

Onset of breeding among Swedish Starlings *Sturnus vulgaris* in relation to spring temperature in 1981–2003

Häckningsstarten hos svenska starar Sturnus vulgaris i förhållande till vårtemperaturen 1981–2003

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Abstract

Both spring temperature and date of the first Starling *Sturnus vulgaris* egg were highly correlated between different study sites and weather stations in the southern half of Sweden. In southern Sweden, but not in northern Sweden, onset of breeding correlated strongly with spring temperature, particularly during the last ten days of April, the period that happens to coincide with the start of breeding. The response was one to two days per degree. No response was found with periods relative to the start of egg-laying, indicating that in the latter part of April the general conditions for breeding are normally satisfied as soon as

temperature reaches a certain level. Possible climatic trends were too weak to be detected in the noise of the annual fluctuations. The best current estimate of long-term spring temperature increase during the next one hundred years is four degrees, which would mean that the Starling will start egg-laying 4–8 days earlier at the end of the present than at the end of the previous century.

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Introduction

For centuries, long-term climate changes as well as short-term weather fluctuations between years or even brief spells of aberrant weather have attracted large interest among naturalists, laymen and professionals alike (e.g. Elkins 1988, Burton 1995). These changes have been used to explain phenomena and properties such as distribution, speciation, migration, breeding biology, and anatomical and physiological adaptations. Currently a strong revival of interest in this field has been inspired by the greenhouse effect, presumed to be mainly anthropogenic, and the consequences that this may exact on wildlife (Hughes 2000, Walther et al. 2002), especially as an additional threat to certain endangered habitats and species (McCarty 2001). Most existing studies indicate that the response to climate change in different species will show few common patterns, which leads to a need to study each species separately. This observation may of course depend on the paucity of relevant studies, but the large variation in response to environmental factors in general provides strong support for a

complex response pattern. Also higher levels of organization must be considered since numerous interactions and functional dependencies exist between species within assemblies, communities and ecosystems.

The different phenophases of the avian life cycles are closely tied to climate change, many of them being adaptations with limited phenotypic flexibility, a constraint that makes it difficult or impossible for birds to adapt further and trace the change in climate (e.g. Visser et al. 1998, Stevenson & Bryant 2000, Both & Visser 2001). But long-term phenological time series are rare. Few are longer than about fifty years, and some of the most informative ones cover only the most recent decades. Hence, in spite of the fact that more than two hundred years of reliable weather data are available from many stations, especially in the northern hemisphere (see recent review in Bernes 2003, particularly p. 37, where temperature trends for Sweden are given for the different seasons separately), it is difficult to find corresponding data about biological events. Occasionally, such time series have been found, for example the so called Marsham phenological record,

covering the period 1736–1947 and containing dates on flowering and leafing of plants, and arrival of migratory birds (Sparks & Carey 1995).

The longest phenological time series usually deal with arrival dates of migrants collected by bird clubs (e.g. Butler 2003). Similar series exist from ringing stations but usually not earlier than from the 1950s (e.g. Sokolov et al. 1998). The best data on the start of the breeding season come from countries where nest record schemes have been in operation for a long period of time, for example in Britain (Crick et al. 1997, Crick & Sparks 1999), or from long-term nest-box studies of tits and flycatchers (e.g. Winkel & Hudde 1997).

Many studies simply confirm the age-old knowledge that the timing of different phenophases of a bird species shifts from year to year in relation to temperature, precipitation, and other weather factors. Most studies concern time of arrival of a migrant species and the onset of breeding in relation to spring temperature, or relate expansion or retraction of distribution ranges to climate change. Recent examples of such studies are those of Crick et al. (1997), Dunn & Winkler (1999), Thomas & Lennon (1999), and Tryjanowski et al. (2002). Some studies (e.g. Butler 2003) re-discover the fact that birds that arrive early (“weather migrants”) show a more flexible response to shifts in spring weather and hence adapt more rapidly to climate change than birds that arrive late (“calendar migrants”; usually species wintering in the tropics), but see Jenni & Kéry (2003) for more complex consequences for later phases of the annual cycle. Some time series are of proper length to be relevant for discussions of climate change (e.g. Tryjanowski et al. 2002), whereas others expand on the climate change issue based on rather brief periods of data that may have little to do with climate change (e.g. Sergio 2003). However, such shorter time series are of great value because they show how birds respond to the weather situation in different years, and such data can be used to predict the prospects of a species under different assumptions about future climatic regimes, particularly when several brief consecutive time series can be concatenated.

A number of studies try to explore the relationships to a deeper level of functional understanding. The most interesting ones point to differential phase shifts between breeding time and essential resources (Stevenson & Bryant 2000, Both & Visser 2001).

Northern Europe, especially the Arctic zone, experienced a general decline of annual mean temperature between 1950 and 1980, particularly a result of more severe winters. This temperature

decline was interrupted in the 1980s although several cold winters also occurred in the late 1970s and in the 1980s. Several authors have assumed that the interruption of the cooling trend was caused by an anthropogenic greenhouse effect. The period covered by the present study (1981–2003) is the period when the former cooling trend no longer continued.

It is not advisable to use annual mean temperature for areas of continental scale when trying to assess effects on birds because the expressions of climatic change differ between both seasons and different parts of a continent. The effects of climatic change may also be very different for birds with different migration strategies, for example a resident species versus a late arriving tropical migrant. Local weather data, relevant to a particular place and time, are necessary. The fact that it is the local weather factors that must be used is, in the case of the Starling, shown by several studies. Havlin & Folk (1961) and Dolenc (1999) suggested a shift towards earlier laying in Czechoslovakia and Croatia, Flux (1987) a shift towards later laying in New Zealand, Feare & Forrester (2002) no change in Britain (1975–1995), and my study, as will be shown, a sudden shift to earlier laying in 1988, but no change thereafter. It all seems to depend on site and selected period.

