

Hypothalamic Thermosensitivity and Adaptations for Heat-Storage Behavior in Three Species of Chipmunks (*Eutamias*) from Different Thermal Environments

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Summary. 1. The characteristics of hypothalamic thermosensitivity in three chipmunk species, *Eutamias speciosus*, *E. amoenus*, and *E. minimus*, were determined at three ambient temperatures (T_a) by manipulating the temperature of the hypothalamus (T_{hy}) with chronically implanted, water-perfused thermodes while continuously measuring metabolic rate. The proportionality constant (α) for the metabolic heat-production (MHP) response to manipulations of T_{hy} was high in all three species. *E. minimus* had a higher hypothalamic thermosensitivity than *E. amoenus* and *E. speciosus*. In all three species the threshold T_{hy} for the MHP response (T_{set}) increased with decreasing T_a (Figs. 1, 2; Table 1).

2. Thermoregulatory responses during and after experimentally induced whole-body and hypothalamic hyperthermia were examined in the three species at $T_a=30^\circ\text{C}$. Body temperatures (T_b) of free-living animals in natural habitats were measured with implanted thermosensitive transmitters. The tolerance to induced hyperthermia differed among the three species. *E. minimus* would allow T_b to rise as high as 41.9°C before activating heat-loss mechanisms, while *E. speciosus* and *E. amoenus* would not tolerate T_b 's above 40.4°C . Following bouts of hypothermia, *E. minimus* and *E. amoenus* would allow T_b to fall considerably below the normally-regulated levels. *E. minimus* reached T_b 's about 0.75°C lower than *E. amoenus* and 2.1°C lower than *E. speciosus* during these episodes of hypothermia (Figs. 3, 4).

3. It is hypothesized that the ability to tolerate hyper- and hypothermia is an adaptation used by *E. minimus* and *E. amoenus* to remain active during the day in hot, arid environments. Calculations based on an energy-budget equation show that in heat-stress conditions *E. minimus* can remain active longer than the other two species and that *E. amoenus* can remain

active longer than *E. speciosus* (Fig. 6; Table 2). The significance of these differences for the distributions of the animals in nature is discussed.

Introduction

The problem of maintaining normal body temperature is a complex one for small, diurnal mammals. Because of their small size, they have high surface/volume ratios and can carry only limited insulation. Also, the depth of the boundary layer of still air decreases as body size decreases. The net result of these factors is a tight coupling of the small mammal's energy balance to environmental conditions. The uneven distribution of solar energy over the environment creates a wide spectrum of microclimates, ranging from cool shaded areas to very hot surfaces in direct sunlight. Most small diurnal mammals are highly mobile and can move rapidly between these very different microclimates. They, therefore, can experience rapid and drastic shifts in energy exchange. To prevent rapid and drastic changes of body temperature, they must have a sensitive thermoregulatory system, quick to command appropriate behavioral and autonomic responses as the thermal environment changes. One therefore expects that evolutionary pressures might result in differences between the thermoregulatory systems of even closely related species from dissimilar habitats. Accordingly, we decided to investigate the thermoregulatory characteristics of three congeneric chipmunks (*Eutamias speciosus*, *E. amoenus*, and *E. minimus*) from very different thermal environments on the eastern slope of the Sierra Nevada. These species are contiguously allopatric and altitudinally zoned (Grinnell and Storer, 1924; Johnson 1943), inhabiting

areas ranging from cool mountain forests (*E. speciosus*) downwards through arid piñon pine-mountain mahogany woodlands (*E. amoenus*) through open sagebrush desert (*E. minimus*). We planned to quantitatively characterize basic properties of the central nervous thermoregulatory systems of these three species, looking for differences related to their different environments. We also wished to examine specific mechanisms for coping with heat stress, since this seemed to be a major problem for the two species from hot, arid habitats.

Materials and Methods

Laboratory Studies

Chipmunks were trapped in Lee Vining Canyon, Mono County, California, transported to our laboratory, and housed individually in glass terraria provided with wooden nest boxes. The animals were fed sunflower seeds, commercial rat chow, and water ad libitum, and received fruit, vegetables, birdseed, and hardboiled eggs approximately once per week. All of the animals were kept on a 12:12 h light-dark cycle in a constant temperature room ($23 \pm 2^\circ\text{C}$).

We used five *E. minimus* (average weight 34 g), three *E. amoenus* (average weight 43 g) and three *E. speciosus* (average weight 72 g) for investigations of CNS thermosensitivity. They were prepared for experimentation by chronic, stereotaxic implantation of two water-perfused thermodes straddling the hypothalamus. A thermocouple reentry tube placed 1.0 mm anterior to the thermodes and 0.5 mm off midline allowed measurements of hypothalamic temperature (T_{hy}). Thermode assemblies and surgical procedures were similar to those described elsewhere (Heller et al., 1974), except that the thermode assembly was bonded directly to the cranium with carboxylate cement (Durelon). We placed the assemblies so that the thermodes penetrated the anterior commissure and straddled the optic chiasm. Anterior-posterior coordinates for the thermodes (using a level skull orientation) were 7.5 mm anterior of ear bar zero in *E. speciosus*, 7.0 mm anterior in *E. amoenus*, and 6.7 mm anterior in *E. minimus*. In all species the thermodes were lowered to the base of the calvarium (approximately 8.5 mm below the skull surface). Radiographic examination of the animals immediately following surgery and inspection of serial brain sections after the conclusion of experiments verified thermode placement.

