increases during the last 30 years (Houghton et al., 2001). Organisms typically reproduce at the most favorable time of the year, when food abundance peaks (Lack, 1954). With extensive changes in environmental conditions we should expect the timing of reproduction also to change, as has been demonstrated for numerous organisms, but not for all (Crick and Sparks, 1999; Dunn and Winkler, 1999; Przybylo et al., 2000; Sanz et al., 2003; Sheldon et al., 2003; Pulido and Berthold, 2004; review in Dunn, 2004). Specific studies of response to changes in local environmental conditions have found a good match between patterns of change in environmental conditions and change in phenology (Dunn and Winkler, 1999; Sanz, 2002, 2003; Sæther et al., 2003; Visser et al., 2003; Both et al., 2004), providing evidence of fine scale patterns of phenological

change matching fine scale patterns of climate change.

Change in breeding date may arise because of phenotypic plasticity, micro-evolutionary response or gene flow (Møller and Merilä, 2004; Pulido and Berthold, 2004). First, a plastic response implies that individuals adjust to changes in environmental conditions by simply changing their timing of reproduction according to their specific reaction norm. This mechanism assumes that the reaction norms will allow an adaptive response even under the high degree of current climate change that may exceed the conditions that have provided the selective regime under which current reaction norms evolved. Second, a micro-evolutionary change implies that populations respond to change in environmental conditions because the effects of natural selection cause the distribution of genotypes in the population to change. Third, directional gene flow from southern to more northern populations would allow individuals in these more northern populations to breed earlier than would otherwise have been the case. There is some empirical evidence for the first of these two mechanisms (Pulido and Berthold, 2004).

Migratory species constitute a group of animals that are of particular interest because migrants and other

species with complex life cycles have to simultaneously adapt to several different environments. Migrants live in both the breeding and the wintering grounds, but also have to survive the migration period. If environmental conditions are not synchronized in these different environments, the environmental cues that would allow a response to climate change may not be present. This problem may be resolved in three different, but not necessarily exclusive ways. First, migration may act as a constraint on adaptation to changing environmental conditions. For example, Both and Visser (2001) have indicated for the pied flycatcher *Ficedula hypoleuca* that advancement of laying date is constrained by arrival date. Although it would be selectively beneficial to start breeding earlier, this is impossible because of late arrival. Hence, migration schedules may constrain breeding dates. Second, selection may act differently on individuals of the two sexes, with males responding more strongly to climate change than females because males generally acquire greater advantages from early arrival to the breeding grounds than females (Møller, 2004). Spottiswoode et al. (2006) have shown that sexual selection may constrain adaptation of spring arrival to climate change. Under this scenario, sexual selection as reflected by the degree of sex difference in arrival date may constrain adaptation to climate change. Third, the entire annual cycle could be advanced due to earlier reproduction. Advanced timing of reproduction would also cause the breeding season to finish earlier, thereby allowing early autumn migration, early molt and hence early spring migration. This would eventually result in breeding date also being advanced the following year, causing the entire annual cycle to be advanced. The effects of such a change could accumulate over the years, but also across generations if timing of breeding was partly determined by timing of fledging. We could imagine two different mechanisms. (1) The simplest mechanism would be that timing of events early during the annual cycle simply had carry-over effects to later events, with timing initially determined by the hatching date of an individual, and that such effects would accumulate over the lifespan of an individual. This mechanism could also account for transfer across generations because early breeding adults would have offspring with early hatching, early autumn migration, early molt and hence early spring migration. Thus, this mechanism relies on hatching setting the clock for subsequent events in the life of an individual. (2) Learning could affect individual responses to timing of breeding if individuals that bred late under environmental conditions that favored early breeding advanced their timing of breeding the following year, if environmental conditions during that year were similar to those during the previous year as is the case with continuously increasing spring temperatures each year in many parts of the arctic and temperate climate zones. Such learning

effects on timing of breeding have been demonstrated experimentally (Grieco et al., 2002). Interestingly, changes in the timing of events in the annual cycle as a consequence of carry-over effects would not require any specific evolutionary change, but only a phenotypic adjustment in the timing of the annual cycle. Although animals have an innate circannual rhythm, as shown by experiments in which animals are kept under constant environmental conditions (Gwinner, 1986), this cycle can be phenotypically adjusted by input from environmental cues (Coppack and Pulido, 2004). Laboratory studies in passerines have suggested strong effects of hatching date on fall migration, although there is no evidence of carry-over effects on spring migration (Coppack and Pulido, 2004). There are only a few field studies suggesting carry-over effects from year to year (Wegglar, 1997; Forstmeier, 2002). Becker et al. (2008) have recently shown that spring arrival date in the close related common tern *Sterna hirundo* has a strong effect on age at first reproduction. This hypothesis (that the entire annual cycle could be advanced due to earlier reproduction in previous years allowing earlier start of molt, migration and breeding) is not to the best of our knowledge described previously, nor has it been subject to empirical test.

