The Journal of Experimental Biology 200, 1451–1458 (1997)
Printed in Great Britain © The Company of Biologists Limited 1997
JEB0852

RATES OF REWARMING, HEART AND RESPIRATORY RATES AND THEIR SIGNIFICANCE FOR OXYGEN TRANSPORT DURING AROUSAL FROM TORPOR IN THE SMALLEST MAMMAL, THE ETRUSCAN SHREW *SUNCUS ETRUSCUS*

ROGER FONS[1], SUSANNE SENDER[2], THOMAS PETERS[2] AND KLAUS D. JÜRGENS[2,]*

[1]*Laboratoire Arago, Université P. and M. Curie (Paris 6), CNRS, URA 2156, F-66650 Banyuls-sur-Mer, France* and [2]*Zentrum Physiologie, Medizinische Hochschule, 30623 Hannover, Germany*

Accepted 10 March 1997

Summary

We investigated the process of rewarming from torpor with respect to respiratory and circulatory oxygen transport properties in the smallest mammal, the Etruscan shrew *Suncus etruscus*. In seven adult Etruscan shrews with a mean body mass of 2.4 g, torpor was induced by deprivation of food and a cold environment. During arousal from torpor at an ambient temperature of 22 °C, the shrews actively rewarmed from the lowest mean (±S.D.) body temperature (T_b) of 12.1±1.2 °C to 20 °C at a rate of 0.43±0.14 °C min^{-1}, from 20 to 24 °C at a rate of 0.8 °C min^{-1}, and from 24 to 36 °C at a rate of 1.1±0.1 °C min^{-1}. The mean rate from 12 °C to normothermia amounted to 0.83 °C min^{-1}, which is among the highest values recorded in mammals. During rewarming, the heart rate increased exponentially (Q_{10}=2.2) from 100 to 800–1200 min^{-1}, whereas the respiratory rate increased linearly from 50 to 600–800 min^{-1}. These rates are higher than the heart and respiratory rates reported for other small mammals at the same T_b.

The fraction of brown adipose tissue (BAT) was 9.2±1.6 % of body mass, which is higher than in any other mammal. Up to a body temperature of approximately 17 °C, the heat for rewarming was mainly produced in the BAT; above this value, considerable activity of the skeletal muscles enhanced thermogenesis. Estimation of the mixed venous oxygen partial pressure showed that, at the tissue level, the rewarming process corresponds to heavy work conditions. The ventilatory system is adapted such that during rewarming, in addition to the appropriate oxygen transport capacity, there is also a capacity for hyperventilation.

Key words: *Suncus etruscus*, Etruscan shrew, torpor, arousal, rate of rewarming, heart rate, respiratory rate, oxygen transport, brown adipose tissue, thermogenesis, electrocardiogram.

Introduction

The Etruscan shrew *Suncus etruscus* is the smallest mammal. The average body mass (M_b) of adult animals trapped in their natural environment is slightly below 2 g. Mainly as a result of its large surface area to volume ratio, this shrew has the highest mass-specific energy turnover of all mammalian species. In a previous study, we investigated the heart (f_H) and respiratory (f_V) rates of normothermic Etruscan shrews under resting and stress conditions and estimated maximal circulatory and respiratory oxygen transport rates of 1000 ml O_2 min^{-1} kg^{-1} body mass (Jürgens *et al.* 1996).

In order to reduce its resting energy expenditure, during food shortage or at low ambient temperatures (T_a), the Etruscan shrew can lower its body temperature (T_b) and enter a torpid state. Under laboratory conditions, daily torpor has also been observed (Frey and Vogel, 1979). Like exercise, active rewarming from torpor requires a high metabolic turnover. Since warm-up rates are higher in *S. etruscus* than in any other heterothermic mammal (Geiser and Baudinette, 1990; Stone and Purvis, 1992), the mass-specific oxygen transport rates must also be higher in the Etruscan shrew.

It is not known how the ventilatory and circulatory oxygen transport systems of *S. etruscus* are adapted to the increased oxygen demands during arousal. As the heart and respiratory rates are the main factors determining the convective oxygen transport rates in the circulatory system and in the lungs, we focus in the present study on changes in these rates during rewarming from torpor. We also measured the rewarming rate over three body temperature ranges and determined the mass of brown adipose tissue (BAT) in the Etruscan shrew. The results are compared with literature data for other heterothermic species.

On the basis of our measurements and on previous studies, we discuss how the circulatory and respiratory oxygen transport rates are adapted to the observed rewarming rates. We also estimate the thermogenetic power of the BAT required for rewarming.

---

*Author for correspondence (e-mail: Juergens.KlausD@MH-Hannover.DE).

Materials and methods

Animals

Adult *Suncus etruscus* (Savi) were caught in southern France in the area around Banyuls-sur-Mer during the summer and were kept in a terrarium until measurements were carried out. The shrews were fed with mealworms and crickets and had access to water *ad libitum*. Torpor was induced by starving the animals for one night and exposing them to a cold ambient temperature the next morning. During this exposure to 4 °C, the animals were carefully supervised until a completely torpid state was entered. For measurements during arousal, the animals were transferred to a measuring chamber in a room with T_a=22 °C. At this temperature, spontaneous rewarming of the animals occurred shortly after transfer to the measuring box.

