

Date and parental quality effects in the seasonal decline in reproductive performance of the Tree Swallow *Tachycineta bicolor*: interpreting results in light of potential experimental bias

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In many bird species early breeders have higher reproductive performance than late breeders from the same population. This could be caused by a reduction in environmental factors related to date *per se* (Date Hypothesis), or because poorer performers nest later (Parent Quality Hypothesis). We manipulated hatch date of Tree Swallows *Tachycineta bicolor* by switching clutches with different lay dates, generating broods with advanced or delayed timing, and assessed the impact of the experiment on nestling mass. The Date Hypothesis better explained the decline in nestling mass in the first half of the season, while the Parent Quality Hypothesis was supported in the second half. We also found that female mass loss was unintentionally reduced in advanced females and suggest that such impacts of the experiment on parent quality, or correlations between nestlings and their actual parents via heritability or maternal effects, could bias hatch-date manipulation experiments towards supporting the Date Hypothesis. Differential costs of incubation, either due to naturally low temperatures early in the season, or due to the unintentional manipulation of female incubation costs, appear to have driven support for the Date Hypothesis early in the season.

Seasonal declines in reproductive performance have been observed in a wide variety of avian taxa. These declines result from a reduction, over the course of the season, in fitness-related parameters such as nestling mass and growth (Hochachka 1990, Sedinger & Flint 1991), clutch size (Winkler & Allen 1996), nestling survival (Norris 1993, Wiggins *et al.* 1994) and nestling recruitment (Hochachka & Smith 1991). Although the occurrence of these declines is well established, the underlying mechanisms remain unclear. The earliest breeders may be those of highest quality (Parent Quality Hypothesis) or some correlate of date *per se* may influence performance independent of individual quality (Date Hypothesis). Attempts to distinguish between these two hypotheses have involved experimentally manipulated timing via induced re-laying or switching clutches with differing lay dates (summarized in Nilsson 1999). The predictions of these experiments assume that parent quality is not altered by the manipulation and, in the case of clutch switching experiments, that nestling performance is not linked to

quality of the actual parents via heritable or maternal effects. These assumptions remain largely uninvestigated due to the difficulty in addressing them. Unfortunately, if they are violated, hatch-date manipulations will be biased towards supporting the Date Hypothesis, despite the presence of parent quality effects.

In general, early breeding is best in seasonal environments but many parents may not be capable of acquiring enough resources to initiate reproduction early on (modelled in Rowe *et al.* 1994). For instance, many studies have demonstrated that younger, less experienced birds breed later in the season (De Forest & Gaston 1996, Daunt *et al.* 1999). Under the Parent Quality Hypothesis, performance of breeding birds over the season is due to some inherent phenotypic characteristic of the parents themselves (e.g. age, provisioning ability), or environmental characteristic of their breeding territory. Alternatively, under the Date Hypothesis, performance of breeding birds may be linked to a gradual change in the environment which affects all individuals equally. This may include seasonally declining food supply, temperature or nestling value (which could lead to parents investing less in later-hatched young).

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Although the Date and Parent Quality hypotheses are not mutually exclusive, they do yield distinct predictions of the outcome of hatch-date manipulation experiments. This clutch-switching experimental design generates both advanced and delayed brood hatch dates experienced by parents. If date *per se* determines nestling mass, performance on a given day in the season should be unaffected by the manipulation. But if parent quality determines nestling mass, performance will match the intended timing. Delayed parents should have the highest performance for a given hatch date (matching their earlier intended date) and advanced parents should perform most poorly (matching their later intended date). These predictions are outlined in Fig. 1(a). Also, see Verhulst and Tinbergen (1991) and Nilsson (1999) for a detailed summary of predictions and previous work involving hatch-date manipulation experiments.