The aim of this study was to test the hypothesis that adaptation to climate change occurs as a consequence of a change in the timing of the annual cycle. We used the Arctic tern *Sterna paradisaea* for this test because this species is the migrant with the longest migrations recorded for any living bird, with annual displacements of up to 44000 km, and more than one million kilometers during the lifetime of an individual (Berthold, 2001). More specifically we tested the predictions that (1) arrival date to the northern breeding grounds was explained by conditions in the breeding and winter quarters. Numerous studies have shown strong responses in arrival date to climate change (review in Lehikoinen et al., 2004), but much less are known about the relative importance of climate change in the breeding and the wintering grounds. Furthermore, we tested (2) whether breeding date is best explained by arrival date in the current or the past breeding seasons. If timing of breeding was determined by timing of migration, we would expect arrival date to account for timing of reproduction. Furthermore, if adaptation to climate change is determined by a change in the timing of the annual cycle, we would expect (i) breeding date in the previous year to determine arrival date in the current year, and (ii) arrival date and breeding date in the previous year to determine breeding date in the current year due to carry-over effects from the previous year. The latter effect could arise due to reproductive costs from mistiming of breeding relative to food availability in the previous year, or from learning effects as described above. (3) If learning is involved in

decisions about timing of reproduction in response to climate change, we can make the prediction that arrival date in year $(i + 1)$ should be negatively correlated with the selection differential in year (i) . In other words, individuals should adjust their timing of breeding to the previously experienced environmental conditions because by doing so, they would improve their reproductive output. An effect of learning will only be adaptive in an environment that provides information about the conditions during the subsequent reproductive event, and changes in timing of breeding in Arctic terns has consistently been for earlier reproduction during the last 70 years (Møller et al., 2006, 2007). Such a learning effect would be particularly likely in long-lived species that may continue to acquire information about their environment throughout their life. To this end we used long-term data on spring arrival and breeding date of Arctic terns in Denmark together with information on environmental conditions in the northern breeding grounds and the Antarctic winter quarters.

Arctic terns are coastal seabirds breeding in large parts of the Arctic and temperate zones of the northern hemisphere (Cramp, 1985; Hatch, 2002). Adults arrive from their Antarctic winter quarters to the Danish breeding grounds in March – May, starting laying eggs by late April. Eggs are laid daily, and a single clutch of 1 – 3 eggs, on average 2.66 eggs, is produced, although replacement clutches in case of failure can be laid until July. Incubation lasts 22.2 days and young are fully able to fly after 22.5 days (Cramp, 1985; Hatch, 2002). The main food is small fish, crustaceans and other marine invertebrates (Cramp, 1985; Hatch, 2002). Arctic terns start leaving the Danish breeding grounds in July – August. The annual molt takes place in the winter quarters and lasts on average five months (from late September or early October to February – March), thus extending the entire period when the birds are in the winter quarters (Ginn and Melville, 1983; Cramp, 1985; Voelker, 1997; Hatch, 2002). The annual migration distance exceeds 40000 km, with the winter being spent in the southern oceans around the Antarctic, with main concentrations in the pack-ice zone between 30° and 150° E (Salomonsen, 1967). Previous studies of the Arctic tern have shown that breeding date has advanced by several weeks during the last 70 years, as environmental conditions in the Antarctic winter quarters and the temperate zone breeding areas have changed (Møller et al., 2006, 2007). This change in breeding date was associated with a change in selection favoring early breeding in recent years, while favoring late breeding at the beginning of the 20th century (Møller et al., 2006, 2007).

1 Materials and methods

1.1 Data sets

We estimated arrival date to the breeding grounds by relying on long-term information collected by the Ornithological Archives of Northern Jutland. This depository has stored observations of birds for over 35 years with data collection going back even further due to note books of a large number of amateurs having been entered subsequently. Amateurs submit their observations on standard cards that are entered into a computer system. These amateurs observe birds throughout the year with little annual variation in effort (Møller, 1979). The number of observers each year has exceeded 100 the last 30 years. Arctic terns are readily observed upon arrival because they fish, rest and display near the coast close to the actual breeding grounds. Because many such sites are preferred bird watching sites, these observations will provide information about annual change in arrival date to the breeding grounds. Information about migration may be biased due to sampling effort. We tested for such effects by analyzing the date for the first observation each year and the date when the tenth Arctic tern had been observed, under the assumption that the date with the tenth individual would be less subject to sampling error. Whether a single early migrant is observed will be subject to large sampling error, while the bias for the tenth or any later observation will be subject to much less bias (Lehikoinen et al., 2004), as a consequence of the central limit theorem. We cross-validated our estimates of arrival dates by using a unique data set on arrival dates collected by the bird ringer A. Schat Kielberg during 29 years between 1935 and 1976. A. Schat Kielberg lived close to several breeding colonies in the Limfjord area, where he daily searched for arriving Arctic terns each year. If the arrival data collected by amateur bird watchers reflected true arrival dates, unbiased by sampling effort, we should expect a strong positive correlation with the first arrival dates recorded by A. Schat Kielberg.

