

Thermal dependence of locomotor capacity

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BENNETT, ALBERT F. *Thermal dependence of locomotor capacity*. Am. J. Physiol. 259 (Regulatory Integrative Comp. Physiol. 28): R253–R258, 1990.—The thermal dependence of locomotor performance capacity, particularly speed and endurance, in vertebrate ectotherms is examined. Most studies have found an optimal speed for performance at relatively high body temperatures, close to upper lethal limits. These performance capacities decrease markedly at low body temperatures and may be compensated by increments in aggressive or evasive behaviors. Relative ranking of performance is maintained among individuals across body temperatures. Acclimation of performance capacities is generally incomplete or entirely absent: most animals compensate locomotor performance rather poorly to cold exposure. Locomotor performance in different groups has been shown to possess the attributes (e.g., variability, repeatability, heritability, and differential survivorship) necessary for evolutionary adaptation, but interpretation of comparative data is complicated by phylogenetic differences among species studied. Controlled studies show partial but incomplete adaptation to environmental temperature.

acclimation; adaptation; amphibian; endurance; evolution; fish; frog; lizard; locomotion; performance; reptile; salamander; speed; temperature

BODY TEMPERATURE exerts a controlling influence on all physiological rate processes (23, 44, 77), retarding in cold and accelerating in heat with temperature coefficients (Q_{10} values) of ~ 1.5 – 3 . Endothermic homeotherms stabilize body temperature at great energetic cost and avoid these perturbations (13, 15), but poikilotherms may be subject to major fluctuations in body temperature daily or seasonally. These fluctuations cause consequent variability not only in physiological processes but also in the behavioral capacities that are directly linked to them. Speed, for example, may be limited by muscle contractile kinetics (9, 58, 68, 69, 70) and endurance by oxygen transport capacities (8, 30), both of which are temperature sensitive.

Performance capacities, that is, the maximum efforts of which an animal is capable, set ultimate limits on behavior (12). If these capacities are temperature sensitive, the potential behavioral repertoire of an animal expands or contracts as body temperature changes. There has been considerable interest in the effects of temperature on locomotor performance capacity as a conse-

quence, asking whether these factors vary with body temperature and, if so, what the consequences are for ectothermic organisms. This paper reviews the effect of temperature on locomotor performance capacities, principally speed and endurance, examines phenotypic plasticity of these traits and their evolutionary lability, and points out areas in which future research is apt to be most productive.

Effect of Acute Temperature Exposure on Locomotor Capacities

Over the past 40 years, a variety of techniques have been developed to quantify locomotor performance capacities under controlled laboratory conditions and to measure the effect of such factors as body temperature on those capacities. Speed is measured as the greatest velocity attained over a short distance (typically <1 m) on electronically timed racetracks (7, 54, 72) or by image analysis. Maximal exertion is measured as the total distance that an animal can move under pursuit before it fatigues or assumes a defensive posture (7). Endurance is measured as the maximum total time (or its distance equivalent) that an animal can maintain position in a water flume or swimming chamber (6) or on a treadmill (74). The effect of body temperature on locomotor performance capacity is measured by acutely exposing an animal to test temperature for only a few hours before assessment.

Most physiological and organismal-level processes (e.g., metabolism, digestion, sensory function, growth) have similar thermal performance curves over a range of acutely experienced body temperatures (46, 55, 86). Above a lower critical temperature, at which function does not occur, rates increase rapidly with increasing temperature, with Q_{10} values of 2–4. At higher temperatures, thermal dependence decreases to Q_{10} of 1–1.5, indicative of a thermally independent plateau of function and an “optimal” temperature (46, 55). Above this range, functional capacities decrease very rapidly over $\sim 5^\circ\text{C}$ with Q_{10} of 0.2–0.8, up to a critical thermal maximum, at which function again ceases. The overall form of the relation is thus strongly skewed toward lower body temperatures, with maximal rates occurring close to upper critical temperatures.

