NOTES AND COMMENTS

ALTERNATIVE MODELS FOR THE EVOLUTION OF OFFSPRING SIZE

Eleven years ago, I proposed a simple model for the evolution of offspring size, pointing out a general correlation between parental care and relatively large offspring size consistent with that model (Shine 1978). My basic premise came from Williams (1966): natural selection should adjust the life history such that organisms spend little time in life-history stages characterized by high mortality. Hence, optimal egg sizes should be determined by the relative survival rates of eggs and free-living juveniles. If the egg stage is a "safe harbor" (as in species with parental care), whereas juvenile life is hazardous, selection should favor an increase in egg size and thus a decrease in the duration of the high-risk juvenile phase. This safe-harbor hypothesis for the evolution of offspring size has recently been criticized on several grounds by Nussbaum (1985, 1987), Sargent et al. (1987), and Nussbaum and Schultz (1989). Important alternative ideas on the topic have also been developed by Ito (1980) and Ito and Iwasa (1981). Analysis of these contributions suggests at least four alternative explanations for the observed correlation between parental care and offspring size: (1) parental care favored the evolution of larger eggs (Shine 1978); (2) larger eggs favored the evolution of parental care (Nussbaum 1985, 1987); (3) parental care and offspring size co-evolved, with an increase in one favoring an increase in the other (Nussbaum and Schultz 1989); or (4) some third factor simultaneously selected for parental care and larger egg size.

Although I maintain that several criticisms of the safe-harbor hypothesis are in error, I also believe that the general correlation between parental care and large offspring size may be due to a combination of processes rather than the single process I envisaged in my 1978 paper. This note outlines my objections to recent criticisms and proposes a method for testing these competing explanations.

CRITICISMS AND ALTERNATIVES

The mathematical formulations of Sargent et al. (1987) and Nussbaum and Schultz (1989) are more sophisticated than my own 1978 version, but they unequivocally support my basic argument that the relative survival of embryos and free-living juveniles should be crucial determinants of optimal offspring size. These authors also extend my model to cover varying intensity and/or effec-
tiveness of parental care, and they examine conditions for the evolution of parental care as well as for the evolution of offspring size.

Sargent et al. (1987)

These authors, in addition to clarifying and extending the safe-harbor hypothesis, identified two shortcomings of the original model; both derive from my assumption that instantaneous mortality during the juvenile stage is independent of egg size. They correctly noted that this assumption is probably unrealistic and that incorporating size-dependent survival and growth rates into the model renders its predictions more accurate in two ways: (1) the model no longer predicts a bimodal distribution in egg sizes (I anticipated this result in 1978, although I did not incorporate it into the mathematical model: "if survivorship rates increase with increasing body size over the size range of juveniles, then the optimal propagule size continues to increase as survivorship during parental care increases"; p. 421); (2) larger egg size can be favored because of advantages to faster growth in larger juveniles, not just because of lower mortality rates. This was an important development of the basic idea, but overall I concur with Nussbaum and Schultz's conclusion that the work of Sargent et al. (1987) was basically an extension of the safe-harbor hypothesis rather than a challenge to its validity.

Nussbaum (1985, 1987)

Nussbaum, in contrast, suggested an alternative approach. Although acknowledging the correlation between parental care and larger egg size, he used both theory and data to dispute the nature of the causal relationship. Most importantly, he argued that my 1978 model (and that of Sargent et al. 1987) may reverse cause and effect: parental care may evolve because of large egg size (and the consequent high mortality of unattended eggs) rather than vice versa. The idea is an excellent one, but I doubt that it explains the widespread occurrence of a correlation between parental care and large egg size for the following reasons.

1. His model assumes that a longer incubation period (a common correlate of larger egg size) necessarily reduces embryonic survival and hence puts a premium on any parental behavior that could combat this high mortality. This assumption may be invalid for well-hidden eggs, for which mortality rates may be low and relatively independent of incubation period (and, hence, egg size).

2. His model does not consider the costs of parental care to the survival rate or food intake of the attending parent. These costs presumably increase with the duration of incubation (and hence with egg size), yielding the opposite prediction to that arising from Nussbaum's model: parental care is less likely to evolve in species with large eggs (see Shine 1978 for a discussion of this point).

3. If the Nussbaum model is the primary explanation for the observed correlation between parental care and large egg size, then the major selective pressure for the evolution of parental care must have been egg survival levels that were low because of large egg size. That is, parental care must have evolved frequently in taxa with large eggs and infrequently in taxa with small eggs; otherwise, we would not see any correlation between parental care and egg size. This view is difficult to
reconcile with the great diversity in the forms of parental care and the presumably complex array of ecological factors that determine whether parental care evolves (e.g., rates of egg predation, vulnerability of eggs to environmental stresses, availability of protected sites for attending parents, vulnerability of attending parents to predators, etc.). In particular, the relative costs faced by the attending parents may facilitate or prevent the evolution of parental care. For example, parental care in reptiles is most common in large and venomous species, presumably because attending parents are invulnerable to predators or are particularly effective at deterring egg predators (Shine 1987). If such factors unrelated to egg size are important in the evolution of parental care, the general correlation between parental care and large egg size is more likely to reflect an adjustment of egg size after parental care has evolved, rather than the scenario suggested by Nussbaum.

