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ARE MOMS MANIPULATIVE OR JUST SELFISH? EVALUATING THE “MATERNAL MANIPULATION HYPOTHESIS” AND IMPLICATIONS FOR LIFE-HISTORY STUDIES OF REPTILES

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ABSTRACT: Recent discussion in the life-history literature has examined “adaptive maternal effects,” defined as maternal effects that benefit offspring, and concluded that this definition is too narrow, because maternal effects may not always benefit current offspring fitness, but can still be adaptive to female lifetime reproductive success. The “maternal manipulation hypothesis” suggests that females modify their physiology and behavior when gravid to increase offspring fitness, an example of adaptive maternal effects in the narrow sense. The maternal manipulation hypothesis has been tested almost exclusively using studies of reptiles, especially viviparous species. We argue that interpretations of modifications of female reptile behavior and physiology while gravid are hampered by the maternal manipulation hypothesis’ exclusive focus on offspring fitness. We suggest broadening the approach of such studies to attempt to determine whether behaviors benefit fitness of the current batch of offspring, or benefit female lifetime reproductive success, or both. Using this approach, researchers acknowledge that females may modify physiology and behavior when gravid to benefit their own lifetime reproductive success, which may, or may not, also enhance fitness of the current batch of offspring. We recommend tests of benefits in reptiles to include the idea that females may increase their lifetime reproductive success by engaging in specific behaviors while gravid, independent of (or in addition to) benefits to offspring. We conclude that a broader view of maternal effects, less focused on offspring fitness and including both mothers and offspring, is the way forward for understanding maternal effects.

Key words: Embryonic development; Maternal effects; Temperature; Thermoregulation; Viviparity

MATERNAL EFFECTS occur when offspring phenotype is causally influenced by maternal phenotype or genotype (Mousseau et al., 2009; Wolf and Wade, 2009). The mechanism for this influence is generally via the maternally provided environment, whether it be direct (e.g., the amount of steroids deposited in an egg) or indirect (e.g., selection of a body temperature (T_b) by the gravid female or selection of a nesting site). Maternal effects can potentially influence nearly every aspect of offspring phenotype, including sex (e.g., Roosenburg, 1996), morphology (e.g., Deeming and Ferguson, 2004), and behavior (e.g.,

Downes and Shine, 1999). Because offspring phenotype is critical to fitness, maternal effects can have important influences on the evolutionary trajectories of populations (Kirkpatrick and Lande, 1989).

Maternal effects may increase, be neutral to, or decrease offspring fitness. As a consequence, some researchers separate “adaptive maternal effects” (defined as those maternal effects that increase offspring fitness; Bernardo, 1996) from maternal effects that are neutral or have negative effects on offspring fitness, which are often interpreted as physiologically unavoidable (e.g., Fox and Czesak, 2000). If the term “adaptive maternal effects” is applied only to instances when offspring

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fitness is enhanced, however, it can cause confusion, because there are situations when the maternal environment may decrease offspring fitness, but still be adaptive to the female (Wilson et al., 2005; Marshall and Uller, 2007). How can maternal effects enhance female reproductive success but not enhance offspring fitness? Indeed, benefits to offspring fitness usually benefit female fitness and vice versa. But maternal lifetime reproductive success has three components: the individual's reproductive life span, its fecundity per reproductive year, and offspring survival (defined in Brown, 1988). Thus, although increasing offspring survival or fitness is one way to increase female lifetime reproductive success, increasing female life span, or fecundity, could also increase her reproductive success, even if offspring survival or fitness is decreased in one or more reproductive episodes. Decreases in offspring fitness relative to female fitness can occur, for example, when there is parent/offspring conflict over resource allocation (Crespi and Semeniuk, 2004). Thus, studying the adaptive function of maternal effects relative to both females and their offspring is necessary. Because of these issues, a productive approach to the study of maternal effects is to remove the focus on adaptive effects on offspring, and simply determine whether maternal effects enhance lifetime reproductive success of the female, in which case they are still adaptive (Marshall and Uller, 2007).

