

FOOD AVAILABILITY AND EGG-LAYING OF CAPTIVE EUROPEAN STARLINGS¹

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Abstract. We investigated egg-laying in captive European starlings, *Sturnus vulgaris*, with moderate differences in food availability. From February–March onwards, experimentally food-rationed (FR) birds got 80% of the food ration of an ad libitum fed control (AL-FR) group, which led to a reduction in body mass and activity, and a redigestion of feces. FR birds showed less courtship behavior than AL-FR birds, and did not start laying until their food ration was increased to 90%, during the second half of the breeding season. Fewer FR than AL-FR females started laying. Among those that did, body mass was 6–7 g lower than that of AL-FR females throughout courtship, laying and incubation. No differences in clutch size, egg mass and egg composition were found. Compared to the AL-FR birds, mean laying date was 11–14 days earlier in ad libitum fed (AL) starlings that had no visual contact with FR birds. Initiation of egg-laying in FR starlings apparently was triggered by increased food availability, whereas that of AL-FR starlings may have been delayed because of the near absence of breeding activity among the FR birds with which they were in visual contact.

Key words: Egg-laying; food availability; egg mass; body mass; social stimulation; starlings.

INTRODUCTION

In temperate regions, there is an enormous seasonal variation in temperature, food availability, and available foraging time, and correct timing of breeding, therefore, is extremely important. Single-brooded bird species should time their breeding effort in such a way that the young are fed in a period when food is most abundant (Lack 1954). However, detailed studies suggest that birds may breed either on the rising or the declining slopes of food availability (Perrins 1970, Daan et al. 1988).

Although environmental conditions may still be suitable for breeding at the end of spring and the beginning of summer, in most temperate bird species the reproductive system (the hypothalamus-hypophyse-gonad axis), is turned off (Farner and Follett 1979). The short days of autumn turn on the reproductive system again. During winter, gonadal development is initially slow, but accelerates during the courtship phase in early spring (Murton and Westwood 1977).

The effect of food availability on reproductive development differs between the two phases. During the winter months, or in short-day laboratory conditions, gonadal development is sometimes slightly affected (Cavé 1968, Huxley

1976, Wingfield 1980, Hiron et al. 1984), sometimes unaffected by food availability (Meijer and Schwabl 1989, Meijer 1991).

The start of the second developmental phase, which is associated with the formation of eggs and egg-laying itself, strongly depends on food availability. In years in which food availability is high or increases earlier, egg-laying is advanced (see e.g., Gibb 1950 for tits *Parus* spp., Dunnett 1955 for European starling *Sturnus vulgaris*, Korpimäki 1987 for Tengmalm's Owl *Aegolius funereus*, and Dijkstra 1988 for European Kestrel *Falco tinnunculus*). Further support for the role of food comes from food supplementation experiments in the field, which almost all show an advance in date of laying (for recent reviews see Davies and Lundberg 1985, Daan et al. 1988, Meijer et al. 1990). By contrast, a drastic food rationing in captive-breeding European kestrels delayed their onset of laying (Meijer et al. 1988).

To unravel the mechanisms influencing egg-laying in the European starling, a large breeding colony was established in captivity (see Meijer 1990, 1992, 1993). This paper addresses (a) how a moderate reduction in food availability affects timing of laying, clutch size and egg quality, and (b) how the behavior of these food-rationed starlings affects the timing of reproduction of ad libitum fed birds, with which they have visual contact.

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METHODS

Starlings were caught in the Netherlands in August 1988 and housed in large outdoor aviaries in Bielefeld (52°01'N, 8°32'E), Germany. In early February 1991, two groups of starlings, one food rationed (from now on called the FR group), the other fed ad libitum (AL-FR group) were housed in *adjacent* aviaries (4.8 × 3.6 × 2.5 m, 1 × w × h), in visual contact. In each group, seven adult males and 14 adult females had access to 14 nestboxes (21 × 21 × 25 cm, nestbox bottom area 371 cm²) from 5 March onwards. A third group of 14 males and 28 females was housed without visual contact with the AL-FR and FR birds in one large aviary (4.4 × 7.2 × 2.5 m) and had access to 30 nestboxes (AL birds).

Birds were fed every morning at 08:00 (MEST). The AL and AL-FR birds were given poultry pellets (Hemo Enten Mast Allein Korn) ad libitum, supplemented with a 100 g mixture of commercial insect food (Claus #3). The FR birds, received (with a delay of 3–4 days) 80% of the amount of both food types eaten by the AL-FR birds. This ration was increased to 90% on 6 May (start of the second half of the starlings' laying period; Meijer 1990, 1992). Bathing and drinking water, supplemented with a vitamin mixture, was renewed every morning.

