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Start of egg-laying in relation to latitude and elevation among Swedish Starlings *Sturnus vulgaris* in 1988–2003

Äggläggningens början i förhållande till breddgrad och höjdläge hos svenska starar Sturnus vulgaris *1998–2003*

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Abstract

The Starlings *Sturnus vulgaris* breeding in sixteen nest-box groups, three in northern and thirteen in southern Sweden, were monitored in 1988–2003. Date of the first egg was found to correlate with both latitude and elevation when all sites were included (13 degrees of latitude; 5–430 m elevation). Restricting the analysis to only the south Swedish sites (4 degrees of latitude; 5–230 m elevation), only elevation had any effect. The absence of an effect of latitude in southern Sweden is interpreted as an effect of the large-scale Atlantic low-pressure systems that rapidly pass Sweden and bring mild spring weather to that whole area almost simultaneously, making local climate as determined by elevation more important than effects of latitude. Onset of laying at the sites in northern Sweden did not differ with more than two days in spite of one site being at the coast and the other two in mountain valleys at 380 and 430 m, possibly because the western birds winter at the Norwegian coast only c. 70 km away.

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Much interest is nowadays devoted to the question of how different bird species may react to short-term weather cycles as well as long-term climate change. In that perspective, better projections could be made with a deeper understanding of how specific aspects of breeding performance are affected by different site properties. Onset of breeding is one such aspect, expected to be affected by temperature, which in turn is related to both latitude and elevation.

There is often, although not always, considerable similarities between phenological events along elevation and latitudinal gradients. Numerous studies have demonstrated a correlation between spring temperature and onset of breeding, and temperature gradients are usually assumed to be the explanation for the effects of latitude and elevation. This also means that the effects sometimes may cancel out each other. For example, Fargallo & Johnston (1997) found that onset of breeding in the Blue Tit *Parus caeruleus* was about the same over latitudes from southern Scandinavia to the Iberian Peninsula in their preferred habitat, oldgrowth deciduous forest, because this habitat only occurred at high elevations in the Mediterranean. Generally, it remains to be determined whether the similarities between the effects of latitude and elevation are direct temperature effects or reflect other functional relationships with the environment. For example, Krementz (1984) concluded that "the evidence suggests that the ecological consequences of increasing altitude and latitude are only in superficial ways similar" and "that in terms of their effects on avian life history characters, changes in the two should not be presumed to be equivalent". This is an almost necessary corollary to the fact that many potentially important environmental factors will be different between, for example, a high elevation site in the south and a low elevation site in the north, such as day length, length of growing season, radiation, rainfall, wind, plant species, and food species. In spite of being well aware of the fact that it is not latitude and elevation as such but the other properties, particularly temperature, that determine onset of breeding, I do not analyse anything else than the effect of latitude and elevation in this paper. Latitude and elevation thus serve as tentative substitutes for temperature (for most of the nest-box groups local temperature data were not available).

During the period 1981–2003 the number of pairs of Starlings *Sturnus vulgaris* and their breeding performance were monitored at several sites in Sweden, between 56 ºN and 68 ºN and at elevations from sea level to 430 m above sea level. These ranges cover the whole distribution of the Starling in Sweden, both of latitudes and elevations. During the course of the study the date of the first egg was one of the things that was determined.

The Starling almost invariably lays only one clutch in Sweden. In southern Sweden it arrives from early February to early March, often more than two months before it lays the first egg in late April or early May. In northern Sweden the arrival time is later and closer to the date of the first egg. For example, at the most northern site of this study (Abisko), the first Starling is normally recorded in early to mid April, only occasionally in late March. In the period 1983–2003, the date of both arrival and first egg were available for 20 of the 21 years (data provided by Nils Åke Andersson, Abisko Reseach Station). The arrival date was 33 ±12 (s.d.) days before the first egg. Only in one year was arrival less than 17 days before the first egg. Although the delay period is shorter, the Starling spends a considerable period at the breeding site before egg-laying also in the north. These rather long intervals between arrival and breeding make it likely that the most important effects governing onset of breeding should be local ones, such as spring temperature as determined by latitude and elevation of the site, and not delayed effects of the conditions at the winter site.

