

## Warm temperatures lead to early onset of incubation, shorter incubation periods and greater hatching asynchrony in tree swallows *Tachycineta bicolor* at the extremes of their range

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The onset of incubation varies in birds, with many species beginning incubation prior to clutch completion. Here we examine whether early onset is more likely to occur during high temperatures, a critical prediction of the egg-viability hypothesis, which suggest that birds begin incubation prior to clutch completion in order to maintain egg-viability. We examined onset of incubation in tree swallows *Tachycineta bicolor* at two locations at the extremes of their breeding range, Alaska and Tennessee. A majority of individuals (68%) began incubation prior to clutch completion. While females in Tennessee were more likely to begin incubation early, there was no difference between sites when differences in temperatures inside nestboxes were controlled in analyses. Rather, early onset of incubation was predicted by the proportion of daily temperatures above physiological zero during laying, a critical prediction of the egg viability hypothesis. Both warm weather and early onset led to shorter incubation periods and increased levels of hatching asynchrony. We found no effect of timing of nesting, female body condition index or clutch size on the probability of beginning incubation prior to clutch completion. Our results are consistent with the egg viability hypothesis, not consistent with a threshold clutch size rule, and do not support the hurry-up hypothesis, that individuals breeding later in the season would begin incubation early to reduce the time spent nesting. Overall, our results suggest that broad scale geographic differences in incubation behaviour may be explained by individual-level responses to environmental conditions.

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Onset of incubation relative to clutch completion varies in birds, with many species beginning incubation before the clutch is complete (Clark and Wilson 1981, Hébert 2002). A large body of literature concerning brood reduction views the early onset of incubation as an evolutionary response to produce hatching asynchrony, which creates a developmental hierarchy and may aid in matching the food supply to the optimal number of chicks (Lack 1968, Nilsson 1993, Forbes et al. 2002). Yet, selection may favor the early onset of incubation per

se, leaving hatching asynchrony as a consequence. The timing of onset may be accounted for by high nest predation that selects for rapid onset of breeding to minimize exposure of the nest (Clark and Wilson 1981, Bollinger et al. 1990). Incubation patterns may also be explained as a determinant rule, where incubation always begins at a threshold clutch size (Smith 1988). Another possible selective force on incubation onset may be the need to “hurry-up”, as seasonal changes in selection pressures may drive early onset of incubation

if there was a benefit to reducing the time spent raising offspring (Slagsvold 1986). Finally, the onset of incubation may have evolved to maintain the viability of eggs due to detrimental effects of high ambient temperatures (Arnold et al. 1987, Veiga 1992, Stoleson and Beissinger 1995) as unincubated embryos exposed to temperatures greater than 26°C but lower than actual incubation temperatures, abnormal development (Webb 1987, Deeming and Ferguson 1991), or microbial growth both on and in the egg can occur (Cook et al. 2003). In this paper, we attempt to distinguish some of these hypotheses, with particular emphasis on the egg viability hypothesis.

Whereas, a handful of studies have investigated the role of ambient temperatures on egg viability (Veiga 1992, Stoleson and Beissinger 1999), few studies have explicitly examined how temperatures experienced by eggs during egg-laying influence individual incubation behaviours (Veiga 1992, Badyaev et al. 2003). We examine two predictions of the egg viability hypothesis: (1) those individuals that laid eggs when temperatures inside nestboxes above 26°C were more likely to initiate incubation before the last egg had been laid and (2) early onset of incubation causes hatching asynchrony.

Here, we assess the role of warm temperatures during egg laying by comparing onset of incubation to temperatures inside nestboxes, lay date, female body condition, actual incubation period, and clutch size in two populations of the tree swallow *Tachycineta bicolor* towards the extremes of its range in Alaska and Tennessee. In tree swallows, only females incubate clutches and onset of incubation varies among individuals with most initiating on the ultimate or penultimate eggs (Zach 1982, Robertson et al. 1992). In tree swallows, laying order tends to predict hatching order, so that last laid eggs are usually the last to hatch, with a mean hatching spread of about 28 hours between first and last eggs (Clotfelter et al. 2000). We examined what role ambient temperatures inside nestboxes play in influencing hatching differences among clutches.

