

## THE EFFECT OF TEMPERATURE ON ISOLATED PERFUSED HEARTS OF HETEROTHERMIC MARSUPIALS

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(Received 10 October 1988)

**Abstract**—1. The thermal response of isolated perfused hearts of four dasyurid marsupials was determined and compared with that of two rodents.

2. Heart beat rate was strongly temperature dependent in all species.

3. The temperature of cardiac arrest in the species investigated in the present study and of others collected from the literature occurred at a mean of about 13°C in homeotherms, 7°C in daily heterotherms, and 1°C in hibernators.

4. For both marsupials and placentals the temperature of cardiac arrest in hibernators and daily heterotherms correlated with the minimum body temperature during torpor.

### INTRODUCTION

An essential requirement for survival at the low body temperatures ( $T_b$ ) encountered during hibernation and daily torpor is the maintenance of cardiac function. Heart rate is strongly temperature dependent and perfused hearts of homeothermic species cease to beat at temperatures between 10 and 25°C (Langendorff, 1897; Adolph, 1951; Lyman and Blinks, 1959; Hubbart *et al.*, 1981). In heterothermic rodents that are capable of shallow, daily torpor, cardiac arrest appears to occur at lower temperatures than in homeotherms; however, maintenance of cardiac function at or below 0°C has only been observed in "deep" hibernators (Lyman and Blinks, 1959; Michael and Menaker, 1963; Hudson, 1967, 1971).

At rest marsupials have lower heart rates than placentals (Kinnear and Brown, 1967). This lower beat rate correlates with a relatively greater heart mass in marsupials, allowing a greater stroke volume (Dawson and Needham, 1981). However, the maximum heart rates during locomotion are similar between the two subclasses, indicating that the scope for increase in heart rate is greater in marsupials than in placentals (Baudinette, 1978).

Because of these differences in cardiac function in marsupials and placentals, we investigated whether the thermal response of the isolated perfused hearts differs between the two mammalian subclasses. For this comparison we determined the temperature dependence of heart rate in four dasyurid marsupials with that of two rodents. We were also interested in whether the temperature of cardiac arrest in heterothermic marsupials and placentals is correlated with the minimum body temperature they reach during periods of torpor. For this comparative analysis we used data from the present study and values from the literature.

### MATERIALS AND METHODS

The thermal response of isolated perfused hearts of the heterothermic dasyurid marsupials *Sminthopsis crassicaudata* ( $n = 2$ ), *Antechinus stuartii* ( $n = 3$ ), *A. flavipes* ( $n = 5$ ), and *Dasyuroides byrnei* ( $n = 3$ ) was compared with that of the rodents *Rattus norvegicus* ( $n = 8$ ) and *Mus musculus* ( $n = 5$ ). Hearts were perfused using the method of Langendorff (1897) using essentially the experimental design described by Hudson (1971). Fifteen minutes prior to the operation procedure animals were injected intraperitoneally with 10,000 units of heparin/kg body mass. Immediately following killing by cervical dislocation, the hearts were cannulated with a modified hypodermic needle, and perfused with standard Krebs–Henseleit medium saturated with 5% CO<sub>2</sub> in O<sub>2</sub>. The perfusion bottle was positioned so that the fluid column was 120–130 cm in height. Both the water-saturated air surrounding the heart and the Krebs–Henseleit medium perfusing the heart were maintained at the same temperature using a water jacket and a heat exchanger. The temperature of the perfusion medium was measured with a thermocouple placed in a small funnel immediately below the heart; the reading was within 0.5°C of the heart temperature. Hearts were allowed to stabilize for 5–10 min at about 35°C. The temperature was then decreased at a rate of 0.5°C/min or less. The beat rate was continuously monitored as a function of temperature and the temperature at which the heart ceased to beat (i.e. where neither electrical activity nor ventricular contractions could be detected) was determined. Heart beat frequency was measured with two Grass E2B subdermal electrodes leading to a Tectronix 5103N oscilloscope or a Grass 7P511 Amplifier and 79D polygraph. At the end of each experiment the hearts were removed from the cannulae, trimmed of excess tissue, and weighed.

Statistical differences between means were determined by Student's *t*-test, one-way ANOVA, and Student–Newman–Keuls test. Significance was assumed at the 5% confidence level.

