

Influence of intraclutch egg-mass variation and hatching asynchrony on relative offspring performance within broods of an altricial bird

Pierre-Paul Bitton, Russell D. Dawson, and Erin L. O'Brien

Abstract: Rates of growth and size of nestlings at fledging have important consequences for future survival and reproductive success in many passerine birds. Within broods of altricial species, these characteristics are often influenced by size hierarchies established early in the nesting period due to hatching asynchrony and within-clutch variation in egg mass, but the concurrent effect of these factors is poorly understood. We investigated the relative influence of these variables on nestling performance within broods of tree swallows, *Tachycineta bicolor* (Vieillot, 1808). Nestlings that hatched earlier within nests were heavier and larger than their later-hatched siblings at 4 days of age. Similarly, earlier-hatched nestlings grew their ninth primary flight feathers faster and had longer ninth primaries just prior to fledging than did later-hatched siblings. Differences in egg mass of siblings also contributed to mass and size hierarchies at 4 days of age, but did not affect any other difference in sibling performance. We conclude that within-clutch variation in performance of offspring is determined primarily by size hierarchies resulting from asynchronous hatching. Intraclutch egg-mass variation appears to have little effect on performance of siblings and may be best explained by proximate constraints on females.

Résumé : Les taux de croissance et la taille des petits au nid au moment de l'envol ont des conséquences importantes sur la survie future et le succès reproductif chez de nombreux passereaux. Dans les portées des espèces nidicoles, ces caractéristiques sont souvent influencées par les hiérarchies de tailles établies tôt durant la période au nid à cause de l'asymétrie de l'élosion et de la variation de la masse des œufs dans une même portée; cependant, les effets concourants de ces facteurs restent mal connus. Nous avons étudié les influences relatives de ces variables sur le succès au nid chez des portées d'hirondelles bicolores, *Tachycineta bicolor* (Vieillot, 1808). Les petits qui éclosent plus tôt au nid sont à l'âge de 4 jours plus lourds et plus grands que les oisillons de même fratrie éclos plus tard. De même, les petits éclos plus précocement développent leurs neuvièmes rémiges primaires plus rapidement et possèdent des neuvièmes rémiges primaires plus longues juste avant le moment de l'envol que les autres oiseaux de la fratrie qui ont éclos plus tard. Les différences de masses des œufs dans une même portée contribuent aussi aux hiérarchies de masses et de tailles à l'âge de 4 jours, mais n'affectent pas les autres performances de la portée. Nous concluons que la variation de la performance des petits au sein de la portée est déterminée principalement par les hiérarchies de tailles résultant de l'asynchronisme de l'élosion. La variation de la masse des œufs dans la portée semble avoir peu d'effets sur la performance des petits d'une même portée et peut s'expliquer le mieux par des contraintes proximales chez les femelles.

[Traduit par la Rédaction]

Introduction

The relative performance of siblings within broods of altricial birds is often a function of sibling competition, which can be affected by size and growth rates of individual nestlings (Stokland and Amundsen 1988; Neuenschwander et al. 2003). To a large extent, the establishment of size and mass hierarchies within a nest is determined by the degree of hatching asynchrony (Krist et al. 2004). When parents start incubating before clutch completion, eggs that are laid first are among the first to hatch and, consequently, have a head-start on their siblings (e.g., Clotfelter et al. 2000). By the

time the entire clutch has hatched, it is not uncommon in some species for the first-hatched chick to be twice as heavy as the last-hatched chick (Zach 1982; Krebs 1999). The ensuing mass hierarchies have been demonstrated to disadvantage late-hatched nestlings and affect their pre-fledging performance (Lago et al. 2000). This has important fitness implications, since a nestling's mass just prior to leaving the nest is a strong predictor of postfledging survival in several species (Magrath 1991; Monros et al. 2002).