Nestboxes were checked each day at 12:00, and all newly laid eggs individually marked. At 15:00 these eggs were weighed to the nearest 0.01 g (Sartorius PT 120). Clutch sizes were only included in the analysis when females incubated normally after the laying period (see Meijer 1990, 1992).

Young were removed when the whole clutch had hatched. Every two to three weeks, all birds were captured at 08:00. Fat in the furcular region was scored on a scale from zero to five (Meijer et al. 1994), and the color of the beak on a scale from one (black) to five (yellow; Berthold 1964, Gwinner 1975). Birds were weighed to the nearest 0.1 g and checked for signs of molt. Birds were also weighed on a balance that was situated in front of the food container. To compare the two mass measurements, birds were weighed only early in the morning before they were fed the insect food.

In 1992, the same experiment was carried out with new groups. Food rationing (80%) started on 5 March, and the amount of food eaten by the AL-FR birds was measured daily, and there-

fore the delay for the FR starlings was shortened to only one day. The AL-FR and FR group consisted of 11 males and 15 females each, with access to 16 nestboxes. The AL aviary was partitioned into two by wire-mesh with 11 males and 15 females (and 16 nestboxes) in each part.

For comparisons between groups, only the first laying period, defined as the period until the first-laying females started a second clutch, was taken into account. Presentation of data will concentrate on the AL-FR and FR group, and only for the timing of laying the AL group will be taken into account.

AL-FR and FR birds were observed during the morning hours, using instantaneous sampling (Martin and Bateson 1986). Twice a week, during the morning hours, each group was observed for half an hour and every minute was recorded which birds showed courtship behavior (sitting in front or inside a nestbox). In the evening, the percentage of sleeping birds was observed once every half hour from 1800 until 2100 hr. Data are presented as means ± SD, unless otherwise stated.

RESULTS

FOOD CONSUMPTION

During March, after introduction of the nestboxes, the starlings' food intake increased. In both years, during the first half of the laying season (mid April–mid May), AL-FR birds consumed around 24 g/bird-day (Fig. 1), of which 4.8 g was insect food. In the FR group, all the food had been eaten around 14:00 (80% ration) or 17:00 (90%). We did not observe any starlings try to monopolize the food. In the late afternoon and evening we observed birds eating feces on the floor of the aviary. During April, May and June FR males and females spent on average 19 and 11% of the time doing so, AL-FR males and females only 5 and 2%, respectively.

BODY MASS

Females. In 1991, morning body masses of *all* AL-FR females (ca. 85 g, Fig. 2) increased slowly during April to reach their highest levels (90 g) during early May (first egg-laying period). During this period, no clear changes in fat reserves (7–8 g) were detectable. Thereafter, body mass and fat levels dropped to minimum levels (78 and 2 g, respectively) during early molt (second half of

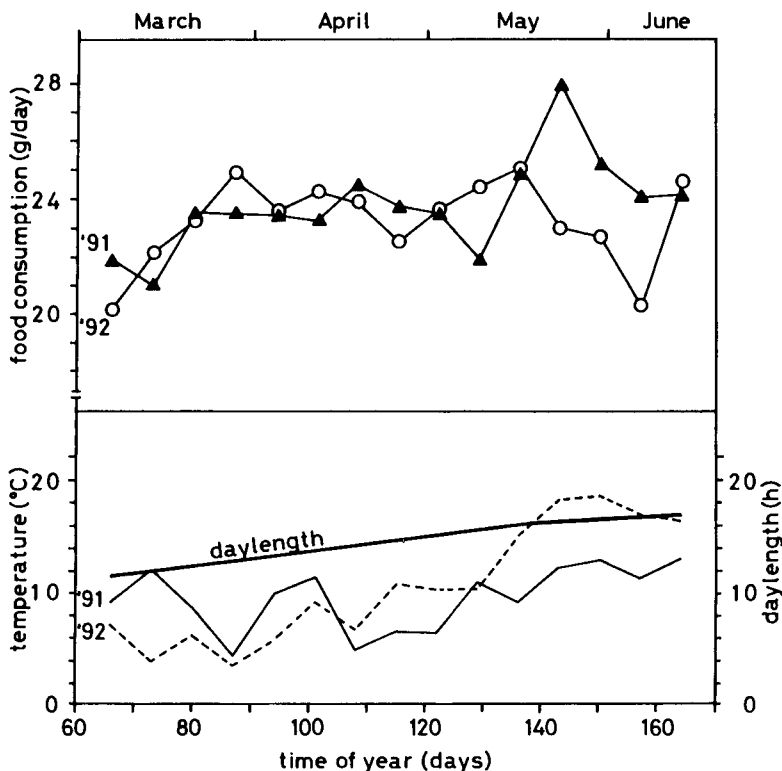


FIGURE 1. Changes in mean food intake (g/bird-day) of ad libitum fed (AL-FR) starlings, daylength (hr) and mean ambient temperature ($^{\circ}\text{C}$) during the spring of 1991 and 1992.

