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AN EXPERIMENTAL TEST OF THE THERMOREGULATORY HYPOTHESIS FOR THE EVOLUTION OF ENDOTHERMY

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Abstract.—The thermoregulatory hypothesis proposes that endothermy in mammals and birds evolved as a thermoregulatory mechanism per se and that natural selection operated directly to increase body temperature and thermal stability through increments in resting metabolic rate. We experimentally tested this hypothesis by measuring the thermoregulatory consequences of increased metabolic rate in resting lizards (*Varanus exanthematicus*). A large metabolic increment was induced by feeding the animals and consequent changes in metabolic rate and body temperature were monitored. Although metabolic rate tripled at 32°C and quadrupled at 35°C, body temperature rose only about 0.5°C. The rate of decline of body temperature in a colder environment did not decrease as metabolic rate increased. Thus, increasing the visceral metabolic rate of this ectothermic lizard established neither consequential endothermy nor homeothermy. These results are inconsistent with a thermoregulatory explanation for the evolution of endothermy.

Key words.—Endothermy, homeothermy, reptile, thermoregulation, *Varanus.*

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Endothermy is the establishment of elevated body temperature by production of large quantities of metabolic heat, whereas homeothermy is the maintenance of a constant body temperature in different thermal environments. Both are familiar and important features of the biology of mammals and birds and are regarded as key innovations or adaptations independently evolved in these lineages. However, understanding the evolution of these thermoregulatory adaptations from their primitive ectothermic condition, that is, the selective factors and mechanistic pathways involved, has proved both elusive and controversial (Hayes and Garland 1995; Ruben 1995). Trying to elucidate macroevolutionary events that occurred millions of years in the past is always difficult, and it is particularly so when these concern physiological or behavioral processes. Only rarely can fossil material inform us about the evolution of metabolic or thermoregulatory characters (e.g., the presence of respiratory turbinates, Hillenius 1992, 1994). Rather, analysis and speculation on the evolution of endothermy have relied on observations on extant animals and the application of the principle of uniformitarianism (Simpson 1963; Beerbower 1968), which assumes that life processes were the same in the past as they are at present.

Endothermy in mammals and birds is fundamentally different from that in other animal groups, such as fishes (Carey et al. 1971; Block and Finnerty 1994), insects (Heinrich 1993), and reptiles (Hutchison et al. 1966). In these latter groups, skeletal muscle is the major source of metabolic heat, and endothermy depends on active contraction of these muscles. Mammals and birds do not depend on myogenic thermogenesis to establish their high resting metabolic rates. Instead, metabolism of the visceral organs, such as the liver, heart, and kidneys, provides the major source of heat (Aschoff et al. 1971), and skeletal muscle serves a thermogenic function only during shivering in the cold or during activity. Hypotheses related to the evolution of mammalian and avian thermoregulatory patterns must therefore assume that the source of the metabolic increment was visceral, as it is in resting mammals and birds, and not myogenically derived.

Several hypotheses have been advanced concerning the selective and mechanistic factors involved in the evolution of endothermy in mammals and birds (Ruben 1995). These include thermoregulation per se (Bartholomew and Tucker 1963; Stevens 1973; Crompton et al. 1978; Taylor 1980; Block 1991), alteration of limb support and locomotor pattern (Heath 1968; Bakker 1971), decreased body size (McNab 1978), and increased aerobic capacity during activity (Bennett and Ruben 1979). The first of these, the thermoregulatory hypothesis, postulates that increments in metabolic rate of ancestral ectotherms elevated body temperature and helped to retard change in body temperature in different thermal environments. This is one of the most widely discussed and accepted ideas in this regard (Ruben 1995) because of its presumptively direct link between metabolism and thermoregulation. Unlike the others, this argument asserts that these thermoregulatory patterns evolved for thermoregulation per se. The others assert that thermoregulation was a secondary adaptation and not the initial selective factor responsible for increased metabolism. The thermoregulatory hypothesis assumes that there must have been immediate thermoregulatory benefits to increments in metabolic rate that outweighed the increased energetic cost. These benefits presumably involved the catalytic effects of high body temperature, optimization of enzyme function at a single temperature, and/or thermal niche expansion (Heinrich 1977; Hochachka and Somero 1984). The costs associated with endothermy, however, are substantial: Average basal metabolic rates of mammals and birds exceed standard rates of reptiles of equal size and body temperature by six- to 10-fold (Bennett and Dawson 1976; Peters 1983), and mammalian and avian field metabolic rates exceed those of equal-sized reptiles by 20- to 30-fold (Nagy et al. 1999). A difficulty with the thermoregulatory model has always been balancing its rather elusive benefits with the very real costs occasioned by the metabolic increments.