In southern Sweden the Starling is common or abundant in many different kinds of open or semi-open habitats, whereas it is rare at most locations in northern Sweden. In the valleys of the mountains in Lapland it is not even annual at all suitable sites. The general population decline in Sweden has been most pronounced in northern Sweden, at many upland sites because of rapidly declining farming activities since the mid-20th century (Svensson et al. 1999). Originally, the study included several more sites in northern Sweden, but only three sites could be used in this analysis.

Study areas and methods

The location and elevation of each study site are given in Table 1. All breedings occurred in nest-boxes. The sites were described and general information about the project was given in Svensson (2004a). The nest-boxes were checked regularly from the start of breeding until the young had fledged. In the majority of cases, the exact date for the first egg was observed, but I have also accepted a few cases when the date of the first egg could be estimated with an error of no more than plus or minus one day.

At two of the sites the nest-boxes were divided among sub-groups at different elevations. This was the case for Svartedalen and Kvill. At Svartedalen there were three subgroups at 35 (Mällby), 60 (Ranebo), and 110 (Komperöd) metres elevation, and at Kvill two subgroups at 130 (Wenzelholm) and 230 (Norra Kvill) metres. Since elevation differed between these subgroups they have been treated as separate sites in this paper.

The data were analysed by regressing average date on latitude and elevation. Since the sites could be grouped into thirteen sites in southern Sweden and three sites much further north, I analysed the data both for all sites together and for the southern sites separately. In order to see if the results obtained with the average dates were the same for individual years, I used the statistical module of Excel to calculate single factor regressions and draw the figures, and STATISTICA to calculate multiple regressions.

The onset of breeding was significantly earlier before 1988 than later, but there was no trend at any site during the period 1988–2003 (Svensson 2004b.). Additionally, for some sites no data were available from before 1988. In order to use comparable data, I therefore restricted this analysis to the period 1988–2003. From some of the sites, data were not available from all years (Table 1). However, the absence of any trend during the study period means that the lack of data from some years does not affect the mean laying dates used in this study.

Results

Latitude, elevation, and average date of egg-laying for all sites are shown in Table 1 and the results are visualised in Figure 1. Laying dates for individual years (except for subgroups) are given in Svensson (2004b). I found a significant correlation between date and both latitude and elevation when all sites were included (multiple R=0.91, $F_{2,13}$ = 32.5, P<0.001) with a higher beta value for latitude (0.67, p<0.01) than that for elevation (0.32, p<0.05). Hence, both factors contributed significantly but latitude more than elevation. However, the opposite was the case when only the sites in southern Sweden were included. In southern Sweden multiple R was 0.82 ($F_{2,10}$=10.4, P<0.01) with significant contribution from only elevation (beta value 0.75, P<0.01) but not from latitude (0.25, P>0.05). Single factor regressions gave R=0.79 ($F_{1,11}$=17.7, P<0.01) for elevation and R=0.35 ($F_{1,11}$=1.5, P>0.05) for latitude. Latitude and

Table 1. Location of the study sites, elevation in meters, average date of first egg (1 = 1 April), and years of study with number of years within parentheses (Starlings ceased to breed at Anjan in 1995 and the Umeå site was closed in 1998). S.E. = standard error of date.
Studieområdenas lägen, höjd i meter, medeldatum för första ägget (1 = 1 april) och undersökningperiod med antal år inom parentes (stararna upphörde att häcka vid Anjan 1995 och Umeågruppen avslutades 1998). S.E. medelvärdets medelfel för datum.

