

Is Parental Care the Key to Understanding Endothermy in Birds and Mammals?

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In a recent paper, Farmer (2000) offered a novel and stimulating hypothesis for the convergent evolution of endothermy in birds and mammals. She proposed that a high level of nonshivering thermogenesis by adults evolved because of the benefits it provided to their developing embryos. Initially, a higher standard metabolic rate (SMR), and consequently a higher body temperature, served only to increase the temperature of embryos during development. Later, increased aerobic capacity arose from the need to meet the energetic demands of parental care. Importantly, Farmer's model of the evolution of endothermy, which we will refer to as the "parental care model," and the long-standing aerobic capacity model (Bennett and Ruben 1979) are mutually exclusive. The aerobic capacity model asserts that endothermy evolved via a correlated response to selection for a greater capacity for sustained aerobic activity. The parental care model states that the relatively high aerobic capacity of mammals and birds is a consequence of parental care rather than a cause for endothermy. Farmer's ideas are intriguing and will hopefully serve to renew empirical interest in a problem that has been dominated by few hypotheses (see Hayes and Garland 1995). Given the potential influence that Farmer's model will have on the direction of future efforts to understand the evolution of endothermy, we feel that it is necessary to scrutinize the arguments in support of the parental care model and those against the aerobic capacity model.

Costs and Benefits of Endothermy for Parental Care

Although Farmer's ideas were inspired by the widespread use of thermoregulatory mechanisms during reproduction, the parental care model must ultimately be evaluated by examining the relative costs and benefits of endothermy as a means of parental care. As Bennett and Ruben (1979) noted, the energetic cost of endothermy is enormous and must be balanced by considerable benefits. An endothermic parent might have produced additional offspring with the energy used for thermogenesis or might have reduced its exposure to predators if it did not have to procure the additional energy for thermogenesis. Given an appreciation of the costs of endothermy, one must compare these costs to the benefits of using endothermy for parental care. Specifically, how would the fitness of offspring be enhanced by a relatively high and constant temperature during development?

Farmer described several mechanisms by which thermogenesis during parental care could influence the fitness of offspring, including a lower risk of developmental abnormalities, a shorter incubation period, a higher probability of survival to hatching, and beneficial effects on the phenotype after hatching. In support of her argument, Farmer identified many cases in which avian and reptilian embryos suffered a greater risk of developmental defect or mortality when incubated at relatively low temperatures. However, these examples cannot be considered strong support for the parental care model. First, there is no way to identify whether the narrow thermal limits of avian embryos are the cause or the effect of care provided by an endothermic parent. Natural selection can favor mothers that maintain a body temperature that is conducive to embryonic development, or it can favor genotypes that produce embryos that develop at the preferred body temperature of the mother. Therefore, avian embryos might have narrow thermal limits because their mothers provide them with a narrow range of body temperatures. Second, Farmer's argument that reptilian embryos have narrow thermal limits was based on studies of development at constant temperatures, but reptilian embryos survive acute

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exposure to temperatures that would be lethal over prolonged periods. For instance, embryos of the eastern fence lizard *Sceloporus undulatus* did not survive to hatching when incubated at constant temperatures $<25^{\circ}\text{C}$ or $>35^{\circ}\text{C}$ (Sexton and Marion 1974). Nevertheless, embryos of *S. undulatus* hatch successfully in nests that drop below 25°C and rise above 35°C on a daily basis (M. J. Angilletta and R. M. Pringle, unpublished data). In the laboratory, embryos of *S. undulatus* survived exposure to 15°C for up to 4 d without a reduction in hatching success (Christian et al. 1986). Similarly, cold exposure for several days had no effect on the survival of embryos of other *Sceloporus* lizards (Andrews et al. 1997). Therefore, the benefits of endothermy for parental care are best quantified by comparing the success of offspring incubated under natural cycles of temperature with that of offspring incubated under the warmer and more stable thermal conditions that would result from care provided by an endothermic parent.