If, however, high-quality parents produce high-quality offspring via heritable or maternal effects, performance of manipulated broods will be influenced by their biological parents. The size of this effect will depend on the aspect of performance assessed in the experiment. Smaller-scale traits such as growth, mass or hatching success may be determined partly by heritability (e.g. Wiggins 1989, Price 1991, Smith & Wettermark 1995, Kunz & Ekman 2000) or maternal effects (e.g. Reid & Boersma 1990, Bernardo 1996, Styrsky *et al.* 1999). It is less likely that this bias will have a significant impact in studies that assess larger-scale traits (such as overall survival or probability of recruitment) because they encompass a suite of smaller-scale traits, only some of which will be significantly determined by genetic or maternal effects. In Tree Swallows, although structural size is known to be largely genetically determined, heritability of nestling growth and body mass is weak at best (Wiggins 1989). Therefore, nestling growth should be a reliable performance measure in this species.

The most critical assumption of hatch-date manipulations is that parent quality is not affected by the experiment. Advanced parents incubate for a shorter period and delayed parents for longer. If incubation comprises a significant portion of the costs of reproduction, as recent research would suggest (Heaney & Monaghan 1996, Reid *et al.* 2000), then altering the incubation period may cause dramatic alterations to the outcome of the breeding attempt. Advanced birds pay reduced incubation costs, resulting in enhanced performance, and delayed birds

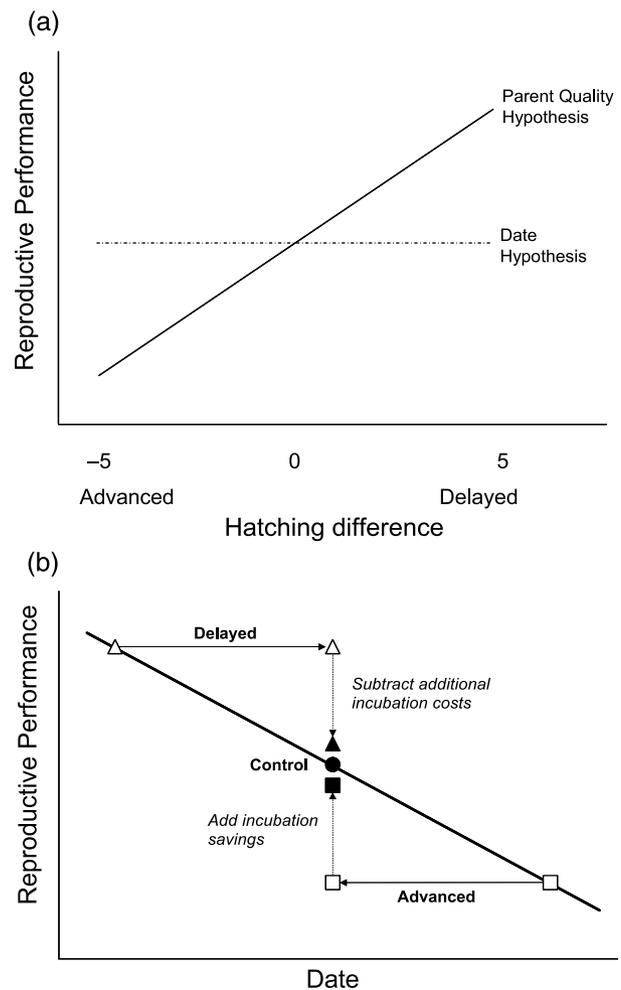


Figure 1. (a) The pattern of reproductive performance predicted under the Date and Parent Quality Hypotheses, on any given day during the season. Under the Parent Quality Hypothesis, the magnitude of the effects on performance should depend on the number of days the brood was either advanced or delayed. Under the Date Hypothesis, performance simply follows the natural seasonal trend. Thus, on any one day, performance should be equal irrespective of the degree of manipulation. (b) If biases such as unanticipated impacts of the experiment on parent quality are present, performance of delayed broods will be reduced and advanced broods increased to more closely approximate the natural seasonal trend (as predicted by the Date Hypothesis). Under the Parent Quality Hypothesis, performance of delayed broods will match their parent's earlier, intended date. Likewise, performance of advanced broods will match their parent's later, intended date. Under the Date Hypothesis, performance will simply follow the natural seasonal trend (solid sloped line). Therefore, if Parent Quality determines reproductive performance, for a given day in the season, performance of delayed broods should be greater than control which should be greater than advanced. The greater the bias, the lower the likelihood of detecting effects of parent quality on nestling performance.

pay increased incubation costs, resulting in reduced performance (Fig. 1b). This could cause the pattern of performance to approximate that predicted by the Date Hypothesis.