The Danish Tern Group was established to ring terns throughout all suitable sites in Denmark during 1970 – 1985. This working group also collected all information on ringing of terns prior to, during and following 1970 – 1985, providing information for the years 1957 – 1998 used for the present study. As an estimate of breeding date we used information on ringing dates for all Arctic tern young reported to the Ringing Centre of the Zoological Museum, Danish Ornithological Central, and all information obtained by the Danish Tern Group was also reported to us directly by bird ringers. The total sample of young ringed in Denmark was 39029, with annual values ranging from one to 2588 per year, with the overall annual mean number being 566 young (see Møller et al., 2006 for further information). The study was based on the fact that Arctic tern young can be ringed for a period of three weeks. Estimates of mean annual breeding date based on ringing dates were not biased compared to estimates when

Arctic tern young were classified into three age classes (Møller et al., 2006), implying that uncertainty about age of young was not a cause of concern.

1.2 Environmental conditions

We used local climate variables for April – May, which just precedes the main period of laying, and two large-scale climate variables reflected by the North Atlantic Oscillation and the Southern Oscillation. We used mean temperature and total precipitation for April and May for Denmark, obtained from the Danish Meteorological Institute, Copenhagen, as indicators of local climate variables at the breeding grounds.

The North Atlantic Oscillation (NAO) is a major source of atmospheric mass balance between pressure centers over Ponta Delgada, Azores and Stykkisholmur, Reykjavik, Iceland (Hurrell, 1995), estimated as the difference in normalized sea level pressures by division of each monthly pressure by the long-term standard deviation (1865 – 1984). High index values are associated with high winter temperatures and high levels of precipitation in Denmark and Scandinavia (Hurrell, 1995). We restricted NAO data to two periods: December – March and April – May, because the first period reflects conditions during winter thereby influencing the start of spring (Ottersen et al., 2001), while the months April – May are the months just before and during start of egg laying. Mean start of laying in our data set was 8 May (assuming an incubation period 22 days, a pre-fledging period of 22.5 days, and one egg of each clutch of three eggs being laid per day).

Sea-surface temperature and the extent of sea-ice in the Southern Ocean are related to El Niño Southern Oscillation events (Park et al., 2004), and a shift in the climate regime of the Southern Ocean has occurred in the 1970's (Masson-Delmotte et al., 2003; Weimerskirch et al., 2003; Jenouvrier et al., 2005), affecting the ecosystem of the Southern Ocean (Reid and Croxall, 2001; Weimerskirch et al., 2003). A proxy for climatic conditions in the Southern Ocean is the Southern Oscillation Index (SOI) (Liu et al., 2002; Park et al., 2004). When SOI is negative, sea-surface temperature and sea-ice extent in the Southern Ocean reduce the abundance of krill and other animals (Loeb et al., 1997). We used values for October – March, which is the period when Arctic terns are in the Southern Ocean. NAO and SOI data were obtained at the Climatic Research Unit, University of East Anglia, Norwich, UK (<http://www.cru.uea.ac.uk/cru>).

We used information on two environmental variables that have previously been shown to impact on the breeding biology of Arctic terns (Møller et al., 2007): the amount of fertilizer used in agriculture and the amount of shrimp. We obtained information on agricultural fertilizer use (both natural and artificial) as reported by Duus and Zinglarsen (2000) (see Møller et al., 2007 for details).

We used information of the amount of shrimp of the species *Palaemon adspersus* landed in Danish fishing harbors during the last century as reported by Pedersen (2005). While many other species of shrimp are caught in significant amounts, we only used information on *P. adspersus* because this species is a common prey of Arctic terns (e. g. Lemmetyinen, 1973). We also assumed that its abundance would correlate with the abundance of many other marine invertebrates (Pedersen, 2005).

We analyzed selection on ringing date as a measure of the timing of breeding, using the quantitative approach developed by Lande and Arnold (1983) and Arnold and Wade (1984), and a summary graph presenting the temporal pattern of selection is reported by Møller et al. (2006, Fig.3). In brief, intensity of directional selection can be estimated from linear regression models, where the dependent variable is a standardized measure of fitness (in this case subsequent survival as shown by the presence or absence of a later recovery of a ringed young, with fitness during a given selection episode being divided by mean fitness to obtain a relative estimate of fitness) and the independent variable is ringing date standardized to a mean of zero and a variance of one. A total of 1278 of the 37491 young were subsequently recovered as adults and used for the selection analyses. Estimated intensities of directional selection provide estimates of selection acting on the trait, with the standardized selection differential reflecting the change in phenotype estimated in standard deviation units for a unit of change in fitness. Rather than ascertaining statistical significance of selection, we used estimates of selection differentials as observations in subsequent analyses. Thirteen out of 47 of the linear selection differentials were statistically significant, according to the significance of the linear regression analyses (see also Møller et al., 2006). However, statistical significance is inappropriate as a measure of effect size, because significance clearly will depend on sample size. Therefore, we used measures of effect size rather than reliance on null hypothesis testing as an approach to evaluate hypotheses (e. g. Burnham and Anderson, 1998).

