

SUPPLEMENTAL FOOD AND LAYING DATE IN THE EUROPEAN STARLING¹

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One can distinguish two main hypotheses concerning the timing of breeding in temperate nidicolous birds: (1) the female starts laying eggs in response to some external cue(s) in such a way that maximum nestling demand coincides with the period of highest food abundance (Lack 1954); (2) laying females are food-constrained and cannot start laying until they can accumulate enough energy to form eggs (Perrins 1970). The latter hypothesis was based on the observation that, while young Great Tits (*Parus major*) and Manx Shearwaters (*Puffinus puffinus*) from early broods survived better than those from late broods, clutches were often started later than would be optimal with regard to the food peak (Perrins 1965, 1966). A third hypothesis, "the food stability hypothesis" (Bryant 1975), is a variant of Lack's original hypothesis. The critical period is that of incubation rather than the nestling period, and females are thought to defer laying until the risk of encountering poor feeding conditions during incubation is minimal.

It follows from Perrins' food limitation hypothesis that experimental provisioning of adequate food should result in an earlier start of laying. This has been supported in a number of studies on different species of birds (for reviews see Arcese and Smith 1988, Daan et al. 1988, Boutin 1990).

The European Starling (*Sturnus vulgaris*) is one of the earliest migrants to return to southern Sweden in spring, arriving in late February or early March. More or less immediately on arrival, prospective nest-holes are visited and defended against other Starlings. Still laying does not start until the last days of April or, usually, the first week of May (median dates in 14 years prior to 1989 were between 29 April and 10 May; Källander and Karlsson, unpubl.). This makes the Starling an appropriate species on which to test the food limitation hypothesis; this paper presents the results of experiments in which Starlings were supplied with extra food prior to laying.

STUDY AREA AND METHODS

The study was carried out in 1982, 1985 and 1990 in the Revinge area about 20 km east of Lund, South Sweden. The ca. 40 km² area is predominantly grazed,

permanent grassland. Starlings are very common, nesting both colonially and solitarily, on buildings, in tree holes, and in nestboxes. For this study, nestbox-breeding colonies were used. Sjötorp has been monitored since 1972 and comprised 44 boxes, the boxes being situated both on abandoned buildings and surrounding trees; V. Tvet was established in 1981 with 16 boxes in a small, open birch grove; at Stensoffa only seven boxes were available, put up in 1985 at the edge of a wood facing rough pasture; at Amenebro 20 boxes were put up in 1986. The nestboxes used were of the same type and dimensions at all the sites; experimental and control sites were 2.4-4.2 km apart.

Experimental Starlings were fed mealworms (*Tenebrio larva*) in plastic cups 10 cm wide and 4 cm deep attached to the side of each nestbox except in 1990 when small cups were placed inside eight boxes at Amenebro. In 1982, provisioning in the V. Tvet colony started on 2 April (30 days before median laying date of control birds). Every evening after the Starlings had gone to roost, each container was supplied with about 50 g of mealworms. This ration was gradually increased, and from 12 April 100 g were supplied daily. In 1985, 100 g mealworms were supplied twice a day at each box in the Stensoffa colony, in the morning and in the evening, starting on 16 April (24 days before median laying date of controls). In 1990, feeding started in the Amenebro colony on 20 March (34 days before median laying date of controls); after 1 April the cups were refilled twice daily. In each year food provisioning stopped when all females had started laying (except in 1982 when two females started laying after food had been withdrawn). The amount of mealworms eaten varied somewhat but 100 g per day and nestbox can be taken as a rough estimate.

The Starlings usually started feeding on the mealworms immediately, and in 1982 cups were almost always empty at the time they were refilled in the evening. In 1985 and 1990, variable amounts of mealworms sometimes remained in one or more cups. Observations suggested that most mealworms were eaten by the Starlings, but it was impossible to prevent other species from using them. In 1982 a pair of Jackdaws (*Corvus monedula*), and in 1985 a Hooded Crow (*C. corone*) and a Great Spotted Woodpecker (*Dendrocopos major*) were the most serious competitors for the artificial food supply.

