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Costs of avian incubation

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Great tits with thin nests delay the onset of full incubation

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ABSTRACT

Birds not only vary their laying dates but are also flexible in their onset of incubation relative to the laying date. Two hypotheses have been formulated to explain this variation in the onset of incubation; birds may delay the onset of full incubation because 1) they are confronted with high energetic costs of early reproduction or 2) they may delay to synchronise hatch date of the offspring with the food peak in order to maximise fitness. In this paper, we report on the delay in onset of full incubation after clutch completion in relation to nest insulation. We measured the onset of full incubation, laying date, clutch size and nest thickness in 109 clutches of great tits *Parus major* (L.) in two breeding seasons (2002 and 2003). For a smaller sample, we determine the relationship between nest thickness and nest insulation. To study possible fitness-related consequences of the delay in onset of full incubation, we measured hatching probability and fledging mass of offspring. The delay in the onset of full incubation was negatively related to nest thickness, clutch size and laying date. Hatching probability was positively related to nest thickness and negatively related to the delay in onset of full incubation. We found no positive effect of incubation delay on nestling growth. The relationships reported in this study are consistent with the idea that delays in the onset of incubation are associated with energetic stress during early reproduction. This means that aspects of the cost of reproduction in the early phase matter to explain the delay in onset of full incubation.

INTRODUCTION

In birds, natural selection is thought to favour those parents that manage to have their nestlings coincide with the peak in food availability (Lack 1968; van Noordwijk *et al.* 1995) or slightly before (Daan & Tinbergen 1997). Since, in a seasonal environment, food peaks during a short period of time in the year, parents have to carefully time laying of the first egg (Perrins 1970; Perrins & McCleery 1989; Verhulst & Tinbergen 1991; Allander & Bennett 1995). Being too early in relation to the food peak may, for instance, lead to high investment for parents given low food availability (Daan *et al.* 1991), while being too late reduces the option for parents to initiate a second breeding attempt or to have sufficient time for moult (Nilsson & Svensson 1993b). Variation in the timing of breeding may, therefore, result in variation in reproductive success (Perrins 1970; Perrins & McCleery 1989; Verhulst & Tinbergen 1991; Allander & Bennett 1995).

Once egg laying has started, the breeding schedule (egg laying, incubation and nestling phase) is relatively fixed in time. Still, birds have some flexibility; they are free to decide when to initiate the onset of full incubation. Most species initiate incubation when laying the penultimate egg or even earlier, while others delay the onset of full incubation until completion of the clutch (Hébert 2002). Initiating incubation with clutch completion has as effect that embryonic development starts at the same time, and thus that eggs hatch simultaneously. In the light of the above, it is interesting that recent studies report that some birds delay incubation not only till clutch completion, but even till one or even more days after it. These studies either looked at blue tits *Parus caeruleus* L. (Nilsson 1994) or great tits *Parus major* L. (Monros *et al.* 1998; Cresswell & McCleery 2003; Naef-Daenzer *et al.* 2004).

Two not mutually exclusive hypotheses have been formulated to explain this phenomenon. The hypothesis most commonly mentioned is that birds delay the onset of full incubation in reaction to variation in environmental conditions. Temperature variation after the first egg has been laid may delay or accelerate the food peak, resulting in either an increase or a decrease in the period between the laying of the first egg and hatching of the eggs. This may cause a mismatch between hatch date and food peak (Visser *et al.* 1998; Cresswell & McCleery 2003). The delay can be a behavioural reaction to synchronise hatch date of the offspring with the food peak (Cresswell & McCleery 2003). The other hypothesis is that birds delay the onset of incubation due to energetic costs of reproduction (Nilsson 1994); delays could be either the result of costs related to the preceding period (i.e. egg laying phase) or a reaction to the expected expenditure during the following period (i.e. incubation phase), assuming that gaps during the incubation period will be more detrimental to developing embryos once full incubation has been initiated. During early reproduction (egg laying and incubation), birds are confronted with high energetic costs due to low and unpredictable ambient tem-

peratures (Ward 1996; Bryan & Bryant 1999; Stevenson & Bryant 2000; Weathers *et al.* 2002; Vézina & Williams 2002; chapter 6 and 7). Moreover, food availability is thought to be limited so that it may be difficult to balance energy expenditure. These hypotheses are referred to as the “strategic hypothesis” and the “constraint hypothesis”, respectively (Cresswell & McCleery 2003; Naef-Daenzer *et al.* 2004). The first hypothesis concentrate on either the benefits of synchronisation with the food peak, while the second hypothesis concentrate on the costs during early incubation. The timing of the onset of incubation represent a decision of the parent that aims to maximise fitness, and thus the optimal solution should both include constraints and the strategic decisions. Therefore, the outcome of the cost benefit analysis of the delay of incubation should both include early costs and late benefits of the timing of the onset of full incubation.