We also examined the role of temperature on actual incubation period, the time from onset of incubation to hatching. Variation in incubation period can primarily be attributed to either variation in the onset of incubation prior to clutch completion (Clark and Wilson 1981) or variation in incubation constancy (% attendance) or incubation rhythms after clutch completion (Sealy 1984, Deeming 2002, Hébert 2002). Among species, variability in nest attendance after clutch completion does not account for variation in incubation period, at least among tropical species (Tieleman et al. 2004). In black kites *Milvus migrans*, both high ambient temperatures during egg-laying and an experimental delay in the start of incubation prolonged the incubation period, while advancing the onset of incubation decreased incubation period (Viñuela 1997). In wood ducks, early onset of

incubation also led to shorter incubation periods (Hepp 2004). However, other studies that have independently examined the role of both onset and temperature have found that early onset per se does not lead to shortened incubation periods (St. Clair 1996, Hipfner et al. 2001). We sought to test whether temperatures experienced by eggs during egg-laying and early onset of incubation lead to shorter incubation periods in tree swallows.

## Methods

Tree swallows are a wide-spread and common cavity-nesting member of the family Hirundinidae. Tree swallow breed from Alaska to northern Mississippi and Alabama and winter in the southern US and Central America (Robertson et al. 1992). During 2002, we studied tree swallows breeding in nestboxes erected for their use in Loudon, Anderson, and Knox Counties, Tennessee, USA (centered on 35° 53'N, 84° 18'W) and in Fairbanks, Alaska, USA (64° 49'N, 147° 52'W).

We checked nests daily to determine date of clutch initiation and clutch size and only followed females making their first breeding attempt of the breeding season. Once a breeding attempt was discovered, we placed a datalogger recording at 2-minute intervals (Thermocron iButton, Dallas Semiconductor, Dallas, TX; accuracy  $\pm 0.5^\circ\text{C}$ ) in each nest cup just to the side of the eggs, so as to not interfere with heat transfer among eggs. This datalogger was intended to measure the onset of incubation by females. Placement of dataloggers in nests did not appear to affect female behavior as there was no difference in abandonment or onset between nests with dataloggers and without (unpubl. data). We defined the beginning of incubation as the Julian date during which, for over 90 minutes: (1) nest cup temperatures were raised to the level later observed as the average nest temperature during incubation, and (2) nest cup temperatures were greater than 10°C above temperatures inside nestboxes. Onset of incubation was calculated by subtracting the date of the beginning of incubation from the date of clutch completion. Incubation period was measured as the number of days from the beginning of incubation to the hatching of the first egg. We placed dataloggers recording at 20-minute intervals (iButton Thermocron) in the upper portion of three randomly selected nests at each site. These dataloggers were intended to measure temperature conditions experienced by eggs during egg-laying. We compared nest-box dataloggers to nest-cup dataloggers to assess whether the nestbox dataloggers accurately measured the temperature experienced by eggs; temperature measured between nest cup vs. nestbox loggers did not differ more than 0.6°C (average 0.4°C). The correspondence between nest cup and nestbox loggers before incubation began indicates

that nestbox loggers accurately measure nest cup temperatures experienced by eggs prior to incubation. Because of a limited number of dataloggers, we only used three dataloggers at each site to assess nestbox temperature, however there was limited microclimate variation among boxes at each site (mean temperature difference among dataloggers  $\pm$ SD: AK  $0.7^\circ \pm 0.2$ , TN  $0.8^\circ \pm 0.02$ ) indicating that these loggers can be used to assess nestbox temperatures across each site. During each daily nest visit, we measured the mass of each freshly-laid egg using a 5-g pesola scale in a wind-protected plastic tube. Eggs were marked at the blunt end with a extra-fine-tip marker.