1.3 Statistical analyses

We made all analyses with JMP (2000). We used regression analyses weighted by sample size to account for uneven sampling effort among years.

Analysis for temporal auto-correlation in the arrival and breeding date time series only revealed auto-correlations at a time lag of one year of 0.47 and 0.59, suggesting that temporal dependence of the data was important for the conclusions. To avoid any problems of effects of temporal auto-correlation on conclusions we used differences in values between subsequent years in the analyses. To this end, we calculated differences between values in subsequent years for all variables, and used these differences in the analyses as statistically

independent data points (Chatfield, 1999). This procedure removed any signs of significant temporal autocorrelation (arrival date 0.05, breeding date 0.19).

We restricted the analyses to a small number of local and large-scale climate variables based on the assumption that temperature, precipitation and pressure differences would capture important aspects of the study system. We assumed that temperature would affect the timing of primary production, while precipitation and pressure differences would reflect the frequency of low pressure passages and hence the conditions for fishing for terns (Dunn, 1972). In these analyses we used a stepwise approach to reduce the number of predictor variables to a minimum. In these models we also included all two-way and three-way interactions. However, no interaction entered the models (see Results). Model selection was based on Akaike's information criterion as an estimate of the improvement in fit for addition of variables (Burnham and Anderson, 1998). Hence, some models contained predictors that were not statistically significant on their own, although these variables significantly improved the fit of the model.

2 Results

2.1 Arrival and environmental conditions

The first observation of Arctic terns on average occurred on 7 April ($SE = 1$), range 16 March to 24 April, $n = 48$ years 1957–2003. The tenth Arctic tern was observed on 14 April ($SE = 1.2$), range 2 April to 8 May, $n = 48$ years. The date for the observation of the first and the tenth individual was positively correlated ($F = 23.22$, $df = 1, 42$, $r^2 = 0.36$, $P < 0.0001$, slope (SE) = $0.56 (0.12)$). Both first and tenth arrival date were positively related to the first arrival date recorded by A. Schat Kielberg (first date: $F = 26.67$,

$df = 1, 18$, $r^2 = 0.56$, $P < 0.0001$, slope (SE) = $0.36 (0.08)$; tenth date: $F = 9.86$, $df = 1, 18$, $r^2 = 0.35$, $P = 0.0057$, slope (SE) = $0.39 (0.12)$). In the remainder of the study we use the date for the tenth Arctic tern as a measure of arrival date in order to use an estimate that is likely to be less affected by sampling bias than the date for the first observation.

Arrival date advanced dramatically during 1957–2003 (Fig.1A), with arrival date now being 17 days earlier than in the 1950's.

We tested if arrival date was related to environmental conditions in the winter quarters and the breeding grounds by using the North Atlantic Oscillation Index, the Southern Oscillation Index and temperature and precipitation in April and May as predictor variables. The only variable that explained arrival date was the Southern Oscillation Index (Fig.2). An increase in the Southern Oscillation Index was associated with a delay in arrival date at the breeding grounds. In contrast, arrival date was not predicted by the amount of shrimp landed in the current year (linear regression based on detrended data: $F = 0.03$, $df = 1, 40$, $r^2 = 0.0007$, $P = 0.87$), or by the amount of fertilizer used (linear regression based on detrended data: $F = 0.01$, $df = 1, 35$, $r^2 = 0.003$, $P = 0.91$). Thus, the effect of climate on arrival date was not a general phenomenon for all environmental variables of relevance for the Arctic tern.

2.2 Breeding date and arrival date

Mean annual breeding date estimated from the ringing dates of young during the period 1957–2003 was 12 June ($SE = 0.7$), range 26 May to 20 June, $n = 42$ years.

There was a significant temporal trend in breeding date (Fig.1B), with breeding date now being 11 days earlier than 42 years ago.

