

The critical thermal maximum: history and critique

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Abstract: We reviewed 725 papers published since Cowles and Bogert's paper on thermal tolerance (R.B. Cowles and C.M. Bogert. 1944. *Bull. Am. Mus. Nat. Hist.* 83: 261–296) to create a data base of studies that used critical thermal maximum or lethal-temperature methods. We found data from 388 of these papers to provide a historical and taxonomic review of various methodologies used in measuring tolerance of high temperature. We conducted this literature review of previous studies to (i) describe the history of the study of thermal tolerance and show the chronological trends in the use of lethal temperature and critical thermal maximum methods, (ii) illustrate the diversity of taxa used in thermal-tolerance studies, (iii) summarize the diversity of protocols (i.e., end points, heating rates, acclimations, etc.) used for determining thermal tolerance, (iv) provide physiological reasons why the onset of spasms is more meaningful biologically than the loss of righting response, and (v) discuss the difficulties in using data from studies in which widely divergent methods were used and the importance of obtaining comparative thermal-tolerance data for comparative physiology. The adoption of the onset of spasms as a standard end point would allow for valid comparisons of data from different studies and among taxa, an important consideration for current investigations of comparative physiology that use the comparative phylogenetic method.

Résumé : Nous avons révisé 725 articles publiés depuis la parution de l'étude de Cowles et Bogert (R.B. Cowles and C.M. Bogert. 1944. *Bull. Am. Mus. Nat. Hist.* 83 : 261–296) sur la tolérance thermique, révision entreprise dans le but de créer une base de données à partir d'études sur le point critique maximal de température ou sur la température létale. Nous avons retenu 388 de ces articles pour faire une révision historique et taxonomique des diverses méthodologies utilisées dans la mesure de la tolérance aux températures élevées. Nous avons procédé à cette revue de la littérature (i) pour décrire l'histoire de l'étude de la tolérance thermique et montrer les tendances chronologiques d'utilisation des méthodes basées sur le point critique maximal de température et la température létale, (ii) pour illustrer la diversité des taxons étudiés dans les recherches sur la tolérance thermique, (iii) pour résumer la diversité des protocoles (i.e., seuils, taux de réchauffement, acclimations, etc.) employés pour déterminer la tolérance thermique, (iv) pour fournir des explications physiologiques à la théorie selon laquelle le début des spasmes est un facteur biologiquement plus valable que la perte de la capacité de récupération et (v) pour faire valoir les difficultés qui entourent l'utilisation de données basées sur des méthodes très différentes et l'importance de comparer des données semblables sur la tolérance thermique en physiologie comparée. L'adoption du début des spasmes comme seuil standard permettrait des comparaisons valables de données de différentes études sur différents taxons, un atout essentiel pour les recherches actuelles en physiologie comparée qui utilisent la méthode phylogénétique comparative.

[Traduit par la Rédaction]

Introduction

The presence and success of organisms in both time and space depend upon a complexity of environmental factors (Odum 1959). Of these factors, temperature is the most pervasive because it directly affects the kinetic energy of reactants (van't Hoff's rule) and thus the biochemical and physiological processes of organisms, including those underlying behavior (Hutchison and Dupré 1992). Temperature, with its temperospatial variability, mediates the effects of almost all environmental and biological factors, explaining

a portion of the diversity of physiological and behavioral adaptations among organisms.

In ectotherms, the study of thermal physiology is increasingly complex, owing to the confounding effects of behavioral plasticity in the regulation of body temperature (T_b). However, in studies of thermal tolerance, particular behaviors (e.g., the onset of spasms) are governed by physiological limits to temperature only, eliminating the ambiguity associated with other behavioral measures (e.g., activity temperature). Although the critical thermal maximum (CTMax) may occur at different temperatures in different species, the behavioral response is the same across a diversity of taxa. For these reasons, CTMax is an excellent index and standard for evaluating the thermal requirements and physiology of an organism.

The ease with which temperature is both measured and controlled has resulted in an enormous body of literature dealing with the effects of thermal conditions on organisms, with a large portion of this literature devoted to organismal

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tolerance of temperature extremes (Precht et al. 1973; Wieser 1973). Because temperature is so easily measured, protocols (as in CTMax studies) have been highly varied and yet have still yielded results for analysis, unlike more complex protocols (e.g., biochemical assays) in which deviation or inattention to the details of a protocol may result in indecipherable or no data.

The two major methods for determining thermal tolerance are (1) the *static* method, which measures the time to death at constant test temperatures, and (2) the *dynamic* method, which involves increasing the test temperatures until an end point is reached. The static or lethal-temperature (LT) method was developed primarily by F.E.J. Fry and colleagues (Brett 1944; Fry et al. 1942; Fry 1957).

The static method uses statistical techniques from pharmacology (Bliss 1937) to determine the equivalent of an LD₅₀ from time–mortality curves where the “dosage” is the time during which animals are exposed to a constant test temperature until death. Median lethal high and low temperatures plotted against acclimation temperature for a species form a polygon that delimits the “zone of resistance” (outside the polygon) from the “zone of tolerance” (inside the polygon). The “ultimate” upper and lower incipient lethal temperatures (UILT and LILT) are also determined by this method and mark the boundary between the zone of tolerance and the zone of resistance. The UILT and LILT are derived from temperatures at which 50% of the population survives an indefinitely long exposure (Fry 1947, 1967). This procedure permits thermal tolerance to be quantified by measuring the area of the polygon in degrees squared.

The dynamic method, represented by the concepts of the critical thermal minimum (CTMin) and critical thermal maximum (CTMax), was introduced by Cowles and Bogert (1944), with CTMax defined as “the thermal point at which locomotory activity becomes disorganized and the animal loses its ability to escape from conditions that will promptly lead to its death.” This definition was modified to include statistical variation (Lowe and Vance 1955) and standardization of methods to include a constant heating rate that allows deep body temperature to follow ambient test temperatures without a significant time lag (Hutchison 1961, 1976). Slower heating rates may allow for partial thermal acclimation (Cox 1974; Hutchison 1961, 1976). Thus, heating rates from about 0.5 to 1.5°C · min⁻¹ are often used. As the temperature increases, an animal usually displays a sequence of responses that includes loss of the righting response (LRR), the sudden onset of muscular spasms (OS), and finally “heat rigor,” “coma,” or “death.” The latter three end points are not definitive, are difficult to determine (Zweifel 1957), and are seldom described fully.