In this paper, we report on the phenomenon of delays in onset of full incubation in a population of nest-box breeding great tits in the Netherlands. Within the framework of a long-term study on the importance of selection on clutch size during the incubation phase for clutch size decisions (chapter 2), we intensively studied the incubation phase. We found interesting correlations between delays in the onset of full incubation in relation to nest thickness. We show that nest thickness is a good determinant of nest insulation and thus energetic costs of incubation. To study possible fitness-related consequences of the delay in onset of full incubation, we measured hatching probability and fledging mass. The latter is a good determinant of post-fledging survival (Naef-Daenzer *et al.* 2001) and of recruitment into the breeding population (Tinbergen & Boerlijst 1990; Verboven & Visser 1998; Both *et al.* 1999). We found that birds with thin nests delayed the onset of full incubation longer and that their eggs had a lower hatching probability. Offspring of the delayed clutches did not differ in condition. This is consistent with the idea that the energetic costs of incubation matter in the decision when to start full incubation.

METHODS

Study population

We conducted this study in the woodlots of the Lauwersmeer, a lake area in the north of the Netherlands (53°20' N - 6°12' E) during the breeding seasons of 2002 and 2003. The Lauwersmeer area was reclaimed in 1969 from the former Wadden Sea. Woodlots were planted starting from 1971 and consist mainly of mixed, deciduous trees of *Populus* sp., *Betula* sp., *Alnus* sp. and *Quercus* sp.. From 1980 till 1993 80 nest-boxes were present in part of the study area and from 1994 onwards it contained around 200 nest-boxes (for a map of the area see Tinbergen 2005).

In great tits, the female incubates the eggs; the male may assist by feeding her. After eggs hatch, both parents invest in feeding the chicks. In the study population

of great tits, clutches contained on average 9.3 ± 1.8 eggs ($n = 1140$; 1994-2003). Part of the females (9-51%; 1994-2003) produced a second clutch after successfully raising a first clutch.

Onset of full incubation

To establish the timing and intensity of breeding, we checked nest-boxes at least once a week from the beginning of April till the end of June. We determined laying date by counting back from the day of observation, assuming that one egg was laid per day. From the sixth egg onwards, we visited nest-boxes daily to estimate the *onset of full incubation*. We defined the onset of full incubation as the day on which either the female was found incubating or the eggs were found uncovered and warm. We defined the *delay in onset of full incubation* as the number of days between clutch completion and the onset of full incubation. After the initiation of incubation, we assumed females to fully incubate throughout the day intermittent with short periods away from the nests for foraging (we refer to this as the *period of full incubation* [days]). We defined the *total period of incubation* as the number of days between clutch completion and hatching of the eggs.

Nest measures and nest insulation

We measured dimensions of the nest once during the incubation period; we performed this measurement on a random day in 2002, and between day 8 and 10 of incubation in 2003 (day 1 is the day when full incubation was initiated). We measured with the use of a knitting needle both the height of the nest rim and the thickness of the nest cup. We defined the *height of the nest rim* (N_{rim} ; in mm) as the distance between the top of the nest and the bottom of the nest; we used the average value of four measurements, one in each corner of the nest. We measured the *thickness of the nest cup* (N_{cup} ; mm) once in the centre of the nest cup. During the measurements, we stored the eggs in an insulated box.

To determine whether nest thickness is a reliable measure of nest insulation, we measured nest insulation for 14 nests in 2003. To standardise the measurements, we took these nests from the field to a nearby laboratory. Meanwhile, we gave birds a replacement nest. We determined the insulation of nests by measuring the cooling curve of a heated plaster hemisphere, which we placed in a standard nest-box. The heat loss measured resembles the heat loss through the nest during contact incubation, and not the heat loss of eggs during the absence of the incubating female. We placed the plaster hemisphere inside the nest cup, after we heated it to about 40°C (body temperature of a female is between 39 and 42°C; Prinzing, Pressmar & Schleucher 1991), and subsequently we covered it with insulating material for standardisation of the measurements. We measured the decline in temperature of the plaster hemisphere with a temperature probe inside the plaster hemisphere. Ambient temperature was measured with a temperature probe in the wall of the nest box. As measure of insulation, we used the slope of the natural

logarithm of the cooling curves (temperature of hemisphere minus ambient temperature) over time (which we refer to as the *cooling coefficient* β in s^{-1}).