Reptiles are an important vertebrate model system for studying maternal effects. As ectotherms, reptiles are strongly affected by environmental temperatures, including during development. Temperature during development can influence sex, developmental rate, size, shape, performance, behavior, and growth rate of offspring (reviewed by Deeming and Ferguson, 2004). Temperature effects on offspring phenotype can be long lasting, and influence offspring survival, growth (e.g., Caley and Schwarzkopf, 2004), and fitness (Warner and Shine, 2008). Specifically, the effects of incubation temperature on offspring phenotype have been used to test the "maternal manipulation hypothesis" (MMH).

The objective of this article is to discuss tests of the MMH, specifically with regards to reptiles. Whereas current studies on birds and

mammals often consider lifetime reproductive success of mothers when evaluating maternal effects (e.g., Crespi and Semeniuk, 2004 [general]; Reed and Clark, 2011 [birds]), current studies on reptiles often do not. We will document the extent of this problem by summarizing recent literature relevant to the MMH, discuss the limitations of a research program that examines only one facet of possible maternal effects, and provide some suggestions for more comprehensive testing of the MMH.

WHAT IS THE MMH?

In general terms, the MMH posits that females could increase offspring fitness by altering their behavior and/or physiology when gravid, or their behavior during oviposition. For example, maternal diet can influence offspring fitness in humans (Mathews et al., 2008) and reptiles (Cadby et al., 2011), and, thus, females could modify their diet to enhance fitness. Similarly, avian mothers could manipulate egg androgens (reviewed by Gil, 2003) or food provisioning (reviewed by Royle et al., 2004) to influence offspring fitness in birds. One of the most obvious kinds of manipulation possible by ectothermic mothers is to vary the temperatures to which offspring are exposed. In oviparous reptiles, this may involve selection of nest sites in microhabitats with specific thermal properties (e.g., Shine and Harlow, 1996; Kamel and Mrosovsky, 2005) or shivering thermogenesis during brooding (e.g., Harlow and Grigg, 1984). Also, both oviparous (e.g., Braña, 1993; Gvoždík, 2005 [newts]; Lourdais et al., 2008 [reptiles]), and viviparous species can vary T_b by basking more or less, or by selecting specific microhabitats while offspring are being carried in utero. The usual expression of the MMH is that females alter the mean and/or variance of their own T_b while gravid, to manipulate the phenotypes of their offspring, so that the latter are more fit than they would have been if females had not altered their "normal" or nongravid thermal behavior (e.g., Shine, 1995; Webb et al., 2006). The MMH has, almost universally, been tested by examining the thermoregulatory behavior of viviparous squamates (Table 1), although effects of thermoregulation on offspring in oviparous species

TABLE 1.—Summary of literature examining effects of maternal body temperature (T_b) on females or offspring, focusing chiefly on reptile species that shift their preferred temperature when gravid. A few studies in which females did not change their T_b when gravid were included. Lab or field = where thermoregulatory measures were made; When? = when during reproduction thermoregulatory behaviors were examined; What kind of shift occurs? = the statistical measure used to document a shift; Nature of shift = a description of the kind of change that occurs, or the treatments to which gravid females were exposed in the lab.