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In principle, an experimental test of the thermoregulatory hypothesis is not difficult. What is required is the experimental elevation of metabolic rate in an ectothermic reptile and an evaluation of its thermoregulatory consequences. However, until recently it was thought that major metabolic elevations could be induced in reptiles only during intense physical activity. Using active animals to test the hypothesis was undesirable from several points of view, primarily because thermogenesis would be myogenic and because patterns of convective heat exchange would be grossly disrupted by the animal's movements. It is now apparent from the research of Secor and Diamond (1995, 1997) that a substantial increase in metabolic rate can be induced in resting reptiles during digestion. These increments are due to tissue growth in the viscera and the energy requirements of metabolite uptake. These can reach levels that approach aerobic metabolic rates during intense activity, and they can be sustained for days. We therefore took advantage of this postprandial metabolic increment to devise an experimental test of the thermoregulatory hypothesis. We induced an elevated metabolic rate in a reptilian ectotherm, the lizard *Varanus exanthematicus,* by feeding it a large meal and measured the thermoregulatory consequences of the increased visceral metabolic rate in these resting lizards.

Modern reptiles have often been similarly used as experimental models to formulate and test hypotheses concerning the evolution of endothermy or the mammalian or avian condition (e.g., Bartholomew and Tucker 1963; Bakker 1971; Regal 1978; Bennett and Ruben 1979; Carrier 1987; Randolph 1994). For example, experimental manipulation of the insulation of a living lizard (Cowles 1958) demonstrated convincingly that evolution of a permanent insulatory coat would have impeded behavioral thermoregulation in ancestral ectotherms. Biophysical studies on heat exchange in modern reptiles (Paladino 1990; Spotila et al. 1991) have altered and framed the debate on endothermy in dinosaurs by indicating the importance of body size to thermal stability. Data from living reptiles are used even in the analysis and interpretation of fossil material (Bennett and Ruben 1986). Although extant reptiles differ in many ways from the ancestral reptilian forms that gave rise to mammals and birds, the underlying assumption is that their patterns of ectothermy and low metabolic rate are so fundamental to their physiology and are so widely shared among extant reptilian taxa that they do not differ in these aspects from their ancestors (Bennett 1991).

Materials and Methods

Animals

Eleven *V. exanthematicus* (mean mass = 0.71 kg) were purchased from a commercial animal dealer for use in these experiments. Varanid lizards may be considered appropriate for investigating the thermoregulatory consequences of increased metabolic rate in reptiles: Their resting metabolic rates are typical for all reptiles of their body size (Bennett and Dawson 1976; Andrews and Pough 1985, Thompson and Withers 1997), and some species, including *V. exanthematicus,* possess relatively high aerobic scopes and levels of activity for reptiles (Gleeson 1981; Thompson and Withers 1997).

Animals were housed in communal pens on a 12:12 L:D photoperiod, given access to a photothermal heat gradient, and fed mouse carcasses weekly. Prior to experimentation, food was withheld for two or more weeks to maximize the calorigenic effect of feeding. During experimentation, animals were fed a large meal (mean % fasting body mass = 17.6%, range = 12.0–23.8%) of homogenized canned beef warmed to experimental temperature. The meal was delivered with a feeding syringe via a stomach tube. The animals accepted these meals well and never regurgitated them. All research was carried out under University of California, Irvine animal permit ARC96–1549.

Experiments at 35°C: Endothermy and Homeothermy

These measurements were done to determine the effect of elevated metabolism on thermoregulation at the preferred body temperature of this species, 35°C (Hicks and Wood 1985). A fasted lizard was weighed and implanted with a thermocouple inserted 5 cm into its rectum to measure deep body temperature (T_B). It was placed in a metabolism chamber fashioned from galvanized steel heating duct (50-cm length, 10-cm diameter) with the interior painted flat black. The chamber also contained a thermocouple to monitor ambient air temperature and a 1.4-cm mesh plastic grid on which the lizard stood, thus avoiding contact with the chamber surface. The chamber containing the lizard was placed in a controlled temperature cabinet maintained between 34°C and 36°C. Experimental measurements were made in the morning, during the light phase of the diurnal cycle. Oxygen consumption was measured continuously by drawing dry air through the chamber at a flow of 250–500 ml min^{-1}, which was maintained by a mass flow controller. Excurrent air was dried and metered into an Amatek oxygen analyzer, model S3A. Temperatures and excurrent oxygen concentration were recorded continuously on a personal computer with Acknowledge data acquisition software (Biopac, Inc., Goleta, CA). Thermocouples were calibrated with a standard thermometer; oxygen consumption (STPD) was calculated according to Withers (1977, eq. 3a). Fasting equilibrium body temperature, ambient temperature, and metabolic rate (mean values for 1 h) were measured for an animal after 24 h in the chamber. Cabinet temperature was then decreased rapidly (0.8°C min^{-1}) to 24–26°C, and the rate of decrease in body temperature of the animal (°C min^{-1}) was measured until body temperature reached 27°C. The cabinet was then returned to 34–36°C, and the lizard was permitted to rewarm to this temperature.

