

Egg Size Variation in Birds with Asynchronous Hatching: Is Bigger Really Better?

J. Dylan Maddox* and Patrick J. Weatherhead†

Program in Ecology, Evolution, and Conservation Biology,
University of Illinois, Champaign, Illinois 61820

Submitted June 1, 2007; Accepted October 18, 2007;
Electronically published January 24, 2008

ABSTRACT: In many animals large size at birth enhances offspring survival, but comparative evidence remains equivocal for birds. Failure to consider asynchronous hatching (ASH) may have confounded previous analyses. We assessed effects of egg size and ASH on growth and survival of common grackle (*Quiscalus quiscula*) nestlings to test the hypothesis that females adjust the size of last-laid eggs to modify effects of ASH. Although positive, the effect of egg size on nestling growth and survival was overwhelmed by the effect of ASH, with late-hatched nestlings being most likely to starve. Egg size did significantly affect growth late in the nestling period, but only because starvation had greatly reduced hatching asynchrony among surviving nestlings. Similarly, in experimentally synchronized nests, egg size and hatching asynchrony both affected offspring growth early in the nestling phase. Our results suggest that there is unlikely to be an adaptive advantage to females from varying the size of last-laid eggs in species with substantial ASH and that studies to assess the effect of a given maternal effect (e.g., varying egg size) should be done in the context of other maternal effects that may be operating simultaneously (e.g., ASH).

Keywords: intraclutch egg size variation, maternal effects, nestling growth, nestling starvation.

Offspring size is among the most extensively studied life-history traits. Across species, offspring size varies enormously, but even within species and within individual clutches, offspring size can also vary substantially (Klomp 1970; Nichols et al. 1976; Stearns 1976). Given finite resources to invest in reproduction, there exists a trade-off between the size of individual offspring and the number

of offspring that a female can produce. Different optimal solutions for this trade-off are thought to explain inter-specific variation in offspring size (Roff 1992; Stearns 1992). Among individuals of the same species, variation in factors such as maternal condition, size, age, or experience may contribute to offspring size variation (Roff 1992; Stearns 1992). Variation in offspring size within clutches has received less attention than variation within and among species but could be a nonadaptive consequence of maternal inability to precisely control resource allocation to developing follicles (McGinley et al. 1987) or, alternatively, could be part of an adaptive maternal strategy to influence competition among siblings (e.g., Slagsvold et al. 1984). The fundamental assumption of adaptive explanations for within-clutch size variation is that egg size affects offspring viability. Here we test that assumption using common grackles *Quiscalus quiscula*, a species with substantial variation in intraclutch egg size and hatching asynchrony (Howe 1976, 1978).

Larger size at birth has been associated with enhanced growth and survival of offspring in a variety of taxa, including lizards (e.g., Sinervo 1990), turtles (e.g., Janzen 1993), snakes (e.g., Jayne and Bennett 1990), arthropods (e.g., Fox and Czesak 2000), fish (e.g., Hutchings 1991), and plants (e.g., Stanton 1984). In organisms that provide extensive parental care, such as birds, siblings must compete with each other for parental provisioning, and when resources are limited, sibling rivalry can cause the death of smaller, weaker individuals (Mock 1984; Magrath 1990; Stoleson and Beissinger 1995; Stenning 1996). Thus, the relative size of eggs within a clutch seems likely to affect which nestlings survive to fledging. However, evidence of a positive relationship between egg size and offspring fitness in birds remains equivocal (Williams 1994).

Variation in size at hatching is not the only factor that can affect the outcome of sibling competition in birds. In many species, females begin incubating their eggs before clutch completion, resulting in asynchronous hatching (ASH), which produces a size hierarchy among nestlings (Clark and Wilson 1981; Magrath 1990; Stoleson and Beissinger 1995). The size and strength advantage that ASH

* Corresponding author; e-mail: jmaddox@uiuc.edu.

† E-mail: pweather@uiuc.edu.

affords earlier-hatched nestlings can result in starvation of those that hatch later. Regardless of the adaptive value of ASH (the evolutionary explanation for ASH is beyond the scope of this article [but see reviews in Magrath 1990; Stoleson and Beissinger 1995; Stenning 1996; and Ricklefs 1997]), the size hierarchy produced by ASH could confound efforts to identify the relative contribution of egg size to offspring fitness (cf. Magrath 1992).

Slagsvold et al. (1984) hypothesized that female birds might adaptively vary egg size to modify the effects of ASH. Species in which the last-laid egg is larger than the clutch mean would be adopting a "brood survival strategy," while species that have a smaller last egg relative to the clutch mean would be adopting a "brood reduction strategy." In the former case, making last-hatched nestlings larger would reduce the negative effects of ASH, while in the latter case, making last-hatched nestlings smaller would compound their disadvantage. Because grackles lay larger last eggs (Howe 1976, 1978), the specific prediction we test here is that the larger size of last-hatched nestlings resulting from hatching from larger eggs should reduce the negative effects of hatching last. Testing this hypothesis requires assessing the independent effects of egg size and hatching asynchrony on nestling growth and survival. Logistical challenges in quantifying those effects have thus far prevented definitive testing of the hypothesis of Slagsvold et al. (1984).