Measurement of body temperature

Body temperature was measured after inserting a thermoprobe (Summit TA1) approximately 8 mm deep into the rectum of the animal. In order to minimize the disturbance of the animal by the measurement, T_b was generally measured only four times between deep torpor and normothermia. This meant that we measured T_b approximately every 2.5 min at T_b<20 °C, approximately every 5 min at 20 °C<T_b<30 °C and approximately every 7 min during the last phase of rewarming (30 °C<T_b<36 °C). Between two temperature measurements, several recordings of heart and respiratory rate were made. To correlate these values with the body temperature prevailing at the time of their recording, the corresponding T_b was determined by linear interpolation between two measured points on the temperature–time relationship. In this way, the generally non-linear increase in T_b with time was approximated stepwise by linear segments.

As long as T_a was higher than T_b, the shrews rewarmed both actively and passively. In order to be able to differentiate between active and passive rewarming effects, in two shrews we measured the passive rewarming shortly after the rate measurements had been completed and the animals had been killed using an overdose of Halothane. The dead shrews were cooled to approximately 10 °C in a refrigerator. They were then transferred into a room with T_a=22 °C, the thermoprobe was inserted rectally and the temperature noted every minute for a total of 25 min. Owing to cessation of the circulation, no convective heat transport will take place inside the body of a dead animal. Therefore, the contribution of internal convection to passive rewarming is not considered in these measurements. The significance of this effect, however, is likely to be negligible since (1) circulatory blood flow is relatively low at low T_b and (2) heat conduction alone causes a rapid rewarming of the animal's core because the distance between the surface and central axis of the nearly cylindrically shaped shrew is only approximately 5 mm.

Recordings of heart and respiratory rate

Heart and respiratory rates were obtained from electrocardiogram (ECG) recordings. These recordings were carried out while a single shrew was confined in a small cylindrical box in which it stood on two stainless-steel electrodes with its fore- and hindlegs. The dimensions of this transparent plastic box were chosen such that the coat of the animal touched the walls and hence induced physical relaxation by thigmotaxis. Sufficient exchange of air and heat with the environment was ensured by numerous holes drilled into the walls of the box. The voltage between the two electrodes was amplified and its time course recorded. The signals were sampled at 5 kHz, stored on a digital oscilloscope (Nicolet 3091) and then transferred to a personal computer for further data-processing and analysis.

The ECG recordings showed two periodic phenomena, the complex of peaks corresponding to each cardiac cycle and, additionally, a periodic pattern characterized by several waves extending over up to 50 % of the heartbeat interval (Fig. 1A,B). This second rhythmic event was clearly different in shape, phase and frequency from the electrical activity of the heart. As has been described in detail previously (Jürgens *et al.* 1996), this signal was due to the electrical activity of the breathing muscles during inhalation; this was confirmed by recording the thoracic movements of the shrews using a laser autofocus system (Jürgens *et al.* 1996). Since the respiratory rate can be identified from the ECG recordings as long as artefacts caused by non-respiratory muscle activity are small, we measured both heart and respiratory rates in this way in most cases.

Mainly over the T_b range between 20 and 30 °C, the ECG recordings also contained large electrical signals arising from the activity of the skeletal muscles due to shivering and to movements of the animal during rewarming.

Preparation of brown adipose tissue

After the experiments with living shrews had been completed, the animals were killed using an overdose of Halothane (Halothan Hoechst). The body mass of seven individuals was determined and their interscapular and dorsal cervical deposits of brown adipose tissue were removed and weighed.

Results

Time course of rewarming

The mean (±S.D.) T_b of seven torpid animals (mean body mass 2.4 g) measured immediately after being transferred to a room with T_a=22 °C, i.e. at the beginning of the rewarming phase, was 12.1±1.2 °C. In three animals, torpor was induced a second time after they had rewarmed completely. They lowered their T_b to the same level as reported above, except in one case, where we observed a considerably lower temperature of 6.3 °C before spontaneous rewarming occurred. In the seven individuals investigated, the mean (±S.D.) rewarming rate between a T_b of 12 and 20 °C was 1.9±0.3 °C min^{-1} (range 1.5–2.3 °C min^{-1}). Since, over this

Table 1. *Measured body temperatures (*T_b*) and their related active rewarming rates (*$\Delta T/\Delta t$*) in* Suncus etruscus *during arousal from torpor*

T_b (°C)	$\Delta T/\Delta t$ (°C min^{-1})	*N*
16 (12–20)	0.43±0.14 (0.29–0.61)	7
22 (20–24)	0.8	1
30 (24–36)	1.10±0.10 (1.0–1.2)	3
(12–36)	0.83*	

*Weighted mean for all three T_b ranges.
Values are means ± S.D. and range (in parentheses).

temperature range, T_a was higher than T_b, the passive rewarming rate of the animals had to be subtracted in order to estimate their active heat production. The non-linear time course of passive rewarming to T_a=22 °C, which was measured rectally in dead animals after being cooled down to the temperatures found in the torpid state, was identical in the two individuals investigated. By subtracting the heat flux from the environment into the shrew, an active rewarming rate (mean ± S.D.) of 0.43±0.14 °C min^{-1} was calculated for the T_b range between 12 and 20 °C (Table 1). In one individual, two successive T_b measurements revealed values of 20 and 24 °C. Thus, in this individual, we were able to observe the rewarming rate over a relatively narrow range around 22 °C, a temperature at which neither passive rewarming nor heat loss through the animal's surface occurs. In three individuals, we measured active rewarming for the T_b range 24–36 °C (Table 1). In the range where T_b exceeds T_a, active heat production must have been larger than that needed for warming up the body mass alone because of the additional heat loss to the environment. From all these data, a mean active rewarming rate of 0.83 °C min^{-1} was calculated for the T_b range between 12 and 36 °C (Table 1).

