EVOLUTION OF THE CONTROL OF BODY TEMPERATURE: IS WARMER BETTER?

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The evolution of increased locomotor and activity capacities has been linked with the evolution of endothermy. Do relatively high and stable body temperatures improve locomotor performance? Studies on acclimation in salamanders and interspecific adaptation to low temperatures in lizards suggest that relatively little compensation for the depressing effects of low temperature has been developed. In regard to locomotion, warmer appears to be better.

INTRODUCTION

The advantages and costs of endothermy are topics of considerable biological interest. Metabolic regulation of body temperature permits both a high and stable thermal regime for physiological function; however, it does so at considerable energetic cost. The balance of cost and benefit and the presumptive selective agents and pathways during the evolution of endothermy have been the subject of much speculation. Several authors (e.g., Bakker, 1971; Crompton et al., 1978; Bennett and Ruben, 1979) have pointed out the increased locomotor capacity associated with the development of endothermy in several vertebrate lineages and suggested that these constituted a significant factor in its evolution. Other authors (e.g., Heinrich, 1977) have pointed out the greater catalytic capacity of biochemical and physiological systems operating at high temperatures, a capacity which in itself may have been an important factor in setting thermostats in endotherms at relatively high levels. In this paper, I wish to discuss

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briefly the intersection of these hypotheses, specifically, to examine the influence of body temperature on locomotor capacity. Is locomotor performance improved by higher body temperature or can performance be maximized at relatively low body temperatures? Do animals necessarily have increased speed and stamina with increasing body temperatures? In short, in regard to locomotor behavior, is warmer better? If so, then the locomotor advantages and the advantages associated with regulation of high temperature may not be completely separate but may have acted as synergistic selective pressures during the evolution of endothermy. I will examine the general influence of temperature on locomotor performance in ectothermic vertebrates and then examine two specific case studies of adjustment to low body temperatures and its locomotor consequences.

THE EFFECT OF BODY TEMPERATURE ON LOCOMOTOR CAPACITY

Locomotor capacity, as discussed here, refers to the highest performance (e.g., greatest burst or sustained speed) of which an animal is capable at a particular body temperature. Maximal locomotor capacity is the greatest level of performance observed at any body temperature. These locomotor capacities set an envelope of limits within which all behavior must occur and consequently form ultimate constraints on the entire behavioral repertoire of an animal. The question examined in this paper is whether maximal locomotor capacity can be obtained at low body temperatures. Endurance and burst speed capacities are considered separately.

Endurance (stamina), performance that can be sustained for more than a few minutes, is limited by the maximal oxygen consumption of an animal. If the demand for energy exceeds that which can be supplied by maximally mobilized aerobic sources, supplemental anaerobic metabolism is activated and endurance decreases rapidly. Maximal oxygen consumption in ectotherms is highly temperature dependent, with temperature coefficients (Q_{10}) generally between 2 and 3. Consequently, maximal aerobic speed, the greatest speed that can be sustained for more than a few minutes, is likewise temperature sensitive and is greatly restricted at low body temperatures. The lizard Dipsosaurus dorsalis, for example, at normally preferred and field active body temperatures of 40°C, can maintain speeds of over 13 m/min. At body temperatures of 25°C, however, it can sustain only 5 m/min (Q_{10} = 1.9) (John-Alder and Bennett, 1981). A similar thermal dependence of endurance is evident in other reptiles (Bennett, 1982) and fish (Beamish, 1978), although in the latter group, endurance may plateau or decline at the highest temperatures measured. Equivalent locomotor performance at any sustainable speed requires more energy at higher body temperatures, but this increased cost must be weighed against expanded endurance capacities.

Burst speed capacity sets the limits on escape or pursuit behavior. The thermal dependence of burst speed in the lizard Dipsosaurus dorsalis is reported in Fig. 1. At low body temperatures (25°C and below), burst speed is apparently limited by muscle twitch kinetics (Marsh and Bennett, 1985) and has a Q_{10} of >2.0. At higher body temperatures (30 to 40°C), the thermal dependence of burst speed is lower (Q_{10} = 1.3 to 1.4) but is still significant. A similar temperature effect has been found in other lizards (e.g., Bennett, 1980; Hertz et al., 1982). Burst speed in swimming animals, especially fish, may be less thermally dependent (see Beamish, 1978), but it has not been intensively investigated.

