

Thermal responses of periodical cicadas: within and between brood parity (Hemiptera: Cicadidae: *Magicicada* spp.)

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Abstract: Measurements of the thermal responses of insects have been used to determine thermal adaptation to various environments. We have compared the thermal responses (minimum flight temperature, maximum voluntary tolerance temperature, and heat torpor temperature) of five periodical cicada species (*Magicicada septendecim*, *M. cassinii*, *M. septendecula*, *M. tredecassini*, and *M. neotredecim*) to test the hypothesis that the thermal responses are similar within and between broods due to the similar environmental conditions experienced by each brood. Cicadas of Brood XIII were collected in 1973, 1990, and 2007 in northern Illinois. Comparisons are made to data from specimens collected during the 1987 Brood X and the 1998 Brood XIX emergences in southeastern Tennessee, and the 1989 Brood XXIII emergence in central Illinois. The maximum voluntary tolerance (an upper thermoregulatory temperature) and the heat torpor temperatures do not differ between the five species examined. Only one species (*M. neotredecim*) differs statistically in the minimum flight temperature from the other species and one species pair (*M. septendecula* and *M. neotredecim*) differs in heat torpor temperature. There were a few examples of between brood statistical differences in the minimum flight temperature (*M. tredecassini*) and heat torpor temperature (*M. tredecassini*, *M. cassinii*) and one species pair differed significantly in heat torpor temperature. The data show that thermal responses generally do not change statistically in different emergences of the same brood or over large portions of a species range and the thermal responses of all species are similar.

Keywords: *Magicicada*, thermal responses, temperature adaptation, cicada

Introduction

Temperature influences the ability of animals to survive because it alters the rate of chemical reactions necessary to maintain living systems and thus sets limits for the viability of species. The daily temperature changes faced by terrestrial animals has meant animal cells cannot function efficiently at every ambient temperature potentially experienced during the day. Diurnal animals generally thermoregulate in order to maintain their body temperature at a level where physiological processes will occur at maximal efficiency despite the changes to ambient temperature over the course of a day.¹ The various habitats used by animals mean that individual species must adapt to specific thermal environments in order to survive.

The thermal responses of insects have been used as a measure of thermal adaptation to specific environments.² Cicadas have been a model system for this type of research as their relatively large body size allowed body temperatures to be measured accurately. The first thermal adaptation study of cicadas investigated a periodical cicada,³ but thermal data for a large number of species from North America, South America, Africa, and Australia have since been published.^{2,4-20}

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The periodical cicadas are a group of seven cicada species that have either a 17-year (*Magicicada septendecim* [L.], *M. cassinii* [Fisher], *M. septendecula* Alexander and Moore) or 13-year (*M. tredecim* [Walsh and Riley], *M. tredecassini* Alexander and Moore, *M. tredecula* Alexander and Moore, *M. neotredecim* Marshall and Cooley) life cycle. The individual year groups are categorized into Broods numbered I–XVII for the 17-year broods and XVIII–XXX for 13-year broods.²¹ Each brood emerges at regular intervals in particular locations (see reviews of periodical cicada biology^{22,23}), but the species extend over large regions of the eastern United States. The 17-year species generally have a more northern distribution than the 13-year species.

Expansive distribution of the periodical cicadas provides an opportunity to investigate regional influences on thermal adaptation. Since thermal adaptation has been shown to be genetically determined in other insects,^{24–28} there is a possibility that local changes in gene frequency have led to differences in the thermal responses over the range of individual species. We studied individual species (*M. septendecim*, *M. cassinii*, *M. septendecula*, *M. tredecassini*, and *M. neotredecim*) from different broods as well as three consecutive emergences of Brood XIII to test the hypothesis that the thermal responses are similar within and between broods due to the similar environmental conditions experienced by each brood.