The lizard was then removed from the metabolic chamber and fed (see above). It was immediately replaced in the chamber and the temperature cabinet. One hour after feeding, the cabinet temperature was again decreased to 24–26°C and the rate of decrease in body temperature of the animal was measured as before. The cabinet temperature was rewarmed to 34–36°C and the animal was left undisturbed for 24 h after feeding. Postprandial equilibrium body temperature, ambient temperature, and oxygen consumption (mean values for the hour at 23–24 h after feeding) were measured, the cabinet temperature was decreased to 24–26°C, and the rate of de-

TABLE 1. Metabolic rate and thermal increment in fasting and 24-h postprandial animals at 35°C. T_B, body temperature; T_A, air temperature in metabolism chamber; postprandial T_B increment = [(postprandial $T_B - T_A$) − (fasting $T_B - T_A$)].

Animal no.	Fasting mass (kg)	Fasting V_{O2} (ml kg^{-1} min^{-1})	Postprandial V_{O2} (ml kg^{-1} min^{-1})	Factorial V_{O2} increment	Fasting $T_B - T_A$ (°C)	Postprandial $T_B - T_A$ (°C)	Postprandial T_B increment (°C)
1	0.46	1.04	3.25	3.1	0.4	1.1	0.7
2	0.59	0.74	1.94	2.6	0.9	1.1	0.2
3	0.63	1.03	4.05	3.9	0.8	1.3	0.5
4	0.80	0.83	3.79	4.6	0.8	1.1	0.3
5	0.85	0.65	3.35	5.2	0.8	1.2	0.4
Mean	0.67	0.86	3.28	3.9	0.74	1.16	0.42
SE	0.071	0.079	0.365	0.46	0.087	0.040	0.086
±95% CL	0.197	0.219	1.013	1.29	0.242	0.111	0.239

crease in body temperature was measured for a third and final time.

Endothermy, that is increments in body temperature associated with increased metabolism, was measured by comparing the difference between body and ambient temperatures in the fasting and postprandial states. Homeothermy, that is resistance to change in body temperature, was measured by comparing the rate of cooling in the fasting and postprandial states. Because the mass of the animal was augmented considerably by feeding and a larger mass has more thermal inertia and should therefore cool more slowly on this basis alone, two comparisons were made. The first was between the fasted and the 24-h postprandial animal and the second between the postprandial animal at 1 h and 24 h after feeding. In the latter comparison, mass is increased but metabolic rate has not yet begun to increase above fasting levels (Hicks et al. 2000). Decline in body temperature over the range of 34–30°C was highly linear in all cases and was used to estimate rates of cooling (°C min^{-1}).

Experiments at 32°C: Endothermy

This series of measurements was made to determine the thermoregulatory consequences of elevated metabolism at a temperature below behaviorally preferred levels. Fasting animals were measured as before, except that the temperature cabinet was regulated at 31–33°C, approximately 3°C below normally regulated levels. Fasting equilibrium and ambient temperatures and metabolic rate (mean values for 1 h) were measured in an animal after it had been in the chamber for 24 h. Animals were removed and fed as before and replaced in the metabolic chamber. They were left undisturbed for 24 h, and equilibrium and ambient temperatures and metabolic rate were measured again. Endothermy was measured by comparing the difference between body and ambient temperatures in the fasting and postprandial states. No measurements of cooling rates were performed in this series of experiments.

RESULTS

Endothermy

Metabolic rates and associated thermal increments are reported in Tables 1 and 2 for lizards at 35°C and 32°C, respectively. At 35°C, metabolic rate nearly quadrupled as a result of digestion, but body temperature increased only 0.4°C. At 32°C, metabolic rate nearly tripled, but body temperature increased only 0.65°C. Although both of these increments are statistically significant ($P = 0.008$ at 35°C and 0.003 at 32°C, paired *t*-test), their absolute size is very small and would have almost no impact on increasing the rate of other physiological processes. Additionally, there is no difference ($P = 0.18$, *t*-test) between the magnitude of these increments at 32°C and 35°C, thus indicating that no more heat is being conserved at the lower, and presumably suboptimal, body temperature. Elevated metabolic rates, in spite of their substantial magnitude and energetic cost, had little impact on body temperature and consequently resulted in minimal endothermy in either experiment.

