

## TEMPERATURE AND TIMING OF EGG-LAYING OF EUROPEAN STARLINGS<sup>1</sup>

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**Abstract.** Many small passerine species breed earlier after a warm rather than a cold spring (long-term effect), and then start egg-formation after a clear increase in ambient temperature ( $T_a$ ) (short-term effect). We investigated the role of  $T_a$  on timing of breeding and the exact time of egg-laying in both a free-living and captive breeding population of European Starlings *Sturnus vulgaris*. The start of the breeding season of free-living starlings in southern Germany was highly correlated with  $T_{min}$  from March. In captivity under ad libitum feeding conditions, low  $T_a$  during February retarded reproductive development and behavior, thereby delaying the onset of breeding. Egg-formation occurred during a period with elevated temperatures. By increasing or decreasing the temperature of the nestbox by 2–3°C, from late March onwards, differences were found in the number of breeding females and the start of egg-laying between groups with heated, unmanipulated, and cooled nestboxes. Most females with cooled nestboxes started egg-formation in the week after the cooling stopped. Experiments under temperature controlled conditions in captivity showed that almost all starlings delayed egg-laying during a period when  $T_a$  was kept at 7°C, then started laying one week after a 5°C increase in  $T_a$ . The sensitivity of the reproductive system of starlings to spring temperatures seems to be an adaptive response, timing the period for laying (short-term effect) and for raising the young (long-term effect) to periods with high food availability.

**Key words:** egg-laying, European Starlings, *Sturnus vulgaris*, temperature.

### INTRODUCTION

In most temperate bird species, early clutches produce more surviving offspring than late ones (Perrins 1965, 1966); thus timing of breeding is extremely important for reproductive success. For timing of breeding, food availability during rearing of the young is the most important factor (Lack 1954). But, to be able to feed the young at the time when food is most abundant, gonadal development, courtship, and egg-laying must have taken place long before. The proximate factors timing these first phases of the breeding cycle are less clear, but photoperiod, ambient temperature ( $T_a$ ), and food availability play a key role (Perrins and Birkhead 1983).

Changes in photoperiod turn on the reproductive system and affect its rate of development (Murton and Westwood 1977). Laboratory experiments showed that the photoperiodic induction of gonadal growth is sometimes slightly reduced under low temperature (Storey and Nicholls 1982, Jones 1986). Timing of breeding is highly correlated with spring temperatures in various species, such as Coots (*Fulica atra*, Per-

deck and Cave 1989), European Kestrels (*Falco tinnunculus*, Meijer et al. 1988), European Starlings (*Sturnus vulgaris*, Dunnnett 1955), and tits (*Parus*, Slagsvold 1976, Van Balen and Potting 1990). An increase in mean spring  $T_a$  of 1°C advances the start of the breeding season of tits by 4–5 days (measured as mean laying date, Nager and Van Noordwijk 1992).

Besides this long-term effect of  $T_a$ ,  $T_a$  also can have a short-term effect. Laying starts in small passerine species, like tits, sparrows, and flycatchers, only a few days after an increase in  $T_a$  (Perrins and McCleery 1989, Lundberg and Alatalo 1992). It seems that in these species the reproductive system is arrested at a point from which egg formation can start immediately. The long-term effect of  $T_a$  seems to set a time-window for breeding, the short-term effect of  $T_a$  acts as a fine-tuner.

Early breeding in a warm spring, and egg-laying after a temperature increase could be a direct effect of  $T_a$  via an allocation of thermoregulation energy to gonadal growth (Kluijver 1952) or an indirect one, via the  $T_a$ -related increase in food availability later on (Perrins and McCleery 1989). Experimental evidence for a  $T_a$  effect on the timing of breeding and the start of

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egg-laying is scarce. In surplus feeding experiments carried out in the field, where  $T_a$  was left unchanged, a moderate advance in onset of laying occurred (review in Meijer and Drent 1998). In a natural temperature experiment, O'Connor (1978) and Dhondt and Eykerman (1979) found earlier laying of tits in nestboxes which provided better insulation or those exposed to the afternoon sun, respectively. Nager (1990) measured local differences in both  $T_a$  and insect availability (mainly caterpillars and spiders) within the same forest, and found that small differences in local  $T_a$  (1–2°C) correlated with differences in onset of laying of Great Tits (*Parus major*). Nager and Van Noordwijk (1992) cooled or heated nestboxes of Great Tits during the night from 2–4 weeks before the start of egg-laying, thereby creating a difference in  $T_{\text{nest}}$  of 3°C without affecting the laying date. Yom-Tov and Wright (1993) started a heating experiment during laying and found that the percentage of Blue Tits (*Parus caeruleus*) that showed an interruption in the laying sequence was lower in heated than in control nests.

