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IN SMALL MAMMALS

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This study was conducted while I was a graduate teaching assistant in the Department of Zoology at the University of Oklahoma. Paper I was prepared for submission to The Journal of Thermal Biology. Paper II was prepared for submission to The Journal of Mammalogy.

TABLE OF CONTENTS

Page

List of Tables v

List of Illustrations vi

PAPER I Critical thermal maximum as a determinant of thermal tolerance in *Mus musculus*

Abstract 1
Introduction 2
Materials and Methods 5
Results 8
Discussion 11
References 15
Tables 19
Table Headings 22
Figures 23
Figure Captions 27

PAPER II Critical thermal maxima in small mammals

Abstract 28
Introduction 28
Methods 31
Results 34
Discussion 36
Literature Cited 40
Tables 44
Figures 46
Figure Captions 48

LIST OF TABLES

PAPER I

Table — Page

I Comparison of critical thermal maxima, elevated defended temperatures, and initial body temperatures of Mus musculus between two photoperiods (LD 12:12 vs LD 18:06) at six times of day 19

II Comparison of the difference between initial body temperature, elevated defended temperature, ΔT, and heating times of Mus musculus between two photoperiods (LD 12:12 vs LD 18:06) at six times of day 20

III Critical thermal maxima, elevated defended temperatures, ΔT, initial body temperature, and heating times of Mus musculus acclimatized to a LD 12:12 photoperiod and one of four thermal regimes 21

PAPER II

Table

I Critical thermal maxima, elevated defended temperatures, ΔT, initial colonic temperature, and heating times for five species of small mammals 44

LIST OF ILLUSTRATIONS

PAPER I

Figure | Page
I Examples of Type I, II, and III heating patterns for *Mus musculus* 23

II Critical thermal maxima and elevated defended temperatures of *Mus musculus* at six times of day 24

III Results of Duncan's New Multiple Range Test for the critical thermal maxima of *Mus musculus* at six times of day 25

IV Critical thermal maxima and elevated defended temperatures of *Mus musculus* acclimatized to LD 12:12 and one of four thermal regimes 26

PAPER II

Figure

I Examples of Type I, II, and III heating patterns for *Mus musculus* 46

II Critical thermal maxima and elevated defended temperatures of five species of small mammals 47

PAPER I

CRITICAL THERMAL MAXIMUM AS A DETERMINANT OF THERMAL TOLERANCE IN *MUS MUSCULUS*

THE CRITICAL THERMAL MAXIMUM AS A DETERMINANT OF THERMAL TOLERANCE IN _MUS MUSCULUS_

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1. The critical thermal maximum (CTM) was used to assess thermal tolerance in _Mus musculus_ acclimatized to two photoperiods and four thermal regimes.

2. Mice acclimatized to 25±1 C and LD 12:12 had a unimodal diel cycle in CTM while mice exposed to 25±1 C and LD 18:06 displayed a bimodal cycle in CTM.

3. Acclimatization to constant temperatures (15 C, 25 C, and 30 C; LD 12:12) had no effect on CTM but acclimatization to a cycling thermal regime 15 C to 30 C; LD 12:12) significantly increased the CTM.

4. These data support the suggestion of susceptibility-resistance cycles to heat stress and indicate that the CTM's of endotherms can be altered by internal and external modifying factors.

INTRODUCTION

The critical thermal maximum (CTM) was originally defined by Cowles and Bogert (1944) 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". Lowe and Vance (1955) modified this definition to include statistical variation and the methodology was standardized by Hutchison (1961). The CTM has since been used extensively in studies of thermal tolerance in terrestrial and aquatic ectotherms. The attractiveness of this method for determining the thermal tolerance of individual animals lies in the economy of time and experimental animals. Because the CTM is determined under short term exposures to high temperatures, the CTM values are generally higher than the lethal temperatures determined from resistance times at elevated temperatures (Fry, 1967). Thus, the CTM is not lethal for ectotherms and is considered an ecological maximum temperature rather than a physiological lethal temperature (Hutchison, 1976). Numerous factors can influence thermal tolerance. Among the modifying influences are seasonal changes, photoperiod, diel variation, body water content, and thermal history (Hutchison, 1976).

Adolph (1947) examined the tolerance to heat and dehydration in seven species of mammals and found that those species varied greatly in their capacities for evaporative cooling and in their temperature sensitivity. He also found delayed deaths in four species of mammals (dog, cat, rabbit, and guinea pig), following heat shock. The duration of this delay appeared to be positively correlated with the size of the animals and with their capacity for evaporative cooling.

The colonic heating patterns of mammalian species exposed to severe heat stress are assigned to one of three forms (Wright et al., 1977) (Fig. 1.).

Type I individuals conform to an approximately linear heating pattern from initial body temperature to CTM. The initial rapid increase in body temperature of Type II individuals during segment 1 of the heating curve is slowed during segment 2 presumably through the action of physiological and behavioral cooling mechanisms. The heating curve during segment 2 is again approximately linear to the CTM. The temperature at which the transition from segment 1 to segment 2 occurs is termed the "equilibrium temperature" (Ohara _et al._, 1975; Wright _et al._, 1977). Type III individuals display a three-stage heating curve. The initial rise in segment 1 is similar to type I and II individuals but segment 2 of the heating curve is characterized by sustained maintenance of body temperature at an elevated level. Often there are decreases in body temperature and/or fluctuations of body temperature around this elevated steady state. Type III individuals undergo an explosive rise in body temperature (segment 3) to the CTM at the end of segment 2. The transition point between segment 2 and 3 is the "thermoregulatory breakdown temperature" (Ohara _et al._, 1975; Wright _et al._, 1977).

Ohara _et al._ (1975) exposed unanaesthetized rats to an ambient temperature of 42.5 C and examined the response pattern of rectal temperature. They were able to derive an equation to predict the survival time for rats exposed to severe heat stress. Others have described the colonic heating patterns of rats exposed to sublethal heat stresses (Hainsworth and Stricker, 1970, 1971 ; Stricker and Hainsworth, 1970).

Wright (1976) first applied the definition of CTM to mammals and Wright _et al._ (1977) examined colonic heating patterns and thermal resistance in rats exposed to high temperatures. Bynum _et al._, (1978) extended the use of CTM to human subjects and attempted to redefine the CTM in terms of both temperature and exposure time. Hutchison (1980) argued that the attempt to redefine the

CTM in terms of subclinical and clinical injuries was inappropriate because the subclinical CTM covered a broad range of physiological events resulting from sublethal hyperthermia.

The CTM has been a popular tool among ichthyologists and herpetologists for determining the temperature sensitivity of ectothermic vertebrates (Hutchison, 1961; Kosh and Hutchison, 1968; Hutchison and Ferrance, 1970; Seibel, 1970; Spellerberg and Hoffman, 1972). However, the CTM has received little attention as a possible indicator of thermal tolerance in endotherms. This study was undertaken to 1) determine if the CTM is a valid index of thermal tolerance in endotherms, 2) attempt to standardize the methodology used in CTM determinations of small mammals, 3) evaluate the influence of external factors on the mammalian CTM, and 4) assess the thermoregulatory capacity of small mammals exposed to acute heat stress.

MATERIALS AND METHODS

Male and non-pregnant female white mice (Mus musculus) were randomly selected from an inbred group (originally derived from mixed strains) and placed into one of two test groups. The animals were housed 5-6 per cage in Sherer environmental chambers. Purina chow pellets and water were available ad libitum. The chambers were opened daily and bedding changed 3-4 times each week. All animals were acclimatized for at least 14 and not more than 21 days prior to CTM determinations.

Animals were removed from acclimatization and weighed to the nearest 0.1 g. A 36 gauge copper/constantan thermocouple sheathed in polyethylene tubing was inserted through the rectum into the colon and taped to the tail. The animals were maintained for a 10-20 minute equilibration period to allow body temperatures to stabilize.

A Temp-Air Convector System (Scientific Instruments, Inc., Skokie, IL) provided dry heated air (relative humidity <15%) to the testing apparatus. The heated air was blown into a centralized separator chamber and then channeled to each of four test chambers (13 cm wide x 18 cm long x 10 cm high) through tygon tubing fitted with Hoffmann pinch clamps to control air flow. The entire apparatus was insulated with styrofoam.

Test chamber temperatures of 40.0±1 C were monitored with a Digitech Model 581C digital thermometer. Animal temperatures were monitored continuously with a Bailey Instruments BAT-8 digital thermometer and recorded every 5 minutes.

Behavioral observations included posturing, forepaw licking, breathing rate, and loss of righting response. The onset of spasms, characterized by uncoordinated spasmodic twitching of the limbs, was used as the endpoint for the CTM determination. Following exposure to the CTM the animal was immediately removed from the test chamber and cooled as rapidly as possible. The thermocouple was then removed and the animal was reweighed.