Locomotor performance capacities share this general form of thermal dependence, as illustrated in Fig. 1 for maximal speed in a lizard and exertion in a frog and in Fig. 2 for endurance in a fish. This general pattern of thermal dependence has been observed for speed in lizards (7, 24, 25, 41, 42, 49, 53, 63, 69, 70, 90, 91), snakes

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(36, 86), salamanders (26, 73), and anurans (43, 55, 58, 67, 73, 78, 81, 93); maximal exertion in lizards (7) and anurans (78); and endurance in lizards (14, 59, 61, 74), salamanders (26), and fish (19, 31, 35, 45, 65, 75; note: many fish studies acclimate animals to test temperature rather than measuring acute thermal effects; see next section). Maximal speed, exertion, and endurance occur at relatively high body temperatures. There is often a good match between these optimal temperatures (46, 55) for locomotion and naturally experienced temperatures: most species of lizards, for instance, have field body temperatures that enable them to run at over 90% of maximal speed (40, 53). However, optimal temperatures for locomotion sometimes exceed those naturally experienced by the animals, particularly those living in colder environments (e.g., 7, 24, 35, 42, 49, 53, 93). Low temperatures greatly constrain behavioral capacities, with implications for a large number of ecologically important

functions, such as thermoregulation, predation, and defense.

In some species, decreased locomotor capacities at low body temperatures are accompanied by increased aggressiveness, creating a thermal dichotomy between fight and flight (25, 41). In the lizard *Agama savignyi*, fewer than one quarter of individuals tested had complete aggressive displays at 34°C, but all individuals were aggressive at 18°C, a temperature at which speed is only one-third that at 34°C (41). Distance before flight on predator approach decreases with increasing body temperature in the lizard *Anolis lineatopus* (79), possibly indicating behavioral compensation for decreased speed capacity. The compensation of aggression, evasion, or other forms of behavior for reduced locomotor capacity at low temperatures is definitely a potentially fruitful area of investigation.

Differences among individuals from a single population in locomotor performance capacities are quite pronounced, even when confounding size-dependent effects are eliminated (11). There are relatively fast and slow individuals and animals of relatively high and low stamina, and these differences persist under field conditions for periods as long as 1 yr (50, 56). These differences also persist across body temperatures (7, 26, 51, 63, 78), so that individuals maintain their relative ranking in performance capacity, even though absolute levels of performance are greatly affected by body temperature. These results suggest that there are no necessary trade-offs in performance at high and low temperatures and that individuals are not thermal specialists (51).

The thermal dependencies of locomotor performance capacities generally accord with the presumptive physiological mechanisms underlying and limiting those activities. Endurance and maximal oxygen consumption appear to be closely linked and have similar temperature dependence (6, 8, 14, 30, 59, 74, but see Ref. 27), and maximal exertion and anaerobic capacity have similar temperature coefficients (7, 78). The thermal dependence of twitch contraction time appears to limit limb cycling frequency and hence speed at low body temperatures in some quadrupeds (26, 58, 60, 68, 69, 70) and perhaps in fish (2).

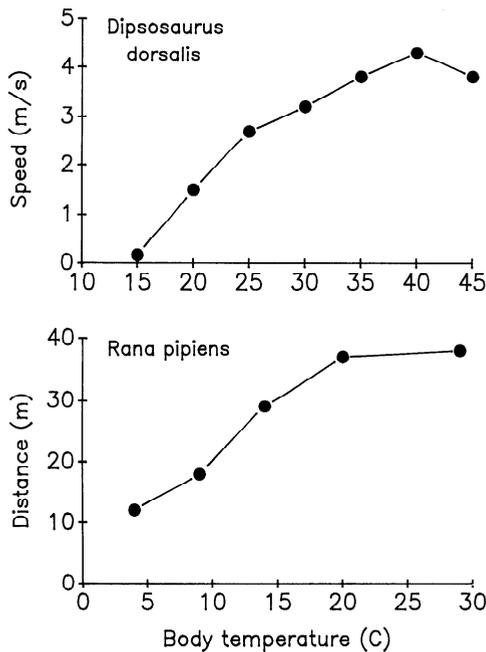


FIG. 1. Speed in lizard *Dipsosaurus dorsalis* (data from ref. 69) and maximal exertion (distance traveled in 5 min) in frog *Rana pipiens* (data from Ref. 78) as a function of body temperature.