Site *Lokal*	Latitude *Latitud*	Longitude *Longitud*	Elevation *H.ö.h.*	Date *Datum*	S.E.	Period (no. of years) *Period (antal år)*
Revinge	55.7	13.5	20	26.3	0.67	1988–1990, 1992–2003 (15)
Gällared	57.1	12.8	140	29.5	0.92	1988–1999, 2001–2003 (15)
Ottenby	56.2	16.4	5	24.9	0.69	1988–2003 (16)
Svartedalen, Komperöd	58.0	11.0	110	30.1	1.03	1988–2001 (14)
Svartedalen, Mällby	58.0	11.0	30	29.3	1.14	1988–2003 (16)
Svartedalen, Ranebo	58.0	11.0	60	28.9	1.52	1988–1999 (10)
Kvill, Wenzelholm	57.7	15.4	130	31.9	0.91	1988–1998 (10)
Kvill, Norra Kvill	57.7	15.4	230	31.0	1.13	1988–1994 (7)
Fleringe	57.8	18.9	20	24.2	0.80	1988–1994, 1996–2003 (15)
Bocksjö	58.6	14.5	105	30.8	1.00	1988–1998 (11)
Tyresta	59.2	18.2	40	27.1	0.73	1988–2003 (16)
Kvismaren	59.2	15.4	25	27.8	0.79	1988–2003 (16)
Grimsö	59.7	15.4	110	30.2	0.82	1988–2003 (16)
Anjan	63.7	12.4	430	40.7	1.66	1988–1994 (7)
Umeå	63.8	20.2	10	38.8	1.98	1988–1997 (10)
Abisko	68.3	18.8	380	41.1	2.13	1988–1992, 1994–2003 (15)

elevation were correlated, but of course only by incidence, being mainly an effect of the once arbitrary selection of sites.

Table 2 shows that the pattern found for average date was also found for individual years. For all Sweden there were significant contributions from latitude in nine years and from elevation in six years. When, however, only southern Sweden was considered, the pattern was clearly in favour of elevation as the factor that explained most of the variation of laying date. Note that fewer sites with egg-laying dates were available for the most recent years. This is probably the explanation for the lower number of significant regressions in these years.

In summary, latitude had an effect only when the range covered all twelve degrees of latitude (almost all Sweden) but not when it covered only the four degrees of latitude south of the so called *Limes Norrlandicus,* i.e. the region south of the northern boreal forest or taiga zone.

Discussion

The small effect of latitude in southern Sweden is probably an effect of the large Atlantic weather systems that usually rapidly pass all of southern Sweden. These systems are normally those that determine the progress of spring, bringing warm Atlantic air within a few hours time to the whole of that region. They are most often connected with rainy and windy conditions that rapidly melt away the snow and start the thawing of the frozen soil almost simultaneously at all southern sites. Such large-scale shifts of spring weather also occur in northern Sweden, although the mountain range in the west often exacts a modifying influence. Another complication is that the ice-covered Bothnian Bay affects the coastal climate. The expectation from this, that breeding should start at about the same time all over southern Sweden if the effect of elevation was removed, was confirmed by this study. However, it is not obvious why there was no difference between the eastern lowland and coastal site at Umeå versus the two high elevation mountain sites to the west (but see below).

In the literature there are several studies that analyse the effects on breeding date of latitude or elevation separately, but few that consider both. Berndt et al. (1981) found effects of both latitude and elevation but did not specifically analyse the relative

