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Consequences of Egg-Size Variation in the Red-winged Blackbird

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Life-history theory predicts that as parents increase their investment in individual offspring, the survival rates of those offspring should also increase (Winkler and Wallin 1987, Stearns 1992, Bernardo 1996). For oviparous taxa, parental investment may be directed toward eggs or hatchlings. Birds are ideal organisms to test general hypotheses of parental investment owing to the substantial interspecific variation in relative investments made by parents toward eggs and hatchlings and because of the ability of researchers to isolate and quantify these investments. The altricial-precocial continuum, based on the development of young at hatching (Nice 1962), provides a convenient description of interspecific patterns in relative energy investment directed toward eggs versus hatched young.

Precocial young hatch from energy-rich eggs and require little parental care after hatching, whereas altricial young hatch from relatively energy-poor eggs and require considerable parental care after hatching (Sotherland and Rahn 1987). We can use these patterns of energy investment in eggs versus young to make predictions about the relative importance of each of these stages in determining offspring performance in different taxa along the life-history continuum. Parents of altricial young spend a large amount of effort during the breeding season feeding and caring for young relative to parents of precocial young. Therefore, we predict that variation in the quality of parental care after hatching should have a larger influence on offspring performance in altricial species than in precocial species. However, because altricial young hatch from energy-poor eggs, factors associated with eggs should have a smaller influence on the performance of altricial species relative to precocial species. Thus, based on interspecific variation in patterns of energy investment, we predicted that the importance of the egg stage to subsequent performance of young birds will increase with increasing precocity of the young.

One measure of parental investments in eggs is size, with large eggs presumably requiring a greater energy investment by females than do small eggs.

Although ornithologists have described the relationship between egg size and offspring performance for some species, interpretations of such descriptions are not straightforward because factors such as parental quality and habitat quality may be correlated with egg size (see Magrath 1992, Williams 1994). One way to isolate egg-size effects is to experimentally manipulate the size of eggs or offspring (Sinervo 1990, Janzen 1993). An alternative is to isolate the effects of egg size on nestling survival by adopting a fostering design in which offspring are moved among nests, thereby randomizing factors not associated with egg size.

Studies that used a fostering design to elucidate the influence of egg size on offspring survival have focused largely on colonial seabirds (e.g. Nisbet 1978, Amundsen and Stokland 1990, Reid and Boersma 1990, Bolton 1991, Meathrel et al. 1993, Bollinger 1994, Amundsen et al. 1996) and have produced mixed conclusions. Few studies have used a fostering design to explore the influence of egg size on survival of passerines (Schifferli 1973, Magrath 1992, Smith et al. 1995), a group whose young are altricial. Although we predict that egg size will have relatively little influence on nestling survival in these birds, at least one study of a bird with altricial young found a significant effect of egg size on juvenile survival (Schifferli 1973). Here, we present the results of an experiment in which we used a fostering design to determine the influence of egg size on nestling growth and survival in a free-living passerine, the Red-winged Blackbird (*Agelaius phoeniceus*).

Methods.—The Red-winged Blackbird is a socially polygynous species that breeds throughout North America in both wetland and upland habitats. We studied a population of Red-winged Blackbirds nesting at the Experimental Ponds Facility of Michigan State University's Kellogg Biological Station in southwestern Michigan in 1993. The Experimental Ponds Facility consists of 18 replicate ponds, each 29 m in diameter, 2 m in depth, and separated by 5 m of grass. A dense ring of cattails (*Typha latifolia*) grows around the margin of each pond, and a large number of Red-winged Blackbirds nest in the cattails. We selected 10 ponds with the highest breeding densities of blackbirds to use in our cross-fostering study. A total of 104 female Red-winged Blackbirds nested on these 10 ponds.

We estimated the size of each egg laid by females nesting on these ponds by measuring linear dimen-

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sions (length and breadth) with calipers, or by measuring egg mass on an electronic balance within 24 h of laying. For a subset of these eggs we measured linear dimensions (mm) and mass (g) and calculated the following linear equation:

$$\text{egg mass} = 0.000510 \times [\text{egg length} \times (\text{egg breadth})^2] + 0.19 \quad (1)$$

($n = 380$ eggs, $r^2 = 0.97$). We used this equation to estimate initial mass for eggs in which only length and breadth were measured. These masses, whether directly measured or indirectly estimated, were used for further analyses of egg-size effects.

We moved eggs of known size between nests with the goal of randomizing factors other than egg size that may influence nestling growth and survival. Most of the variation in egg size of Red-winged Blackbirds occurs among rather than within nests (Muma and Ankney 1987). We focused our study on understanding the importance of egg-size variation among females and not within broods. Therefore, we exchanged whole clutches of eggs between nests and used individual nests as the experimental unit in all analyses. Our cross-fostering consisted of trading clutches between nests that were completed within 24 h of each other. We used 50 nests in the cross-fostering study. All experimental clutches consisted of four eggs, and all switches were done within a pond. We switched eggs within 48 h after the fourth egg was laid.