**Nussbaum and Schultz (1989)**

Recently, these authors have proposed an elegant model that combines the main features of the two preceding hypotheses. Egg size and the intensity of parental care coevolve, with increases in either variable favoring subsequent increases in the other. I have pointed out, above, a number of reasons for doubting that increased egg size consistently imposes selection for an intensification of parental care. However, I agree with Nussbaum and Schultz that the reverse is also true. The evolution of parental care in a lineage may not affect optimal egg size for several reasons.

1. Parental care may be more likely to evolve in taxa experiencing higher egg mortality than in their congeners (e.g., the terrestrial-breeding ambystomatid discussed by Nussbaum). A similarity in egg sizes among congeners may thus reflect an overall similarity in egg survival rates among taxa, with parental care in some species merely bringing egg survival levels back up to the norm for that group. No correlation between parental care and egg size would be expected.

2. Food resources or predation pressures on neonates may set the optimal size at hatching, whereby small changes in offspring body size effect large changes in offspring fitness. Under such circumstances, selection is likely to favor the same offspring size over a wide range of egg survival rates (Lloyd 1987).

3. Physiological constraints or the ecological disadvantages of late hatching may prevent any increase in egg size or incubation period in some lineages.

Hence, one would expect under all three models that the correlation between egg size and parental care would be imperfect. Nussbaum and Schultz (1989) also substantively criticized the basic safe-harbor model in their discussion of the effects of changing embryo or juvenile survival rates. Lower embryo survival relative to juvenile survival selects for both smaller egg size (because the egg is no longer a safe harbor) and parental care (because it increases the probability of egg survival). Hence, egg size and parental care may be negatively correlated if environmental differences impose widely different embryo or juvenile survival rates among populations. Nonetheless, any such correlation should exist only transiently; as soon as parental care evolves, selective pressures on egg size immediately reverse. Certainly, the negative correlation between parental care
and egg size that one might expect from this hypothesis seems not to be evident in nature (Shine 1978). One further point from Nussbaum and Schultz (1989) is that the correlation between parental care and large egg size should be weak in environments that readily allow the survival of very large embryos or very small juveniles, because there is little difference in survival rates between the egg and juvenile stages. I agree with this prediction; it can be derived directly from the safe-harbor hypothesis.

An Alternative Model

Little attention has been paid to a fourth alternative explanation for the correlation between parental care and larger egg size: this correlation may not reflect any cause-and-effect relationship between the two variables but may arise from a common, causally based correlation of each with a third variable. Larger eggs and parental care may be integral parts of an overall, coevolved, life-history strategy adaptive in particular environments (e.g., Ito 1980; Ito and Iwasa 1981). Although the models Ito proposed deal primarily with the availability of food in different environments for juveniles of various body sizes (and thus are similar to Nussbaum's models in that the primary focus of selection would seem to be offspring size rather than parental care), conditions could simultaneously select for parental care and an increase in egg size. The most obvious possibility is some source of size-specific mortality. Imagine a species with small eggs and without parental care, living in an area invaded by a new predator capable of consuming eggs and small juveniles but not larger juveniles. Under such conditions, the arrival of this predator may impose simultaneous selection for parental care (because it massively increases egg survival) and an increase in egg size (because it means that newly hatched juveniles are too large to be subject to predation). This explanation for the resulting correlation between parental care and large offspring size is entirely different from that proposed under the safe-harbor hypothesis or the models of Nussbaum and Schultz. It should apply to any form of mortality (including desiccation, etc., as well as predation) that affects eggs and small juveniles more than large juveniles and that can potentially be minimized by parental care or larger hatchling size. Availability of food for hatchlings (Ito 1980; Nussbaum 1985, 1987) does not fall into this category because it obviously applies only to juveniles and not to eggs.

TESTING AMONG ALTERNATIVE HYPOTHESES

The preceding discussion identifies four alternative explanations for the correlation between parental care and large egg size. Predictions derived from these hypotheses differ in the sequence of events in the evolutionary history of a taxon with large, parentally protected eggs: did parental care evolve before, after, or simultaneously with the increase in egg size? Unfortunately, these alternatives may be difficult to distinguish in practice: (1) because the evolutionary transitions may be brief, comparative data from related species may reveal nothing more than the correlation between egg size and parental care; (2) parental care and increased
Egg size may appear to coevolve, even when one is leading the other. Under the safe-harbor hypothesis, a slight increase in the intensity of parental care may favor a corresponding increase in egg size, whereas the reverse would be expected under Nussbaum’s hypothesis. Neither case is likely to be distinguishable from a simultaneous shift in both variables, as predicted by the two remaining hypotheses (the coevolutionary model of Nussbaum and Schultz and the hypothesis of size-specific vulnerability suggested above).