An additional six *E. minimus*, five *E. amoenus*, and four *E. speciosus* received simpler caps consisting of a single thermocouple reentry tube in the hypothalamus. These preparations were used only for heat tolerance and heat storage studies. Placements and surgical procedures were similar to those for thermode implanted animals.

In two thermode implanted animals (one *E. minimus* and one *E. amoenus*), approximately 4 cm of 18-gauge polyvinyl tubing sealed at one end was inserted under the skin of the head and neck so that the closed end rested subcutaneously over the scapular musculature. The open end protruded from the skin and was cemented to the thermode assembly. Thermocouples inserted into this tube measured the interscapular temperature (T_{sc}), which we used as a measure of body core temperature (T_{b}) because the animals did not tolerate rectal thermocouples. T_{sc} and T_{hy} corresponded closely when T_{hy} was not being manipulated.

At least two weeks were allowed for recovery from surgery

before animals were used in experiments. We observed no behavioral or physiological abnormalities resulting from the surgical preparations.

Hypothalamic thermosensitivity measurements were conducted at three ambient temperatures (T_{a}): 10, 20, and 30°C . We never used animals in experiments more often than every other day, nor for more than 6 h at a time. Experimentation always took place during the animal's active periods (between 0800 and 1900 PST). The experimental protocol consisted of a series of hypothalamic heatings and coolings, during which the animal's metabolic rate was recorded. Detailed descriptions of the equipment and procedures can be found in Heller et al. (1974) and Heller and Henderson (1976).

Studies of heat stress responses and tolerance for hyperthermia were performed in the same metabolism chamber setup as the hypothalamic thermosensitivity work. A thin-walled water-cooled ($18\text{--}22^\circ\text{C}$) floor was added to the chamber to provide a heat-sink surface for the animals. All of these experiments took place at $T_{\text{a}} = 30^\circ\text{C}$. Animals with thermode implants received stepwise hypothalamic heatings to determine the maximum tolerated T_{hy} . These heatings began at 0.5°C above the unmanipulated T_{hy} and were stepped in 0.2°C increments. Animals were observed closely for at least one minute following each increase in T_{hy} . When behavioral criteria (sprawling or frantic escape activities) indicated that the maximum tolerated T_{hy} had been reached, we terminated the heatings and allowed the animals to rest until T_{hy} returned to normal levels.

The maximum T_{b} tolerated under a radiation heat load at $T_{\text{a}} = 30^\circ\text{C}$ was also investigated. For these experiments we installed a 150 W photoflood lamp 20 cm above the clear Plexiglass lid of the metabolism chamber. A 2–3 cm deep water bath in the light path decreased the infrared energy reaching the animal so that most of the energy incident on the animal was in the visible spectrum. Under these conditions the animal's T_{b} increased at approximately $1^\circ\text{C}/\text{min}$. The lamp was turned on when the animal was sitting quietly, and the behavior of the subject was observed (as described above) to determine when T_{b} reached the maximum tolerated level (at which point the lamp was immediately extinguished).

After both hypothalamic and whole-body heatings, we allowed the animals to cool themselves without disturbance. The lowest T_{b} reached was noted; this was the minimum T_{b} attained before the onset of activity or of increased metabolic heat production. We attempted to ascertain whether the chipmunks were awake or asleep during the cooling phase (sprawled animals with closed eyes and regular, slow respirations were assumed to be asleep). Successive heatings were not performed until the animal had reattained its normal T_{b} .

Field Studies

Behavioral studies and telemetering of body temperatures of free-ranging chipmunks took place during the summers of 1975–1976 in the Lee Vining Canyon area. All three species inhabited the study site. We made behavioral observations from blinds set in trees, for a total time of about 1000 h. Temperatures of microclimates under various weather conditions and times of day were measured with a Bailey BAT-4 thermocouple thermometer. This instrument was calibrated at the beginning and end of summer against an accurate mercury thermometer (Ertco ATSM). A feeding station attracted animals for the telemetry work. Chipmunks visiting the feeder were trapped and marked with easily recognizable pelage clipping patterns as well as ear tags. Frequently returning individuals were recaptured and taken to our field station for implantation of miniature temperature telemetering devices in their abdominal cavities.

Transmitters (Minimitter model V) were prepared for implantation by sealing them with a layer of epoxy cement and a layer of sterile plastic wound dressing (Aeroplast). The sealed units (2 cm by 1 cm cylinders) weighed approximately 3.0 g. Minimitters transduce temperature as the pulse rate of emitted clicks. Each unit was individually calibrated against the Bailey BAT-4 thermometer in a well-stirred water bath. Calibrations were made at three or more temperatures within the physiological range (33–45 °C). The responses of the units approached linearity over this temperature interval, and measurements were repeatable to within 0.3 °C. Several of the units ($n=4$) were not implanted immediately and were checked for accuracy several days after initial calibration. There were no significant drifts from the initial temperature-pulse rate relationship. Three transmitters were recovered when animals were retrapped, two to four weeks after implantation, and these units also were within 0.5 °C of their initial calibration values.

The implantation procedures were quite simple. A sealed, calibrated transmitter would be sterilized in a cold sterilization solution (Urolicide) and placed in the peritoneal cavity of a chipmunk after the animal had been anesthetized (sodium pentobarbital, 115 mg/kg). We closed the 2.5 cm ventral abdominal incision with fine sutures, and released the animal the following morning near the feeder. Nine of 10 implanted animals were subsequently seen in the vicinity of the feeder, and 4 returned frequently.