Once egg switches were completed, we did not disturb nests until 10 days after the initiation of incubation, at which time we monitored nests closely to determine hatching. Nestlings were weighed to the nearest 0.1 g on a spring balance within 24 h of hatching. Nests were revisited and surviving nestlings were weighed again at two days of age and just prior to fledging (i.e. leaving the nest) at 10 days of age. All nestlings used for this experiment hatched within 10 days of one another. Because hatching date had no effect on nestling performance over this time period, we did not include hatching date as a variable in our analyses.

We focus our analyses of egg-size effects on nestling survival, nesting success, and nestling mass. Nestling survival was calculated as the proportion of nestlings surviving from hatching to fledging and does not include mortality during the egg stage. Nesting success was defined as a complete nest failure (no fledglings produced) or as a success when at least one of the young survived to fledging.

In addition to testing for egg-size effects, our cross-fostering design allowed us to assess whether females that lay large eggs are better able to produce fledglings than those that lay small eggs. A previous study on this population of Red-winged Blackbirds found that males made fewer than 5% of the total feeding visits to nestlings (Turner and McCarty 1998); therefore, we concentrate our discussion of pa-

rental quality on females. We simultaneously evaluated the effects of two independent variables (1) mean egg size a female received in the fostering (egg-size effects), and (2) mean egg size a female produced (female-quality effects), on nestling survival, nesting success, and nestling mass. Egg-size and female-quality effects on nestling survival and nestling masses were evaluated with a multiple linear regression. We used Type III sums of squares to test whether egg size or female quality influenced nestling performance. The multiple regression tested whether each factor influenced the dependent variable after first accounting for the effects of the other factor(s). Nestling masses were log-transformed to normalize the residuals and to compare the slopes of the relationships for each age. Nesting success is a binomial response variable, and we evaluated egg-size effects and female-quality effects with a multiple logistic regression analysis.

The above analyses tested for a linear effect of egg size and female quality on nestling performance. A significant linear relationship would suggest directional selection. In addition to directional selection, we tested for nonlinear selection (i.e. disruptive or stabilizing selection) by squaring each independent variable and adding them to the multiple regression model (Lande and Arnold 1983, Brodie et al. 1995).

Results.—Eggs varied in mass from 3.06 to 5.01 g ($\bar{x} = 4.04 \pm \text{SD of } 0.38$ g, $n = 196$), and egg mass was normally distributed about the mean (Shapiro-Wilk test, $W = 0.98$, $P = 0.31$). The mean egg mass at individual nests varied from 3.18 to 4.72 g ($\bar{x} = 4.03 \pm 0.35$ g, $n = 50$) and also was normally distributed about the mean ($W = 0.98$, $P > 0.50$). Based on a hierarchical analysis of variance, 24% of the overall variation in egg size resulted from differences among ponds, 56% of the variation was due to differences among nests within ponds, and the residual 20% of variation was due to variation among individual eggs within nests. Thus, the largest component of variation was due to variation among females in the average size of eggs that they produced.

On average, 3.78 eggs hatched from the original 4-egg clutch, and of the eggs that hatched, an average of 1.96 survived to fledging at each nest (overall mortality rate of 48%). The multiple regression model indicated that the number of fledglings produced in each nest was not related to egg size ($F = 0.32$, $df = 1$ and 47 , $P > 0.20$) or female quality ($F = 0.004$, $df = 1$ and 47 , $P > 0.20$). Neither egg size nor female quality were under significant nonlinear selection with respect to nestling survival ($P > 0.20$ for both terms).

The nest-failure rate in our experimental nests was 16%, and all failures appeared to have resulted from starvation or abandonment rather than from predation (i.e. no nests were found empty or damaged). We found little evidence that nest failure rate was related to egg size. The average egg mass was $3.86 \pm \text{SD of}$