We use a clutch-switching experiment to investigate the cause of seasonal declines in mass of nestling Tree Swallows, and compare the results with the predictions outlined above. We then attempt to address whether potential biases could have a bearing on interpretation of the results of this experiment.

METHODS

Study area and breeding phenology

This study was carried out during May and June of 1999, on the Creston Valley Wildlife Management Area, a managed wetland in south-eastern British Columbia, Canada (49°05'N, 116°35'W). Here, 200 Tree Swallow nestboxes are mounted on stakes approximately 15–30 m apart along dykes surrounding a series of ponds. Lay date of each egg, clutch completion date, hatch date and incubation date were recorded. Hatch date was the first day on which half or more of the eggs in a clutch had hatched, and was considered day 1 of the nestling period. Onset of incubation was typically easy to detect by feeling egg temperature, but was occasionally ambiguous. In these cases, the date on which the last egg was laid was considered to be the first day of incubation, as 79% of all broods with known incubation timing initiated incubation on that day. Eggs were weighed on a portable pan balance to the nearest 0.01 g on the day they were laid.

Experimental protocol

Hatch date was manipulated by switching clutches differing in onset of incubation. Eggs were moved quickly, and transported in small plastic containers nestled in cotton balls and heated with 'Hot Pocket' air-activated handwarmers. All clutches were adjusted to six eggs and at hatching adjusted again if necessary to a brood of six with nestlings from elsewhere on the study site. This was done to ensure that all birds experienced equal incubation and provisioning costs. Previous studies of this species found no evidence of a cost of rearing a natural, rather than a manipulated, brood of equal size (Wheelwright *et al.* 1991). Clutches at day 6 of incubation were paired with those at day 10, and switched. As a result, those parents whose eggs had been incubated for 6 days

were incubating eggs that had been developing for 10 days and would therefore hatch 4 days earlier than expected. These are referred to as 'advanced' broods. Parents that had been incubating for 10 days received eggs that had been developing for only 6 days and would therefore hatch 4 days later than expected. These are referred to as 'delayed' broods. Broods at the same incubation timing were switched at day 10 to serve as controls. A manipulation of 4 days represents a significant adjustment to an individual's relative reproductive timing, as hatch dates in the entire population varied by only 16 days. The actual magnitude of the manipulation varied, with broods advanced or delayed by as much as 5 days because the natural incubation period in this population is 13–15 days. Negative values represent advanced broods and positive values delayed broods. This measure will be referred to as 'hatching difference'. It was calculated as the hatch date of the fostered brood minus the hatch date of the parent's own brood in the foster nest. Thus, if the average incubation period is 14 days, differences between advanced and delayed broods could be as much as 10 days (incubation period of advanced = $14 - 5 = 9$ days; delayed = $14 + 5 = 19$ days).

In all, 47 clutches were manipulated. Of those, one clutch did not hatch and eight broods died before day 15, leaving a sample of 38 nests that survived to the end of the study. Females in their first year, distinguished by their brown plumage (Stutchbury & Robertson 1988), were excluded from the study to avoid possible confounding effects of age.

Parental characteristics

Females were captured on the nest 8 days after the onset of incubation, and were weighed on a spring balance to the nearest 0.5 g. This is termed 'incubation mass'. Females were captured and weighed a second time on day 8 of chick rearing. This is termed 'provisioning mass'. Mass loss is the difference in mass between day 8 of incubation and day 8 of chick rearing. The duration between measurements varied across treatments. For example, the time between measuring incubation and provisioning mass in advanced birds was as little as 9 days (time from day 8 to hatch = $1 + 8 = 9$ days), in controls was 14 days (time from day 8 to hatch = $6 + 8 = 14$ days) and in delayed broods was as much as 19 days (time from day 8 to hatch = $11 + 8 = 19$ days). Birds were marked with numbered, metal leg bands. Four females were not captured

during incubation and one female was not captured at either time.

