

Accepted Manuscript

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PII: S0944-2006(16)30013-7

DOI: <http://dx.doi.org/doi:10.1016/j.zool.2016.03.001>

Reference: ZOOL 25491



To appear in:

Received date: 1-3-2016

Accepted date: 3-3-2016

Please cite this article as: Tattersall, Glenn J., Reptile thermogenesis and the origins of endothermy. *Zoology* <http://dx.doi.org/10.1016/j.zool.2016.03.001>

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Invited Perspectives

Reptile thermogenesis and the origins of endothermy

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Highlights

- Proposed proximate and ultimate origins of endothermy in vertebrates are numerous.
- In this context, all possible heat generation and heat conservation capacities need to be considered.
- The reproductive capacity/parent care model for endothermy has received recent support from tegu lizards.

Abstract

Extant endotherms have high rates of metabolism, elevated body temperatures, usually tight control over body temperature, and a reasonable scope for further increases in metabolism through locomotor activity. Vertebrate ectotherms, on the other hand, rely on behavioural thermoregulation and cardiovascular adjustments to facilitate warming, and generally lack specific biochemical and cellular mechanisms for sustained, elevated metabolism. Nevertheless, the ancestral condition to endothermy is thought to resemble that of many extant reptiles, which raises the question of the origins and selection pressures relevant to the transitional state. Numerous hypotheses have emerged to explain the multiple origins of endothermy in vertebrates, including thermoregulatory, locomotory, and reproductive activity as possible drivers for these sustained and elevated metabolic rates. In this article, I discuss recent evidence for facultative endothermy in an extant lepidosaur, the tegu lizard. Since lepidosaurs are a sister group to the archosaurs, understanding how a novel form of endothermy evolved will open up opportunities to test the compatibility or incompatibility of the various endothermy hypotheses, with potential to elucidate and resolve long contentious ideas in evolutionary physiology.

Keywords: Evolution of endothermy; Body temperature; Parental care; Activity capacity; Assimilation capacity

The evolution of endothermy has long interested zoologists, driven in part by an interest in the reconstruction of dinosaur physiology, but also perhaps because being warm is so strongly ingrained in the human condition. Two major groups within the vertebrates, birds and mammals, exhibit elevated rates of basal metabolism that sustain their high body temperatures; however, phylogenetic evidence supports separate origins for their endothermic physiology, in lineages separated by approximately 320 million years (Farmer, 2016) (Fig. 1). The reason why the origin of endothermy is such an interesting evolutionary question is tied up with explaining how an energetically expensive strategy originated and competed alongside less intensive energetic strategies. High rates of metabolism demand high rates of foraging, and in resource-limited environments, these strategies would be expected to have relatively lower fitness unless the benefits outweigh the costs. Investigating the context within which endothermy arose has involved competing and overlapping concepts to construct viable hypotheses to test in extant animals. In short, the arguments can be distilled down to whether a capacity for an enhanced locomotor-based muscle activity evolved prior to an enhanced visceral organ metabolism. Other arguments related to cardiovascular and respiratory capacity driving endothermy focus on the supply side of the oxygen cascade (Hillman and Hedrick, 2015) rather than the demand side; in a proto-endothermic ancestor, it is the latter which is more likely subject to direct selection on behaviours related to survival and reproduction, since the cardio-respiratory system already has inherent scope available. To date, much attention has been paid to the obvious physiological conditions supporting extant endothermy, namely the elevated metabolic, cardiovascular and respiratory capacity of birds and mammals. The challenge to the field, however, is that endothermy in extant birds and mammals is highly derived, and assessing its origins requires hypotheses that incorporate both proximate and ultimate causation. One might argue that we have been too focused on proximate mechanisms, while assuming the ultimate causes are either already known or not germane. Although augmented cardiovascular and respiratory capacities are clearly required for modern mammals and birds, these endotherms are also efficient at retaining body heat through convergently evolved insulation (i.e., fur and feathers).

Thus, making inferences regarding endothermy requires consideration of the capacity to produce, as well as the capacity to conserve, body heat (McNab, 1978). For example, rattlesnakes fed meals up to 50% of their body mass raised their metabolism enormously ($\sim 10x$) for days at a time, yet achieved only a modest amount ($\Delta T \sim < 2 \text{ }^\circ\text{C}$) of warming (Tattersall et al., 2004). Similarly, varanid lizards, renowned for their elevated aerobic capacities, were exercised and fed large meals, in order to augment metabolic rate significantly, but without substantial change ($\Delta T \sim 1 \text{ }^\circ\text{C}$) in T_b , which led to the conclusion that thermal conductance can be high and thermoregulation per se is not a sufficient driver for the evolution of endothermy (Bennett et al., 2000).