Species	Lab or field	When?	What kind of shift occurs?	Nature of shift	Effects of shift on offspring	Effects of shift on mother	Authors	Date
Measured effects of maternal T_b on offspring								
<i>Acanthophis praelongus</i>	Lab	Pregnancy	Mean, variance	Females more precise, same mean	Offspring larger, large offspring higher survival in field	Not measured	Webb et al.	2006
<i>Eremias multiocellatus</i>	Lab	Pregnancy	Preferred temperature in pregnancy 29.6°C	No shift	29°C 'best' for growth rates, no other differences among treatments	Not measured	Yan et al.	2011
<i>Eulamprus heatwolei</i>	Lab	Pregnancy	Mean, variance	Long and short basking opportunities (2 or 8 h 30°C+ available, temperature dropped to 23°C)	Cooler treatment short, better condition, good runners, lasted 2 mo after birth	Not measured	Shine and Harlow	1993
<i>Eulamprus quoyii</i>	Lab	Pregnancy	Mean, variance	Higher, less variable	High temperature, longer tails, higher survival rates	Not measured	Borges-Landaez	1999
<i>Gloydius brevicaudus</i>	Lab, field	Pregnancy	Mean, variance	Variance less, mean same	Offspring deformed at high temperatures, poor performing at low temperatures	Not measured	Gao et al.	2010
<i>Mabuia multifasciata</i>	Lab	Pregnancy	Mean, variance	Gravid females select lower, less variable temperatures	Offspring differed in morphology, variation mostly from extreme temperatures, sprint speed influenced by mean not variance.	Not measured	Ji et al.	2007
<i>Niveoscincus ocellatus*</i>	Lab	Pregnancy	Not reported	Long and short basking opportunities (4 or 10 h 30–35°C available, temperature dropped to 10°C)	Warmer treatment longer, heavier, better condition, grew faster	Not measured	Wapstra	2000
<i>Oligosoma maccanni*</i>	Lab	Pregnancy	Not reported	Allowed to bask 7 d/wk, 5 d/wk, 3.5 d/wk	Survival low in low-bask treatment	Not measured	Hare and Cree	2010
<i>Sceloporus jarrovi</i>	Lab	Pregnancy	Mean temperature	Down	High temperatures caused death and deformity of offspring	Not measured	Beuchat	1986, 1988
<i>Sceloporus virgatus</i>	Lab	Gravid (oviparous)	Mean temperature	Down 1°C	Fluctuating temperatures enhanced embryonic growth and development, nest and gravid female temperatures not much different	Not measured	Andrews and Rose	1994

TABLE 1.—Continued.

Species	Lab or field	When?	What kind of shift occurs?	Nature of shift	Effects of shift on offspring	Effects of shift on mother	Authors	Date
<i>Thamnophis elegans</i>	Lab	Pregnancy	Females maintained at nine constant temperatures between 21°C and 33°C	Compared to field-selected temperatures by females	Optimal temperature for embryo survival 26.6°C, also minimal developmental abnormalities	Not measured	O'Donnell and Arnold	2005
<i>Vipera aspis</i>	Field	Pregnancy	Mean, variance	Higher, less variable	Cool temperatures late in gestation caused mortality and scalation changes, cool temperatures in mid-gestation lengthened gestation	Not measured	Lourdais et al.	2004
<i>Zootoca vivipara</i>	Lab	Egg incubation inside gravid female	Gravid females forced to thermoregulate like nongravid females	Usually lower for gravid females	High temperatures reduced offspring survival, body size, and running speed	Not measured	Rodriguez-Diaz and Brana	2011
Measured effect of T _b on females								
<i>Crotalus horridus</i>	Field	Pregnancy	Mean temp	Higher for gravid females	Not measured	Females moved less when gravid	Gardner-Santana and Beaupre	2009
<i>Crotalus viridis oregonus</i>	Lab	Pregnancy	Mean, variance	Higher, less variable	Not measured	Females moved less when gravid	Gier et al.	1989
<i>Crotalus viridis viridis</i>	Field	Pregnancy	Mean temperature	Higher for gravid females	Not measured	Females moved less when gravid	Graves and Duvall	1993
<i>Molpodon monspessulanus</i>	Field	Gravid (oviparous)	Mean temperature	Higher	Not measured	Gravid females moved more	Blazquez	1995
<i>Sceloporus grannicus</i>	Field	Pregnancy	Median temperature	Down (33°C to 31°C)	Not measured	Mothers avoided thermoregulating in field when difficult, caused shift to lower mean temperature in field	Andrews et al.	1997
<i>Thamnophis elegans</i>	Lab, field	Pregnancy	Mean, variance	Higher, less variable	Not measured	Females ate less by choice, moved less	Gregory et al.	1999

TABLE 1.—Continued.