June). In 1992, similar changes in body mass were observed, but AL-FR females weighed only 78 g (Fig. 2), on average 7 g less than in March 1991.

After food rationing started in mid February 1991, body mass and fat of FR females dropped rapidly during the first two weeks, after which they stayed more or less constant (74 and 4 g) until mid April when body mass increased slowly by 3–4 g. After getting 90% of the ad libitum food ration, body mass increased within a week by 6 g. Fat reserves, however, remained the same. Thereafter, as in the AL-FR females, body mass and fat decreased slowly until early molt. In 1992, food rationing did not start until early March. Body mass of FR females levelled off at about 77 g during March and April, and did not increase until the food ration was raised to 90% (Fig. 2).

Males. Body mass in AL-FR males was highest at the end of March–early April (84–86 g), and decreased slowly to 78 g during early molt. Dur-

ing the courtship and laying periods, FR males weighed ca. 4–6 g less than AL-FR males.

BEAK COLOR

The beak color, an indicator of gonadal development (Berthold 1964, Gwinner 1975) showed no overall differences between AL-FR and FR females over the period from February to May when beaks became yellow (two-way analysis of variance, 1991: $F_{1,26} = 0.17$, $P = 0.68$; 1992: $F_{1,28} = 1.06$, $P = 0.31$) nor did we find a different development rate within this period (two-way ANOVA, interaction, 1991: $F_{4,104} = 0.48$, $P = 0.74$; 1992: $F_{4,112} = 0.58$, $P = 0.67$).

Male beak colors did not differ significantly (two-way ANOVA, 1991: $F_{1,12} = 2.89$, $P = 0.11$; 1992: $F_{1,4} = 1.98$, $P = 0.17$). In both years, however, beaks of FR males started with slightly lower scores than those of AL-FR males. During May, both groups reached similar maximum scores. Male beak colors developed similarly