The mean mass of adult Starlings in our study area was ca. 82 g. From the formula given by Walsberg (1980), an individual Starling's daily energy expenditure (DEE) can be estimated at 172 kJ. The energy content of a mealworm was ca. 0.02 kJ per g dry mass

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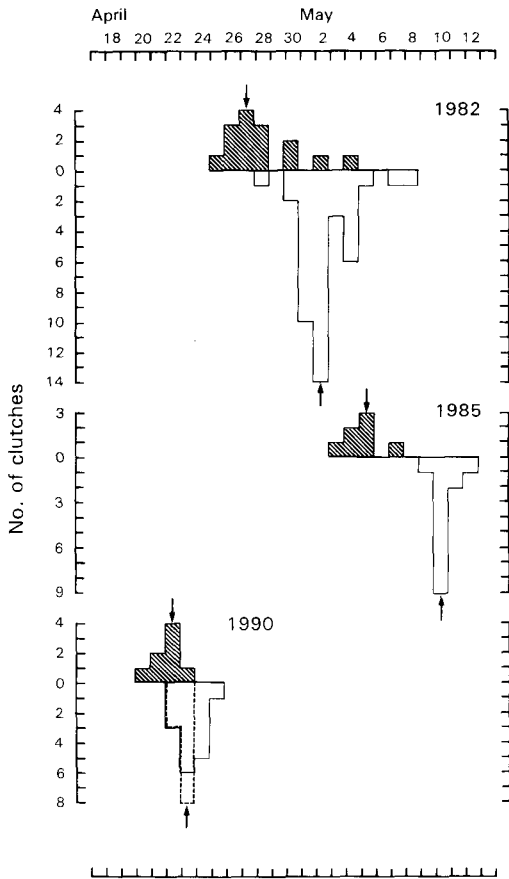


FIGURE 1. Distributions of laying dates of experimental (hatched bars) and control Starlings (open bars) in the three study years. In the bottom histogram, bars delimited by a broken line refer to control birds within the experimental colony, those delimited by an unbroken line to birds in a separate control colony. Arrows indicate median laying dates.

(37% of fresh mass). With a digestive efficiency of 74% (Taitt 1973), the daily intake requirements correspond to 237 kJ, or 31 g mealworms (fresh mass). In feeding trials using mealworms, Taitt (1973) measured DEE values of 181 and 153 kJ for male (75 g) and female (73 g) Starlings, respectively. This is close to the 172 kJ (for birds weighing 82 g) given by the Walsberg equation. Thus, most of the time, experimental birds were fed mealworms in amounts considerably exceeding the total energy requirements of a pair.

The nestboxes were checked regularly, and after laying had started the eggs were weighed every (1985) or every other day (1982). In 1982 nestlings were weighed when 13 days old. The length of the nestling period was not checked in order not to cause premature leaving, but observations from a distance showed that nestlings of experimental pairs fledged after the normal

time of ca. 20 days. Soon after fledging the boxes were checked for dead chicks.

RESULTS

Experimental birds started laying eggs significantly earlier than controls in 1982 and 1985 (Fig. 1; Mann-Whitney U -test, $U = 58.5$ and $U = 0$, respectively, $P < 0.001$ in both years), the median laying dates being five days earlier. In 1990, when mealworms were supplied inside eight nestboxes, fed birds started slightly earlier than unfed ones both within the colony ($U = 13$, $P = 0.005$) and compared with birds in a control colony ($U = 12$, $P = 0.001$; Fig. 1). In years without supplementary feeding no significant differences in median laying dates were found between the different colonies we monitored in the Revinge area (Källander and Karlsson, unpubl.). We thus conclude that the extra food advanced laying in Starlings at Revinge.

Mean clutch size was 5.40 ± 0.83 SD ($n = 15$) for experimental vs. 5.39 ± 0.79 ($n = 38$) for control birds in 1982, 5.71 ± 0.49 ($n = 7$) vs. 5.64 ± 0.74 ($n = 14$) in 1985, and 6.00 ± 0.53 ($n = 8$) vs. 5.82 ± 0.60 ($n = 11$) in 1990; none of these differences is statistically significant.

In 1982, eggs were 4% heavier in the experimental colony than in the control, and the masses of both the first (7.62 g vs. 7.37 g) and the last (7.37 g vs. 6.97 g) egg in the laying sequence were significantly greater in the experimental colony (t -test, $P < 0.01$). However, neither in 1985 nor in a similar experiment in 1984 (L. Gezelius and M. Grahn, unpubl.) was there a difference in egg mass between experimental and control birds.