Although the use of these standardized methods has been urged (Hutchison 1979; Paladino et al. 1980) and would allow for comparisons of data from different studies, a wide variety of heating rates and end points remain in use. Even combinations of the static and dynamic methods have been attempted (e.g., Pough and Wilson 1970; Punzo and Rosen 1984; Whitfield and Livezey 1973). The problem is further exacerbated by “phylogenetic provincialism,” many authors being unaware of the techniques used for, and the results obtained from, diverse taxonomic groups.

Although CTMax was first described in reptiles (Cowles

and Bogert 1944), various modifications of the method have been used for other ectothermic vertebrates (e.g., Brattstrom 1963; Matthews 1987) and many invertebrates (e.g., Lagerspetz and Bowler 1993; Lahdes 1995; Korhonen and Lagerspetz 1996; Spidle et al. 1995). The concept has been extended to mammals (Erskine and Hutchison 1982a, 1982b; Wright 1976), including humans (Bynum et al. 1978; Hutchison 1980). The convulsions accompanying heat stroke in humans have been equated to the OS of CTMax in ectothermic vertebrates (Attia and Khogali 1983; Attia et al. 1983).

Lutterschmidt and Hutchison (1997) support OS as a better CTMax end point than LRR by showing that OS (i) had greater precision among different ectothermic vertebrates and (ii) shows this greater precision across taxa (i.e., in fish, amphibians, and reptiles). To illustrate why OS may be more relevant biologically than LRR, and the importance of standardizing methods for determining upper-temperature tolerance, we conducted a literature review of previous studies to (i) describe the history of the study of thermal tolerance and show the chronological trends in the use of LT and CTMax methods, (ii) illustrate the diversity of taxa used in thermal-tolerance studies, (iii) summarize the diversity of protocols (i.e., end points, heating rates, acclimations, etc.) used for determining thermal tolerance, (iv) provide physiological reasons why OS is more meaningful biologically than LRR, and (v) discuss the difficulties in using data from studies with widely divergent methods and the importance of obtaining thermal-tolerance data comparable to those obtained from ecophysiological and comparative phylogenetic investigations (Felsenstein 1985).

Materials and methods

Literature review

We surveyed 1045 papers on thermal tolerance published since Cowles and Bogert (1944). We discarded 320 papers that described cold-tolerance or cellular/molecular investigations (and were thus inappropriate for addressing organismal responses). From the remaining 725 papers we created a data base of studies in which the CTMax or LT method was used. These were reviewed to determine the procedures and methods used in determining thermal tolerances of vertebrates and invertebrates. We found that 388 of the papers provided original data or review material on measures of organismal thermal tolerance. We used these 388 papers to provide a historical and taxonomic review of various methodologies used in the CTMax literature (Table 1). The total for taxa and methods shown in Table 1 is 604 and not 388 because some papers dealt with multiple methods and (or) taxa.

Results

Literature review

The best represented taxonomic group in the literature survey was Cypriniformes with 92 accounts of thermal tolerance, 64 (i.e., 70%) of which were measured with CTMax. Most of these accounts (53 of 64, or 83%) were observations of LRR and not OS. A similar trend was found for the other groups of fishes.

LRR was used more often than OS for reptiles. Only frogs and salamanders had more accounts for OS than for LRR. However, studies on anurans also represent the greatest number of accounts (i.e., 14 of 40, or 35%) in which alternative

Table 1. Methods used in determining vertebrate and invertebrate thermal tolerance, according to taxon.

	CTMax method/end point				LT	Mixed methods	Taxon total
	OS	LRR	Other	Unknown			
Mammalia	5	—	—	—	4	—	9
Aves	—	—	—	—	2	1	3
Reptilia							
Serpentes	—	3	—	—	—	1	4
Lacertilia	14	17	4	2	6	2	45
Testudines	5	1	—	—	—	—	6
Crocodylia	—	—	—	—	—	1	1
Amphibia							
Anura	16	9	14	1	11	7	58
Caudata	27	10	3	1	1	3	45
Actinopterygii							
Pleuronectiformes	—	—	—	—	1	—	1
Perciformes	4	33	—	—	11	22	70
Scorpaeniformes	1	1	—	—	1	1	4
Cyprinodontiformes	1	16	3	1	16	3	40
Beloniformes	—	—	2	—	—	—	2
Atheriniformes	—	1	—	—	2	—	3
Salmoniformes	—	12	—	1	19	5	37
Osmeriformes	—	—	—	—	1	—	1
Esociformes	3	—	—	—	1	—	4
Siluriformes	1	4	—	—	2	—	7
Cypriniformes	9	53	1	1	24	4	92
Clupeiformes	—	3	—	—	4	4	11
Anguilliformes	—	—	—	2	1	—	3
Cephalaspidomorphi							
Petromyzontiformes	—	—	—	—	4	—	4
Oligohymenophora	—	—	—	—	3	—	3
Turbellaria	—	—	—	—	1	—	1
Phasmeidea	—	—	—	—	1	—	1
Hydrozoa	—	—	—	—	3	—	3
Copepoda	—	—	—	—	3	1	4
Ostracoda	—	—	—	—	1	—	1
Cirripedia	—	—	—	—	2	—	2
Gastropoda	2	1	3	—	12	2	20
Bivalvia	—	—	1	—	12	1	14
Echinoidea	—	—	—	—	1	—	1
Merostomata	—	—	—	—	1	—	1
Branchiopoda	—	—	—	—	3	—	3
Malacostraca	—	5	—	1	39	2	47
Arachnida	2	—	1	—	1	1	5
Insecta	5	1	10	2	25	5	48
Total for methods	95	169	42	12	219	66	604

CTMax end points were used (e.g., increase in evaporative water loss; Geise and Linsenmair 1988).