We investigated the relation between spring weather and timing of breeding in a free-living population of European Starlings, as well as starlings breeding in captivity. Additionally, in captivity, the short-term effect of temperature on timing of egg-laying was investigated: in one experiment by manipulating the temperature of the nestboxes, and in a second experiment by manipulating the temperature of the whole aviary during the last weeks before the start of laying.

## METHODS

### FIELD

We analyzed the data of a 10-year period (1981–1990) on timing of breeding of a free-living colony of starlings in Fischen, southern Germany. Starlings arrived at the colony during the second half of February. During April, the nestboxes were checked daily to determine onset of laying. Laying date of a clutch was the day on which the first egg was laid. Almost all starlings from one colony start laying within one week (Karls-son 1983). Annual laying date was the median of the laying dates within this synchronized period.

$T_a$  was recorded continuously a few kilometers away at the Max Planck Institute in Erling-

Andechs (48°N, 11°11'E). Correlations between the warmth sum (sum of  $T_a$  during a certain period, Kluijver 1951) and timing of laying were calculated for minimum and maximum  $T_a$  ( $T_{\text{min}}$  and  $T_{\text{max}}$ , respectively) during the period from 1–28 March (10 days before the earliest laying date). Because vegetation development in spring seems to be related to  $T_{\text{min}}$  of 5°C or more (Wallen 1970, Cannell and Smith 1983), we made similar calculations using only days with  $T_{\text{min}}$  above 4°C.

### CAPTIVITY

Starlings were caught in the Netherlands in August 1991 and kept in captivity in Bielefeld (52°01'N, 8°32'E). During the spring of 1992, these starlings were given the opportunity to breed in one large aviary (7 × 21 × 6 m) equipped with an excess of nestboxes. Nine females laid and incubated their eggs. In early February 1993, the starlings were divided into three groups in adjacent aviaries (4.8 × 3.6 × 2.5 m), in visual contact with each other. Each group consisted of 8 males and 12–13 females, of which 3 had laid and incubated in the previous year. In each group, birds had access to 14 nestboxes (21 × 21 × 25 cm, bottom area 371 cm<sup>2</sup>) from 5 March onwards. Birds were offered poultry pellets (HEMO Enten Mast Allein) ad libitum and each group was given additionally 100 g day<sup>-1</sup> of commercial insect food (CLAUS #3).

*Nestbox experiment.* Female starlings sleep in nestboxes before laying (pers. observ.). Starting on 25 March 1993, we heated nestboxes in one group (WARM) and cooled nestboxes in the other outermost aviary group (COLD), whereas the group in the middle aviary served as a control (CONTROL).  $T_{\text{nest}}$  was increased by 2–3°C by a small electric resistor (UTM 216-8, 4R7 10%) and decreased by 2–3°C (Fig. 1) by placing, in the top of the nestbox, two 220 g ice packs, which were exchanged at 08:00 and 18:00. To maintain the temperature difference between nestbox and aviary, the entrance of all the nestboxes was covered by a small piece of rubber, which was easily pushed away by the starlings. Nestboxes were checked each day at 08:00 and 12:00 to assess reproductive behavior (nest-building, egg-laying, and incubation). The eggs were removed on the 10th day of incubation. Because laying in captivity was less synchronized than in the field, the day the fifth captive

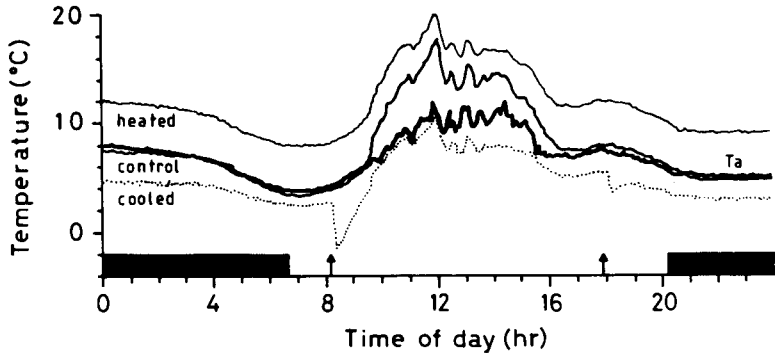


FIGURE 1. Example of the daily temperature pattern between a heated, a control, and a cooled nestbox on 17 April 1994. Ambient temperature ( $T_a$ , thick line) and light/dark period also are indicated.

female started laying refers to the peak of egg-laying (see Fig. 3).