In 1982, nestlings were weighed when 13 days old. The mean mass of 61 young in the experimental colony was identical to that of 104 young in the control colony, 73.07 g (SD 6.31 and 6.07, respectively). However, mean nestling mass on Day 14 tended to increase with the progress of the season. This trend was suggested for the experimental colony (0.85 g/day, $r = 0.439$, $df = 12$, n.s.) and was statistically significant for the control (2.92 g/day, $r = 0.753$, $df = 21$, $P < 0.001$). The same was true in the preceding year for 69 broods at Sjötorp and surrounding areas (0.95 g/day, $r = 0.296$, $df = 67$, $P < 0.02$). The trend was not caused by early broods being larger and therefore lighter than later broods (correlations between brood size and date were non-significant in all cases).

In 1982, the mean number of fledglings was 4.07 ± 1.71 in the experimental, and 4.21 ± 1.53 in the control colony, a non-significant difference. Fledging success could not be determined in 1985, but in 1990 there was a difference in the mean number of young fledging from experimental and control boxes at Amenebro (4.25 ± 1.39 vs. 5.64 ± 0.81 , $t = 2.96$, $P < 0.01$).

DISCUSSION

Perrins (1970) observed that Great Tits often started laying later than would be optimal with regard to brood-raising and fledging survival and suggested that this was because females were food-constrained. Following the early experiments by Källander (1974) and Yom-Tov (1974), numerous food supplementation experiments have been carried out to test this hypothesis in

a variety of birds (reviews in Arcese and Smith 1988, Daan et al. 1988, Boutin 1990; also see Nilsson and Svensson 1993; Nilsson, in press). As in the present study, in nearly all of these studies food-supplemented females have started laying earlier than control females. However, the response has mostly been moderate (see Table 1 of Meijer et al. 1990), suggesting that the birds do not base their decision when to start laying entirely on their own nutritional state but use other cues as well (Högstedt 1981).

This problem has recently been elaborated by Meijer et al. (1990) and Schultz (1991). The former authors suggested that there exists a "reproductive window," during which breeding can take place and also envisage a linear relationship between food abundance or food acquisition rate and start of laying. However, one of the problems with this attractive interpretation is how to define the window's lower limit in the field. For instance, during 14 years at Revinge, the earliest date that clutch initiation was recorded among unmanipulated Starlings was 26 April. In the extremely warm (and thus phenologically early) years of 1989 and 1990, however, control birds started egg-laying on 19 and 22 April, respectively. Thus the Starling's reproductive window in southernmost Sweden at least must include 19 April. Why then did not food-provisioned Starlings start much earlier in 1982 and 1985? One possibility, of course, is that, although abundant, the extra food they received was not sufficient (with respect to energy or protein, or some limiting nutrient). Only new feeding experiments using more, and a more varied, food can determine this.

Schultz (1991) looked at the problem from a different perspective. He argued that there exists a "saturation" (i.e., threshold) level of energy below which breeding cannot start. Above this level, however, breeding date is unrelated to nutritional state, and breeding is initiated in response to some environmental cue(s) correlating with parental fitness. Such a cue could be any or a combination of intercorrelated variables such as ambient temperature, bud burst, invertebrate activity, etc. that indicate an optimum starting date. This hypothesis, which agrees with Perrins' (1970) original idea, would explain why food provisioning experiments usually have advanced laying by only a few days up to a week (but see exceptions in Meijer et al. 1990). The question, however, is how, in the field, one can determine that the saturation level has indeed been reached well before the birds start laying.

One prediction from the saturation level hypothesis is that effects of food supplementation should be weaker in situations when natural food is more abundant, for instance in certain years (Schultz 1991). This prediction has been supported in some of the studies he quotes, as well as in recent feeding experiments with Blue Tits (*Parus caeruleus*) (Nilsson, in press). The results of our study are also consistent with this prediction. In 1982 and 1985, which were the coolest of the three spring seasons (the means of mean daily temperature 10 days before control birds started laying were 6.4 and 6.5°C, respectively), median laying date of experimentally fed Starlings was advanced by five days. In 1990, the warmest spring (8.5°C), the difference between fed birds and controls was only about

one day. Thus, one could argue that, in the latter year, both food supplemented and control birds had been able to reach the saturation level necessary for breeding and that they initiated laying in response to some phenological information from the environment.