We also include accounts of several invertebrate classes. Only 22% of all invertebrate accounts used CTMax methods, only 5% of these being observations of OS. The popularity of the LT method for invertebrates may be due to difficulty in observing OS in many invertebrate species. However, investigators have described OS in arachnids (Krakauer 1972), insects (Moulton et al. 1993; O'Neill and O'Neill 1988), and gastropods (Ohsawa and Tsukuda 1955, 1956a, 1956b).

Discussion

History of CTMax

Since Cowles and Bogert (1944) introduced the concept of the critical thermal maximum, there has been an increasing trend for its use in preference to LT methods (Figs. 1a, 1b). This increase indicates how Cowles and Bogert's classic paper impacted the field of thermal ecology. This trend toward the use of CTMax methods may also reflect its ease of use and the requirement for fewer animals and less time

than for LT methods. Although Cowles and Bogert's (1944) theoretical concepts and explanations of thermal ecology and tolerance were unparalleled for that time, they did not give detailed explanations and descriptions of an appropriate end point for CTMax. Their measurements of CTMax were taken from tethered reptiles under field conditions. They allowed animals to struggle toward shade until "effective coordinated movements had ceased." The "coordinated movements" were not described and "loss of righting response" was not mentioned. However, Brattstrom (1968) claimed that "coordinated movements" referred to elimination of the righting response. After removal of the animal to shade to prevent additional heat absorption, measures of T_b provided indices of CTMax (Cowles and Bogert 1944). Thus, an unstated heating rate, and an unclear definition of the end point in this widely cited work, may have led to the diversity of techniques subsequently used in CTMax procedures.

Zweifel (1957) was apparently the first to use and define OS as an end point (defined as "when movements became spasmodic"). Until Lowe and Vance (1955), no defined heating rate, and until Hutchison (1961), no attempts to define clearly the physiological basis for Cowles and Bogert's (1944) observations of "loss of effective coordinated movement" were made. These publications attempted to standardize the experimental protocol for measuring organismal thermal tolerance with the CTMax method. However, these and later attempts (e.g., Hutchison 1980; Paladino et al. 1980) failed to convince many investigators of the importance and physiological basis of OS in these protocols. The decreasing trend toward protocols using the OS end point (Fig. 1c) and an appropriate heating rate may be due to the 11 and 17 years of acceptance of diverse methods prior to Lowe and Vance (1955) and Hutchison (1961), respectively.

Acclimation and heating rate

Of all environmental parameters that influence thermal tolerance, the most important is the thermal history of an organism, especially just before testing. The effects of acclimation on CTMax have been well documented under laboratory conditions (e.g., Hutchison and Rowland 1974). Holland et al. (1974) demonstrated further differences in CTMax for fish acclimated under natural conditions (i.e., acclimatized) to higher temperatures in a nuclear cooling reservoir. Rates of acclimation to temperature are quite rapid in ectotherms, full acclimation usually occurring within hours to a few days. Acclimation is also significantly faster to high than to low temperatures (Hutchison 1976). Less than 24 h is required for full acclimation at temperatures above 20°C, but resistance to very low temperatures may be much greater: 4 days for acclimation from 20 to 4°C in newts (Hutchison 1961) and as much as 20 days for complete acclimation from 26 to 14°C in fishes (Brett 1944, 1946). Exposure to cyclic temperatures with "natural" 24-h periodicities usually results in faster acclimation than exposure to a constant temperature equal to the highest temperature during the cycle (Edney 1964; Heath 1963; Hutchison and Ferrance 1970; Lowe and Heath 1969).

Despite a large body of information on acclimation rates, some investigators use heating rates that allow acclimation to occur during observations of thermal tolerance. For example,

some investigators used a heating rate between 1.0 and 5.0°C · h⁻¹ (e.g., Baker and Heidinger 1996; Graham 1971; Hecht 1994; Kita et al. 1996; Smale and Rabeni 1995). Others (Guest 1985; Sadler 1979) used rates as low as 1.0°C · day⁻¹. Read and Cumming (1967), with an end point of "death," used a heating rate of 1.0°C per 3.5 days. Clearly, such low rates would allow acclimation to occur during the tests. These examples show that the effects of acclimation on thermal tolerance have often been ignored and may limit the validity of the results for future investigators. In the LT method, acclimation is incorporated in the procedure; exposure of fishes to a constant test temperature for 7 or more days is common (Fry 1967).

Temperature gain or loss by an organism during heating is dependent on thermal inertia. In addition to physiological influences such as vasomotor changes in circulation (Lillywhite 1987), the heating rate is greatly dependent on body mass (M_b) and the surface area to volume ratio. A rapid change in environmental temperature (T_e) can produce long lag times between T_e and T_b and may induce heat-shock effects (Barker et al. 1981; Hutchison and Murphy 1985). Using a heating rate of 1.0°C · min⁻¹, we found a highly significant relationship (Lutterschmidt and Hutchison 1997) between T_b and the chamber-water temperature (T_e) for different-sized fishes (*Lepomis macrochirus*) and frogs (*Rana catesbeiana*). These results showed that M_b , with no significant lag time between T_e and T_b , could be as great as 165 g at a heating rate of 1.0°C · min⁻¹ ($R^2 = 0.991$; T_e explained 99.1% of the variation in T_b). We believe that M_b could be considerably greater than 165 g and the R^2 value would still be high with the use of an appropriate heating rate (i.e., 1.0°C · min⁻¹).

