Integrating Thermal Physiology and Ecology of Ectotherms: A Discussion of Approaches

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SYNOPSIS. An understanding of interactions between the thermal physiology and ecology of ectotherms remains elusive, partly because information on the relative performance of whole-animal physiological systems at ecologically relevant body temperatures is limited. After discussing physiological systems that have direct links to ecology (*e.g.*, growth, locomotor ability), we review analytical methods of describing and comparing certain aspects of performance (including optimal temperature range, thermal performance breadth), apply these techniques in an example on the thermal sensitivity of locomotion in frogs, and evaluate potential applications.

INTRODUCTION

Body temperature (T_b) profoundly affects the ecology of ectotherms by influencing both physiology and behavior. The effects of temperature on many physiological systems are known (Dawson, 1975), and the responses used by amphibians and reptiles in regulating T_b are well established (Cowles and Bogert, 1944; Brattstrom, 1963; Heath, 1965; Lillywhite, 1970). An understanding of the interactions between physiological performance and ecology is, however, still elusive (Huey and Slatkin, 1976). This gap partly results from a surprising lack of information on whole-animal physiological systems (*e.g.*, growth, locomotion, reproductive output) that have direct links to ecology and from the difficulty of defining and estimating statistics (*e.g.*, optimal temperature range, thermal performance breadth) that characterize the thermal sensitivity of these responses. In this paper we enumerate some ecologically relevant physiological systems, review methods of describing their thermal sensitivity with an example, and discuss ecological problems that can be attacked by similar approaches.

Our interest in thermal physiology and ecology evolved from field studies on temperature regulation in lizards. Certain species regulated precisely only in habitats where the potential costs (time and energy) or risks (predation) of raising T_b appear low (Ruibal, 1961; DeWitt, 1967; Regal, 1967; Hertz, 1974; Huey, 1974; Lister, 1976), suggesting that the behavior of lizards cannot be understood solely from physiological considerations.

Huey and Slatkin (1976) formalized the

view that thermoregulatory behavior should reflect a compromise between the benefits and the associated costs or risks of temperature regulation and then derived a cost-benefit model with three parameters (the benefit at various T_b, the frequency distribution of environmental temperatures in a habitat at a given time, and the cost to achieve particular T_b). This model predicts, for example, the extent of temperature regulation that maximizes energy gain or the relative advantages of thermal generalists *vs.* thermal specialists (eurytherms, stenotherms).

In attempting to estimate the physiological benefits of T_b, these or related analyses confront serious problems. First, the available data on physiological effects of T_b, which have been gathered to determine the physiological significance of the preferred T_b (the T_b selected in a laboratory thermal gradient; Licht *et al.*, 1966), are usually focused on tissue or cellular systems (Dawson, 1975) rather than on whole-animal systems, which are ecologically more relevant (Bartholomew, 1958). Second, important descriptive statistics such as the physiologically "optimal" T_b (herein defined as the best-performance T_b; Fig. 1) or the "thermal performance breadth" (herein defined as the range of T_b over which an animal performs well; Fig. 1) are normally estimated indirectly (*e.g.*, inferring optimal T_b from preferred T_b). These estimates can be useful as first approximations, but have limitations (Huey and Slatkin, 1976; Reynolds, 1977;

Beitinger and Fitzpatrick, 1979): most importantly, such estimates convey no information on the relative physiological disadvantage of activity at other T_b.

A partial solution to these difficulties was pioneered by several biologists (Moore, 1939; Fry and Hart, 1948; Brett, 1971). Basically, one measures an animal's performance over a broad spectrum of T_b and then fits a curve to these performance data. One can then estimate optimal T_b, thermal performance breadth, or relative performance at any T_b from these curves. These procedures and their applications are the subjects of this discussion.