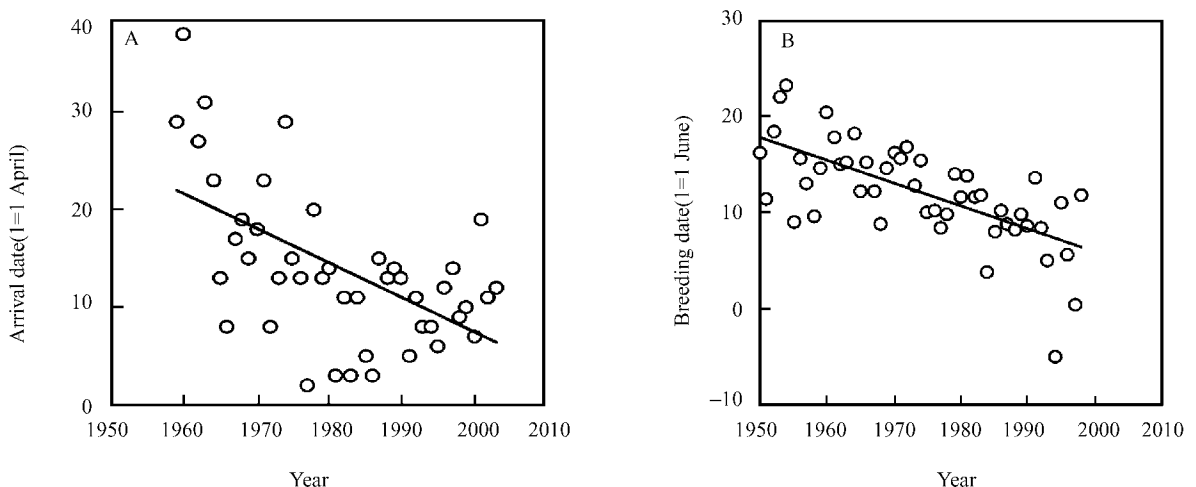


Fig.1 Arrival date (A) and mean annual breeding date of Arctic terns in Denmark 1957–2003 (B)

Arrival date was the date when the 10th Arctic tern was observed in a given year, while mean breeding date was the mean date of ringing of Arctic tern young. The regression lines have the statistics (A) $F = 20.18$, $df = 1, 42$, $r^2 = 0.32$, $P < 0.0001$, slope (SE) = $-0.35 (0.08)$, and (B) $F = 29.94$, $df = 1, 40$, $r^2 = 0.43$, $P < 0.0001$, slope (SE) = $-0.25 (0.05)$ and are shown in the graphs.

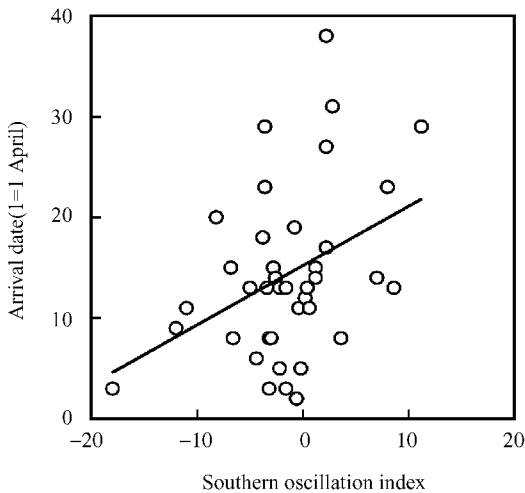


Fig.2 Mean arrival date of Arctic terns in Denmark in relation to the Southern Oscillation Index the previous winter

The regression line has the statistics $F = 6.60$, $df = 1, 37$, $r^2 = 0.15$, $P = 0.014$, slope (SE) = $0.59 (0.23)$ and is shown in the graph.

The mean of the annual estimates of selection differential for breeding date was -0.108 ($SE = 0.044$), range -1.358 to 1.115 , $n = 36$ years during 1957 – 2003, differing significantly from zero (one-sample t -test weighted by sample size: $t = -2.47$, $df = 35$, $P = 0.019$). The temporal trend in selection differential was weakly significant during 1957 – 2003 (linear regression weighted by sample size: $F = 4.86$, $df = 1, 34$, $r^2 = 0.14$, $P = 0.035$, slope (SE) = $0.014 (0.006)$). Likewise, the annual estimates of selection differentials did change from negative to positive values during 1932 – 1992 as breeding date advanced (linear regression weighted by sample size: $F = 9.27$, $df = 1, 34$, $r^2 = 0.21$, $P = 0.0045$, slope (SE) = $-0.041 (0.014)$; see Møller et al., 2006 for further details).

If events in one year carried over to the following year, we would expect arrival date in the current year to be predicted by breeding date the previous year. In fact, annual arrival date was predicted by mean annual breeding date the previous year [linear regression of detrended data weighted by sample size: $F = 8.01$, $df = 1, 33$, $r^2 = 0.20$, $P = 0.0078$, slope (SE) = $0.60 (0.21)$].