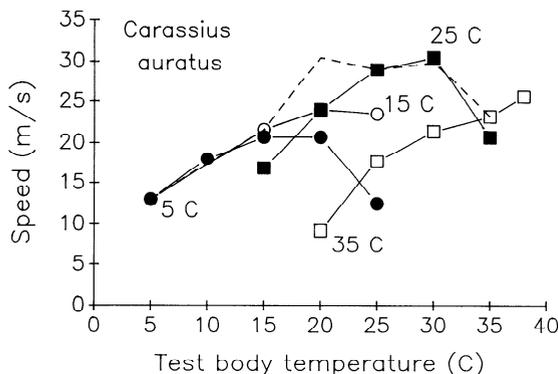


FIG. 2. Endurance (measured as sustainable speed) as a function of body temperature in goldfish *Carassius auratus* acclimated to different temperatures, as indicated (data from Ref. 31). Dashed line indicates endurance of fish acclimated to test temperature.

Acclimation: Effects of Long-Term Temperature Exposure

To what extent can the acute effects of variation in body temperature be overridden by longer term temperature exposure? Can animals modify their functional capacities to adjust to the thermal environment in which they find themselves? Such phenotypic plasticity, acclimation, is very common in many physiological systems of ectotherms (e.g., metabolism, enzyme kinetics, nervous function) (44, 76, 77). When an organism is moved into a colder temperature, acute thermal effects on rate processes are ameliorated over a period of a few weeks. Rate processes in the cold increase above original levels, either partially (incomplete compensation) or totally (complete compensation) in comparison with rates in the previous warmer environment. Opposite responses (progressive depression of rates) occur during warm accli-

mation. Thus acutely determined rate processes are usually greater at any temperature in cold-acclimated than in warm-acclimated animals, being reflected in the translation of the thermal performance curve of the process on the thermal axis, to the left in the cold, to the right in the warm. To what extent do locomotor capacities show such acclimatory temperature adaptation? Does performance improve, for instance, during prolonged cold exposure and does it ever reach levels attained during exposure to higher temperatures?

Acclimation of speed capacities has been studied primarily in amphibians. Most studies have found that maintenance at cold temperatures does not improve speed performance in the cold (26, 73, 78, 81, 93), results that are in accord with the lack of acclimatory effects observed in the mechanical properties of skeletal muscle (see Refs. 26, 80, 82, 83, although myofibrillar ATPase may acclimate in some fish; 1, 38, 62). One study (67) on the toad *Bufo woodhousii* reported significant but incomplete compensation (<10%) in speed at low temperatures with cold acclimation but inverse acclimatory effects on jump length. Speed in the lizard *Xantusia vigilis* is affected by acclimation temperature only at extremes approaching critical thermal limits (63); over natural ranges of body temperature, speed is not modified by acclimation (Fig. 3). Maximal velocity and acceleration of rainbow trout are not fully compensated between 5 and 15°C even after 8 wk of acclimation; these factors are equal in animals acclimated and measured at 15–25°C (92). On the basis of these admittedly few studies, it appears that ectotherms acclimate poorly or not at all in their capacity for rapid locomotor speed: exposure to low temperature permanently depresses speed performance.