Species	Lab or field	When?	What kind of shift occurs?	Nature of shift	Effects of shift on offspring	Effects of shift on mother	Authors	Date
Measured effect of Tb on both mothers and offspring								
<i>Bassiana duperreyi</i>	Lab	Egg incubation inside gravid female, and after laying	Basking available for females 3 or 8 h/d, eggs in 22 ± 7.5°C and 16 ± 7.5°C	Long and short basking opportunities (3 or 8 h/d, 33°C available, temperature dropped to 15°C)	Warmer temperatures led to large offspring	Daily food intake of crickets by females measured while gravid, larger females ate more	Telemeco et al.	2010
<i>Eremias przewalskii</i>	Lab	Pregnancy	Mean, variance	Females selected lower mean when gravid, thermoregulation not more precise, offered 14 or 10 h basking daily	Tail length, number of ventral scales differed, longer basking treatment led to faster runners and growers	No effect on mothers' mass, snout-vent length of treatments	Li et al.	2009
<i>Hoplodactylus maculatus</i>	Lab	Pregnancy	Mean temperature	Females selected higher mean when gravid	100% offspring mortality at cold temperatures—but note that lab temperatures much colder than in field	No effect on mothers' size, condition, or sprint speed	Rock and Cree Werner and Whitaker	2003 1978
<i>Liasis fuscus</i>	Lab	Maternal brooding, maternal choice of nest site	Mean, variance	Higher, or higher less variable	Earlier hatching and therefore increased food availability, constant most willing to feed, brood grew faster, constant 32 needed more taps, cold more active	Increased risk of mortality to females	Shine et al.	1997
<i>Podarehis muralis muralis</i>	Field	Pregnancy	Mean temperature	Lower	Not measured	Not measured	Braña	1993
<i>Podarehis muralis</i>	Lab thermal gradient	Pregnancy	Mean temperature	Not different	Not measured	Mothers avoided thermoregulating in field, caused shift to lower mean temperature in field	Brana	1993
<i>Podarehis muralis</i>	Lab	Egg incubation	Mean constant temperatures	32°C	High temperatures detrimental: hot worst performance, smaller, smaller extremities	Not measured	Brana and Ji	2000

TABLE 1.—Continued.

Species	Lab or field	When?	What kind of shift occurs?	Nature of shift	Effects of shift on offspring	Effects of shift on mother	Authors	Date
<i>Podarchis muralis</i> **	Lab	Egg incubation	Mean constant, variation different, early cold, early hot	Females “provided” early cool period in field	Morphological effects of early hot, no performance effects	Not measured	Brana and Ji	2007
<i>Pseudemola pagenstecheri</i> *	Lab	Pregnant	Not reported	Experimentally reduced basking opportunities by 85%	Offspring from females with restricted thermoregulation opportunities born later, bigger, ran slowly	Maternal body condition did not differ due to treatment	Shine and Downes	1999
<i>Sceloporus jarrovi</i>	Lab	Pregnancy	Mean, variance	Lower mean, less variance; in particular, avoiding upper extremes	Neonates exposed to low temperatures smaller, survival and growth equal among treatments	No ill effects, females grew equal amounts	Mathies and Andrews	1997
<i>Zootoca vivipara</i>	Lab	Egg incubation inside gravid female	Mean temperature	Lower for gravid females, increased after laying	Optimum for embryonic development (not measured this study)	Reduced activity to avoid predation (not measured for this study)	Carretero et al.	2005

* Natural maternal T_b during pregnancy not documented.
 ** Interpreted as support for the MMH, although females did not modify T_b when gravid in the lab.

(Braña 1993; Lourdais et al., 2008) and nest site selection as a method of manipulating offspring T_b (Shine, 2006; Patterson and Blouin-Demers, 2008) have also been examined.

TESTING THE MMH

Typically, any evidence that gravid female reptiles increase or decrease their T_b , or reduce variance in T_b when gravid, is interpreted as support for the MMH (Shine, 1995, 2004a; Webb et al., 2006; Ji et al., 2007; Li et al., 2009; Rodriguez-Diaz et al., 2009). Similarly, differences among neonatal phenotypes associated with different thermal regimes during gestation are also interpreted as support for the MMH (Shine, 1995, 2004a; Webb et al., 2006; Ji et al., 2007; Patterson and Blouin-Demers, 2008; Li et al., 2009; Rodriguez-Diaz et al., 2009). Thus, studies of the MMH in squamates often (1) demonstrate a change in female thermoregulatory behavior while gravid, (2) demonstrate a change in offspring phenotype, and (3) suggest that the change in offspring phenotype is adaptive, and conclude that the reason females change their T_b while gravid is to manipulate offspring phenotype.

