

“SELFISH MOTHERS” USE “MATERNAL MANIPULATION” TO MAXIMIZE LIFETIME REPRODUCTIVE SUCCESS

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ABSTRACT: Females should behave in ways that maximize lifetime reproductive success (the “selfish mother” hypothesis [SMH]). Very often, this will mean that female behavior during reproduction maximizes fitness of the current batch of offspring. In some cases, however, females may maximize lifetime reproductive success by behaving in ways that are neutral, or even detrimental, to current offspring fitness. The “maternal manipulation hypothesis” (MMH), proposed by Shine (1995), argues that females should behave in ways that maximize fitness of the current batch of offspring. We argued, however, that if researchers focus solely on measuring benefits to offspring of female behavior during reproduction, they will not consider the possibility that female behavior is neutral or even detrimental to offspring fitness, thereby missing an important facet of behavior during reproduction. Here we reply to comments by Shine (2012) and DeNardo et al. (2012), mainly to emphasize our point that contrasting the MMH and the SMH as if they operated exclusively and independently is not productive, because females enhance their lifetime reproductive success by enhancing current offspring fitness or their own long-term fitness, or both.

WE thank Richard Shine, Dale DeNardo, Olivier Lourdais, and Zachary Stahlschmidt for their thorough and considered responses to our recent Point-of-View article (Schwarzkopf and Andrews, 2012). Our intention was to broaden the perspective of researchers on the adaptive value of thermoregulation (and, by extension, other behaviors) of female reptiles during reproduction. In general, the critiques, comments, and suggestions for further work by these authors will help focus attention on this important issue.

Females should behave in ways that maximize their lifetime reproductive success (Marshall and Uller, 2007). Very often, maximizing lifetime reproductive success for a mother will involve maximizing the fitness of offspring in most, or every, reproductive episode. As pointed out by Shine (2012) and DeNardo et al. (2012), in the case of females that only produce offspring once in their lifetime (semelparity), maximizing offspring fitness is synonymous with maximizing lifetime reproductive output. Many species are iteroparous, however, in which case maximizing lifetime reproductive success for a female will not necessarily be coincident with maximizing fitness for any given reproductive bout (e.g., Stearns, 1992, p. 28). For example, provisioning offspring less when there is less food available might reduce offspring fitness, but

will preserve female fitness when food availability is variable, allowing females higher lifetime reproductive success (e.g., some birds; Hussell, 1988). Therefore, in cases when there is parent–offspring conflict, we expect that females will continue to behave in ways that maximize lifetime reproductive success, even if it does not maximize fitness of the current batch of offspring. Females must take a longer-term view—if they are unlikely to be successful at producing offspring now, then the best strategy is to survive, in good condition, to reproduce again in the future, rather than to invest heavily in offspring likely to have low fitness (Williams, 1966).

The maternal manipulation hypothesis (MMH), or the idea that females should behave in ways that maximize the fitness of the current batch of offspring (Shine, 2012), is a special case of the more-general argument that females should always maximize lifetime reproductive success (the selfish mother hypothesis, or SMH; Table 1). The two hypotheses cannot be compared as if they were alternatives, because one (the MMH) is a subset of the other (the SMH; Table 1). In our Point-of-View article, we specifically stated that our aim was not to indicate that the MMH was incorrect (see the section entitled “Evidence Supporting the MMH”). Rather, we ask researchers to consider the broader context, and not to search only for

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TABLE 1—Conceptual framework showing the relationship of the MMH (maternal manipulation hypothesis) to the SMH (selfish mother hypothesis).

Hypotheses	Females act:
SMH	To maximize their lifetime reproductive success, in two nonexclusive ways: (1) enhance current reproductive fitness (maternal manipulation of offspring fitness—MMH) (2) enhance future reproductive success of the female (e.g., in cases in which females must abandon maximizing current fitness of offspring)
Nonadaptive	In ways neutral to current and future offspring and female fitness

evidence that a change to maternal thermoregulatory behavior during pregnancy would benefit offspring fitness, because it might not (Schwarzkopf and Andrews, 2012). As correctly pointed out by Shine (2012), the arguments we made, specifically about thermoregulation, could be expanded to many other behaviors that occur during pregnancy, including nest site selection, offspring provisioning, and nest attendance.