Starlings *Sturnus vulgaris* are short-distance migrants that arrive in Sweden in early spring after having wintered mainly in Britain (Svensson 1990). They arrive at the breeding sites long before they build a nest and lay the first egg. In southernmost Sweden the earliest birds may arrive already in February. In the rest of southern Sweden they arrive successively during March, and almost immediately start to visit, clean and defend a nesting cavity. The first eggs are laid in late April or early May. At the most northern site of this study (Abisko), the mean arrival date over 20 years was 33 days before laying of the first egg (data provided by Nils Åke Andersson, Abisko Scientific Research Station). Hence, Starlings spend at least one month, sometime up to two months, in the breeding area before egg-laying.

The long period between arrival and onset of breeding makes it likely that the start of breeding is determined by the local weather and other conditions experienced during March and April at the breeding sites. One cannot exclude completely that weather in the wintering area could affect time of breeding through delayed effects. However, I consider it unlikely that substantial causal effects could be transmitted over such a long period. Hence, it seems evident that the sensitive period for the onset of breeding in the Starling must be the three spring

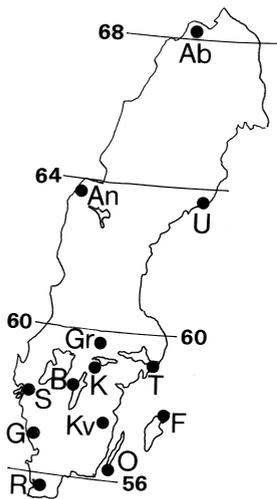


Figure 1. Location of the Starling study sites. The name of the SMHI weather station used for each study site together with its distance in kilometres to the Starling site is given within parenthesis. Figures in the map denote latitudes. Ab = Abisko (Abisko, 0), An = Anjan (Storlien, 55), U = Umeå (Umeå, 3), Gr = Grimsö (Stålldalen, 35), T = Tyresta (Stockholm, 23), K = Kvismaren (Örebro, 15), B = Bocksjö (Jönköping, 90), S = Svartedalen (Säve, 32), F = Fleringe (Visby, 40), Kv = Kvill (Målilla, 42), G = Gällared (Varberg, 35), O = Ottenby (Ölands södra udde, 5), R = Revinge (Lund, 15).

Placeringen av undersökningsområdena. Den väderstation som använts ges inom parentes tillsammans med dess avstånd i kilometer till starområdet. Siffrorna på kartan anger breddgrad.

months of March through May or a certain period within that time frame.

This study is based on a data set collected during a long-term Starling study at thirteen different locations distributed all over Sweden, from the very north (Abisko in northern Lapland) to the very south (the Revinge area in Skåne). The study hence covers thirteen degrees of latitude, almost from the northern range limit of the species and almost to the southern border of the area where only one breeding attempt per season is made. In Sweden, second clutches, after a successful first one, are extremely rare, which means that double-brooding, and possible time constraints because of that, are not considered in this study.

The original purpose of the project was long-term monitoring of population size and breeding performance of the Starling in relation to the load of environmental pollutants, being a part of the general environmental monitoring activities of the Nature

Conservation Agency as described in a previous paper (Svensson 2004). This particular report is a by-product of that project and a partial analysis of the total data set.

Study areas

The location of the study sites is shown in Figure 1. The study sites have been described in a previous report (Svensson 2004). In this paper I have used data from three sites in northern and ten sites in southern Sweden. The length of the time series from other sites included in Svensson (2004) was not sufficient. I restricted this analysis to sites with laying dates from at least ten years.

Methods

All studied Starlings bred in nest-boxes, up to one hundred at each site (Svensson 2004). At some of the sites, the nest-boxes were divided into sub-groups located several kilometres away from each other. These distances between the subgroups were small and much shorter than between even the most nearby sites: less than 3 km at Revinge, 5–11 km at Svartedalen, 7 km at Ottenby, 2 km at Kvill, 1.5 km at Kvismaren, and 4.5–9 km at Grimsö. There was no significant difference of mean date of first egg between the subgroups within the same site. A maximum difference of 1.3 days was found between two subgroups at Grimsö. In individual years the difference was two days, or less, in 91% of the comparisons, and it was more than four days in only one case. The correlation coefficients between dates were in no case lower than 0.9. Hence, the first date within a site, independent of which subgroup it derived from, was accepted as a proper measure to use for that site.

All nest-boxes were inspected several times during the breeding season in order to determine the date of the first egg, final clutch size, and the number of fledglings. In the majority of cases the date of the first egg was determined exactly by at least one visit during the laying period (the Starling lays one egg per day). In a few cases, the laying period was missed. In most of these cases, the laying date could be back-calculated on the basis of information from the other visits. Data were accepted for this study if laying date could be determined with an error no larger than plus or minus one day. The back-calculations were made on the basis of visits close enough to the laying period to permit this precision or from a known hatching date, assuming that

hatching occurs eleven days after the last egg. Among the areas in southern Sweden this level of precision was not reached for Grimsö in 1981 and 1982. For the areas in northern Sweden, this lack of precision prevailed in several years. All these cases have been excluded from the analysis. At Kvill in 1996, only one pair bred, laying the first egg extremely late (on 29 May); this case was also excluded.