Collecting the data necessary to investigate the independent effects of intraclutch egg size variation and ASH on offspring fitness requires three things that can be difficult to achieve for a suitable sample of nests. First, nests must be found before clutch initiation to determine laying order and egg size. Second, nestlings must be accurately matched to the egg from which they hatched, even though in ASH species the first few eggs of a clutch can hatch within a few minutes of each other. Thus, nests must be checked every few minutes on days when eggs are predicted to hatch. Although eggs generally hatch early in the morning, they can hatch at any time of the day or night. Third, nestlings must be monitored and measured throughout the entire nestling stage. Here we use a study design that allowed us to obtain these data from a population of common grackles. We compare the effect of egg size on nestling growth and survival when the effects of ASH have been experimentally eliminated with egg size effects under normal patterns of ASH.

Methods

Study Species

Common grackles are well suited to the objectives of this study. First, females substantially vary egg size with laying

order and hatch their eggs asynchronously (Howe 1976, 1978), although the variation in egg size and asynchrony is well within the range found in altricial bird species (Clark and Wilson 1981; Slagsvold et al. 1984). Second, grackles are not territorial (Peer and Bollinger 1997), eliminating territory quality (e.g., food availability) as a confounding factor affecting offspring survival. Finally, grackles experience a high incidence of brood reduction (20%; Howe 1978), which should increase the opportunity to detect fitness consequences of egg size variation.

Field Methods

We studied common grackles in 2006 in Champaign County, Illinois, at the Ridge Road Tree Farm (RRTF). Christmas tree farms often attract large nesting colonies of grackles in central Illinois (Maddox and Weatherhead 2006). All grackle nests were 1–3 m off the ground, which allowed us to find most nests before clutch initiation. Nests found before egg laying were checked daily to determine clutch initiation. We weighed and uniquely marked each egg on the day it was laid. To match nestlings with eggs, we collected all eggs from a nest when at least one egg was starting to hatch, temporarily replacing the real eggs with wooden eggs of similar appearance and size, which the grackles readily accepted. Real eggs were placed individually in compartments in an incubator maintained at approximately 30°C (Hova-Bator Incubator, model 1602N). To identify individuals throughout the entire nestling stage, we marked nestlings with a unique color combination on the foot (left or right) using a nontoxic permanent marker. Nestlings were then weighed to the nearest 0.1 g and returned to their respective nests, and a wooden egg was removed for each nestling. We repeated this process until all eggs from a particular nest hatched. Nestlings were generally returned to their nests within 2 h of hatching, but nestlings that hatched during the night were returned the next morning, resulting in some nestlings being held without food for ≥ 6 h. This timing is identical to what occurs naturally because parents do not feed nestlings at night. Hatching rates comparable to those in unmanipulated nests and high initial survival of nestlings indicated that our manipulation did not negatively affect nestling performance. Furthermore, because all eggs and nestlings were treated identically, any potential methodological effects would not have introduced any bias relative to the goals of the study.

Nests were checked daily to estimate starvation and fledging dates. Starvation was easy to identify because nestlings that subsequently disappeared were emaciated, were substantially smaller than their siblings, and had gained little or no mass for 1–3 days. Five and 10 days after the first nestling hatched in a given nest, each nestling was

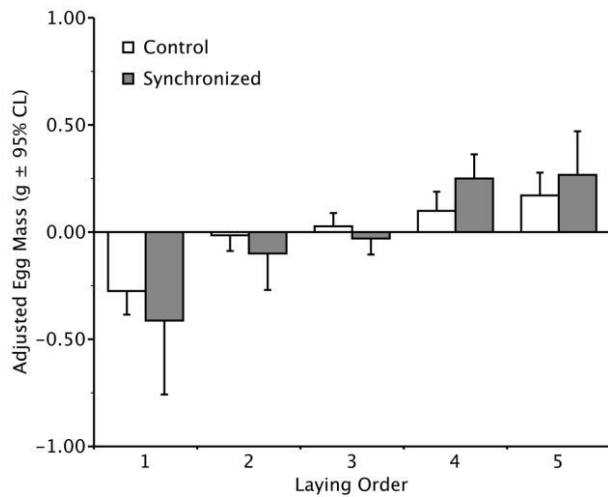


Figure 1: Mean adjusted egg mass ($g \pm 95\%$ confidence limits [CL]) relative to laying order in control nests and experimentally synchronized nests.

reweighed. Fledging generally occurs 12–14 days after hatching, but weighing nestlings >10 days old can force nestlings to fledge prematurely.