Thermogenetic activity and BAT

During rewarming from a torpid state, heat production is mainly due to the activity of brown adipose tissue and skeletal muscle. Electrical activity from the skeletal muscles was only visible in the ECG recordings at T_b values above 17–20 °C (e.g. see Fig. 1). Below this temperature range, the activity of brown adipose tissue must be the main source of thermogenesis. In the seven Etruscan shrews examined, large stores of BAT were present, mean (±S.D.) BAT mass represented 9.2±1.6 % of the total body mass.

Heart rate during rewarming

Fig. 2 shows the relationship between heart rate (f_H) and body temperature during rewarming from a torpid state. The lowest rates were approximately 100 beats min^{-1}, and heart rate increased with increasing T_b to give values of 800–1200 min^{-1} in normothermic individuals, as found previously (Jürgens *et al.* 1996). From the slope of a linear regression of the semilogarithmic heart rate/body temperature relationship (r^2=0.94, P<0.001), a Q_{10} of 2.22 was calculated. The corresponding exponential function (solid line in Fig. 2) is $f_H=65.8e^{0.0796T_b}$.

Respiratory rate during rewarming

Fig. 3 shows the respiratory rate as a function of T_b during rewarming, measured in the same seven individuals from which heart rates (Fig. 2) were obtained. For the evaluation of the respiratory data, fewer recordings were available than for determination of heart rate. For the T_b range 20–30 °C, movements and shivering of the shrews caused considerable

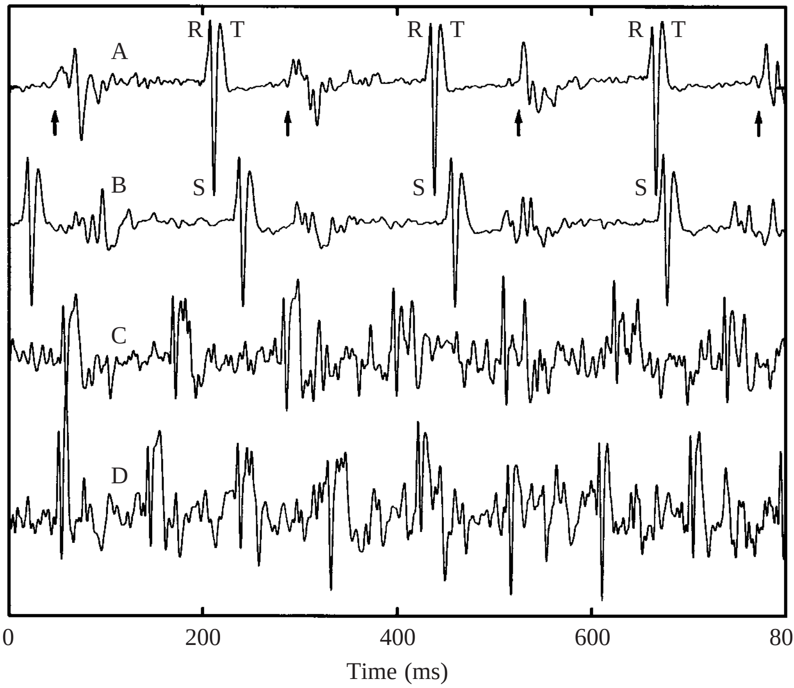

Fig. 1. Electrocardiogram recordings at four different body temperatures, 15 °C (A), 17 °C (B), 20 °C (C) and 22 °C (D). Pronounced electrical activity due to skeletal muscle activity is superimposed on the cardiac activity only at T_b>17 °C. In A and B, periodic activity patterns (in A starting at the arrows) occur between the R-T complexes of the cardiac cycles. They represent the electrical activity of the breathing muscles during inhalation (Jürgens *et al.* 1996).

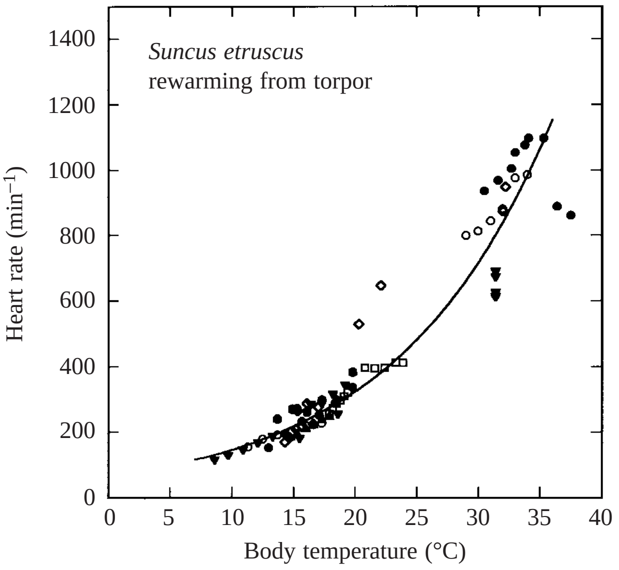

Fig. 2. Heart rates of *Suncus etruscus* rewarming from torpor. The different symbols represent seven different individuals. The solid line is the best-fit of an exponential function.