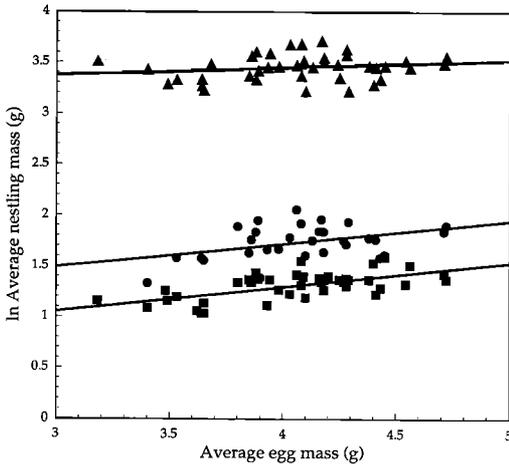


FIG. 1. Average nestling mass in foster Red-winged Blackbird nests at 1 (squares), 2 (circles), and 10 (triangles) days posthatching as a function of average egg mass for that nest. A semilog plot was used to allow for comparison of slopes among nestling ages. Regression equations are: \ln day 1 mass = $0.2396 \times \text{egg mass} + 0.3338$ ($r^2 = 0.41$); \ln day 2 mass = $0.2267 \times \text{egg mass} + 0.8094$ ($r^2 = 0.18$); and \ln day 10 mass = $0.0782 \times \text{egg mass} + 3.1341$ ($r^2 = 0.05$).

0.29 g for failed nests and 4.06 ± 0.35 g for successful nests ($t = 1.54$, $P = 0.13$). Statistical significance aside, the magnitude of the differences was not large: the average egg size in nests that failed to produce fledglings was 5% lower than that in nests that succeeded in producing fledglings. The logistic multiple regression model simultaneously accounting for female quality and egg-size effects explained only 5.4% of the variation in nesting success, and neither female quality nor egg size explained a significant amount of the variation in nesting success (female quality, $\chi^2 = 0.0006$, $P > 0.20$; egg size, $\chi^2 = 2.16$, $P = 0.14$). Neither egg size nor female quality were under significant nonlinear selection with respect to nesting success ($P > 0.20$ for both terms).

The effects of egg size and female quality on nestling mass were evaluated simultaneously. Egg size had a positive effect on initial nestling mass, but this effect weakened as nestlings grew (Fig. 1). Nestling mass on days 1 and 2 were positively related to egg size (day 1, $F = 26.03$, $df = 1$ and 41 , $P < 0.0001$; day 2, $F = 5.90$, $df = 1$ and 29 , $P = 0.02$). However, 10 days after hatching, egg mass had little effect on nestling mass ($F = 1.39$, $df = 1$ and 39 , $P > 0.20$). Effects of female quality on nestling mass were negligible throughout the nestling period (day 1, $F = 1.13$, $df = 1$ and 41 , $P > 0.20$; day 2, $F = 1.80$, $df = 1$ and 29 , $P = 0.19$; day 10, $F = 0.02$, $df = 1$ and 39 , $P > 0.20$).

Discussion.—Although the mass of Red-winged

Blackbird eggs varies considerably (40% difference between the largest and smallest eggs), we found little evidence to suggest that egg size is an important determinant of survival or growth of nestlings. We acknowledge, however, that our study lacks the power to detect small effects. For example, nests composed of eggs larger than the median size fledged 13% more offspring than did nests composed of eggs that were smaller than the median size. Given the large amount of variability we observed in female reproductive success, effects of this size are not statistically detectable without much larger sample sizes, but these differences potentially represent strong selection differentials and may be important in the evolution of egg size. Thus, our study highlights the importance of very large sample sizes in investigations aimed at testing whether egg size is under natural selection.

Our results show clearly that even if the small egg-size effects on offspring performance were real, the survival and growth of nestlings are still influenced primarily by factors other than egg size. Egg size and female quality together accounted for less than 1% of the variation in nestling survival. Although nestling mass at one and two days of age was related to egg size, this effect disappeared by day 10. On average, experimental nestlings increased their mass by 65% during the first day after hatching (Fig. 1). This suggests that any variation among nests in average growth rates likely overwhelms any differences in initial size. A previous study of this population showed that nestling growth was dependent on food availability (Turner and McCarty 1998). Because growth rates of altricial nestlings generally are a function of food provisioning (Searcy and Yasukawa 1995) and other aspects of female efficacy (i.e. parasite loads; Møller 1990, Roby et al. 1992), differences in female quality should have large effects on nestling growth and survival.

Egg size has often been used as a measure of female quality. Females that lay large eggs are assumed to be of better quality than females that lay small eggs (Amundsen and Stokland 1990, Reid and Boersma 1990, Bolton 1991); however, our experiment provides no support for this idea (see also Amundsen et al. 1996). In this population, a female's ability to rear nestlings was independent of the size of her eggs. Although it is likely that variation in female quality compensated for the initial differences in nestling size, this variation was not related to the size of the eggs a female produced.

Overall, our results are consistent with the idea that the sensitivity of offspring performance to egg-size variation is related to the degree of precocity of hatched young. Females that raise altricial young invest relatively little in the egg stage compared with females that raise precocial young. Because of this fact, factors associated with the egg stage should have less of an influence on performance of altricial

young relative to that of precocial young. Clearly, testing the generality of this pattern will require additional studies on the consequences of egg-size variation in a wide range of avian taxa.

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