Ectotherms active at high body temperatures, such as Dipsosaurus, may thus be able to achieve nearly maximal locomotor performance. At preferred or field active body temperatures, maximal burst and aerobic speeds are attainable. But what about species active at low body temperatures? For instance, the lizard Gerrhonotus multicarinatus is normally active at 20 to 25°C, but maximal running speed and distance running capacity are attained only above 35°C (Bennett, 1980). Can animals active at low

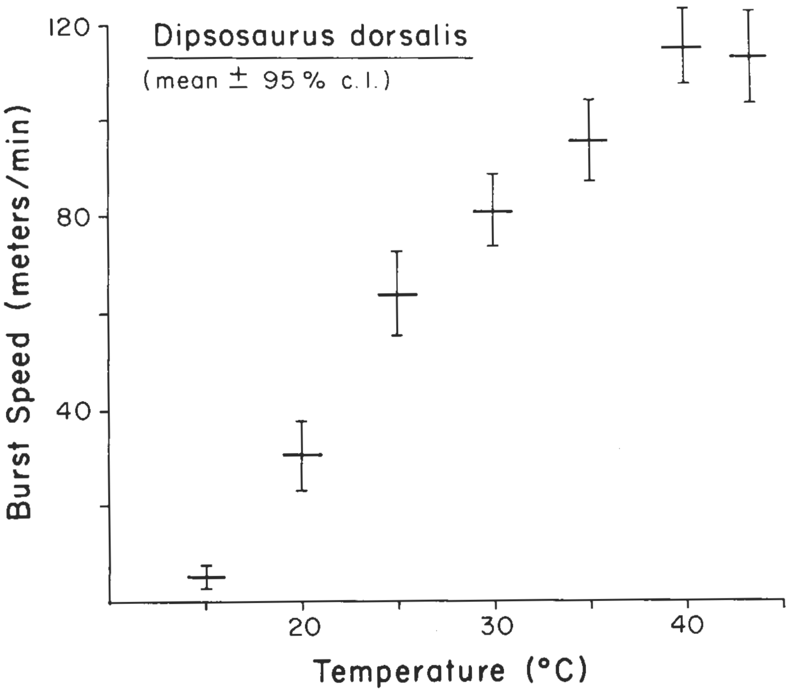

Fig. 1. Burst speed as a function of body temperature in the lizard Dipsosaurus dorsalis (data from Bennett, 1980).

temperatures achieve maximal performance at those temperatures? The following case studies examine this issue in two different taxa of ectotherms naturally active at low temperatures.

ACCLIMATION TO LOW BODY TEMPERATURE BY A SALAMANDER

The salamander *Ambystoma tigrinum* is the most geographically widespread amphibian in North America. Adults overwinter underground and migrate to ponds in the very early spring, sometimes through snow. In these ponds, which still may be ice-covered and have water temperatures of 0 to 10°C, they court, mate, and lay eggs. Courtship behavior involves intense physical activity, with males attempting to displace one another from a female (Arnold, 1976). Thus locomotor performance at low temperatures is crucial to successful reproduction in this species.

Paul Else and I investigated whether these salamanders are able to achieve maximal locomotor capacity at low body temperatures and whether they undergo any behavioral or physiological compensation (acclimation) when maintained at low temperatures. We maintained groups of animals at 10 and 20°C for approximately one month and measured burst speed and endurance capacities on land and in water at 10 and 20°C for each group. Burst speeds were analyzed from

Table 1. Thermal dependence of locomotion in *Ambystoma tigrinum* (unpublished data, Else and Bennett).

Performance	Q_{10} (10 to 20°C)	Probability of Acclimation
Running burst speed	1.35	0.65
Swimming burst speed	1.00	0.96
Running endurance	1.57	0.56
Swimming endurance	1.66	0.59

videotapes. Endurance was measured with a treadmill or water tunnel; speed was increased step-wise until animals became exhausted.