Materials and methods

Brood XIII *Magicicada* emergences were studied in Raccoon Grove (41° 23' 35" N 87° 45' 21" W), Will County, Illinois in 1973 and the same collecting sites in Des Plaines (42° 00' 22" N 87° 51' 52" W) and Brookfield (41° 49' 59" N 87° 50' 02" W), Cook County, Illinois during both 1990 and 2007. Brood X specimens were captured south of Walland (35° 42' 01" N 83° 48' 13" W), Blount County, Tennessee (*M. septendecim*) or in Knoxville (35° 52' 39" N 84° 02' 30" W), Knox County, Tennessee (*M. cassinii*) in 1987. Brood XXIII specimens were collected in Clinton Lake (40° 08' 54" N 88° 52' 39" W), DeWitt County, Illinois. Finally, Brood XIX specimens were collected in Friendsville (35° 45' 07" N 84° 07' 30" W), Blount County, Tennessee. The data published³ on *M. cassinii* from Brood IV were collected at Dirty Creek (35° 26' 47" N 95° 06' 07" W), near Webbers Falls, Muscogee County, Oklahoma.

The thermal responses were determined using the methodology outlined in the original cicada thermal response studies.^{3,4} Specimens were transported to the laboratory in a cardboard container with a moist paper towel in a cooler in an effort to minimize metabolism until experiments could be

performed. Experiments were generally performed during the afternoon or evening of the day of capture.

Body temperature (T_b) was measured in the laboratory with either a telethermometer and a 26-gauge hypodermic thermistor probe (1973 data) or a Physitemp Model BAT-12 digital thermocouple thermometer with a type MT 29/1 29 gauge hypodermic microprobe copper/constantan thermocouple accurate to ± 0.1 °C and a time constant of 0.15 s^{-1} (Physitemp Instruments, Inc., Clifton, NJ, USA). All thermocouple probes were calibrated to a National Institute of Standards and Technology thermometer to insure accuracy. Deep T_b was measured by inserting a probe midway into the dorsal mesothorax. Specimens were handled only by the wings prior to insertion of the thermocouple to prevent conductive heat transfer between the insect and experimenter. Each T_b was recorded within 5 s of the animals performing the desired behavior.

Prior to beginning the thermal experiments, specimens were cooled to torpor by placing them in a container above ice or in a refrigerator. Specimens were then tossed 1–2 m into the air, warming passively, until they made a controlled flight or landing, after which their T_b was measured. This T_b is the minimum flight temperature (MFT) and represents the lowest T_b of fully coordinated flight activity. Individual specimens were placed under a heat lamp to determine the maximum voluntary tolerance (MVT) or shade-seeking temperature. When the animal walked or flew from the heat source, its T_b was measured. The MVT is an upper thermoregulatory temperature representing the T_b when thermoregulation takes precedence over other behaviors.²⁹ The final T_b to be recorded was the heat torpor temperature (HTT). HTT was determined by heating an insect with the heat lamp within a paper container until it stopped moving. The procedure is nonlethal as animals recover motor control within a few minutes as they cool passively. The HTT represents the upper limit of activity and may be an ecologically lethal T_b since the animals are no longer able to move to avoid any continued increase in T_b . MFT and HTT delineate the T_b range within which a species is fully active as cicadas are torpid outside of this T_b range.

Statistical analyses were performed using InStat 3.0a for the Macintosh (GraphPad Software, San Diego, CA). Statistical significance is considered to be $\alpha = 0.05$ for all tests. Statistics are reported as mean \pm standard deviation.

Results

The thermal responses for all species and broods within species are summarized in Table 1. No data for the MFT of the

Table I Thermal responses of *Magiscada* species. Minimum flight temperatures are not provided for the 1973 and 1987 emergences due to problems with the experiments (see Results). The data for Brood IV *M. cassinii* are provided for comparative purposes but were not used to determine the species averages or in the statistical analyses. The Brood IV data do not differ from the average determined for *M. cassinii* (MFT $t = 0.0613$, d.f. 72, $P = 0.9513$; MVT $t = 1.698$, d.f. 119, $P = 0.0921$). Complete statistical analyses are provided in the text