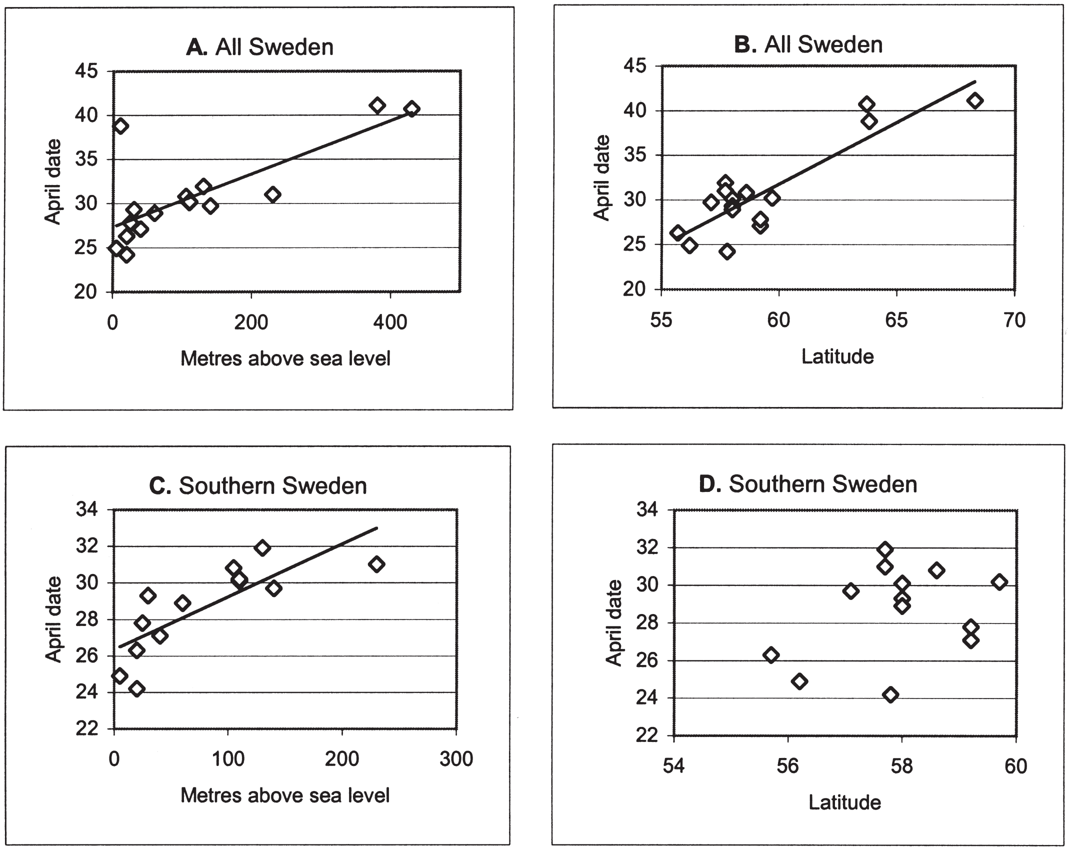

Figure 1. Relationships between date of first egg (1 = 1 April), elevation (metres above sea level), and latitude in Starling populations at different sites in Sweden. A and B: all sites; C and D: thirteen sites in southern Sweden. Regression lines have been drawn when significant.

Sambanden mellan datum för första ägget (1 = 1 april), höjdläget (meter över havet) och breddgraden för olika svenska starpopulationer. A och B: alla lokaler; C och D: sydsvenska lokaler. Regressionslinjer utritade när de är signifikanta.

importance of each factor. He used elevation delay data found by Zang (1980) in order to correct for elevation when analysing the latitudinal effect on the Pied Flycatcher *Ficedula hypoleuca.* Järvinen (1989) also found, when comparing data from 103 sites between north Africa and north Norway, that the mean date for the first egg in the Pied Flycatcher was correlated with both latitude and elevation. The partial correlation coefficients were 0.96 for date versus latitude and 0.44 for date versus elevation, and both were highly significant. I know of no such study dealing with the Starling.

The fact that onset of breeding is so closely connected with spring temperature rise is usually explained in terms of insect abundance, especially the larval peak after leafing of the trees. This is because some of the most well-studied species, such as tits and flycatchers, depend on that peak. The Starling is mainly a ground feeder both before onset of breeding and during the incubation and nestling periods. Although insects form a substantial part of the diet also earthworms are important, especially for adults in early spring. Hence, the feeding habits of the Starling are more similar to those of thrushes and some waders. The feeding conditions of such species in spring are mainly determined by melting of the snow layer, thawing of the frozen soil, and the delay period before the soil invertebrates have become available or increased sufficiently in size and abundance.

In spite of the limited scope of this study (one species and one aspect of its annual cycle) it confirms that there cannot be any simple relationships between breeding performance and climate (cf. e.g. Slagsvold 1975). Different populations with different adaptations may be involved. Different rates of change of a phenophase may prevail within different parts of a distribution range, and the effects of latitude and elevation may be different under different environmental regimes. This complicates the analysis of time series in relation to climate change and points to a need for long phenological time series from sites with different local properties.