Group 1: This experimental group was used to examine diel variation in critical thermal maximum. Photoperiods of LD 12:12 and LD 18:06, with the photophases centered at 1200 CST, were used for comparison. Environmental chamber temperature was 25±1 C in both cases. Animals were removed from acclimatization and CTM determinations were carried out at each of six times (0200, 0600, 1000, 1400, 1800, 2200 CST). CTM determinations made in the scotophase of each group were done under red light or low light conditions.

Group 2: To examine the effect of immediate thermal history these animals were divided into three groups and acclimatized to one of three temperatures (15 C, 30 C, or a cycling thermal regime of 15 C to 30 C) and a LD 12:12 photoperiod with the photophase centered at 1200 CST. A Sherer environmental chamber equipped with a Partlow Temperature Programmer provided a controlled temperature cycle; 15 C was maintained for 1 hour (0600-0700 CST) in the environmental chamber and temperature was then increased linearly to 30 C and held for 1 hour (1800-1900 CST); chamber temperature was then returned to 15 C and the cycle was repeated. All CTM determinations were carried out between 1000 and 1200 CST.

Heating curves were determined for each animal by plotting colonic temperature (Tc) every 5 minutes (Fig. 1.). Each curve was inspected to determine if an individual exhibited a Type I, II, or III heating pattern and a best fit line was computed for each segment with the method of least squares (Sokal and Rohlf, 1969). The intersections of the best fit lines for Type II and III heating curves were determined to compare the heating times in segments 1 and 2. Type III individuals typically exhibited an immediate decline in colonic temperature at the onset of segment 2. However, Tc fluctuated above and below the best fit line throughout segment 2. Rather than compute an "equilibrium temperature" (Ohara, et al. 1975; Wright, et al. 1977) at the intersection of segments 1 and 2, a mean body temperature around which Tc fluctuated during segment 2 was calculated. The increased level in body tmeperature calculated for segment 2 was termed the elevated defended temperature (EDT) (Fig. 1.). The difference between initial body temperature and the EDT, ΔT, was used for further comparisons between those animals exhibiting a Type III heating pattern. Total time spent in segments 1 and 2 of the heating curve and total time to thermoregulatory breakdown were also examined.

All data were initially tested for normality and homogeneity of variance. Single classification analysis of variance, Student's t-test, and Duncan's New Multiple Range Test (Duncan, 1955) were used for further analyses. All statistical analyses were performed with the Statistical Analysis System (Barr et al. 1976).

RESULTS

Type III heating patterns predominated in both experimental groups. However, Type I and Type II patterns did occur: 3 Type II in LD 12:12, 10 Type II and 4 Type 1 in LD 18:06; 2 Type II in 30 C, 2 Type II, and 1 Type I in the 15 to 30 C cycle. The distribution of heating patterns and weight loss were not related to sex of the animals or time of day, nor were there sex related differences in CTM, EDT, ΔT, heating time in segment 1 or 2 of the heating curve, or in total time to thermoregulatory breakdown.

The mortality rate in this study was effectively 100%; of those animals that did survive the initial exposure to the CTM (less than 5%) none survived for more than 6 hours. The mortality remained at 100% despite rapid cooling and administration of water. All experimental animals exhibited a set sequence of behavioral responses to the induced hyperthermia. During the initial heating period, when the animals were most active, there was an apparent passive increase in colonic temperature. When an active defense of body temperature was undertaken the animals would reduce activity, spread saliva for evaporative cooling, increase breathing rate, and assume a prostrate posture.

Experimental Group 1: Significant diel variation in critical thermal maximum occurred under both photoperiod regimes (Figs. 2. and 3.). A significant ($F=3.13$, $P<0.02$) unimodal cycle existed in LD 12:12 with mid-photophase values significantly lower than scotophase values. A diel cycle ($F=5.85$, $P<0.01$) in CTM was also present in those animals exposed to a LD 18:06 photoperiod. However the latter cycle was bimodal with peak values at 0600 (three hours after lights-on) and 2200 (one hour after lights-off). The results of a multiple comparison test on the CTM in each photoperiod is summarized in Fig. 3.

There was no diel variation in the elevated defended temperature in LD 12:12. However, a bimodal cycle ($F=2.66$, $P<0.05$) was present in LD 18:06. Peak values for EDT in 18:06 occurred at 0200 (one hour before lights-on) and 1400 (two hours after mid-photophase). The diel variation in EDT did not coincide with the cycle for CTM in 18:06 although a bimodal cycle was exhibited in both instances.

The CTMs of the 18:06 group were significantly lower than those of the LD 12:12 group at 0200, 1400, and 1800 hours (Fig. 1., Table 1.). The EDTs of the LD 18:06 group were significantly lower at all times except 1400 (Fig. 1., Table 1).

Those animals exposed to a LD 12:12 photoperiod showed no significant diel variation in ΔT, heating time in segments 1 or 2, heating time to thermoregulatory breakdown, or weight-specific weight loss. Animals exposed to a LD 18:06 photoperiod showed significant differences ($P<0.05$) in all the above categories except heating time in segment 1. The ΔT at 1000 was lower than at all other time periods and total heating time in segment 2 and heating time to thermoregulatory breakdown were greater ($P<0.01$) at 1000 than at any other times (Table 2). Weight loss was greater ($P<0.05$) at 2200 (0.087 $g\ g^{-1}$ initial body weight) than at 1400 (0.051 $g\ g^{-1}$ initial body weight). There were no differences in weight loss among any other times of day.

Heating time in segment 1 was shorter ($P<0.05$) in the LD 18:06 group at all hours except 0600 (Table 2.). Total heating time to thermoregulatory breakdown and total time in segment 2 were longer ($P<0.01$) in the LD 18:06 group at 1000 when compared to LD 12:12 at 1000. There was no significant diel variation in the initial Tc in either photoperiod. However, the initial Tc was lower ($P<0.01$) in the 18:06 group at 0200, 0600, 1800, 2200 and ($P<0.05$) 1400 (Table 1.). The mean initial Tc for all 18:06 animals (36.65±0.31 C) was significantly lower (t=3.95, P<0.01) than the mean initial Tc for all 12:12 animals (38.35±0.30 C). The ΔT was significantly (P<0.05) higher in LD 18:06 animals at 0200, 0600, and 2200 (Table 2.). The ΔT was also higher in LD 18:06 animals at 1400 and 1800 although the difference was not significant. There was no difference in weight loss among the two groups at any time of day.

Experimental Group 2: The mean CTM of those animals exposed to a cycling thermal regime of 15 to 30 C (43.75±0.25 C) was significantly (P<0.05) higher than the CTM of 25 C (42.62±0.23 C) and 30 C (42.89±0.27 C) acclimated animals but was not different from 15 C (43.26±0.27 C) acclimated animals (Fig. 2., Table 2.). There were no differences between 15, 25, and 30 C acclimated animals. There were also no differences among the EDTs at each acclimation temperature.

Animals acclimatized to the cyclic thermal regime also had significantly higher (P<0.01) ΔTs than all other groups (Table 3.). Heating time in segment 1 of the heating curve was significantly longer (P<0.05) in 25 C animals than in the other three groups and longer in 15 to 30 C cycle animals than in 30 C animals (Table 3.). The mean initial Tc of animals in the 15 to 30 C cycle was significantly lower (P<0.05) than all other groups (Table 1.). Total time to thermoregulatory breakdown and heating time in segment 2 of the heating curve were not different in any of the groups (Table 3.). There were no differences in weight loss of animals among any of the acclimatization conditions.

DISCUSSION

Circadian rhythms in body temperature and activity have been studied extensively in endotherms. Randall and Thiessen (1980) examined daily variation in activity and body temperature in the mongolian gerbil. Body temperature rhythms have also been studied in man (Czeisler et al., 1977), primates (Fuller et al., 1978, 1979), and birds (Farner, 1956). Nakayama et al. (1979) reviewed the evidence implicating the suprachiasmatic nucleus as the central region for controlling body temperature rhythms in endotherms.

Diel cycles in temperature tolerance occur in reptiles (Kosh and Hutchison, 1968; Spellerberg and Hoffman, 1972) and amphibians (Mahoney and Hutchison, 1969; Seibel, 1970; Johnson, 1971). Changes in thermal resistance of ectothermic animals in response to changes in the photoperiod to which they are exposed have been reported by Hoar (1956), Roberts (1961), Hutchison (1961), and Hutchison and Kosh (1965).

There are also indications that the time of day when a stress is applied will have an effect on the susceptibility of an animal to the stress (Halburg, 1969; Reinberg and Halberg, 1971). Vener et al. (1977) studied the susceptibility-resistance cycle in heat stress in chinchillas. These animals were acclimatized to 22±1 C and a photoperiod of LD 12:12 with the photophase centered at 1200. Their results indicated an increased ability to resist whole body hyperthermia during the time period around 0600 and increased susceptibility to heat stress around 1800. When Wright et al. (1977) studied colonic heating patterns and lethal temperatures in rats they found significantly lowered lethal temperatures in animals tested between 1200 and 1600. Acclimatization conditions were 23±2 C and an LD 14:10 photoperiod.