Homeothermy

Rates of cooling are reported in Table 3. If metabolically produced heat were being retained and used to stabilize body temperature or retard its change, rates of cooling in 24-h postprandial animals would be lower (i.e., change in body

TABLE 2. Metabolic rate and thermal increment in fasting and 24-h postprandial animals at 32°C. T_B, body temperature; T_A, air temperature in metabolism chamber; postprandial T_B increment = [(Postprandial $T_B - T_A$) − (Fasting $T_B - T_A$)].

Animal no.	Fasting mass (kg)	Fasting V_{O2} (ml kg^{-1} min^{-1})	Postprandial V_{O2} (ml kg^{-1} min^{-1})	Factorial V_{O2} increment	Fasting $T_B - T_A$ (°C)	Postprandial $T_B - T_A$ (°C)	Postprandial T_B increment (°C)
6	0.55	0.77	1.55	2.0	0.5	0.7	0.2
7	0.58	1.07	1.96	1.8	0.6	1.2	0.6
8	0.62	0.49	1.32	2.7	1.4	1.8	0.4
9	0.80	0.25	1.02	4.1	0.3	1.3	0.9
10	0.94	0.32	0.53	1.7	0.6	1.5	0.9
11	1.03	0.27	1.22	4.5	0.3	1.3	0.9
Mean	0.75	0.53	1.27	2.8	0.62	1.30	0.65
SE	0.082	0.134	0.197	0.50	0.166	0.148	0.123
±95% CL	0.211	0.345	0.507	1.28	0.427	0.381	0.317

TABLE 3. Cooling rates (°C T_B min^{-1}) to 30°C T_B in a 24–26°C environment for fasting, 1-h postprandial, and 24-h postprandial animals. More negative values indicate more rapid cooling.

Animal no.	Fasting	1-h postprandial	24-h postprandial
1	−0.134	−0.103	−0.206
2	−0.128	−0.105	−0.133
3	−0.117	−0.109	−0.187
4	−0.143	−0.091	−0.086
5	−0.138	−0.069	−0.114
Mean	−0.132	−0.095	−0.145
SE	0.0045	0.0073	0.0224
±95% CL	0.0120	0.0201	0.0625

temperature min^{-1} would be less negative) than in fasting animals or in 1-h postprandial animals. As anticipated, the added mass of the meal significantly retarded heat loss ($P = 0.03$, paired *t*-test) in 1-h postprandial animals in comparison to fasting animals. One-hour postprandial animals have increased mass, but have not yet developed a metabolic increment. However, cooling rates in 24-h postprandial animals were not significantly different from fasting animals ($P = 0.63$, paired *t*-test), which have 15–20% less mass. Rather, they were even marginally significantly *higher* than 1-h postprandial ones ($P = 0.058$, paired *t*-test), which have the same mass. These animals did not become more homeothermic as their metabolic rate increased. There is no indication that the increased heat production was used to stabilize body temperature.

DISCUSSION

The energy expenditure during digestion was very high in our experimental animals. The metabolic rate of the 24-h postprandial animals at 35°C was indistinguishable ($P = 0.17$, *t*-test) from the basal metabolic rate of a hedgehog, *Paraechinus aethiopicus*, a perfectly competent mammalian endotherm and homeotherm of equal size and body temperature (34.2°C; Shkolnik and Schmidt-Nielsen 1976). In spite of this sizable metabolic increment, there was negligible thermoregulatory impact. Body temperature increased less than 0.5°C. This increment, although statistically significant, has little biological impact: Assuming a temperature coefficient (Q_{10}) of 2.0, a body temperature increment of 0.5°C would increase rate processes by only 4%. Although it might be argued that a 4% increment in such a factor as running speed could be selectively beneficial, we point out that this value is well within interindividual variability of most physiological variables, including running speed (e.g., Garland 1984, table 1). Given this high level of interindividual variablility, there appears to be many other ways to increase such factors as speed, without spending the prodigious amounts of energy associated with these minor thermal increments.

Because 35°C is the preferred body temperature of this species, perhaps animals already at this temperature had no incentive to retain excess heat and, in fact, were thermoregulating to release it. However, when the animals were maintained at 32°C, a temperature below preferred thermal levels, they likewise did not conserve body heat and incremented temperature again by only 0.65°C and remained below preferred thermal levels. If they had they access to an environmental thermal gradient, they would likely have raised their body temperature above 32°C by behavioral thermoregulation. Thus, we find no evidence that increased visceral metabolic rate in this reptile results in substantial endothermy.