Every 2–3 weeks all birds were captured before 08:00, their bill color scored on a scale from 1 (black) to 5 (yellow; see Meijer and Langer 1995), weighed to the nearest 0.1 g, and checked for signs of molt. During the morning hours, the starlings were observed from a dark shelter through a one way window. Each group was observed for 15 min twice a week, using the instantaneous sampling method (Martin and Bateson 1986). Every 30 sec we recorded for each nestbox which bird was sitting in front or inside the nestbox, sang, or showed wing flailing. Every day at 18:00, together with the exchange of the ice packs, nestbuilding was scored on a scale from 0 (no nest material present) to 5 (a complete nest was built). In 1994 we repeated the experiment with minor differences. The number of females increased to 14 in all three groups, and females of the WARM and COLD group were exchanged. The group in the middle was the CONTROL group in both years. In this way, differences in laying date between both years should be caused by differences in  $T_a$  only. We are aware of the fact that the design was one of pseudoreplication (Hurlbert 1984). Because captive starlings held in small groups do not breed, we were not able to increase the sample size.

*Climate chamber experiment.* In 1997 we were able to let the starlings breed in three large climate chambers, equipped with wire aviaries ( $1.8 \times 1.8 \times 1.8$  m) in which four males and seven females had access to eight nestboxes. Four plastic screens ( $1.0 \times 0.4$  m) were put up between two adjacent nestboxes, making it impossible for the birds, sitting in front of their

own nestbox, to see each other. Earlier experiments had shown that in this way, fighting over nestboxes was reduced substantially and birds started laying shortly after introduction of the screens (Meijer and Gwinner, unpubl. data). Birds were introduced into the aviaries on 19 March 1997, the temperature was set at 9°C during the day and 5°C (lower limit of the chamber) during the night. Daylength (time between sunrise and sunset without twilight) was adjusted to natural variation in weekly steps.  $T_a$  in the first chamber was increased by 5°C on 10 April, in the second chamber on 17 April, and in the third on 24 April.

## RESULTS

### FIELD

Starlings in southern Germany synchronized their laying. During the 10 years, 91% of the first clutches ( $n = 164$ ) were started during a 6-day period. Between years, the absolute start of this laying period varied by 14 days: in the warm spring of 1989 laying already started on 5 April (median), whereas in the cold spring of 1984 and 1986 laying did not start before 19 April. Days in March with  $T_{\min}$  above 4°C explained 81% of the variation in annual laying date ( $P < 0.001$ , Table 1 and Fig. 2). Deviations from the expected median annual laying date (residuals) were significantly correlated with  $T_{\min}$  during early April, just before laying (week 6 from 5–11 April,  $r = 0.52$ ,  $P < 0.05$ ). Although  $T_{\min}$  seemed to increase around laying (Fig. 3a), temperature before and during egg-formation was not significantly different (Wilcoxon signed-ranks test,  $T = 12.5$ ,  $P = 0.13$ ).

TABLE 1.  $R^2$  of the negative relation between annual laying date ( $n = 10$  years) of free-living European Starlings and March ambient temperatures.

Weeks in March	$T_{min}$	$T_{min} > 4^{\circ}C$	$T_{max}$
1	0.40	0.35	0.52
1, 2	0.39	0.58	0.55
1, 2, 3	0.43	0.69*	0.49
1, 2, 3, 4	0.54	0.81**	0.59
2, 3, 4	0.55	0.75**	0.58
3, 4	0.71*	0.86**	0.54
4	0.31	0.45	0.37

Bonferroni transformation was used to decrease Type I error to 0.05 using a value for  $\alpha$  equal to 0.05/7 = 0.007 (Beal and Khamis 1991); \*  $P < 0.007$ , \*\*  $P < 0.001$ .