The differences in elevated defended temperatures, initial colonic temperatures, and ΔTs between the two photoperiods are somewhat puzzling. The EDTs of the LD 18:06 group were lower at all times of day and the ΔTs were higher at all times except 1000. Further, the initial Tc was lower at all times in the LD 18:06 group and the differences in ΔT can be nearly accounted for by the differences in initial Tc. Thus, the degree of total body heating to the EDT is approximately the same in both groups and the amount of total body heating to the EDT may be a controlled variable. Animals exposed to the longer photoperiod showed longer heating times through segment 2 of the heating curve at 1000, corresponding to the time of day when ΔT was lowest. Heating time in segment 1, from initial Tc to the beginning of segment 2, was shorter in LD 18:06 animals at all times, although this difference was not significant at 0600. Because initial Tc was lower in LD 18:06 animals it appears that the animals heated more rapidly to a critical point where physiological and behavioral mechanisms acted to control the amount of total body heating.

Increases in thermal tolerance as a result of increasing acclimation temperature have been reported in fish (Brett, 1952), frogs (Dunlap, 1960), and salamanders (Hutchison, 1961). The CTMs of mice acclimated to 15 C were lower than for mice acclimated to 30 C; and the CTMs of mice acclimated to 30 C were also higher than controls (25 C) but there was no indication of whether this difference was significant (Wright, 1976). Acclimation to constant temperatures of 15 and 30 C had no effect on the CTM of mice in this study. However, acclimation to a cycling thermal regime significantly increased the CTM. The thermal tolerance of the Sonoran desert pupfish was increased in the thermally cycled natural environment when compared to animals acclimated to constant laboratory temperatures (Lowe ane Heath, 1969). The rate of acclimation was faster in leopard frogs exposed to a cycling thermal regime than in frogs exposed to constant temperature acclimation (Hutchison and Ferrance, 1970). The CTM was higher in animals exposed to only one 24-hour thermoperiod than in those exposed to constant acclimation temperatures.

In this study the initial Tc was lower and the ΔT was higher in the group exposed to the cycling thermal regime. Because there were no differences in EDTs, the differences in ΔTs can be accounted for by the lower initial Tc. Again, it appears that the amount of total body heating was controlled.

Wright (1976) found that the CTM of control (25 C) mice was approximately 44 C. The CTM in this study ranged from 42.62 C to 43.61 C in LD 12:12 and from 42.25 C to 43.38 C in LD 18:06. Also, the time to thermoregulatory breakdown and the heating time in segment 2 were longer, in both photoperiods, than in Wright's study. However, comparisons are difficult to make because acclimation conditions differed between the studies as did genetic background (strain) of the experimental animals, testing apparatus, and test temperatures.

Wright (1976) reported mortality rates ranging from 54% at 30 min to 72% at 16-20 hours after exposure to the CTM in mixed strain male white mice. The extreme mortality in the present study suggests that the CTM may also be a lethal temperature for endotherms. Thus, application of the CTM to endotherms may require adherence to the original definition of CTM (Cowles and Bogert, 1944) rather than the modified definition (Hutchison, 1961, 1976) which is applicable to ectotherms.

The CTM can be a useful tool for determining the temperature sensitivity of endotherms. The CTM of endotherms will be affected by external and internal factors as are the CTMs of ectotherms. Thus, future investigations should take into account such factors as thermal history, photoperiod, season, diel variation, geographic variation, age, nutritional status, state of hydration, behavior, and general health of the experimental animals. Moreover, standardization of acclimatization and testing conditions should be undertaken so that meaningful comparisons can be made between various studies of mammalian thermal tolerance.

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TABLE 1

Time	Group	CTM (C)	t	EDT (C)	t	Initial Tc (C)	t
0200	12:12	43.61±0.15 (12)	3.30**	41.19±0.16 (8)	2.65**	38.29±0.30 (12)	5.13**
	18:06	42.78±0.19 (12)		40.54±0.21 (11)		36.38±0.22 (12)	
0600	12:12	43.35±0.19 (9)	0.19 ns	40.93±0.13 (9)	2.91**	38.44±0.29 (9)	6.24**
	18:06	43.40±0.17 (12)		40.34±0.16 (10)		36.01±0.26 (12)	
1000	12:12	42.62±0.23 (11)	1.09 ns	41.04±0.11 (8)	6.74**	37.85±0.30 (11)	1.12 ns
	18:06	42.85±0.15 (12)		39.82±0.14 (9)		37.13±0.57 (12)	
1400	12:12	42.98±0.18 (11)	2.91**	40.82±0.14 (8)	0.91 ns	37.92±0.24 (11)	2.56*
	18:06	42.33±0.16 (12)		40.63±0.17 (9)		37.12±0.20 (12)	
1800	12:12	43.31±0.22 (12)	3.38**	41.09±0.15 (10)	2.91*	38.81±0.35 (10)	4.81**
	18:06	42.25±0.24 (12)		40.29±0.23 (8)		36.56±0.31 (12)	
2200	12:12	43.38±0.21 (12)	0.01 ns	41.26±0.11 (7)	7.37**	38.81±0.32 (10)	4.73**
	18:06	43.38±0.27 (12)		40.12±0.12 (7)		36.67±0.32	

TABLE 2

Time	Group	Mean ΔT (C)	Heating Time in Segment 1 (min)	Heating Time in Segment 2 (min)	Total time to Thermoregulatory Breakdown (min)
0200	12:12	2.99 ±0.34 (8)*	21.07 ±1.72 (9)*	39.52 ±5.24 (8)	61.31 ±5.77 (8)
	18:06	4.26 ±0.36 (11)	16.14 ±1.47 (12)	56.18 ±12.16 (11)	73.12 ±12.28 (11)
0600	12:12	2.49 ±0.23 (9)*	21.92 ±3.44 (9)	58.51 ±9.67 (9)	80.43 ±11.55 (9)
	18:06	4.29 ±0.33 (10)	17.24 ±1.88 (11)	38.73 ±8.98 (10)	56.81 ±8.65 (10)
1000	12:12	2.86 ±0.20 (8)	20.39 ±1.17 (8)*	50.66 ±6.34 (8)**	71.00 ±5.94 (8)**
	18:06	2.26 ±0.55 (9)	15.14 ±1.23 (9)	126.88 ±20.79 (9)	142.03 ±20.77 (9)
1400	12:12	2.84 ±0.26 (8)	27.33 ±2.24 (8)**	65.03 ±8.31 (8)	92.36 ±9.83 (8)
	18:06	3.56 ±0.25 (9)	14.13 ±0.78 (10)	64.96 ±10.45 (9)	79.83 ±10.56 (9)
1800	12:12	2.28 ±0.41 (10)	20.68 ±1.30 (10)**	53.34 ±11.50 (10)	74.02 ±11.83 (10)
	18:06	3.41 ±0.47 (8)	12.92 ±1.45 (12)	72.87 ±19.61 (8)	86.30 ±19.72 (8)
2200	12:12	2.44 ±0.35 (7)*	20.09 ±2.05 (9)*	66.75 ±21.06 (7)	88.70 ±22.14 (7)
	18:06	3.73 ±0.44 (7)	13.96 ±1.17 (10)	74.14 ±19.08 (7)	88.96 ±19.45 (7)