Species	Brood emergence	Minimum flight temperature (°C)	Maximum voluntary tolerance temperature (°C)	Heat torpor temperature (°C)
<i>M. septendecim</i>		20.2 ± 1.50 ^b n = 52	33.3 ± 2.76 n = 88	42.5 ± 1.48 n = 76
	Brood X 1987		33.6 ± 2.82 n = 12	43.2 ± 1.61 n = 12
	Brood XIII 1973		32.8 ± 3.29 n = 20	41.8 ± 1.46 n = 10
	1990	20.4 ± 1.51 n = 38	33.3 ± 2.69 n = 40	42.4 ± 1.26 n = 38
	2007	19.5 ± 1.34 n = 14	33.6 ± 2.29 n = 16	42.8 ± 1.73 n = 16
<i>M. cassinii</i>		20.8 ± 1.78 ^c n = 64	33.0 ± 2.55 n = 107	42.5 ± 1.59 n = 92
	Brood X 1987		32.4 ± 2.70 n = 20	41.7 ± 1.97 ^g n = 20
	Brood XIII 1973		33.0 ± 2.75 n = 23	42.4 ± 0.90 n = 10
	1990	20.7 ± 1.71 n = 41	33.2 ± 2.45 n = 41	42.6 ± 1.48 n = 39
	2007	20.9 ± 1.95 n = 23	33.3 ± 2.49 n = 23	43.1 ± 1.36 ^g n = 23
	Brood IV ^a 1964	20.9 ± 2.84 n = 10	31.8 ± 2.51 n = 14	
<i>M. septendecula</i>	Brood XIII			
	2007	20.6 ± 2.24 ^d n = 19	32.6 ± 2.01 n = 21	43.0 ± 1.22 ^h n = 20
<i>M. neotredicim</i>	Brood XXIII			
	1989	18.0 ± 1.09 ^{b,c,d,e} n = 10	31.2 ± 1.62 n = 10	41.4 ± 1.45 ^h n = 10
<i>M. tredicassini</i>		20.1 ± 2.41 ^e n = 25	33.3 ± 1.83 n = 24	41.8 ± 1.66 n = 25
	Brood XXIII 1989	18.4 ± 1.48 ^f n = 10	33.0 ± 1.53 n = 10	40.4 ± 1.07 ⁱ n = 10
	Brood XIX 1998	21.2 ± 2.29 ^f n = 15	33.5 ± 2.05 n = 14	42.7 ± 1.32 ⁱ n = 15

Notes: ^aHeath³; ^b $P < 0.01$; ^c $P < 0.001$; ^d $P < 0.01$; ^e $P < 0.05$; ^f $P = 0.0026$; ^g $P < 0.05$; ^h $P < 0.05$; ⁱ $P = 0.002$.

1973 *M. septendecim* are included because the experiments could not be performed on the day of capture. This meant the animals were kept in a cold environment overnight decreasing their willingness to fly during the experiments the next morning. Similarly, no MFT data are provided for the 1987

emergence of *M. septendecim* as the refrigerator in which the specimens were stored prior to experimentation was so cold that the animals would not fly after being removed and rewarmed. Both groups behaved normally with respect to the MVT and HTT experiments.

Comparisons of the data from the 1973, 1990, and 2007 emergence of Brood XIII *M. septendecim* show no statistical difference between MFT ($t = 1.918$, d.f. = 50, $P = 0.0608$), MVT (ANOVA $F = 0.3907$, d.f. = 2, 73, $P = 0.6780$), or HTT (ANOVA $F = 1.495$, d.f. = 2, 61, $P = 0.2324$) (Figures 1–3). The same trends are seen for the MFT ($t = 0.0286$, d.f. = 62, $P = 0.7968$), MVT (ANOVA $F = 0.05124$, d.f. = 2, 84, $P = 0.9501$), and HTT (ANOVA $F = 1.569$, d.f. = 2, 69, $P = 0.2157$) for *M. cassinii* collected from Brood XIII.

The same lack of statistical differences is found when Brood X data are added to the analysis. The data are not significantly different for *M. septendecim* (MFT

$t = 1.918$, d.f. = 50, $P = 0.0608$, MVT ANOVA $F = 0.3274$, d.f. = 3, 84, $P = 0.8056$, or HTT ANOVA $F = 2.066$, d.f. = 3, 72, $P = 0.1208$) or *M. cassinii* (MFT $t = 0.0286$, d.f. = 62, $P = 0.7968$, or MVT ANOVA $F = 0.5334$, d.f. = 3, 103, $P = 0.6604$). Only the HTT (ANOVA $F = 3.413$, d.f. = 3, 88, $P = 0.0209$) shows a significant difference in *M. cassinii*. A Tukey–Kramer multiple comparison test shows the 1987 and 2007 ($q = 4.498$, $P < 0.05$) are the only data sets to show a statistical difference for *M. cassinii*.