How well do relevant data support the evolutionary scenario described by the parental care model? To date, only two teams have simultaneously manipulated the mean and variance of incubation temperature in a manner consistent with the parental care model and have examined the effects on the phenotypes of hatchlings: first, Shine et al. (1997b) incubated embryos of the water python *Liasis fuscus* at a constant temperature of 32°C or a diel cycle of $24.3^{\circ}\text{--}32.9^{\circ}\text{C}$, and second, Andrews et al. (2000) incubated embryos of *S. undulatus* at a constant temperature of 33°C or a diel cycle of $23^{\circ}\text{--}33^{\circ}\text{C}$. In the study by Shine et al., individuals from the two thermal regimes did not differ in hatching success, size at hatching, or locomotor capacity after hatching. However, the growth of hatchlings was affected by incubation temperature; by 30 d after hatching, individuals incubated at 32°C were 6% longer than those incubated under the cycling thermal regime. In the study by Andrews et al., individuals from the two thermal regimes did not differ in hatching success or size at hatching, but individuals incubated at 33°C grew more slowly in the laboratory than those incubated at $23^{\circ}\text{--}33^{\circ}\text{C}$. Hatchlings from both treatments were released in the field at an age of 2 wk so that growth and survival could be monitored under natural conditions, but neither growth nor survival differed between groups during the first 8–9 mo after hatching. These studies provide mixed support for the notion that warmer and more stable thermal conditions during embryonic development would benefit offspring.

Other investigators have incubated embryos at diel cycles of temperature, providing different means but identical amplitudes, and the results of these studies are mixed as well. Overall, there is little evidence that the mean of incubation temperature has a strong influence on hatching success when embryos are incubated under diel cycles that span the range of variation in natural nests (Castilla and

Swallow 1996; Qualls and Shine 1996, 1998; Qualls 1997; Shine et al. 1997b; Elphick and Shine 1998; Qualls and Shine 1998; Shine 1999). Additionally, both laboratory and field studies indicate that warmer conditions do not usually alter the size of individuals at hatching (Cagle et al. 1993; Castilla and Swallow 1996; Qualls and Shine 1996, 1998; Shine et al. 1997a, 1997b; Elphick and Shine 1998; Shine 1999). A notable exception is *Sceloporus virgatus*, in which individuals that were incubated at a diel cycle of $20^{\circ}\text{--}30^{\circ}\text{C}$ hatched more successfully and were larger at hatching than those that were incubated at a diel cycle of $15^{\circ}\text{--}25^{\circ}\text{C}$ (Qualls and Andrews 1999). In some species, higher temperatures enhance either the condition, locomotor performance, growth, or survival of hatchlings, but these traits are unaffected or are detrimentally affected in other species (e.g., see Castilla and Swallow 1996; Qualls and Shine 1996, 1998; Qualls and Andrews 1999; Andrews et al. 2000). A strong case for or against the parental care model cannot be made without additional studies like those of Shine et al. (1997b) and Andrews et al. (2000). Furthermore, the relationship between the phenotype and the fitness of offspring must be resolved. Finally, one would like to know the extent to which the fitness of offspring is further reduced when low incubation temperatures are combined with other stressors (e.g., dry or acidic soils).

If there are major benefits of thermogenesis during parental care, they are likely to arise from a reduction in the incubation period and a lengthening of the reproductive season. Both Shine et al. (1997b) and Andrews et al. (2000) observed a dramatic reduction in the incubation period of embryos from the warmer, more stable thermal treatment relative to the colder, more variable thermal treatment. An increase in the mean of incubation temperature is probably more beneficial than a decrease in the variance because incubation period is either unaffected (Georges et al. 1994; Andrews et al. 2000) or is lengthened (Shine and Harlow 1996) when the variance of incubation temperature is decreased without altering the mean. A shorter incubation period provided by endothermy could benefit both parent and offspring. Parents that provide extensive care during incubation would be freed from these duties earlier, increasing the chance for brooding additional clutches in a given year. However, the added energetic expenditure for endothermy might negate any energetic savings that would result from a shorter incubation period. One can conceive that the exposure of adults to predation would be reduced by shortening the incubation period. Similarly, embryos would be exposed to predators of nests for a shorter period of time, but the survival benefit for offspring would depend on the relative risk of predation for embryos and hatchlings. Furthermore, offspring that emerge earlier in the active season may have a better opportunity to acquire resources for growth and storage,

which could confer a higher probability of survival or an earlier opportunity for reproduction (Qualls and Shine 2000; but see Andrews et al. 2000).