Throughout I have used the date of the first egg in each colony. Alternatives would have been to use the mean, modal or median date. Mean date is not well suited for the purpose since the distribution of laying dates is biased towards later dates because of replacement clutches. Modal and median date would both be proper measures but would differ little from the first date because of the strong laying synchrony in this species (Karlsson 1983, Feare 1984). Modal or median dates lied only 2–3 days later than the first date. In my colonies in southern Sweden and the one at Umeå, there was only eleven cases when there was an interruption in the sequence of days with layings, and only two cases when this interruption was longer than one day (two days at Umeå in 1994 and 4 days at Tyresta in 1987). Hence, for all these sites, the date of the first egg gives the same results as if I had used modal or median date. At Anjan and Abisko, the frequency of delays between the first and next date with laying was higher and the intervals longer. At Anjan there were 1 (1987), 1 (1992), 3 (1989), and 4 (1988) days between the first and next laying in these four different years. At Abisko the intervals were 3 (2000), 4 (1983), 4 (1995), 4 (2001), 4 (2002), 7 (1997), and 13 (1992) days. The small number of clutches at the latter site (often only 1–3; Svensson 2004) makes it, however, impossible to determine which date would be the most appropriate to compare with spring temperature, so I have arbitrarily chosen the first date also for this site.

Temperature data were obtained from the Swedish Meteorological and Hydrological Institute. The weather station selected for each Starling study site and its distance from the study site are listed in the caption of Figure 1. In most cases, the nearest weather station was selected, but with some exceptions they were rather distant away, or at a different elevation. Consequently, the absolute temperatures were not the same as at the Starling sites. However, for studying correlations between temperature and onset of breeding, this is of lesser importance.

In this paper I use mean daily temperature. Since the analysis of Easterling et al. (1997) suggested that the global temperature increase is to a large extent

due to an increase of minimum temperature, I initially performed a number of calculations based also on daily minimum or maximum temperatures. However, I soon found that the results were identical to those based on mean temperature. This is in good accordance with the findings in Easterling et al. (1997) that, in Scandinavia, neither mean nor minimum or maximum temperature has shown any trend since 1950. I analysed trends in mean temperature for both calendar periods and for periods relative to the date of egg-laying. I first studied the monthly means of March, April and May, and the mean for the period 1 March through 10 May. Although there was no significant trend in temperature, either in northern or southern Sweden during the period, the stations in southern Sweden indicated a weakly positive trend for April. Therefore I also analysed the temperature trends for a number of shorter calendar periods: 1–15 and 16–31 March, 1–10, 11–20, and 21–30 April, and 1–10 May.

I calculated the correlations between laying date and temperature for these different calendar periods and for the following relative periods setting the laying date as day 0: days 24–15, 14–10, 9–0, 9–5, and 4–0 before the first egg, and days 1–5 after the first egg. The correlation coefficients were calculated using the regression function of the Excel data analysis module.

In order to summarize my findings for southern Sweden in a simple way, I did as follows. I calculated the mean temperature of all ten weather stations for the period 21–30 April. To summarize laying dates, I first calculated the annual relative laying date for each site, using the mean laying date in 1988–2003 for that site as datum. Then I calculated the mean annual relative laying date for all stations. Note that for 1991 and 1992, data from only two and three sites, respectively, were available.

Throughout the paper, significance levels are as follows: * $P < 0.05$, ** $P < 0.01$, and *** $P < 0.001$.

Results

Date of first egg

The dates when the first egg was laid at each of the study sites are given in Appendix 1. The regressions of laying date on year are given in Table 1. Almost all trends were negative, indicating that laying occurred earlier in more recent years ($P = 0.12$; binomial test). However, the correlations were weak and significant ($P < 0.05$) at only five of the thirteen sites. Appendix 1 shows that there were a number of comparatively late years before 1988. No trend was found at any of

Table 1. Linear regression of date of first egg on year, and a comparison of mean date of first egg in 1981–1987 vs. 1988–2003 (date 1 = 1 April). The number of years is given within parentheses. For the specific years included, see Appendix 1. The difference in days between the two periods was tested by t-test. n.d. = no data.
Linjär regression för datum för första ägget mot år, samt jämförelse mellan medeldatum för första ägget under perioderna 1981–1987 och 1988–2003 (datum 1 = 1 april). Antal år ges inom parenteser. För vilka specifika år som ingår, se Appendix 1. n.d. = inga data.

| | Slope all years <i>Lutning alla år</i> | Slope 1988–2003 <i>Lutning 1988–2003</i> | Mean date 1981–1987 <i>Medeldatum 1981–1987</i> | Mean date 1988–2003 <i>Medeldatum 1988–2003</i> | Difference in days <i>Skillnad i dagar</i> |
|-------------|--|--|---|---|--|
| Revinge | -0.30* | +0.04 | 33.0 (4) | 26.3 (15) | 6.7*** |
| Gällared | -0.26 | +0.04 | 36.0 (3) | 29.5 (15) | 6.5* |
| Ottenby | +0.03 | +0.03 | n.d. | | |
| Svartedalen | -0.27 | +0.08 | 34.0 (7) | 28.4 (16) | 5.6* |
| Kvill | -0.22 | +0.42 | 35.5 (6) | 31.5 (10) | 4.0* |
| Fleringe | -0.29* | -0.09 | 29.0 (5) | 24.2 (15) | 4.8** |
| Bocksjö | -0.26 | +0.46 | 35.7 (6) | 30.8 (11) | 4.9* |
| Tyresta | -0.29* | -0.07 | 32.0 (5) | 27.1 (16) | 4.9** |
| Kvismaren | -0.24 | -0.24 | n.d. | | |
| Grimsö | -0.31* | -0.16 | 34.8 (5) | 30.2 (16) | 4.6* |
| Anjan | -0.16 | +0.92 | 44.0 (3) | 40.7 (7) | 3.3 |
| Umeå | -0.19 | -0.19 | n.d. | | |
| Abisko | -0.64* | -0.69 | 48.0 (4) | 41.1 (15) | 6.9 |

the sites for the period 1988–2003 (Table 1). This means that the weak negative trends for the whole time series were caused by the late springs before 1988. This is confirmed by comparing mean laying dates for the two periods 1981–1987 and 1988–2003. Laying occurred 3–7 days later in the former period, and the difference was significant at all sites in southern Sweden (Table 1).