Temperature measurements from these animals in the field were made by timing click rates and referring to the calibration plot for the particular transmitter. Because of the short range of these units (about 0.5 m) we surrounded the feeder area with a closed-loop antenna and connected it to a radio at the observing station. Timed periods as short as 10 clicks were considered adequate, but we attempted to time at least 30 clicks to increase accuracy. Time of day and the approximate air temperature were also recorded for each visit of a transmitter-equipped animal.

Results

Hypothalamic Thermosensitivity

There are many similarities in the thermoregulatory characteristics of the three *Eutamias* species. Hypothalamic thermosensitivity is extremely high in these animals, and inputs to the thermoregulatory system from extrahypothalamic core receptors seem to be relatively unimportant. These points are apparent in Figure 1, which represents a portion of an experiment run on *E. speciosus* M15 at $T_a=10$ °C (results from other species did not differ qualitatively). At time zero the animal had been in the chamber for approximately one hour and T_{hy} and metabolic rate (MR) had stabilized. A hypothalamic heating of 3 °C to 39.4 °C produced an immediate drop in MR; a further increase in T_{hy} to 41.0 °C reduced MR to levels approximating those seen in resting animals under thermoneutral conditions. When the T_{hy} clamp was released, T_{hy} fell immediately to 34.2 °C. This drop represents the equilibration of T_{hy} with core T_b as blood at core temperature entered the brain, and indicates that core T_b fell below normal levels when MR was depressed by heating the hypothalamus. When T_{hy} decreased, an immediate and large increase in

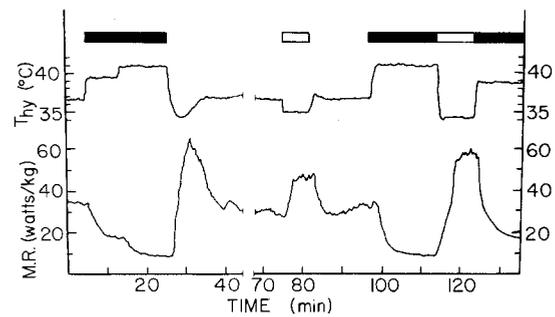


Fig. 1. Responses in metabolic rate to manipulations of hypothalamic temperature at a T_a of 10 °C (*E. speciosus* M15). Open bars at the top of the figure indicate periods of T_{hy} cooling and solid bars indicate periods of T_{hy} heating

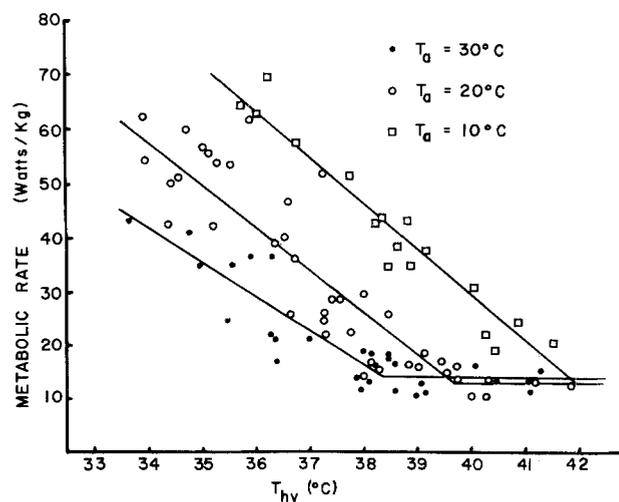


Fig. 2. Metabolic rate of *E. minimus* M20 as a function of T_{hy} during hypothalamic coolings and heatings at three ambient temperatures

MR occurred, raising T_b (and T_{hy}) to premanipulation levels, with the magnitude of the MR response declining as T_{hy} increased. This indicates that extrahypothalamic core inputs are not important, or are overridden by T_{hy} . When the hypothalamus was cooled to 35.2 °C (time = 75 min) MR increased immediately. Releasing the thermal clamp after 7 min of cooling allowed T_{hy} to equilibrate with T_b at about 1 °C above premanipulation levels (occasionally, with other animals, a 2–3 °C increase was noted). The fact that MR did not decrease during the hypothalamic cooling, even though T_b was rising, again indicates the relative unimportance of extrahypothalamic core inputs to the thermoregulatory system.

When metabolic rate is plotted as a function of T_{hy} , a threshold temperature for the metabolic heat production (MHP) response is seen in animals run at T_a 's of 20 or 30 °C (Fig. 2). At T_{hy} values below threshold, MR was inversely proportional to T_{hy} , but at T_{hy} 's above threshold MR was constant and mini-