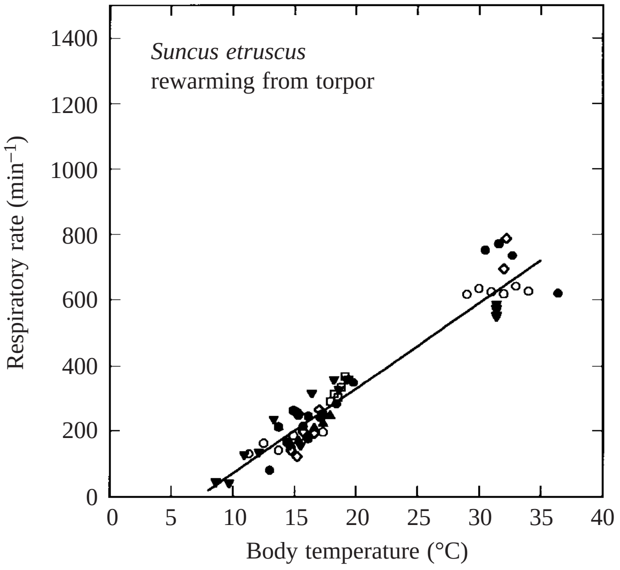

Fig. 3. Respiratory rates of *Suncus etruscus* rewarming from torpor. The different symbols represent seven different individuals. The solid line is the least-squares regression line.

noise in the electrical recordings, so that the electrical signals related to breathing could not be clearly identified (Fig. 1C,D). The lowest respiratory rates were approximately 50 breaths min^{-1}, increasing with T_b to give a final range of 600–800 min^{-1} at normothermia, similar values to those recorded previously (Jürgens *et al.* 1996). The relationship between the recorded respiratory rates (f_V) and T_b can best be described by a straight line ($f_V=25.94T_b-188.8$, $r^2=0.92$, $P<0.001$). A semilogarithmic approximation gave a Q_{10} of 2.19, but was a poorer fit to the data ($\log f_V=0.034\log T_b+1.752$, $r^2=0.81$, $P<0.001$).

Discussion

Minimal torpor temperature and rewarming rates

The body temperature of *S. etruscus* exposed to $T_a=4\,°C$ dropped to a mean minimal value of 12 °C. This is in agreement with the results of Frey (1979), who also reported a minimal torpor T_b of 12 °C for these shrews. However, the Etruscan shrew can withstand body temperatures below this value without losing its capability for active rewarming, as was observed for one individual cooled to 6.3 °C. This temperature is close to the average T_b of 7 °C at which cardiac arrest occurs in mammals undergoing daily torpor cycles (Geiser *et al.* 1989).

The mean rate of active body temperature increase between 12 and 36 °C was 0.83 °C min^{-1}. This is a little lower than that calculated from the data of Frey and Vogel (1979), who reported a duration of the rewarming phase of 25 min for *S. etruscus* arousing from $T_b=12\,°C$ to normothermia at an ambient temperature of 8 °C, giving a mean rate of increase in body temperature from torpor to normothermia of approximately 1 °C min^{-1}. Nagel (1977) reported a range of rewarming rates of 1–2 °C min^{-1} for this species but did not give the body and the ambient temperature ranges for these observations. Increases in T_b at rates slightly higher than 1 °C min^{-1} have also been found in *Sorex cinereus* (M_b 3–4 g; Morrison *et al.* 1959). It has been shown that mean warm-up rates are negatively correlated with body mass in heterothermic mammals and that the values observed in the smallest shrew species are the highest rates found in mammals (Stone and Purvis, 1992).

Energy demand and oxygen consumption during rewarming

In order to assess which adaptations of the circulatory and respiratory oxygen transport system have evolved to ensure the oxygen transport rates required for active rewarming, we first estimated the amount of heat produced during this process. Since this heat results from oxidative metabolic processes, the amount of oxygen transported to the metabolically active tissues can therefore also be calculated.

During arousal from torpor, neither external work is performed nor energy stored and, therefore, all the energy liberated by the metabolism of the animal is turned into heat. Most of this heat is generated by the activity of the brown adipose tissue and the skeletal muscles. BAT represents 9.2 % of the total body mass in *S. etruscus*. This proportion is greater than that reported for any other mammal, emphasising its role in nonshivering thermogenesis. For thermogenesis homogeneously rewarming an animal's body at a rate of $\Delta T/\Delta t$, where T is temperature and t is time, a mass-specific oxygen consumption of:

$$(\dot{V}_{O_2}/M_b)_{rew} = (c/k)(\Delta T/\Delta t) \qquad (1)$$

is required, where c is the specific heat of the body (the value for water of 4.2 J g^{-1} °C^{-1} is taken) and k is the calorific equivalent for oxygen (assumed to be $20\,\mathrm{J\,ml^{-1}\,O_2}$ for a diet mainly consisting of fat and protein). At T_b values above ambient temperature, in addition to the energy required for rewarming, the heat loss to the environment must be taken into account. This is given by:

$$(\dot{V}_{O_2}/M_b)_{hl} = G(T_b - T_a)\,, \qquad (2)$$

where G is the thermal conductance of the shrew. A minimum conductance of $10\,\mathrm{ml\,O_2\,min^{-1}\,kg^{-1}\,°C^{-1}}$ (T_a range 0–25 °C) was reported by Nagel (1977) for awake *S. etruscus*.

The oxygen consumption values calculated from equations 1 and 2 are for STPD (standard temperature, pressure, dry) conditions and must be converted to BTPS (body temperature, pressure, saturated) conditions when considering oxygen transport within the body. For the three body temperatures 16, 22 and 30 °C, we calculate mass-specific oxygen consumption rates of 97, 186 and $360\,\mathrm{ml\,O_2\,min^{-1}\,kg^{-1}}$ (see Table 2). These rates represent approximately 10–30 % of the maximal oxygen consumption possible under normothermic conditions (Jürgens *et al.* 1996).