TABLE 3

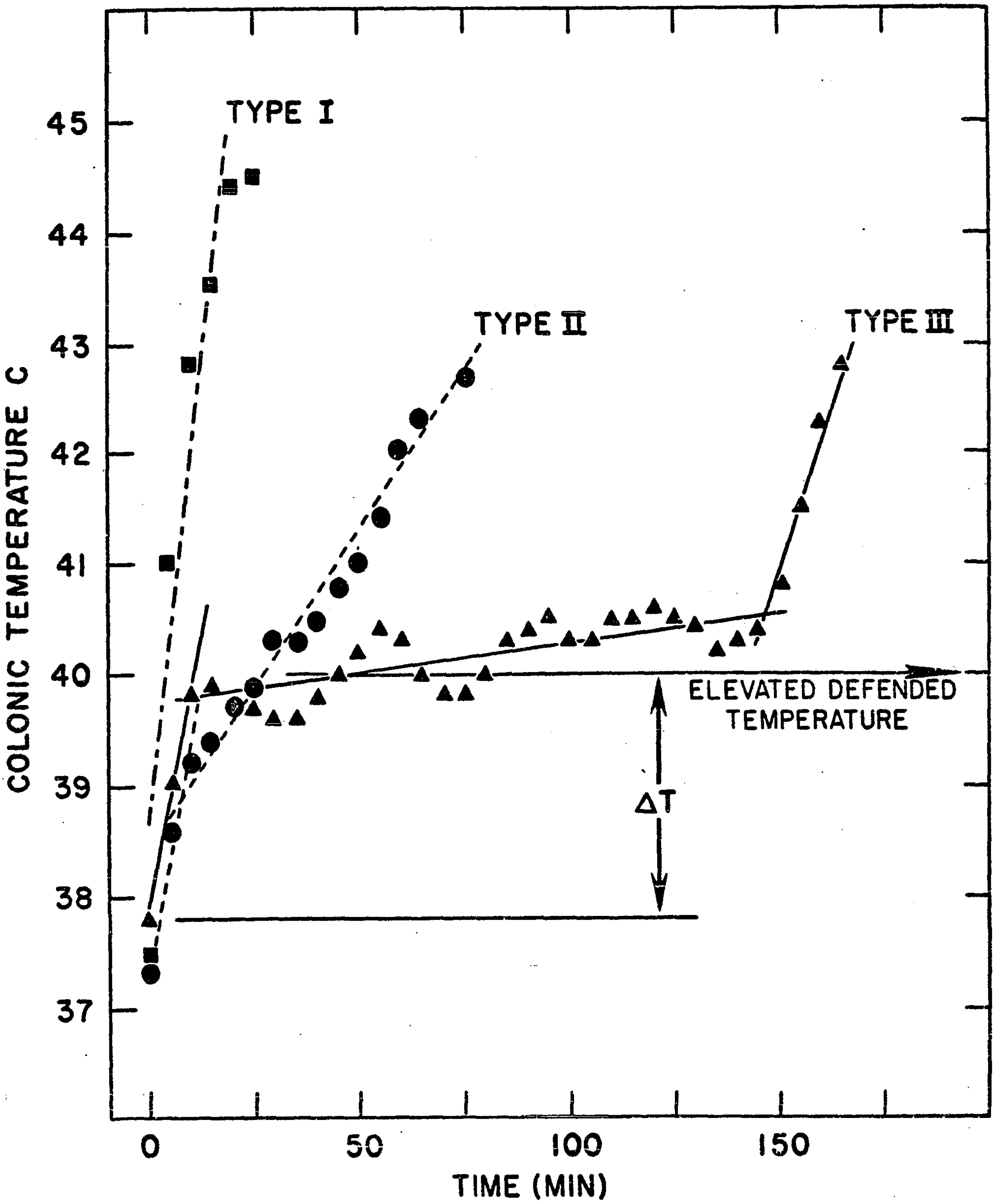
	Acclimation Temperature			
	15 C	25 C	30 C	15:30 C Cycle
CTM (C)	43.26±0.23 (10)	42.62±0.23 (11)	42.89±0.27 (11)	43.75±0.25 (11)
EDT (C)	40.25±0.33 (10)	41.05±0.11 (8)	40.26±0.19 (8)	40.86±0.29 (8)
ΔT (C)	2.65±0.46 (10)	2.86±0.20 (8)	2.75±0.23 (8)	4.39±0.44 (8)
Initial Tc (C)	37.60±0.41 (10)	37.85±0.30 (11)	37.81±0.21 (11)	36.75±0.41 (11)
Heating Time in Segment 1 (min)	14.33±1.16 (10)	20.39±1.17 (8)	13.09±0.92 (10)	17.13±0.89 (8)
Heating Time in Segment 2 (min)	56.35±8.00 (10)	50.61±6.34 (8)	79.92±16.24 (8)	58.92±14.36 (8)
Total Time to Thermoregulatory Breakdown (min)	70.68±7.00 (10)	71.00±5.94 (8)	93.86±16.35 (8)	76.05±14.65 (8)

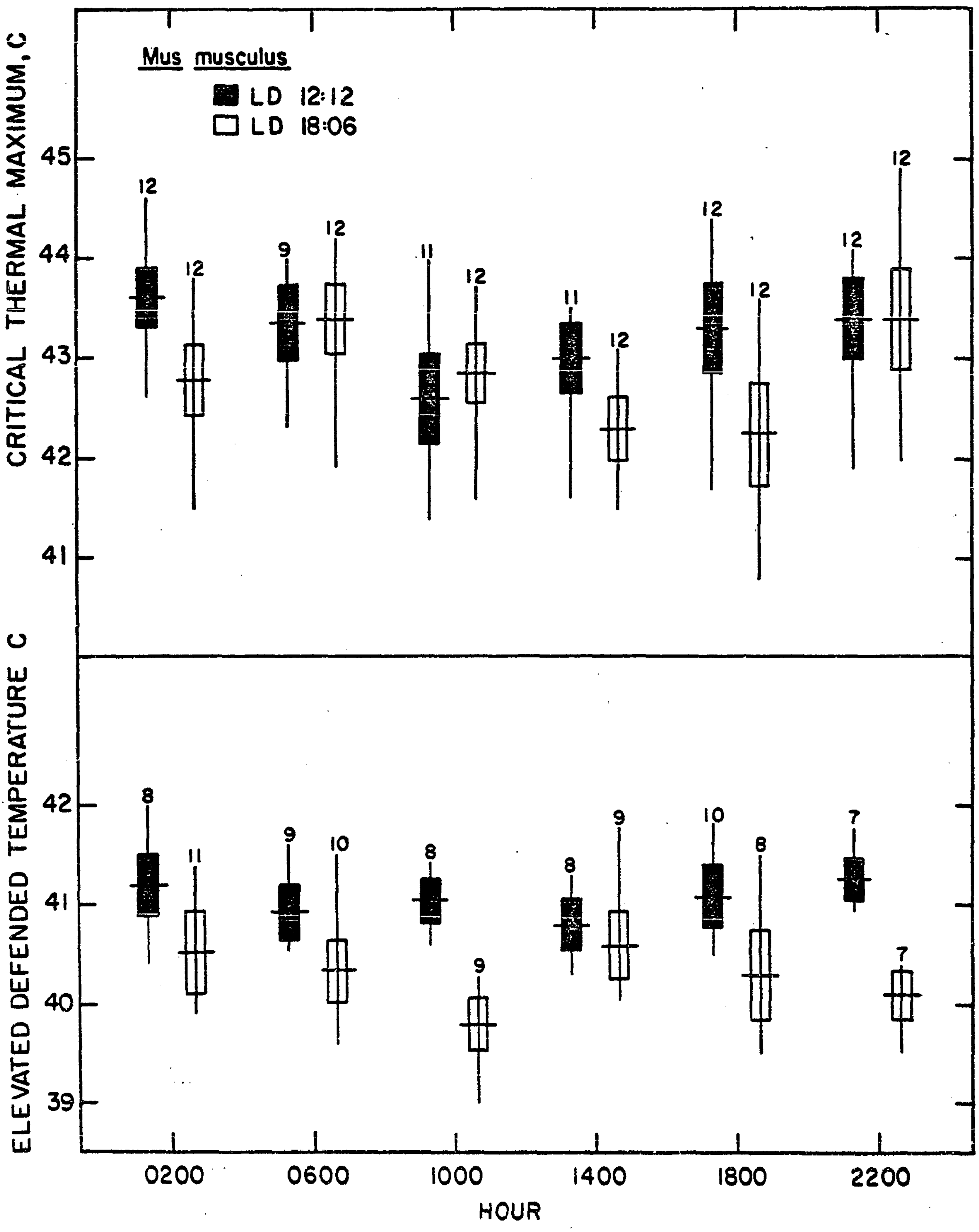
TABLE HEADINGS

Table 1. Comparison of critical thermal maxima (CTM), elevated defended temperature (EDT), and initial colonic temperature (Tc) of Mus musculus between two photoperiods (LD 12:12 vs LD 18:06) at six times of day. Means and one standard error are shown. Sample sizes are in parentheses. (*, $P<0.05$; **, $P<0.01$; ns, no significant difference)

Table 2. Comparison of the difference between initial body temperature, elevated defended temperature, ΔT, and heating times of Mus musculus between two photoperiods (LD 12:12 vs LD 18:06) at six times of day. Means and one standard error are shown. Sample sizes are in parentheses. (*, $P<0.05$; **, $P<0.01$)

Table 3. Critical thermal maxima (CTM), elevated defended temperatures (EDT), ΔT, and heating times of Mus musculus acclimatized to a LD 12:12 photoperiod and one of four acclimation temperatures (15, 25, 30, and 15 to 30 C cycle). Means and one standard error are shown. Sample sizes are in parentheses.