Table 1. CNS Thermoregulatory characteristics of *Eutamias sp.* α_{MHP} values in watts $\text{kg}^{-1} \text{ } ^\circ\text{C}^{-1}$; minimal MR values in watts kg^{-1} ; T_{set} and T_a values in $^\circ\text{C}$

| | T_a 10 | | | | T_a 20 | | | | T_a 30 | | | |
|---------------------|-----------------------|-------|------------------|-------------------|-----------------------|-------|------------------|-------------------|-----------------------|-------|------------------|------------|
| | α_{MHP} | r^2 | T_{set} | Minimal MR | α_{MHP} | r^2 | T_{set} | Minimal MR | α_{MHP} | r^2 | T_{set} | Minimal MR |
| <i>E. minimus</i> | | | | | | | | | | | | |
| F1 | | | | | -4.0 | 0.83 | 39.6 | 12.0 | -4.2 | 0.80 | 38.6 | 14.1 |
| F3 | -9.6 | 0.93 | 41.5 | 15.4 ^a | -6.8 | 0.78 | 40.3 | 15.4 | -6.5 | 0.81 | 40.2 | 15.3 |
| F5 | | | | | -6.6 | 0.95 | 39.0 | 7.9 | | | | |
| M1 | | | | | | | | | -3.4 | 0.75 | 38.1 | 11.6 |
| M20 | -8.0 | 0.90 | 42.0 | 13.0 ^a | -7.9 | 0.77 | 39.6 | 13.0 | -6.3 | 0.77 | 38.4 | 14.3 |
| Mean | -8.8 | | 41.75 | 14.2 | -6.3 | | 39.63 | 12.1 | -5.1 | | 38.83 | 13.8 |
| <i>E. amoenus</i> | | | | | | | | | | | | |
| M1 | | | | | -3.3 | 0.70 | 41.0 | 12.9 ^a | -3.0 | 0.78 | 36.9 | 12.9 |
| F4 | -5.1 | 0.60 | 42.7 | 14.8 ^a | -3.3 | 0.75 | 40.6 | 14.8 | -4.1 | 0.72 | 36.4 | 13.5 |
| F3 | -6.8 | 0.88 | 41.0 | 17.9 ^a | -5.4 | 0.73 | 40.4 | 17.9 | -5.6 | 0.94 | 39.6 | 16.9 |
| Mean | -6.0 | | 41.85 | 16.4 | -4.4 | | 40.5 | 15.2 | -4.3 | | 38.25 | 14.4 |
| <i>E. speciosus</i> | | | | | | | | | | | | |
| F12 | | | | | -5.2 | 0.81 | 40.8 | 9.4 ^a | -6.4 | 0.74 | 37.9 | 9.4 |
| F14 | -3.7 | 0.90 | 42.2 | 10.0 ^a | -5.7 | 0.76 | 39.5 | 10.0 | -3.9 | 0.75 | 37.6 | 11.1 |
| M15 | -6.1 | 0.91 | 40.6 | 6.7 ^a | -5.9 | 0.87 | 40.6 | 6.7 ^a | -4.7 | 0.75 | 37.2 | 6.7 |
| Mean | -4.9 | | 41.40 | 8.4 | -5.0 | | 40.30 | 8.7 | -5.0 | | 37.55 | 9.1 |

^a Minimal MR values used to compute T_{set} were obtained at higher T_a 's

mal. The threshold temperature (T_{set}) and the proportionality constant for metabolic heat production, α_{MHP} , were estimated through least-squares analysis, as described in Heller and Henderson (1976).

Hypothalamic thermosensitivity in *Eutamias amoenus* and *E. minimus* (as indicated by α_{MHP}) tends to decrease with increasing T_a (Table 1). Pairwise comparisons with individual animals tested at different T_a 's show an increase of α_{MHP} with decreasing T_a 6 out of 7 times with *E. minimus* and 5 out of 7 times with *E. amoenus*. Although the sample sizes for each species are not large enough to allow statistical significance, the trends are clear. Combining data from *E. minimus* and *E. amoenus* gives increases of α_{MHP} with decreasing T_a 11 times out of 14, which is significant at the 0.05 level. Average α_{MHP} for the three *E. speciosus* tested was not significantly different at dissimilar T_a 's. This may be an artifact of small sample size; one individual (M15) did show a decrease in thermosensitivity as T_a increased.

In all species T_{set} decreased consistently with increasing T_a . There were no significant interspecific differences in T_{set} , which dropped from a mean of 41.6 $^\circ\text{C}$ at $T_a = 10^\circ\text{C}$ to 38.2 $^\circ\text{C}$ at $T_a = 30^\circ\text{C}$ (Table 1). Figure 2 shows the changes in α_{MHP} and T_{set} with different T_a 's for 1 animal.

We did not note any change in hypothalamic thermosensitivity or T_{set} following bouts of elevated T_b in any of the three *Eutamias* species. Such shifts have

been reported in another small diurnal desert mammal, the antelope ground squirrel (Heller and Henderson, 1976).

Hyperthermia Tolerance

Three types of experimental procedures were used to determine the maximum T_b tolerated by each of the *Eutamias* species: Hypothalamic heatings, whole-body heatings with incandescent lamps, and field experiments with implanted thermosensitive transmitters. All three lines of evidence support the hypothesis that *E. minimus* is significantly more tolerant of hyperthermia than *E. amoenus* or *E. speciosus*.

There were definite interspecific differences in the behavioral response to heatings. With both hypothalamic and whole-body heatings, *E. minimus* and *E. amoenus* almost always assumed a prone, sprawling posture as the critical temperature was reached, while *E. speciosus* never sprawled. Instead, *E. speciosus* simply became very quiet when subjected to T_{hy} heatings. They usually assumed a crouching "alarm" posture with ears flattened back as T_{hy} rose above 40 $^\circ\text{C}$, and remained immobile even when T_{hy} reached high levels (above 42.5 $^\circ\text{C}$). In contrast, whole-body heatings of *E. speciosus* invariably resulted in frantic activity as T_b approached 41 $^\circ\text{C}$. Typical records of heatings of *E. speciosus* and *E. minimus* are shown in Figure 3.