Locomotor performance capacity is generally greater at 20°C than at 10°C (Table 1). Terrestrial burst speed and endurance in water and on land improve significantly with increasing temperature. Only burst swimming speed shows no significant thermal dependence over this temperature range. Further, no significant acclimation effect is apparent for any of the variables examined: animals maintained at cold temperatures do not compensate with altered locomotor abilities (Table 1). In this salamander, there is no maximization of locomotor performance at low temperature: cold exposure results in a significant depression of locomotor capacities that is not compensated by long-term physiological adjustment. These results concur generally with most other studies on fish and amphibians (e.g., Beamish, 1978; Putnam and Bennett, 1981; Renaud and Stevens, 1983).

EVOLUTION OF LOWER THERMAL PREFERENDA BY LIZARDS

Locomotor capacity appears to acclimate poorly if at all in individual animals. Perhaps, however, over substantially longer time periods, it is possible for different species to adapt to low body temperatures and attain maximal performance at those temperatures. In investigating such a possibility, it is important to examine an assemblage of closely related species. Comparative studies have been correctly criticized (e.g., Gould and Lewontin, 1979) when they draw inferences from observations on very distantly related animals, as historical patterns of adaptive or developmental constraints may be significant in influencing the results obtained.

An ideal group in which to examine interspecific thermal adaptation is the scincid lizards of Australia, consisting of over

200 species of skinks all belonging to the same subfamily. Thermal preferenda of these species vary broadly, from 24 to 36°C (Bennett and John-Alder, 1986). Ancestral thermal preference of the group was determined by a minimum-evolution analysis based on parsimony to be approximately 32°C (Huey and Bennett, unpublished data). Consequently, several species of skinks have evolved lower preferenda, and we can ask whether these species have successfully adapted locomotor capacity to attain maximal speeds at these low temperatures.

Ray Huey and I (unpublished data) examined burst speed in 12 species of Australian skinks in 6 different genera with a computer-controlled, photocell-timed raceway. These species had thermal preferenda ranging from 24 to 36°C and were run at body temperatures ranging from 15 to 40°C. Some results of this study are reported in Table 2. The temperature at which maximal burst speed is attained has indeed decreased during the evolution of lower thermal preferenda. However, it has not changed equivalently ($T_{max\ burst\ speed} = 26.4 + 0.25\ T_p$; p slope = 1.0 is <0.001): for every 4°C decrement in preferred temperature, temperature of maximal burst speed declines only 1°C. Consequently, cryophilic species do not attain maximal burst performance at naturally experienced temperatures. Genera with

Table 2. Thermal preference (T_p) and performance in Australian skinks (unpublished data from Huey and Bennett).

Genus	# spp.	T_p (°C)	T of Maximal Burst Speed	% Maximal Speed at T_p
Ctenotus	3	35.4	35.0	94
Egernia	1	33.7	35.3	93
Leiolopisma	2	33.2	34.0	93
Sphenomorphus	3	29.8	32.1	93
Eremiascincus	1	24.4	34.0	50
Hemiergis	2	24.2	31.7	62

preferenda of >29°C attain over 90% of their maximal speeds at their thermal preferenda; genera with preferenda <25°C achieve only 50 to 62% of their capacity at these temperatures. Evolution and adaptation in this group have not resulted in maximizing locomotor performance at low temperatures. Species with low thermal preferenda must pay a behavioral price of low locomotor capacity at normally experienced body temperatures.

SUMMARY: WARMER IS BETTER

Relatively little information on the topic of thermal adaptation of locomotor performance is available and consequently any conclusions must be very tentative. At a minimum, it is safe to conclude that complete compensation of locomotor performance at low body temperature is not universal. It may be very rare or absent. It was not found in individual salamanders acclimated to different temperature. Only partial compensation was found among different lizard genera, resulting in submaximal performance at body temperatures normally chosen by cryophilic animals.

These observations and others in the literature suggest that, in regard to locomotor performance, warmer may indeed be better. In other words, animals generally do not or can not maximize locomotor speeds at low body temperatures, even if exposure to these temperatures is prolonged. Consequently, the evolution of high and stable body temperatures had important consequences for both endurance and burst speed capacities. The high levels of performance that can be attained only at these temperatures may have represented very significant selective advantages during the evolution of endothermy.

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