Heart rate during rewarming from torpor

The heart rate of the Etruscan shrew rises approximately tenfold during rewarming from 12 to 36 °C. This increase in f_H with increasing T_b can be described using a single exponential function. The Q_{10} of 2.2 so obtained is in the range usually found for biological functions dependent on body temperature, although this does not prove that the activity of the heart passively follows body temperature. As has been shown by Heldmaier and Ruf (1992), it is not possible to distinguish between active thermoregulatory control mechanisms and passive temperature effects on biochemical reactions, because both mechanisms can lead to the same function/temperature relationships.

A pronounced non-linear, non-exponential concave relationship between f_H and organ temperature (range 10–35 °C) has been observed in artificially rewarmed isolated hearts of heterothermic marsupials (Geiser *et al.* 1989). An increasing slope of the f_H/T_b relationship with increasing T_b was also reported for the western jumping mouse *Zapus princeps* during arousal (T_b 5–36 °C; Cranford, 1983), whereas an almost linear relationship was recorded for the deer mouse *Peromyscus maniculatus* upon rewarming from torpor (T_b 19–34 °C; Morhardt, 1970). The effect in *P. maniculatus* may be due to the fact that the investigated temperature range was greater than 20 °C, since the pronounced non-linear behaviour found in the other species was mainly for a temperature range below 20 °C.

It is therefore very likely that the concave non-linear increase in f_H with T_b found in *S. etruscus* is a common feature of heterothermic mammals during rewarming from torpor. The tenfold increase in f_H during arousal in the Etruscan shrew is also similar to values observed in other heterothermic species such as western jumping mice (Cranford, 1983) and deer mice (Morhardt, 1970), but these factorial increases can be even larger, depending on the temperature range investigated, e.g. in rewarming hibernators. The absolute heart rate of the Etruscan shrew, however, is higher at any T_b during rewarming than in the other species from which data are available, and at a T_b approaching normothermia f_H is approximately twice that found in western jumping mice (mean M_b 26 g) and in deer mice (mean M_b 20 g). Such high heart rates of up to $1200\,\mathrm{beats\,min^{-1}}$ are unique and indicate the importance of this variable for enhancing the circulatory oxygen transport rate during rewarming in *S. etruscus*.

Estimation of circulatory oxygen transport parameters during rewarming

The circulatory oxygen transport rate is given by:

$$\dot{V}_{O_2}/M_b = f_H\,(V_S/M_b)\,C_{a-v_{O_2}}\,, \qquad (3)$$

where V_S/M_b is the body-mass-specific stroke volume and $C_{a-v_{O_2}}$ is the arterio-venous difference in blood oxygen content.

For the T_b range between 12 and 20 °C, the mean active rewarming rate $\Delta T/\Delta t$ was $0.43\,\mathrm{°C\,min^{-1}}$. In fact, the actual rewarming rate was not constant over this interval, so this mean value was taken to correspond to the mean T_b of 16 °C. At this T_b, an oxygen consumption rate of $97\,\mathrm{ml\,O_2\,min^{-1}\,kg^{-1}}$ was calculated as described above to account for the required heat production. From Fig. 2, the mean heart rate at T_b=16 °C is $235\,\mathrm{beats\,min^{-1}}$. From this heart rate and a given maximal body-mass-specific stroke volume of $3.5\,\mathrm{ml\,kg^{-1}}$ (a relatively high value due to a high relative heart mass, which was estimated in a previous study; Jürgens *et al.* 1996), a mass-specific cardiac output ($\dot{Q}/M_b$) of $820\,\mathrm{ml\,min^{-1}\,kg^{-1}}$ can be calculated. To satisfy the oxygen consumption rate of $97\,\mathrm{ml\,O_2\,min^{-1}\,kg^{-1}}$, an arterio-venous difference in oxygen content ($C_{a-v_{O_2}}$) of $118\,\mathrm{ml\,O_2\,l^{-1}}$ blood is therefore required, corresponding to 49 % of the mean blood oxygen-carrying capacity of $242\,\mathrm{ml\,O_2\,l^{-1}}$ blood found in *S. etruscus* (Bartels *et al.* 1979). In order to estimate the oxygen partial pressure head available for oxygen diffusion into the tissue at such a blood oxygen desaturation, the blood oxygen-binding properties of the shrew at 16 °C must be known. In a previous investigation (Bartels *et al.* 1979), we found a standard oxygen half-saturation pressure (P_{50}) for *S. etruscus* of 35.2 mmHg (1 mmHg=133 Pa). The temperature coefficient of P_{50} ($\Delta\log P_{50}/\Delta T$) is not known for the Etruscan shrew, but there seems to be little variation in this factor in heterothermic mammals (0.014–0.017; Willford and Hill, 1986); we therefore used a value of 0.0167 (T_b range 4.5–39 °C) obtained for another insectivore, the hedgehog *Erinaceus europaeus* (Bartels *et al.* 1969), to estimate the change in blood oxygen-affinity with temperature. This correction gave a P_{50} of 15.7 mmHg at 16 °C. Neglecting the minor effects of changes in pH and Hill coefficient (for which a value of 2.8 has been measured previously, Bartels *et al.* 1979) with body temperature, at this oxygen affinity a $C_{a-v_{O_2}}$ of $118\,\mathrm{ml\,O_2\,l^{-1}}$ blood gives a mixed venous P_{O_2} ($P_{v_{O_2}}$) of approximately 16 mmHg. Such a low $P_{v_{O_2}}$ is found in normothermic mammals during heavy work conditions.