ECOLOGICALLY INTERPRETABLE PHYSIOLOGICAL SYSTEMS

Although ecologists and physiologists are keenly interested in thermal biology, they usually have different goals. Consider their contrasting approaches to studies on locomotion. To an ecologist, the thermal sensitivity of locomotion is critical for evaluating an animal's ability to capture prey, escape predators, and interact socially. To a physiologist, the thermal sensitivity of this whole-animal activity provides a baseline for focusing ever sharper on the mechanisms of thermal adaptations at the tissue, cellular, and biochemical levels.

Our contention here is that attempts to integrate physiology and ecology should usually rely on studies of *whole-animal functions* rather than of tissue or cellular activities (Bartholomew, 1958). In other words, a study on acceleration is more directly related to ecological performance than is a study on the rapidity of muscle contraction (the latter is, of course, appropriate for mechanistic evaluations). Licht (1967) discovered, for example, a classic case where biochemical data appear ecologically misleading: the "optimal" temperatures for alkaline-phosphatase activity were above the lethal temperatures for some of the lizards he studied!

From this intentionally restricted perspective, examples of whole-animal activities that should make significant contributions to fitness include growth rates
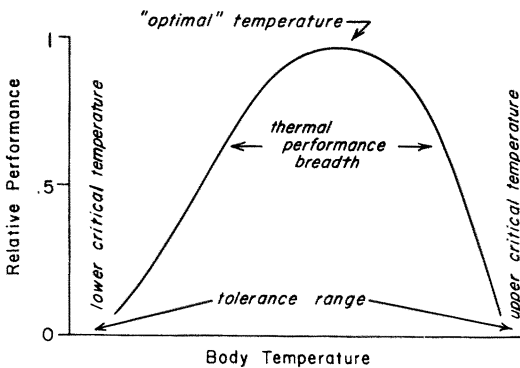

FIG. 1. Hypothetical performance curve of an ectotherm as a function of body temperature.
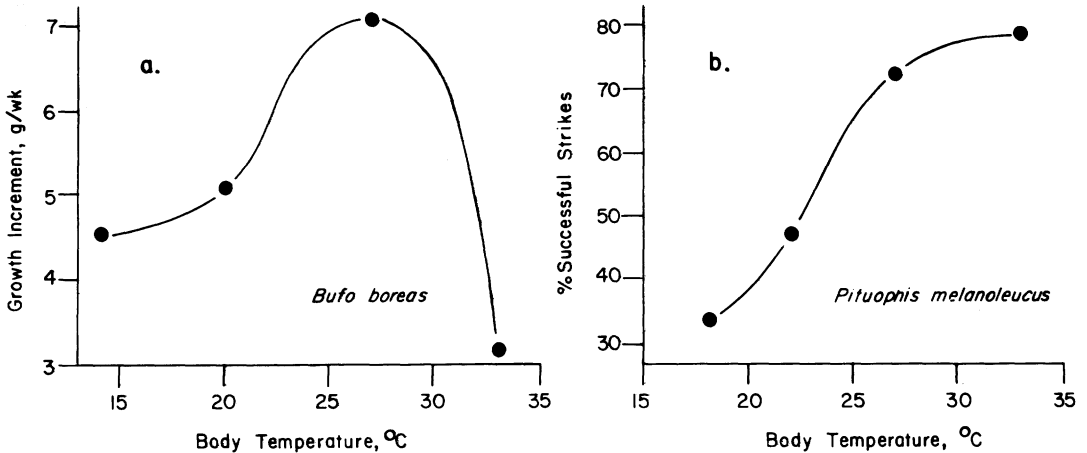
FIG. 2. *A*. Growth (g/wk) of *Bufo boreas* juveniles during third week since metamorphosis (from Lillywhite *et al.*, 1973). *B*. Percentage of strikes by gopher snakes (*Pituophis melanoleucus*) that resulted in capture of a mouse (from Greenwald, 1974). Curves for both graphs fitted by eye.