After clutches were complete, we captured, weighed, measured and aged by plumage (after-second year vs. second year) each breeding female. We measured body mass with a 30-g pesola scale and head-bill length with digital calipers to the nearest 0.05 mm. We estimated female body condition as the residual body mass from a regression of body mass vs. head-bill length (Ardia 2005). We visited nests daily, beginning four days prior to the estimated hatching date, to determine actual hatching dates and the number of eggs hatching on each day; asynchrony was characterized in each nest as the proportion of nestlings hatching on the day following the commencement of hatching.

## Data analyses

Before conducting statistical analyses we arc-sine square root transformed the proportion of time that daily temperatures in nestboxes exceeded  $26^\circ\text{C}$  and the proportion of eggs hatching asynchronously to normalize these variables (Shapiro-Wilk's  $W$ : temperature  $W = 0.97$ ,  $P = 0.22$ ; asynchrony  $W = 0.98$ ,  $P = 0.45$ ). In addition, because clutch initiation dates vary by site, we standardized clutch initiation date to a mean of 0 for each site. We used linear regression (forward selection with exit and entry probabilities = 0.10) to examine factors affecting the onset of incubation (PROC REG(SAS 1988) with the following covariates: standardized clutch initiation date, clutch size, female body condition, and the proportion of daily temperatures in nestboxes  $> 26^\circ\text{C}$ . In addition, we included two categorical variables converted to dummy variables: female age and breeding site. Because variables with  $P$ -values  $> 0.10$  were removed from models, we are unable to generate exact  $P$ -values for insignificant variables.

We also used linear regression to examine factors affecting incubation period and proportion of young hatching asynchronously. These models contained the covariates mentioned above along with the timing of onset of incubation. In addition, the model predicting asynchrony included incubation period as a covariate. For all linear regression models we produced partial

regression plots to examine relationships between predictors and the variable of interest while taking other variables into account. Partial regression plots are the best method of examining the relationship between two variables while accounting for covariation with other independent variables in a model (Neter et al. 1996). Partial regression plots for a pair of variables are created by plotting the residuals of two regression analyses: the first variable of interest against all independent variables vs. the first variable of interest against all independent variables excluding the second variable. We also used  $t$ -tests to compare mean clutch size between sites and chi-square to compare the distribution of early onset among sites.

## Results

We examined incubation behaviour in 95 nests (40 in Alaska, 55 in Tennessee). Clutch size did not differ between sites (mean clutch size  $\pm$ std. error: Alaska  $5.67 \pm 0.655$ , Tennessee  $5.52 \pm 0.68$ ,  $t_{93} = 1.01$   $P = 0.29$ ).

We observed early onset of incubation in 65 of 95 nests (68%), with most individuals beginning incubation one day prior to clutch completion (Fig. 1). More females in Tennessee initiated incubation prior to clutch completion than did females in Alaska (82% vs. 50%;  $\chi^2_4 = 14.19$ ,  $P = 0.006$ ), but when other covariates were taken into consideration, breeding site per se was not a significant predictor of the probability of initiating incubation before clutch completion ( $P > 0.10$ ). Rather, as the proportion of daily temperatures above  $26^\circ\text{C}$  during laying increased, the probability of initiating incubation prior to clutch completion increased (overall model  $F_{1,93} = 10.45$ ,  $P = 0.002$ ; effect of daily temperatures

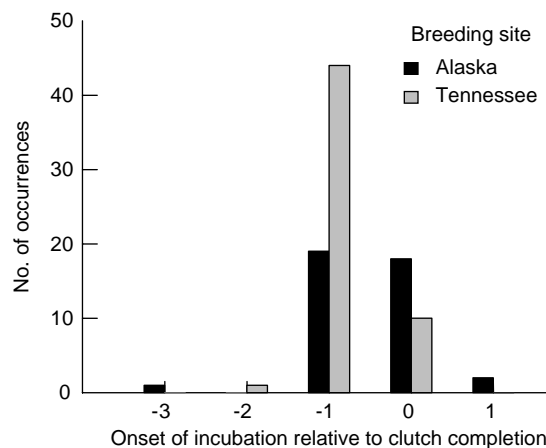


Fig. 1. Histogram of timing of onset of incubation relative to clutch completion date for two breeding locations of the tree swallow. Onset refers to the number of days incubation began prior to clutch completion. A higher proportion of females in TN than in AK start incubation early.

