

HEART AND RESPIRATORY RATES AND THEIR SIGNIFICANCE FOR CONVECTIVE OXYGEN TRANSPORT RATES IN THE SMALLEST MAMMAL, THE ETRUSCAN SHREW *SUNCUS ETRUSCUS*

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Summary

Heart and respiratory rates of the smallest mammal (mean adult body mass 2 g), the Etruscan shrew *Suncus etruscus*, were determined at rest and under stress conditions. Heart rate was obtained from electrocardiograms (ECGs), recorded *via* foot electrodes. The mean \pm S.D. heart rate of resting animals (ambient temperature 22 °C) was $835 \pm 107 \text{ min}^{-1}$, the mean maximal rate amounted to $1093 \pm 235 \text{ min}^{-1}$. The highest single value recorded was 1511 min^{-1} , which is the highest heart rate reported so far for an endotherm. The respiratory rate was also obtained from ECG recordings, which showed the electrical activity of the breathing muscles during inhalation, and additionally by recording the movements of the thoracic wall with a laser autofocus system. The mean resting respiratory rate was $661 \pm 93 \text{ min}^{-1}$, the mean maximal rate was $758 \pm 109 \text{ min}^{-1}$ and the highest single value recorded was 894 min^{-1} . At 22 °C, the specific oxygen consumption rate is 67 times higher in resting *S. etruscus* than in resting humans. Under these conditions, the

respiratory rate of the shrew is 47 times higher but the heart rate only 12 times higher than in man. Therefore, to achieve an adequate circulatory oxygen transport rate, the product of relative stroke volume and arterio-venous O₂ difference has to be 5.6 times higher in the shrew than in man, whereas for an appropriate ventilatory oxygen transport rate the product of relative tidal volume and oxygen extraction has to be only 1.4 times higher in this small insectivore than in man. The maximal possible oxygen transport rates of the ventilatory and the circulatory system have been estimated and compared with the diffusional transport capacity of the lung. These rates amount to approximately $1000 \text{ ml O}_2 \text{ kg}^{-1} \text{ min}^{-1}$. According to our results and data in the literature, an aerobic scope of 7–10 seems to be realistic for the Etruscan shrew.

Key words: heart rate, respiratory rate, oxygen transport, electrocardiogram, laser autofocus, insectivore, symmorphosis, Etruscan shrew, *Suncus etruscus*.

Introduction

The Etruscan shrew *Suncus etruscus* is the smallest mammal. The adult body mass of animals caught from their natural habitat ranges between 1.6 and 2.4 g. This species has the highest mass-specific energy consumption of all mammals. At its thermoneutral ambient temperature of 35 °C, a resting Etruscan shrew consumes a mean of $100 \text{ ml O}_2 \text{ kg}^{-1} \text{ min}^{-1}$. At an ambient temperature of 22 °C, which is the mean temperature encountered by *S. etruscus* while resting in its nest within the stone walls of the vineyard terraces around Banyuls-sur-Mer (Fons, 1975), the Etruscan shrew consumes $267 \text{ ml O}_2 \text{ kg}^{-1} \text{ min}^{-1}$, 67 times as much as resting humans. Consequently, there must be adaptation to this outstandingly high oxygen demand at all levels of the oxygen transport system. Previous studies have provided information on the oxygen diffusion capacity of the lung (Gehr *et al.* 1980), the capillary density (Pietschmann *et al.* 1982), the mitochondrial

content of muscle tissue (Mathieu *et al.* 1981; Hoppeler *et al.* 1984; Oron and Mandelberg, 1985) and the oxygen capacity and oxygen affinity of the blood (Bartels *et al.* 1979) of *S. etruscus*. In the present study, we have measured the respiratory rate and heart rate of this mammal under resting and stress conditions. These frequency data are required for a quantitative examination of convective oxygen transport from the air into the lung by the respiratory system and from the lung into the tissues by the circulatory system. Using these measured rates as well as data from the literature for other oxygen transport parameters, we compare adaptations at the convective oxygen transport level in the smallest mammal with those of man. We also estimate the maximal respiratory and circulatory convective oxygen transport rates of *S. etruscus* and relate them to the maximal diffusional oxygen transport rate of its lung.

Materials and methods

Animals

Adult *Suncus etruscus* (Savi) were caught in southern France in the area around Banyuls-sur-Mer during 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*.

ECG recordings

In order to obtain electrocardiogram (ECG) recordings, single shrews were confined in a small cylindrical box in which they stood on two stainless-steel electrodes with their 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 achieved through numerous holes drilled into the walls of the box. According to the recorded heart rates, the animals had adjusted to this new environment after approximately 15 min, by which time a plateau of comparatively low frequencies was reached. These heart rates were considered to be typical for resting conditions. An increase in heart and respiratory rate was provoked by touching the snout of the animal using a small stick. This procedure simulates a physical attack by an enemy and seems to cause a maximal cardiac effect, comparable with that produced by pharmacological stimulation of the sympathetic nervous system of small shrews (Vornanen, 1992). The heart rates measured directly after physical stimulation were considered to represent maximal heart rates.