To additionally determine whether difference in nest thickness really matters for the energy expenditure of an incubating female, we calculated the difference in heat transfer for females with different nest insulation (different cooling curves) at several ambient temperatures. We calculated the costs of keeping the nest at a certain temperature (E [$J s^{-1}$]) using Newton's law of cooling: $E = \beta \cdot C \cdot (T_{\text{nest}} - T_a)$, whereby C is the heat capacity of the plaster hemisphere ($J/^\circ C$), T_a is the ambient temperature ($^\circ C$) and T_{nest} is the temperature in the nest ($^\circ C$). We assumed incubation temperature to be $35^\circ C$ (Haftorn & Reinertsen 1985).

Ambient temperature

At a central location in the study area, a temperature sensor (Tinytalk II, Gemini Data Loggers, INTAB Benelux) recorded ambient temperatures ($^\circ C$) at 10 min interval at a height comparable to that of the nest-boxes. We calculated mean, minimum and maximum ambient temperature per day.

Fitness approximations

Around the expected hatch date – we assumed a minimal incubation period of 12 days – we visited nests daily to determine the number of hatchlings. Hatching probability was determined as the number of hatchings divided by the number of eggs laid. To approximate fledging mass, we measured mass of nestlings on day 14 (day of hatching is 0).

Statistical analysis

We used in total 109 first clutches (2002, $n = 28$; 2003, $n = 81$) in the analyses. We excluded those clutches from the analyses that were deserted during incubation, that contained one or more eggs of blue tits or that had abnormal large clutches (>15 ; such a clutch size is presumably a combination of two clutches). Although, the occupation of the nest-boxes was similar in the two years, sample size was smaller for the year 2002. In that year, we did not measure the nest dimensions of clutches that were involved in an experiment (chapter 2; $n = 63$) to minimize handling of the eggs in these clutches. In 2003, we did measure the nest dimensions of the experimental clutches to ensure larger sample size.

We used multiple regression analyses to determine whether delays in the onset of full incubation varied with nest thickness, clutch size, laying date and year. Subsequently, we analysed whether hatching probability and fledging weight were correlated with delays in onset of full incubation, nest thickness, clutch size, laying date and year. For the analysis on hatching probability, we performed binomial analysis with the use of program MLwiN (version 2.02; Rasbash *et al.* 2000). For the analysis concerning the delay in onset of full incubation, we included all

clutches. In all other analyses, we excluded the experimental clutches ($n = 38$) because the manipulation may have affected the response variables other than delay. Sample size varied per analysis due to missing values in the data; they are reported in the text. All values presented concern means \pm SD, unless stated otherwise.

RESULTS

General

Incubation started on average one week earlier in 2002 than in 2003 (2002: 18.1 ± 4.0 days; 2003: 26.8 ± 4.9 days starting with the first of April as day 1; year: $F_{1,108} = 8.1$, $p = 0.005$). In 2003, clutches were also one egg smaller than in 2002 (2002: 9.1 ± 1.4 ; 2003: 8.1 ± 1.6 ; year: $F_{1,108} = 69.7$, $p < 0.001$). Clutch size is negatively correlated to laying date ($t_{1,107} = -3.3$, $p < 0.001$). Minimum daily ambient temperature (T_{a_min}) was strongly correlated with date of the season in both years (Pearson's correlation: 2002; 0.60, $p = 0.01$, $T_{a_min} = 0.89$ ($[SE]1.45$) + 0.25 (0.08) · April date; 2003; 0.65, $p = 0.01$, $T_{a_min} = 1.57$ (1.20) + 0.20 (0.05) · April date).

Nest dimensions and nest insulation

Nests had an average rim height of 60.6 ± 15.5 mm in 2002, and 51.5 ± 11.7 mm in 2003, and an average cup thickness of 15.8 ± 12.1 mm in 2002, and 11.2 ± 9.4 mm in 2003. The height of the nest rim (N_{rim}) and the thickness of the nest cup (N_{cup}) were strongly correlated ($R^2 = 0.77$). In further analyses, the thickness of the nest cup was used. Variation in nest cup thickness was neither explained by clutch size ($t_{1,108} = -0.02$, n.s.), nor by laying date ($t_{1,108} = 0.06$, n.s.), but nests were thicker in 2002 than in 2003 ($t_{1,108} = -2.0$, $p = 0.04$).