Nestling mass

Nestling mass determines the probability of fledgling survival to independence in many altricial bird species (Hochachka & Smith 1991, Macgrath 1991, Brown & Brown 1996, Both *et al.* 1999). Although it is not known whether this is the case in Tree Swallows specifically, Brown and Brown (1996) have demonstrated that day 10 nestling mass of Cliff Swallows *Hirundo pyrrhonota* correlates with mass just after their leaving the nest, and both masses are correlated with first-year survival. This, and the fact that nestling mass is also well-known to predict first-year survival in many other passerine species, suggests that it should serve as a useful performance measure in this study.

A high incidence of runt nestlings could indicate that the mean nestling mass per brood might not be a good indicator of the probability of survival of each nestling within that brood. Nestling masses at day 15 were therefore evaluated for the presence of runt nestlings (arbitrarily defined as any nestling that was at least 25% smaller than the average of the rest of the brood). Only one runt was found, with a body mass 36% smaller than the average of its brood-mates. Two other nests had chicks that were approximately 20% smaller than the average of the rest of the brood. The low incidence of runt nestlings indicates that this is not an issue in this study.

Chicks were weighed to the nearest 0.01 g on a portable electronic balance and measured on days 4 and 15 of the nestling period. Nestling tarsus length was also measured at day 15. Nestlings were marked with soft, plastic, coloured leg bands at day 4, and were re-marked with permanent, numbered, metal leg bands at around day 8.

Statistical analysis

To test whether hatching difference influenced brood mass, a backward stepwise multiple regression procedure was used with mean 15 days nestling mass as the response variable and hatch date (to control for the expected seasonal decline in nestling mass), hatching difference and hatch date by hatching difference interaction as predictors. Correlation coefficients were calculated using a partial correlation analysis. All analyses were done using JMPIN 3.2.1 (SAS Institute Software, 1997).

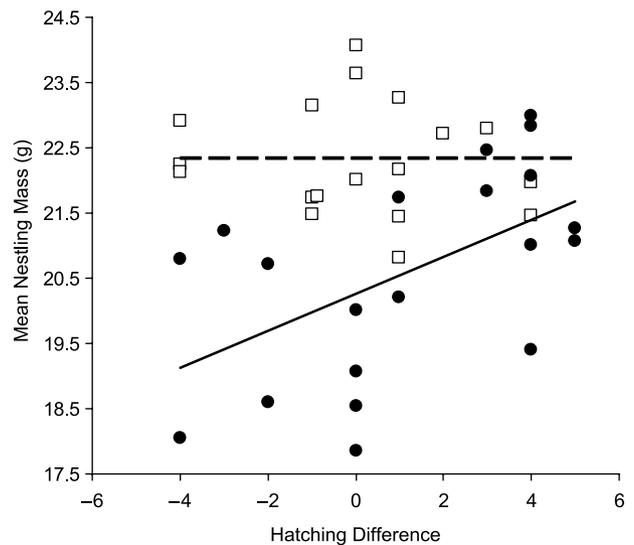


Figure 2. Mean nestling mass is associated positively with hatching difference late in the season (solid line and circles; $F_{1,19} = 6.83$, $P = 0.018$, $n = 20$, $R^2 = 0.275$, slope = 0.269 g/day, $se = \pm 0.103$ g) but not early (broken line and squares; $F_{1,17} = 0.245$, $P = 0.627$, $n = 18$, $R^2 = 0.015$, slope = -0.043 g/day, $se = \pm 0.087$ g). Negative values of Hatching Difference represent 'advanced' broods, while positive values represent 'delayed' broods. The early part of the season was 4–10 June. The late part of the season was 11–20 June. Note that there is about a 3-g or 15% difference between day 15 nestling mass of controls (0 Hatching Difference) in the early vs. late portion of the season. This further illustrates the presence of a seasonal decline in Tree Swallow nestling mass in the year of this study.