Table 2. *Measured and estimated circulatory oxygen transport parameters of* Suncus etruscus *during rewarming*

T_b (°C)	$\Delta T/\Delta t$ (°C min^{-1})	f_H (min^{-1})	$\dot{V}_{O_2}/M_b$ (ml O$_2$ min^{-1} kg^{-1})	V_S/M_b (ml blood kg^{-1})	$\dot{Q}/M_b$ (ml blood min^{-1} kg^{-1})	C_{a-vO_2} (ml O$_2$ l^{-1} blood)	C_{a-vO_2} (% of O$_2$-cap.)	P_{50} (mmHg)	P_{vO_2} (mmHg)
16	0.43	235	97	3.5	820	118	49	15.7	16
22	0.8	380	186	3.5	1330	140	58	19.8	17.5
30	1.1	716	360	3.5	2500	144	60	28.3	24

T_b is the body temperature, $\Delta T/\Delta t$ is the rate of rewarming, f_H is the heart rate, $\dot{V}_{O_2}/M_b$ is the mass-specific oxygen consumption, V_S/M_b is the mass-specific stroke volume, $\dot{Q}/M_b$ is the mass-specific cardiac output, C_{a-vO_2} is the arterio-venous difference in blood oxygen content, O$_2$-cap. is the blood oxygen capacity, P_{50} is the blood oxygen half-saturation pressure, P_{vO_2} is the mixed venous oxygen partial pressure.

$\dot{V}_{O_2}$ is calculated from equations 1 and 2 and is converted to BTPS.

1 mmHg = 133 Pa.

Similar calculations were made for T_b=22 °C and 30 °C. The results are given in Table 2. The P_{vO_2} value estimated in this way for T_b=22 °C was 17.5 mmHg, very similar to the result at T_b=16 °C. At T_b=30 °C, a slightly higher P_{vO_2} of 24 mmHg was calculated. These three P_{vO_2} values are typical for heavy work conditions in other mammals. The corresponding end-capillary P_{O_2} values are very likely to ensure a sufficient driving pressure for oxygen diffusion into the tissues in the Etruscan shrew, since the diffusion distances, at least in muscle tissue, are shorter in *S. etruscus* than in other mammals (Pietschmann *et al.* 1982). The exponential increase in heart rate, and hence, cardiac output, as well as the shift to the right of the oxygen binding curve with increasing temperature guarantee that the increasing oxygen demand during rewarming is met by the convective oxygen transport system without a reduction in the capillary O$_2$ partial pressure head. This will also hold for body temperatures in excess of ambient temperatures, i.e. where heat loss to the environment occurs. The slight increase in our calculated P_{vO_2} with increasing T_b suggests that even higher rates of rewarming may be possible; in fact, higher values have been reported previously (Frey and Vogel, 1979; Nagel, 1977). The P_{vO_2} values calculated for *S. etruscus* at body temperatures of 16 and 22 °C (Table 2) are in very good agreement with P_{vO_2} values measured at these T_b values in the little pocket mouse *Perognathus longimembris* (M_b 7–11 g) during arousal from torpor (Withers, 1977).

Heat production by BAT

Over the temperature range 12–20 °C, a sufficient oxygen partial pressure head is required to supply O$_2$ to BAT. As can be seen from the ECG traces at the lower temperatures (see Fig. 1), at a T_b of 16 °C most of the heat used for rewarming must be produced in the BAT. Assuming that 97 ml O$_2$ min^{-1} kg^{-1} body mass, giving a rewarming rate of 0.43 °C min^{-1}, is consumed by this organ exclusively, which represents 9.2 % of the body mass, the mass-specific oxygen consumption rate of BAT must be 1054 ml O$_2$ min^{-1} kg^{-1} BAT in *S. etruscus*. This is a realistic value, although higher values have been measured in other small mammalian species. In hamster, mouse and rat, maximal mass-specific oxygen consumption rates of BAT of 1050–1440 ml O$_2$ min^{-1} kg^{-1} BAT have been obtained following noradrenaline injection (see Puchalski *et al.* 1987). On the basis of these data for maximal oxygen consumption rates of BAT, the rewarming rate of 0.8 °C min^{-1} measured for the T_b range 20–24 °C (equivalent to a $\dot{V}_{O_2}/M_b$ of 186 ml O$_2$ min^{-1} kg^{-1} body mass), cannot be explained by the activity of BAT alone. This is in accordance with our observation from the ECG recording that skeletal muscle activity in *S. etruscus* begins at T_b>17 °C (Fig. 1). The exact value of the maximal specific oxygen consumption of the BAT of *S. etruscus* and whether there are seasonal variations remain to be investigated.

Respiratory rate during rewarming

The linear increase of the respiratory rate between approximately 50 min^{-1} at the lowest mean T_b and 600–800 min^{-1} at T_b values approaching normothermia in *S. etruscus* during rewarming is quite different from the results for *Perognathus longimembris* (Withers, 1977), in which a steep increase occurred in the T_b range between 10 and 20 °C, followed by relatively constant values in the range 20–40 °C. In *Peromyscus maniculatus* during arousal, Morhardt (1970) measured a steep linear increase in the respiratory rate for the T_b range 19–26 °C followed by a plateau phase between 26 and 35 °C.

The respiratory rates of the Etruscan shrew during rewarming are higher at any specific T_b than those found in other small species such as pocket mice and deer mice (Withers, 1977; Morhardt, 1970). The rate at T_b values approaching normothermia of up to 800 breaths min^{-1} is unique; it is more than twice the rates in pocket mice (M_b 7–11 g) and in deer mice (mean M_b 20 g). This high f_V could be the reason for the absence of a clear plateau phase in the f_V *versus* T_b relationship of *S. etruscus*, because the shrew may not be capable of generating such a high breathing frequency at body temperatures considerably below the normothermic range.