$\beta = -1.56$ ,  $R^2 = 0.10$ ,  $P = 0.002$ ). Standardized clutch initiation date, clutch size, female age, and female body condition had no influence on early onset of incubation ( $P_s > 0.05$ ).

Incubation period varied from 13 to 18 days (mean 14.3 days  $\pm 0.1$  SE). The length of the incubation period varied as a function of three variables: early onset of incubation, clutch size, and the proportion of daily temperatures  $> 26^\circ\text{C}$  during laying (overall model  $F_{4,90} = 6.79$ ,  $P < 0.001$ ). Females that began incubation early tended to incubate their clutches for fewer days than did females that began incubation on the day of clutch completion ( $\beta = -0.65$ ,  $R^2 = 0.09$ ,  $P = 0.003$ ). As clutch size increased, incubation period decreased ( $\beta = -0.44$ ,  $R^2 = 0.06$ ,  $P = 0.01$ ). Lastly, as temperatures during laying increased, incubation period decreased ( $\beta = -1.09$ ,  $R^2 = 0.05$ ,  $P = 0.02$ ). There was no direct effect of female age, female body condition index, standardized clutch initiation date, or breeding site on incubation period ( $P_s > 0.05$ ).

We observed asynchronous hatching (eggs hatching over more than a 24 hour period) in 65% of nests (62 of 95) with the proportion of nestlings hatching asynchronously ranging from 0.14 to 0.40 (Fig. 2). Early onset of incubation, clutch size and temperature conditions predicted the proportion of eggs hatching asynchronously (overall model  $F_{3,91} = 21.32$ ,  $P < 0.0001$ ). The strongest effect on asynchrony was the timing of onset of incubation. In nests where incubation began prior to clutch completion, there was a higher degree of asynchrony ( $\beta = -0.22$ ,  $R^2 = 0.36$ ,  $P < 0.001$ , Fig. 3). While increasing clutch size and warmer temperature conditions also had significant effects on hatching asynchrony, they explained very little of the variation (clutch size  $\beta = 0.06$ ,  $R^2 = 0.02$ ,  $P = 0.04$ ; temperature conditions  $\beta = 0.26$ ,  $R^2 = 0.1$ ,  $P = 0.09$ ). There was no

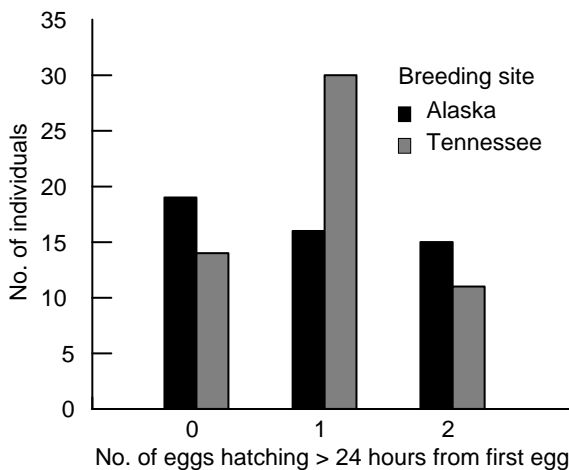


Fig. 2. Histogram of number of breeding female tree swallows that had nests where nestlings hatched asynchronously (over greater than a 24-hour period)

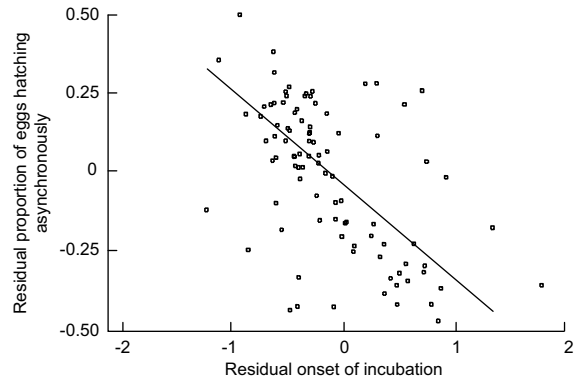


Fig. 3. Partial regression plot of the relationship between residual onset of incubation and residual proportion of eggs hatching asynchronously. Onset refers to the number of days incubation began prior to clutch completion. Negative values represent early onset of incubation. Proportion of eggs was arc-sine square root transformed prior to entry in model.

direct effect of female age, female body condition, standardized clutch initiation date, breeding site, or incubation period on hatching asynchrony ( $P_s > 0.05$ ).