In regard to homeothermy, animals did not have lower cooling rates 24 h after feeding, when metabolic rates were high, than they did 1 h after feeding, when metabolism was not yet elevated. These cooling rates were no different than those of fasting animals, even though fasting animals had 15–20% less mass and less thermal inertia and should consequently have cooled more quickly. Therefore, the increased visceral heat production was not used to retard the rate of change of body temperature. These results provide no support for the view that increased visceral metabolic rate enhances homeothermy in this reptile.

What happened to the increased heat production associated with digestion? At 35°C, if total thermal conductance had remained constant, the metabolic increment would have been sufficient to increase body temperature by about 1°C h^{-1} (assuming an incremental heat production of 0.47 kcal h^{-1} determined from oxygen consumption and a specific heat of 0.82 cal g^{-1} $°C^{-1}$). But the increased heat production was not retained, but was lost nearly as fast as it was produced. Obviously, thermal conductance increased and most of it was lost to the environment. We do not know how much of this heat production was lost through the integument and how much was due to increased respiratory heat loss. We have previously determined (Hicks et al. 1996, 1999, 2000) that ventilation increases substantially during digestion in these animals. Perhaps the increased heat production is lost as a consequence of the increased ventilation needed to supply oxygen to support the metabolic increment itself.

Would a larger thermal increment be expected in larger animals? Endothermy is thought to have first appeared in the mammalian lineage in lion- to bear-sized therapsids (Hillenius 1994; see below). Could substantial endothermy have been achieved through visceral metabolic increments in ectothermic animals as large as this? An allometric analysis suggests that the anticipated thermal increment remains small even in very large animals. Conductance may be expected to scale as surface area to mass ($mass^{0.67}$) and metabolic rate scales as $mass^{0.75}$. Therefore, the thermal increment may be expected to scale as conductance to metabolic rate, or $mass^{0.08}$. Assuming an average body temperature increment of 0.5°C for our experimental animals of 0.7 kg and an allometric scaling factor of $mass^{0.08}$, we can calculate an allometric constant (a in $y = aM^b$) of 0.51 for the thermal increment. Anticipated thermal increments ($y = 0.51$ $[mass]^{0.08}$) for 100-kg and 1000-kg animals are, respectively, 0.7°C and 0.9°C. Therefore, tripling or even quadrupling metabolic rate can be anticipated to raise body temperature less than 1°C, even in very large ectothermic reptiles.

These experimental observations contradict fundamental predictions of the thermoregulatory hypothesis for the evolution of endothermy. According to the latter, graded increments in visceral metabolic rate should be matched with concomitant increments in endothermy and homeothermy. In our experimental animals, increased energetic metabolism equivalent to a several-fold increment in metabolic rate had almost no impact on increasing or stabilizing body temperature.

From a thermoregulatory viewpoint, this is cost without benefit. In light of these results, it is difficult to see how natural selection would continue to increase metabolic rate if the only goal were a thermoregulatory condition that was not being established. We therefore conclude: (1) that the elevated metabolic rates associated with endothermy in mammals and birds probably evolved initially for other selective reasons; and (2) that endothermy and homeothermy may be adaptations that developed later than the evolution of increased metabolic rate. From this viewpoint, the thermoregulatory condition of mammals and birds would be a secondary refinement of an elevated metabolic condition developed by other selective factors.

These conclusions are in accord with paleobiological observations (Hillenius 1992, 1994; Ruben 1995, 1996) that the first mammalian endotherms were unlikely candidates for selection on enhanced metabolic thermogenesis. Nasal turbinates are used as morphological indicators of endothermy in the mammalian lineage. Turbinates are interpreted principally as water reclamation organs, necessitated by high metabolic rates and consequent high ventilation rates associated with endothermy. In the mammalian lineage, these structures first appear in late Permian glanosuchid therapsids. These were lion- to bear-sized carnivores living in subtropical or tropical climates. Animals of this size were most likely inertial homeotherms (Paladino 1990; Spotila et al. 1991), with stable body temperatures resulting from their bulk alone. Given the equable thermal environments in which they lived, it seems unlikely that high metabolic rates in these animals evolved principally for thermoregulatory purposes. Our results also suggest a possible additional thermoregulatory benefit of nasal turbinates. Although originally interpreted principally as a water conservation devices (Hillenius 1992, 1994), they may additionally serve to conserve body heat. If significant amounts of heat are lost through ventilation, by restricting evaporation and consequent respiratory heat loss, nasal turbinates may also act to minimize rates of heat loss in cooler thermal environments and promote homeothermy.

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