(Fig. 2A), digestive efficiencies and rates, healing from injury, surviving disease, predation success (Fig. 2B) and avoidance, maximum acceleration or velocity, agility, metabolic scope, rate of egg production, and social dominance. Despite the impressive variety and quality of studies on the physiological significance of temperature regulation at tissue or lower levels (Dawson, 1975), information on whole-animal performance is scattered and rare (*e.g.*, Moore, 1939; Avery, 1971; Lillywhite *et al.*, 1973; Greenwald, 1974; Huey, 1975; Kluger, 1978; Bennett, 1978, unpublished data; Waldschmidt, 1978; Tracy, unpublished data). A major and immediate goal of research in this area must be to fill this gap.

DESCRIBING THERMAL SENSITIVITY

Measures of performance

Many physiological systems show maximum response at intermediate T_b and reduced response at higher or lower T_b (Figs. 1, 2, 3). Similar response curves approximate the performance of many systems (Brett, 1971).

To characterize the thermal sensitivity of such systems, we need at least three descriptive measures (Fig. 1): the "optimal" temperature (or optimal temperature range), the thermal performance breadth

(or degree of thermal specialization), and the tolerance range (Fry *et al.*, 1946), with associated upper and lower threshold or lethal temperatures. When completeness is required, fitting a curve to performance data allows specification of predicted performance at any T_b (Huey, 1975).

These measures differ in physiological significance. Optimal temperatures and thermal performance breadth describe temperatures at which animals perform "*best*" or "*well*," respectively, and are closely related to the physiological concept of capacity adaptation (Precht *et al.*, 1973). In contrast, the tolerance range estimates the range of temperatures over which *any* activity or survival is possible, and is thus related to the concept of resistance adaptation (Precht *et al.*, 1973).

These measures differ in ecological significance as well. Thermal performance breadth is relevant to the important ecological concept of niche width (Roughgarden, 1972). Threshold or lethal temperatures set absolute limits on where or when animals can survive (Porter and Gates, 1969; Heatwole, 1970; Spellerberg, 1972*a*, 1973). However, lizards are rarely active at near-threshold T_b, except in emergencies (DeWitt, 1967). For example, the difference between the maximum T_b ever recorded for active individuals and the upper T_b at loss of coordination (Critical
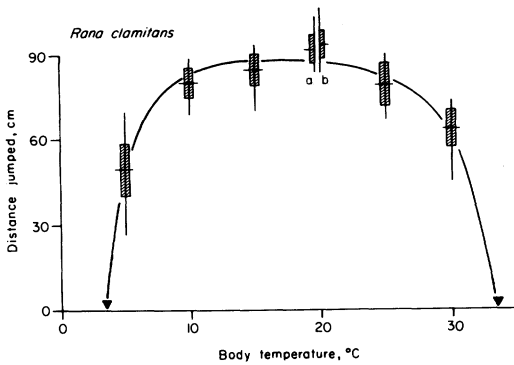
FIG. 3. Distance jumped by *Rana clamitans* as a function of T_b (from Huey, 1975; see Appendix I). The fitted curve is a product exponential (see Appendix II).

Thermal Maximum) for 33 species of lizards is $6.0 \pm 0.58°C$, range $= 1.0° - 19.4°C$ (calculated from Heatwole, 1970) and the difference between the minimum T_b ever recorded for active lizards and the lower T_b at loss of coordination (=Critical Thermal Minimum) for 4 species of lizards is even larger ($12.8 \pm 1.21°C$, range $= 10.2° - 15.3°C$: calculated from Spellerberg, 1972*a,b*). Because activity T_b are thus very different from threshold T_b, the cessation of activity before reaching near-threshold temperatures is probably not a result of avoiding such temperatures. We believe that this cessation is instead related to the general decline in physiological performance at non-optimal T_b (Fig. 1). [Extremely high-temperature ectotherms like *Dipsosaurus dorsalis* may, however, be exceptions.] Thus tolerance limits seemingly have less relevance to temperature regulation per se or to the day-to-day activities of ectotherms than do optimal temperatures or thermal performance breadths (Bartholomew, 1958; Warren, 1971; Huey, 1975; Feder, 1978; Humphreys, 1978: but see Spellerberg, 1973).