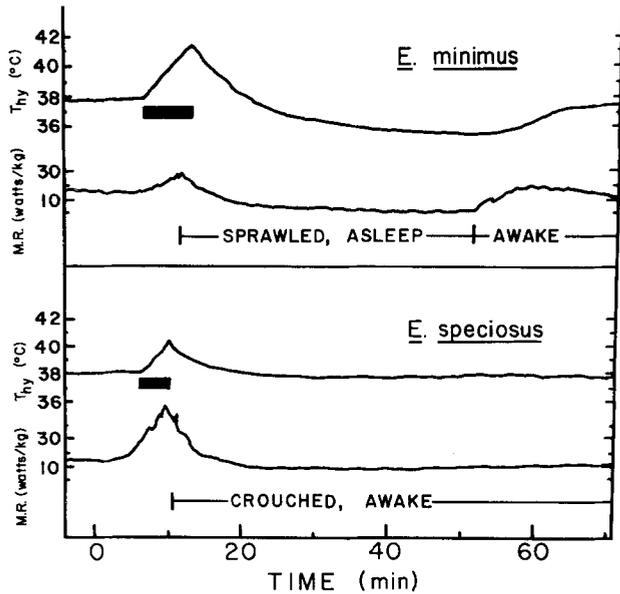


Fig. 3. Changes in T_b , arousal state, and metabolic rate during and after whole-body heatings in *E. speciosus* and *E. minimus* (*E. amoenus* responses were qualitatively similar to those of *E. minimus*). Solid bars mark times when the photoflood lamp was on. $T_a = 30^\circ\text{C}$

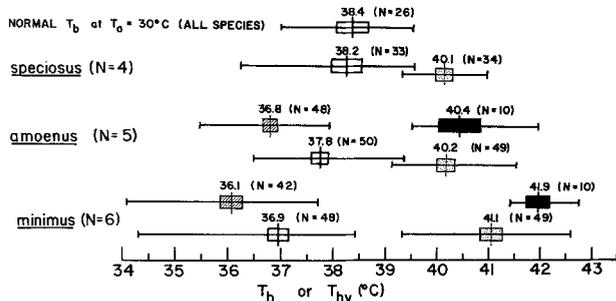


Fig. 4. Maximum and minimum temperatures tolerated by the three *Eutamias* species. Lines represent ranges of the data, bars represent two standard deviations on each side of the mean. Open bars signify data from awake animals, diagonally-stripped bars signify data from sleeping animals, stippled bars signify data from animals subjected to whole-body heatings, and solid bars signify data from animals subjected to hypothalamic heatings

E. minimus and *E. amoenus* tolerated higher temperatures when T_{hy} alone was raised than when T_b was increased (Fig. 4). The difference in maximum temperature tolerated between hypothalamic and whole-body heatings was about 0.8°C for *E. minimus* ($p < 0.05$, t-test) and 0.2°C for *E. amoenus* (not significant). With either procedure *E. minimus* had a significantly higher tolerance than *E. amoenus* for elevated T_b or T_{hy} ($p < 0.01$, t-test), and a significantly higher tolerance than *E. speciosus* for elevated T_b ($p < 0.01$, t-test) (*E. speciosus* were not evaluated for hypothalamic heatings because of their ambiguous responses to this procedure).

Hypothermia

E. speciosus did not show any tendency to become hypothermic following periods of elevated T_b ; the lowest temperature reached by this species was not significantly different from the normal T_b (Fig. 4). In contrast, both *E. amoenus* and *E. minimus* regularly allowed their T_b 's to drop to subnormal levels after heatings. The minimum temperature attained depended upon the arousal state of the animal. *E. minimus* and *E. amoenus* fell asleep (as determined by behavioral criteria) in about 50% of these experiments (no interspecific difference), but *E. speciosus* always remained awake. Minimum T_b 's for sleeping animals were significantly cooler than for awake animals ($p < 0.01$, pairwise t-test); the difference was approximately 1°C . Sleeping in *E. minimus* and *E. amoenus* only occurred following episodes of hyperthermia; the animals invariably remained awake during other experiments and control runs. We found no correlation between the amount of previous heating and the subsequent arousal state, and there was also no relationship between the degree of heating and the amount of hypothermia tolerated in any of the species.

Values for minimum temperatures reached were lower for *E. minimus* than similar measurements for *E. amoenus* (Fig. 4). The lowest temperatures observed were from sleeping *E. minimus* (mean 36.1°C), 2.3°C cooler than the normal T_b and significantly less ($p < 0.01$, t-test) than the mean T_b from sleeping *E. amoenus*. Awake *E. minimus* reached a mean minimum temperature not significantly different than the value for sleeping *E. amoenus* but cooler ($p < 0.01$, t-test) than the mean minimum for awake *E. amoenus*. In all cases the mean minimum temperature values for sleeping and awake *E. minimus* and *E. amoenus* were significantly less ($p < 0.01$, pairwise t-Test) than the average nonmanipulated T_b .