The effect of temperature acclimation on endurance has been studied primarily and extensively in fish (3–5, 16, 20, 31, 33–35, 37, 65, 84, 85). The typical response is illustrated in Fig. 2 for the goldfish *Carassius auratus*. Acclimation to colder temperatures translates the endurance performance curve to the left; fish maintained at colder temperatures have greater endurance in the cold. This compensation, however, is incomplete. In goldfish, animals acclimated at 15°C have greater endurance than 25°C-acclimated animals at 15°C, but the latter have greater endurance at their own acclimation temperature

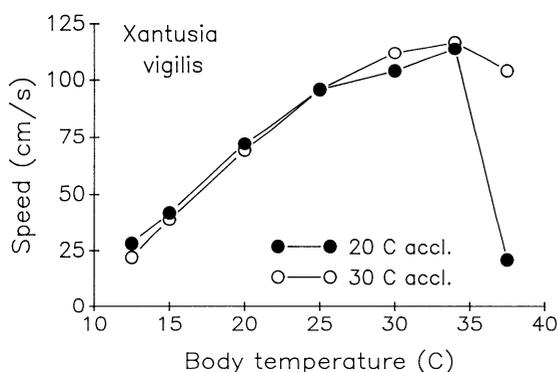


FIG. 3. Speed in lizard *Xantusia vigilis* acclimated to 20 and 30°C (data from Ref. 63). Acclimation groups are different only at 12.5 and 37.5°C.

than the 15°C-acclimated animals attain at any temperature. Thus thermal performance curves for endurance of fish acclimated to test temperatures also demonstrate a strong thermal dependence, albeit lower than that observed for acute temperature exposure. Complete acclimation would result in thermally independent plots of endurance on test (i.e., acclimated) temperatures. No acclimation was found in endurance capacities at acclimation temperatures of 10°C and above in two species of salamanders (26, 27).

On the basis of the foregoing, it appears that locomotor performance capacity has limited phenotypic plasticity in different thermal environments. Acclimation is either entirely absent or incomplete for both speed and endurance in all species investigated. Exposure to lower body temperatures or occupation of colder environments seems therefore to restrict capacities for locomotion, to exact a price in behavioral scope that cannot be completely compensated through physiological mechanisms. Conversely, warmer body temperatures and thermal environments seem to afford an expansion of locomotor performance space, resulting in an increased potential behavioral repertoire. These results support previous arguments (10, 39, 52) that "warmer is better" for organisms, that the greater catalytic power attainable at higher temperatures can translate into increased performance capacities.

The data cited above are limited in several ways, making these generalizations tentative. Phylogenetic coverage is spotty, heavily emphasizing fish for endurance and amphibians for speed. Studies have been done only on adult organisms and only under laboratory conditions. Studies more comprehensive in these regards are desirable, particularly in view of the pattern of constraint on thermal adjustments that is currently emerging and is so puzzling from an adaptive perspective.

Evolutionary Adjustments to Temperature

From the foregoing section, it is apparent that individual organisms adjust their locomotor capacities incompletely or not at all during exposure to different temperatures. To what extent have these capacities been adjusted, that is, become adapted, during evolution of animal groups to warm and cold environments?

To evolve, functions such as performance capacity must possess several attributes, among them variability, repeatability, and heritability, and they must be under natural selection. To a varying extent, all of these attributes have been demonstrated for locomotor performance capacities. Capacities are highly variable among individuals, even at birth (11); for example, among neonatal snakes (*Thamnophis sirtalis*), some individuals are four times faster than others, and some individuals have 100 times the endurance of others (56). Repeatability of performance, as mentioned above, is significant through time in nearly all species examined (11). Performance capacity is also heritable (18, 32, 56, 64, 88, 91). Speed has been indirectly linked to predator avoidance in both lizards (22) and fish (87), with implications for differential survivorship and reproduction associated with fitness (40). Greater speed and maximal exertion have been