In addition to hatching asynchrony, differences in egg mass within a clutch also have the potential to contribute to size hierarchies. Egg mass varies with laying sequence in numerous bird species (review in Slagsvold et al. 1984), and this variation may have adaptive value. Laying a relatively small final egg, for example, may represent a brood reduction strategy by which females can enhance the size hierarchy established by hatching asynchrony, thus giving them more control over their brood size (Parsons 1970). Alternatively, a relatively large final egg could compensate for the size differences among siblings due to hatching asynchrony (Rosivall et al. 2005), thereby reducing the mortality

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rates of last-hatched chicks (Viñuela 1997). In studies that have investigated sources of variation in egg mass of tree swallows, *Tachycineta bicolor* (Vieillot, 1808), an altricial passerine, both Zach (1982) and Wiggins (1990) observed significant increases in egg mass with laying order. As a result, Wiggins (1990) suggested that this investment pattern may be strategic and would allow females to reduce the mass hierarchy caused by hatching asynchrony. The underlying assumption that variation in egg mass within a clutch has performance consequences for nestlings, however, was not tested. Indeed, the relative importance of egg mass and hatching asynchrony in determining offspring quality in species of altricial birds is poorly understood. In this study, we examined how hatching asynchrony and variation in egg mass influenced the mass, size, and growth of siblings within broods of tree swallows.

Materials and methods

Study area and field procedures

The study was conducted from May to July 2003 near Prince George, British Columbia, Canada ($53^{\circ}45'N$, $122^{\circ}33'W$). Birds nested in boxes that were mounted 1.5 m above the ground on fence posts, in an area mainly composed of open agricultural fields with patches of mixed deciduous and coniferous forest. Tree swallows arrived on the site near the end of April and began initiating clutches in late May.

Starting in mid-May, nest boxes were inspected every 1–2 days until the first egg was found, after which every box was checked daily. On the day it was laid, each egg was weighed to the nearest 0.01 g using an electronic balance and numbered with a nontoxic permanent marker according to laying sequence. After clutches were complete, nests were not visited again until 2 days before the predicted hatching date, at which time they were visited at least once per day. When the eggs showed signs of hatching (i.e., star cracks), a piece of fine thread was glued around the longitudinal axis of each egg to temporarily restrain the chick (Mayoh and Zach 1985). Nests were then visited hourly from dawn to dusk (approximately 0500–2200 PDT) to determine time of hatching. When a hatchling had pecked around the girth of the egg, the thread was removed, and the chick was given an individual identification mark using a nontoxic marker. These marks were refreshed as needed, usually every other day. Although chicks were often able to free themselves before we removed the thread, we were able to match all chicks with their egg in 33 nests (all clutches five–seven eggs). When the penultimate egg had hatched, the thread was also removed from the remaining egg to avoid further disturbance of the nest. This prevented us from determining the exact hatching time of the last chick and, therefore, total asynchrony of most nests; however, our goal was to compare chicks differing in hatching time (see below), and this did not require that we determine total hatching asynchrony. We defined hatching date as the day the first egg in a clutch hatched; hatching time of the first egg was time zero.

Nestlings were measured every other day, from 4 days after hatching until they were 16 days old (just prior to fledging, which begins at 18 days of age). At every visit, each chick was weighed (nearest 0.125 g) using a spring

scale, and their right tarsus was measured 4 times (nearest 0.01 mm) with digital callipers. We calculated the average of the measurements of tarsus length and used these values for all analyses. Since ninth primary feathers of most nestlings do not begin growing until after 6 days of age, we measured length of primary from 8 to 16 days of age using a ruler (nearest 0.5 mm). We then calculated growth rate constants for body mass, ninth primary, and tarsus for each nestling within a brood using methods described by Dawson et al. (2005). We used logistic, Gompertz, and linear models to describe growth of mass, tarsus, and ninth primary, respectively, which allowed us to test how egg mass and hatching asynchrony influenced nestling development.