Temperature trends 1981–2003

No significant temperature trends were found during the 23-year study period for mean temperature of any of the whole months of March, April, and May separately, or for the whole three-month period. The result was the same whether the daily minimum, maximum or mean temperature was used. There was, however, a weak but non-significant positive regression for April. When the shorter calendar periods were analysed, significant positive trends were found for the last ten days of April at ten of the thirteen stations. The regression coefficients were 0.07–0.17 for the three non-significant and 0.11–0.22 for the ten significant ones. The average coefficient for all thirteen weather stations was 0.16 degrees per year. This late April period happens to

coincide with the laying period for the Starling in most of the study areas (Appendix 1).

For the other five periods, the regression coefficients were significant for none of the stations. However, the coefficients clearly tended to be positive in a majority of the cases: all were positive in the period 1–15 March (range 0.07–0.14, mean 0.09), 12 positive and one negative 15–31 March (range –0.02–0.12, mean 0.04), seven positive and six negative 1–10 April (range –0.07–0.10, mean 0.00), nine positive and four negative 11–20 April (range –0.03–0.12, mean 0.02), and all positive 1–10 May (range 0.01–0.11, mean 0.06).

Correlations between areas

Appendix 2 shows correlations of laying dates between the study areas. The correlation coefficients were high and most of them significant for the sites in southern Sweden. Also laying dates at Anjan (North Sweden) correlated with those at the southern sites although significantly so in only half of the cases. The correlations with the two most northern sites were, however, weak. There was no significant correlation between the three northern sites.

Correlation between mean temperature and laying date, relative periods

The correlations between laying date and temperature during the different periods relative to laying date were non-significant in almost all cases. For the areas in southern Sweden they were even far from significant. In northern Sweden they were actually positive in several cases indicating an inverse relationship between laying date and temperature. However, the only significant correlation was a positive one at Abisko for the period 4 to 0 days before laying ($r=0.52$, $P<0.05$).

Correlation between mean temperature and laying date, calendar periods

When correlating laying date with mean temperature during the different calendar periods it was found that the northern sites differed from the southern ones (Appendices 3 and 4). There seemed to be no correlation between temperature and laying date at the northern sites. The single correlation at Anjan for the period 16–31 March is likely to be spurious. In southern Sweden, the onset of breeding correlated with temperature, most often strongly, at all sites for April but much less strongly and only for five of the ten sites for March (Appendix 4). There were no significant correlations for the whole of May. There were also strong correlations between breeding date and mean temperature for the whole period 1 March through 10 May, but this was of course mainly an effect of the April correlations. When the briefer periods were analysed (Appendix 3) it was found that the main reason for the strong correlations with April temperature was the period 21–30 April. Also for other periods, there were negative correlations, particularly for the period 16–31 March, but, interestingly, not for the period 1–10 April. Almost all correlations, independently of period, were negative also when they were not significant. This result strongly indicates a general relationship between onset of breeding and spring temperature, but that the effect was most pronounced for the period 21–30 April, the period when the Starlings started egg-laying in most years.

Discussion

Past climate change, and change during 1981–2003

For a discussion of Starling phenology and climate change, a focus on only the most recent decades is of

course relevant in the present study. However, a brief review of what has happened in the more distant past and of what may happen in the future will put our current brief period in perspective. The temperature changes in Sweden have been analysed by Alexandersson & Eriksson (1989) for the period from 1860 through 1987, thus until the early years of this study. The analysis was made for northern and southern Sweden separately and also, and more importantly, separately for spring, summer, autumn and winter. Spring (March–May) temperature is the relevant factor in the current study. In northern Sweden there was an increase of the ten-year mean temperature of about one degree between 1860 and 1930, then no trend during the rest of the period but with higher values around 1950 and 1980 and lower values during the 1970s. In southern Sweden the ten-year means increased with about half a degree between 1860 and 1900. After 1900, no trend can be observed. We can conclude that spring temperature changed little during the fifty years preceding this Starling study. This also means that the Starling had a long time to adapt to the spring temperature patterns characterizing the time when this study started. If no further changes were found thereafter, no selection on spring phenology needs to be considered.

As quite clear from the results obtained in this study there was no general trend in spring temperature during 1981–2003. No trend would therefore be expected for the dates of onset of breeding. However, such trends were found for the whole period, although only weakly significant in most cases (but none was found for the period 1988–2003). The analysis of shorter calendar periods revealed that the reason for the trends in egg laying dates was probably that there were significant temperature trends for the last ten days of April, and this happens to be the period when the Starlings start or are about to start breeding. This would indicate that the most important phenological response is an immediate, not a delayed one.

In order to make projections into the future, we must go to different climatic models, for example those used by SWECLIM (Bergström 2003), which suggest a long term spring temperature increase of about four degrees during the next one hundred years.

Correlations between areas

In spite of the fact that the laying dates emanated from slightly different years, and in some cases from rather few years, the correlation coefficients were impressively high, and all were positive, for the

thirteen sites in southern Sweden (Appendix 2). This result strongly indicates that a common factor governs the onset of breeding over the whole of southern Sweden. Local factors, such as latitude and elevation, of course determine the absolute mean date, but the co-variation cannot depend on site-specific factors. It is likely that spring temperature shifts between years, similar over a large region, is the most important factor that explains the strong correlations.

The three northern areas showed few significant correlations among them, and only Anjan showed some correlations with the southern sites. However, it is not possible to conclude much from this because the number of clutches was small in many years, and the three sites were much more distant from each other than were those in southern Sweden.

Spring temperature and onset of breeding

This analysis has been limited to a maximum period of 23 years for two of the thirteen sites and briefer periods of variable length for the other sites. Even the longest runs of years are brief when climate effects are to be analysed. Meteorologists usually use periods of at least 30 years when analysing anomalies around climate “normals” in order to eliminate the effects of short-term weather cycles, many of which are driven by the periodic North Atlantic front oscillations in Scandinavia. Briefer periods are therefore difficult to analyse in terms of climate change, and many authors have drawn too far-reaching conclusions from too brief time series, and I am of course at risk of doing the same with my mere two decades of data.