The cases with the greatest potential to discriminate among the competing hypotheses are lineages containing species with and without parental care, with a range in egg sizes and with imperfect correlation between parental care and large egg size. Cladistic analysis of such taxa may reveal whether the initial evolutionary shift was in parental behavior (as predicted by the safe-harbor hypothesis) or egg size (as predicted by Nussbaum’s model). The hypotheses of coevolution and of size-specific vulnerability predict that both patterns will occur, but the two variables may be more tightly coupled under the coevolution hypothesis (because it posits a causal relationship between the variables) than under the model of size-specific vulnerability. Detailed phylogenetic analysis of a variety of lineages from this perspective would be an interesting exercise.

An alternative means of distinguishing between these hypotheses may come from ecological correlates of large egg size. If there is obvious selective pressure for an increase in offspring size, independent of parental care, then the safe-harbor hypothesis is unlikely to be the correct interpretation. Egg size in salamanders may offer an example: large eggs have evolved in terrestrial or lentic environments where prey sufficiently small for smaller hatchlings is scarce (Nussbaum 1985, 1987; Nussbaum and Schultz 1989). Terrestrial habitats may also favor the evolution of parental care, perhaps to prevent the desiccation of eggs. However, the evolution of parental care may have had little effect on the already-large egg sizes in such a group. In this example, the resulting correlation between parental care and large offspring size could be either causal (an increase in egg size favors the evolution of parental care) or non-causal (egg size evolves because of available prey sizes for hatchlings; parental care evolves for other reasons). In either case, the correlation cannot be attributed to the safe-harbor hypothesis. Nonetheless, the data are entirely consistent with predictions from the basic premise of the safe-harbor model: relative rates of survival for eggs and juveniles of different sizes are the crucial determinants of optimal offspring size. In this specific case, it may well be prey-size spectra (or other size-dependent advantages relating to feeding or survival) that determine the relative viabilities of various-sized hatchlings.

**Generality of the Safe-Harbor Hypothesis**

Some of the criticisms of the safe-harbor hypothesis result from a misunderstanding: the model was proposed not simply as an explanation for the correlation between offspring size and parental care but as a general model for the evolution of optimal offspring size. Its central tenet is that natural selection should adjust
offspring sizes in accordance with the rates of survival and growth of hatchlings of
different sizes relative to the rates of mortality of embryos from eggs of different
sizes. Large egg size is likely to evolve whenever the survival rate of embryos is
significantly higher than that of free-living juveniles of similar body sizes. I used
parental care to test the hypothesis in my 1978 paper only because it offered a
straightforward case in which related taxa differed predictably in rates of embryo
survival. Nussbaum and Schultz interpreted the trends in egg size among salaman-
ders noted above as evidence against the safe-harbor model because large egg size
evolved before the evolution of parental care in such lineages. However, it is
entirely consistent with the basic premise of the safe-harbor hypothesis: a factor
that reduces viability of small juveniles relative to the viability of embryos of
comparable size (lack of food resources in the environment) favors an evolution-
ary increase in offspring size until the relative rates of survival for embryos and
for juveniles are more nearly equivalent. (Because larger offspring size reduces
maternal fecundity and because juveniles are able to feed, the optimal offspring
size from the viewpoint of maternal fitness will always be smaller than the size at
which embryonic and juvenile viabilities are equal.) I agree that a higher embry-
onic survival rate due to parental care may not be the reason for the correlation
between parental care and offspring size in this case, but I emphasize that the data
are in accord with the general principle that relative viabilities of eggs and ju-
veniles over a range of body sizes are the crucial evolutionary determinants of
offspring size.

SUMMARY

al. (1987), and Nussbaum and Schultz (1989) has done much to clarify possible
reasons for the general correlation between parental care and large offspring size.
On the basis of this literature, I suggest that at least four explanations for the
above correlation are plausible: parental care favors an increase in offspring size;
increased offspring size favors the evolution of parental care; the two variables
coevolve; or some third factor (perhaps size-dependent mortality of eggs and
embryos) simultaneously selects for both parental care and larger offspring size.
Tests between these alternative models should be feasible and would be of great
interest. These discussions also illuminate more-general models for offspring size,
because any comprehensive model for evolutionary shifts in offspring size must
explain the consistent correlation of this variable with parental care. In my
opinion, the net effect of the work reviewed above has been to support the safe-
harbor hypothesis and to extend and clarify its nature, rather than to challenge its
basic validity. It is perhaps unfortunate that most discussion of the safe-harbor
model has been focused so strongly on the role of parental care in the evolution of
offspring size. It seems not to have been widely appreciated that the safe-harbor
hypothesis—the idea that optimal offspring size is determined by relative viabili-
ties of eggs versus free-living juveniles—is applicable to the evolution of offspring
size in any situation.
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LITERATURE CITED


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