The data for *M. tredecassini* show significant differences between Broods XIX and XXIII for MFT ($t = 3.379$, d.f. = 23, $P = 0.0026$) and HTT ($t = 4.528$, d.f. = 23, $P = 0.002$).

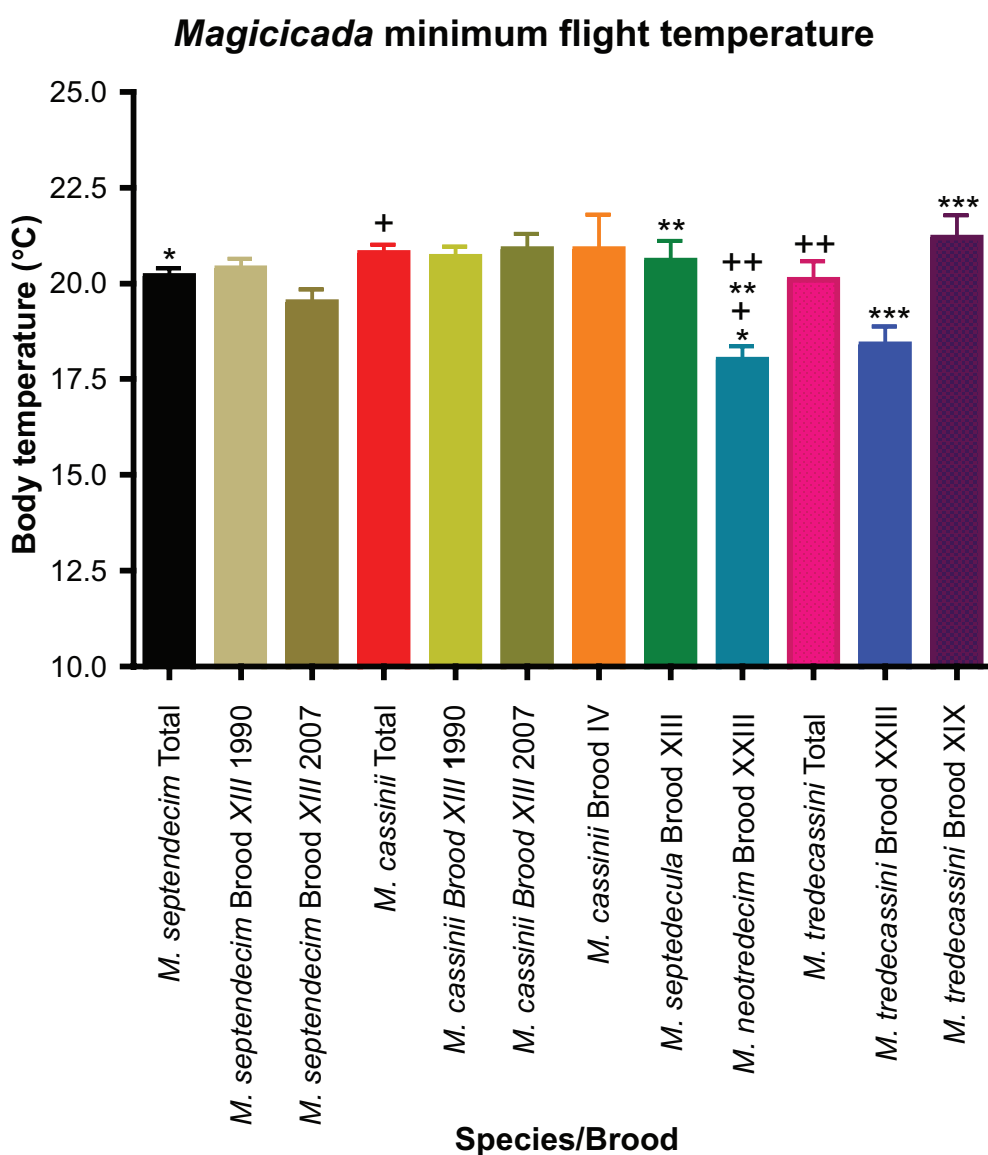


Figure 1 Minimum flight temperature determined for the periodical cicadas. *Magicicada neotredecim* differs significantly from the remaining species and the two broods of *M. tredecassini* differ from each other. Complete statistical analysis is provided in the text.