Experimental Manipulation

We largely eliminated hatching asynchrony by collecting each egg on the morning it was laid, replacing it with a wooden egg, and storing it at 10° – 15°C to suspend embryo development. After clutch completion, all eggs from a given clutch were returned to their nest simultaneously and thereafter were treated exactly as we described above for control nests. Daily air temperature in April 2006 (i.e., during egg laying) averaged $14.0^{\circ} \pm 4.7^{\circ}\text{C}$ SD (range 4.3° – 22.8°C), so before incubation, experimental and control eggs experienced similar mean temperatures.

Data Analysis

Because maternal effects vary with clutch size in common grackles (Howe 1976, 1978), we limited analyses to five-egg clutches—the modal clutch size across the entire breeding range (Peer and Bollinger 1997)—which accounted for 71% of the 172 clutches found at RRTF. We were interested in the effect of within-clutch egg size variation on offspring performance, so we determined relative egg mass (our measure of egg size) as the difference between the mass of each egg and its clutch mean (Krist and Remes 2004; Krist et al. 2004). To determine the effects of hatching asynchrony on nestling growth and survival for each laying position, we calculated the time (in hours)

between the hatching of the first nestling and that of each of its siblings. For all nestlings, including those that hatched at night, we considered hatching time for each nestling to be the time it was returned to its nest, because that is the point at which parents could begin to feed it.

To determine the effects of hatching asynchrony and egg size, we constructed models in R 2.5.0 (R Development Core Team 2007), using nestling mass and survival as response variables. For all models, we retained hatching asynchrony and egg size as fixed effects of interest. Initial models included mean clutch mass, laying order, and the interaction between hatching asynchrony and egg size as fixed-effects covariates. Final models were selected using the Akaike Information Criterion following the recommendations of Johnson (1998). Nest was included as a random effect in all models to account for nonindependence of nestlings within a nest. Models assessing nestling mass were fitted using linear mixed-effects (LME) models (lme, package nlme; Pinheiro and Bates 2000). Models assessing nestling survival were fitted using generalized linear mixed models (GLMMs) with a penalized quasi-likelihood (PQL) method, a binomial error structure, and a logit link function (glmmPQL, package MASS; Venables and Ripley 2002). Both model types were fitted to data for control and synchronized nests at 5 and 10 days post-hatching. To estimate the relative importance of egg size versus hatching asynchrony on nestling performance, we used logistic and linear regressions to calculate univariate coefficient of determination r^2 values for nestling survival and mass, respectively. For graphical purposes, we used

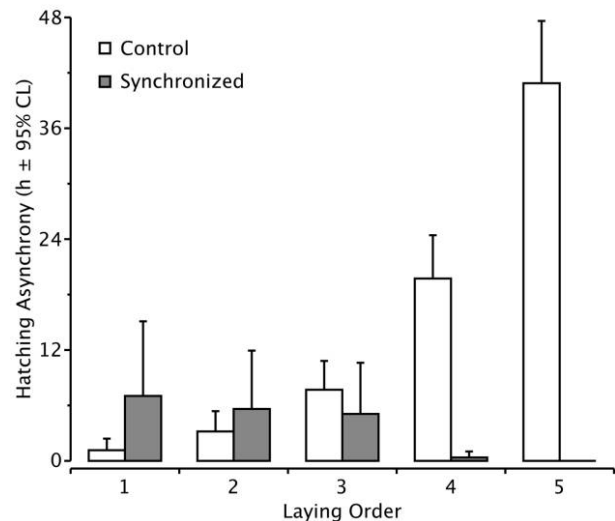


Figure 2: Mean within-clutch hatching span (hours $\pm 95\%$ CL) relative to laying order in control nests and experimentally synchronized nests. The span is determined relative to the first egg to hatch.

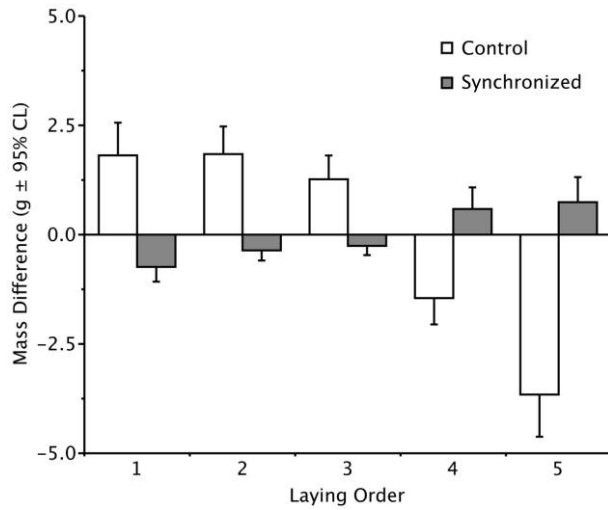


Figure 3: Mean difference between nestling mass and clutch mean ($g \pm 95\%$ CL) at the completion of hatching relative to laying order in control nests and experimentally synchronized nests.