TYPE I
TYPE II
TYPE III
ELEVATED DEFENDED TEMPERATURE
ΔT
COLONIC TEMPERATURE C
45
44
43
42
41
40
39
38
37
0
50
100
150
TIME (MIN)


Mus musculus
LD 12:12
LD 18:06
CRITICAL THERMAL MAXIMUM, C
45
44
43
42
41
12
12
9
12
11
12
11
12
12
12
12
12
ELEVATED DEFENDED TEMPERATURE C
42
41
40
39
8
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0200
0600
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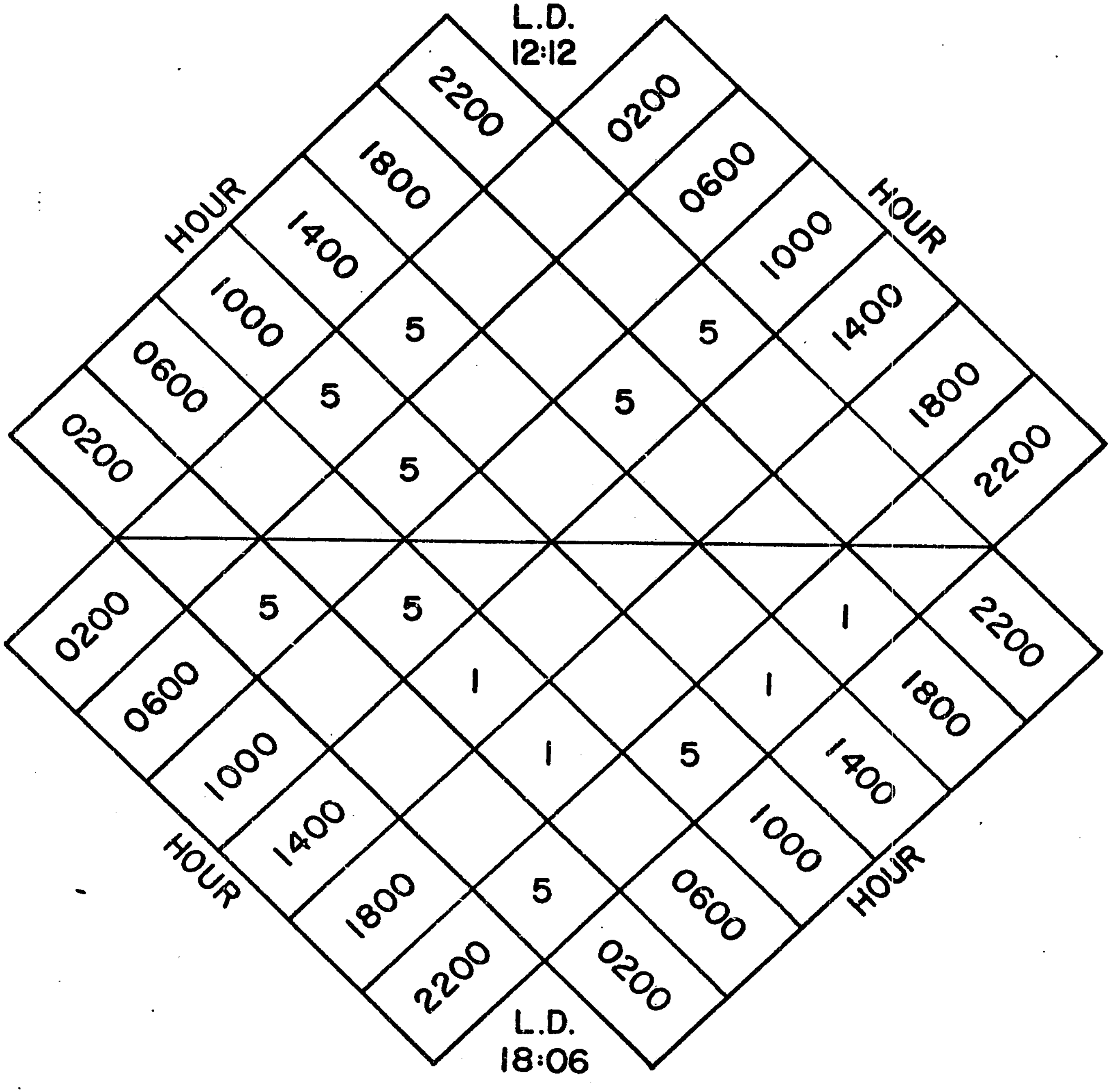
L.D.
12:12
HOUR
2200
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L.D.
18:06

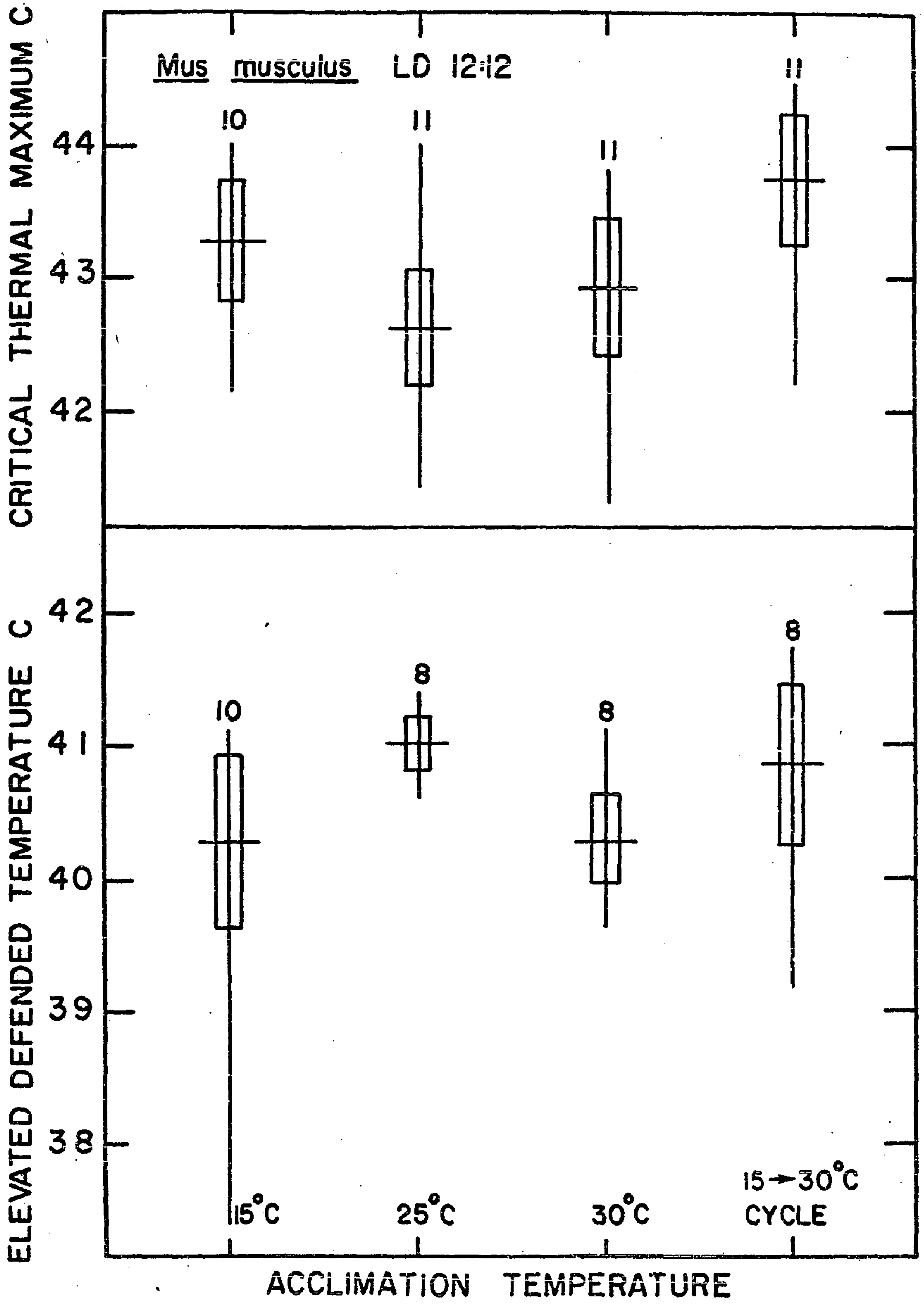
CRITICAL THERMAL MAXIMUM C
44
43
42
Mus musculus LD 12:12
10
11
11
11
ELEVATED DEFENDED TEMPERATURE C
42
41
40
39
38
10
8
8
8
15°C
25°C
30°C
15→30°C CYCLE
ACCLIMATION TEMPERATURE

FIGURE CAPTIONS

Figure 1. Examples of Type I, II, and III heating patterns (Ohara *et al.*, 1975; Wright *et al.*, 1977) plotted for colonic temperature in *Mus musculus*. Best fit lines for each segment were computed by the method of least squares. The final point on each curve is the critical thermal maximum (CTM) for each individual. Elevated defended temperature and ΔT are explained in detail in the text.

Figure 2. Critical thermal maxima (CTM) and elevated defended temperatures (EDT) at six times of day for *Mus musculus* acclimatized to 25±1 C and a LD 12:12 or LD 18:06 photoperiod with the photophase centered at 1200 CST. Vertical lines are ranges, horizontal lines are means, rectangular boxes represent two standard errors of the mean, and sample sizes are shown above each group.

Figure 3. Results of Duncan's New Multiple Range Test for the critical thermal maxima (CTM) of *Mus musculus* at six times of day. The animals were acclimatized to 25±1 C and a photoperiod of LD 12:12 or LD 18:06 with the photophase centered at 1200 CST. Comparisons can be made from the probability level (1, $P<0.01$; 5, $P<0.05$) at the intersect of any two time periods, within either photoperiod.