RESULTS

Hatching difference

The multiple regression analysis found hatch date to be negatively correlated with nestling mass ($F_{1,34} = 16.8$, $P = 0.0002$, $n = 38$, $r = -0.42$). Thus, a seasonal decline in nestling mass was present in the year of this study, a necessary prerequisite for the predictions of the hatch-date manipulation experiment. Hatching difference was correlated positively with nestling mass ($F_{1,34} = 7.20$, $P = 0.011$, $n = 38$, $r = 0.32$). This result matches the predictions of the Parent Quality Hypothesis. The effects on mean nestling mass were, however, complicated by a highly significant interaction between hatching difference and hatch date ($F_{1,34} = 2.23$, $P = 0.007$, $n = 38$). Figure 2 displays the nature of this interaction, with the season divided into early and late at the median date. This figure illustrates that the significant interaction in the model was due to differing effects of hatching difference on nestling mass in the two

halves of the season. Early in the season, there was no effect of the manipulation on nestling mass, which is consistent with the Date Hypothesis. In the second half of the season, there was a positive effect of hatching difference on nestling mass, which is consistent with the Parent Quality Hypothesis (compare with predictions in Fig. 1a). Comparisons of the standard deviation, using Levene's ($F_{1,32} = 5.95, P = 0.02$) and Bartlett's ($F_{1,32} = 5.37, P = 0.03$) tests for heterogeneity of variance ($sd_{\text{early}} = 0.859, sd_{\text{late}} = 1.519$), indicate that variation in nestling mass in the first half of the season was significantly less than in the latter portion.

Egg mass

There was no relationship between egg mass and nestling mass at day 15 ($F_{1,38} = 1.39, P = 0.24, n = 39, R^2 = 0.036$, slope = 2.1 g chick/g egg, $se = \pm 1.78$ g) or tarsus length at day 15 ($F_{1,38} = 0.14, P = 0.70, n = 39, R^2 = 0.004$, slope = 0.11 mm tarsus/g egg, $se = \pm 0.30$ mm) but there was a weak positive correlation between nestling mass at day 4 and egg mass ($F_{1,46} = 4.87, P = 0.03, n = 47, R^2 = 0.10$, slope = 1.93 g chick/g egg, $se = \pm 0.86$ g). This indicates that the influence of egg mass on nestling characteristics was transitory and most important early in the nestling period. It is worth noting, however, that more nestlings were measured at day 4 than at day 15 (47 vs. 39). It is possible, given the similarity of slopes (day 4 slope = 1.93 g chick/g egg; day 15 slope = 2.1 g chick/g egg) that there is a very weak effect of egg size on nestling mass at day 15 which was simply not detectable given the sample sizes available. Nevertheless, any relationship between egg mass and nestling mass at day 15 is weak at best. Nestling mass at day 4 did not decline over the season ($F_{1,46} = 0.363, P = 0.55, n = 47, R^2 = 0.008$, slope = 0.019 g/d, $se = \pm 0.03$ g), while egg mass increased over the season ($F_{1,46} = 5.08, P = 0.03, n = 47, R^2 = 0.10$, slope = 0.01 g/d, $se = \pm 0.005$ g).

Impacts of the experiment on parent quality

Our manipulation affected the amount of mass lost by foster females during the late incubation and early brood-rearing periods. The degree of mass loss in advanced females was inversely related to the number of days they were advanced. There was no effect of the treatment on delayed females (Fig. 3). The amount of mass that all females lost declined