Notes: *, ** $P < 0.01$; + $P < 0.001$; ++ $P < 0.05$. *** $P = 0.0026$.

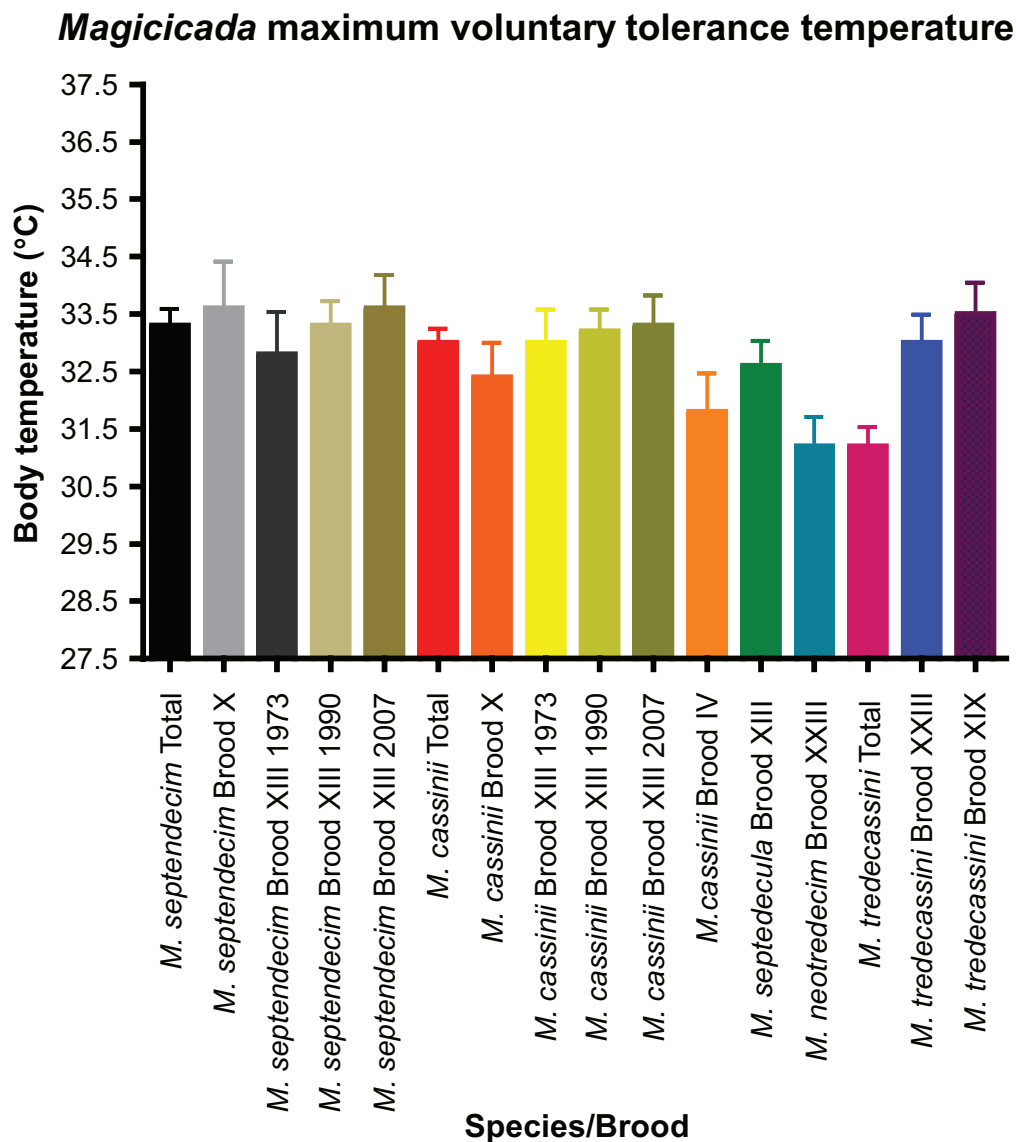


Figure 2 Maximum voluntary tolerance temperature determined for the periodical cicadas. There are no statistically significant differences in the means determined within or between broods or between species.

However, the MVT data did not differ significantly between broods ($t = 0.6748$, d.f. = 22, $P = 0.5069$).