95% confidence limits (CL) constructed from 1,000 replicate bootstrap samples.

Results

We obtained data for 10 synchronized and 39 control nests. A predation episode eliminated all synchronized nests before day 10, and starvation before day 5 was rare, so analysis for those nests is limited to mass at day 5. Egg size increased with laying order for both control and synchronized nests (fig. 1). Experimental manipulation of hatching asynchrony produced the desired result in that the hatching span was reduced by 79% from 39.6 ± 6.3 h (95% CL; range 0–90) in control nests to 8.2 ± 6.6 h (95% CL; range 0–23) in synchronized nests. Eggs generally hatched in the order in which they were laid in control nests, with last-laid eggs hatching most asynchronously (fig. 2). In synchronized nests, however, eggs tended to hatch in the order opposite that in which they were laid, suggesting that embryonic development and laying order are positively correlated (Nicolai et al. 2004), possibly due to increased concentrations of yolk androgens (Gil 2003; Groothuis et al. 2005). Consequently, at the end of hatching, the weight difference between a given nestling and the mean of its siblings decreased substantially with laying order in control nests but increased slightly with laying order in synchronized nests (fig. 3). These patterns were still evident at 5 days posthatching (fig. 4).

Both egg size and hatching asynchrony had a significant effect on nestling survival in control nests at 5 and 10 days posthatching (table 1). Similarly, hatching asynchrony af-

fected nestling growth at 5 and 10 days posthatching in control nests, while egg size had a significant effect on nestling mass only at 10 days posthatching (table 2). In synchronized nests, both egg size and hatching asynchrony significantly affected nestling mass at 5 days posthatching. Univariate r^2 values indicated that hatching asynchrony affected both nestling growth and survival in all treatments, while egg size had limited effects (table 3). Egg size did affect nestling growth in control nests at 10 days but not at 5 days, and in synchronized nests, egg size had an effect equivalent to that of hatching asynchrony at 5 days. Consistent with these results, starvation rates in control nests were substantially higher for nestlings from the fourth and fifth egg positions at both 5 and 10 days posthatching (fig. 5), indicating that larger egg size did not compensate for delayed hatching. Furthermore, starvation rates for each egg position were higher later in the nestling period, except for nestlings from first-laid eggs, for which starvation rates remained constant (fig. 5).

Discussion

Our population of common grackles exhibited pronounced hatching asynchrony and intraclutch egg size variation, both of which were positively correlated with laying order. Because these patterns are nearly identical to those found for grackles studied in a variety of habitats (Howe 1976, 1978; J. D. Maddox, unpublished data) and are typical of many altricial birds (Clark and Wilson 1981; Slagsvold et al. 1984), our results are unlikely to be unique to

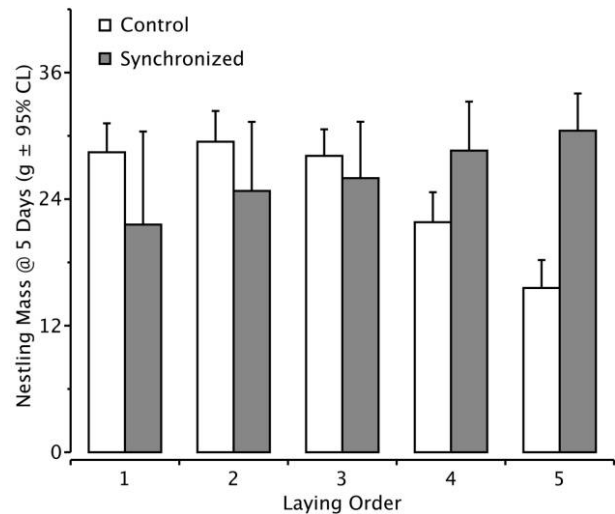


Figure 4: Mean nestling mass ($g \pm 95\%$ CL) 5 days after the hatching of the first nestling relative to laying order in control nests and experimentally synchronized nests.

