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RESEARCH ARTICLE

Increased homeothermy during reproduction in a basal placental mammal

Danielle L. Levesque* and Barry G. Lovegrove

ABSTRACT

Homeothermic endothermy, the maintenance of a high and stable body temperature (T_b) using heat produced by elevated metabolism, is energetically expensive. There is increasing evidence that the earliest endotherms were heterotherms that, rather than maintaining strict homeothermy, allowed T_b to fluctuate with large variations between active and rest-phase T_b. The high level of homeothermy observed in modern mammals is therefore likely to have evolved from an ancestral heterothermic state. One of the hypotheses for the evolution of endothermy is that homeothermy allows for greater energetic output during reproduction (parental care model). We tested this hypothesis by measuring metabolic rates over a range of ambient temperatures in both reproductive and non-reproductive greater hedgehog tenrecs (*Setifer setosus*), a physiologically primitive mammal from Madagascar. Tenrecs have some of the lowest metabolic rates and highest levels of T_b variability of any mammal and are therefore good models of the ancestral eutherian state. During pregnancy and lactation, there was an increase in metabolism and T_b below the thermoneutral zone, accompanied by a decrease in T_b variability. The lower critical limit of the thermoneutral zone was estimated at ~25°C. However, whereas increases in resting metabolism were substantial below 20°C (up to 150% higher during reproduction), daytime rest-phase ambient temperatures at the study site rarely reached equivalent low levels. Thus, *S. setosus* provide an example for how relatively low-cost increases in homeothermy could have led to substantial increases in fitness by allowing for the faster production of young. The mechanisms necessary for increases in thermogenesis during reproduction would have further benefited the development of homeothermy in mammals.

KEY WORDS: Evolution of endothermy, Parental care hypothesis, Thermoregulation, Reproduction, Torpor, Madagascar, *Setifer setosus*, Tenrecinae

INTRODUCTION

All extant mammals are endotherms, capable of maintaining core body temperature (T_b) above ambient temperatures (T_a) through the production of heat from metabolism (Bartholomew, 1972; Schmidt-Nielsen, 1997). The precision of T_b regulation varies considerably among modern mammals (Clarke and Pörtner, 2010; Lovegrove, 2012a), ranging from species that maintain a high degree of homeothermy (small circadian variations in T_b), to those that have highly labile T_b (Angilletta et al., 2010; Boyles et al., 2013; Clarke and Pörtner, 2010; Lovegrove, 2012a; Refinetti and Menaker, 1992). In addition to circadian rhythms, in which T_b typically decreases during the rest phase (but see Lovegrove et al., 2014), many mammals also lower T_b and metabolic rate (MR) for extended periods of time during daily torpor and hibernation (Geiser and Ruf, 1995; Lyman et al., 1982).

Strict homeothermy could have evolved as early as 200 million years ago (mya), coincident with increased encephalization and a shift to a nocturnal lifestyle, or as late as 66 mya before the crown placental groups diversified following the mass extinctions at the Cretaceous–Paleogene (K–Pg) boundary (Crompton et al., 1978; Grigg et al., 2004; Lovegrove, 2012b; O'Leary et al., 2013; Rowe et al., 2011). Moreover, there is increasing evidence that endothermy evolved in a tropical environment from an ancestral state in which T_b was highly labile and T_a-dependent (Crompton et al., 1978; Grigg et al., 2004; Lovegrove, 2012a; Lovegrove, 2012b). Under this hypothesis, the ancestral eutherian mammal was small, nocturnal, insectivorous, and likely to have expressed either short- or long-term periods of torpor (Lovegrove, 2012a; Luo, 2007; O'Leary et al., 2013). It is this plesiomorphic heterothermic capacity that is thought to have been the most likely means by which the ancestral eutherian was able to have survived the short- and long-term devastation of the K–Pg boundary asteroid impact (Lovegrove, 2012b).

A number of hypotheses have been proposed in an attempt to explain how and why endothermy, a costly method of thermoregulation and existence in general, evolved in mammals (Bennett and Ruben, 1979; Crompton et al., 1978; Farmer, 2000; Koteja, 2000). In this study, we argue that the study of modern mammals that putatively retained plesiomorphic heterothermic characteristics, that is, physiological characteristics that are thought to have prevailed in Cretaceous eutherian ancestors, should shed light on the transition from ectothermic-like heterothermy to homeothermy (Crompton et al., 1978; Eisentraut, 1960; Grigg et al., 2004; Lovegrove, 2012a). Termed 'protoendotherms' by Grigg, Beard and Augee (Grigg et al., 2004), and 'basoendotherms' by Lovegrove (Lovegrove, 2012a), extant basal eutherians, often found on low-latitude islands with little paleoclimatic history of Cenozoic cooling, are highly heterothermic, with variable T_b and frequent use of torpor. The large amplitudes in the circadian rhythm of T_b in these animals can lead to difficulties in differentiating between torpor and normothermy using T_b alone (Brice et al., 2002; Canale et al., 2012; Kuchel, 2003; Lovegrove and Génin, 2008; Poppitt et al., 1994). Also, the determination of a distinct thermoneutral zone (TNZ), a range of T_a over which MR remains minimal and constant, is highly problematic if T_b is not maintained at a constant level (Brice, 2008; Scholander et al., 1950). The high thermolability of basoendotherms generates a relatively linear relationship between T_b and T_a, with no clear inflection points in MR at the lower and upper critical limits of thermoneutrality that typically define the TNZ in classic homeothermic endotherms (Brice, 2008; Stephenson and Racey, 1993b; Nicoll, personal communication in Stephenson and Racey, 1994).

School of Life Sciences, University of KwaZulu-Natal, P/Bag X01, Scottsville 3209, South Africa.

*Author for correspondence at present address: Institute of Biodiversity and Conservation, Univeristi Malaysia Sarawak, 94300 Kota Samarahan, Sarawak, Malaysia (lldanielle@ibec.unimas.my)

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