The most plausible scenario is that thermogenesis during parental care evolved in populations at the northern limits of species' ranges, where thermal challenges limited the survival and reproduction of individuals. One might even speculate that the evolution of endothermy for parental care would have extended the range of a species. However, the cost of endothermy is also greater in colder environments because either a greater quantity of insulation or heat must be produced to maintain a certain body temperature (Scholander et al. 1950*a*, 1950*b*). Given the energetic cost of endothermy, a shift in the thermal tolerance of embryos seems to be a more likely course of evolution. In fact, an implicit assumption of the parental care model is that the evolution of embryonic physiology is either constrained by genetic variation or carries a greater fitness cost than endothermy. The validity of this assumption is questionable, as the thermal reaction norms of ectotherms are capable of evolving in response to environmental temperature (Angilletta et al. 2002). Recently, Shine (1999) demonstrated that thermal reaction norms for hatchling phenotypes have diverged between two lineages of skinks living in a montane environment of Australia. Embryos of *Nannoscincus maccoyi* experience lower temperatures in natural nests than do embryos of *Bassiana duperreyi*. Accordingly, hatchlings of *N. maccoyi* tended to be smaller and suffered decreased locomotor performance when incubated under warmer conditions, but hatchlings of *B. duperreyi* exhibited the opposite response to an increase in incubation temperature. Although geographic variation in the physiology of reptilian embryos has not been investigated extensively, the capacity for the thermal tolerances of embryos to evolve is a key piece of information needed to evaluate the parental care model.

Reexamining a Criticism of the Aerobic Capacity Model

Although the aerobic capacity model has enjoyed an enduring position as the most popular explanation for the evolution of endothermy (reviewed by Hayes and Garland 1995), Farmer and others have questioned its underlying assumption: the aerobic capacity model requires a mechanistic link between the cellular machinery involved in maintenance metabolism and that required for sustained aerobic activity. Farmer noted that the primary source of endogenous heat in endothermic amniotes is the leaky membranes in the visceral organs and not the ATP-consuming reactions of skeletal muscle. Similarly, Bennett (1991) noted that the viscera constitute only 7% of a human's body mass but account for almost 70% of the heat

produced during inactivity. How can selection for increased aerobic capacity explain the relatively high contribution of the viscera to SMR? More important, how could selection for greater aerobic capacity be linked to the rate of thermogenesis caused by leaky membranes? The lack of a mechanistic link between the processes that contribute to SMR and those that contribute to sustained aerobic activity has cast doubt on the aerobic capacity model.

Biochemical studies have provided a clearer picture of the relative contribution of different tissues and different cellular processes to SMR. First, the relative contribution of different tissues to SMR varies within and among amniotes because of the size and metabolic intensity of organs (Hurlbert and Else 1999). Although the viscera account for almost 70% of the SMR of humans, they account for only 39% of the SMR of rats (Rolfe and Brown 1997). Therefore, a comparative analysis of data for a greater number of amniotes is needed to reconstruct the physiological states of the endothermic ancestors of mammals and birds. Second, leaky membranes may well constitute the primary source of endogenous heat in endotherms, but this does not necessarily mean that the aerobic capacity model is in trouble. In fact, there is a growing body of evidence that the metabolic processes of cells are functionally linked. The proportion of SMR that is generated by particular activities (e.g., proton leaks, protein synthesis) within similar tissues is relatively constant in a variety of organisms, including both ectotherms and endotherms (Hurlbert and Else 1999, 2000). The rates of these processes seem to be governed by the composition of phospholipids in the cellular and mitochondrial membranes, with polyunsaturated lipids enabling greater metabolic activity (Hurlbert and Else 1999). Based on these observations, Hurlbert and Else (2000) proposed that turning up the level of metabolic activity within a cell involves changes in membranes that increase rates of all cellular processes proportionally. If such a linkage among cellular processes does exist, selection for higher metabolic activity in cells might simultaneously increase thermoregulatory ability, growth rate, and aerobic capacity (Hurlbert and Else 2000). Indeed, plausible arguments exist for causal relationships between greater aerobic capacity and an increase in each of the major cellular processes: sodium-potassium transport, protein synthesis, and proton leaks (Hochachka and Somero 2002). Although these ideas are promising, data for additional species of ectotherms and endotherms are needed to establish that this hypothetical linkage among cellular processes is a general property of amniotes.

Finally, there is no reason to think that increased metabolic activity of the visceral organs could not be a target of selection for greater aerobic capacity. The assimilation of energy, the mobilization of energetic reserves, and the

elimination of wastes are all essential tasks of a system designed for sustained aerobic activity (Ricklefs et al. 1996). Steady demands imposed on the viscera by high and prolonged levels of activity can cause a higher standard metabolic rate (Nilsson 2002). Increased metabolic activity of both viscera and skeletal muscle would be anticipated as a response to selection for greater aerobic capacity, especially if the greater aerobic capacity leads to a greater daily energetic expenditure on activity (Koteja 2000). Consequently, the aerobic capacity model cannot be refuted solely by comparing the relative contribution of different organs to SMR.