Table 1: Parameter estimates for model of nestling survival at 5 and 10 days posthatching in control nests

| | Estimate | SE | df | <i>t</i> | <i>P</i> |
|------------------------|----------|-------|-----|----------|----------|
| Control at 5 days: | | | | | |
| Intercept | 4.173 | .687 | 144 | 6.075 | <.001 |
| Hatching asynchrony | -.068 | .018 | 144 | -3.699 | <.001 |
| Egg size | 2.526 | 1.270 | 144 | 1.989 | .049 |
| Control at 10 days: | | | | | |
| Intercept | -7.198 | 8.803 | 56 | -.818 | .417 |
| Hatching asynchrony | -.157 | .028 | 56 | -5.695 | <.001 |
| Egg size | 3.103 | 1.129 | 56 | 2.749 | .008 |
| Mean clutch egg weight | 1.774 | 1.298 | 13 | 1.366 | .195 |

Note: Final models were selected using the Akaike Information Criterion with hatching asynchrony and egg size as fixed effects.

our study population or species. Given that our study design was effective—nestlings were unambiguously matched to their respective eggs, and hatching asynchrony in experimental nests was substantially reduced—our control and synchronized nests allowed us to investigate the importance of egg size variation with and without hatching asynchrony. Although predation prevented us from collecting the full suite of information from experimental nests, our greater interest was in the relative importance of egg size and hatching asynchrony as they occur naturally. Our control nests provided adequate data for those analyses.

In control nests, both egg size and hatching asynchrony significantly affected nestling survival throughout the nestling phase, although their importance varied depending on laying order. Nestlings from the last-laid egg were usually the largest at hatching because they came from the largest eggs, but they were the most susceptible to star-

vation because they hatched approximately 40 h after their first sibling. Nestlings from fourth-laid eggs also exhibited this pattern but to a lesser extent because they had hatched 50% less asynchronously than last eggs. Overall, hatching asynchrony overwhelmed the effects of egg size on nestling survival in control nests. Although the loss of experimental nests after day 5 prevented us from obtaining starvation data later on, the lack of starvation by day 5 is itself supportive of the results from control nests. By experimentally reducing hatching asynchrony, we substantially reduced the size differences among siblings. The fact that so few of these nestlings starved (unlike in control nests) demonstrated that asynchrony was necessary for early brood reduction.

Nestling growth was also significantly affected by hatching asynchrony at both 5 and 10 days posthatching, whereas egg size affected only older nestlings. The reason that egg size apparently affected older nestlings but not

Table 2: Parameter estimates for model of nestling mass for control nests at 5 and 10 days posthatching and synchronized nests at 5 days posthatching

| | Estimate | SE | df | <i>t</i> | <i>P</i> |
|-------------------------|----------|-------|-----|----------|----------|
| Control at 5 days: | | | | | |
| Intercept | 1.337 | 9.100 | 129 | .147 | .883 |
| Hatching asynchrony | -.422 | .020 | 129 | -20.839 | <.001 |
| Egg size | 1.455 | 1.021 | 129 | 1.425 | .157 |
| Mean clutch egg mass | 4.297 | 1.349 | 37 | 3.185 | .003 |
| Control at 10 days: | | | | | |
| Intercept | 56.341 | 4.255 | 40 | 13.240 | <.001 |
| Hatching asynchrony | -.432 | .131 | 40 | -3.305 | .002 |
| Egg size | -12.787 | 5.423 | 40 | -2.358 | .023 |
| Laying order | 2.451 | 1.702 | 40 | 1.440 | .158 |
| Synchronized at 5 days: | | | | | |
| Intercept | 27.573 | 1.808 | 34 | 15.246 | <.001 |
| Hatching asynchrony | -.338 | .096 | 34 | -3.519 | .001 |
| Egg size | 7.368 | 1.516 | 34 | 4.860 | <.001 |

Note: Final models were selected using the Akaike Information Criterion with hatching asynchrony and egg size as fixed effects.

Table 3: Univariate coefficient of determination r^2 values for egg size and hatching asynchrony

| | Nestling survival | | Nestling growth | | |
|---------------------|-------------------|--------------------|-------------------|--------------------|------------------------|
| | Control at 5 days | Control at 10 days | Control at 5 days | Control at 10 days | Synchronized at 5 days |
| Hatching asynchrony | .23 | .20 | .53 | .25 | .40 |
| Egg size | .02 | <.00 | NS | .22 | .19 |

Note: NS = not significant.

younger nestlings is that by the time nestlings were 10 days old, many of the most asynchronously hatched individuals (i.e., those from fourth- and fifth-laid eggs) had starved. Thus, variation in hatching asynchrony among surviving nestlings effectively declined steadily through the nestling period, allowing the effect of egg size to be detected. This situation in control nests late in the nestling period is similar to the effect we created in the experimental nests, which produced similar outcomes. With asynchrony experimentally much reduced, egg size and asynchrony had similar effects on nestling growth (up to day 5, when measurements ended). Over the whole nestling period, however, natural levels of hatching asynchrony were much more important than egg size in the extent to which each affected nestling growth.

Although we treated growth and starvation separately, the two are obviously linked because it is the slowest-growing nestlings that die first. The level of starvation we observed was high relative to that in most studies of passerines (although consistent with that in a previous study of grackles; Howe 1976, 1978). However, even had the starvation rate been lower, factors that affect nestling growth were still likely to affect survival eventually. Where fledgling or juvenile survival has been estimated reliably for passerines, evidence indicates that nestlings that weigh more at fledging survive better (Tinbergen and Boerlijst 1990; Magrath 1991; Naef-Daenzer et al. 2001). Therefore, we would expect that, given the similar variation in hatching asynchrony and egg size that we reported here, their relative importance to offspring survival would be the same whether nestlings starved in the nest or most mortality occurred after fledging.