Apart from activity or thermoregulation, an alternative hypothesis involves reproductive capacity, with extension to parental care, as a driver for endothermy. Farmer (1998) posited that the initial selective advantage of endothermy in both the avian and mammalian lineages was its usefulness as an adaptation for improving parental care (warming embryos and hatchlings), and that the initial mechanism for thermogenesis would have been the increased biosynthesis that accompanies reproduction. Body heat, or endothermy, would thus be a by-product of a reproductive trait. Farmer (2001) also predicted that burrowing animals could quite effectively conserve any metabolic heat production, even if they lack their own insulation. Recently we demonstrated that tegu lizards exhibit an elevated body temperature during the reproductive season (Tattersall et al., 2016) (Fig. 1), consistent with the reproductive capacity/parental care model for endothermy. Their rise in body temperature could not be explained by heat retention from basking nor from digestion-related thermogenesis, since the endothermy occurs toward the end of the hibernation fast while within an underground burrow, and accompanies the surge in reproductive and thyroid hormones that precede the reproductive season. Interestingly, thermogenesis associated with reproduction also occurs in the echidna, a mammalian protoendotherm (Grigg et al., 2004) which allows for stable body temperatures (Nicol and Andersen, 2006). In reptiles, only pythons are known to exhibit thermogenesis associated with reproduction, which

appears restricted to female egg incubation (Harlow and Grigg, 1984). On the other hand, in tegu lizards, both sexes exhibit facultative endothermy; males establish and defend territories and show large changes in secondary sexual characteristics, whereas females appear to remain with their eggs for a period of time following laying, possibly enhancing embryo development. Significantly, this discovery is inconsistent with the assimilation capacity model for endothermy (Koteja, 2000), which places emphasis on selection for higher metabolism to aid foraging and parental feeding (i.e., post-reproductive events), and also not directly supportive of the activity capacity model for endothermy origins (Bennett and Ruben, 1979), in the sense that the elevated metabolism is not associated with movement, activity, or foraging.

Nevertheless, much remains to be investigated to fully resolve these questions. Do tegus sustain this endothermy throughout the incubation period? Does nest guarding provide thermal benefits to the developing embryos? Discovering the tissue localisation for the facultative thermogenesis, its hormonal control, and, most importantly, the fitness consequences of endothermy in a normally ectothermic lizard would bring clarity to the reproductive capacity/parental care model for endothermy. Tegus also are an interesting model in other regards. Since both sexes adopt endothermy, this extends the reproductive hypothesis to traits related to mate competition well known for its potential to drive positive selection on traits that enhance reproductive fitness.

Acknowledgements

I would like to thank Cleo Leite, William Milsom, Denis Andrade, Colin Sanders, and Augusto Abe for their assistance over the years of data collection and discovery with this research, and Thomas Bosch for inviting me to write this perspective article. The research discussed here has been supported by the Natural Sciences and Engineering Research Council of Canada (NSERC) and by the Brazilian funding agencies UNESP, CNPq, and FAPESP.

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Figure Captions

Fig. 1. (A) Phylogenetic relationship of the amniotes showing the lepidosaurs (includes Sphenodontia and Squamata) as sister group to the archosaurs (dashed line); extant endotherms are shown in red, ectotherms in blue, and turtle placement is currently contentious depending on whether morphological or molecular data are used (Hedges, 2012). (B) Thermal conductance of vertebrates decreases with body size due to thermal inertia (McNab, 1978), and differs between reptiles (blue area) and mammals (red area) due to differences in insulation and greater vascular control; however, the tegu lizard (*Salvatore*) thermal conductance is more similar to that of mammals than that of other reptiles. (C) Tegu lizards are normally ectothermic, with heart rates (data obtained from a year-long study of tegus in their burrows at the coldest time of the day) following a typical biochemical sensitivity where $Q_{10} = 1.7$. This heart rate/temperature relationship (if holding temperature constant; dotted lines in C) shifts when tegus enter the reproductive period, with heart rates (proxy for metabolic rate) rising $\sim 2x$ during arousal from hibernation and $3-5x$ during the reproductive period. (D) Elevated body temperatures ($T_{\text{body}} - T_{\text{burrow}}$) result from the seasonal shift to higher rates of metabolism in the breeding season, but are driven by metabolism, not basking or heat storage. (E-F) Tegu lizards are typically ectothermic ($T_{\text{b}} - T_{\text{ambient}} \sim 0-2 \text{ }^{\circ}\text{C}$) outside of the breeding season or if unable to enter the burrow at night (E; thermal image taken at 6 am prior to sunrise), whereas inside their burrows, they can sustain body temperatures up to $10 \text{ }^{\circ}\text{C}$ higher than the burrow (F; thermal image of two co-habiting tegu lizards of slightly different body temperatures), resulting in a facultative endothermy derived from a combination of enhanced metabolism and control over thermal conductance. All data from tegu lizards in (C-F) derived from Sanders et al. (2015), Piercy et al. (2015), and Tattersall et al. (2016).