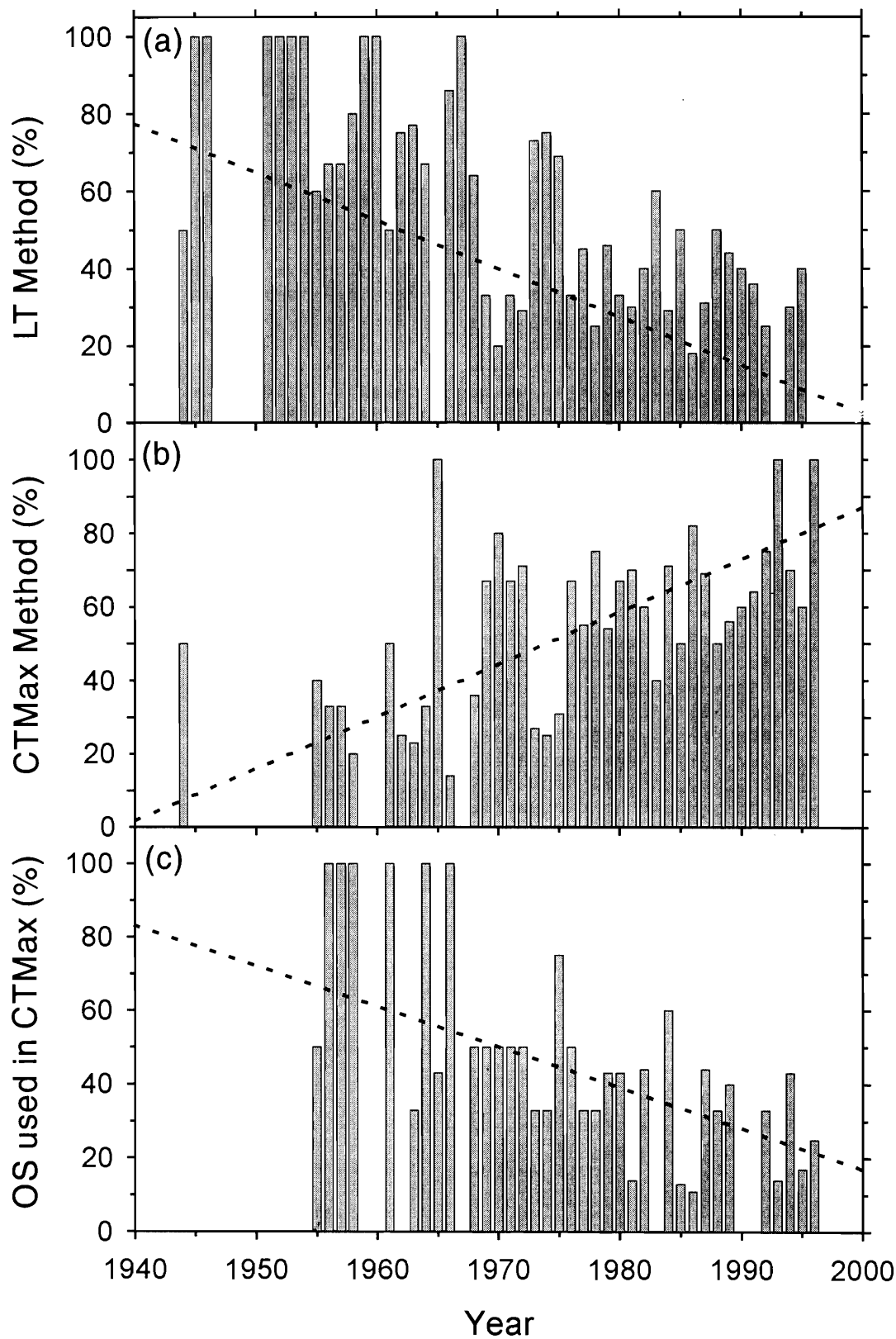
Most researchers recognize these concerns and avoid high heating rates. However, we found examples of 3.5°C · min⁻¹ (Lubin and Henschel 1990), 3.8°C · min⁻¹ (Heatwole et al. 1965), and 10.0°C · min⁻¹ (Martin and Gentry 1974). The latter rate is probably too high to avoid heat-shock effects and allow T_b to follow T_e without a significant lag time, regardless of the organism's small M_b . Some investigators failed to provide information on heating rate (e.g., Brown 1996; Hirth 1963; Larson 1961; Nietfeldt et al. 1980; Punzo and Rosen 1984). Some workers mixed static and dynamic methods by using a heating rate with the LT method (e.g., Whitfield and Livezey 1973) or a constant temperature (static method) with CTMax end points (Sanders and Jacob 1981).

Photoperiod: diel and seasonal cycles

Despite abundant evidence that photoperiod influences thermal tolerance as determined by either the LT (e.g., Hoar 1956; Roberts 1961) or CTMax method (e.g., Hutchison 1961), many investigators failed to control for day length. In general, long photophases result in increased heat tolerances and short photoperiods result in increased cold resistance (Hoar and Robertson 1959). Thus, conditions for acclimatization should include control for day length as well as temperature (Hutchison 1976).

Significant diel and seasonal cycles in thermal tolerance occur in most organisms (e.g., Dunlap 1969; Hutchison 1976; Kowalski et al. 1978; Layne et al. 1987). Both types of cycles result from the photoperiod exposures of animals under either laboratory or field conditions (Hutchison 1976).

Fig. 1. Chronological trends (shown by broken lines) in the use of various thermal-tolerance methods since Cowles and Bogert (1944); *a* and *b* illustrate the increased use of critical thermal maximum (CTMax) in preference to lethal temperature (LT) methods. However, *c* shows a decrease in the use of the onset of spasms (OS) end point in studies determining thermal tolerance with CTMax methods. Trend lines were generated by Sigmaplot® 1.0 (Jandel Scientific Software Corp. 1994).



Thus, time of day and season should be considered and reported with all measures of thermal tolerance. Time of day is especially important in the CTMax method, where test times are relatively short. In the LT method, exposure times to test temperatures are long (up to several days) and will usually mask diel cycles.

CTMax end points

Much of the confusion in selecting an appropriate end point for CTMax derives from the sequelae of the symptoms and behaviors observed during heating of an animal to stressful levels (Hutchison 1961; Brattstrom 1968; Paladino et al. 1980). As the temperature increases in a test chamber, an experimental animal increases its activity in an attempt to escape. Bouts of activity are often interspersed with inactive periods. These attempts to escape often continue until there is a period of inactivity in which LRR occurs; this is sometimes followed by another period of inactivity, and then OS. The spasms in ectothermic tetrapods often begin posteriorly with jerky, convulsive movements, spastic opening and closing of the jaw, and tremors of the digits (sometimes with an interlocking of digits on the hind limbs of salamanders and front limbs of frogs). The spasms may continue, sometimes intermittently, for up to 40–50 s. The animal is then motionless, and rigidity of the body (rigor) and finally death will follow. Animals usually survive if removed at OS and placed in a cold environment. In fishes the sequelae are similar, but may vary slightly. Becker and Genoway (1979) stated that OS “is much less distinct in fish and cannot be considered a reliable characteristic.” We found that rapid quivering of the opercula, although more difficult to observe than muscular spasms in amphibians and reptiles, serves as a clear and reliable marker for OS. These opercular spasms in fish are usually accompanied by body shuddering, gill distension, and mouth gaping (Lutterschmidt and Hutchison 1997; Paladino et al. 1980; Schaefer et al.¹). With continued heating, death occurs at various intervals after cessation of breathing, marked by a lack of opercular movement. The quivering of the opercula, however, always occurred in our tests, even when some other sequelae were absent or difficult to detect.