When comparing the mean values for all species studied, the MFT data show the greatest variability (ANOVA $F = 5.430$, d.f. = 4, 165, $P = 0.0004$). A Tukey-Kramer multiple comparison test shows MFT of *M. neotredecim* shows significant differences from *M. septendecim* ($q = 4.877$, $P < 0.01$), *M. septedecula* ($q = 5.192$, $P < 0.01$), *M. cassinii* ($q = 6.369$, $P < 0.001$), and *M. tredecassini* ($q = 4.335$, $P < 0.05$). The corrected Bartlett statistic (12.872, $P = 0.0119$) suggests differences in the standard deviations of the MFT means are different so nonparametric test was then performed. The Kruskal-Wallis test ($KW = 18.579$, $P = 0.0010$) also suggests

there are differences between means. The Dunn's multiple comparisons test suggests that *M. neotredecim* differs from *M. septendecim* ($P < 0.05$), *M. septedecula* ($P < 0.05$), and *M. cassinii* ($P < 0.001$). The MVT (ANOVA $F = 1.900$, d.f. = 4, 245, $P = 0.1111$) shows no significant differences between species. The HTT (ANOVA $F = 3.153$, d.f. = 4, 218, $P = 0.0152$) suggests significant differences between species. A Tukey-Kramer multiple comparison test suggests only the HTT of *M. neotredecim* shows a significant difference from *M. septedecula* ($q = 3.928$, $P < 0.05$).

Discussion

The parity within and between groups suggests that all species are adapted to similar thermal conditions. This is not