Figure 4. Critical thermal maxima (CTM) and elevated defended temperatures (EDT) of *Mus musculus* acclimatized to a LD 12:12 photoperiod (photophase centered at 1200 CST) and one of four thermal regimes (15 C, 25 C, 30 C, or a 15 to 30 C cycle). Vertical lines are ranges, horizontal lines are means, rectangles represent two standard errors of the mean, and sample sizes are shown above each group.

CRITICAL THERMAL MAXIMA
IN SMALL MAMMALS

DALE J. ERSKINE

ABSTRACT. -- The critical thermal maximum (CTM) was used to compare the thermal tolerances of five species of small mammals (*Mus musculus*, *Rattus norvegicus*, *Peromyscus leucopus*, *Meriones unguiculatus*, and *Dipodomys ordi*). All experimental animals were acclimatized to 25±1 C and a 12L:12D photoperiod. The CTM of *D. ordi* (45.03±0.22 C) was significantly higher ($P<0.01$) than that of all other species. The CTM of *M. musculus* (42.62±0.23 C) was significantly lower ($P<0.01$) than the CTMs of the other four species. The CTM of *P. leucopus* (43.48±0.22 C) was lower than that for *R. norvegicus* (44.22±0.30 C) and there were no differences between the CTMs of *M. unguiculatus* (44.00±0.23 C) and *R. norvegicus*.

The critical thermal maximum (CTM) has been a popular tool for measuring temperature sensitivity in terrestrial and aquatic ectotherms (Hutchison, 1961; Hutchison and Kosh, 1965; Hutchison et al., 1966; Mahoney and Hutchison, 1969; Cox, 1974; Miller and Packard, 1974; Hassan and Spotila, 1976; Maness and Hutchison, 1979). As a result, the CTM has proven to be a sensitive indicator of thermal tolerance in ectotherms.

The CTM was originally defined by Cowles and Bogert (1944) 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". Lowe and Vance (1955) modified this definition to include statistical variation and the methodology was standardized by Hutchison (1961). Since the CTM is determined under short term exposures to high temperatures and CTM values are generally higher than the lethal temperatures determined from resistance times at elevated temperatures (Fry, 1967). The CTM is not lethal and is considered an ecological maximum temperature rather than a physiological lethal temperature for ectotherms (Hutchison, 1976).

Adolph (1947) examined the tolerance to heat and dehydration in seven species of small mammals and found that those species varied greatly in their capacities for evaporative cooling and in their temperature sensitivity. He found delayed deaths in four species (dog, cat, rabbit, and guinea pig) following heat shock. The duration of the delay appeared to be positively correlated with the size of the animals and with their capacity for evaporative cooling. There have been several studies of temperature regulation and metabolism of M. unguiculatus (Robinson, 1959); McManus and Mele, 1969; Mele, 1972), D. ordi (Yousef and Dill, 1970, 1971), and Peromyscus sp. (Sealander, 1952; Morrison and Ryser, 1959; Wickler, 1980).

Ohara et al. (1975) exposed unanaesthetized rats to an ambient temperature of 42.5 C and examined the response pattern of rectal temperature. Wright et al. (1977) examined heating patterns and thermal resistance in rats exposed to high temperatures. Other studies have described the colonic heating patterns of rats exposed to sublethal heat stresses (Hainsworth and Stricker, 1970, 1971; Stricker and Hainsworth, 1970). Colonic heating patterns of mammalian species exposed to severe heat stress are assigned to one of three forms; Types I, II, and III (Fig. 1.). A detailed description of these patterns can be found in Ohara et al. (1975) and Wright et al. (1977).

Although mammalian thermoregulation and thermal resistance have received much attention only one study (Wright, 1976) has attempted to apply directly the definition of CTM to mammals. Bynum et al. (1978) estimated the CTM in sedated humans in which hyperthermia had been induced and attempted to redefine the CTM in terms of both temperature and exposure time. Hutchison (1980) argued that the attempt to redefine the CTM in terms of subclinical and clinical

PAPER II

CRITICAL THERMAL MAXIMA IN SMALL MAMMALS

injuries was inappropriate because the subclinical CTM covered too broad a range of physiological events resulting from sublethal hyperthermia.

Erskine (1981) demonstrated that the CTM is a useful experimental tool for examining thermal tolerance in endotherms. This study was undertaken to compare the thermal tolerance (CTM) and thermoregulatory capacity of several species of small mammals.

METHODS

Mixed strain male and non-pregnant female white mice (Mus musculus), white rats (Rattus norvegicus), and mongolian gerbils (Meriones unguiculatus) were randomly selected from laboratory breeding groups. White-footed mice (Peromyscus leucopus) and kangaroo rats (Dipodomys ordi) were trapped on the flood plain of the South Canadian River near Norman, Cleveland County, Oklahoma, USA. Small animals were housed 5-6 per cage and large animals 2-3 per cage in Sherer environmental chambers; acclimatization conditions were 25 1±C and a 12L:12D photoperiod. Purina chow pellets and water were available ad libitum. The chambers were opened daily and bedding changed 3-4 times each week. All animals were acclimatized for at least 14 and not more than 21 days prior to CTM determinations.

Animals were removed from acclimatization and weighed to the nearest 0.1 g. A 36 gauge copper/constantan thermocouple sheathed in polyethylene tubing or a Yellow Springs Instrument thermistor was inserted through the rectum into the colon and taped to the tail; except for D. ordi (see below). The animals were maintained for a 10-20 minute period to allow body temperatures to stabilize.

A Temp-Air Convector System (Scientific Instruments, Inc., Skokie, IL) provided dry heated air (relative humidity <15%) to the testing apparatus. The heated air was blown into a centralized separator chamber and then channeled to each of four test chambers (13 cm wide x 36 cm long x 10 cm high) through tygon tubing fitted with Hoffmann pinch clamps to control air flow. A removable partition was used to reduce the dimensions to 13 x 18 x 10 cm for the smaller animals. The entire apparatus was insulated with styrofoam.

Test chamber temperatures of 40±1 C were monitored with a Digitech Model 581C digital thermometer. Animal temperatures were monitored continuously with a Bailey Instruments BAT-8 digital thermometer and recorded every 5 minutes.

Behavioral observations included posturing, forepaw licking, breathing rate and loss of righting response. The onset of spasms, characterized by uncoordinated spasmodic twitching of the limbs, was used as the endpoint for the CTM determination. Following exposure to the CTM the animal was immediately removed from the test chamber and cooled as rapidly as possible. The thermocouple was then removed and the animal was reweighed.

Heating curves were determined for each animal by plotting colonic temperature (Tc) every 5 minutes (Fig. 1.). No satisfactory means could be found to maintain attachment of the thermistor to the tail of D. ordi. Therefore, only initial body temperature and the body temperature at the onset of spasms were recorded for this species. Each curve was inspected to determine if an individual exhibited a Type I, II, or III heating pattern and a best fit line was computed for each segment with the method of least squares (Sokal and Rohlf, 1969). The intersections of the best fit lines for Type II and III heating curves were computed to compare the heating times in segments 1, 2, and 3. Type III individuals typically exhibited an immediate decline in colonic temperature at the onset of segment 2. However, Tc fluctuated above and below the best fit line throughout segment 2. Rather than compute an "equilibrium temperature" (Ohara et al. 1975; Wright et al. 1977) at the intersection of segments 1 and 2, mean body temperature around which Tc fluctuated during segment 2 was computed. The increased level in body temperature calculated for segment 2 was termed the elevated defended temperature (EDT) (Fig. 1.). The difference between initial body temperature and the EDT, ΔT was used for further comparisons between those animals exhibiting a Type III heating pattern. Heating time in segments 1 and 2 of the heating curve and total time to thermoregulatory breakdown were also examined.

All data were initially tested for normality and homogeneity of variance. Single classification analysis of variance, Student's t-test, and Duncan's New Multiple Range Test (Duncan, 1955) were used for further analyses. All statistical analyses were performed with the Statistical Analysis System (Barr et al. 1976).

RESULTS

Type III heating patterns predominated in all species except D. ordi. One P. leucopus and three M. unguiculatus displayed Type II heating curves. D. ordi appeared to be exclusively Type I. Total time to CTM in D. ordi ranged from 35 to 38 minutes (36.67±0.87 min) and the rate of heating ranged from 0.20 to 0.23 C min^{-1} (0.22±0.009 C min^{-1}). This heating rate was comparable to the heating rate in segment 1 for all other species. The distribution of heating patterns was not related to sex of the animals nor were there sex-related differences in CTM, EDT, ΔT, heating time in segments 1 or 2 of the heating curve, total time to thermoregulatory breakdown, or weight loss.