CAPTIVITY

*Nestbox experiment.* During 1993, CONTROL females started laying around 10–15 April, and in 1994 at the end of April (Fig. 4). Observations on free-living starlings around Bielefeld showed a one week delay in the start of laying in 1994 compared to 1993 (Meijer, unpubl. data). Surprisingly,  $T_{min}$  of March was lower in 1993 than in 1994, but the opposite was true for the last two weeks in February and the first two weeks in April.

In both years, female body mass in captivity decreased during March and increased during the last weeks before laying. In 1993, mass decreased from  $93.6 \pm 5.0$  g on 1 March to  $83.7 \pm 3.6$  g on 15 March. However, in 1994, mass loss was much more gradual. Until 21 March the same females had lost only 1.7 g (Wilcoxon  $T = 0.0$ ,  $P < 0.01$ ) and reached minimum mass ( $82.5 \pm 4.2$  g) at the end of March or early April. A similar delay was observed for changes of bill color, female nest occupancy, and nest-building. The change in female bill color from black to yellow slowed down in March 1994 (an increase of 0.04 points  $day^{-1}$ ) compared to 1993 (0.06 points  $day^{-1}$ , Wilcoxon  $T = 6.0$ ,  $n = 9$ ,  $P = 0.05$ ). On 12 March, one week after introduction of nestboxes, 20 of 38 females occupied at least one nestbox in 1993, compared to only 7 of 42 females in 1994 ( $\chi^2_1 = 11.5$ ,  $P < 0.001$ ). On 24 March 1993, just before the start of the temperature experiment, the mean score of all CONTROL nests was  $3.4 \pm 1.6$  compared to  $1.7 \pm 1.1$  in 1994 (Mann-Whitney  $U$ -test;  $Z = -2.9$ ,  $P < 0.01$ ). Between the two years, we found no differences in color changes of the bill of CONTROL males (at the end of March a mean of 4.4 [1993] and 4.6 [1994]), or the number of males

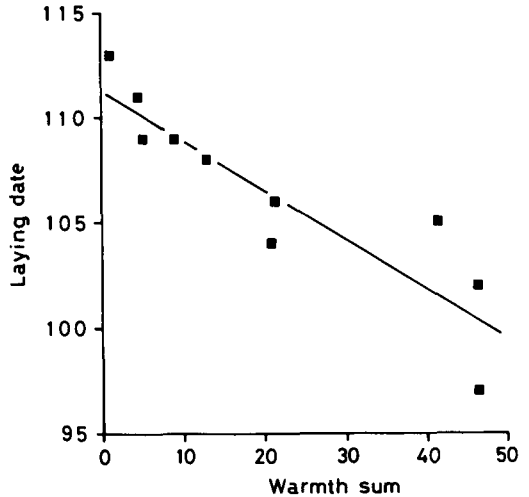


FIGURE 2. The relation between annual start of egg-laying (median) of free-living European Starlings and the warmth sum (WS) of the first four weeks in March (i.e., the temperature sum of days with  $T_{min} > 4^{\circ}C$ ). Laying date (LD) is presented as days from 1 January (day 100 = 10 April). Linear regression:  $LD = 111.3 - 0.236(WS)$ ,  $r^2 = 0.81$ ,  $P < 0.001$ .

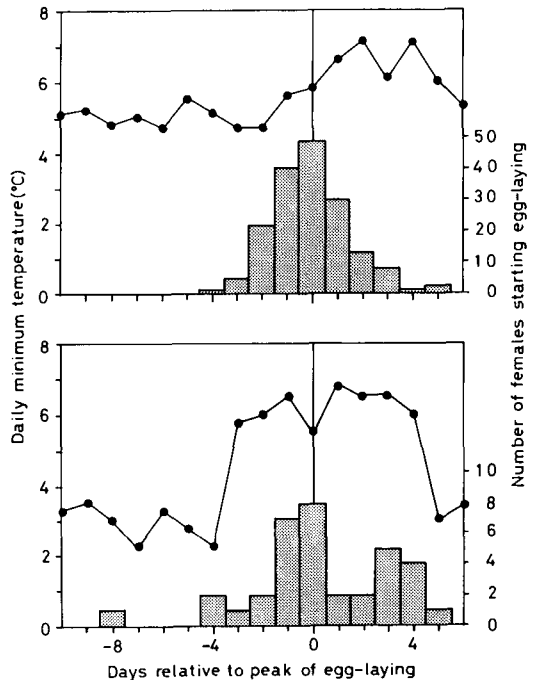


FIGURE 3. The start of egg-laying of free-living (upper panel, for 10 years) and captive European Starlings (lower panel, for 4 years) in relation to  $T_{min}$  around the peak of egg-laying.