### RESULTS

Beat rate of the isolated perfused hearts decreased with decreasing temperature (Fig. 1). The thermal

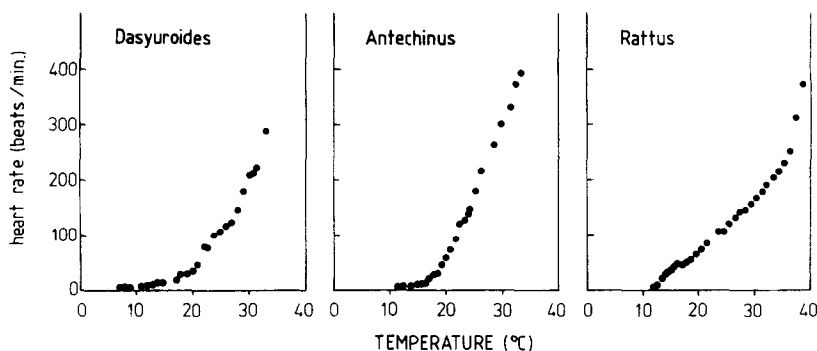


Fig. 1. The beat rate as a function of temperature during cooling of isolated perfused hearts from *Dasyuroides byrnei*, *Antechinus flavipes* (female), and *Rattus norvegicus*. Each point represents a single determination of beat rate.

response of heart rate was similar in *Dasyuroides byrnei* and *Rattus norvegicus* above 14°C. However, the heart of *R. norvegicus* ceased to beat at about 12°C, while that of *D. byrnei* still showed spontaneous activity at temperatures down to 7°C. The heart rate of a female *A. flavipes*, the species with the smallest hearts of the three species, was faster at temperatures equivalent to normal body temperature than those of the other two species (Fig. 1; Table 1).

The heart rate of all species decreased curvilinearly with temperature; however, the log-transformed data could not be described by single or dual slopes. The mean  $Q_{10}$  ( $\pm$ SD) for heart rate between 30°C and the normal resting  $T_b$  was  $2.4 \pm 0.38$  and was significantly less than the  $Q_{10}$  observed between 20 and 30°C ( $Q_{10} = 3.2 \pm 0.75$ ;  $P < 0.01$ ;  $t$ -test). Below 20°C, the  $Q_{10}$  increased to mean values of 2.8 (*S. crassicaudata*), 4.7 (*M. musculus*), 4.9 (*A. stuartii*), 9.5 (*D. byrnei*), and  $> 50$  (*A. flavipes* and *R. norvegicus*).

The beat rate as a function of temperature differed between species (Table 1). At the temperature corresponding to the normal body temperature the fastest rates were observed in species with small hearts. This relationship also was seen at 30°C; at 20°C heart rate did not appear to be linked with heart size. The temperature of cardiac arrest also differed significantly between the species (Table 1). In the marsupials, cardiac arrest occurred between 6.0°C in

*D. byrnei* and 12.6°C in *A. flavipes* females. For the rodents, heart beat ceased at 10.5–12.5°C.

The temperature of cardiac arrest correlates with thermoregulatory strategy in 22 endothermic species (Table 2). Hearts stop beating between 6 and 25°C in homeotherms, between 1.5 and 12°C in daily heterotherms (species that enter shallow, daily torpor), and between  $-1.0$  and 3.3°C in deep hibernators and the means of the three groups were significantly different ( $P < 0.001$ ; one-way ANOVA). When species of similar body mass and heart rates were compared, e.g. the homeothermic *R. norvegicus* with the daily heterotherm *D. byrnei* and the hibernators *S. tridecemlineatus* and *M. auratus* the differences between the three groups became even more obvious (one-way ANOVA;  $P < 0.0001$ ). However, the cessation temperature of heart beat in the daily heterotherms was significantly lower than the minimum body temperatures of this group ( $P < 0.001$ ;  $t$ -test). In hibernators the difference between the minimum  $T_b$  and the temperature of cardiac arrest was not significant ( $t$ -test). The minimum  $T_b$  during torpor of daily heterotherms and hibernators was linearly related with the temperature of cardiac arrest (Fig. 2). It appears that both marsupials and placentals fit this linear relationship well because the means of the residuals of species in both subclasses did not differ significantly ( $t$ -test).