Field Experiments

Our laboratory results strongly suggested that the two species from arid habitats, *E. minimus* and *E. amoenus*, were much more tolerant of hyperthermia, and showed a greater tendency to become hypothermic following heat exposure, than the forest-inhabiting *E. speciosus*. Field data on hyperthermia tends to support the laboratory findings, but results are limited, because the transmitter-implanted animals were reluctant to return to the site of capture. We obtained recordings of T_b from 2 *E. minimus* (13 and 7 records) and 2 *E. amoenus* (9 and 6 records) at various times of the day (Fig. 5).

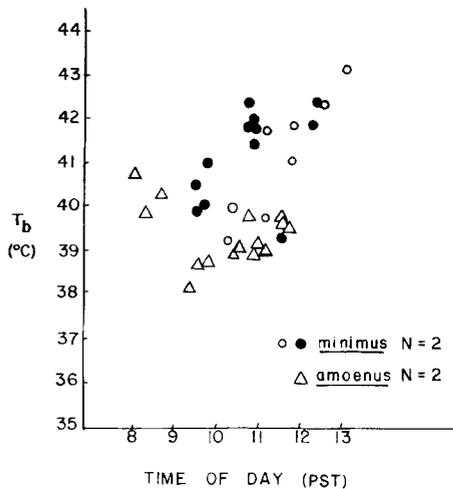


Fig. 5. Body temperatures as a function of time of day telemetered from animals returning to a feeding station in the natural habitat. Open circles are data obtained from one *E. minimus* on one day

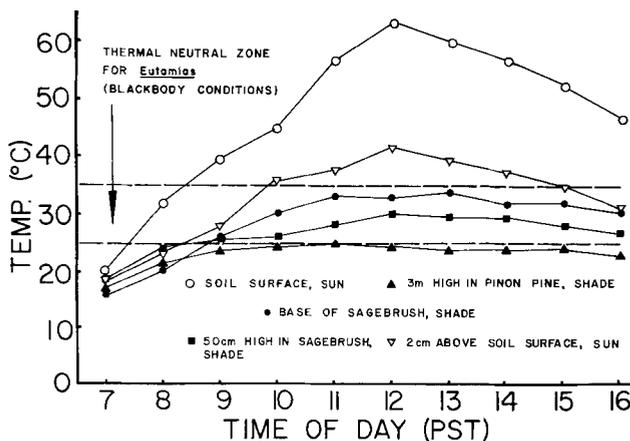


Fig. 6. Average microhabitat temperatures as a function of time of day. Data obtained from a representative site at the habitat border between pinon pine-mountain mahogany forest and open sagebrush in August 1976. Each point represents the average of at least three measurements on clear days with moderate (less than 200 cm s^{-1}) wind speeds. At this time of year, sunrise occurs at about 0600 h and sunset at about 1900 h at the study site

Several aspects of these results are noteworthy. First, both *E. minimus* and *E. amoenus* appear to commonly experience unusually high T_b 's during normal environmental conditions and activity levels. Means of T_b 's were 41.2°C for *E. minimus* and 39.7°C for *E. amoenus*. The value for *E. minimus* is significantly higher than that for *E. amoenus* ($p < 0.01$, t-test). A second point of interest is the apparently extremely high upper tolerance limit of T_b in *E. minimus*. One female had a T_b of 43.1°C , a temperature more than 0.5°C hotter than any tolerated by laboratory animals in hyperthermia experiments. This individual was behaving normally at the time of recording and

did not appear stressed. She was later retrapped and her transmitter calibration was checked and found to be accurate. A third interesting observation is the apparent increase in the T_b 's of *E. minimus* from morning to early afternoon (animals were inactive later in the day). For example, the T_b of one *E. minimus* recorded 8 times during one morning rose from 39.3°C at 10:25 PST to 43.1°C at 13:03 PST (Fig. 5, open circles). This change in T_b appears to be correlated with the rise in environmental heat load with time of day, since air and ground temperatures as well as solar radiation loads increase as the sun approaches its zenith (Fig. 6). The two *E. amoenus* did not show a similar change in T_b with time of day. However, we have no data for this species at times later than 11:40 PST.

Discussion

Values of α_{MHP} for the three chipmunks are among the highest yet reported (Heller, in press). Heller et al. (1974) found high α_{MHP} values, similar to those of *Eutamias*, in two ground squirrels, *Citellus lateralis* and *C. beldingi*, and offered two hypotheses to explain this unusually high hypothalamic thermosensitivity. One hypothesis proposed that it was the consequence of the need to maintain thermoregulation during hibernation. If hypothalamic thermosensitivity were adequate to drive thermoregulatory responses at the low T_b 's of hibernation, and if the thermoregulatory system were continuous from euthermia to deep hibernation, then Q_{10} effects on the neurons involved should require a high euthermic hypothalamic thermosensitivity. The second hypothesis postulated that the high hypothalamic thermosensitivity might be a consequence of small body size. Because of its greater weight-specific coefficient of heat loss, a small species must respond to a given drop in T_a below thermoneutrality with a larger weight specific heat production response than a larger species if both are to maintain a constant T_b . Data from a wide variety of hibernators and nonhibernators support the body size hypothesis (Heller, in press).

The three *Eutamias* species provide an interesting test of these two hypotheses. All are hibernators (Heller and Poulson, 1970) and hence would be expected to show similar thermosensitivities if the first hypothesis were true. However, if body size is of primary importance, the smaller species should show greater thermosensitivity than the larger species. Although small sample sizes and variation in the data (probably due to slight differences in thermode placement and some interindividual variation) preclude statistical significance, hypothalamic thermosensitivity as re-

flected by α_{MHP} does seem to be inversely related to body size in *Eutamias* (Table 1). Interspecific differences are most pronounced at low T_a 's, when thermosensitivity is maximal. These results, though not conclusive, support the body size hypothesis and argue against the hibernation hypothesis.