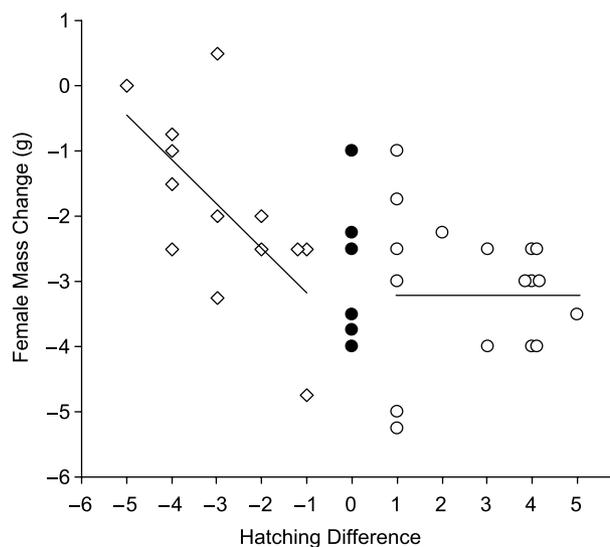


Figure 3. Female mass change is associated with the difference between actual and intended hatch date, but only in advanced broods (diamonds: $F_{1,12} = 7.86, P = 0.017, n = 13, R^2 = 0.417$). There is no relationship in delayed broods (open circles: $F_{1,16} = 0.01, P = 0.75, n = 17, R^2 = 0.007$). There were six broods whose actual and intended hatch dates were exactly matched (filled circles). Mass change is the difference in grams between incubation and provisioning in females.

significantly through the season ($F_{1,35} = 24.63, P < 0.0001, n = 36, R^2 = 0.41$, slope = -0.227 g/d, $se = \pm 0.045$ g). This was due to a decline in incubation mass as there was no seasonal trend in provisioning mass (Fig. 4). The effect of the experiment on mass loss was due to advanced females retaining higher provisioning masses, as there was no relationship between incubation mass and hatching difference ($F_{1,43} = 0.89, P = 0.35, n = 44, R^2 = 0.02$, slope = 0.08 g/d, $se = \pm 0.086$ g) while there was a negative correlation between provisioning mass and hatching difference ($F_{1,36} = 7.11, P = 0.01, n = 37, R^2 = 0.17$, slope = -0.14 g/d, $se = \pm 0.05$ g).

DISCUSSION

Experimental results

Mean nestling mass declined significantly over the season, and early in the season mean nestling mass was apparently uninfluenced by the hatch-date manipulation, a response predicted by the Date Hypothesis. Late in the season, however, delayed nestlings were heavier, as predicted by the Parent Quality Hypothesis.

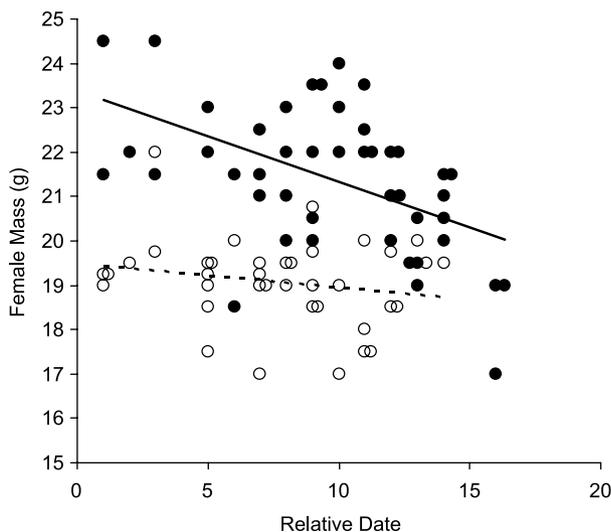


Figure 4. Incubation mass declined over the season (filled circles, solid line: $F_{1,44} = 15.36$, $P = 0.0003$, $n = 45$, $R^2 = 0.25$, slope = -0.209 g/day, $se = \pm 0.053$ g) while provisioning mass did not (open circles, broken line: $F_{1,37} = 1.34$, $P = 0.25$, $n = 38$, $R^2 = 0.009$, slope = -0.05 g/day, $se = \pm 0.045$ g). Relative Date is the number of days from when the first mass was measured (e.g. Day 1 is the day the first incubation mass was measured, Day 5 was 5 days after the first mass was measured; the same process was used for provisioning mass). The difference between these two lines is mass loss. Note that mass loss declines over the course of the season.