Although most regressions were positive, it is clear from this analysis that spring temperature, with the exception of late April, has not shown any significant trend in Sweden since the early 1980s. It is therefore not surprising that few significant trends were found for date of the first egg. The trends of the first egg depended on a few late years before 1988 (Table 1) with no trends at all in 1988–2003, in agreement with the absence of a temperature trend.

Two main patterns emerge from the study. First, there was a very strong correlation between different sites in southern Sweden. Second, of the two components of variation, trend and residual variation about the trend, the latter was by far the most important one for the Starling in spite of the time series being up to 23 years long. Thus, until now, annual variation of spring weather, not climate change, has been the factor, directly or indirectly, determining onset of breeding in the Starling.

This result may be valid for a wider area than only Sweden. A British study also found no trend towards earlier laying during the period 1975–1994 (Feare & Forrester 2002, their figure on p. 77). Using their data I found that the slope of the linear trend was -0.23 which is far from significant ($P > 0.2$). However, the fact that this time series, as well as most of mine, demonstrated a negative slope, may indicate that actually there is a long-term trend towards earlier breeding in the Starling although this cannot be statistically ascertained because the time series are yet too short. The average slope at the ten sites in southern Sweden was -0.24 and at all thirteen sites -0.26 , slopes that are very similar to the one from the British site. But again, these slopes depended only on a difference between the early and late parts of the period; there was no significant trend after 1987 (Table 1).

One of my time series, the one from Revinge, can be expanded backwards to 1973 thanks to the data provided by Karlsson (1983) who worked at exactly the same site and used the same number of nest-boxes. The first egg was laid as follows: 1 May 1973, 26 April 1974, 29 April 1975, 4 May 1976, 2 May 1977, and 30 April 1980. These data strengthen the assumption that there is no real long-term trend but that the trends found rather depend on a number of late years in 1976–1987. The years 1973–1975 were about as early as 1988–2003.

Some results from other studies

There are a number of time series on different phenophases of birds that are long enough to have the potential to reveal effects of climate change on the start of breeding and not only the effects of short-term weather cycles. There are several detailed population studies, one being the Great Tit *Parus major* study at Marley Wood (Crick et al. 1997), which shows that laying date closely tracked the warmth sum for March and April.

Other types of data are those on the timing of spring migration at ringing stations (e.g. Sokolov et al. 1998). That kind of data becomes particularly valuable when the arrival of the birds can be tied to the breeding time of local populations (Sokolov & Payevski 1998).

Dolenec (1999) found a non-significant trend towards earlier laying (0.25 days per year) in Croatia for the period 1980–1999. Havlin & Folk (1961) provided data from Czechoslovakia on the number of ringed broods in different five-day periods during 1940–1944 and 1948–1957. I read the modal periods

of ringed first broods from their figure 2 for this 18-year period. The linear trend was less than 0.01 days per year towards earlier breeding but sequences of years differed so much from each other that this trend was far from significant ($P > 0.2$).

Conclusions and projection

The general relationship between temperature during the last ten days of April and onset of breeding in southern Sweden is summarized in Figure 2. The slope of the regression line is very close to a shift of onset of breeding by one day for every degree of temperature change. The corresponding shift in relation to temperature during the whole of April or all spring is about two days per degree temperature (Appendix 4).

This study shows that spring temperature has not changed much in Sweden since the early 1980s. In accordance with this, the main effect on date of breeding was the annual variation of spring temperature and not climate change. Starlings followed the general pattern for birds that arrive early. They were flexible and traced spring temperature, particularly that of late April. This indicates that if the climate will change in the future, we would expect the Starling to respond to that change. The absence of correlations between the relative periods before onset of laying shows that the present spring climate will always create suitable breeding conditions in southern Sweden on about 20 April, and likely earlier, if mean temperature increases in the future. The exact date of egg laying will then be modified by the temperature about that date.

The range of dates when the “Starling spring” arrived was not wide enough in this study to show what would happen if spring would arrive very much earlier. This remains to be seen, and the result would be very interesting in the perspective of possible adaptive constraints, as suggested for tits and flycatchers (Visser et al. 1998). If Starlings are able to adapt to much earlier springs will mainly depend on whether or not their food species will be able to adapt.

If, however, we assume that the response of one or two days per degree temperature (Figure 1, Appendix 3 and 4) will remain the same even if average April temperature will increase considerably, we can estimate when the Starling will start to breed in the future. The current best estimate of climate change for Sweden is probably that produced by SWECLIM (Bergström 2003). Mean spring temperature is projected to be about four degrees higher in 2071–

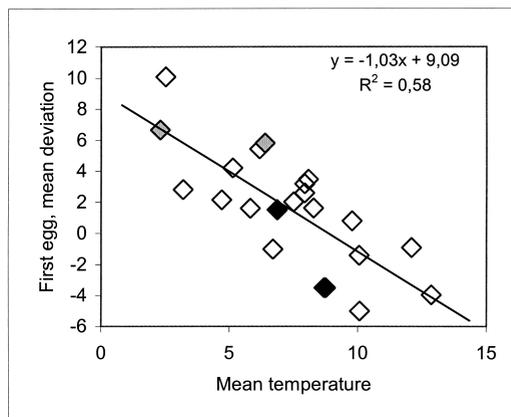
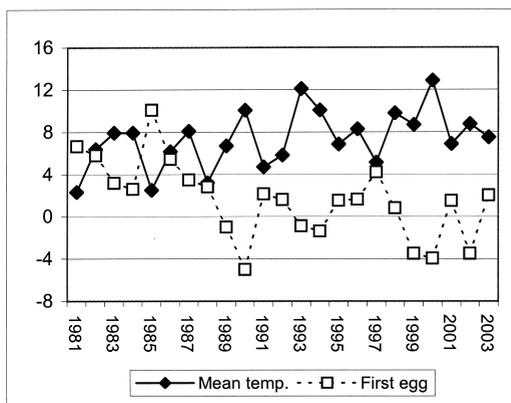