Most altricial passerine species hatch their eggs asynchronously (Clark and Wilson 1981), yet the majority of studies investigating egg size and nestling performance have neglected potential effects of hatching asynchrony (cf. Williams 1994). In his review, Williams (1994) noted that most authors subjectively indicated whether ASH had a noticeable effect on nestling performance. In our study, hatching asynchrony had a significant effect on nestling performance even in experimental nests where hatching asynchrony was greatly reduced. Thus, even in species for which hatching asynchrony is much less pronounced than

we found for grackles, its effects are still likely to be important (Krist et al. 2004; Bitton et al. 2006).

Our results support the assumption underlying Slagsvold et al.'s (1984) hypothesis, that is, that egg size can affect the growth and survival of nestlings. Because we found that the importance of egg size is contingent on the degree of ASH, however, support for the hypothesis itself is qualified. Slagsvold et al. (1984) proposed that by varying egg size with laying order, birds could modify the competitive disadvantage of last-hatched nestlings resulting from ASH. Where the last egg is larger, such as in grackles, increased size at hatching should make those nestlings more likely to survive. However, we found that the size disadvantage to last-hatched grackle nestlings resulting from ASH overwhelmed any advantage from hatching from a larger egg. In fact, the egg size advantage was most detectable among early-hatched nestlings, where ASH had little effect. In general, then, the importance of egg size on offspring performance will be largely dependent on the degree of ASH. When ASH is pronounced, females will have little scope for affecting the survival of last-laid eggs by varying egg size. Egg size variation is likely

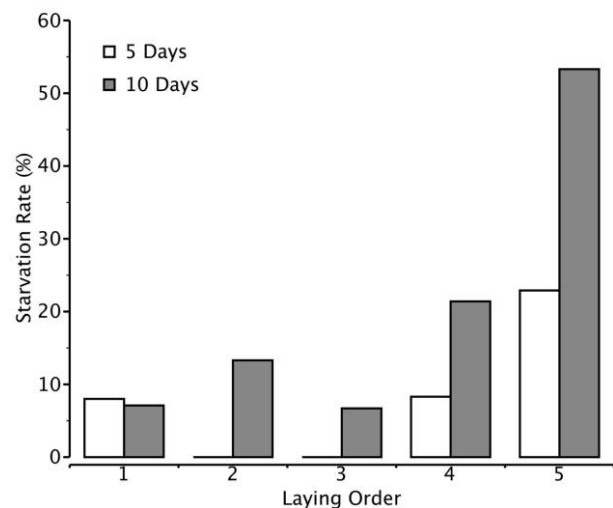


Figure 5: Nestling starvation rates (%) in control nests relative to laying order at 5 and 10 days posthatching.

to be important only in species that exhibit levels of ASH similar to that in our experimentally synchronized nests (i.e., ≤ 12 h). The hatching pattern of these species is generally classified as synchronous (Clark and Wilson 1981).

Other factors not considered here, such as yolk hormones and nestling sex, may also have important effects on nestling growth and survival. For example, yolk hormones can vary with laying order (Schwabl 1993; Schwabl et al. 1997; Groothuis and Schwabl 2002) or embryo sex (Petrie et al. 2001; Badyaev et al. 2005) and can positively (Schwabl 1993; Eising et al. 2001) or negatively (Sockman and Schwabl 2000) affect nestling performance. In species that are sexually size dimorphic, offspring sex can affect nestling starvation (Teather and Weatherhead 1989) because the larger sex is more costly to raise (Weatherhead and Teather 1991). Additionally, the sequence in which males and females are produced within the laying order can also affect nestling growth (Badyaev et al. 2003) and survival (Badyaev et al. 2002). Thus, the suite of factors that female birds can potentially manipulate to influence survival of their offspring is substantial (Bernardo 1996a).

Given the suite of factors available to female birds, two questions arise. First, from a practical perspective, given that researchers have yet to consider the effects and interactions of all the factors simultaneously, how do we interpret results of studies that focus on one or two factors? Experimental evidence suggests that some maternal effects are substantial when considered separately (Mousseau and Fox 1998). In our study, hatching asynchrony had such a pronounced effect on grackle nestlings that other factors could only modify but not substantially alter that effect. Problems of interpretation seem more likely to arise when the effects of individual factors are more subtle. The second, more conceptual issue is whether multiple maternal effects are likely to be adaptive, with each interacting with others to maximize offspring performance. It is possible that some mechanisms are inconsequential, being swamped by other effects, or, alternatively, they could be antagonistic, canceling out other effects that on their own appear adaptive. It seems implausible that females simultaneously and independently select optimal levels of multiple interacting factors to maximize offspring fitness, particularly given varying environmental conditions (Bernardo 1996b). Judging whether this expectation is truly implausible can be achieved only by empirical studies in which multiple maternal effects are measured simultaneously.