Mean annual breeding date was predicted by arrival date with a peak in predictability at a time lag of one year (Fig.3). Breeding date in the current year could potentially be affected by arrival in the current year, but also by delayed effects from previous years. Mean annual breeding date was predicted by arrival date the previous year rather than arrival date the current year, which did not enter as a significant predictor [Fig.4; linear regression of detrended data, weighted by sample size: $F = 10.58$, $df = 1, 35$, $r^2 = 0.23$, $P = 0.0025$, slope (SE) = $0.69 (0.21)$]. There was no problem of

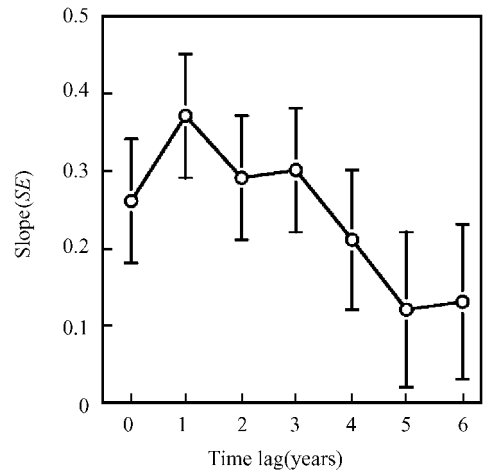


Fig.3 Slope (SE) of the relationship between mean annual breeding date of Arctic terns in Denmark 1957 – 2003 in relation to arrival date with different time lags (years)

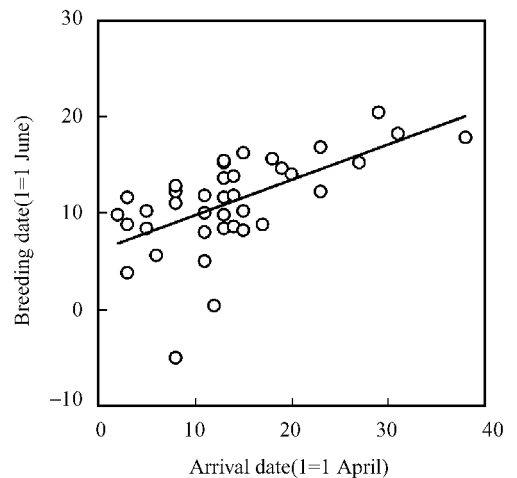


Fig.4 Mean annual breeding date of Arctic terns in Denmark 1957 – 2003 in relation to arrival date the previous year

The regression line weighted by sample size has the statistics $F = 20.71$, $df = 1, 36$, $r^2 = 0.37$, $P < 0.0001$, slope (SE) = $0.37 (0.08)$ and is shown in the graph.

collinearity because the correlation coefficient between the two time series was only $r = 0.46$. There was no significant effect of arrival date two or more years ago (partial regression of detrended data, weighted by sample size: $F < 1.95$, $df = 1, 35$, $P > 0.17$).

The best fit model of mean annual time of breeding including breeding date in the previous year, arrival date in the current and the previous year, environmental conditions in the current and the previous year as predictor variables produced a model that explained 58% of the variance (Table 1). The best predictor was arrival date the previous year, explaining 20% of the variance, with arrival date the current year only explaining 8% of the variance (Table 1). In addition, breeding date in the

previous year explained 12% of the variance (Table 1). Finally, two environmental variables explained small amounts of variance: The North Atlantic Oscillation Index for April – May the current year explained 12% of the variance, while the Southern Oscillation Index explained a non-significant 7% of the variance (Table 1). Including year as a continuous predictor variable in the model did not qualitatively change this conclusion (model: $F =$

9.65, $df = 4, 32, r^2 = 0.55, P < 0.0001$), with arrival date the previous year being the best predictor ($F = 21.42, df = 1, 32, P < 0.0001, \text{slope (SE)} = 0.29 (0.06)$), and the North Atlantic Oscillation Index for April-May the current year being the only other significant predictor variable ($F = 4.88, df = 1, 32, P = 0.034, \text{slope (SE)} = 2.40 (1.08)$).

Table 1 Multiple regression model with mean annual breeding date of Arctic terns as the dependent variable and arrival date the previous and the current year, breeding date the previous year and environmental variables the previous and the current year as predictor variables

Variable	Sum of squares	df	F	P	Slope (SE)
Arrival date year (i)	146432	1	2.86	0.10	0.09 (0.05)
Arrival date year (i - 1)	407040	1	7.95	0.008	0.17 (0.06)
Breeding date year (i - 1)	312320	1	6.10	0.019	0.31 (0.12)
North Atlantic Oscillation Index April – May year (i)	225792	1	4.41	0.044	0.38 (0.18)
Southern Oscillation Index year (i - 1)	112128	1	2.19	0.15	-0.10 (0.07)
Error	1587200	31			

The model for mean breeding date weighted by sample size had the statistics $F = 8.70, df = 5, 31, r^2 = 0.58, P < 0.0001$.

2.3 Arrival date and learning

Arrival date in year (i + 1) relative to date of breeding in year (i) advanced in years when it was advantageous to breed early in year (i) (Fig.5). On average, arrival date advanced by almost 18 days in year (i + 1) relative to breeding date in year (i) when the advantage of early breeding increased by one standard deviation in year (i). This effect could potentially be caused by selection rather than learning. If that was the case, we should expect selection in the previous year to affect breeding date. However, there was no significant effect of selection differential in year (i + 1) ($F = 0.48, df = 1, 27, P = 0.50$).