Transections of the central nervous system at various levels and blockage of the myoneural junction in anurans showed that the origin of the stimulus for muscular spasms at OS was anterior to the cerebellum; likely candidates include the hypothalamus and motor chain elements such as those in the tectum or tegmentum (Paulson and Hutchison 1987).

Because endotherms defend themselves against changes in T_b through a variety of physiological mechanisms, the sequelae during heating to stressful levels are significantly different from those in ectotherms. There is no clear LRR as such in mammals, but spasms (convulsions) occur and serve as an excellent end point for CTMax (Erskine and Hutchison 1982a, 1982b; Hutchison and Hart 1984; Wright 1976; Wright et al. 1977). Bynum et al. (1978) suggested that in endotherms, especially humans, CTMax is defined as “the

particular combinations of exposure time at elevated body temperatures that result in either subclinical (CTMs) or clinical (CTMc) injuries.” Hutchison (1980) pointed out that (i) this labeling of the sequelae seen in humans as subsets of CTMax was unnecessary and did not follow the original definition, and (ii) the catastrophic clinical symptomatology of heat stroke in humans fits the classic definition of CTMax and OS. As far as we know there have been no CTMax determinations in birds, although the LT method has been used extensively (e.g., Arjona et al. 1990; Bennett et al. 1981; Dawson and Bennett 1981; Johnson and Cowan 1975; Lahiri 1982a, 1982b; Marder and Bernstein 1983; Webb 1987), especially for poultry (e.g., Ait-Boulaheh et al. 1995; Cogburn et al. 1976; Collier and Schlesinger 1986; Nilsen 1981a, 1981b, 1984a, 1984b).

A variety of end points other than LRR and OS have been used as a measure of CTMax. These end points have included cessation of movement or absence of a response to prodding or similar disturbance (e.g., Buchanan et al. 1988; Dunlap 1968; Hoppe 1978; Kivivuori and Lahdes 1996; Menke and Claussen 1982; Miller and Packard 1974, 1977; Sanborn and Phillips 1996), loss of the nictitating membrane response (Krakauer 1970), posterior locomotor paralysis (Lashbrook and Livezey 1970), rigor (Feder and Pough 1975; Pough and Wilson 1970), coma (Gatz 1973; McMahon and Payne 1980), arching of the back (Burke and Pough 1976), absence of muscle tone (Pough et al. 1977), cessation of opercular motion in fishes (Chung 1981), failure to move one body length when probed (Appel 1991; Sponsler and Appel 1991), initial and total “disorientation” (Rodríguez et al. 1996), a sharp increase in evaporative water loss (Geise and Linsenmair 1988), knock-down temperature (Jenkins and Hoffmann 1994), inability to regain the righting response within 30 s (Layne et al. 1987), salivation (Hailey and Coulson 1996), and sudden secretion from the parotoid glands (Schmid 1965).

The problem of data interpretation caused by the use of such a diversity of end points has been exacerbated by inappropriate citations. For example, some investigators used end points other than OS but cited Hutchison (1961), who used spasms (e.g., Brattstrom 1963, 1965; Gatz 1973; Hlohowskyj and Wissing 1985; Lohr et al. 1996; Watenpaugh and Beiting 1985). Even end points not used in the determination of thermal tolerance have been incorrectly cited as appropriate for CTMax. Krakauer (1970) “used the loss of a nictitating membrane response (see Hutchison and Dady 1964).” However, the latter authors used this end point to measure submergence survival, not thermal tolerance, in anurans. Other investigators simply stated that their methods followed Cowles and Bogert (1944), but did not describe an end point (e.g., Curry-Lindahl 1979; Lemos-Espinal and Ballinger 1995) or simply miscited the methods and end points from earlier works (i.e., Cowles and Bogert 1944 and Lowe and Vance 1955), causing confusion (e.g., Brattstrom 1968; Graham 1971). Wedemeyer and McLeay (1981) define the CTMax end point as “permanent loss of equilibrium or death” and cite Hutchison (1961) and Paladino and Spotila (1978) as examples; the latter two papers used OS as the end point. CTMax values have been given with no description of the methods used (e.g., Bauwens et al. 1995). Becker and Genoway (1979) gave a definition of the CTMax concept in quotation marks and cited Cox (1974) as the source, when

¹ J.F. Schaefer, W.I. Lutterschmidt, and L.G. Hill. 1997. Physiological performance and stream microhabitat use by two centrarchids (*Lepomis megalotis* and *Lepomis macrochirus*). Submitted for publication.

the material described was originally from Hutchison (1961). Others have used the LT method but labeled the results CTMax (e.g., Grande and Andersen 1991). We emphasize that the conclusions drawn from the studies cited in the preceding two paragraphs are mostly valid, *based upon the end points used*.

The application of the CTMax concept has been mostly to ectothermic vertebrates, but it is clearly applicable to invertebrates. The OS end point works well with most invertebrates, where it is marked by spasms of the legs or muscle tremors in arthropods (e.g., Moulton et al. 1993; Perttunen and Lagerspetz 1956; Seymour and Vinegar 1973) and sudden foot extrusion due to spasmodic contractions of the annular muscles in molluscs (Hamby 1975; Ohsawa and Tsukuda 1955, 1956a). The latter authors, however, did not label their method CTMax. Polcyn (1994) used loss of muscle coordination as a measure of heat tolerance in dragonflies; although he did not use the term CTMax, the end point is likely the equivalent of OS.