Table 1. Beat rates of isolated perfused hearts as a function of temperature and the temperature of cardiac arrest in four marsupial and two placental mammals

| Species                          | $T_b$ rest (°C) | $T_b$          | Heart beats/min at |                | Cardiac arrest (°C) | Heart mass (g)  | <i>n</i> |
|----------------------------------|-----------------|----------------|--------------------|----------------|---------------------|-----------------|----------|
|                                  |                 |                | 30°C               | 20°C           |                     |                 |          |
| <i>Sminthopsis crassicaudata</i> | 34              | (420)          | $287 \pm 38.2$     | $108 \pm 33.9$ | $11.0 \pm 1.4$      | $0.12 \pm 0.03$ | 2        |
| <i>Antechinus stuartii</i>       |                 |                |                    |                |                     |                 |          |
| Female                           | 34              | (470)          | 336                | 140            | 8.6                 | 0.25            | 1        |
| Male                             | 34              | 250            | $162 \pm 0$        | $52 \pm 10.6$  | $12.0 \pm 0.7$      | $0.28 \pm 0.01$ | 2        |
| <i>Antechinus flavipes</i>       |                 |                |                    |                |                     |                 |          |
| Female                           | 35              | $375 \pm 21$   | $259 \pm 61.7$     | $65 \pm 7.5$   | $12.6 \pm 1.7$      | $0.29 \pm 0.05$ | 4        |
| Male                             | 35              | 300            | 180                | 63             | 11.0                | 0.31            | 1        |
| <i>Dasyuroides byrnei</i>        | 34              | $279 \pm 12.7$ | $226 \pm 15.1$     | $48 \pm 16.9$  | $6.0 \pm 1.4$       | $1.0 \pm 0.22$  | 3        |
| <i>Rattus norvegicus</i>         |                 |                |                    |                |                     |                 |          |
| Weaner                           | 37              | 430            | 260                | 104            | 12.3                | 0.8             | 1        |
| Adult                            | 37              | $325 \pm 7.1$  | $175 \pm 9.8$      | $62 \pm 23.1$  | $12.5 \pm 1.9$      | $1.4 \pm 0.15$  | 8        |
| <i>Mus musculus</i>              | 37              | 495            | $253 \pm 42.5$     | $75 \pm 12.7$  | $10.6 \pm 0.9$      | $0.16 \pm 0.9$  | 5        |

Data expressed as mean  $\pm$  SD. Values in parentheses represent extrapolated beat rate using the  $Q_{10}$  between measurements at 30 and 20°C. *Antechinus* males and females are listed separately because of distinct sexual dimorphism (Geiser, 1988b). Temperatures of cardiac arrest differed significantly between the six species (one-way ANOVA;  $F = 6.36$ ;  $df = 5,24$ ;  $P < 0.01$ ). When pairwise comparisons were made, differences in cardiac arrest could be observed between *D. byrnei* and *M. musculus*, *D. byrnei* and *R. norvegicus*, and *D. byrnei* and *A. flavipes* (Student–Newman–Keuls test;  $P < 0.05$ ). Body temperatures of normothermic resting *R. norvegicus* and *M. musculus* were taken from Altmann and Dittmer (1973), those for the marsupials from Geiser (1985a).

Table 2. The minimum body temperatures during torpor and the temperature of cardiac arrest in 22 endothermic species