It follows from the above reasoning that advancement of laying in response to experimental food provisioning should only be expected in species in which females are food-constrained (sensu Perrins 1970), i.e., females that, in natural conditions, cannot attain the saturation level until after the optimal laying date. It remains to be seen how common this situation is; judging from the experimental feeding experiments reported so far, it seems to be the rule.

In agreement with most other feeding experiments, we found no effect of the food supplementation on clutch size, and no, or only a slight, influence on egg mass (see Nilsson and Svensson [1993] for a discussion of how birds use extra food to increase their fitness). There was a tendency for 13-day old nestlings to become heavier as the season proceeded and also for fledgling production to be better in control broods. Thus, there may exist a trade-off between early laying and nestling quality in the European Starling.

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SEXUAL DIMORPHISM IN BASAL METABOLISM AND BODY TEMPERATURE OF A LARGE BIRD, THE EMU¹

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Key words: Basal metabolism; body temperature; *Dromaius novaehollandiae*; Emu; ratite; sexual dimorphism.

The relationship between body mass and basal metabolic rate (BMR) for birds has had many revisions since Kleiber (1932) included three birds in his initial examination of this relationship for homeotherms. Lasiewski and Dawson (1967) calculated separate relationships for the passerines and non-passerines. Later, Aschoff and Pohl (1970) showed significant differences between the BMR measurements of birds in their normal quiet phase (ρ), as opposed to the active phase (α), of the daily activity cycle. Dann et al. (1989) recently presented an equation based on the ρ -phase BMR measurements of 263 species. They demonstrate that some orders, such as Falconiformes, diverge from the general relationship. This also appears to be so for ratites. Withers (1983) found the BMR of the Ostrich (*Struthio camelus*) to be about 40% lower than usual for birds. Calder and Dawson (1978) also reported similar low BMRs for three species of kiwi (*Apteryx oweni*, *A. australis*, and *A. haasti*). They also obtained low values for the Emu (*Dromaius novaehollandiae*), but an earlier study by Crawford and Lasiewski (1968) suggested that the BMR of the Emu was not different from other non-passerine species. There are problems with both studies of the Emu; in the 1968 study, Emus were hooded and restrained, and the 1978 measurements were made in the late afternoon on birds with little experience of the procedures. We re-examined the BMR and resting body temperature of the Emu. We also examined the possibility of differences in BMR due to sex and time of year because of the long inactive period (eight weeks)

that males face during their incubation fast in winter (Davies 1974).

MATERIALS AND METHODS

Five Emus of each sex were examined, sex being determined by cloacal examination. Experiments were carried out in winter (July–September) and summer (November–February). None of the Emus were laying or incubating during the study. Birds were familiarized with the experimental procedure for at least two weeks before data collection began.

Experiments were carried out at night during the quiet phase of the Emu's diurnal cycle between 18:00 and 03:30 local time. After 24 hr without food, an animal was placed in a large lexan chamber (1.8 × 1.0 × 0.6 m). This chamber was in a temperature-controlled room in which air temperature was controlled at 25 ± 0.5°C.

Dry air, which flowed into the chamber at approximately 150 liters/min, was measured with a Hastings Mass Flowmeter (Model HFM-201). A 125 ml/min sample of excurrent air was dried, scrubbed of CO₂ with ascarite®, redried and passed through an Applied Electrochemistry S3A-II oxygen analyzer. Five-second averages from the sensors measuring mass flow and O₂ concentration were logged on a personal computer via a 12-bit analog/digital converter (Sable Systems, USA) resulting in a maximum resolution of 0.001% O₂. The system was calibrated several times in each season by the Iron-burn method of Young et al. (1984). Calibration factors varied between 0.97 and 1.02.

Before being placed in the metabolism chamber, each Emu was weighed to the nearest 0.1 kg. After 1–2 hr, data collection was initiated and lasted for an additional 2–3 hr. Body temperature (T_b; measured 10 cm into the cloaca) was taken within 5 min of completion of metabolic measurements with a Jenco electronic thermometer, calibrated against a mercury-in-glass

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