Traditional methods of estimating descriptive measures

The *a priori* assumption of early workers (*e.g.*, Cowles and Bogert, 1944) that the mean T_b of field-active lizards represents

their optimal T_b was altered by the subsequent realization that field T_b's reflect a compromise between physiology and ecology (Soulé, 1963; Licht *et al.*, 1966; DeWitt, 1967; Regal, 1967; Huey, 1974). Workers then often substituted the "preferred" T_b of lizards in laboratory thermal gradients (Licht *et al.*, 1966). With some exceptions, many tissue and cellular functions do proceed fastest near the preferred T_b (Dawson, 1975). Nevertheless, preferred T_b may be altered by time, hormonal or physiological state, and behavioral context (Huey and Slatkin, 1976; Reynolds, 1977), suggesting that the preferred T_b is somewhat labile and may also reflect a compromise between physiology and ecology. More importantly, as noted above, preferred T_b conveys no information about the actual disadvantages to an animal of being active at any other T_b. However, when direct measures of physiological performance are unavailable or impractical, preferred T_b is probably the most meaningful measure of thermal behavior (Reynolds, 1977) and may also provide important insight into the nature of behavioral integration.

In contrast, tolerance range can be directly measured by calculating the difference between the Critical Thermal Maximum and Minimum (Moore, 1939; Kour and Hutchinson, 1970; Spellerberg, 1972*a*, Snyder and Weathers, 1975). Fewer measures of performance breadth as implied herein have been suggested, partly because performance breadth is infrequently distinguished from tolerance range and partly because the renewed attention to the theoretical significance of niche width is recent (Janzen, 1967; Brattstrom, 1968; Levins, 1969; Kour and Hutchison, 1970; Ruibal and Philibosian, 1970; Huey and Slatkin, 1976; Lister, 1976; Hertz, 1977; Huey, 1978; Feder, 1978). Most field or laboratory measures are imprecise or rely on untested assumptions (Huey and Slatkin, 1976, p. 370). The use of tolerance range to estimate performance breadth not only confounds the important physiological and ecological distinctions between these measures (above), but may also be unreliable. For

example, the known tolerance ranges of amphibians and reptiles do not in fact correlate directly with intuitive predictions by herpetologists of performance breadths. Most herpetologists that we have informally queried believe that frogs have wider performance breadths than do lizards. Yet sample tolerance ranges of lizards ($\overline{X}$ = 36.7±.52°C, N = 29; calculated from Spellerberg, 1972a) are actually broader than those of frogs ($\overline{X}$ = 30.1±.91°C, N = 5; calculated from Brattstrom, 1963). Moreover, a correlation between tolerance range and performance breadth is seemingly possible only to a limited extent: a precise correlation would imply that physiological performance curves are geometrically similar — an improbable occurrence in biology! Therefore, until a strong correlation is actually demonstrated, it seems appropriate to maintain a distinction between tolerance range and performance breadth.

Of the traditional measures of describing thermal performance, only tolerance range can be easily and directly estimated. Estimates of other measures are less suitable for detailed analyses of physiology and ecology.

Direct measures of descriptive statistics

Optimal temperatures and thermal performance widths can be estimated by measuring the performance of an animal over a spectrum of T_b and fitting a curve to the data. To exemplify this procedure, we use some preliminary data (Fig. 3, from Huey, 1975) on the acute effect of T_b on distance jumped (Appendix I) by a green frog (*Rana clamitans*) and fit these data to a product-exponential equation (Appendix II). [When possible, data should be fitted to a theoretical curve. In the absence of such a curve, as is the case here, standard curve-fitting procedures should be followed.]