Although it is possible that females change T_b when gravid specifically to manipulate offspring phenotype, concluding that any or all reproduction-related changes in T_b enhance offspring fitness can be problematic, because the link between hatchling phenotype and evolutionary fitness is not known, and, more importantly, changes in thermoregulatory behavior of females could have other causes that were not considered or examined experimentally when the MMH was tested. For example, females may change their thermoregulatory behavior while gravid, and it may influence offspring phenotype, but the change in offspring phenotype may not be the ultimate reason for the change in thermoregulatory behavior. Essentially, the challenge is to discover not only whether females change their thermoregulatory behavior when gravid, but why, i.e., to determine whether and how both maternal and offspring fitness are influenced by this behavior.

Determining the drivers of maternal change in thermoregulation while gravid is important for at least two reasons. First, the ideas underpinning the MMH are being used to support other hypotheses. For example,

one hypothesis for the evolution of viviparity suggests that maternal manipulation of offspring phenotype is the selective basis for increased egg retention (i.e., oviparous females, while retaining eggs, can manipulate gestation temperatures to enhance offspring fitness, leading to longer retention and eventually to viviparity; Shine and Thompson, 2006). If females are not manipulating T_b to manipulate offspring phenotypes, then a major assumption of this hypothesis is not supported, and increased periods of egg retention probably evolve for other reasons. Second, by focusing solely on offspring fitness, as studies of the MMH have traditionally done, researchers might miss factors influencing maternal fitness, which also determine female lifetime reproductive success.

We argue that to properly test the MMH, it is important to widen the focus of experiments to determine the influence of changes in thermoregulation while gravid on female fitness. We propose, more generally than the MMH and consistent with life-history theory in general, that females should behave in ways that maximize their own lifetime reproductive success (Wilson et al., 2005; Marshall and Uller, 2007). Although maximizing lifetime reproductive output does not preclude providing benefits to offspring, it may also mean that females sometimes alter their behavior in ways that are neutral, or even detrimental, to offspring fitness (e.g., Shine and Downes, 1999; Rock and Cree, 2003; [viviparous female lizards aborted offspring under unsuitable thermal conditions, but themselves survived with little mass loss]; Lloyd and Martin, 2004 [birds may provision offspring inadequately, and themselves survive while offspring starve]).

Because females should maximize lifetime reproductive success, their behavior during any given reproductive episode could enhance their own fitness, rather than that of their offspring (Wilson et al., 2005; Marshall and Uller, 2007). Such selfish activities should be relatively easy to detect in viviparous reptiles. Viviparous squamates are gravid for longer periods than oviparous species and must survive throughout their long period of pregnancy if they are to have current, and any future, reproductive success, compared to oviparous species that need only survive past

oviposition to obtain at least some possibility of current reproductive success (Schwarzkopf, 1994). Viviparous females may, therefore, maximize their own survival, potentially even over obtaining high fitness for offspring, compared to oviparous females.

Our review of the literature relevant to the MMH (Table 1) identified 30 papers published 1986–2011 that met these minimal criteria: observations were made on T_b or other thermal behaviors when females were gravid, and the effect of natural or experimentally controlled female T_b on offspring or females or both, were determined. Earlier studies that documented changes in maternal T_b , but did not examine effects on offspring or females, were excluded from our review. We included studies of both oviparous and viviparous species, as both can potentially influence offspring phenotype during the time embryos are retained, and retention time can be extensive in some oviparous species (Andrews, 2004). Of these studies, the greatest number (13 studies; 43%) examined the effects of thermoregulation, basking, or temperature treatments on offspring fitness only; 20% (six) examined the effects of changes in thermoregulation on females without examining effects on offspring; and 23% (eight) examined the effects of changes in thermoregulatory behavior while gravid on both females and their offspring (note that all studies by F. Braña and coworkers are on one species, and build on each other—we have counted these as a single study of both mothers and offspring, which means the total of our percentages does not reach 100). Our review also includes two studies that examined temperature effects on offspring in laboratory experiments without measuring female thermal preferences when gravid and nongravid in the field. Although difficult to obtain, information on female thermoregulatory behavior while gravid is useful to ensure that temperature treatments are not more extreme than actual thermal tolerances of female and offspring.