3 Discussion

Timing of spring arrival to the breeding grounds by the Arctic tern advanced by 17 days and timing of breeding by 11 days during the last 47 years. Timing of spring arrival from the Antarctic wintering quarters was correlated with timing of breeding the previous year. Timing of breeding was mainly correlated with spring arrival in the previous rather than the current year and with timing of breeding in the previous year. The change in arrival date was affected by learning, as suggested by the advancement in arrival date in a given year being greater following a year when it was advantageous to breed early. These findings support the hypothesis that change in phenology occurs due to changes in the timing of the annual cycle as mediated by learning.

Arrival date of Arctic terns from their Antarctic winter quarters was partly determined by environmental conditions in the winter quarters, but not by environmental conditions in the breeding areas (there was no significant effect of NAO). In addition, there was a

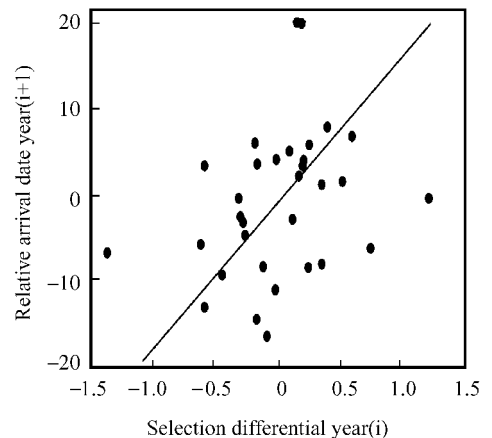


Fig.5 Interval between breeding date in year (i) and arrival date in year (i + 1) of Arctic terns in Denmark in relation to selection differential for breeding date in year (i)

The regression line based on detrended data weighted by sample size has the statistics $F = 7.01, df = 1, 30, r^2 = 0.19, P = 0.013, \text{slope (SE)} = 17.64 (6.66)$ and is shown in the graph.

delayed effect of breeding date the previous year. This effect could have arisen from the timing of breeding the previous year affecting autumn migration and timing of molt and subsequently spring migration. Because the annual molt occupies most of the time spent in the winter quarters (Cramp, 1985; Ginn and Melville, 1983; Voelker, 1997; Hatch, 2002), a change in spring arrival can only come about due to a change in the start of the annual molt. The analyses of breeding date suggested that the timing of breeding in the current year was determined to a larger extent by timing of spring arrival and breeding date the previous year than arrival date the current year. The simplest interpretation of these findings is that

breeding date mainly is affected by delayed effects of timing of spring arrival and breeding in the previous year rather than spring migration in the current year, suggesting carry-over effects from one year to the next. We suggest that hatching date of an individual will determine its subsequent timing of migration and molt, as shown for passerine birds in the laboratory (review in Coppack and Pulido, 2004). Consistent arrival dates of individuals in subsequent years, as shown for common terns (Becker et al., 2008), will imply that an early-hatched individual will tend to arrive early and hence start to breed early (Becker et al., 2008). Further phenotypically plastic adjustment of breeding date in subsequent years due to climate change could further advance breeding date across generations. If such effects are carried over from one generation to the next, this could eliminate the need for genetic variation and micro-evolutionary change to be invoked in order to explain changes in timing of breeding. Experimental evidence from the barn swallow *Hirundo rustica* shows that manipulation of parasite load of first clutch nests affects timing of breeding in the second clutch, with carry-over effects on spring arrival and timing of breeding the following year (Møller et al., 2004b).

Learning is a potential mechanism generating adjustment in arrival date to environmental conditions experienced during previous years. Learning may affect life history decisions when experience during one reproductive event can be used to change subsequent decisions. Grieco et al. (2002) showed for blue tits *Parus caeruleus* that females receiving additional food during the nestling period in one year changed the timing of egg laying the following year. This delay in breeding made experimental females reproduce much later in the second year than the peak period of nestling food availability. Indeed, long-lived species like the Arctic tern would benefit from learning if environmental conditions in one year provides reliable information about conditions during subsequent reproductive events, as shown by temporal auto-correlation in environmental conditions. We found evidence consistent with learning because Arctic terns arrived earlier in a given year relative to breeding date the previous year if it was particularly advantageous to breed early the previous year. We have found no alternative explanation for this effect, although an individual-based model may provide a more rigorous test of this hypothesis. Our data on Arctic terns do not provide sufficient rates of recaptures to allow such a test.