Thermal tolerance range. Curve fitting is not required; merely compute the difference between the upper and lower threshold T_b. For *Rana clamitans* (Fig. 3), this range is 30.0°C. By calculating this range for individuals in several popula-

tions, one can compare the relative breadth of ranges among populations. Methods for estimating whether one range is hotter than another will be suggested below in the discussion on comparing optimal temperature ranges.

Optimal temperature vs. optimal temperature range. While many of us casually refer to "*the* optimal temperature" of an animal, we should probably refer instead to its optimal temperature range (see Heath, 1965). The continuity of many physiological systems strongly implies a zone of temperatures within which performance does not change substantially (Fig. 1). The width of this temperature-insensitive zone has profound implications for ecological and behavioral analyses (Huey and Slatkin, 1976) and even for selection of an appropriate statistical method for comparing optima.

We should therefore initially determine whether an individual has an optimal temperature or an optimal temperature range. First, we might determine the mean and variance of the animal's performance at each of several test temperatures (Fig. 3). Then we might determine the number of test temperatures in the maximal performance range that are statistically identical. A consistent pattern of insignificant differences among three or more intervals implies a broad optimal temperature range. Statistical identity of only two temperatures, which could indicate either that an optimal range exists or that the optimal temperature is intermediate between the two test temperatures, is ambiguous. For *Rana clamitans* (Fig. 3), jumps at 15°C and 20°C do not differ significantly. The temperature intervals (5°C) in this study were large, so these data are somewhat ambiguous. Nonetheless, the general jumping pattern suggests a broad optimal temperature range.

When an optimal temperature exists, one can estimate the optimal T_b by 1) selecting the single best performance T_b (*e.g.*, by ANOVA); 2) selecting the midpoint between the two best performance T_b; or 3) fitting a curve to the data and solving for the optimal T_b. Solution of the product-exponential (Fig. 3, Appendix II) yields an estimate of 16.8°C, whereas the

midpoint estimate is 17.5°C.

When the object of curve fitting is for a comparison of populations, data for individuals must be examined separately. Lumping data for individuals, while decreasing the experimental load considerably, has two serious drawbacks. First, unless data are normalized, individual differences in magnitude of performance increase the variance at each test temperature. Second, if optimal T_b is genetically polymorphic or is affected by age, season, time of day, or acclimation (see Reynolds, 1977), one might conclude that individuals have broad optimal temperature ranges when instead the population is merely heterogeneous for optimal T_b (Roughgarden, 1972).

Thermal performance breadth. To estimate thermal performance breadth, select an arbitrary performance level (*e.g.*, 80% of maximum performance) and then solve the curve to determine the range of T_b over which that performance standard is equalled or exceeded (Huey, 1975). For example, the estimate from the product-exponential curve for *Rana clamitans* is 21.7°C (Fig. 3). The choice of performance level is arbitrary, of course; and the estimate for thermal performance breadth will vary between the estimates for tolerance range and the optimal temperature range, depending on the selected performance level. [Because performance breadth is measured in degrees Celsius, one can compare performance breadths of animals having very different forms of locomotion (*e.g.*, jumping by frogs *vs.* sprinting by lizards).]

Comparing placement of tolerance ranges and optimal temperature ranges. When an optimal temperature range exists (or when comparing tolerance ranges), the above methods, which compare optimal temperatures, would be biologically misleading. In this case, we rephrase the problem to determine whether the optimal temperature range of population A is higher than that of population B. The simplest method is to compare midpoints (*e.g.*, 17.5°C for *Rana clamitans*) for individuals among populations. A more general technique that has greater information content can

also be derived. After determining the optimal temperature range (*e.g.*, 15°C to 20°C, Fig. 3) for each individual, compare average "lower bound" temperatures (15°C, Fig. 3) among populations. Next, set criteria for differential placement of ranges. For example, specify that range A is higher than range B only if the lower bound and the upper bound of A are both significantly higher than those of B. [Alternatively, one could specify that A is higher than B if at least one bound is significantly higher in A.] Although this "bound" method is more complex than a "midpoint" approach, more information is gained. Thus we determine not only that A is higher than B "on average," but also the basis for this average difference. Moreover, the bound approach would alert us to situations where the range of B is entirely contained within the range of A.