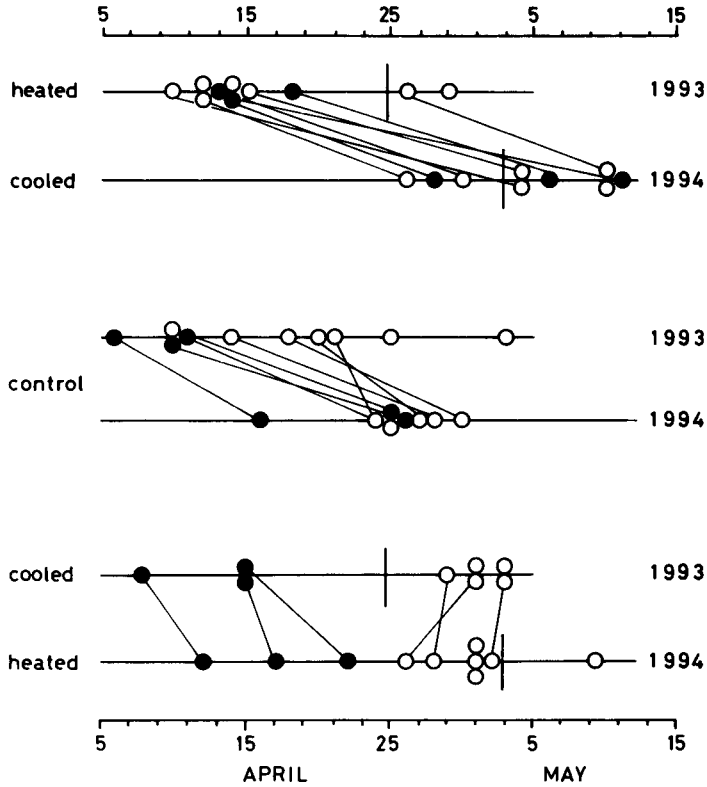


FIGURE 4. Laying dates of individual females in 1993 and 1994: the first group occupied heated nestboxes in 1993 and cooled ones in 1994, the second group had unmanipulated nestboxes in both years and served as controls, whereas the third group had cooled boxes in 1993 and heated ones in 1994. Laying dates of the same females are connected with lines. Solid and open dots represent females with and without breeding experience, respectively in 1992. Vertical lines show the end of the temperature manipulation.

occupying and defending nestboxes (7 and 6, respectively).

In 1993 female R (CONTROL) laid the first egg (laying date 6 April) followed by female YY (8 April, COLD). When we stopped the experiment (in the afternoon of 23 April), 8 of the 13 CONTROL and 8 of the 13 WARM females had almost finished laying (Fig. 4). At that time only 3 of the 12 COLD females (25%; all three with breeding experience in the previous year) had laid. During the experiment, significantly fewer COLD females started breeding compared to the females of the other two groups combined ( $\chi^2_1 = 5.4$ ,  $P = 0.02$ ). Within 6–10 days after removal of the ice packs, another five COLD females started laying and incubated their clutches. At the same time, only two CONTROL and two WARM females started laying (Fig. 4).

In 1994, in which the two experimental groups had changed position (treatment),

WARM female YY was the first to start laying (12 April), followed by CONTROL female R (16 April). Compared to 1993, CONTROL females started laying 12.5 (median) days later in 1994 (Wilcoxon  $T = 0.0$ ,  $P = 0.01$ ). As in the year before, the number of laying females of the WARM and CONTROL group (9 vs. 8, respectively) did not differ. WARM females started egg-laying only one day later as in the year before (with cooled nestboxes). Within this group, those three females which laid in 1993 during the cooling period, started 2–7 days later (Fig. 4), whereas those that laid directly after the end of the cooling period, laid 1–5 days earlier in 1994 (two-way ANOVA: interaction,  $F_{1,4} = 11.4$ ,  $P = 0.03$ ).