The cooling constant β decreased with the thickness of the nest cup. This indicates that thicker nests cooled more slowly, and thus that they were better insulated than thinner nests ($\beta \times 10^3$ [s^{-1}] = $-1.2718 + 0.1731 \cdot \ln(N_{cup}$ [mm]); $R^2 = 0.33$, $F_{1,12} = 5.82$, $p < 0.05$; Fig. 5.1A). Calculations on the costs of keeping nests at a certain temperature (Fig. 5.1B), and thus on the energetic costs of incubation, revealed that energetic costs are higher for birds with thinner nests than for those with thicker nests. Additionally, the energetic costs depended on ambient temperature, but females with thicker nests were less affected by ambient temperatures than those with thinner nests (Fig. 5.1B).

Delay in onset of full incubation

The onset of full incubation relative to the laying date of their last egg differed strongly between individuals. Some females started incubating before laying the third last egg, while others waited up to 8 days after clutch completion before ini-

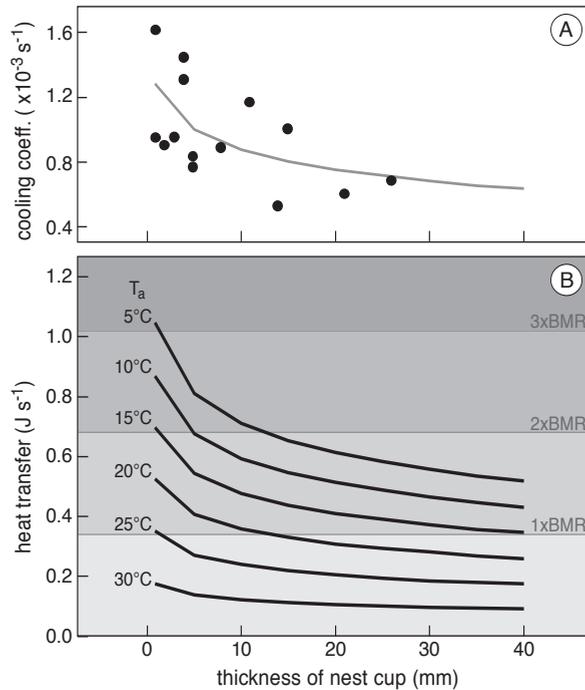


Figure 5.1. A) The cooling coefficient as function of the thickness of the nest cup. B) Warmth transfer against thickness of the nest cup, as measure of nest insulation. Lines represent the energy expenditure of an incubating female that keeps her eggs at 35°C with different nest thickness and at several ambient temperatures (T_a). Reference lines (horizontal lines) are included in the figure to show energy expenditure in relation to basal metabolic rate (BMR).

tiating full incubation (Fig. 5.2). On average, females initiated full incubation 0.8 ± 1.6 days and 1.0 ± 2.3 days after clutch completion in 2002 and 2003, respectively. Incubation delay was negatively related to thickness of the nest cup, after corrected for variation in laying date and clutch size (Table 5.1). Females with smaller clutches, and females that started egg laying early in the season had greater delays in the onset of full incubation (Table 5.1).

Consequences of delay in onset of full incubation

Due to the delay in onset of full incubation the total incubation period was longer ((total incubation period [days]) = $13.5 + 0.82 \cdot$ (delay in onset of full incubation [days])); $F_{1,69} = 71.7$, $p < 0.001$). The period of full incubation decreased with increasing delay in onset of full incubation; this correlation was approximately significant ($F_{1,69} = 3.5$, $p = 0.07$). After exclusion of one outlying point, the period of full incubation decreased with increasing delay in onset of full incuba-

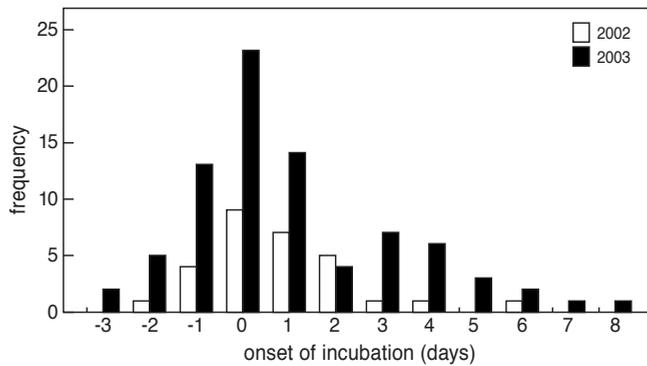


Figure 5.2. Frequency distribution of delay in onset of full incubation for the two years.