Death, coma, and rigor as end points have seldom been defined. Just when does "death" occur? How is death distinguished from coma and rigor? The physiological point of death is difficult to determine unless cessation of heart contractions or central nervous system activity or other criteria are stated as end points and measured directly. Physiological "death" does not often occur at the time that breathing movements stop, especially in aquatic animals with cutaneous and branchial gas-exchange structures. For example, we always observed continued heart beats and blood circulation in animals after both LRR and OS, sometimes right up to the point of rigor (i.e., when the body becomes rigid). In contrast to the LT method, animals exposed to OS will survive if removed immediately from the heating chamber and placed in a low-temperature environment. We do not object to death being measured as an additional end point, as suggested by Becker and Genoway (1979), but a clear definition is required and death should not be equated with CTMax but reported as an additional measurement.

Measures of generalized tissue damage (serum levels of glutamic oxaloacetic and glutamic-pyruvic transaminases, total proteins, and urea nitrogen were not altered significantly by exposure to OS in toads (Paulson and Hutchison 1987). Also unaffected were hematocrit, numbers of erythrocytes in circulation, mean cell volume, and hemoglobin concentration. There were significant increases in blood glucose, lactic acid, and creatine phosphokinase (CPK) concentrations, blood pH, PO_2 , and HCO_3 concentration; P_{CO_2} decreased. Frogs exposed to CTMax developed heart lesions (Carlsten et al. 1983). Additional studies on both the short- and long-term effects of exposure to LRR and OS are needed.

For many species, tolerance of low temperature may be more important than heat tolerance in governing geographic distribution. Although we have limited our discussion to CTMax, we emphasize that LRR is an appropriate end point for CTMin. LRR fits Cowles and Bogert's original definition, since LRR at low temperatures prevents an animal from moving any significant distance in order to escape.

At LRR in many animals, locomotion is in a fairly straight direction and often persists beyond the point of LRR. For example, fishes can still swim and some reptiles can still

move with lateral undulatory motion after LRR and could therefore escape from conditions that would, if continued, lead to their death. Thus, LRR does not meet the criteria of Cowles and Bogert's (1944) original definition. Berkhouse and Fries (1995) agree that at LRR in salamanders (*Eurycea nana*), the animals "conceivably could have escaped local high temperatures by random whole body movements," and at OS "the salamanders effectively were immobile."

Unlike T_b associated with OS, the temperature at LRR is not high enough to produce heat-hardening (Maness and Hutchison 1980), which is a transitory increase in heat tolerance following exposure to lethal high temperatures. Heat-hardening is likely adaptive; it provides a means of acute adjustment to extreme fluctuations in ambient temperature (reviewed by Maness and Hutchison 1980). Thus, OS temperatures provide information not available from LRR data.

Frogs, and presumably other vertebrates, can learn to inhibit the righting reflex. Such a response may serve as an ecologically relevant passive-avoidance response to predators, although habituation as an explanation of LRR is not ruled out (Rice and Taylor 1995). Since the inhibition of the righting response can easily be increased by operant-avoidance procedures (reviewed by Suboski 1992), and species differ in learning abilities with such procedures (Harvey et al. 1981), the use of LRR as an end point of thermal tolerance may be suspect. No similar mechanisms have been demonstrated or suggested for OS.

Statistical comparisons of the CTMax end points LRR and OS

Lutterschmidt and Hutchison (1997) demonstrated that there is significantly more variance associated with the end point LRR than OS for a diversity of taxa. Additionally, tests of the homogeneity of paired variances of LRR and OS showed that these variances differed significantly only when LRR variance was greater than OS variance. Although OS variance was sometimes greater than LRR variance for some species, the homogeneity of these within-species LRR and OS variances did not differ statistically. These results suggest that OS is a more valuable and meaningful CTMax end point than LRR because of its greater precision.

Ontogenetic differences in LRR occur in the lizard *Cophosaurus texanus* (Lutterschmidt and Durtsche),² but differences in OS were observed among size classes. This further suggests the appropriateness of OS as the definitive end point in determining species-specific thermal tolerance.

Heat-shock proteins

When cells or whole organisms are exposed to high but sublethal temperatures, as well as to other stressors, synthesis of a set of special proteins is induced. These heat-shock proteins (HSP) occur in organisms from archeobacteria to mammals and are thought to protect normal cellular protein during heat (or other) stress and to facilitate cellular recovery after the

² W.I. Lutterschmidt and R.D. Durtsche. Thermal physiology and metabolic capacities of a desert dwelling lizard (*Cophosaurus texanus*): answers to behavioral and ecological observations. Submitted for publication.

stress is removed (Craig 1985; Morimoto et al 1990). The HSP response may be a mechanism for surviving what would otherwise be a lethal temperature (Spotila et al. 1989). At least some HSPs are in cells under normal (no heat shock) temperatures and the amount of HSP in ectotherms may be correlated with the mean temperatures of their habitats as well as whole-animal thermoresistance (Ulmasov et al. 1992). In adult salamanders, synthesis of HSPs increased after exposure to OS, but did not always coincide with increased thermal tolerance (Easton et al. 1987). In the frogs *Lepidobatrachus laevis* (Carroll 1996) and *Xenopus laevis* (Heikkilä et al. 1985), HSP synthesis was correlated with tolerance of heat shock. Larvae of *Lepidobatrachus* spp. formed two different sets of HSPs that were independent of developmental stage or severity of heat shock. There may be two states of thermal tolerance, a temporary response that does not require synthesis of HSPs and a longer term delayed response that does require synthesis of new HSPs (Boon-Niermeijer et al. 1986). Since the temperatures necessary to induce synthesis of HSPs vary from species to species, as do the molecular weights of the HSPs at different temperatures (Lindquist 1986; Lindquist and Craig 1988), the HSPs produced at the temperatures of LRR and OS may vary both quantitatively and qualitatively. The more severe stress of OS may produce different HSPs than that of LRR. More studies of the relationships of HSP production at LRR and OS and increased thermal tolerance of the organism are needed (Near et al. 1990).