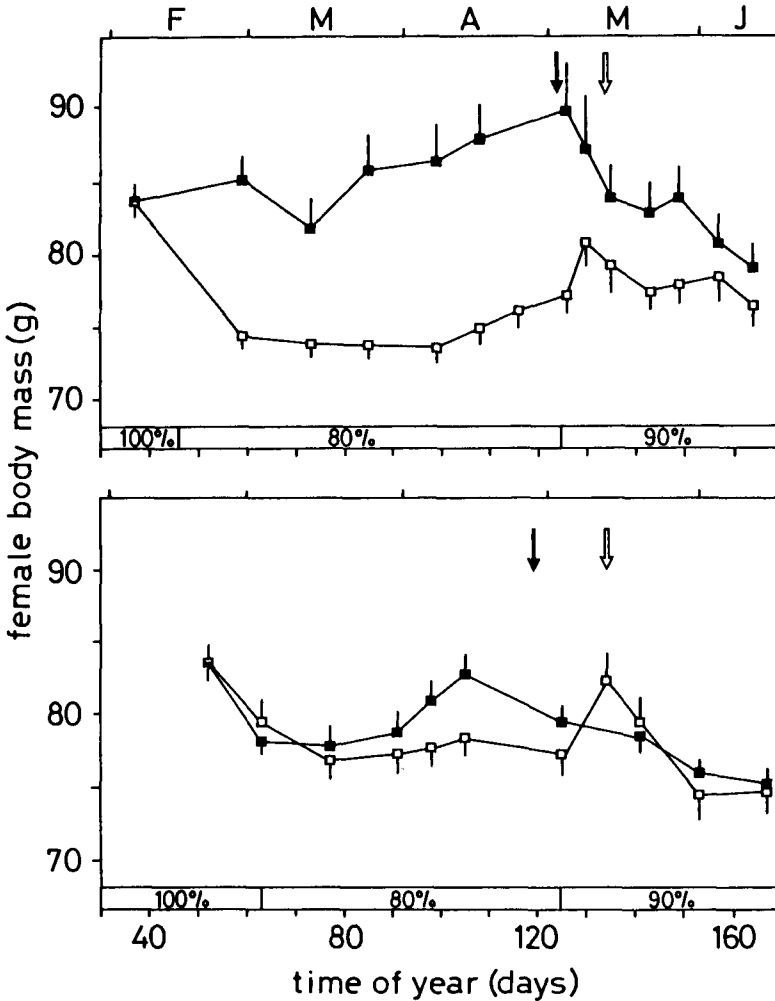


FIGURE 2. Mean (\pm SD) body mass (g) of *all ad libitum fed* (AL-FR, closed squares) and *food-rationed* (FR, open squares) female starlings. In 1992 (lower graph), food rationing (80% of ad libitum = 100%) started two weeks later than in 1991 (upper graph). On 6 May, the food ration was raised to 90%. Median date of laying for first clutches is indicated by arrows.

within the season (1991: $F_{4,48} = 0.53$, $P = 0.71$; 1992: $F_{4,80} = 1.65$, $P = 0.16$).

MATING PATTERN

Not all males occupied and defended one or two nestboxes. From the time nestboxes were introduced, a few of the males occupied most of them. Some males defended up to five nestboxes and 6–7 males occupied all the nestboxes. In the two years, three AL-FR males (on 19 April 1991, 4 and 7 May 1992) and one FR male (15 May 1992) died during the breeding season (no females died during the experiments). All four

deaths were associated with fights over nestboxes. In the two years, 8 out of 13 paired AL-FR males were polygynous, versus only 3 out of 14 paired FR males (Fisher exact test, $P = 0.04$).

BEHAVIOR

During March and April, almost twice as many AL-FR birds as FR birds showed courtship behavior (sitting in front of or inside their nestboxes and therefore occupying one or more nestboxes). For instance, during two morning observations in the first week of April 1992, four FR versus seven AL-FR males showed this behavior

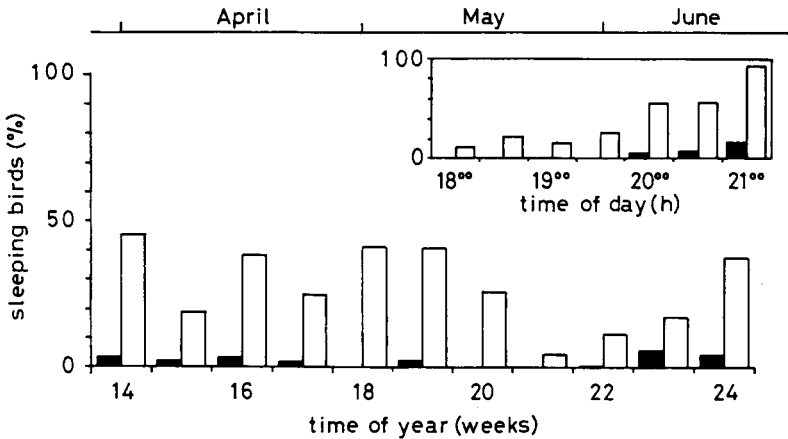


FIGURE 3. The percentage of sleeping AL-FR (black bars) and FR birds (open bars) during the course of the season between 18:00–21:00, and as an example the increase in sleeping birds after 18:00 for the first week in June (insert).

(Fisher test, $P = 0.19$), and five FR versus 11 AL-FR females (Fisher test, $P = 0.03$). This pattern was more or less constant, and also observed in the previous year.

In the evening after 18:00, the percentage of sleeping starlings (head under the wing) was much higher in the FR group ($26 \pm 13\%$ of the birds which we could observe) than in the AL-FR group ($2 \pm 2\%$, mean over 11 weeks of observation, Fisher test, $P = 0.02$, Fig. 3). Additionally, FR birds went to sleep earlier than AL-FR birds. In early June, for example, 55% of FR birds were sleeping at 20:00 versus 5% of the AL-FR birds (Fisher test, $P < 0.001$, Fig. 3).

DATE OF LAYING

The three groups of starlings (AL, AL-FR and FR), differed significantly in their timing of egg-laying (Kruskal-Wallis ANOVA, for 1991: $H_{(2,38)} = 26.5$, $P < 0.001$; and for 1992: $H_{(2,46)} = 27.7$, $P < 0.001$, Fig. 4).

In both years, AL groups of starlings that could not see FR birds laid earlier than AL-FR birds which were in visual contact with them (Mann-Whitney test, AL vs. AL-FR in 1991: $Z = -3.85$, $P = 0.0001$, and in 1992: $Z = -3.29$, $P = 0.001$).