Figure 2. Upper panel: Mean laying date of the Starling (open symbols), relative to the mean laying date in 1988–2003, at the ten study sites in southern Sweden, and mean temperature for the period 21–30 April at the ten corresponding weather stations. Lower panel: Diagram showing the correlation, using the same data set. Black symbols: years with two almost identical values. Grey symbols: 1991 and 1992, when data from only two and three sites, respectively, were available (cf. Appendix 1). The mean shift of laying date is one day per degree temperature.

Övre diagrammet. Medeldatum för äggläggningen hos staren (övre), relativt till medeldatum för 1988–2003, vid de tio undersökningsområdena i södra Sverige samt medeltemperaturen (övre) för perioden 21–30 april vid de tio motsvarande väderstationerna. Nedre diagrammet. Korrelationsdiagram för samma värden. Svarta symboler: år med två nästan identiska värden. Grå symboler: 1991 och 1992 med värden från bara två resp. tre undersökningsområden (se Appendix 1). Den genomsnittliga ändringen av läggdatum är en dag per grad temperaturförändring.

2100 than it was during the last decades of the 20th century. That means that one would expect the Starling to start breeding about four to eight days earlier at the end of the present century. This means that the long-term change is within the normal annual variation and explains why it is so difficult to detect long-term trends among the noise of annual weather fluctuations when data from only a few decades are available and climate change is slow.

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Sammanfattning

Klimat och väder, och dess effekter på fåglarnas tidsschema, har fascinerat människor i alla tider, men frågan har blivit ännu mera aktuell under senare decennier på grund av uppmärksamheten kring den växthuseffekt som antas vara orsakad av människan. Det är förvisso ingen nyhet att fåglarnas ankomst på våren och deras häckningsstart påverkas av temperaturen. Det finns dock skäl att närmare studera förhållandena och speciellt hur olika arter reagerar lokalt. Det är nämligen så att de globala växthuseffekter som man oftast hör talas om inte behöver gälla för ett mindre område. Och eftersom många fåglar rör sig inom rätt begränsade områden är det bara vad som sker i dessa områden som kan påverka deras fenologi. Vidare kan utvecklingen vara olika under olika årstider. De svenska starna flyttar till Storbritannien under vinter, varför det bara är förhållandena i Skandinavien och Nordsjöområdet som är avgörande och sannolikt speciellt eventuella temperaturförändringar mellan ankomsten i mars och häckningsstarten i slutet av april eller början av maj.

Under åren 1981–2003 insamlades data om när första ägget lades i tretton holkområden spridda över hela Sverige från Abisko i norr till Revinge i söder (Figur 1, Appendix 1). Jag erhöll temperaturuppgifter för månaderna mars, april och maj från SMHI. Först studerade jag hur datum för häckningsstarten hade förändrats under dessa drygt tjugo år, därefter eventuella förändringar i temperaturen under hela våren eller delar av våren, och slutligen undersökte jag vilka korrelationer det fanns mellan temperatur och häckningsstart.

Det fanns en antydning till att häckningsstarten inföll successivt tidigare (Tabell 1), men effekten var svag och signifikant bara för några områden. En närmare analys (Tabell 1) visade att effekten berodde på några sena år under perioden 1981–1987, men att det därefter inte funnits någon som helst trend mot tidigare datum. Genom att analysera tempera-

turutvecklingen de olika vårmånaderna separat och dessutom under olika kortare perioder kunde jag visa att den positiva temperaturutvecklingen var koncentrerad till de sista tio dagarna i April. Detta råkar vara den period då starna lägger ägg inom större delen av södra Sverige. En jämförelse mellan de olika områdena (Appendix 2) visade att det var mycket hög korrelation för läggningsdatum bland alla sydsvenska områden.

Det var med utgångspunkt från detta inte förvånande att den bästa korrelationen mellan starnens läggningsdatum och temperaturen erhöles för perioden 21–30 april (Appendix 3). Betydligt svagare och fåtaligare korrelationer erhöles för de två första tio-dagarsperioderna i April. Det var litet överraskande att flera korrelationer också erhöles med de sista tio dagarna i mars. Men även med hela april och med hela våren erhöles signifikanta korrelationer (Appendix 4).

Förutom att studera starnens äggläggning i förhållande till bestämda kalendariska perioder beräknade jag också regressionen mellan häckningsstart och temperaturen under relativa perioder av olika längd i förhållande till första äggets läggning. Det visade sig att inga samband fanns mellan läggdatum och medeltemperaturen olika perioder före detta datum.

Slutsatsen från denna studie är att om det pågår en höjning av vårtemperaturen så har den gjort sig gällande i mycket ringa grad under de senaste två decennierna och i konsekvens med detta har starnens äggläggning i genomsnitt ändrats mycket litet. Det som helt dominerar bilden är de årliga fluktuationerna i äggläggningsdatum, vilka är nära korrelerade med temperaturen i slutet av april det aktuella året. Svaret på temperaturvariationerna är ungefär en dag per grad om man använder perioden 21–30 april (Figur 2) och ungefär två dagar per grad om man använder hela våren (Appendix 4).

Vill man göra en långsiktig prognos utifrån de förmodligen bästa klimatförutsägelser vi har för Sverige så finner vi att SWECLIM räknar med ungefär fyra graders temperaturökning under vårmånaderna under de kommande ca 100 åren. Det skulle innebära att starnen i genomsnitt kommer att lägga sitt första ägg fyra till åtta dagar tidigare vid slutet av detta sekel än den gör i dag.