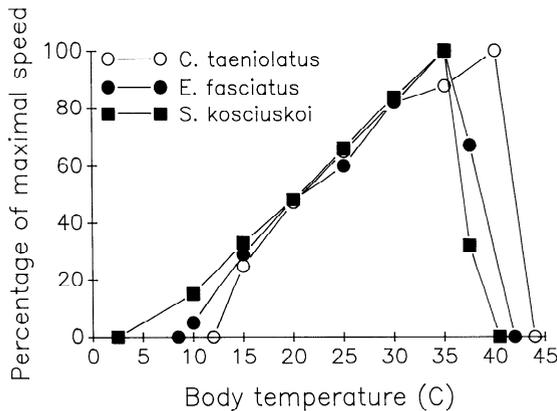


FIG. 4. Speed in scincid lizards *Ctenotus taeniolatus* [preferred body temperature (PBT) = 35.3°C], *Eremiascincus fasciolatus* (PBT = 24.4°C), and *Sphenomorphus kosciuskoi* (PBT = 29.8°C) as a function of body temperature (data from Ref. 49).

shown to be associated with differential survivorship in garter snakes (*T. sirtalis*) (57), again with presumptive implications for selection and differential fitness. These findings imply that locomotor performance capacity may be under selection in particular systems and these systems are therefore capable of evolution.

An examination of animals living in greatly different climatic environments suggests in general that evolutionary adjustments to temperature regimes have occurred. Antarctic fish, for example, are able to swim at temperatures that kill more temperately occurring species (94), and vice versa (6). The amount of evolutionary compensation involved is, however, very controversial. In regard to endurance, for instance, some authors (71) maintain that no compensation is evident in Antarctic fish, while others (2) suggest that it is, at least in adult fish. Maximal speeds of fish from different thermal environments have been reported to be similar (6, 17), suggesting complete evolutionary compensation for temperature.

The problem with such comparisons and analyses is the very great phylogenetic difference among the animals being compared, which may belong to different families or even different orders. They have very different evolutionary histories and, as a consequence, very different morphology and physiology. Differential performance ability, such as speed, at different temperatures may be the result of evolutionary adaptation to temperature, but it may also be the result of numerous different factors, including different body size, feeding habits, muscle fiber composition, limb or fin morphology, etc. An assertion of adaptation should be tested against a null hypothesis (28), and a useful one is ancestral inheritance (e.g., Ref. 21). Studies that seek to demonstrate adaptation to a specific environmental factor such as temperature should be done within a restricted phylogenetic context, among populations or species groups of known relatedness to minimize extraneous factors that complicate comparisons (29, 47, 48). The incorporation of phylogenetic and historical information also permits determination of directionality in the evolutionary process (a "transformational" rather than an "equilibrium" analysis of comparative data, Ref. 66), an aspect particularly useful in regard to adaptation to temperature.

An example of this approach is provided by a study (49) on the evolution of different species of Australian scincid lizards to different thermal environments. Body temperatures of extant species were mapped onto a preexisting phylogenetic tree, one based on morphological features and therefore independent of the thermal data. A parsimonious minimum-evolution algorithm was used to determine that the group ancestrally possessed relatively high body temperatures (~33°C). More temperately distributed and nocturnally active species, represented by the genera *Eremiascincus* and *Sphenomorphus*, secondarily occupied and evolved in cooler thermal niches. Analysis of maximal speed capacities in these animals demonstrated the evolution of partial but incomplete compensation to these cooler environments (see Fig. 4). Optimal temperatures for running are lower in the cooler genera, and they are able to run at lower temperatures than the warmer genera (e.g., *Ctenotus*). But optimal temperatures are always higher than preferred or natural body temperatures, so genera from cool environments are able to attain only a fraction of their potential speed capacities. Occupation of cooler environments has led to a reduction in locomotor performance space in these genera that has not been completely compensated through evolution. Other studies on species active at low body temperatures (7, 53, 58, 89, 93) also indicate that performance at naturally experienced temperatures is less than optimal, that is, less than the animals are capable of attaining at higher body temperatures.

Few studies have been undertaken in the above context. The methodology, however, shows great promise for unravelling the opportunities and constraints that different thermal environments offer organisms and an alternative to the simple and untestable assumption of adaptation in every case investigated.

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