In 1991, 11 of the 14 AL-FR females laid eggs during the first "synchronized" period (median date of laying of the first egg was 3–4 May), and 10 incubated their first clutch. In 1992, all 15 AL-FR females laid (median laying date 24 April), and incubated.

None of the FR females laid before 6 May in

1991, the day the food ration was increased to 90%. Within two weeks of this eight females started laying (median 14 May), and later incubated their clutches. Laying dates differed significantly between the FR and AL-FR groups (Mann-Whitney test, $Z = -2.75$, $P < 0.01$).

In 1992, two FR females laid eggs on the 80% food ration during the period in which the AL-FR females started egg-laying. After the food-ration was raised to 90% another nine females started laying. Median laying date for all 11 FR clutches was 16 May, again significantly later than for the AL-FR group (Mann-Whitney test, $Z = -3.50$, $P < 0.001$, Fig. 4). The proportion of females that laid eggs differed between the AL-FR and FR groups (the two years combined: Fisher exact test, $P = 0.028$).

BODY MASS OF LAYING FEMALES

Weighing the birds before 08:00 on a balance placed in front of the food container, showed that before laying the first or second egg (of first clutches), AL-FR females weighed 91.5 ± 3.4 g ($n = 17$, both years combined since mass of laying females was exactly the same, Fig. 5), and were significantly heavier than FR females (85.6 ± 3.7 , $n = 14$, MWU test, $Z = -3.57$, $P < 0.001$). This 5–7 g difference was found already during late courtship, and later on also during incubation (Fig. 5).

EGGS

The first clutches of the AL-FR females contained 3.9 ± 0.6 eggs (1991) and 4.3 ± 0.7 eggs