There were marked differences between the three *Eutamias* species in their responses to heat stress, including (1) the degree of whole-body or hypothalamic hyperthermia tolerated, (2) the type of countermeasures initiated when the maximum tolerated temperature was attained, and (3) the amount of hypothermia following bouts of hyperthermia. The evidence suggests that *E. minimus* and *E. amoenus* have well-developed passive heat-loss mechanisms. After a heating they would sprawl on the cool floor, bringing the thinly-furred ventral surface into maximal contact with the substrate and facilitating conductive heat loss. Additionally, these two species fell asleep after heatings in about half of these experiments. This was a specific response to hyperthermia, since they never fell asleep at other times. Finally, both *E. minimus* and *E. amoenus* allowed themselves to become significantly hypothermic following heatings. In contrast, *E. speciosus* never sprawled, always remained awake, and did not exhibit a tendency to become hypothermic, in any of our heat stress experiments.

The rather wide ranges of T_b tolerated by *E. minimus* and *E. amoenus* without evoking active thermoregulatory responses are unusual, especially the high upper limit of *E. minimus*. Lethal T_b 's are usually only a few degrees above normal levels, and elevations in T_b more than one or two degrees above normal levels are almost always countered by heat-loss responses (in nonfebrile animals). The extreme conditions encountered by diurnally active desert mammals, such as *E. minimus* and *E. amoenus*, lead to exceptions to this general rule. Several species, such as the camel (Schmidt-Nielsen et al., 1957) and the antelope ground squirrel (Hudson, 1962), utilize heat storage mechanisms to maintain activity without resorting to evaporative cooling. The antelope squirrel has two interesting modifications of its CNS thermoregulator which seem to be correlated to heat storage behavior: (1) reversal of the normal inverse relationship of α_{MHP} to T_a , such that hypothalamic thermosensitivity is highest at high T_a 's, and (2) a marked depression of hypothalamic thermosensitivity following T_{hy} heatings (Heller and Henderson, 1976). We believe that the large tolerance for hypo- and hyperthermia exhibited by *E. minimus* and *E. amoenus* are also adaptations for heat-storage behavior, although these species lack the CNS adaptations displayed by the antelope squirrel.

The typical behavior pattern of an animal utilizing

heat storage consists of activity bouts, during which T_b rises, followed by retreats to a cool shelter (e.g., a burrow) for passive heat dissipation. The length of each activity bout is directly related to the range of T_b 's tolerated by the animal—the larger the T_b “scope”, the longer an activity bout can last. There are large differences in the T_b scopes of the three *Eutamias* species (Fig. 4), which range from 6–7 °C in *E. minimus* through 3.5 °C for *E. amoenus* to less than 2 °C for *E. speciosus*. The scopes can be used to estimate the approximate lengths of activity bouts via a modified energy budget equation (Porter and Gates, 1969) which yields the rate of heat gain for each species:

$$S = Q_{\text{abs}} + M - E - \varepsilon \gamma (T_r)^4$$

where S = rate of thermal energy storage, Q_{abs} = rate of radiation absorption, M = rate of metabolic heat production, E = rate of evaporative heat loss, ε = pelt emissivity, γ is the Stephan-Boltzmann constant, and T_r = surface temperature. Conductive heat exchange is unimportant because the animals are well insulated from the substrate. If T_a and T_b are assumed to be 40 °C and wind speed to be moderate (10–100 cm s⁻¹), convection also becomes negligible since there is very little gradient between T_b , T_r , and T_a . As can be seen in Figure 6, 40 °C is a commonly experienced T_a for chipmunks in open areas. Q_{abs} can be computed from incident radiation and pelt absorptivity. Incident radiation was assumed to approximate 1.35 cal cm⁻² min⁻¹, as a reasonable figure for desert conditions. Pelt absorptivities and other energy exchange parameters (Tables 2a and 2b) were obtained from Heller and Gates (1971). In order to accommodate for activity, resting values for MHP were multiplied by 3, an increase seen in moderately active animals in the laboratory. Similarly, E values were set at 3 times resting levels, since evaporative water loss is primarily respiratory and should therefore change approximately in proportion to MR. Chipmunks do not sweat and use thermoregulatory evaporative water loss only as a last resort in extremely critical situations (Heller and Poulson, 1972) unlike other sciurids which commonly utilize evaporative cooling (Hudson and Deavers, 1972; Hudson et al., 1972). Solutions for S are shown in Table 2b.