Finally, I add a note of speculation that possibly could explain the absence of a difference between the coastal Umeå site and the two western mountaineous sites Anjan and Abisko. It is not known if the whole Starling population of Sweden is a homogeneous one. Recoveries and observations suggest that there may be a migratory divide somewhere in northern Sweden (Delin et al. 1957, Svensson 1990, Andersson 1996). Three of eight recoveries of nestlings ringed in northern Sweden came from the Norwegian coast, suggesting that they either overwintered there or flew directly to the British Isles rather than via Denmark and the Netherlands as the Starlings from southern Sweden do. One bird ringed in western Lapland was recovered at the Norwegian coast close to the breeding site. Two later recoveries of Starlings ringed at Abisko suggest that the normal wintering area of the Starlings from at least western Lapland may be to the west. Andersson (1996) also reports that Starlings arrive earlier at Abisko than at Kiruna, 80 km to the south-east. This means that the birds from Abisko and Anjan could belong to a distinct population wintering in Norway. Whether the birds breeding in the eastern parts of northern Sweden mainly winter in Norway or Britain is not known (in this study the birds from the Umeå site). The distance between Abisko and Anjan and the Norwegian coast is very short (60–70 km) compared with the distance to Britain. If the Starlings of the western part of northern Sweden winter in Norway, the temporal progress of spring would be quite similar at their wintering and breeding sites even if the conditions in absolute terms are

Table 2. Multiple regressions investigating whether annual laying date (dependent variable) was later at higher latitude and elevation. N = number of sites with data. R = multiple R. P, Lat., and Elev. = significance levels of R, latitude, and elevation, respectively. NS = not significant (a minus sign indicates negative value), * = P < 0.05, ** P < 0.01, *** P < 0.001. Lat. and Elev. not tested for P < 0.001.
*Multipla regressioner som visar om årligt läggningsdatum (beroende variable) var senare för högre latitud och höjdläge. N = antal områden med data. R = multipel R. P, Lat. och Elev. = signifikansnivåer för respektive R, latitud och höjdläge. NS = ej signifikant (minustecken anger negativt värde), * = P < 0,05, ** P < 0.01, *** = P < 0.001. Lat. och Elev. ej testade för P < 0.001.*

Year	All Sweden *Hela Sverige*					Southern Sweden *Södra Sverige*				
År	N	R	P	Lat.	Elev.	N	R	P	Lat.	Elev.
1988	16	0.95	***	**	NS	13	0.66	NS	*	NS
1989	16	0.69	*	**	NS–	13	0.78	**	NS	*
1990	16	0.94	***	**	**	13	0.82	**	NS	**
1991	15	0.67	*	NS	NS	12	0.84	**	NS–	**
1992	16	0.97	***	**	**	13	0.74	*	*	NS
1993	15	0.93	***	**	**	13	0.84	**	NS–	**
1994	16	0.93	***	**	**	13	0.63	NS	NS–	*
1995	13	0.79	**	*	NS–	11	0.81	*	NS	*
1996	13	0.88	***	**	NS	11	0.47	NS	NS	NS
1997	13	0.83	**	*	NS	11	0.63	NS	NS–	NS
1998	12	0.74	*	NS–	NS	11	0.81	*	NS	*
1999	11	0.90	**	NS–	**	10	0.74	NS	NS–	*
2000	9	0.92	**	NS	NS	8	0.82	NS	NS–	NS
2001	10	0.73	NS	NS–	NS	9	0.58	NS	NS	NS
2002	9	0.95	**	NS–	**	8	0.76	NS	NS–	*
2003	9	0.85	*	NS–	NS	8	0.76	NS	NS	NS

different. The risk of arriving too early to these sites would be small since they would be able to return to the coast in the case of a cold and snowy spell.