When on 2 May the ice packs were removed, only three COLD females had laid, again significantly less than in the other two groups combined ( $\chi^2_1 = 5.8$ ,  $P = 0.02$ ). Another six COLD

females started laying between 4–11 May, 2–9 days after the cooling was stopped. Within this period, only one WARM female started laying (Fig. 4). The overall change from heated nest-boxes in 1993 to cooled ones in 1994 delayed the onset of laying by 20.5 days, significantly more than the 12.5 days delay in the control group (Mann-Whitney  $U$ -test;  $U = 9.0$ ,  $P = 0.01$ ).

*Climate chamber experiment.* To investigate further if Starlings would start egg-formation after a rise in  $T_a$  only, we increased  $T_a$  by 5°C in the first chamber on 10 April, in the second on 17 April, and in the third one on 24 April. In the three chambers, laying started on 18 April (median, range 16–25 April,  $n = 7$  females), 25 April (21–29 April,  $n = 7$ ), and 1 May (19 April–6 May,  $n = 6$ ), respectively. In the last chamber, one female did not start laying and two females started before  $T_a$  was increased. Therefore, 18 out of 20 females started laying more than four days after  $T_a$  increased. Overall, absolute Julian laying-date differed significantly between the three aviaries (Kruskal-Wallis test,  $H_{2,20} = 7.4$ ,  $P = 0.03$ ). Relative to the increase in  $T_a$ , the start of egg-laying in the three groups did not differ ( $H_{2,20} = 2.2$ ,  $P = 0.33$ ). The delay was 7–8 days in all three groups.

## DISCUSSION

### TIMING OF THE BREEDING SEASON

Between years, onset of laying of both free-living and ad libitum fed captive European Starlings differed by as much as two weeks. Ambient temperature and/or food availability seem to influence timing of the breeding season. Low  $T_a$  during the end of the winter seems to retard the development of the reproductive system of ad libitum fed starlings and thereby the start of the breeding season. That 1994 would be a “late” year was clear from our observations during the first half of March, like delayed color changes of the bill (which follow gonadal development with a delay of some weeks, Gwinner 1975), delayed body mass changes, fewer females occupying nestboxes, and less nestbuilding behavior. It seems that the extremely cold second half of February 1994, with  $T_{\min}$  of  $-10^\circ\text{C}$  from 14–24 February compared with the steadily increasing  $T_a$  from late February ( $-5^\circ\text{C}$ ) until mid March in 1993 ( $7^\circ\text{C}$ ), slowed down the development of the reproductive system.

Spring temperature affected the onset of the breeding season of free-living starlings, especially the weather during March which seemed to set a time window for laying (Table 1). The yearly shift of the laying window could be affected by  $T_a$  directly via allocation of energy normally used for gonadal development to thermoregulation, but the daily energetic cost of development accounts for a few percent of basal metabolic rate (Ricklefs 1974). However, laboratory experiments show that low temperature delays the photoperiodic induction of gonadal growth in female White-crowned Sparrows (*Zonotrichia leucophrys*, Lewis and Farner 1973), domestic male Canaries (*Serinus canarius*, Storey and Nicholls 1982), male Black-billed Magpies (*Pica pica*, Jones 1986), and Willow Tits (*Parus montanus*, Silverin and Viebke 1994). These, together with our own experiments, were all carried out under ad libitum feeding conditions and show that development of the reproductive system, which influences the laying window, may be sensitive to  $T_a$  in an adaptive way, independent of food availability. Even by severe food restriction, resulting in a 20% body mass reduction, Meijer (1991) was unable to slow down the development of the gonads of male and female starlings.