If S is known, the time available for activity can be calculated easily from body weight, T_b scope, and heat capacity (assumed to be 0.82 cal °C⁻¹ gm⁻¹):

$$\text{activity time} = \frac{(\text{scope} \times \text{weight} \times \text{heat capacity})}{S}$$

These computations (Table 2c) predict that *Eutamias minimus* can remain exposed to severe heat loads

Table 2. a) Energy exchange parameters for *Eutamias* species

| | Body weight | Weight specific minimal MR ^a | 35 °C Weight specific EWL ^{a,b} | Minimal MR | Resting EWL | Absorptivity to solar energy ^a | Emissivity to thermal energy ^a | A _{ee} area for radiant energy exchange ^a |
|---------------------|-------------|--|--|--------------------------|-------------|---|---|---|
| | (g) | (cal g ⁻¹ min ⁻¹) | | (cal min ⁻¹) | | (%) | (%) | (cm ²) |
| <i>E. speciosus</i> | 72 | 0.12 | 0.046 | 8.64 | 3.30 | 73 | 99 | 130 |
| <i>E. amoenus</i> | 43 | 0.12 | 0.054 | 5.16 | 2.32 | 75 | 99 | 113 |
| <i>E. minimus</i> | 34 | 0.12 | 0.041 | 4.08 | 1.39 | 73 | 99 | 89 |

b) Rates of energy storage (S) for *Eutamias* species. All values in cal min⁻¹; assumes T_r = T_b = T_a = 40 °C; incident radiation load = 1.35 cal cm⁻² min⁻¹)

| | M 3 × minimal MR | – | E 3 × resting EWL | + | Q _{abs} Absorbed radiation | – | Q _{em} Emitted radiation | = | S Rate of energy storage |
|---------------------|------------------------|---|-------------------------|---|---|---|---|---|--------------------------------|
| <i>E. speciosus</i> | 25.8 | | 9.9 | | 130 | | 101.4 | | 44.5 |
| <i>E. amoenus</i> | 15.5 | | 7.0 | | 113 | | 88.2 | | 33.3 |
| <i>E. minimus</i> | 12.2 | | 4.2 | | 89 | | 69.4 | | 27.6 |

c) Time available for activity before T_b maximum is exceeded

| | Rate of energy storage (cal min ⁻¹) | Heat capacity (cal °C ⁻¹ g ⁻¹) | Rate of rise of T _b (°C min ⁻¹) | Body tem- perature scope (°C) | Time available for activity (min) | Relative time available for activity |
|---------------------|---|---|--|-------------------------------------|---|--|
| <i>E. speciosus</i> | 44.5 | 0.82 | 0.76 | 2.0 | 2.64 | 1 |
| <i>E. amoenus</i> | 33.3 | 0.82 | 0.94 | 3.5 | 3.71 | 1.4 |
| <i>E. minimus</i> | 27.6 | 0.82 | 0.99 | 7.0 | 7.09 | 2.68 |

^a Data from Heller and Gates (1971)

^b EWL = evaporative water loss

approximately twice as long as *E. amoenus*, and more than 2.6 times as long as *E. speciosus*. These findings have obvious implications for the distributions of the animals in their natural habitats. Heller and Gates (1971) calculated the climatic spaces of the three species (all combinations of T_a, wind speed, and Q_{abs} in which the animal can maintain a constant T_b), and found that they were very similar. Thus steady-state physiological factors should not be responsible for establishing the contiguously allopatric distributions of these animals. Studies of interspecific behavioral dominance hierarchies (Chappell, 1977) show that *E. speciosus* dominates both *E. minimus* and *E. amoenus*, and that *E. amoenus* in turn dominates *E. minimus*. Thus behavioral interactions may account for the upper range limits of *E. amoenus* and *E. minimus*, but do not explain the restriction of *E. speciosus* from *E. amoenus* habitat, or of *E. amoenus* from *E. minimus* habitat. We feel that the differences in heat storage ability in the chipmunks are important in determining these boundaries. The climate space diagrams of Heller and Gates reveal that none of the three species can remain in steady-state thermal equilibrium under

the extremely severe conditions commonly experienced in the arid piñon pine-mountain mahogany and sagebrush zones. However, the ability to effectively utilize heat storage behavior (a transient excursion beyond the climate space followed by a retreat back within its limits) allows *E. minimus* and *E. amoenus* to colonize these areas. *E. amoenus* is not as well adapted as *E. minimus* for this behavior (it has a smaller T_b scope than *E. minimus*), and therefore is at a competitive disadvantage to *E. minimus* in the severe open sagebrush desert. However, in piñon pine areas the trees apparently provide enough patches of shade and elevated perches out of the hot boundary layer to tip the competitive balance in favor of the more aggressive *E. amoenus*.

The hypotheses are strengthened by behavioral observations of animals in the field (Chappell, 1977; States, 1976). In forest edge areas where both occur, *E. amoenus* spends a much greater percentage of its time in and around trees than *E. minimus*. In open sagebrush areas *E. minimus* is commonly observed far from tree cover, but *E. amoenus* is rarely seen except close to the widely scattered trees.

This study of thermoregulatory characteristics in *Eutamias speciosus*, *E. amoenus*, and *E. minimus* has revealed marked differences in autonomic and behavioral mechanisms for coping with heat stress. These differences are adaptive in view of the animals' behavior and ecology, and may be important in determining their distribution patterns in the natural habitat. The ability to utilize heat storage seems to allow *E. minimus* and *E. amoenus* to occupy habitats which would be otherwise intolerable. Interestingly, the chipmunks have evolved a specialized heat storage mechanism which is functionally very similar to that of the antelope ground squirrel, but without requiring the modifications to the CNS thermoregulator seen in this animal. Physiological regulatory systems as basic and important as the regulator of body temperature are often believed to be fundamentally conservative and resistant to evolutionary change. This study has shown that thermoregulatory differences can arise even between very similar species if they are subjected to dissimilar selective pressures. It is becoming increasingly clear that great evolutionary plasticity does exist in the mammalian thermoregulatory system.

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