Table 5.1. General Linear Model of delay in onset of full incubation (days, dependent variable) in relation to clutch size, laying date and thickness of the nest cup.

	$\beta \pm SE$	$F_{1,105}$	p
Intercept	10.0 ± 1.4	50.9	<0.001
Clutch size	-0.6 ± 0.1	24.5	<0.001
Laying date	-0.15 ± 0.03	25.2	<0.001
Thickness nest cup	-0.05 ± 0.02	8.5	0.004

tion analyses ((period of full incubation [days]) = $13.3 - 0.19 \cdot$ (delay in onset of full incubation [days]): $F_{1,68} = 7.6$, $p = 0.01$). The outlying female incubated very irregularly for several days and had an extremely long total period of incubation. Still six of her ten eggs hatched and four young fledged.

Hatching probability did not differ between the two years (year: $\chi^2_{1,68} = 1.2$, $p = 0.27$). On average $90 \pm 13\%$ ($n = 27$) and $87 \pm 14\%$ ($n = 43$) of the eggs hatched in 2002 and 2003, respectively. Hatching probability decreased when females had a longer delay in the onset of full incubation ($\beta \pm SE$; -0.16 ± 0.07 ; $\chi^2_{1,68} = 7.6$, $p = 0.01$; Fig. 5.3), and increased with nest thickness (N_{cup} ; 0.03 ± 0.02 ; $\chi^2_{1,68} = 5.8$, $p = 0.02$). Fledging mass neither differed between year (year effect: $F_{1,65} = 0.71$, $p = 0.40$), nor was it related to the number of fledglings in the nest ($F_{1,65} = 0.25$, $p = 0.62$). The delay in onset of full incubation did not explain any variation in fledging mass, when variation in laying date was taken into account (residual delay in onset with laying date: $F_{1,64} = 0.65$, $p = 0.42$; Fig. 5.4).

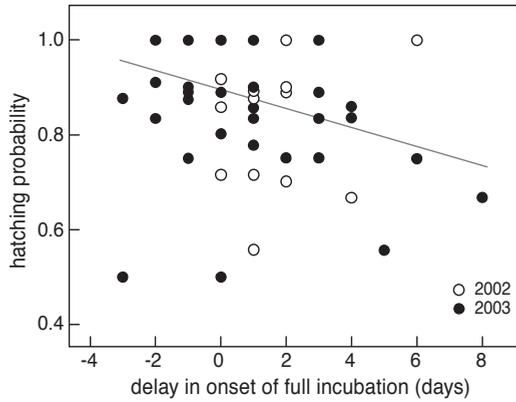


Figure 5.3. Hatching probability (number of hatchlings divided by number of eggs in the clutch) in relation to delay in onset of full incubation for the two years; 2002 and 2003. Grey line is regression line through all points.

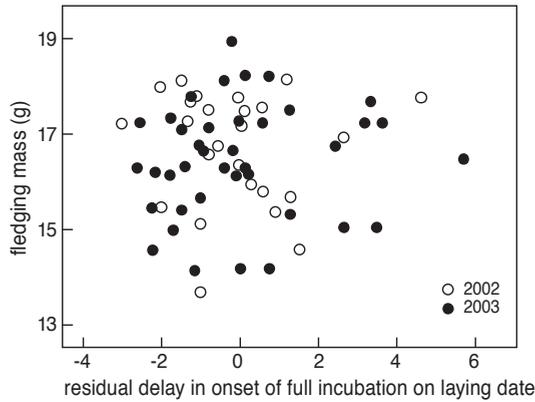


Figure 5.4. Average fledging mass per nest in relation to residual delay in onset of full incubation on laying date for the two years; 2002 and 2003.

DISCUSSION

Females with thinner nests had longer delays in the onset of full incubation. Hatching probability increased with nest thickness, and declined with delay in onset of full incubation. Following the analysis by Naef-Daenser (2004), we did not find that fledging mass was correlated with the delay in onset of full incubation, when corrected for laying date. These results imply that in our study in con-

trast to the findings of Naef-Daenser the delay in onset of full incubation did not result in benefits in terms of increased fledging mass.