Estimation of respiratory oxygen transport parameters during rewarming

Oxygen is transported from the air into the lungs by ventilation. The mass-specific ventilatory oxygen transport rate is given by:

$$\dot{V}_{O_2}/M_b = f_V(V_T/M_b)C_{in-ex_{O_2}}\,, \tag{4}$$

Table 3. *Measured and estimated ventilatory oxygen transport parameters for* Suncus etruscus *during rewarming*

T_b (°C)	$\Delta T/\Delta t$ (°C min^{-1})	f_V (min^{-1})	$\dot{V}_{O_2}/M_b$ (ml O$_2$ min^{-1} kg^{-1})	$(V_T/M_b)(C\text{in–ex}_{O_2})$ (ml O$_2$ kg^{-1})	$C\text{in–ex}_{O_2}$ (ml O$_2$ ml^{-1} air)	V_T/M_b (ml air kg^{-1})	V_T (µl)
16	0.43	226	97	0.43	0.03	14	34
					0.05	9	21
22	0.8	382	186	0.49	0.03	16	39
					0.05	10	24
30	1.1	593	360	0.61	0.03	20	49
					0.05	12	29

T_b is the body temperature, $\Delta T/\Delta t$ is the rate of rewarming, f_V is the respiratory rate, $\dot{V}_{O_2}/M_b$ is the mass-specific oxygen consumption, $C\text{in–ex}_{O_2}$ is the amount of oxygen extracted from the inhaled air, V_T/M_b is the mass-specific tidal volume, V_T is the tidal volume required by a 2.4 g shrew for ventilatory oxygen transport at the respective temperature (without accounting for a capacity for hyperventilation).

$\dot{V}_{O_2}$ is calculated from equations 1 and 2 and is converted to BTPS.

1 mmHg = 133 Pa.

where V_T/M_b is the mass-specific tidal volume and $C\text{in–ex}_{O_2}$ is the oxygen extraction from the inhaled air.

From Fig. 3, f_V is 226 breaths min^{-1} at T_b=16 °C. Using this value in equation 4, (V_T/M_b) $C\text{in–ex}_{O_2}$ must be 0.43 ml O$_2$ kg^{-1} when the rate of oxygen consumption is 97 ml O$_2$ min^{-1} kg^{-1} body mass. In normothermic mammals, $C\text{in–ex}_{O_2}$ does not vary systematically with body size (Stahl, 1967). According to the literature, the mean ventilatory oxygen extraction ranges between 0.03 and 0.05 ml O$_2$ ml^{-1} air, with more recent studies reporting higher values (e.g. Chappel, 1992; Chappel and Roverud, 1990) than did earlier ones (e.g. Stahl, 1967; Withers, 1977). With a $C\text{in–ex}_{O_2}$ of 0.05 ml O$_2$ ml^{-1} air, a relative tidal volume of 9 ml kg^{-1} body mass is required at T_b=16 °C, which is only slightly higher than the mean value of 7.7 ml kg^{-1} obtained for normothermic resting mammals from an interspecific allometric relationship (Stahl, 1967). Applying the lower oxygen extraction of 0.03 ml O$_2$ ml^{-1} air gives a V_T/M_b of 14 ml kg^{-1} body mass. In a 2.4 g shrew, the corresponding tidal volumes are 21 and 34 µl, respectively.

Similar calculations were made for T_b=22 °C and 30 °C. The results are given in Table 3. Tidal volumes between 21 and 29 µl, obtained using the higher oxygen extraction value of 0.05 ml O$_2$ ml^{-1} air, are comparable with the value of 24 µl estimated for normothermic resting *S. etruscus* (Jürgens *et al.* 1996). Withers (1977) reported that tidal volumes of *Perognathus longimembris* during arousal in the T_b range 15–40 °C were also in the same range as in resting normothermic individuals.

The tidal volumes of 34–49 µl, calculated using the lower oxygen extraction, are rather high given the mean total lung volume of *S. etruscus* of 100 µl (Jürgens *et al.* 1996). These values correspond to the maximal possible tidal volume found under working conditions, which in humans would amount to approximately 40 % of the total lung volume (see Jürgens *et al.* 1996), and, therefore, will exhibit little potential for a further increase. A large increase in V_T to approximately twice the normothermic resting value has been found in *Perognathus longimembris* during arousal shortly after the onset of rewarming in the T_b range 11–13 °C; this was associated with a pronounced hyperventilation. It is known from other heterothermic mammals that torpor can be associated with an acidosis (Withers, 1977) and/or that CO$_2$ accumulated during entrance into torpor (in order to prevent a rise in pH with falling T_b) must be released during rewarming (Bickler, 1984). A potential for a V_T larger than that required for the oxygen transport rate alone may therefore be important, so the V_T values estimated in Table 3 for the higher extraction rate are more likely to be correct.

The mean warm-up rate of an Etruscan shrew during arousal from torpor is among the highest found among heterothermic mammals. In our experiments at T_a=22 °C, the heat for rewarming in the T_b range 12–17 °C was generated almost exclusively by the brown adipose tissue of the shrew, of which *S. etruscus* has larger deposits than any other mammal. Above this temperature range, activity of the skeletal muscles served as an additional heat source. Certain adaptations allow for such a high metabolic rate during rewarming from a low T_b. The heart rate of *S. etruscus* during arousal from torpor is higher than that found in other small mammals at the same T_b. Since, for biophysical reasons, blood oxygen-affinity is considerably higher at low T_b, the ability to release oxygen to the tissues is impaired. Calculations show that, as a result, mixed venous P_{O_2} is reduced to values that, in normothermia, are found only under heavy work conditions; i.e. at the tissue level, the oxygen transport system is operating at close to its maximal possible performance. Heat production and, hence, oxygen consumption increases with increasing body temperature but, as a result of an exponential increase in heart rate and a shift to the right of the blood oxygen-binding curve with increasing T_b, a further reduction in mixed venous P_{O_2} is prevented.