There are two possible explanations for why this experiment found support for both hypotheses within the same season. The first is that different mechanisms are dominant at different points in the season. Forces influencing reproductive performance of early and late breeders may differ. The second is that there are biases inherent in the experiment that made it difficult to detect parent quality effects in the first part of the season. It should be noted that the failure to detect parent quality effects in the first part of the season could simply be due to the fact that there was insufficient variability in quality among the early breeders. Variation in nestling mass was lower in the early portion of the season, though the difference in variability between early and late was small. It is possible that the reduced variability early in the season can explain the observed support for the Parent Quality Hypothesis only in the late portion of the season. Early broods are much more synchronous, as indicated by the fact that the first half of the study population hatched within 6 days while the late half encompassed 9 days. Unfortunately, parent quality was not assessed directly, so

whether differences in variation in parent quality between early and late breeders can explain the observed discrepancy between the two halves of the season is unknown.

Climate and food abundance clearly influence reproductive success in birds (Daan *et al.* 1989), but it is not clear that systematic declines in these parameters are responsible for seasonal declines in reproductive performance. In this experiment, temperature increased during the first half of the laying period, and then stabilized around a mean of 15 °C. The earliest breeders faced lower temperatures during egg production and early incubation. Thus, if higher quality parents were breeding earliest in the season, these were also the parents paying the highest incubation costs, an influence opposing the hypothesized effect of parental quality. In the first half of this season, a delayed bird experienced lower temperatures during incubation than control birds whose brood hatched on the same day. This is because delayed birds had initiated egg-laying up to 5 days earlier than controls, at a time when ambient temperature was lower. If lower temperatures during incubation impose significant costs on reproduction, the performance of delayed broods could be reduced simply because of the environmental conditions experienced during incubation and before any experimental manipulation was carried out. Similarly, advanced birds experienced higher incubation temperatures, and would thus have higher reproductive performance than predicted under the Parent Quality Hypothesis. Systematic increases in incubation temperature could have countered differences in parent quality early in the season. Later in the season, when temperature during incubation stabilized, all birds experienced, on average, the same incubation temperature of 15 °C. Thus, later in the season, parent quality differences would not have been masked by natural variation in incubation costs, and so it should be possible to detect real differences in parent quality. Given recent compelling evidence that temperature during incubation can have a significant impact on subsequent reproduction (Heaney & Monaghan 1996, Reid *et al.* 2000), this seems the most plausible explanation for the observed support for the Date Hypothesis in the first half of the season only.

Heritability or maternal effects

We could not assess heritability as a possible bias in this experiment, as we did not know the mass of parents when they were nestlings. Previous research

that has assessed the heritability of nestling characteristics in other species has found evidence for heritability of body size and nestling growth or mass, though heritability of body mass or growth tends to be low (Price 1991, Smith & Wettermark 1995, Kunz & Ekman 2000). Wiggins (1989) found no evidence of heritability in growth in the population of Tree Swallows studied in this experiment. Therefore, heritable variation in body mass was probably not a source of bias causing the observed support for the Date Hypothesis early in the season that we found.

There were, however, potential maternal effects acting via the egg that could have biased the experiment towards supporting the Date Hypothesis. We found a positive correlation between egg mass and nestling mass early in the nestling period. However, this effect was not detected in any nestling characteristic by the time nestlings were 15 days old. Egg mass appears to be a maternal effect that translates to heavier nestlings early in the nestling period. A number of studies have demonstrated a transitory effect of egg size on nestling size (e.g. Reid & Boersma 1990, Meathrel *et al.* 1993, Amundsen *et al.* 1996) although few have demonstrated long-term fitness advantages to emerging from a large egg (but see Styrsky *et al.* 1999). Although egg size seems unlikely to contribute strongly to nestling performance, it is possible that there are other maternal effects acting via the egg. Reid and Boersma (1990) suggest that the benefits from emerging from a large egg are due to maternal effects via egg composition rather than fitness advantages of emerging from a large egg. A possible mechanism is the passive transfer of antibodies to nestlings via the egg (e.g. Burley & Vadehra 1989). We suggest that if passive immune transfer enhances immune responses in nestlings, and this corresponds to increased performance, this would bias towards support for the Date Hypothesis in hatch-date manipulation experiments.