Acknowledgments

We thank D. Kikuchi, T. O'Connor, N. Owens, and P. Wesley for their help in the field; the Shoemaker family for allowing us to work on their tree farm; G. Bollero, J.

Brawn, and F. Miguez for statistical advice; two anonymous reviewers for comments on the manuscript; and the University of Illinois and the American Ornithologists' Union for funding.

Literature Cited

- Badyaev, A. V., G. E. Hill, M. L. Beck, A. A. Dervan, R. A. Duckworth, K. J. McGraw, P. M. Nolan, and L. A. Whittingham. 2002. Sex-biased hatching order and adaptive population divergence in a passerine bird. *Science* 295:316–318.
- Badyaev, A. V., G. E. Hill, and M. L. Beck. 2003. Interaction between maternal effects: onset of incubation and offspring sex in two populations of a passerine bird. *Oecologia (Berlin)* 135:386–390.
- Badyaev, A. V., H. Schwabl, R. L. Young, R. A. Duckworth, K. J. Navara, and A. F. Parlow. 2005. Adaptive sex differences in growth of pre-ovulation oocytes in a passerine bird. *Proceedings of the Royal Society B: Biological Sciences* 272:2165–2172.
- Bernardo, J. 1996a. Maternal effects in animal ecology. *American Zoologist* 36:83–105.
- . 1996b. The particular maternal effect of propagule size, especially egg size: patterns, models, quality of evidence and interpretations. *American Zoologist* 36:216–236.
- Bitton, P. P., R. D. Dawson, and E. L. O'Brien. 2006. Influence of intraclutch egg-mass variation and hatching asynchrony on relative offspring performance within broods of an altricial bird. *Canadian Journal of Zoology* 84:1721–1726.
- Clark, A. B., and D. S. Wilson. 1981. Avian breeding adaptations: hatching asynchrony, brood reduction, and nest failure. *Quarterly Review of Biology* 56:253–277.
- Eising, C. M., C. Eikenaar, H. Schwabl, and T. G. G. Groothuis. 2001. Maternal androgens in black-headed gull (*Larus ridibundus*) eggs: consequences for chick development. *Proceedings of the Royal Society B: Biological Sciences* 268:839–846.
- Fox, C. W., and M. E. Czesak. 2000. Evolutionary ecology of progeny size in arthropods. *Annual Review of Entomology* 45:341–369.
- Gil, D. 2003. Golden eggs: maternal manipulation of offspring phenotype by egg androgen in birds. *Ardeola* 50:281–294.
- Groothuis, T. G. G., and H. Schwabl. 2002. Determinants of within- and among-clutch variation in levels of maternal hormones in black-headed gull eggs. *Functional Ecology* 16:281–289.
- Groothuis, T. G. G., W. Müller, N. von Engelhardt, C. Carere, and C. Eising. 2005. Maternal hormones as a tool to adjust offspring phenotype in avian species. *Neuroscience and Biobehavioral Reviews* 29:329–352.
- Howe, H. F. 1976. Egg size, hatching asynchrony, sex, and brood reduction in the common grackle. *Ecology* 57:1195–1207.
- . 1978. Initial investment, clutch size, and brood reduction in the common grackle (*Quiscalus quiscula* L.). *Ecology* 59:1109–1122.
- Hutchings, J. A. 1991. Fitness consequences of variation in egg size and food abundance in brook trout *Salvelinus fontinalis*. *Evolution* 45:1162–1168.
- Janzen, F. J. 1993. An experimental analysis of natural selection on body size of hatchling turtles. *Ecology* 74:332–341.
- Jayne, B. C., and A. F. Bennett. 1990. Selection on locomotor performance capacity in a natural population of garter snakes. *Evolution* 44:1204–1229.
- Johnson, D. E. 1998. Applied multivariate methods for data analysts. Duxbury, Pacific Grove, CA.