Within-brood comparison

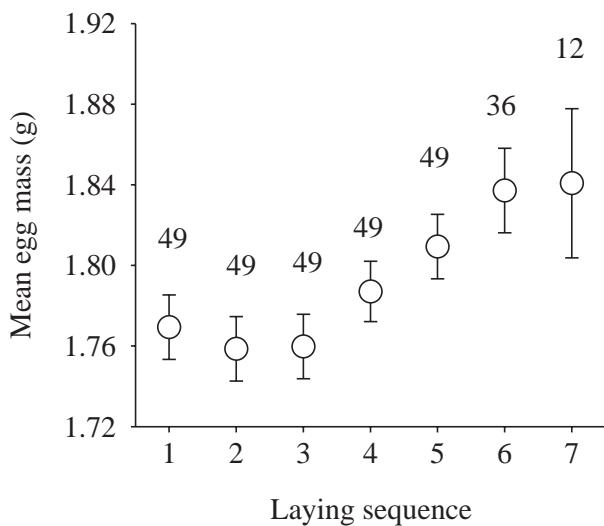
Because we often lacked precise information on hatching time of the last-hatched chick, and thus could not include all nestlings within a brood in our analyses, we compared the performance of a pair of siblings, one of which had hatched from a relatively small egg and one that had hatched from a relatively large egg. We compared the performance of these nestlings within a dyad by calculating the difference in egg mass, hatching time, and performance characteristics (size and growth) between them. For each pair of siblings, we randomly assigned whether values associated with the nestling that hatched from the smaller egg would be subtracted from those from its sibling coming from a larger egg, or vice versa.

Within broods, mass hierarchies established by hatching asynchrony are a function of feeding time, with the first hatchlings being fed while other siblings are still within their eggs (Zach 1982). For this reason, for nests where members of a dyad hatched on different days, we calculated differences in hatching time excluding nighttime (2200 to 0500). Also, because we wanted to analyse the effect of intraclutch egg-mass variability, we converted absolute egg-mass difference to a relative difference in egg mass. This relative index was calculated as the difference in mass of the two eggs in a dyad, divided by the mean egg mass of the clutch. This procedure eliminated the effects of among-clutch egg-mass variation.

Statistical analyses

We described the pattern of variation in egg size with laying sequence using Spearman's rank correlations and tested whether egg mass and hatching times within a dyad differed using Student's *t* tests. We investigated the early influence of egg mass and hatching asynchrony on mass and length of tarsus of nestlings at 4 days of age and the influence of these variables later in the nestling period on growth rates of mass, tarsus, and ninth primary, and size (tarsus, ninth primary) and mass of nestlings at age 16 days. For each variable, we used a general linear model with differences in egg mass and hatching asynchrony as independent variables as well as the interaction term. In addition, we included hatching date and brood size in each model because these two factors have been shown to influence the effects of sibling competition (Arroyo 2002; Neuenschwander et al. 2003). We used a backward stepwise procedure to eliminate nonsignificant terms for each model, always keeping differences in hatch time and egg mass in the final model. Our

Fig. 1. Mean mass of eggs (\pm SE) of tree swallows, *Tachycineta bicolor*, according to order of laying. Numbers of nests are indicated above error bars.



sample sizes for mass and size of offspring at 16 days of age, as well as for growth rates, are lower than those for mass and size at 4 days of age because many complete broods died during the nestling period as a result of unseasonably cold and inclement weather during the year of our study (unpublished data). For this same reason, all nestlings within a large majority of broods either survived or died, and therefore, we did not analyse the effects of hatching asynchrony and egg-mass variation on nestling survival. Nonetheless, the variables we included in our analyses are known to be related to fitness in passerine birds (e.g., Magrath 1991) and specifically in tree swallows (McCarty 2001). All statistical analyses were performed using SPSS® (Norušis 2000). Results were considered significant at the 0.05 level, and we present means \pm 1 SE.