There was a wide variation in the CTM for individuals ranging from a low of 41.3 C in M. musculus to a high of 45.7 C in D. ordi (Table 1., Fig. 2.). The mean CTM of D. ordi (45.03±0.22 C) was significantly higher than that of M. musculus (42.62±0.23, $P<0.01$), P. leucopus (43.48±0.20, $P<0.01$), M. unguiculatus (44.0±0.23, $P<0.01$), and R. norvegicus (44.22±0.30, $P<0.01$). The mean CTM of M. musculus was significantly lower than the mean CTM of R. norvegicus, M. unguiculatus, and D. ordi ($P<0.01$) and P. leucopus ($P<0.05$). The CTM of P. leucopus was lower than that of R. norvegicus ($P<0.05$) but was not different from the CTM of M. unguiculatus. There was no difference in CTM between M. unguiculatus and R. norvegicus. The EDT of M. unguiculatus (39.98±0.17 C) and R. norvegicus (40.38±0.17 C) were significantly lower ($P<0.01$) than those of M. musculus (41.05±0.11) and P. leucopus (41.04±0.20) (Table 1., Fig. 2.).

The length of time spent in segment 1 by R. norvegicus (27.01±0.95 min) was significantly longer than that for M. unguiculatus (16.53±3.49 min, $P<0.01$), P. leucopus (16.38±0.96 min, $P<0.01$), and M. musculus (20.39±1.17 min, $P<0.05$). Total time to thermoregulatory breakdown was greater in R. norvegicus

(180.48±18.93 min) than in P. leucopus (103.68±14.41 min, $P<0.01$) or M. musculus (71.00±5.94 min, $P<0.01$) and greater in M. unguiculatus (136.19±29.01 min) than in M. musculus ($P<0.05$). Total time in segment 2 of the heating curve was also greater in R. norvegicus (153.47±20.06 min) than in P. leucopus (87.15±14.91, $P<0.01$) and M. musculus (50.61±6.34, $P<0.01$) and greater in M. unguiculatus (118.08±26.36 min) than in M. musculus ($P<0.01$) (Table 1.). There were no differences in weight-specific weight loss between any of the species.

All species, except Dipodomys ordi, exhibited a set sequence of behavioral responses to the induced hyperthermia. During the initial heating period, when the animals were most active, there was a somewhat passive increase in body temperature. When an active defense of body temperature was undertaken, at the beginning of segment 2 of the heating curve, the animals became relatively inactive, spread saliva for evaporative cooling, assumed a prostrate posture, and increased breathing rate. D. ordi, in contrast, became inactive almost immediately and assumed a prostrate posture. These animals did not spread saliva for cooling or increase breathing rate appreciably. They remained in the prostrate posture until the onset of spasms.

The mortality rate in this study was essentially 100%; of those animals that did survive the initial exposure to the CTM (less than 5%) none survived for more than 6 hours. The mortality remained at 100% despite rapid cooling and administration of water.

DISCUSSION

Wright (1976) reported mortality rates ranging from 54% at 30 min to 72% at 18 to 20 hours after exposure to the CTM in mixed strain male white mice. Adolph (1947) found delayed deaths in four species of mammals following heat shock; the delay appeared to be related to body size and capacity for evaporative cooling. Erskine (1981) found a mortality rate of 100% in mixed strain male and female white mice exposed to the CTM; the extreme mortality in this study indicates that the CTM may also be a physiological lethal temperature for endotherms. The suggestion has been made that application of the CTM to endotherms may require adherence to the original definition of the CTM rather than to the modified definition which is applicable to ectotherms (Erskine, 1981).

There was wide variation in the CTM of the five species of mammals studied. There was also great variability in the resistance to heat stress, indicated by the distribution of heating patterns and the heating times in each segment of the heating curves. The differences in thermal tolerance and in the resistance to heat stress may be related to behavior and habitat of each species.

Kangaroo rats (_Dipodomys_ sp.) inhabit arid regions of the southwestern United States and tend to lack the capacity for thermoregulation of more wide ranging species when exposed to heat stress. _D. merriami_ is a good example of an animal which is remarkably well adapted to the desert environment (Schmidt-Nielsen and Schmidt-Nielsen, 1950; Schmidt-Nielsen, 1964a, 1964b). The most obvious adaptations are nocturnal activity and fossorial habits which allow the animal to avoid stressful daytime temperatures. _Dipodomys_ sp. can rely on oxidative and preformed water and the physiology of the animal permits water retention (concentrated urine and feces, absence of sweat glands, and nasal-tidal water conservation). There may be some interspecific variation in the capacity for thermoregulation in this species because D. merriami sometimes inhabit shallow burrows (Dawson, 1955). Thus, Dipodomys have a broad range of adaptations that allow them to occupy arid regions. The results of this study suggest that, in addition to this suite of physiological and behavioral adaptations, Dipodomys possess an enhanced tolerance to high body temperatures. That their heating patterns were exclusively Type I supports previous findings that Dipodomys lack the capacity to resist thermal stress. An increased tolerance to high body temperatures (ie., a high critical thermal maximum) would allow Dipodomys more time to escape from heat stress in the wild.

Desert rodents of the genus Meriones are distributed throughout North Africa, most of Asia, and southern Russia. The Mongolian gerbil, Meriones unguiculatus, is native to arid and semi-arid regions of China. Since its introduction into the United States as an experimental animal, M. unguiculatus has been the focus of several physiological, behavioral, and ecological studies. Photoperiodic control of gerbil activity has been studied extensively (Thiessen et al., 1968; Stutz, 1972; Roper, 1976). Robinson (1959) studied temperature regulation in M. unguiculatus at several ambient temperatures and found that they were efficient thermoregulators with a broad thermal neutral zone. Other studies of gerbil bioenergetics and thermoregulation also suggest a high resistance to heat stress (McManus and Mele, 1969; Mele, 1972). The gerbil is also a burrower and is thought to be nocturnal in the wild. However, Randall and Thiessen (1980) found that gerbils in an outdoor enclosure avoided temperature extremes by emerging from their burrows when ambient temperature fell below burrow temperature in hot weather and rose above burrow temperature in cold weather. They concluded that gerbils probably time their activity in the wild to avoid temperature extremes and are likely to shift from nocturnal activity in summer to diurnal activity in winter.

The efficient thermoregulation of gerbils under a wide range of environmental conditions may account for a CTM that was lower than that of Dipodomys, an inhabitant of similar environs. The increased capacity to tolerate heat stress for longer periods by the gerbil probably does not preclude the necessity for enhanced thermal tolerance when in heat stressed habitats since the gerbil did have a CTM above those of M. musculus and P. leucopus.

Laboratory white mice derived from wild M. musculus and P. leucopus (found in more mesic grassland habitats in the central United States) had the lowest CTMs. Heating patterns for animals from both groups were almost exclusively Type III, which suggests efficient thermoregulatory mechanisms and an enhanced ability to resist whole body heating. The distribution of P. leucopus ranges from the northern and eastern United States to Central America and the possibility exists that geographical variation in thermal tolerance and thermoregulatory capacity exists in this species.

The laboratory rat is derived from wild Rattus norvegicus, perhaps the most widely distributed of the small mammals studied and occupies a wide range of habitat types. This species appears to be an intermediate form in terms of thermal tolerance and thermoregulatory capacity. The CTM of this species was not different from that of M. unguiculatus indicating thermal tolerance and the heating pattern of all animals in this group (exclusively Type III) suggests an effective thermoregulatory ability.

These results indicate that the CTM is an easily determined measure of thermal tolerance that can be applied to small mammals in much the way that the technique has been used with ectothermic vertebrates. However, as has been suggested (Erskine, 1981), acclimatization and testing conditions should be standardized so that meaningful comparisons can be made and investigators should be aware of possible external and internal modifying factors that may influence individual CTMs.