TESTING THE ASSUMPTIONS OF THE MMH WITHIN THE BROADER CONTEXT OF FEMALE LIFETIME REPRODUCTIVE SUCCESS

The ideal means of testing the MMH would be to determine how changes in female

thermoregulatory behavior affect offspring fitness relative to female fitness. This approach requires longitudinal studies on the fitness of offspring and mothers whose thermal behavior while gravid changed, and comparisons with individuals that did not make such changes, or made a different change. This approach can be difficult with vertebrates, especially long-lived species, although longitudinal studies of birds, mammals, and reptiles have compared life history outcomes of different maternal strategies (e.g., reptile case study by Brown and Weatherhead, 1997; birds and mammals reviewed by Lindstrom, 1999). Another approach is to examine the main assumptions of the MMH in the context of possible alternative explanations, using measures of fitness that are presumably correlated with lifetime reproductive success.

Assumption 1. Changes in Female Thermal Behavior while Gravid Increase the Fitness of Offspring

The MMH is supported by evidence that current offspring fitness was enhanced by maternal thermoregulatory behavior during reproduction, while female fitness was either unaffected or reduced (e.g., Braña, 1993; Mathies and Andrews, 1997; Braña and Ji, 2000). On the other hand, observations that thermoregulatory behavior of gravid females (A) maximized their lifetime reproductive success and was neutral to current offspring fitness, or (B) maximized their lifetime reproductive success at the expense of their current offspring's fitness, would refute the MMH. We present evidence supporting these alternatives to the MMH. In both cases, operational tests could determine the effects of T_b while gravid on the fitness of females and on their offspring, relative to such effects if T_b were not altered.

(A) *Females maximize their own lifetime reproductive success, while not greatly influencing current offspring fitness.*—Gravid females may change their thermoregulatory behavior while gravid, not as a strategy to increase offspring fitness, as suggested by the MMH, but because their movement is restricted or their survival compromised by the burden imposed by pregnancy. Pregnancy

often reduces female performance, and after parturition, performance typically improves (Olsson et al., 2000). Also, gravid females are often more susceptible to predation than other members of a population, either because of reduced performance (Shine, 1980), or increased detectability (Schwarzkopf and Shine, 1992). Predation risk or energetic costs of movement may alter the thermoregulatory priorities of females, independent of the needs of offspring. For example, in some species, females only alter T_b while gravid if thermoregulation is relatively easy, and not if the cost of thermoregulation is high (Braña 1993; Andrews et al., 1997). Such evidence suggests that changes in thermoregulatory behavior while gravid may sometimes be driven more strongly by enhancement of female lifetime reproductive fitness than by enhancement of current offspring fitness.

Encumbrance, and associated risks, may be one reason gravid females alter mean T_b and, especially, lower variance in T_b compared to nonreproductive females (Gier et al., 1989; Graves and Duvall, 1993; Webb et al., 2006; Lourdais et al., 2008). For example, gravid rattlesnakes (*Crotalus horridus*) have 50% smaller home ranges, and move significantly less, as well as having less variable T_b than nongravid females (Gardener-Santana and Beaupre, 2009). Decreased variability in incubation temperature is often neutral to offspring survival or fitness compared to fluctuating temperatures with the same mean, as long as temperatures do not fluctuate to detrimental extremes (Andrews et al., 2000; cf. Shine, 2004b; Ji et al., 2007; Lin et al., 2008 in which variable temperatures influenced offspring fitness).