The majority of the response written by Shine (2012) was a contrast of the MMH with the SMH assuming that the two hypotheses were mutually exclusive. He made that contrast by casting the component of the SMH in which females enhance their future reproductive fitness (our Item 2, Table 1) as the SMH itself. For example, he stated: “For the SMH to offer a better explanation than the MMH, maternal thermoregulatory modifications need to enhance maternal lifetime reproductive success more than they enhance offspring viability” (Shine, 2012). In response, we argue that contrasting the MMH and the SMH as exclusive alternatives cannot be productive because the MMH is one of two nonexclusive alternatives of the SMH. With this logic in mind, we examine three aspects of Shine’s (2012) argument in detail: first, that there is more evidence to support the MMH than the SMH, second, that interspecific differences in thermoregulation during pregnancy refute the SMH, and third, that the direction and magnitude of maternal shifts support the MMH more than the SMH.

(1) Shine (2012) argued that there is ample evidence in support of the MMH, and little in support of the SMH. We concur, and suggest that there are two reasons for this dichotomy. First, the MMH is a subset of, and is consistent with, the

SMH, so we expect the two to act in concert. We did not intend our paper to refute the MMH in favor of the SMH. Instead, we hoped to encourage researchers to consider that mothers must optimize both current and future reproductive success. Female selfish behavior in the absence of behavior that also maximizes offspring fitness (i.e., exclusive female focus mainly on future reproductive success) is most likely to be observed when there is parent–offspring conflict (Crespi and Semeniuk, 2004), which is relatively rare. Our more important point was that few investigators have determined the wider fitness effects of particular strategies adopted by female reptiles (see Table 1 in Schwarzkopf and Andrews, 2012), and therefore that evidence for the SMH is not that common because researchers do not look for it. Our research program suggested that researchers should examine the influences of pregnant female behavior on female condition in laboratory studies, and on condition and survival in field studies, in addition to effects on offspring. Adding such measurements constitutes a modest increase in data collected (depending on the study system) that could help address more widely the question of which aspects of maternal fitness are increased by particular strategies. Shine (2012) concurred that an examination of environmental influences on maternal traits could be interesting; that was exactly the response we were hoping to elicit with our paper.

(2) Shine (2012) argued that females alter their thermoregulatory preferences to suit offspring requirements, which supports

the MMH. We noted the alternative, that correlation between optimal temperatures for embryonic development and female selected body temperatures (T_b) during reproduction could indicate that embryonic thermal optima match female thermal preferences during reproduction, supporting the SMH. Shine (2012) claimed that females must be changing their thermoregulation preferences for their offspring, because embryonic thermal optima are evolutionarily conserved compared with female thermal optima. However, data on phylogenetic patterns of embryonic thermal optima are not available, so this “chicken and egg” (or perhaps it is “reptile and egg”?) dilemma is yet to be definitively resolved. Data on relative levels of variation in thermal optima of embryos across a wide range of species (e.g., Andrews and Schwarzkopf, 2012) could be compared with data on adults (e.g., Clusella-Trullas et al., 2011) to determine which group is more conservative.

- (3) Shine (2012) also claimed that variation in the direction and magnitude of changes in female thermoregulatory behavior provides evidence in favor of the MMH over the SMH, because the MMH predicts such variation. He supported this contention by pointing out that, depending on species or ecology, embryos may require warm or cold, variable or constant conditions to enhance fitness. He listed four ways that T_b alterations during pregnancy may enhance female fitness (by reducing predation, accelerating embryogenesis, reducing food intake, or reducing energy expenditure). Shine (2012) said that each of these mechanisms supports a unidirectional prediction of change in T_b , and concluded that these unidirectional predictions demonstrate that the SMH cannot be the factor driving T_b changes in general, because T_b changes are multidirectional among species. However, we argue that, taken together, these advantages to females do predict variation in female T_b during reproduction, because any one of these changes may enhance female fitness in any particular case.

Similarly, there are unidirectional predictions for any given enhancement of offspring fitness (e.g., higher female T_b for early birth date, lower female T_b for larger offspring body size, etc.), but a prediction of variation if taken together. Thus, a variety of different unidirectional changes in maternal T_b are predicted whether or not females are manipulating offspring phenotype in the current reproductive event, and hence there is a prediction of variation in maternal T_b during reproduction.

DeNardo et al. (2012) provided an excellent discourse on the ways that consideration of the SMH can be included in studies of reptile thermoregulation, and indeed other behaviors, during reproduction. They gave examples of cases, using pythons, in which “SMH thinking” allows for an examination of the complete fitness benefits of particular strategies. They noted that although females frequently manipulate offspring phenotype by selecting or providing particular nest environments, females also sometimes act in ways that benefit themselves and not their offspring. Similarly, Shine (2012) suggested that measuring the effects of reproduction on female condition and survival is likely to be profitable. Both Shine (2012) and DeNardo et al. (2012) also discussed a series of experiments that would add to our understanding of reproductive behavior of reptiles. We applaud these suggestions, and hope that herpetological researchers will broaden their thinking about maternal manipulations of offspring fitness to include measurements of female fitness more generally.

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