The voltage between the two electrodes was amplified and its time course recorded. The signals were stored on a digital oscilloscope (Nicolet 3091) and then transferred to a personal computer for further data processing and analysis. Sampling frequency was 5000 s^{-1} .

The shape of the recorded ECGs varied because of changes in the type of contact between the animals and the electrodes. Sometimes both pairs of legs were in contact, sometimes only one foreleg and one hindleg, and sometimes other parts of the body also touched the metal. These differences resulted in differences in the characteristic peaks of the cardiac cycle: the T waves were sometimes larger than the R waves and negative P waves sometimes appeared. Fig. 1 shows two examples of such recordings. The heart rate was calculated from the intervals between the R peaks.

Body temperature

After ECG recordings were obtained, body temperature was measured by inserting a thermoprobe (Summit TA1) approximately 8 mm deep into the rectum of the animal. This was necessary in order to determine whether the heterothermic shrew was still in its normothermic body temperature range of 34–38 °C.

Respiratory rate

The ECG recordings showed two periodic phenomena (see

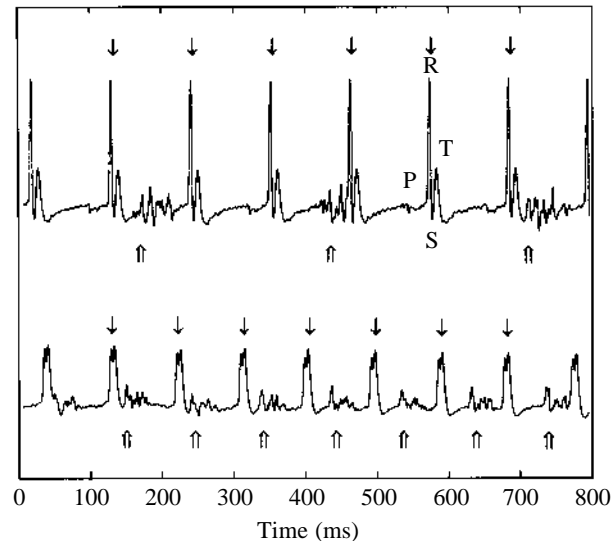


Fig. 1. Electrocardiogram recordings from *Suncus etruscus*. In the upper trace, characteristic peaks of the cardiac cycle (indicated by the internationally recognised symbols P, R, S and T) are identified. Heart rates were determined from intervals between R peaks (single arrows), respiratory rates from the electrical phenomena associated with breathing muscle activity (open arrows indicate the beginning of each breathing pattern). The two traces (recorded from different animals) are examples of the different shapes of the ECG recordings resulting from differences in the type of contact made with the electrodes (see Materials and methods).

Fig. 1): (1) the complex of peaks corresponding to each cardiac cycle (P, R, S and T on Fig. 1) and (2) periodic patterns characterized by several waves extending over approximately 50% of the heartbeat interval. The beginning of each of these groups of waves is marked by an upward arrow in Fig. 1. This second rhythmic event is clearly different in shape, phase and frequency from the electrical activity of the heart and was found to be due to the electrical activity of the breathing muscles during inhalation. This was confirmed independently by recording the thoracic movements of the animal using a laser autofocus system (Rodentstock RM600) normally used for optical scanning of the surface profiles of materials. This system can measure displacements of the thorax in the micrometer range without touching the animal. The laser is fixed at a distance of a few centimeters from the animal and the beam is adjusted to be perpendicular to the investigated area. In order to obtain a better reflection of the laser beam, a small area of the animal's coat was shaved and covered with white correction fluid. An example of such a recording is shown in Fig. 2.

Since the respiratory rate can be identified from the ECG recordings as long as artefacts caused by nonrespiratory muscle activity are small, we measured both heart and respiratory rates in this way in most cases. In an earlier study, Morrison *et al.* (1959) recorded ECGs from the shrew *Sorex cinereus* (mass 3–4 g). They identified a breathing pattern in their electrical recordings by simultaneously measuring movement of the thorax using a strain gauge.

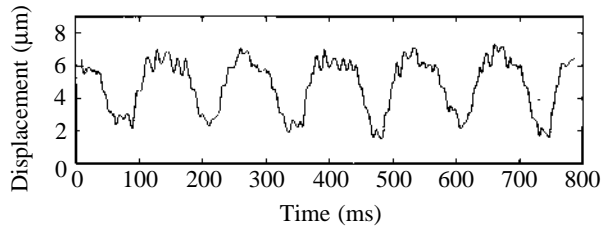


Fig. 2. Recording of the thoracic wall movements of *Suncus etruscus* obtained using a laser autofocus system.