- Klomp, H. 1970. The determination of clutch size in birds: a review. *Ardea* 58:1–124.
- Krist, M., and V. Remes. 2004. Maternal effects and offspring performance: in search of the best method. *Oikos* 106:422–426.
- Krist, M., V. Remes, L. Uvirova, P. Nadvornik, and S. Bures. 2004. Egg size and offspring performance in the collared flycatcher (*Ficedula albicollis*): a within-clutch approach. *Oecologia* (Berlin) 140:52–60.
- Maddox, J. D., and P. J. Weatherhead. 2006. Nests without eggs: abandonment or cryptic predation? *Auk* 123:135–140.
- Magrath, R. D. 1990. Hatching asynchrony in altricial birds. *Biological Reviews* 65:587–622.
- . 1991. Nestling weight and juvenile survival in the blackbird, *Turdus merula*. *Journal of Animal Ecology* 60:335–351.
- . 1992. Roles of egg mass and incubation pattern in establishment of hatching hierarchies in the blackbird (*Turdus merula*). *Auk* 109:474–487.
- McGinley, M. A., D. H. Temme, and M. A. Geber. 1987. Parental investment in offspring in variable environments: theoretical and empirical considerations. *American Naturalist* 130:370–398.
- Mock, D. W. 1984. Siblicidal aggression and resource monopolization in birds. *Science* 225:731–733.
- Mousseau, T. A., and C. W. Fox. 1998. The adaptive significance of maternal effects. *Trends in Ecology & Evolution* 13:403–407.
- Naef-Daenzer, B., F. Widmer, and M. Nuber. 2001. Differential post-fledging survival of great and coal tits in relation to their condition and fledging date. *Journal of Animal Ecology* 70:730–738.
- Nichols, J. D., W. Conley, B. Batt, and A. R. Tipton. 1976. Temporally dynamic reproductive strategies and the concept of *r*- and *K*-selection. *American Naturalist* 110:995–1005.
- Nicolai, C. A., J. S. Sedinger, and M. L. Wege. 2004. Regulation of development time and hatch synchronization in black brant (*Branta bernicla nigricans*). *Functional Ecology* 18:475–482.
- Peer, B. D., and E. K. Bollinger. 1997. Common grackle (*Quiscalus quiscula*). *The Birds of North America*, ed. A. Poole and F. Gill. No. 271. Academy of Natural Sciences, Philadelphia; and American Ornithologists' Union, Washington, DC.
- Petrie, M., H. Schwabl, N. Brande-Lavridsen, and T. Burke. 2001. Sex differences in avian yolk hormone levels. *Nature* 412:498.
- Pinheiro, J. C., and D. M. Bates. 2000. *Mixed-effects models in S and S-Plus*. Springer, New York.
- R Development Core Team. 2007. *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org>.
- Ricklefs, R. E. 1997. Hatching asynchrony in birds. *Trends in Ecology & Evolution* 12:229.
- Roff, D. A. 1992. *The evolution of life histories: theory and analysis*. Chapman & Hall, New York.
- Schwabl, H. 1993. Yolk is a source of maternal testosterone for developing birds. *Proceedings of the National Academy of Sciences of the USA* 90:11446–11450.
- Schwabl, H., D. W. Mock, and J. A. Gieg. 1997. A hormonal mechanism for parental favouritism. *Nature* 386:231.
- Sinervo, B. 1990. The evolution of maternal investment in lizards: an experimental and comparative analysis of egg size and its effects on offspring performance. *Evolution* 44:279–294.
- Slagsvold, T., J. Sandvik, G. Rofstad, O. Lorentsen, and M. Husby. 1984. On the adaptive value of intraclutch egg-size variation in birds. *Auk* 101:685–697.
- Sockman, K. W., and H. Schwabl. 2000. Yolk androgens reduce offspring survival. *Proceedings of the Royal Society B: Biological Sciences* 267:1451–1456.
- Stanton, M. L. 1984. Seed variation in wild radish: effect of seed size on components of seedling and adult fitness. *Ecology* 65:1105–1112.
- Stearns, S. C. 1976. Life-history tactics: a review of the ideas. *Quarterly Review of Biology* 51:3–47.
- . 1992. *The evolution of life histories*. Oxford University Press, New York.
- Stenning, M. J. 1996. Hatching asynchrony, brood reduction and other rapidly reproducing hypotheses. *Trends in Ecology & Evolution* 11:243–246.
- Stoleson, S. H., and S. R. Beissinger. 1995. Hatching asynchrony and the onset of incubation in birds, revisited: when is the critical period? *Current Ornithology* 12:191–270.
- Teather, K. L., and P. J. Weatherhead. 1989. Sex-specific mortality in nestling great-tailed grackles. *Ecology* 70:1485–1493.
- Tinbergen, J. M., and M. C. Boerlijst. 1990. Nestling weight and survival in individual great tits (*Parus major*). *Journal of Animal Ecology* 59:1113–1127.
- Venables, W. N., and B. D. Ripley. 2002. *Modern applied statistics with S: statistics and computing*. Springer, New York.
- Weatherhead, P. J., and K. L. Teather. 1991. Are skewed fledgling sex ratios in sexually dimorphic birds adaptive? *American Naturalist* 138:1159–1172.
- Williams, T. D. 1994. Intraspecific variation in egg size and egg composition in birds: effects on offspring fitness. *Biological Reviews* 69:35–59.

Associate Editor: Robert Montgomerie
 Editor: Michael C. Whitlock