## Discussion

By examining factors affecting the onset of incubation at two sites at the extremes of the species breeding range we found support for a key prediction of the egg viability hypothesis. First, as the proportion of daily temperatures in nestboxes above physiological zero increased, the probability that female tree swallows begin incubating prior to clutch completion also increased. Second, early onset of incubation was linked with a greater degree of hatch asynchrony. Our findings indicate that broad scale geographic differences in incubation behaviour may be explained by individual-level responses to environmental conditions that vary geographically rather than by population-specific differences as geographic differences were attributable to the difference in temperatures inside nestboxes; when temperatures are included in analyses, there was no site-level difference in early onset per se. Our results are correlational and other interpretations are possible; without a manipulation it is difficult to conclude that temperature alone drives the onset of incubation, rather individuals may be breeding at certain times of year for other reasons, and this timing is correlated with warmer temperatures. In addition, the low amount of variation explained by temperature indicates that other factors also play a strong role in influencing early onset of incubation.

In contrast to our results relative to the egg viability hypothesis, we found limited support for predictions of the “hurry-up” hypothesis (Slagsvold et al. 1995), which predicted that seasonal differences both within and among sites would influence early onset. Rather, we

found that later-laying individuals in both sites did not show patterns of onset different from early laying individuals. In addition, females in Alaska were not more likely to show early onset than Tennessee females. The last observation is particularly damaging to the “hurry-up” hypothesis, as the short breeding season in Alaska should create strong selection pressures to accelerate reproduction, and the “hurry-up” hypothesis predicts that early onset is one method to reduce total breeding time. We found no support for the clutch size threshold hypothesis; females regardless of clutch size showed similar patterns of incubation onset, even though eggs in larger clutches may have a greater chance of being exposed to warmer temperatures.

We found that warm temperatures shortened incubation periods regardless of clutch size, suggesting more complex dynamics than just temperature influencing incubation periods. Females initiating incubation early also tended to have shorter incubation periods, even when controlling for ambient temperatures inside nestboxes and clutch size. We also found that larger clutches have shorter incubation periods. Since large clutches cool more slowly, they may incubate at higher average temperatures (Frost and Siegfried 1977, Moreno and Hillstrom 2000, Reid et al. 2000, Reid et al. 2002) and therefore exhibit shorter incubation periods. But thermal inertia during cooling is more important under cooler ambient temperatures and we observed that short incubation periods tended to occur during warmer temperatures. Cooper et al. (2005) reported shorter durations between clutch completion and hatching for Eastern bluebirds and red-winged blackbirds with larger clutches, primarily at lower latitudes and later in the season. They suggested the pattern might be due to early onset of incubation to minimize loss of egg viability under warm ambient temperatures (Cooper et al. 2005).

Overall, our results are consistent with a critical prediction of the egg viability hypothesis, that early onset of incubation is more likely to occur when temperatures rise above physiological zero. While temperature inside nestboxes alone can not explain the complicated intersection of selection pressures on clutch size, reproductive investment, incubation behaviour and egg quality, the pattern of variation we observed makes it clear that hatching asynchrony is not an absolute rule for tree swallows. Rather, female incubation behaviour is driven by individual-level responses to environmental conditions, and those responses can be independent of individual condition. The consequences of these individual-level decisions combine to produce geographic variation in incubation behaviour and differences in offspring hatching patterns. It appears that early onset in tree swallows does not occur solely to induce hatching asynchrony, though asynchrony and early onset may be

linked if hatching asynchrony may also be more beneficial when ambient temperatures are warm.

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