Predictive models of thermal tolerance

Several investigators have suggested that UILT and CTMax end points may be related in some predictable manner (Becker and Genoway 1979; Cox 1974; Fry 1967). Kilgour et al. (1985) provided a useful model of the static method for determining lethal high temperatures in fishes. Applications of the model to data in the literature predicted "UILTs usually within 0.5°C and almost always within 1.0°C of observed values." The model allows UILT to be predicted from measurements of shorter term exposures, thus reducing the time usually needed for accurately measuring LT. Kilgour and McCauley (1986) also constructed a heuristic model in an attempt to reconcile results from the LT and CTMax methods for upper lethal temperatures. Although they concluded that "data from either type of experiment can be used to predict the observations from an experiment of the other type under certain assumptions," they caution that the two methods are "technically different" and "measure different things." In both the static and dynamic methods, tolerance of high temperatures increases with acclimation temperature only to a certain point. AT temperatures above this point, thermal tolerance (CTMax or thermal resistance) does not increase; either a plateau occurs (i.e., often in the LT method) or the slope of the line decreases significantly (mostly in the CTMax method; Fry 1967; Hutchison 1976). Thus, the lines delimiting resistance polygons determined from static versus dynamic methods are often not parallel. This nonlinearity makes the construction of predictive models difficult. Because of these differences and the limited verification observed, we believe that the model is not yet adequate for general use, but the results emphasize the importance of acclimation and

heating rates in both the CTMax and LT methods. Hopefully, new revisions of the model will make it a better tool for valid predictions.

Bennett and Beiting (1997) discuss the use of thermal tolerance polygons for CTMax and CTMin data, but with LRR as an end point. They show that these polygons are useful in a similar manner to polygons constructed from LT data.

Natural occurrence of CTMax

Over many years, critics have suggested that measurements of LT or CTMax are unrealistic in that such temperatures are seldom experienced by organisms in the field. Such views are exemplified by Rome et al. (1992): "Although compensatory acclimation to CTMax is real, reproducible, and widespread among amphibians, the changes are small in magnitude, and the ecological significance of this response and the benefit to the animal are unproven." According to Feder (1982): "The evident capabilities for behavioral thermoregulation and the paucity of field body temperature records that are at or near lethal temperatures suggest that amphibians generally do not experience extreme temperature." Rome et al. (1992) also suggest that thermal tolerance is not directly important but "is correlated with thermal responses that have a more direct bearing on the ecology of amphibians." They then discuss the likelihood that desert amphibians may be an exception. Bradshaw (1992) expresses the view that desert reptiles may never be exposed to thermal stress in their environment. These critics have apparently failed to consider that it is the extremes of environmental conditions, not the means, which exert the most selective pressures. Extreme conditions are relatively rare and thus not frequently observed, but over evolutionary time can certainly exert a major influence (Huey and Kingsolver 1989). Indeed, most field biologists recognize that temperatures in many environments can exceed the tolerance limits of ectotherms (e.g., Gunter 1941). These animals have mostly behavioral characteristics that approach their thermal tolerance. However, animals trapped in conditions that do not allow escape will often die from heat before they would have succumbed to other lethal conditions. Examples include desert amphibians (especially tadpoles) in ephemeral pools, fish trapped in shallow tidal pools or isolated pools in stream beds, lizards trapped in rocks, and aquatic organisms in or near hot springs (e.g., Bailey 1955; Heatwole and Harrington 1989; Littlewood 1989; Matthews and Hill 1982; O'Neill and O'Neill 1988; Tramer 1977). The concept of "excessive construction" suggests that the phenotypic capacities of animals are shaped by rare events that may be critical to an animal's survival, rather than by routine activities or events; thus, "most aspects of phenotypes will, at any moment of an individual's life, be capable of fulfilling demands much greater than those routinely encountered" (Gans 1979). The assertion by Rome et al. (1992) that tolerance of high temperature is not directly important but is related to other thermal responses more important to an animal's ecology is a caution against a Panglossian fallacy (Gould and Lewontin 1979). However, conventional wisdom and direct observations suggest that animals do indeed meet, though rarely, lethal thermal conditions in natural environments.

CTMax and its importance to ecophysiological theory

Physiological tolerances are central to an understanding of species distribution and adaptation. Liebig's "Law of the Minimum" states that species distribution is governed by those factors for which a species has the narrowest tolerance range or the least adaptability (Bartholomew 1958). The investigation and quantification of thermal tolerance across geographical clines (e.g., Christian et al. 1988; Howard et al. 1983; Lemos-Espinal and Ballinger 1995; Manis and Claussen 1986; Matthews 1986) have allowed for an evaluation of differences in the ability of a species to cope with and adapt to variation in temperature. However, unlike thermal acclimation, temperature adaptation requires genetic change over evolutionary time. Investigators (e.g., Ward and Seely 1996) have examined how harsh thermal environments select for genotypes that allow plasticity in physiological traits. Such investigations are essential to ecophysiological theory, for they explain how physiological plasticity in adapting to extremes (e.g., CTMax) increases performance breadths having a direct influence upon activity, niche diversification, and geographic distribution, which ultimately lead to changes in communities and ecosystems.

Although we do not address thermal tolerance in plants, the amount of recent literature is overwhelming. Many of the studies on thermal tolerance in plants address important questions (e.g., Loik and Harte 1996), and their discussions of ecophysiological theory should not be overlooked.

CTMax in comparative physiology and the comparative phylogenetic method

Studies in comparative animal physiology involve "the comparing and contrasting of physiological mechanisms, processes, or responses of different species of animals, or of a single species under differing conditions" (Withers 1992). An underlying assumption of any comparative study, however, is that all individuals and species have received identical experimental treatments. Additionally, current trends in comparative physiology require controls for phylogeny (Felsenstein 1985, 1988), if valid comparisons and contrasts are to be made among taxa. Although these controls for phylogeny have now become common practice in studies in comparative physiology (e.g., Bauwens et al. 1995; Huey and Bennett 1987; Walton 1993; Ward and Seely 1996), the validity of combining data from different studies in which various experimental protocols have been used has received little attention. This is an important consideration, since investigators of comparative physiology are encouraged to use data from different studies to address more theoretical and evolutionary questions in physiological ecology (e.g., Huey and Bennett 1987; Huey et al. 1991; Snyder and Weathers 1975). Garland et al. (1991) investigated possible evolutionary changes in thermal physiology by using phylogenetic analysis and data from different studies (i.e., Bennett and John-Alder 1986 and Huey and Bennett 1987). This comparative study controlled for both phylogenetic relationships among taxa and valid comparisons of thermal tolerance by using data obtained with identical methodologies.