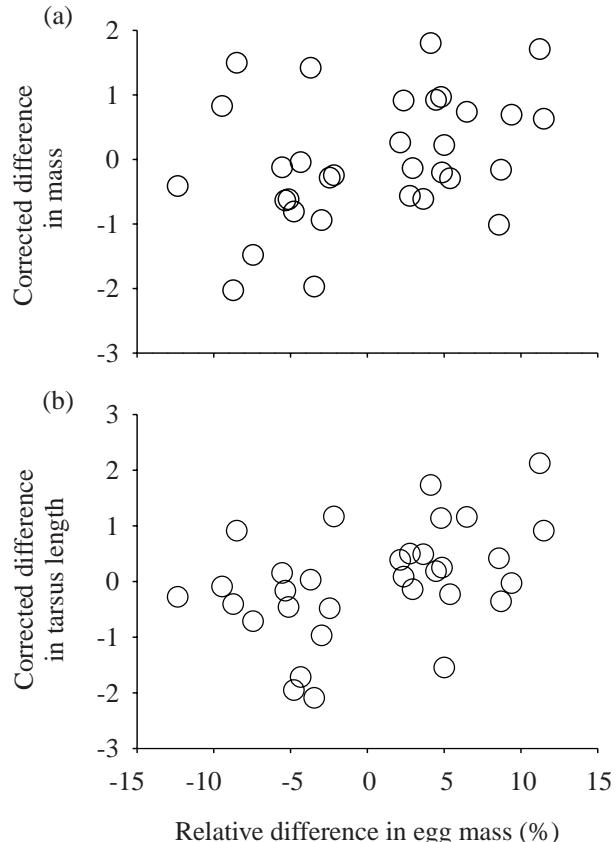
Results

The mean mass of all eggs (293 eggs from 49 clutches) was 1.79 ± 0.01 g (range 1.49–2.12 g), with the largest egg in a clutch being on average 0.14 ± 0.07 g ($7.8\% \pm 3.9\%$) heavier than the smallest egg. Similar to patterns previously observed in tree swallows (Zach 1982; Wiggins 1990), the average mass of eggs increased significantly with the order in which they were laid, both when all clutch sizes were pooled for analysis ($r_S = 0.89$, $n = 7$, $P < 0.01$; Fig. 1) and when analyzed by clutch size (all P values < 0.05). Within the dyads that we compared in this study, the heavier egg had an average mass of 1.82 g, while the lighter egg averaged 1.72 g (paired $t_{[32]} = 11.31$, $P < 0.0001$). Time elapsed between hatching of the two eggs in a dyad averaged 3.24 ± 0.99 h (range –6.52 to 17.48 h, $n = 33$) and differed significantly from 0 (one-sample t test: $t_{[32]} = 3.26$, $P < 0.01$).

Nestling performance

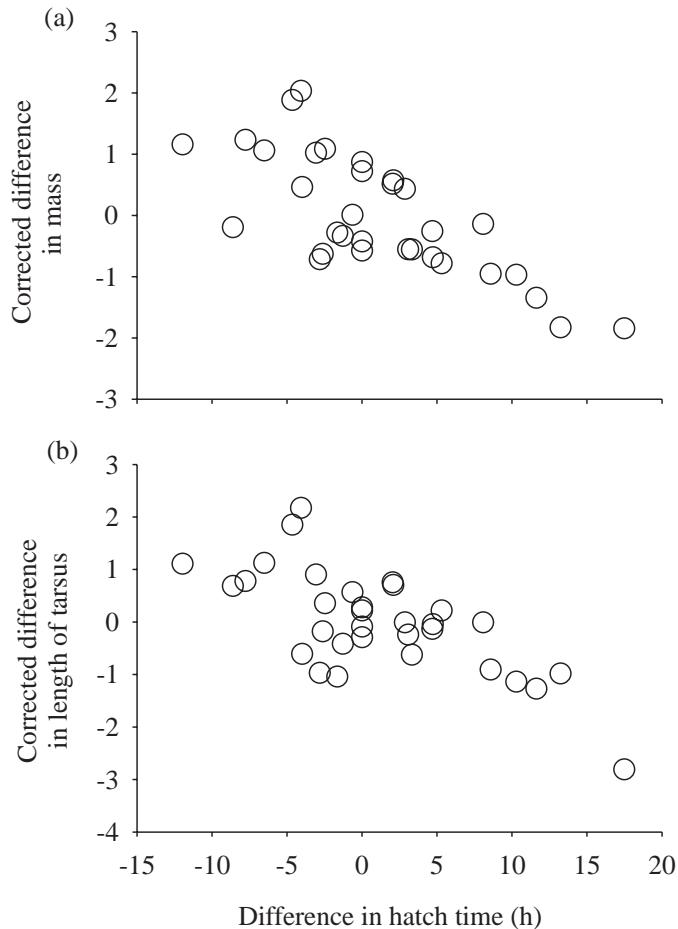
Differences in both egg mass ($F_{[1,29]} = 6.06$, $P = 0.02$, $R_{\text{partial}} = 0.42$; Fig. 2a) and hatching time ($F_{[1,29]} = 87.66$, $P < 0.001$, $R_{\text{partial}} = -0.87$; Fig. 3a) were significantly related to differences in mass of siblings at 4 days of age,