Should Models Based on Parental Care and Aerobic Capacity Be Mutually Exclusive?

According to Farmer, the primary purpose of endothermy was initially parental care, but we doubt that this was the only factor responsible for the evolution of endothermy. If it were, why is the endothermy of birds and mammals not facultative, being expressed only in the reproductive season? Such a strategy would limit the costs of endothermy to periods in which benefits would accrue. Even more puzzling is the notion that the endothermy of males can be explained by parental care. Pythons are a perfect example to consider. Some species of pythons (e.g., *Morelia spilota*) use shivering thermogenesis during brooding to raise the temperature of their eggs, and these species are the only animals that are known to use endothermy strictly for parental care. As one might expect, the endothermy of pythons is facultative and is only expressed by females (Slip and Shine 1988). When the ancestors of mammals and birds achieved endothermy through a permanent increase in SMR, they would have incurred far greater energetic costs than those incurred by pythons. The benefits derived from the increase in thermogenesis must have been considerable to override the obvious costs. To justify the costs of obligate endothermy, we suspect that some benefits were enjoyed at all stages of the life cycle, not just during periods of parental care. In which case, the parental care model and models based on the thermoregulatory benefits of endothermy (e.g., the niche expansion model of Crompton et al. 1978) are not mutually exclusive. Alternatively, better parental care via endothermy could have been a byproduct of selection for other phenotypes. Koteja (2000) proposed that selection for a greater capacity to assimilate energy during parental care led to the evolution of higher metabolic activity of the visceral organs; ultimately, locomotor limits to foraging and greater energetic requirements would feed back to promote further increases in the metabolic capacities of muscular and visceral tissues. In the context of either Koteja's model or the aerobic capacity model, the high rate of thermogenesis during rest

could have been used to heat embryos during their development.

Whether parental care is the key to understanding the convergent evolution of endothermy in mammals and birds or just one of the many factors that influenced the evolution of endothermy is an important question. Certainly, more studies that define thermal effects on the fitness of offspring will be critical to evaluating the parental care model, particularly if those studies include comparisons of groups incubated under natural conditions with those incubated under warmer, more stable conditions. Attempts to test the parental care model might be focused on the benefits of a shorter incubation period and the energetic expenditure that would be required to heat nests sufficiently to obtain these benefits. Ultimately, these costs and benefits should be evaluated in a phylogenetic context to determine the likelihood that endothermy evolved for parental care in a reptilian ancestor. In the end, however, the aerobic capacity model may prevail as we learn more about the processes that underlie the metabolism of endotherms.

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Literature Cited

- Andrews, R. M., C. P. Qualls, and B. Rose. 1997. Effects of low temperature on embryonic development of *Sceloporus* lizards. *Copeia* 1997:827–833.
- Andrews, R. M., T. Mathies, and D. A. Warner. 2000. Effect of incubation temperature on morphology, growth, and survival of juvenile *Sceloporus undulatus*. *Herpetological Monographs* 14:420–431.
- Angilletta, M. J., P. H. Niewiarowski, and C. A. Navas. 2002. The evolution of thermal physiology in ectotherms. *Journal of Thermal Biology* 27:249–268.
- Bennett, A. F. 1991. The evolution of activity capacity. *Journal of Experimental Biology* 160:1–23.
- Bennett, A. F., and J. A. Ruben. 1979. Endothermy and activity in vertebrates. *Science* 206:649–654.
- Cagle, K. D., G. C. Packard, K. Miller, and M. J. Packard. 1993. Effects of the microclimate in natural nests on the development of embryonic painted turtles, *Chrysemys picta*. *Functional Ecology* 7:653–660.
- Castilla, A. M., and J. G. Swallow. 1996. Thermal dependence of incubation duration under a cycling temperature regime in the lizard, *Podarcis hispanica atrata*. *Journal of Herpetology* 30:247–253.
- Christian, K. A., C. R. Tracy, and W. P. Porter. 1986. The