Correlations between physiology and aspects of behavior or ecology have been frequently explained as being adaptations through natural selection (Endler 1986; Feder 1987).

The practice of testing correlates of physiological traits among species and then assuming that the results demonstrate adaptation has been criticized for its failure to consider the phylogenetic history of the organism studied (Felsenstein 1985, 1988). However, differences in species-specific thermal tolerance (due to varying experimental protocols) among species are rarely criticized.

To illustrate the problems of combining data from different studies using varying protocols, we collected species-specific thermal tolerance data on *Cyprinella (Notropis) lutrensis* from seven independent studies (Table 2). The CTMax values reported for this species ranged from 31.9 to 39.65°C. We used these seven values to calculate a grand mean and variance of 35.86 and 6.59°C, respectively. This variance of the values from the combined studies and protocols is more than eight times our reported variance, and differs significantly ($F_{[6,19]} = 8.24$, $P < 0.001$). Thus, the species-specific variability in *C. lutrensis* is presumably due to differences in experimental method (e.g., acclimation temperature, T_a). If we consider comparisons of independent studies using identical experimental protocols (e.g., $T_a = 21^\circ\text{C}$, Matthews 1986, 1987; or $T_a = 15^\circ\text{C}$, Kowalski et al. 1978; Maness and Hutchison 1980; Schubauer 1980), we find very similar CTMax values among studies. For *C. lutrensis*, Matthews (1986, 1987) showed a difference of only 0.5°C in CTMax values. More interestingly, Kowalski et al. (1978), Maness and Hutchison (1980), and Schubauer (1980), using identical experimental protocols (Table 2), show a difference of only 0.1°C among three different (in the taxonomy of that time) *Notropis* species. This suggests that the method used may have a greater influence on CTMax than real species differences.

Our CTMax for *C. lutrensis* is approximately 2°C higher than that reported in the latter three papers. This may be due to the seasonal effects of summer thermal regimes prior to measurement of CTMax in early fall; determinations of thermal tolerance in the other studies were made during winter. This observation again emphasizes the importance of using similar methods, and to include controls for seasonality.

Conclusion

The tolerance of animals toward a single environmental factor such as temperature is typically greater than their tolerance of combinations of environmental factors studied simultaneously. Reproduction of the holocoenotic environment and its variability in the laboratory is not feasible, but the modification of thermal tolerance by many environmental factors (e.g., photoperiod, diel and seasonal cycles, concentrations of respiratory gases, pH, salinity, diet, reproductive status) should be recognized and controlled for as far as possible. Thus, tolerance of high temperature must eventually be studied as part of multiple-factor interactions. The use of standardized methods and terminology will allow for comparisons of data obtained by different investigators and will ultimately facilitate the necessary multiple-factor approach (Hutchison 1976).

We have demonstrated that OS is a more meaningful end point than LRR, owing to its precision and greater physiological relevance. Although OS is more biologically meaningful, we recommend that both LRR and OS be determined and

Table 2. Summary of experimental protocols used in 10 different studies in which CTMax data were collected on the fish *Cyprinella (Notropis) lutrensis* and three closely related species.

Acclimation temp. (°C)	Photoperiod	Acclimation length	Heating rate	End point	CTMax	s ²	n	Reference
20	Unknown	≥ 1 week	0.3°C · min ⁻¹	LRR	35.03	1.69	11	Carrier and Beiting 1988
15	12 h L: 12 h D	2–4 weeks	1.0°C · min ⁻¹	OS	31.8	0.80	5 ^a	Kowalski et al. 1978
10	12 h L: 12 h D	2 weeks	1.0°C · min ⁻¹	OS	34.04	0.80	20	Lutterschmidt and Hutchison 1997
15	12 h L: 12 h D	≥ 1 week	1.0°C · min ⁻¹	OS	31.9	0.30	82	Maness and Hutchison 1980
21	12 h L: 12 h D	14–20 days	1.0°C · min ⁻¹	LRR	35.90	0.17	15	Matthews 1986
21	12 h L: 12 h D	14–20 days	1.0°C · min ⁻¹	LRR	36.41	1.69	86	Matthews 1987
Unknown	Unknown	≤ 3 h	0.5–0.8°C · min ⁻¹	LRR	36.2	1.00	6 ^b	Mundahl 1990
30	12 h L: 12 h D	≥ 2 weeks	0.3°C · min ⁻¹	LRR	39.65	0.05	10	Rutledge and Beiting 1989
26	14 h L: 10 h D	63–160 days	2.0°C · h ⁻¹	LRR	38.1	0.18	11	Smale and Rabeni 1995 ^c
15	12 h L: 12 h D	3 weeks	1.0°C · min ⁻¹	OS	31.9	1.00	8 ^d	Schubauer et al. 1980

Note: LRR, loss of righting response; OS, onset of spasms; s², variance.

^aFor *Notropis rubellus*.

^bFor *Notropis chryscephalus*.

^cAuthors termed the end point the critical maximum temperature and did not use the term critical thermal maximum.

^dFor *Notropis cornutus*.

reported (e.g., Berkhouse and Fries 1995) for future comparisons with the results of past studies. We also encourage the use of additional end points, if they are clearly defined and if the value of OS is determined. Most importantly, when comparing and contrasting thermal tolerance of species from different studies, we recommend that investigators consider possible differences in experimental method (i.e., acclimation, heating rate, etc.), otherwise phylogenetic, ecological, and (or) evolutionary conclusions drawn from studies using different protocols may be invalid. We advocate the use of OS, as the most biologically relevant end point, and hope that its adoption will facilitate the development of standard definitions and techniques for making valid comparisons of the results of future studies.

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