Fig. 2. Relationship between the relative difference in egg mass of sibling tree swallows in a dyad (see Materials and methods for details) and difference in (a) mass and (b) length of tarsus at 4 days of age. To illustrate the relative contribution of variation in egg mass to differences in mass and size, we removed the effect of hatching asynchrony (see Results) by calculating the residuals from regressions between the differences in each variable and differences in hatching time; these residuals are presented in the figures.



such that those hatching earlier within a nest and coming from relatively large eggs were heavier. Similarly, greater differences in egg mass ($F_{[1,29]} = 9.42$, $P < 0.01$, $R_{\text{partial}} = 0.50$; Fig. 2b) and hatching time ($F_{[1,29]} = 63.02$, $P < 0.001$, $R_{\text{partial}} = -0.83$; Fig. 3b) were associated with greater differences in length of tarsus at 4 days of age. At 16 days of age, however, only difference in hatching time appeared to influence variation in mass of siblings, but this relationship only approached significance (hatching time: $F_{[1,18]} = 4.07$, $P = 0.059$, $R_{\text{partial}} = -0.43$; egg mass: $F_{[1,18]} = 2.43$, $P = 0.14$, $R_{\text{partial}} = 0.35$). Similarly, hatching asynchrony ($F_{[1,18]} = 24.15$, $P < 0.001$, $R_{\text{partial}} = -0.76$; Fig. 4), but not egg mass ($F_{[1,18]} = 0.02$, $P = 0.88$, $R_{\text{partial}} = -0.04$), was significantly related to differences in length of ninth primary between siblings at day 16. Difference in length of tarsus at 16 days of age was not related to either differences in egg mass ($F_{[1,17]} = 1.56$, $P = 0.23$) or hatching time ($F_{[1,17]} = 1.35$, $P = 0.26$), but the interaction between the two terms was significant ($F_{[1,17]} = 5.25$, $P = 0.04$). To investigate the nature of this interaction, we separated the data into two groups based on whether the difference in egg mass was larger or smaller than the unsigned average difference in egg mass and analysed the effects of hatching

Fig. 3. Influence of the difference in hatching time between sibling tree swallows included in a dyad (see Materials and methods for details) and difference in (a) mass and (b) length of tarsus at 4 days of age. We removed the effect of egg mass by calculating the residuals from regressions between the differences in each variable and differences in egg mass; these residuals are presented in the figures.



asynchrony separately for the two groups. If the difference between the egg mass was small, there was a trend for earlier-hatched nestlings to have longer tarsi at day 16, but this relationship only approached significance ($F_{[1,9]} = 4.93$, $P = 0.054$, $R^2 = 0.35$). In contrast, if the egg mass difference was large, there was no relationship between differences in hatching time and differences in length of tarsus at 16 days old ($F_{[1,8]} = 1.41$, $P = 0.27$, $R^2 = 0.15$).

Differences in growth rates of mass were not influenced by either differences in egg mass ($F_{[1,11]} = 0.52$, $P = 0.49$, $R_{\text{partial}} = -0.21$) or hatching time ($F_{[1,11]} = 1.15$, $P = 0.31$, $R_{\text{partial}} = -0.31$). Likewise, there was no significant relationship between differences in egg mass ($F_{[1,11]} = 2.80$, $P = 0.12$, $R_{\text{partial}} = 0.45$) or hatching time ($F_{[1,11]} = 0.24$, $P = 0.63$, $R_{\text{partial}} = -0.15$) and differences in growth rates of tarsus. We did find, however, a significant relationship between difference in hatching time and differences in growth rates of ninth primaries ($F_{[1,12]} = 5.13$, $P = 0.04$, $R_{\text{partial}} = -0.55$; Fig. 5), but differences in egg mass had no effect ($F_{[1,12]} = 0.01$, $P = 0.96$, $R_{\text{partial}} = -0.02$), suggesting that earlier-hatched nestlings were able to grow their feathers faster than later-hatched siblings.