The relationships that we found in this study are consistent with the idea that the delay in onset of incubation is associated with energetic stress during early reproduction. Birds with thinner nests had greater delays than birds with thicker nests. Nest thickness was found to be a good indicator of nest insulation, which has previously also been reported for penduline tits *Remiz pendulines* (Szentirmai *et al.* 2005) and blackbirds *Turdus merula* (Møller 1990). Better insulated nests reduce energetic costs of incubation (chapter 6) and cooling rates of eggs in the absence of the incubating bird (Reid *et al.* 1999; Reid *et al.* 2002b; Szentirmai *et al.* 2005). Therefore, thicker nests may allow for longer periods away from the nest and for a reduction of energy requirement, when rewarming the clutch upon return (Reid *et al.* 1999; Cresswell *et al.* 2003). Additionally, better nest insulation makes incubating females less vulnerable to unfavourable environmental conditions (Hansell 2000). We would not expect delays in onset of full incubation and nest thickness to be negatively related if birds would delay the onset of full incubation to only synchronise the hatching date with the food peak.

Birds with smaller clutch sizes had longer delays. Clutch size likely represents differences in quality between females or in territories females are living in. This implies that females laying smaller clutches experienced either higher costs or lower benefits of reproduction. During early reproduction (both egg laying and incubation), birds are confronted with high energetic expenditures (Ward 1996; Bryan & Bryant 1999; Stevenson & Bryant 2000; Engstrand *et al.* 2002; Vézina & Williams 2002; chapter 7), which are equivalent to that of a female provisioning food to their nestlings (Williams 1996; Ward 1996; Tinbergen & Williams 2002). Energy expenditure during early reproduction is relatively high due to low ambient temperatures (Bryan & Bryant 1999; Weathers *et al.* 2002), and limited food availability to balance the expenditures. Birds with smaller clutches were likely unable to continue laying or to initiate the onset of full incubation.

Delays were negatively correlated with laying date. Since ambient temperature and food availability increases with time during the season (Perrins 1970), females that started laying late in the season will be less likely to be energetically constrained. In line with this idea, experiments in which birds receive supplementary feeding show that birds receiving additional food have an earlier onset of laying (Nilsson & Svensson 1993b), a reduction of laying gaps (Nilsson & Svensson 1993a) or an earlier onset of incubation (Nilsson & Svensson 1993b). In another experiment by Nilsson (1994), females blue tits that were manipulated to lay early in a season had greater delays in the onset of incubation than the unmanipulated females who bred later in the season. The explanation that the negative correlation between delays in onset of full incubation and laying date occurs due to energetic stress early in the season is very plausible, though it is not conclusive. This negative correlation can also be explained by the fact that birds may time

reproduction better later in the season, because environmental conditions such as ambient temperature are likely to become more predictable later in the season (Perrins 1970).

The delays in onset of full incubation were negatively correlated with breeding parameters. This suggests that there are costs to the delays in onset of full incubation. Birds with greater delays in onset of the incubation had a longer total period of incubation. Such prolongation of the incubation period may have negative consequences, since the probability of nest predation may increase with an increasing reproductive period (Bosque & Bosque 1995; Tombre & Erikstad 1996) or due to detrimental effects on developing embryos (Vleck *et al.* 1980; chapter 3). Moreover, birds with greater delays had lower hatching probability, like previously found by Naef-Daenzer *et al.* (2004). In contrast to the study by Naef-Daenzer *et al.* (2004), we did not find that due to the delays nestlings were heavier. This suggests that in our study, nestlings of clutches in which females delay the onset of incubation did not have more food as a result of the delay. In case of the strategic hypothesis, we would have expected to find an advantage of delays in onset of incubation, which we did not find.

Although the two hypotheses are not mutually exclusive, the most likely explanation of our findings is that the energetic costs of incubation plays a role in determining the decision to initiate the onset of full incubation. The correlation between delay and nest thickness suggest an important role of nest traits in reducing the energetic costs. Nevertheless, since we rely on correlations, there are alternative explanations possible for our findings: variation in nest thickness may be correlated to variation in either the quality of the environment (i.e. territories) birds live in or the quality of parents in association to the delay in onset of full incubation. An experiment manipulating nest insulation is therefore needed. Such experiments may help to raise our understanding of the breeding biology in birds.

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