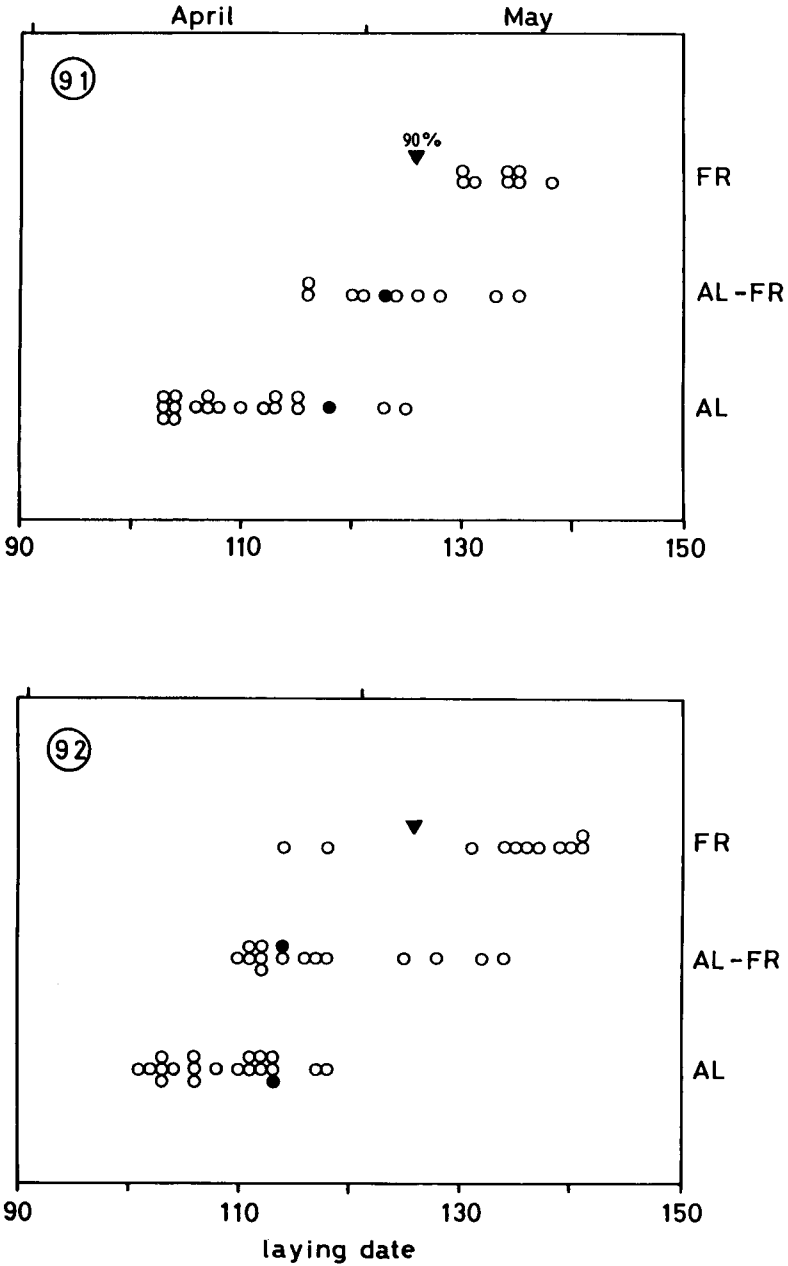


FIGURE 4. Date on which first clutches were started by food-rationed (FR), ad libitum fed (AL-FR) birds in visual contact with FR birds, and of AL birds which had no visual contact with FR birds. Filled circles indicate repeat clutch of females which deserted first clutch during laying.

(1992). The FR females laid 3.6 ± 1.1 (1991) and 3.8 ± 1.0 (1992) eggs per clutch, not significantly different from that of AL-FR females.

In neither year did the number of eggs in the first clutches of AL-FR females decrease with the

progress of the season. However, the clutches of the FR females, laid after the food ration was increased to 90%, decreased significantly in size by 0.18 egg/day ($n = 17, P < 0.01$).

The mean mass of eggs in clutches laid by

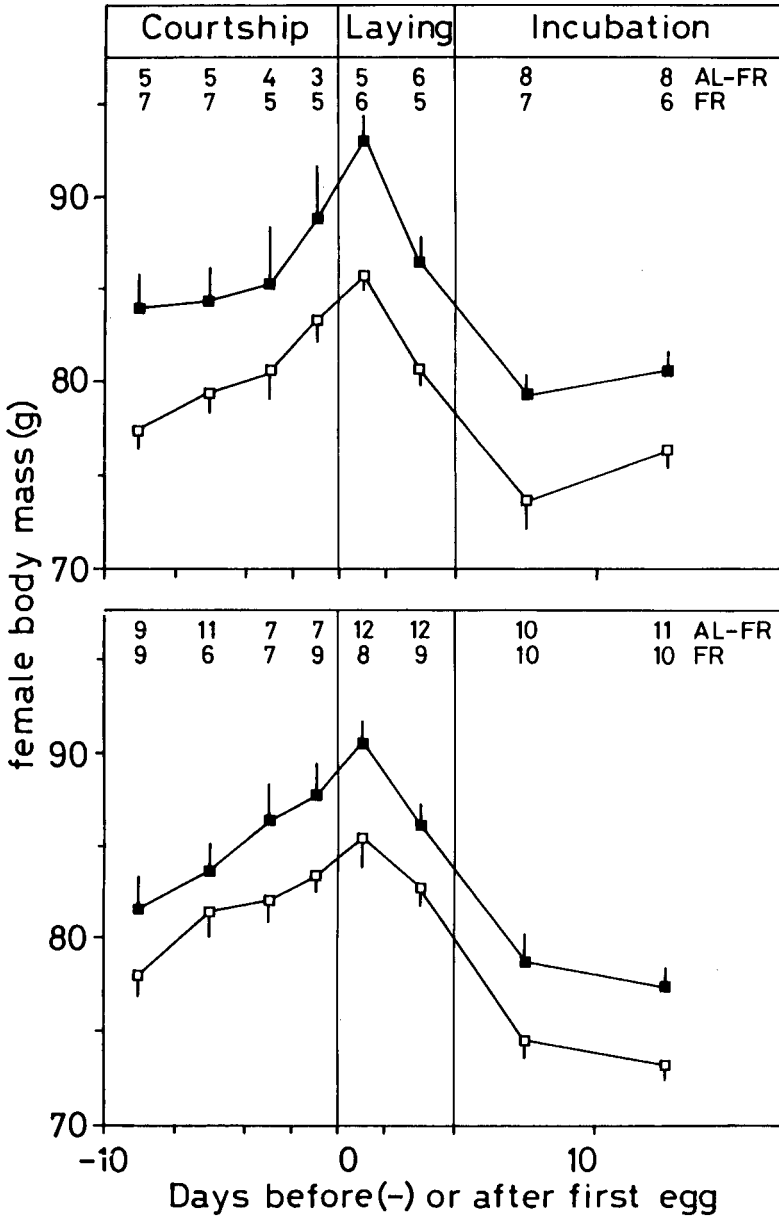


FIGURE 5. Mean (\pm SD) body mass (g) of AL-FR (closed squares) and FR (open squares) females during the courtship, (first) laying and incubation period in 1991 (upper graph) and 1992 (lower graph).

females with ad libitum or restricted food did not differ significantly (for AL-FR and FR females in 1991: 6.97 ± 0.59 and 6.86 ± 0.58 g; in 1992: 7.01 ± 0.77 and 6.87 ± 0.58 g, respectively).