For the 6 weeks before laying, the warmth sum accumulated to a level of 200–250 in early laying years, that is a mean  $T_{\min}$  of  $5\text{--}6^\circ\text{C}$ , whereas in late years it did not reach a level of 100 (mean  $T_{\min}$  of  $2\text{--}3^\circ\text{C}$ ). For all 10 years, this relation was highly significant ( $r^2 = 0.81$ ,  $P < 0.001$ ): this means that in late years, temperature during the six weeks before laying was much lower than during the same period in early years. Similar observations were reported for other starling colonies (Nagy and Merkel 1986), as well as for tits (Schmidt 1984, Perrins and McCleery 1989). Kluijver (1951) suggested that breeding would start relatively earlier with regard to any given warmth sum, the later the date (see also Perrins and McCleery 1989), which could be an effect of the increase in daylight hours (and thereby longer foraging time) and the decrease in night hours (and thereby shorter fasting time). Furthermore, during the 10 years of data collection,  $T_a$  increased steadily during spring in southern Germany ( $0.10\text{--}0.15^\circ\text{C day}^{-1}$ ,  $r^2 = 0.76$ ,  $P < 0.01$ ), thereby reducing thermoregulation costs later on in the season. Besides these more energetic considerations, speeding up

of the breeding season in late years is adaptive, because in most species survival of the young decreases with progressive laying date. Furthermore, in tits, late breeding has negative consequences for the parents' molt (Nilsson and Svensson 1996).

#### TRIGGERING OF EGG-LAYING

Within the laying window, the start of egg-laying, especially in small species, follows after an increase in  $T_a$ . The 5-day period between an increase in  $T_a$  and the laying of the first eggs of tits, sparrows, and flycatchers indicates that egg-formation is triggered immediately by an increase in  $T_a$ , because 5 days is the time needed for rapid yolk formation in these species (Ricklefs 1974, Walsberg 1983). Our data show that  $T_a$  has a similar effect in starlings, which also need 5 days for egg-formation (Ricklefs 1974, 1976). Our free-living starlings shifted their onset of laying in relation to the weather in early April. Finnish starlings laid one week after a temperature increase (Korpimäki 1978). In captivity, CONTROL starlings laid during a period with elevated temperatures, shortly after  $T_{min}$  had increased by 4–5°C (Fig. 3b, Meijer and Langer 1995). After the cooling of the nestboxes was stopped, the COLD females started laying within 2–10 days, and in the climate chamber experiment, a 5°C increase in  $T_a$  resulted in egg-laying 7–8 days later in all three groups.

Could egg-formation be so costly (Perrins 1970) that it is only possible on warm days by using energy normally used for thermoregulation? This allocation principle was suggested by Jones (1973 in Perrins 1979) to explain the fact that small individual tits (with lower thermoregulation costs) start egg laying before larger individuals, and by Perrins (1979) and Magrath (1991) for the fact that  $T_a$  differences during egg formation correlate with differences in egg mass within the clutch of tits and blackbirds *Turdus merula*, respectively. The energetic cost of egg formation for small passerines (< 100 g) is relatively low and averages only 3–5% of their daily energy expenditure of 3 times basal metabolic rate (Meijer and Drent 1998). Only a small increase in daily foraging time would yield enough energy to produce the eggs. But eggs not only need energy in the form of fat or carbohydrates, but also protein. Compared to the requirements during the non-laying period, the laying female needs 30–70% more protein (Rob-

bins 1981). Therefore, not energy but protein availability, normally represented by insects, could be important for the timing of egg-laying. Because temperature strongly affects insect behavior and growth (Jones 1973 in Ojanen et al. 1981), females could use an abrupt increase in temperature as a predictor for the increase in protein availability and thereby as a trigger for the start of egg-formation. Insects would become available one week later, during the second half of the egg-formation period (Ojanen et al. 1981) when albumen is built up and most of the egg-protein is needed. Laying interruptions and the decrease in egg mass in relation to low  $T_a$  during laying could result from a decrease in insect availability. Furthermore, smaller females need less protein for maintenance and could therefore allocate more of the total protein intake to egg-formation and thereby start laying before larger females.

Because  $T_{min}$  affects the timing of the breeding season and the decision to start egg-formation more than does  $T_{max}$  (Table 1 and Fig. 2), it seems that the starlings are sensitive to  $T_{min}$ , which is usually lowest at night. Roosting in the cooled nestboxes led to a delay in the start of egg-laying. WARM and CONTROL females started egg-laying at the same moment, probably triggered by the same increase in  $T_{min}$ .

Because the energetic cost of gonadal development and of egg-laying for starlings and other small passerines amounts to only a few percent of their daily energy budget, the sensitivity of the reproductive system to spring temperatures seems to be an adaptive response, timing the period for laying (short-term  $T_a$  effect) and for raising the young (long-term effect) to periods with high food availability.

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