Females may preferentially preserve their own condition under thermal stress. For example, offspring performance was negatively affected (offspring ran more slowly) when gravid female skinks (*Pseudemoia pagenstecheri*) were exposed to experimentally reduced basking opportunities (Shine and Downes, 1999), but there were no negative effects on female body condition. Similarly, offspring fitness was negatively affected in gravid female *Eremias przewalskii* exposed to a series of different constant temperatures while gravid, but there was no influence of these treatments on female body condition

(Li et al., 2009). These observations, taken together, suggest that changes in thermoregulation while gravid may sometimes enhance female lifetime reproductive success more than that of the current batch of offspring as a bet-hedging strategy, because fitness of offspring varies more than that of females.

One way to test whether decreases in maternal thermoregulatory variability or variations in T_b while gravid are caused chiefly by encumbrance or by other factors, would be to determine if nongravid females respond to any physical burden in the same way that gravid females respond to pregnancy (i.e., by shifting mean T_b and/or decreasing the variability in T_b and movement rates). This prediction could be tested by adding weights, or implanting objects inside the body cavity of females, to simulate the burden of pregnancy (similar to experiments by Shine, 2003; Du et al., 2005). The response should be graded: light loads should cause smaller shifts in behavior than heavy loads, because females should be more inconvenienced by heavy loads. Experimental support of this prediction would challenge one aspect of the MMH.

More generally, to focus on female fitness, studies relevant to the MMH should include observations on female pre- and postpartum mass, condition, and other performance measures. Observations on performance measures likely to be correlated with female fitness are critical to the determination of the costs and benefits of specific thermal behaviors to females while gravid.

(B) *The female's response to pregnancy may actually reduce fitness of the current batch of offspring.*—Females may preserve their own condition at the expense of their offspring's survival. For example, gravid female skinks (*Pseudemoia pagenstecheri*; Shine and Downes, 1999) and geckos (*Hoplodactylus maculatus*; Rock and Cree, 1993) exposed to (apparently inappropriate) laboratory thermal conditions aborted and consumed their offspring, but there were no negative effects on female body condition. In general, poor thermal conditions while gravid can cause increased offspring mortality, but often do not appear to influence female mortality (e.g., Arnold and Peterson, 2002). Death or negative outcomes for offspring in experiments can

be difficult to interpret, however, because for many laboratory treatments, it may not be possible for females to “protect” their offspring by their behavior (e.g., in some treatments they may not be able to thermoregulate, or do so sufficiently, to stop negative phenotypic effects on offspring), so failure to produce viable offspring may not be a “choice” by the female to preserve her own life at the expense of her offspring. Consequently, knowledge of three things is required to fully test the MMH: the preferred temperature and thermoregulatory precision of females when gravid, the preferred temperature and precision when not gravid, and the effects of variation in these parameters on both females and offspring.

Determining whether phenotypic effects on offspring are actually negative is not always straightforward. Females of some species reduce T_b while gravid, slowing embryonic development (reviewed in Shine, 2006; Table 1). Slowed embryonic development can be detrimental to offspring phenotype in some species (e.g., Qualls and Andrews, 1999; Hare et al., 2008). On the other hand, females of other species increase T_b or basking duration during gestation, which speeds development (reviewed in Shine, 2006). A shorter gestation period can be beneficial to female lifetime reproductive success, because it reduces the period females are gravid, and attendant costs (e.g., Caley and Schwarzkopf, 2004). But fast development may produce smaller offspring, which might be detrimental to the fitness of any specific batch of offspring (Qualls and Andrews, 1999). In these cases, it is difficult to determine the influence of female thermoregulatory choices on offspring fitness, because the consequences are not predictable.

Taken together, these observations suggest that simply documenting changes in T_b while gravid does not necessarily provide support for the MMH; a clear understanding of the effects of changes in T_b on the fitness of the current batch of offspring of that species (e.g., whether slow or rapid development is good or bad for offspring fitness in that particular species) relative to effects on the lifetime reproductive success of the female are required before the MMH can be evaluated.