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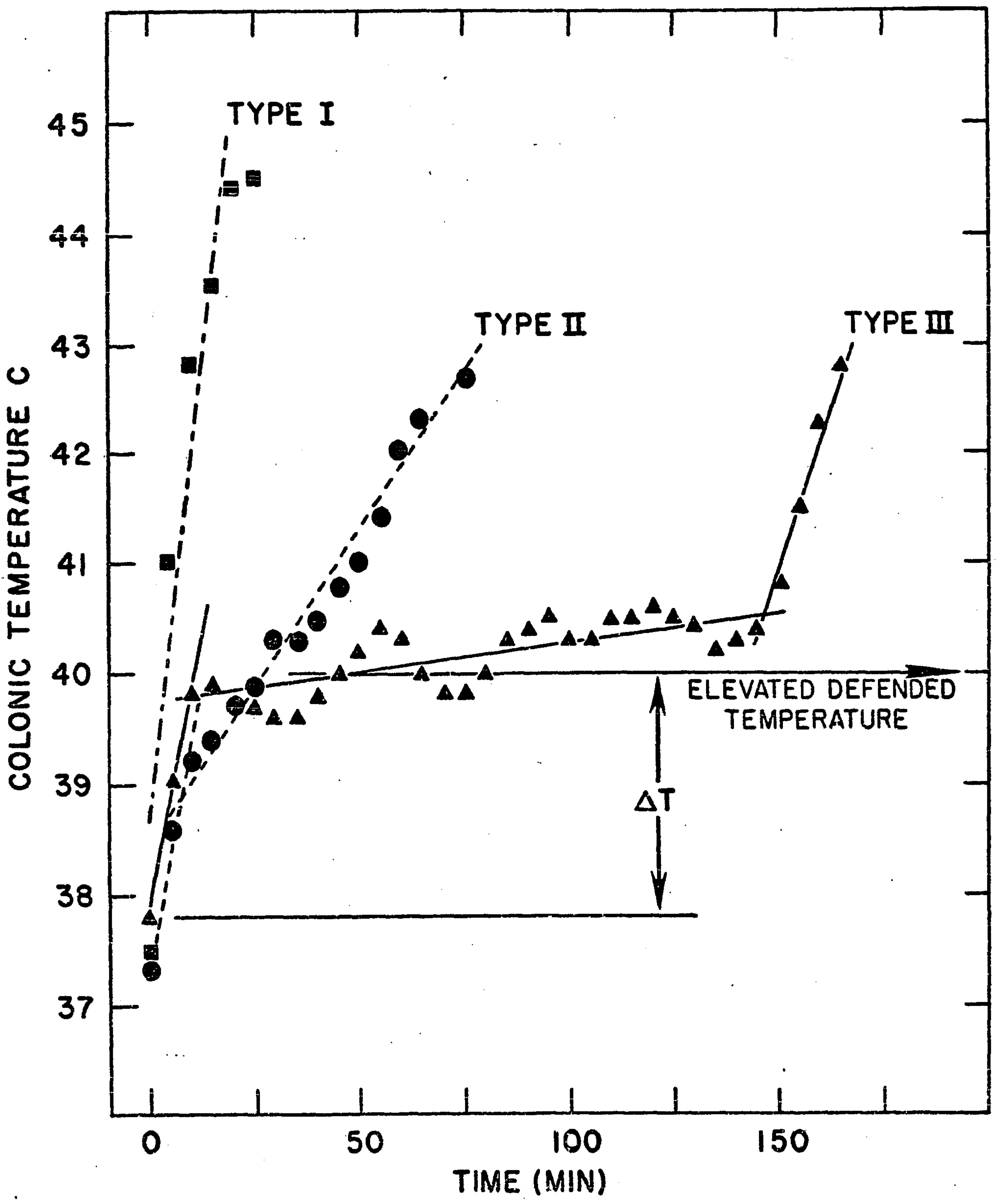
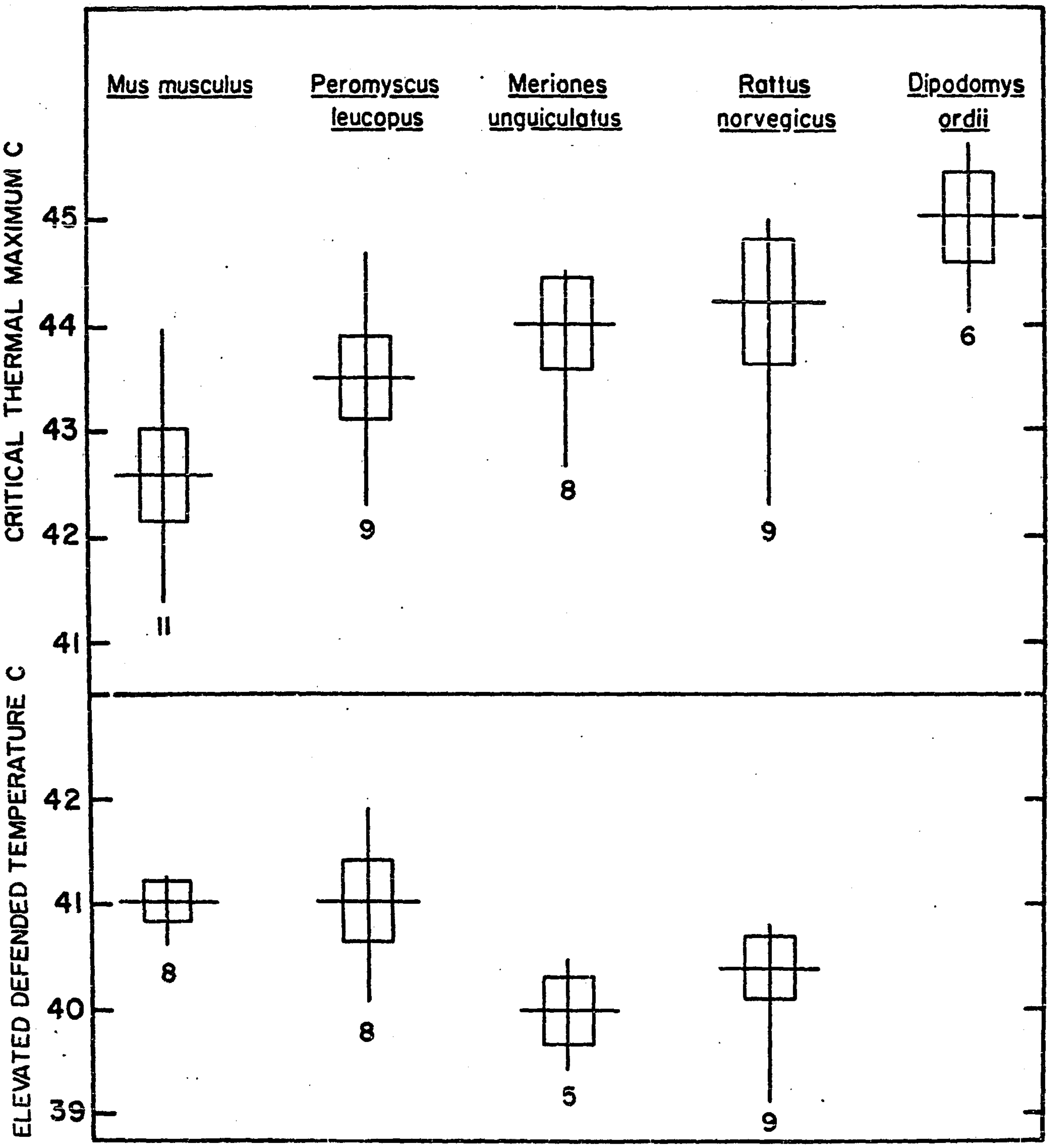
TABLE 1

	Mus musculus	*Peromyscus leucopus*	*Meriones unguiculatus*	*Rattus norvegicus*	*Dipodomys ordii*
CTM (C)	42.62±0.23 (11)	43.48±0.22 (9)	44.00±0.23 (8)	44.22±0.30 (9)	45.03±0.22 (6)
EDT (C)	41.05±0.11 (8)	41.04±0.20 (8)	39.98±0.17 (5)	40.38±0.17 (9)	
ΔT (C)	2.86±0.20 (8)	2.44±0.19 (8)	2.04±0.32 (5)	2.43±0.21 (9)	
Initial Tc (C)	37.85±0.30 (11)	38.51±0.30 (9)	37.83±0.28 (8)	37.96±0.19 (9)	37.47±0.18 (6)
Heating Time in Segment 1 (min)	20.39±1.17 (8)	16.38±0.96 (9)	16.53±3.49 (7)	27.01±1.95 (9)	
Heating Time in Segment 2 (min)	50.61±6.34 (8)	87.15±14.91 (8)	118.08±26.36 (5)	153.47±20.06 (9)	
Total Time to Thermoregulatory Breakdown (min)	71.00±5.94 (8)	103.68±14.41 (8)	136.19±29.01 (5)	180.48±18.93 (9)	

TABLE LEGEND

Table 1. Critical thermal maxima (CTM), elevated defended temperatures (EDT), ΔT, initial colonic temperatures (Tc), and heating times for five species of small mammals previously acclimatized to 25±1 C and a photoperiod of 12L:12D with the photophase centered at 1200 CST. Means and one standard error are shown. Sample sizes are in parentheses.


TYPE I
TYPE II
TYPE III
ELEVATED DEFENDED TEMPERATURE
ΔT
COLONIC TEMPERATURE C
45
44
43
42
41
40
39
38
37
0
50
100
150
TIME (MIN)



Mus musculus
Peromyscus leucopus
Meriones unguiculatus
Rattus norvegicus
Dipodomys ordii
CRITICAL THERMAL MAXIMUM C
45
44
43
42
41
11
9
8
9
6
ELEVATED DEFENDED TEMPERATURE C
42
41
40
39
8
8
5
9

FIGURE CAPTIONS

Figure 1. Examples of Type I, II, and III heating patterns (Ohara et al., 1975; Wright et al., 1977) plotted for colonic temperature in *Mus musculus*. Best fit lines for each segment were computed by the method of least squares. The final point on each curve is the critical thermal maximum (CTM) for each individual. Elevated defended temperature and ΔT are explained in detail in the text.

Figure 2. Critical thermal maxima and elevated defended temperatures of five species of small mammals. All animals were previously acclimatized to 25±1 C and a 12L:12D photoperiod. Vertical lines are ranges, horizontal lines are means, and rectangles represent two standard errors of the mean. Sample sizes are shown below each group.