INTEGRATING THERMAL PHYSIOLOGY AND ECOLOGY

The above methods can be used to quantify the sensitivity of physiological performance to T_b, a prerequisite for integrating thermal physiology and ecology. Knowledge of optimal T_b alone may suffice for many analyses, but curve fitting permits further analytical power. It can be useful, for example, to know that *Rana clamitans* should jump about twice as far at $T_b = 16.8°C$ than it should at $T_b = 5.0°C$ or 31.5°C.

Some basic applications

Measures of optimal T_b are particularly appropriate to analyses of geographic distributions of animals (Spellerberg, 1973; Huey and Slatkin, 1976; see also Clark and Kroll, 1974), of times of activity and of habitats (Rand, 1964; Corn, 1971; Huey and Webster, 1976; Huey and Pianka, 1977), and of competitive interactions (Inger, 1959; Ruibal, 1961; Rand, 1964; Huey and Webster, 1976; Lister, 1976; Schoener, 1977). Optimal T_b could be used to estimate patterns of geographic variation (Moore, 1949) and even to measure rates of evolution of phenotypic characters (see

Bogert, 1949; Brown and Feldmeth, 1971).

Thermal performance breadth is relevant to discussions of habitat occupancy and competition (Ruibal and Philibosian, 1970; Huey, 1974; Huey and Webster, 1976; Huey and Slatkin, 1976; Lister, 1976; Hertz, 1977) as well as of the precision of temperature regulation in various ecological and behavioral contexts (De-Witt, 1967; Huey and Slatkin, 1976; Greenberg, 1976). Moreover, selection pressure for thermal performance breadth may differ between constant and fluctuating environments (Levins, 1969; Kour and Hutchison, 1970; Huey and Slatkin, 1976), and knowledge of thermal performance breadths is necessary for certain zoogeographic analyses (Janzen, 1967; Feder, 1978; Huey, 1978).

As we have argued, tolerance range and associated threshold or critical temperatures have restricted ecological significance (Warren, 1971; Feder, 1978; Humphreys, 1978). They relate primarily to analyses of "thermal safety margins" (Heatwole, 1970), to adaptations to extreme conditions, and to understanding why animals avoid extreme temperatures.

Extensions

An immediate extension of this methodology involves increasing the dimensionality. May (1975) demonstrated interactions between salinity and temperature on embryonic development of the fish *Bairdiella icistia*. C. R. Tracy (personal communication) is similarly examining the effects of T_b and hydration state on jumping ability of a frog.

A second extension involves the dimension of time. Acclimation results in a time-dependent shift (presumably adaptive) in the performance curve (Fry and Hart, 1948). [Holding an animal at constant, moderately high T_b may produce a time-dependent impairment in performance: thus not all shifts are adaptive (Hutchison and Ferrance, 1970).] The extent and rate of acclimation, which can easily be quantified with the above methods, also gives a longer term estimate of niche

width (see Levins, 1969; Hertz, 1977) than the acute estimates discussed here.

A more specific application concerns analyses of differences in preferred T_b among samples. Mayhew and Weintraub (1971) demonstrated seasonal changes in preferred T_b of *Sceloporus orcutti*. This shift can be interpreted as evidence of seasonal acclimatization of optimal body temperature. Alternatively, perhaps the physiological optimum is unaffected by season, but instead only the preferred T_b, which is a behavior (Reynolds, 1977), is changing. Given a constant, physiologically "optimal" T_b, a lower preferred T_b during winter can be adaptive by reducing costs associated with attempting to maintain a high T_b (see Huey and Slatkin, 1976). A direct comparison of optimal T_b for growth or locomotion for lizards at different seasons might discriminate by strong inference (Platt, 1964) between these competing (but non-exclusive) hypotheses.