Fig. 4. Effect of difference in hatching time of sibling tree swallows included in a dyad (see Materials and methods for details) on the difference in length of ninth primary flight feathers at 16 days of age.

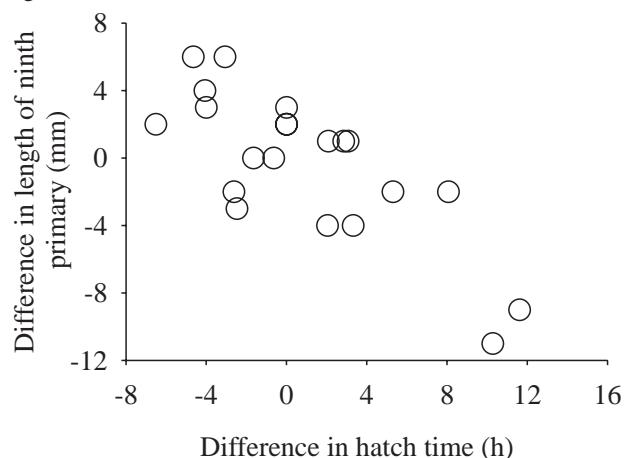
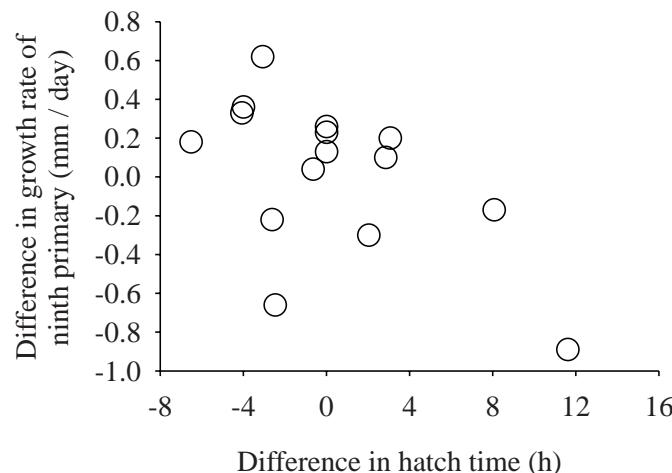


Fig. 5. Effect of hatching time differences on the differences in growth rate of the ninth primary of sibling tree swallows included in a dyad (see Materials and methods for details).



Discussion

Influence of hatching asynchrony and egg mass on nestling performance

The difference in hatching time between sibling tree swallows explained a large proportion of the observed differences in structural size at 4 and 16 days of age. Nestlings that hatched earlier within a nest performed better throughout the brood-rearing period compared with their later-hatched siblings. Similarly, differences in hatching times seemed to have influenced long-term differences in mass between siblings, and the magnitude of hatching asynchrony was also associated with the differences between nestmates in growth rates of ninth primary flight feathers. In contrast, within-clutch variation in egg mass had detectable effects on the establishment of brood hierarchies in the days following hatch, but this effect was not maintained throughout the nestling period. Therefore, nestling performance primarily reflected differences in hatching time. Although sample sizes for some of these tests were limited, our results are in accordance with

previous studies that concluded hatching asynchrony is more influential than egg mass in mediating nestling competition (e.g., Krist et al. 2004) and likely represent true trends.

In tree swallows, females usually start incubating after laying their penultimate egg (Robertson et al. 1992), and eggs may hatch over a period of up to 4 days (Zach 1982). Although documenting total hatching asynchrony was not a goal of our study (see Materials and methods), we nonetheless showed that differences in hatching times of siblings played an important role in their relative performance within a brood. These differences are most likely due to the fact that nestlings which emerge first are fed before the other eggs hatch, and these first-hatched nestlings are able to maintain their initial advantage. Whittingham et al. (2003) have shown that parental provisioning of food to nestling tree swallows is not influenced by nestling size, sex, or paternity but rather by begging behaviour and proximity to the nest entrance. Similarly, Leonard and Horn (1996) found that large and small nestlings were fed at similar rates. Mass hierarchies throughout the brood-rearing period are therefore probably not controlled by parent favouritism but rather are likely a direct effect of hatching asynchrony.