Appendix 1. Dates of first egg in each area and year. Date 1 is 1 April. Empty cell = no data. The acronyms denote the study areas according to Appendix 2.

Datum för första ägget i varje område och år. Datum 1 = 1 April. Tom cell = uppgift saknas. Förkortningarna anger området enligt Appendix 2.

| | REV | GÄL | OTT | SVA | KVL | FLE | BOC | TYR | KVS | GRI | ANJ | UME | ABI |
|-------|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|
| 1981 | 32 | | | 36 | | | | | | | | | |
| 1982 | | | | 35 | 35 | | 37 | | | | | | |
| 1983 | 31 | | | 28 | 36 | 28 | 33 | 31 | | 33 | | | 44 |
| 1984 | | | | 31 | 33 | 28 | 32 | 32 | | 31 | | | 49 |
| 1985 | 38 | 39 | | 37 | 41 | 34 | 42 | 35 | | 42 | 49 | | 48 |
| 1986 | | 36 | | 37 | 34 | 28 | 36 | 32 | | 36 | 39 | | |
| 1987 | 31 | 33 | | 34 | 34 | 27 | 34 | 30 | | 32 | 44 | | 51 |
| 1988 | 28 | 28 | 29 | 33 | 32 | 30 | 33 | 31 | 31 | 33 | 43 | 40 | 45 |
| 1989 | 24 | 29 | 23 | 25 | 30 | 22 | 30 | 26 | 30 | 31 | 34 | 51 | 33 |
| 1990 | 22 | 25 | 20 | 20 | 26 | 19 | 24 | 24 | 24 | 26 | 35 | 27 | 51 |
| 1991 | | 39 | 25 | 29 | 34 | 27 | 30 | 27 | 29 | 33 | 44 | 42 | 36 |
| 1992 | 28 | 27 | 26 | 31 | 32 | 25 | 32 | 31 | 31 | 33 | 44 | 38 | 57 |
| 1993 | 27 | 29 | 25 | 27 | 30 | 23 | 28 | 27 | 27 | 28 | 41 | 33 | |
| 1994 | 27 | 29 | 24 | 28 | 28 | 25 | 27 | 26 | 25 | 27 | 44 | 36 | 43 |
| 1995 | 27 | 31 | 25 | 28 | 34 | | 33 | 25 | 31 | 35 | | 42 | 40 |
| 1996 | 26 | 28 | 25 | 36 | | 24 | 34 | 28 | 30 | 32 | | 39 | 56 |
| 1997 | 32 | 35 | 30 | 32 | 35 | 26 | 35 | 31 | 32 | 34 | | 40 | 46 |
| 1998 | 26 | 28 | 26 | 27 | 34 | 26 | 33 | 28 | 29 | 31 | | | 34 |
| 1999 | 25 | 27 | 23 | 26 | | 25 | | 21 | 22 | 25 | | | 34 |
| 2000 | 22 | | 20 | 25 | | 19 | | 25 | 25 | 27 | | | 35 |
| 2001 | 29 | 31 | 26 | 32 | | 26 | | 29 | 29 | 29 | | | 34 |
| 2002 | 25 | 27 | 24 | 24 | | 20 | | 24 | 23 | 26 | | | 35 |
| 2003 | 27 | 32 | 28 | 32 | | 26 | | 30 | 27 | 33 | | | 37 |
| Mean | 28 | 31 | 25 | 30 | 33 | 25 | 33 | 28 | 28 | 31 | 42 | 39 | 43 |
| Years | 19 | 18 | 16 | 23 | 16 | 20 | 17 | 21 | 16 | 21 | 10 | 10 | 19 |

Appendix 2. Correlations between first egg laying date for all areas. The correlation coefficients in percent in the upper right part. Number of years common to the compared areas at the lower left. The column acronyms are the three capital letters of the area names in the first column.

Korrelationer mellan första ägglägningsdatum för samtliga områden. Korrelationskoefficienterna i procent uppe till höger. Antal gemensamma år för områdena nere till vänster. Kolumnförkortningarna är de tre versala bokstäverna i områdesnamnen i första kolumnen.

| | REV | GÄL | OTT | SVA | KVL | FLE | BOC | TYR | KVS | GRI | ANJ | UME | ABI |
|---------------|-----|-------|-------|-------|-------|-------|-------|-------|-------|-------|------|-----|-----|
| REVinge | | 91*** | 90*** | 77*** | 88*** | 88*** | 84*** | 82*** | 62* | 79*** | 88** | 19 | 33 |
| GÄLlared | 16 | | 54* | 60** | 77** | 74** | 62* | 59** | 41 | 73*** | 52 | 40 | -2 |
| OTTenby | 15 | 15 | | 76*** | 75* | 81*** | 80** | 79*** | 65** | 70** | 70 | 30 | 14 |
| SVArtealdalen | 19 | 18 | 16 | | 72** | 76*** | 84*** | 78*** | 65** | 74*** | 67* | 30 | 44 |
| KVILi | 12 | 13 | 10 | 16 | | 86*** | 92*** | 74** | 83*** | 91*** | 69* | 54 | -1 |
| FLERinge | 16 | 16 | 14 | 19 | 14 | | 82*** | 78*** | 59* | 80*** | 79** | 35 | 23 |
| BOCKsjö | 13 | 14 | 11 | 17 | 16 | 15 | | 80*** | 92*** | 93*** | 59 | 56 | 13 |
| TYResta | 18 | 18 | 16 | 21 | 15 | 19 | 16 | | 77*** | 79*** | 65* | 18 | 48* |
| KViSmaren | 15 | 15 | 16 | 16 | 10 | 14 | 11 | 16 | | 91*** | 26 | 68* | 32 |
| GRImso | 18 | 18 | 16 | 21 | 15 | 19 | 16 | 21 | 16 | | 56 | 63* | 33 |
| ANJan | 8 | 10 | 7 | 10 | 10 | 10 | 10 | 10 | 7 | 10 | | -7 | 31 |
| UMEå | 9 | 9 | 10 | 10 | 9 | 10 | 10 | 10 | 10 | 10 | 7 | | -63 |
| ABIsko | 17 | 16 | 15 | 19 | 13 | 17 | 14 | 19 | 15 | 19 | 8 | 9 | |

Appendix 3. Correlation between date of first Starling egg and mean daily temperature at 13 sites and for six different spring periods during years with data on egg-laying available. The trend is number of days per degree mean temperature. The other figures are Pearson correlation coefficients.