CONCLUDING REMARKS—UNSOLVED PROBLEMS

The above discussion implicitly assumes that different physiological systems of an ectotherm have similarly shaped and positioned performance curves. This is undoubtedly an oversimplification (Dawson, 1975). If optimal temperatures vary among physiological systems (or with age, sex, or time), then no single T_b simultaneously optimizes all systems. One potential approach to solving this complex problem would be to order physiological systems by their importance to the animal: thus (if optimal T_b for locomotion is higher than that for growth) an animal might select a high T_b only when the ability to run quickly is of more immediate (or long term) importance than is the ability to grow quickly. [Why selection might have resulted in multiple optima rather than converging systems to a single optimum seems a fundamental question. Not all systems are used simultaneously: perhaps optimal T_b of a system is related to its temporal activity pattern (see Brett, 1971).]

A second problem is that physiological and ecological performance probably do not scale directly. Greenwald's (1974)

unique data on gopher snakes (*Pituophis melanoleucus*) provide a suggestive example. Relative velocity of strikes at mice were correlated with percentage of strikes that were successful (r = .80), but major changes in percent success were associated with minor changes in relative strike velocity (slope = 1.81, calculated from data, courtesy of O. E. Greenwald). Thus a 50% improvement in physiological performance (strike velocity) does not necessarily imply a 50% increase in ecological performance (predation success). Extrapolation from tissue or biochemical systems to ecological performance must also be very sensitive to this scaling problem: This is an additional reason why such systems are unsuitable for ecological analyses.

Because metabolism represents an important and constant drain of energy, metabolic costs may also influence the outcome of interactions between physiology and ecology and further complicate analyses. Very likely, animals sometimes select T_b that are suboptimal for certain physiological systems but that maximize growth rate (Brett, 1971; Warren, 1971) or that minimize metabolic losses or risk of predation (Regal, 1967; Huey and Slatkin, 1976; Hainsworth and Wolf, 1978; Humphreys, 1978).

The existence of these and other significant complications suggests that attempts to integrate physiology and ecology are at a nascent stage of development. Nevertheless, this is a stage that appears to promise rapid gains in the immediate future.

before repeating the test. Ten sets of jumps were measured at 5°C, and then at 5°C intervals between 10° and 30°C following the above protocol. At a T_b of 33.5°C, the frog was again unable to jump when prodded. To test for fatigue effects or possible acclimation during the experiment, the frog was cooled to 20°C and another series of jumps recorded (b in Fig. 3). Mean distance jumped for the two series at 20°C did not differ significantly suggesting that the decrease in distance at high T_b (Fig. 3) was unrelated to fatigue and that acclimation did not occur.

APPENDIX II

Various curves were fit to the frog jumping data (Fig. 3, Appendix I). The best-fitting curve was the product of 2 exponential equations (see Thornton and Lessem, 1978, for a similar model that uses the product of 2 logistic equations):

$$P = SC(1 - e^{-K_l (T_b - T_l)}) (1 - e^{K_u (T_b - T_u)})$$

where P is performance, SC is the scale parameter (estimated value = 87.50 cm), $-K_l$ is the initial slope for the lower (left) side of the curve (.44°C^{-1}), T_b is body temperature, T_l is the lower threshold temperature (3.45°C), K_u is the initial slope for the upper (right) side (.34°C^{-1}), and T_u is the upper threshold temperature (33.50°C). The product exponential was estimated using the SPSS nonlinear regression (Marquardt's method) subprogram.

APPENDIX I

To determine the thermal dependence of distance jumped by a 45 g, adult male *Rana clamitans* (acclimated for 2 weeks at about 7°C), Huey (1975) cooled the frog until it was unable to jump when prodded (3.5°C). The frog was transferred to a water bath (5°C). After 30 min, the frog was placed on the floor and induced to jump by lightly tapping its urostyle (the average of 3 jumps was recorded). The frog was returned to the water bath for 5 min

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