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Sammanfattning

Under åren 1983–2003 bestämdes datum för första äggets läggning i ett antal starkolonier (alla i holkar) på olika breddgrader (från 56º N till 68º N) och i olika höjdlägen (från havsnivå till 430 meter över havet). I princip täcktes därmed starens hela svenska utbredning både latitudinellt och vertikalt.

I södra Sverige anländer staren ofta mer än två månader före äggläggningen. I norra Sverige är perioden mellan ankomst och äggläggning kortare, men så långt norrut som i Abisko i medeltal en månad. Detta gör att det är troligt att det är de lokala förhållandena under våren som är viktigast för när häckningen börjar och inte några kvardröjande effekter av förhållandena i övervintringsområdet.

I dag intresserar man sig mycket för vilka effekter som vädercykler och eventuella klimatförändringar kan få på fåglarnas förekomst och häckningsframgång. Prognoserna kan bli säkrare om vi bättre känner till relationen mellan klimat och fenologi på olika lokaler. Därför analyserade jag vilka effekter som breddgrad och höjdläge kunde ha på starens häckningsstart. Det är naturligtvis inte latitud eller höjdläge som är den avgörande faktorn utan det lokalklimat, främst temperaturen, som bestäms av dessa faktorer. I avsaknad av temperaturdata från flera av kolonierna tjänar latitud och höjdläge som ett surrogat för temperaturdata.

De undersökta lokalernas latituder och höjdlägen samt genomsnittligt datum för första ägget redovisas i Tabell 1. Eftersom det föreföll finnas skillnader mellan södra och norra Sverige analyserades materialet både för hela landet och för södra Sverige separat. För vissa av områdena fanns datum för första ägget från före 1988. Emellertid var läggningsdatum något senare under de tidigare åren, medan det inte fanns någon trend i något område under perioden 1988–2003. Dessutom saknades data från före 1988 för vissa områden. Därför begränsades analysen till perioden 1988–2003.

Resultatet (Figur 1) blev att det fanns en korrelation mellan datum och både latitud och höjdläge när jag inkluderade samtliga områden (12 breddgrader). För de tretton sydsvenska holkgrupperna fanns däremot korrelation bara mellan datum och höjdläge, inte mellan datum och breddgrad. Intressant nog var det ingen skillnad mellan kust- och låglandskolonin vid Umeå och de två högt belägna kolonierna vid Anjan och Abisko, och inte heller mellan de två sistnämnda. Tabell 2 visar att de samband som fanns för genomsnittligt läggdatum också fanns inom de flesta enskilda år.

Som förklaring till frånvaron av effekt av breddgrad inom södra Sverige anför jag det faktum att våren (i termer av tillräckligt lång period av varmt vårväder för staren att komma igång med häckningen) bestäms av de västliga lågtrycken som för in mild luft över hela Sydsverige samtidigt. Effekten av höjdläget (lokalklimatet) kommer därför att dominera över effekten av breddgrad. I norra Sverige kan förhållandena vara mer komplicerade, bl.a. för att det är möjligt att vi har att göra med två olika starpopulationer, en som övervintrar vid norska kusten (den västligaste) och en annan som likt Sydsve-

riges starar övervintrar i England (den vid kusten). Det finns observationer och återfynd som tyder på att så kan vara fallet. Det har också observerats att stararna anländer tidigare till Abisko än till Kiruna, vilket också tyder på att de anländer västerifrån.

I litteraturen finns det åtskilliga studier som behandlar läggningsdatum i förhållande till antingen höjdläge på enskilda lokaler eller breddgrad på många lokaler. Däremot finns få studier som studerar båda faktorerna samtidigt. De studier som finns pekar på att det sannolikt inte går att likställa effekter av breddgrad och höjdläge utan att man måste försöka fastställa den relativa betydelsen av respektive faktor. Detta bekräftas av denna studie av staren. För prognoser om vad som kommer att hända med fåglars läggningstid och andra fenologiska aspekter av deras livscykel kan man därför inte utan vidare schablonmässigt korrigera för höjdlägen och breddgrad när man analyserar fenologiska data; långa tidsserier från platser med olika lokala egenskaper är nödvändiga.