Unintentional impacts of the experiment on parent quality

Recent research has demonstrated experimentally that females that expend more energy during incubation produce nestlings with poorer performance than those that paid lower incubation costs (Reid *et al.* 2000). Tombre and Erikstad (1996) advanced and delayed Barnacle Goose *Branta leucopsis* broods by exchanging clutches (as in this experiment), and looked for effects of the manipulation on female

body condition. They showed that body condition was affected negatively in females with extended incubation periods and enhanced in females with reduced incubation periods. Sanz (1999) delayed timing in Blue Tits *Parus caeruleus* by inducing relaying by clutch removal. He found that delayed females were lighter than unmanipulated females with equivalent reproductive timing. Hansson *et al.* (2000) used a natural experiment in which first clutches of Great Reed Warblers *Acrocephalus arundinaceus* were removed by predators and determined that reproductive success is reduced in relaying females. The authors interpreted this as an indication that parent quality is reduced in relaying females, a violation of the major assumption of hatch-date manipulation experiments. Verboven and Verhulst (1996) attempted to assess whether parent quality was influenced by a clutch switching experiment in Great Tits *Parus major* by looking for a correlation between the number of days by which hatch date was manipulated, and nestling mass at fledging. They found no evidence that their experiment altered parent quality. It should be noted, however, that they did not measure any parental characteristics directly.

Female mass loss declined over the season within the general population in this study. This seasonal decline in mass loss is due to later females having lower body mass during incubation. The subset of advanced females, however, retained higher provisioning masses, contrary to the natural pattern of mass loss. Female mass loss is well-known in birds, but the reason for this loss is still unresolved. The two main hypotheses, which are not mutually exclusive, are the Flight Adaptation Hypothesis and the Reproductive Stress Hypothesis. Under the Flight Adaptation Hypothesis, females lose mass before their clutch hatches in order to reduce wingloading and therefore increase flight efficiency while provisioning nestlings. Under the Reproductive Stress Hypothesis, mass loss simply reflects the energetic resources used during incubation and chick rearing. Most experiments designed to distinguish between these two hypotheses find support for the Flight Adaptation hypotheses (Sanz & Moreno 1995, Merkle & Barclay 1996, Cavitt & Thompson 1997, Slagsvold & Johansen 1998) though there are exceptions (Merilä & Wiggins 1997, Gebhardt-Heinrich *et al.* 1998). The observed retention of higher provisioning masses in this study may have reflected energetic savings in advanced females due to reduced costs of incubation. Delayed females would not have continued

to lose mass as there is likely to be a lower limit on body mass in Tree Swallows. Although we did control for hatch date in the regression model, there are no delayed birds for comparison in the earliest part of the season, and no advanced birds in the latest part. Therefore, since by definition, nestlings of advanced females hatched earliest in the season, the observed support for the Date Hypothesis early in the year could be due to the fact that there were proportionally more advanced females early in the year. Given the growing body of literature supporting Flight Adaptation as the primary explanation for mass loss in female birds, however, the interpretation that mass loss reflects reproductive expenditure in Tree Swallows should be considered with great caution.

The significance of mass loss in female Tree Swallows remains unknown; however, the fact that female mass was affected by the manipulation in this experiment, and the fact that previous work has demonstrated links between incubation costs and female quality, underscores the need to assess the impact of hatch-date manipulations on parent quality in the future.

In summary, there was no evidence in this experiment that heritability or maternal effects caused a bias towards support for the Date Hypothesis early in the season. The high cost of incubation was the most likely explanation, acting either through low ambient temperatures early in the season, or the experimentally altered costs of incubation in advanced broods. Previous research has not considered the impact of hatch-date manipulations on incubation costs. Norris (1993) states that the clutch switching design is superior to induced relaying because '... the experimental bias introduced is relatively minor compared with laying an extra clutch: a female has to incubate for a few more or a few less days.' This view of incubation is sensible because, until very recently, incubation costs were thought to be minor compared to the costs of chick rearing. It is now becoming apparent that incubation costs may be significant (Reid *et al.* 2000). The results of this and other experiments may be biased by these unintentional impacts of the experiment on parent quality and this potential bias must be assessed in order both to interpret past experiments, and to design new ones that attempt to determine the cause of seasonal declines in reproductive success.

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