Korrelationen mellan datum för starens första ägg och dygnsmedeltemperaturen under sex sex olika kalenderperioder. Trenden är antal grader per dag. Övriga siffror är Pearson korrelationskoefficienter.

| | Years År | Trend (slope) | 1–15 March | 16–31 March | 1–10 April | 11–20 April | 21–30 April | 1–10 May |
|---------------------|-------------|------------------|---------------|----------------|---------------|----------------|----------------|-------------|
| <i>South Sweden</i> | | | | | | | | |
| Revinge | 19 | -0.30 * | -0.40 | -0.60 ** | -0.12 | -0.48 * | -0.69 ** | -0.65 ** |
| Gällared | 18 | -0.26 | -0.22 | -0.37 | -0.20 | -0.29 | -0.52 ** | -0.41 |
| Ottenby | 16 | +0.03 | -0.33 | -0.59 ** | -0.25 | -0.71 ** | -0.81 *** | -0.45 |
| Svartedalen | 23 | -0.27 | -0.51 * | -0.59 ** | -0.26 | -0.54 ** | -0.56 ** | -0.52 * |
| Kvill | 16 | -0.22 | -0.22 | -0.51 * | -0.22 | -0.48 | -0.61 * | -0.71 ** |
| Fleringe | 19 | -0.35 * | -0.39 | -0.58 ** | -0.06 | -0.49 * | -0.74 *** | -0.34 |
| Bocksjö | 17 | -0.26 | -0.22 | -0.50 * | -0.37 | -0.38 | -0.63 ** | -0.58 * |
| Tyresta | 21 | -0.29 * | -0.19 | -0.60 ** | -0.54 * | -0.51 * | -0.57 ** | -0.18 |
| Kvismaren | 15 | -0.20 | -0.27 | -0.39 | -0.36 | -0.25 | -0.71 ** | -0.37 |
| Grimsö | 21 | -0.31 * | -0.08 | -0.39 | -0.54 * | -0.37 | -0.78 *** | -0.48 * |
| <i>North Sweden</i> | | | | | | | | |
| Umeå | 10 | -0.19 | +0.29 | -0.29 | +0.21 | +0.18 | -0.49 | -0.60 |
| Anjan | 10 | -0.16 | -0.33 | -0.64 * | +0.53 | -0.36 | -0.35 | -0.59 |
| Abisko | 19 | -0.64 * | +0.27 | -0.27 | -0.33 | -0.09 | -0.37 | -0.16 |

Appendix 4. Correlation between date of first Starling egg and mean daily temperature at 13 sites and for March, April, and whole spring (1 March–10 May) during years with data on egg-laying available. R is the Pearson correlation coefficient. B is the trend in number of days per degree mean temperature.

Korrelationen mellan datum för starens första ägg och dygnsmedeltemperaturen under mars, april och hela våren (1 mars–10 maj). Trenden är antal dagar per grad. Övriga siffror är Pearson korrelationskoefficienter.

| Study site Område | Years År | March | | | April | | | March – 10 May | | |
|----------------------|-------------|-------|-------|----|-------|-------|-----|----------------|-------|-----|
| | | R | B | P | R | B | P | R | B | P |
| <i>South Sweden</i> | | | | | | | | | | |
| Revinge | 19 | 0.54 | -1.13 | * | 0.86 | -2.87 | *** | 0.81 | -2.40 | *** |
| Gällared | 18 | 0.31 | -0.69 | | 0.58 | -1.85 | * | 0.53 | -1.65 | * |
| Ottenby | 16 | 0.50 | -1.07 | * | 0.89 | -2.91 | *** | 0.71 | -2.01 | ** |
| Svartedalen | 23 | 0.63 | -1.66 | ** | 0.77 | -1.75 | *** | 0.87 | -3.37 | *** |
| Kvill | 16 | 0.40 | -0.60 | | 0.77 | -2.16 | *** | 0.75 | -1.81 | *** |
| Fleringe | 19 | 0.56 | -1.17 | ** | 0.75 | -2.07 | *** | 0.77 | -2.27 | *** |
| Bocksjö | 17 | 0.39 | -0.64 | | 0.79 | -2.54 | *** | 0.65 | -2.01 | ** |
| Tyresta | 21 | 0.48 | -0.85 | * | 0.77 | -1.75 | *** | 0.72 | -1.83 | *** |
| Kvismaren | 15 | 0.12 | -0.22 | | 0.88 | -2.46 | *** | 0.56 | -1.54 | * |
| Grimsö | 21 | 0.29 | -0.47 | | 0.71 | -1.32 | *** | 0.59 | -1.20 | ** |
| Mean Medeltal | | | -0.85 | | | -2.17 | | | -2.01 | |
| <i>North Sweden</i> | | | | | | | | | | |
| Umeå | 10 | 0.03 | +0.09 | | 0.11 | -0.57 | | 0.20 | -1.13 | |
| Anjan | 10 | 0.51 | -1.02 | | 0.18 | -0.51 | | 0.61 | -2.01 | |
| Abisko | 19 | 0.04 | +0.14 | | 0.36 | -1.58 | | 0.18 | -0.93 | |