| Group<br>Species                     | Minimum $T_b$<br>(°C) | Cardiac arrest<br>(°C) | Source   |
|--------------------------------------|-----------------------|------------------------|--|
| <b>Homeotherms</b>                   |                       |                        |  |
| <i>Rattus norvegicus</i>             | —                     | 12.5                   | Present study                                      |
|                                      | —                     | 9.2–15                 | Lyman and Blinks (1959)                            |
| <i>Aplodontia rufa</i>               | —                     | 10.6                   | Lyman and Blinks (1959)                            |
| <i>Sigmodon hispidus</i>             | —                     | 6                      | Lyman and Blinks (1959)                            |
| <i>Sciurus vulgaris</i>              | —                     | 13–16                  | Lyman and Blinks (1959)                            |
| <i>Oryctolagus cuniculus</i>         | —                     | 12.5                   | McMurchie <i>et al.</i> (1973)                     |
| <i>Felis silvestris</i>              | —                     | 6.4–9                  | Langendorff (1897)                                 |
| <i>Canis lupus familiaris</i>        | —                     | 25                     | Adolph (1951)                                      |
| <i>Sturnus vulgaris</i>              | —                     | 15                     | Weller <i>et al.</i> (1978)                        |
| <b>Daily heterotherms</b>            |                       |                        |  |
| <i>Sminthopsis crassicaudata</i>     | 13.0                  | 11.0                   | Present study; Geiser <i>et al.</i> (1986)         |
| <i>Antechinus stuartii</i>           | 20                    | 9                      | Present study; Geiser (1988b)                      |
| <i>Antechinus flavipes</i>           | 24.5                  | 12                     | Present study; Geiser (1985b)                      |
| <i>Dasyuroides byrnei</i>            | 20.4                  | 6                      | Present study; Geiser and Baudinette (1987)        |
| <i>Mus musculus</i>                  | 16                    | 10.5                   | Present study; Hudson and Scott (1979)             |
| <i>Baiomys taylori</i>               | 21                    | 1.5                    | Hudson (1965, 1967)                                |
| <i>Perognathus hispidus</i>          | 11                    | 2.1                    | Hudson (1967); Wang and Hudson (1970)              |
| <i>Perognathus californicus</i>      | 15                    | 6.5                    | Hudson (1967); Tucker (1965)                       |
| <i>Peromyscus boylei</i>             | 18                    | 6.5                    | Hudson (1967); Morhardt (1970)                     |
| <i>Peromyscus eremicus</i>           | 16                    | 4.0                    | Hudson (1967); MacMillen (1965)                    |
| <i>Peromyscus leucopus</i>           | 13                    | 7.2                    | Hudson (1967); Gaertner <i>et al.</i> (1973)       |
| <b>Hibernators</b>                   |                       |                        |  |
| <i>Spermophilus tridecemlineatus</i> | 1.1                   | –1.0                   | Lyman and Blinks (1959)                            |
|                                      |                       | –1.0                   | Lyman and O'Brian (1972); Hudson (1971)            |
| <i>Tamias striatus</i>               | 5                     | 1.7–3.3                | Lyman and Blinks (1959);<br>Wang and Hudson (1971) |
| <i>Mesocricetus auratus</i>          | 2.2                   | 2.5                    | Lyman and Blinks (1959); Lyman (1948)              |
| <i>Myotis lucifugus</i>              | 2                     | –1.0                   | Michael and Menaker (1963); Hock (1951)            |
| <b>Mean:</b>                         |                       |                        |  |
| Homeotherms                          | —                     | 13.0 ± 6.2 (8)         |  |
| Daily heterotherms                   | 16.7 ± 4.5            | 6.9 ± 3.5 (11)         | $P < 0.01$ ; $t$ -test                             |
| Hibernators                          | 2.6 ± 1.7             | 0.8 ± 2.0 (4)          | NS; $t$ -test                                      |
|                                      | $P < 0.001$           | $P < 0.001$            |  |
|                                      | $t$ -test             | one-way ANOVA          |  |

When a range of temperatures was given the mean of the two values was used to calculate the mean for each group. NS = not significant ( $P > 0.05$ ).

The hearts of all species showed the ability to regain spontaneous beat after rewarming for a few degrees above the cessation temperature. In several instances the temperature was increased above the normothermic  $T_b$  after the initial cooling experiment and the heart rates increased further with temperature. At about 40°C fibrillation was observed in *R. norvegicus* and *M. musculus*. The highest temperatures where a coordinated beat was observed was 43.5°C in a *A. flavipes* male at a rate of 444 beats/min.

## DISCUSSION

The present study reveals significant differences in the temperature-dependence of cardiac function with regard to the thermoregulatory mode of the various species considered. In homeothermic species which always maintain a high and steady  $T_b$ , cardiac arrest occurred at much higher temperatures than in hibernators; daily heterotherms were intermediate. The thermal response of isolated perfused hearts of the heterothermic marsupials did not show major differences from the heterothermic rodents. Within all heterothermic species (hibernators and daily heterotherms) the minimum  $T_b$  and the temperature of cardiac arrest were linearly related, suggesting that these variables may be functionally linked. Because the temperature of cardiac arrest and the minimum  $T_b$  in the daily heterotherms differ significantly, it appears, however, that cardiac arrest determines the range of body temperatures in endotherms indirectly rather than directly.