At the ventilatory level, the respiratory rate, which is higher than in other small mammals during rewarming, must provide a sufficient oxygen supply to the lungs. The increasing oxygen demand with increasing T_b is largely met by a linear increase in the respiratory rate. We cannot determine from our respiratory rate measurements alone whether the maximal possible respiratory rates are reached, because maximal tidal volume and maximal oxygen extraction are unknown. Calculations based on a relatively high oxygen extraction value are consistent with the assumption that, besides fulfilling the ventilatory demand for oxygen transport during rewarming, the respiratory system has the capacity for hyperventilation, i.e. that it can be used for acid–base regulation during arousal.

We thank Jean-Pierre Clara for his excellent technical assistance.

References

BARTELS, H., BARTELS, R., BAUMANN, R., FONS, R., JÜRGENS, K. D. AND WRIGHT, P. G. (1979). Blood oxygen transport and organ weights of two shrew species (*S. etruscus* and *C. russula*). *Am. J. Physiol*. **236**, R211–R224.

BARTELS, H., SCHMELZLE, R. AND ULRICH, S. (1969). Comparative studies of the respiratory function of mammalian blood. V. Insectivora: shrew, mole and nonhibernating and hibernating hedgehog. *Respir. Physiol*. **7**, 278–286.

BICKLER, P. E. (1984). CO_2 balance of a heterothermic rodent: comparison of sleep, torpor and awake state. *Am. J. Physiol*. **246**, R49–R55.

CHAPPEL, M. A. (1992). Ventilatory accommodation of changing oxygen demand in sciurid rodents. *J. comp. Physiol*. B **162**, 722–730.

CHAPPEL, M. A. AND ROVERUD, R. C. (1990). Temperature effects on metabolism, ventilation and oxygen extraction in a neotropical bat. *Respir. Physiol*. **81**, 401–412.

CRANFORD, J. A. (1983). Body temperature, heart rate and oxygen consumption of normothermic and heterothermic western jumping mice (*Zapus princeps*). *Comp. Biochem. Physiol*. **74**A, 595–599.

FREY, H. (1979). La température corporelle de *Suncus etruscus* (Soricidae, Insectivora) au cours de l’activité, du repos normothermique et de la torpeur. *Rev. suisse Zool*. **86**, 653–662.

FREY, H. AND VOGEL, P. (1979). Etude de la torpeur chez *Suncus etruscus* (Savi, 1822) (Soricidae, Insectivora) en captivité. *Rev. suisse Zool*. **86**, 23–36.

GEISER, F. AND BAUDINETTE, R. V. (1990). The relationship between body mass and rate of rewarming from hibernation and daily torpor in mammals. *J. exp. Biol*. **151**, 349–359.

GEISER, F., BAUDINETTE, R. V. AND MCMURCHIE, E. J. (1989). The effect of temperature on isolated perfused hearts of heterothermic marsupials. *Comp. Biochem. Physiol*. **93**A, 331–335.

HELDMAIER, G. AND RUF, T. (1992). Body temperature and metabolic rate during natural hypothermia in endotherms. *J. comp. Physiol*. B **162**, 696–706.

JÜRGENS, K. D., FONS, R., PETERS, T. AND SENDER, S. (1996). Heart and respiratory rates and their significance for convective oxygen transport rates in the smallest mammal, the Etruscan shrew *Suncus etruscus*. *J. exp. Biol*. **199**, 2579–2584.

MORHARDT, J. E. (1970). Heart rates, breathing rates and the effects of atropine and acetylcholine on white-footed mice (*Peromyscus* sp.) during daily torpor. *Comp. Biochem. Physiol*. **33**, 441–457.

MORRISON, P., RYSER, F. A. AND DAWE, A. (1959). Studies on the physiology of the masked shrew *Sorex cinereus*. *Physiol. Zool*. **32**, 256–271.

NAGEL, A. (1977). Torpor in the European white-toothed shrews. *Experientia* **33**, 1455–1456.

PIETSCHMANN, M., BARTELS, H. AND FONS, R. (1982). Capillary supply of heart and skeletal muscle of small bats and non-flying mammals. *Respir. Physiol*. **50**, 267–282.

PUCHALSKI, W., BÖCKLER, H., HELDMAIER, G. AND LANGEFELD, M. (1987). Organ blood flow and brown adipose tissue oxygen consumption during noradrenaline-induced nonshivering thermogenesis in the Djungarian hamster. *J. exp. Zool*. **242**, 263–271.

STAHL, W. R. (1967). Scaling of respiratory variables in mammals. *Am. J. Physiol*. **22**, 453–460.

STONE, G. N. AND PURVIS, A. (1992). Warm-up rates during arousal from torpor in heterothermic mammals: physiological correlates and a comparison with heterothermic insects. *J. comp. Physiol*. B **162**, 284–295.

WILLFORD, D. C. AND HILL, E. P. (1986). Modest effect of temperature on the porcine oxygen dissociation curve. *Respir. Physiol*. **64**, 113–123.

WITHERS, P. C. (1977). Metabolic, respiratory and haematological adjustments of the little pocket mouse to circadian torpor cycles. *Respir. Physiol*. **31**, 295–307.