Assumption II. Optimal incubation temperatures for embryonic development do not vary among species, or at least not as much as female T_b . Females must, therefore, change their thermal biology when gravid to produce offspring with the highest fitness

This assumption is based on the idea that changes in preferred temperature while gravid are caused by a mismatch between optimal temperatures for offspring development, and temperatures selected by females, such that females must change their T_b while gravid to achieve an optimal temperature for embryonic development (e.g., Beuchat, 1988). This assumption would be challenged if the optimal incubation temperatures for embryos and selected body temperatures (T_{sel}) of females were correlated (O'Donnell and Arnold, 2005). This seems to be the case. For example, species with adults with high T_{sel} also have high optimal temperatures for embryonic development (e.g., *Dipsosaurus dorsalis* embryos at 36°C [Muth, 1980]; adult T_{sel} 42°C [DeWitt, 1967]), whereas those with low T_{sel} have low optimal temperatures for development (e.g., *Anolis carolinensis* embryos 27°C [Goodman, 2007]; adult T_{sel} 31°C [Goodman and Walguarnery, 2007]). Similarly, fitness (as measured by postbirth growth rates) of neonatal water skinks (*Eulamprus quoyii*) is enhanced when females have the opportunity to thermoregulate while gravid at temperatures to which they are evolutionarily adapted, but lowered when they must thermoregulate in different thermal regimes (Caley and Schwarzkopf, 2004). These examples indicate coadaptation of the thermal biology of embryos and adults. The most likely evolutionary scenario, given that gestation is often a relatively brief part of the life span of individuals posthatching, is that optimal temperatures for embryonic development accommodate T_b s preferred by adults when gravid (Arnold and Peterson, 2002), rather than the other way around.

Comparative methods could be used to test the assumption that females alter their T_b when gravid to accommodate the optimal temperatures of embryos. Positive correlations between optimal temperatures for embryonic development and adult T_b for squamates in general and for taxa with relatively homoge-

neous thermal biologies (e.g., *Sceloporus*, Andrews, 1998) would indicate that shifts in T_b of females when gravid were related to factors other than embryonic thermal optimum. On the other hand, little evolutionary change in the optimal temperature for development, when there has been evolution in female T_b , would suggest that optimal development temperatures are constrained in some way unrelated to the evolution of T_b .

EVIDENCE SUPPORTING THE MMH

Our comments are not intended to refute the MMH, but instead to widen the scope of studies designed to test it. Here we discuss several studies that provide credible support for the MMH. For example, egg attendance in free-ranging water pythons (*Liasis fuscus*) creates a warmer, more stable environment for developing embryos, and includes a reproduction-related shift in behavioral thermoregulation, which improves offspring phenotype, increasing size and growth rate, and improving escape behavior and willingness to feed (Shine et al., 1997; Madsen and Shine, 1999). At the same time, prolonged egg attendance and, thus, prolonged periods of elevated T_b , reduce females' rates of survival and reproduction (Madsen and Shine, 1999). Furthermore, immune function of females is reduced at the temperature preferred during reproduction (31.5°C) relative to the temperatures preferred at other times (28.5°C; Lourdaïs et al., 2008; Z. Stahlschmidt, personal observation). Observations of brooding pythons thus support the MMH, whereby reproduction-related shifts in T_b appear to benefit offspring and incur costs to females. Similarly, the MMH is supported when female behavior during reproduction enhances offspring fitness, but is neutral to females (e.g., Li et al., 2009). Simultaneous maximization of maternal lifetime reproductive success and current offspring fitness (mentioned above) would very likely select for that very outcome.

CONCLUSIONS

We have suggested a variety of scenarios by which focusing exclusively on offspring fitness, as does the MMH, leads researchers to reach unsupported conclusions about the function

of the thermal behaviors of reproductive females. One conclusion of our summary of the available literature (Table 1) is that relatively few studies examine outcomes for both offspring and females. We strongly recommend that both groups are included in such studies. The second conclusion is that the experimental design of some studies is weak in that they establish experimental temperature treatments prior to determining female preferences when gravid and nongravid in the field. Use of treatments that are outside optimal temperatures for normal embryonic development are likely to produce spurious outcomes.

Our view is that focusing the search for adaptation of maternal effects solely on fitness benefits to offspring will be counterproductive (Wilson et al., 2005; Marshall and Uller, 2007). Instead, we recommend that the view of adaptive maternal effects be broadened to include behavior that maximizes lifetime reproductive success of females, which provides testable alternatives to the MMH, and enhances the significance and applicability of such research.

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