The  $Q_{10}$  of beat rate increased with decreasing temperature in the species investigated in the present study. The  $Q_{10}$ 's of beat rate remained  $< 10$  in most species even when heart temperature decreased below 20°C. In contrast, the  $Q_{10}$  of heart rate below 20°C was increased to  $> 50$  in *R. norvegicus* which is homeothermic and *A. flavipes* which, although heterothermic, has the highest minimum  $T_b$  of all heterothermic species investigated (Table 2). Normal biological functions show  $Q_{10}$ 's between 2 and 3. This

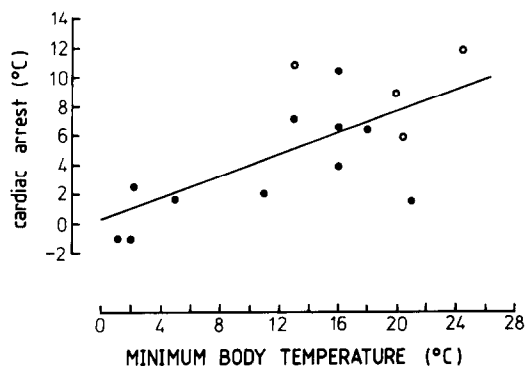


Fig. 2. The temperature of cardiac arrest as a function of the minimum body temperature during torpor of 15 heterothermic placental (●) and marsupial (○) mammals. A linear regression analysis resulted in the equation:  $y = 0.11 + 0.39x$ ;  $r = 0.69$ ;  $P < 0.005$ . Data from Table 2.

high  $Q_{10}$  of heart rate would result in a more rapid reduction of supply of oxygen and nutrients than that of metabolic requirements (Geiser, 1988a) and thereby in a failure of energetic homeostasis. The change in  $Q_{10}$  of heart rate with temperature in homeotherms and daily heterotherms is not observed in hibernating bats and rodents which exhibit a constant  $Q_{10}$  over the range of temperatures investigated (Michael and Menaker, 1963; Hudson, 1971, reanalysed). These observations suggest that the marked increase in  $Q_{10}$ , and therefore decrease in cardiac work, below a critical temperature is more important in determining the range of body temperatures available to the animal than the temperature of cardiac arrest.

The change in the  $Q_{10}$  of heart rate may be a reflection of temperature-induced alterations in cardiac membrane function or ion permeability critical for the excitation-coupling process. Potassium efflux from the hearts of the rodent *Peromyscus leucopus* increased close to the minimum  $T_b$  of that species (Hudson and Eller, 1974). Similarly, the thermal response of heart mitochondrial respiration of *Sminthopsis crassicaudata* showed an increase in  $Q_{10}$  close to the minimum  $T_b$  and correlated with seasonal changes in their minimum  $T_b$  (Geiser *et al.*, 1986). Moreover, the increase in  $Q_{10}$  of heart mitochondrial respiration in homeothermic species occurs at a higher temperature than in daily heterotherms (McMurchie *et al.*, 1973; Geiser and McMurchie, 1984). As for heart rate no changes in the  $Q_{10}$  of cardiac respiratory enzymes could be observed in deep hibernators (Aloia *et al.*, 1986). These observations suggest that cell membranes of daily heterotherms and hibernators are less temperature sensitive than those of homeotherms and therefore allow normal physiological function at low temperatures.

The beat rates of isolated perfused hearts at the temperature of their respective  $T_b$  were similar to the minimum heart rates determined for living *A. flavipes*, *M. musculus*, and *R. norvegicus* (Kinnear and Brown, 1967; Penzlin, 1977). For intact *S. crassicaudata* the minimum heart rate was 460 beats/min (present study), a value slightly above that from the isolated perfused hearts at body temperature.

The present study suggests that the thermal response of isolated perfused hearts in placental and marsupial mammals is similar. Differences in cardiac function at low temperatures appear to reflect differences in thermoregulation of the animal rather than the phylogenetic separation of the two subclasses.

**Acknowledgements**—Supported by a Flinders University Research Scholarship to F.G. and grants to R.V.B. from the Flinders University Research Committee and the Australian Research Grants Scheme.

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