The findings reported here have implications for the three hypotheses. Clearly the data support the changing annual cycle hypothesis because the timing of events in one year was carried over to the following year with consequences for arrival date and breeding date in that year. We only had information on arrival and breeding time for unsexed birds, preventing us from assessing the

protandry hypothesis (Møller, 2004). However, we can assess the constraints hypothesis (Both and Visser, 2001) as an explanation for the findings. The Arctic tern has the longest migrations of any species, and the annual molt occupies over 40% of the annual cycle (Cramp, 1985; Ginn and Melville, 1983; Voelker, 1997; Hatch, 2002). This makes it a particularly strong test case for the constraints hypothesis because timing of migration would be particularly likely to constrain timing of breeding under these circumstances. This test failed because timing of breeding was less strongly affected by timing of spring arrival in the current year (accounting for 8.4% of the variance) than in the previous year (accounting for 20.4% of the variance according to test statistics in Table 1). A corollary of these analyses is the question whether data suggested to support the constraints hypothesis may also support the alternatives. The main empirical finding supporting the constraints hypothesis is the observation that the selection differential on breeding date in the pied flycatcher has changed, but not changed sufficiently to remove any advantage of early arrival to the breeding grounds (Both and Visser, 2001). Despite earlier arrival during recent years, pied flycatchers would benefit from even earlier arrival, suggesting that adaptation to climate change is constrained by timing of migration. This conclusion was based on analyses of selection differentials with the number of local recruits as the fitness measure (Both and Visser, 2001). It is possible that not all fitness components will act in the same direction because opposing selection pressures are an inherent characteristic of life history theory (Roff, 2001). Conclusive evidence for the hypotheses listed here would require that total selection and hence total fitness was evaluated in relation to timing of breeding. Obviously, this is much easier said than done, and such a test would require considerable research effort, but until this has been done, none of the hypotheses would be conclusively supported. Finally, using Occam's razor as a guideline the annual cycle hypothesis is a much simpler alternative relying on fewer assumptions than the constraint hypothesis.

Migratory birds differ in life history strategies (Berthold, 2001), and pied flycatchers and Arctic terns are very different in many respects. Could the findings reported here be due to the Arctic tern being a long-lived seabird, while the pied flycatcher is a short-lived passerine? The experimental evidence for barn swallows concerning carry-over effects of timing of reproductive events in one year on timing of events in the following year (Møller et al., 2004b) suggests that the mechanism proposed here can also work in short-lived passerines. This raises the question whether there are species in which there are no changes in the timing of the annual cycle (i.e., changes in the timing of different components of the annual cycle, and not just changes in spring migration or breeding date)? Therefore, a next step

would be to investigate a number of other species in order to determine the limits of the explanatory power of the different hypotheses. Analyses of the timing of breeding of two other tern species have shown similar patterns as we have reported here for the Arctic tern (A. P. Møller, E. Flensted-Jensen and W. Mardal unpublished data). A second point of interest is whether there are limits to changes in timing of annual cycles? Would continued climate change eventually constrain changes in the timing of the annual cycle? The Arctic tern provides a test of such constraints. Based on a 70 years time series of breeding dates and selection on breeding dates, we have previously shown that mean annual breeding date has advanced by over 18 days during this period (Møller et al., 2006), and that there is no indication that selection on breeding date is constrained by arrival date in the current year, as shown by the present study. This suggests that if such constraints exist, they are certainly not ubiquitous, nor are they of a magnitude so that they prevent further change in breeding date in the Arctic tern, even after 70 years of directional change in breeding date.

Finally, we would like to consider potential sources of error and bias. The findings reported here could not be due to temporal auto-correlation in the data because the auto-correlation was only present for a time lag of one year, and because the conclusions remained unchanged when the analyses were based on detrended data that controlled statistically for auto-correlation. The arrival date information was based on extensive bird watching activity by amateurs, as is commonly the case for studies of effects of climate change on bird migration (Lehikoinen et al., 2004). We tested explicitly for effects of sampling bias that is particularly important for first date records of spring arrival, while biases are much less prominent for the 5th or the 10th percentile (Lehikoinen et al., 2004; Møller and Merilä, 2004). First arrival dates were strongly positively correlated with the date when the tenth Arctic tern was observed, suggesting that the two measures reflected the same phenomenon. Furthermore, we verified that two independent estimates of arrival derived from the population of amateur ornithologists and from a single specialist ringing Arctic terns were strongly positively correlated, providing cross-validation of the data. The arrival of the tenth bird precedes mass arrival of the entire breeding population by just a few days (Møller et al., 1978), suggesting that this estimate of arrival is representative for the entire population. The changes in breeding date and selection on breeding date reported here are typical of changes estimates for the last 70 years in Denmark (Møller et al., 2006, 2007). We have found no evidence of bias in dates of breeding due to lack of information on exact age of young (Møller et al., 2006, 2007). Likewise, there is no indication that ringing practices have changed during the study period, as verified by numerous bird ringers that have been active for

periods of up to 60 years. Finally, there is no indication of consistent changes in population size during the last century (Grell, 1998). Therefore, we do not consider the data to be biased with respect to any of the proposed hypotheses.

In conclusion, we have shown that Arctic terns have changed timing of spring arrival by adjusting to timing of breeding in previous years, and that this adjustment is likely to have been achieved through learning. This phenotypically plastic response to climate change provides a novel mechanism to account for changing phenology in response to climate change.

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