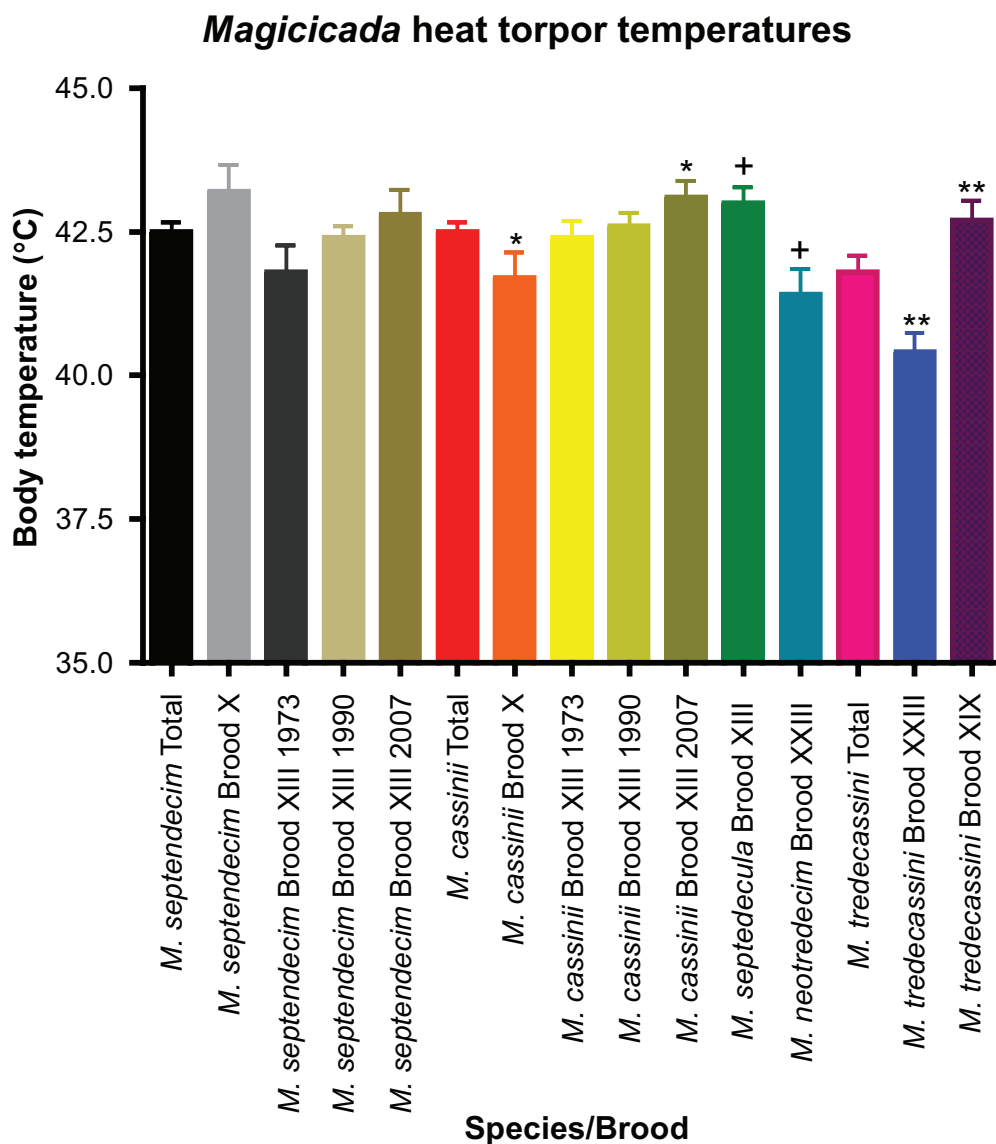


Figure 3 Heat torpor temperature determined for the periodical cicadas. The Brood X and the 2007 Brood XIII data differ significantly within *M. cassinii* as do the data for *M. tredecassini* Broods XXIII and XIX. The only species data to differ significantly are the data species for *M. septedecula* differ from *M. neotrededecim*. Complete statistical analysis is provided in the text.

Notes: *, * $P < 0.05$; ** $P = 0.002$.

surprising since the 17-year and 13-year species of individual broods have evolved to emerge synchronously. The survival benefits of the periodic and short-term emergences are only sustained if all individuals emerge in a brood emerge synchronously. The results are supported by the thermal responses of other closely related cicada species having been shown to be similar as well.^{10,11,13,14,16}

The MFT is the thermal response that showed statistically significant differences within and between broods or species. MFT does not seem to be dependent on the environment in which a species lives. Instead, MFT is dependent on the morphology of the flight system.³⁰ The variability in MFT

values is probably the result of the morphological influence of individual species on MFT. The MFT of *M. neotrededecim* is significantly different from most other species suggesting that there is a difference in the flight system. However, determining when a specimen reaches the MFT is the most subjective of the thermal response experiments. This may be partially responsible for the differences in MFT values for the different broods of *M. tredecassini*.

The MVT was consistent both within and between broods as well as between species. The thermal environment to which each brood will be exposed during an emergence will be consistent as well. Similar MVT would be expected as all

species have the same thermal environment to manipulate in order to regulate T_b . Adapting to function more efficiently at higher or lower T_b would put ectothermic species like the periodical cicadas at a disadvantage in terms of maintaining activity. Fewer hours of activity would lead to less time to find a potential mate, decreasing the reproductive potential of individuals that are adapted to the higher or lower T_b for peak activity, which would select against different MVT values in the different species. Combining these data with the MFT and MVT data in Heath³ (which do not differ significantly from the data provided here, MFT $t = 0.0613$, d.f. 72, $P = 0.9513$; MVT $t = 1.698$, d.f. 119, $P = 0.0921$), the thermal responses of *M. cassinii* are the same from Oklahoma to northern Illinois to southeastern Tennessee.

The similarity in HTT within and between broods and species would be expected for the same reasons as similarity in the MVT. The only difference found was between *M. septendecula* and *M. neotredcecim* and the two broods of *M. tredecassini*. The statistical significance of the difference between *M. septendecula* and *M. neotredcecim* is barely significant ($q = 3.928$ with significance if $q > 3.900$) and may be the result of one low value determined during the experiments (significance disappears if the datum is eliminated from the analysis). The differences observed in the *M. tredecassini* HTT are more difficult to explain but may be related to the age of the population in 1989. There were many dead animals in the habitat when the experimental group was collected so the low HTT may be a result of deterioration of function with aging of the population. Similarly, the one pair of *M. cassinii* that showed a statistical difference in HTT included the 1987 group which may have been altered due to the fact that these specimens were nearly frozen prior to experimentation. The extreme cold may have weakened the group producing the lower HTT.

Thermal adaptation has been shown to be genetically determined in insects other than cicadas.^{24–28} The similarities of the thermal responses of periodical cicadas suggest that they are also genetically determined and maintained within populations of cicadas as well. The long life cycle of periodical cicadas would mean that these species would not be able to adapt quickly to changing climate as has been seen in other insects.²⁴

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where experiments could be performed. The authors report no conflicts of interest in this work.

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