- effect of cold exposure during incubation of *Sceloporus undulatus* eggs. *Copeia* 1986:1012–1014.
- Crompton, A. W., C. R. Taylor, and J. A. Jagger. 1978. Evolution of homeothermy in mammals. *Nature* 272: 333–336.
- Elphick, M. J., and R. Shine. 1998. Long-term effects of incubation temperatures on the morphology and locomotor performance of hatchling lizards (*Bassiana duperreyi*, Scincidae). *Biological Journal of the Linnean Society* 63:429–447.
- Farmer, C. G. 2000. Parental care: the key to understanding endothermy and other convergent features in birds and mammals. *American Naturalist* 155:326–334.
- Georges, A., C. Limpus, and R. Stoutjesdijk. 1994. Hatching sex in the marine turtle *Caretta caretta* is determined by proportion of development at a temperature, not daily duration of exposure. *Journal of Experimental Zoology* 270:432–444.
- Hayes, J. P., and T. Garland, Jr. 1995. The evolution of endothermy: testing the aerobic capacity model. *Evolution* 49:836–847.
- Hochachka, P. W., and G. N. Somero. Biochemical adaptation. Oxford University Press, Oxford.
- Hurlbert, A. J., and P. L. Else. 1999. Membranes as possible pacemakers of metabolism. *Journal of Theoretical Biology* 199:257–274.
- . 2000. Mechanisms underlying the cost of living in animals. *Annual Review of Physiology* 62:207–235.
- Koteja, P. 2000. Energy assimilation, parental care and the evolution of endothermy. *Proceedings of the Royal Society of London B, Biological Sciences* 267:479–484.
- Nilsson, J. 2002. Metabolic consequences of hard work. *Proceedings of the Royal Society of London B, Biological Sciences* 269:1735–1739.
- Qualls, C. P. 1997. The effects of reproductive mode and climate on reproductive success in the Australian lizard, *Lerista bougainvillii*. *Journal of Herpetology* 31:60–65.
- Qualls, C. P., and R. M. Andrews. 1999. Cold climates and the evolution of viviparity in reptiles: cold incubation temperatures produce poor-quality offspring in the lizard, *Sceloporus virgatus*. *Biological Journal of the Linnean Society* 67:353–376.
- Qualls, C. P., and R. Shine. 1996. Reconstructing ancestral reaction norms: an example using the evolution of reptilian viviparity. *Functional Ecology* 10:688–697.
- Qualls, F. J., and R. Shine. 1998. Geographic variation in lizard phenotypes: importance of the incubation environment. *Biological Journal of the Linnean Society* 64: 477–491.
- . 2000. Post-hatching environment contributes greatly to phenotypic variation between two populations of the Australian garden skink, *Lampropholis guichenoti*. *Biological Journal of the Linnean Society* 71:315–341.
- Ricklefs, R. E., M. Konarzewski, and S. Daan. 1996. The relationship between basal metabolic rate and daily energy expenditure in birds and mammals. *American Naturalist* 147:1047–1071.
- Rolfe, D. F. S., and G. C. Brown. 1997. Cellular energy utilization and molecular origin of standard metabolic rate of mammals. *Physiological Reviews* 77:731–758.
- Scholander, P. F., V. Walters, R. Hock, and L. Irving. 1950a. Body insulation of some arctic and tropical mammals and birds. *Biological Bulletin* 99:225–236.
- Scholander, P. F., R. Hock, V. Walters, F. Johnson, and L. Irving. 1950b. Heat regulation in some arctic and tropical mammals and birds. *Biological Bulletin* 99:237–258.
- Sexton, O. J., and K. R. Marion. 1974. Duration of incubation of *Sceloporus undulatus* eggs at constant temperature. *Physiological Zoology* 47:91–98.
- Shine, R. 1999. Egg-laying reptiles in cold climates: determinants and consequences of nest temperatures in montane lizards. *Journal of Evolutionary Biology* 12: 918–926.
- Shine, R., and P. S. Harlow. 1996. Maternal manipulation of offspring phenotypes via nest-site selection in an oviparous lizard. *Ecology* 77:1808–1817.
- Shine, R., M. J. Elphick, and P. S. Harlow. 1997a. The influence of natural incubation environments on the phenotypic traits of hatchling lizards. *Ecology* 78: 2559–2568.
- Shine, R., T. R. L. Madsen, M. J. Elphick, and P. S. Harlow. 1997b. The influence of nest temperatures and maternal brooding on hatchling phenotypes in water pythons. *Ecology* 78:1713–1721.
- Slip, D., and R. Shine. 1988. Reptilian endothermy: a field study of thermoregulation by brooding diamond pythons. *Journal of Zoology* 216:367–378.