Unlike mass hierarchies that seem to have been maintained until the birds fledged, patterns of structural growth were not as consistent. In this study, differences in hatching time explained a large proportion of the differences in length of tarsus at 4 days of age but not at age 16 days. Instead, hatching asynchrony had a long-term influence on the growth rate and pre-fledging length of primary flight feathers. It is probable that control of feather growth is less constrained than growth of bones such as the tarsi. Previous studies on tree swallows have shown that tarsus length is highly heritable (Wiggins 1989) and that bone growth may be limited by the availability of specific nutrients such as calcium (Dawson and Bidwell 2005). This would reduce the influence that factors such as hatching asynchrony and egg mass have on growth of tarsus. In addition, Michaud and Leonard (2000) demonstrated that long-winged nestlings fledge before short-winged nestlings and suggested that there is a risk for short-winged nestlings to be left behind when larger siblings fledge. Similar findings were obtained by Johnson et al. (2003) when investigating the fate of last-hatched offspring in tree swallows. They found that size-disadvantaged nestlings gained mass and grew their primary feathers more slowly than their earlier-hatched nestmates, and, as in our population, they also observed that late-hatched nestlings had shorter primaries just prior to fledging. Nestlings that hatch first, therefore, seem to outcompete their later-hatched siblings by prioritizing feather growth as opposed to allocating resources to other processes. Since length of feathers at fledging has also been found to affect postfledging survival in tree swallows, this strategy would likely increase the nestlings' fitness (McCarty 2001).

Is intraclutch egg-mass variation adaptive?

Although some studies of passerine birds have shown that there are fitness consequences associated with egg-mass variation among clutches (e.g., Styrsky et al. 1999), the effects of within-clutch variation are less clear. In this study, egg

mass within clutches increased with laying order (Fig. 1), a pattern previously reported in tree swallows (Zach 1982; Wiggins 1990) as well as in other altricial passersines (e.g., Briskie and Sealy 1990; Cichón 1997; Cichón et al. 2003; Rutkowska and Cichón 2005). This pattern is consistent with the brood survival strategy, which suggests that species with asynchronously hatching clutches may decrease the mortality rate of last-hatched chicks by laying relatively large final eggs (Slagsvold et al. 1984; Viñuela 1997). The brood survival hypothesis implies that within-clutch egg-mass variation has consequences for brood mass and size hierarchies, but this assumption has rarely been tested.

In an experimental synchronization of incubation onset, Rutkowska and Cichón (2005) showed that nestling survival probability was positively related to egg mass in synchronous broods but not in asynchronous broods. In contrast, there was no evidence of long-term effects of egg mass on nestling growth. This last finding concurs with correlational studies that have examined the influence of intraclutch egg-mass variation (e.g., Stokland and Amundsen 1988; Magrath 1992; Viñuela 1996; Magrath et al. 2003; Krist et al. 2004), including our own, which have shown that egg mass had an effect on the initial mass or size of hatchlings, but did not influence hierarchies over the long term (but see Rosivall et al. 2005). Many of these studies have concluded that intraclutch egg-size variation has little adaptive value and invoke proximate constraints on laying females to explain these trends. Indeed, heritability estimates for egg size are high (77% in tree swallows and generally over 60% in most species; see Wiggins 1990; Christians 2002), indicating that variation in this trait is largely due to genetic factors. In addition, factors such as changes in temperature before or during the egg-laying period (Saino et al. 2004; Hargitai et al. 2005), changes in food availability or quality (Perrins 1970; Bidwell and Dawson 2005), and evolutionary pressure for laying early (Slagsvold and Lifjeld 1989) could induce variation in egg mass. As noted by Krist et al. (2004), differences in the relative importance of these constraints at the individual or population level could be responsible for the diversity in patterns of intraclutch egg-mass variation observed in birds. Confirming these ideas, Ardia et al. (2006) found that egg mass and egg composition in tree swallows was highly influenced by a combination of environmental conditions, food availability, female quality, and allocation trade-offs during the egg-laying period. Taken together, these results seem to indicate that females have little control over resource allocation to individual eggs within the same clutch and that adaptive explanations of within-brood egg-mass variation must be invoked with prudence.

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