In 1991, we analyzed the eggs of second clutches (19 eggs from five AL-FR clutches, 14 eggs

from four FR clutches) for differences in composition. The proportions of shell (7.5 and 8.1%), albumen (76.9 and 75.2%) and yolk (15.6 and 16.7%) were not significantly different between AL-FR and FR clutches. Neither did the dry mass of the three egg components differ between the groups.

DISCUSSION

REPRODUCTIVE SYSTEM

In temperate zone birds, the development of the reproductive system (hypothalamus-hypophyse-gonad axis) starts in early autumn after molt. Especially in females, the system develops slowly during the winter months, and only shortly before the start of egg-laying, the oviduct and ovary increase enormously in mass. This short second phase of four to ten days precedes egg-laying directly, and is the period in which eggs are formed (rapid yolk formation, see Ricklefs 1974, Murton and Westwood 1977).

How does food availability affect the reproductive system in the first (slow) and second (rapid) phase of development? European Kestrels which were drastically food rationed for more than four months (January until May), did not show differences in levels of reproductive hormones to ad libitum fed birds (Meijer and Schwabl 1989).

Decreasing the feeding time of photosensitive starlings from 12 to only 2 hr, led to a 15 g decrease in body mass compared to control birds, but the development of the gonads in both males and females was very similar in the two groups (Meijer 1991).

The change in beak color from black to yellow, an indicator of gonadal development (Berthold 1964, Gwinner 1975), progressed in parallel in AL-FR and FR starlings. As long as the amount of food remains above the starvation level, it thus appears to have little or no influence on the first phase of gonadal development.

ONSET OF LAYING

Egg formation depends entirely on body reserves in "capital" breeders such as swans, geese and ducks, but depends on food availability in "income" breeders, such as most passerine species (see Drent and Daan 1980, Thomas 1988). Almost all feeding experiments in the field have been carried out on income breeders and have shown that fed pairs of a large number of species advance laying compared to unfed pairs (for reviews see Davies and Lundberg 1985, Daan et al. 1988, Meijer et al. 1990). Starlings, fed for four weeks during late courtship with large amounts of mealworms, advanced laying by five days, compared to control birds (Källander and Karlsson 1993).

It is clear that in capital breeders only those females can start egg-laying *early* in the breeding season which have enough body reserves and nutrients (Schultz 1991). In those early laying females, it is the photoperiod which opens the temporal window for laying and sets the date of laying. Late females wait until the food situation improves, and more reserves can be built up, but still lay with lower reserve levels than early ones. Almost all body reserves are depleted during the egg-laying and incubation periods (see e.g., data for the mute swan *Cygnus olor* of Reynolds 1971, Beekman 1991).

Dawn body mass of laying females increased from late courtship to early laying by ca. 8–10 g, both in the ad libitum and the food restricted females (Fig. 5). Half of this mass increase represents oviduct growth; the other half is due to egg formation (see Ricklefs and Hussell 1984). This amount of increase is therefore a prerequisite for laying in starlings, and was observed in both AL-FR and FR females (Fig. 5).

Egg formation in the starling takes 4–5 days (Ricklefs 1974, 1976). After the food level was increased from 80 to 90% of that of the AL-FR group, FR females started laying within a week. Although body mass in these females increased immediately, over the whole period of (late) courtship, laying and incubation, they weighed 5–7 g less than AL-FR females. Therefore, it is not absolute mass, but the increase in food availability and so the possibility to increase (oviduct, ovarium and fat) mass, which triggers egg formation in the starling. Female starlings showed a moderate increase in fat levels shortly before laying, and lost fat during egg formation (4–5 g, Meijer, unpubl. data). The regression of oviduct and ovary, together with the loss of fat, in both groups resulted in a 11–14 g decrease in body mass between early laying and early incubation (Fig. 5). Only 1.5–1.9 g of fat is needed for a clutch of 4–5 eggs (Ricklefs 1974); the rest probably covers the cost for foraging on protein-rich food items such as insects.

