GENERAL SCIENCE NOTES

TEMPERATURE REGULATION IN TETRAPOD VERTEBRATES: ECTOTHERMS VS. ENDOTHERMS

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Amphibians and reptiles have often been considered to be primitive, and to illustrate steps in an evolutionary pathway to higher vertebrates, the birds and mammals. However, in a notable recent review Pough (1980) points out that the anatomy and physiology of amphibians and reptiles are as complex as in birds and mammals, but fit a different mode of life. They have a system based on low energy flow rather than the high energy flow of birds and mammals.

Birds and mammals maintain a constant high temperature by a high metabolic rate; they are called "endotherms" to specify that the source of heat is internal. On the other hand, amphibians and reptiles (and many other animals), choose a warm environment at the time of activity, and this supplies the necessary heat; they are called "ectotherms,'' indicating that the heat source is external to the animal. One consequence is that an active amphibian or reptile may use less than a tenth as much metabolic energy as an endotherm! Even when at rest the metabolic rate is only 10-20% of that of birds and mammals of similar size. Further, in nonactive periods of the day (or year), the body temperature can also drop, further reducing overall metabolic energy usage.

Part of what makes this low energy flow system possible is that most of the energy used for muscular activity is limited to anaerobic metabolism, rather than aerobic as in endotherms. Anaerobic energy stores (glycogen) are immediately available within the muscles and hence facilitate bursts of activity. But in many cases the animals would be completely exhausted by 3 to 5 minutes of maximum activity and could require several hours to completely regenerate their energy stores. At this point one might ask, "How then do they manage?" The answer is that bouts of activity are brief, interspersed with "sitting and waiting" (follow the next frog or lizard you see). In this way these animals may normally avoid the oxygen debt ensuing from continuous activity.

This might seem a high price to pay. On the other hand, consider the benefits of low energy flow (see Table 1). Small endotherms, with their large surface/mass ratio, lose heat so rapidly that they require more food per unit weight. This explains the incessant food gathering required by

TABLE 1

Costs and benefits of ectothermy and endothermy. The items listed are not mutually exclusive: some follow from others in the list. Based on Bennett & Ruben 1979 and Pough 1980.

	Ectothermy	Endothermy
Disadvantages	Rapid exhaustion	Require *much* food
	Activity restricted to brief bouts	Require *continuous* supply of food, water, and O_2
	Activity restricted to certain hours or habitats	
Advantages	Avoids cost of high basal metabolic rate	Work capacity many times that of ectotherms
	Endure shortages of food, water, or O_2	Capable of sustained high activity
	Can be elongate in shape or tiny in size	Can be active at a variety of times of day and in a wide range of habitats
	Can live in very sandy desert	

small animals such as shrews. In fact, the metabolic rate rises so fast with decreasing body size that an endotherm smaller than 5 grams would have an energy demand impossible to meet. But amphibians and reptiles, with a weight-specific daily energy requirement of less than a tenth that of birds and mammals, may have body weights of much less than 5 grams. Over 300 of 5000 species surveyed (Pough 1980) weigh less than 1 gram (!) (calculated from his Table 2). Thus amphibians and reptiles can occupy a whole size range (i.e., <5 grams) unavailable to birds and mammals.

Further, an elongate form is possible (long salamanders, lizards, snakes). To endotherms, this form would result in prohibitive loss of heat across the body surface. Again we see the variety possible in terms of thermal physiology.

Or suppose there is a food shortage. Because of their low energy approach, many ectotherms can go for months without food.

Many species of lizards and snakes can survive the extremes of the desert even in an area of shifting sand, by burrowing under. A mammal could not get enough oxygen at the depth required, and a tunnel system in this instance, which might provide oxygen elsewhere, would collapse.

What benefits do endotherms gain from their costly high energy flow system? The *resting* levels of oxygen consumption for endotherms equal the maximum levels for ectotherms, and the *maximum* levels for endotherms are 5-10 x the resting levels. Hence the capacity of endotherms for supporting work is many times that of ectotherms.

Birds and mammals are capable of much higher sustained speeds than ectotherms and can have a much broader behavioral repertoire than ectotherms because of the greater range of possible speeds and activities. Furthermore, there is greater independence in timing daily activity, because of constant maintenance of the high temperature that provides for maximal oxygen consumption.

In summary, here is yet another example of what has been seen before: when a phenomenon is studied with enough depth and in enough animals, it may show great design or value in its own right, rather than primitiveness or progressive evolution. It also may show more diversity in the underlying design than previously suspected — a little surviving reminder that Eden must have been a more intriguing place, even physiologically, than we had imagined.

LITERATURE CITED

Bennett A, Ruben J. 1979. Endothermy and activity in vertebrates. Science 206:649-654.

Pough F. 1980. The advantages of ectothermy for tetrapods. American Naturalist 115:92-112.

[As specific examples of current research see (a) Hulbert A, Else P. 1981. Comparison of the "mammal machine" and the "reptile machine'': energy use and thyroid-activity. American Journal of Physiology 241:R350-R356; and (b) Schall J, Bennett A, Putnam R. 1982. Lizards infected with malaria: physiological and behavioral consequences. Science 217:1057-1059].