In food-rationed European kestrels as well, it is higher food intake that triggered egg formation. Though body mass was very low, kestrels started egg formation immediately after food was again offered ad libitum (Meijer and Schwabl 1989). Experiments on starlings (this paper) and kestrels (Meijer and Schwabl 1989) thus show clearly that poor food supply arrests growth of the reproductive system before the start of egg formation.

In this state, the birds can react immediately if the food situation improves.

Because fed starlings in the field (Källander and Karlsson 1993) and ad libitum fed birds in captivity do not start egg-laying at the same date each year (Meijer, unpubl. data) there must be other factors besides food availability, which influence the start of laying. Many bird species breed earlier in warm springs than in cool ones, and for tits, laying normally starts four days after an increase in temperature (Kluyver 1952, Perrins and McCleery 1989). This four-day period is exactly the time tits need for egg formation (Haftorn 1981, 1985). Also in starlings, the start of egg-laying was preceded by a sharp increase in daily mean temperature about 6–7 days earlier (Korpimäki 1978, see also Fig. 1). This temperature effect on laying date can act directly on the birds, or indirectly via its effect on the food supply (Perrins and McCleery 1989). Earlier laying of fed starlings in 1990 compared to 1982 and 1985 correlated with higher ambient spring temperature (Källander and Karlsson 1993) and supports a direct effect, as does advanced laying by tits in nestboxes exposed to afternoon sun (Dhondt 1979) and in artificially heated nestboxes (Nager and van Noordwijk 1992, Yom-Tov and Wright 1993) in which temperature could not have affected food availability but only the energetics of the laying female.

SOCIAL ASPECTS

For a colonial species such as the starling, the “decision” to lay may not only be influenced by food but social factors may also be involved (Feare 1984). Members of the same colony start laying within one or two weeks, and it seems that this synchronization is brought about by social stimulation, e.g., singing (Feare 1984).

In both years, ad libitum fed (AL) starlings that could not see food-rated (FR) birds, laid earlier than ad libitum fed (AL-FR) birds which had visual contact with food-rated starlings. A similar effect was probably observed by Källander and Karlsson (1993). The difference in laying date between fed and unfed colonies was five days in 1982 and 1985 but only one day when only half of one colony was fed in 1990. Therefore, synchronization might be more important in the starling than the earliest possible start of breeding.

Which factors could be responsible for the retarded egg-laying of AL-FR birds relative to AL

birds? Firstly, the presence of a number of FR males showing almost no courtship behavior could have delayed the start of egg-laying. Secondly, not only the number of “active” males, but also the intensity of their singing could have been different. Unfortunately, we did not measure this. Further experiments are needed, but already at this moment we support Feare’s (1984) statement that the initiation of egg-laying in the starling seems to be influenced by a complex of factors involving photoperiod, climate, food availability and social stimulation.

EGGS

Unexpectedly, the food situation did not influence clutch size or eggs in any systematic way. AL-FR and FR females laid the same number of eggs per clutch. Total egg mass and the mass distribution over shell, albumen and yolk also were similar for the two groups. This confirms the findings of feeding experiments with free-living birds, both for the starling (Källander and Karlsson 1993) and other species (see Table 1 in Meijer et al. 1990). That is, there is a moderate advancement of laying date, but no change in clutch size. For the FR starlings this is remarkable, because during the courtship and laying periods, food intake and body mass were still lower than for the AL-FR group. The same was observed in free-living European Kestrels, in which late-laying females consumed 30% less food and had almost 50% less body reserves than early-laying females (Meijer et al. 1989). This does not necessarily mean that late-laying kestrels (or FR starlings) have less energy for egg formation than early layers (or AL-FR females). Lower body mass reduces energetic costs for maintenance and flight, and thermoregulation costs later in the breeding season are also lowered. Furthermore, FR starlings clearly saved energy by decreasing their activity, especially in the evening. Note also that FR starlings were often seen eating feces.

After the food ration was raised to 90%, FR females laid progressively smaller clutches over a period of ten days. Karlsson (1983) used the term “hypersynchronisation” to describe the phenomenon by which late laying starlings seem to synchronize their nestling or fledging period with that of late layers (also see Feare 1984). That FR females synchronized laying more than AL-FR females was probably due to more monogamous pairs in the first group (see also Meijer 1992).

In summary, it appears that after photoperiodic changes have set the onset and end of the breeding season of the starling, the prevailing food situation, and perhaps temperature, time the egg-laying more precisely. Social stimulation of the colony members apparently acts as a final fine-tuning. Reduced food availability is not reflected in the number or quality of eggs: the female may compensate by a reduction of body mass and activity, and by redigestion of feces.

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