Lung volume

In a separate set of experiments, in which the biochemical properties of the blood-free perfused lung of *S. etruscus* were studied, we measured the lung volume of five animals. The animals were killed using an overdose of halothane (Halothan, Hoechst), the trachea was catheterized, the chest opened and the lung inflated using a small syringe.

Statistics

The *t*-test for unpaired samples was used to test the significance of the difference between two means.

Results

Heart rate

Table 1 shows the heart rates (f_H) measured in seven normothermic *S. etruscus* (body temperature $T_b=34-37.5^\circ\text{C}$, ambient temperature $T_a=22^\circ\text{C}$) and those of several other shrew species taken from the literature. Mean resting and mean maximal heart rates of *S. etruscus*, which are significantly different ($P<0.05$), were found to be higher in this mammal than in any other small shrew species. Table 1 also presents the highest frequencies recorded in these species. The value of

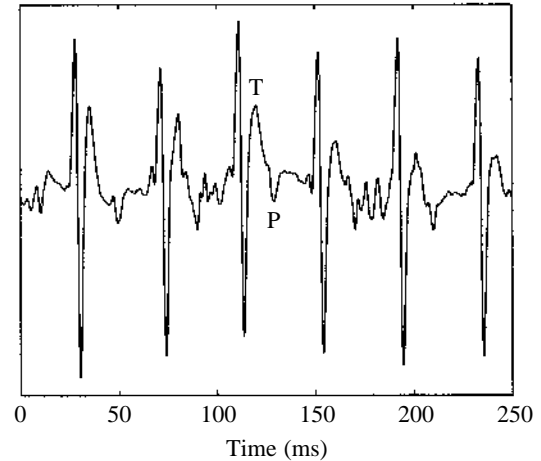


Fig. 3. Electrocardiogram recording showing the maximal heart rate observed in *Suncus etruscus*. Skeletal muscles electrical activity is superimposed on the electrical activity of the heart.

1511 min^{-1} recorded in *Suncus etruscus* is the highest heart rate ever reported for a mammal (Fig. 3).

Respiratory rate

Table 2 shows the results obtained from the ECG recordings of the respiratory rate (f_v) of seven normothermic Etruscan shrews at an ambient temperature of 22°C . For comparison, data from the literature for other small shrews are given. In *S. etruscus*, the mean breathing rate at rest and the mean maximal rate observed after physical stimulation of the animals are significantly different ($P<0.1$). Table 2 also shows the highest single recorded value (894 min^{-1}). The mean resting respiratory rate obtained from the movements of the thoracic wall using the laser system yielded a result identical to that obtained from the ECG recordings.

Table 1. Resting and maximal heart rates of *Suncus etruscus* and other small shrew species

Species	N	Body mass (g)	$f_{H\text{rest}}$ (min^{-1})	$f_{H\text{max}}$ (min^{-1})	Source
<i>Suncus etruscus</i>	7	2.4 ± 0.3	835 ± 107	1093 ± 235 (1511)	This study ($T_a = 22^\circ\text{C}$)
<i>Sorex minutus</i>	3	3.0 ± 0.8	750 ± 48	$1043\pm 66^*$ (1091*)	Vornanen (1992) (T_a not given)
<i>Sorex cinereus</i>	7	2.9–4.0	780	– (1320‡)	Morrison <i>et al.</i> (1959) (T_a not given)
<i>Sorex araneus</i>	7	7.2 ± 1.5	656 ± 40	$938\pm 29^*$ –	Vornanen (1992) (T_a not given)
<i>Crocidura russula</i>	7	8.1–15.3 (mean 11.4)	Approx. 530	$779\pm 108^\dagger$ (Approx. 900‡)	Nagel (1991) ($T_a=22^\circ\text{C}$)
<i>Neomys fodiens</i>	6	12.8 ± 1.5	466 ± 39	$887\pm 21^*$ –	Vornanen (1992) (T_a not given)

Values are means \pm S.D.

Highest single values are given in parentheses.

Maximal heart rates of *S. etruscus* were provoked by physical stimulation.

*Provoked by isoproterenol injections; †provoked by an ambient temperature of 0°C ; ‡spontaneous.

Approximate values are estimated from a plotted data range.

Table 2. Resting and maximal respiratory rates of *Suncus etruscus* and other small shrew species

Species	N	Body mass (g)	fV_{rest} (min ⁻¹)	fV_{max} (min ⁻¹)	Source
<i>Suncus etruscus</i>	7	2.4±0.3	661±93 668±140*	758±109 (894)	This study ($T_a=22^\circ\text{C}$)
<i>Sorex cinereus</i>	7	2.9–4.0	800†	– (1080†)	Morrison <i>et al.</i> (1959) (T_a not given)
<i>Crocidura russula</i>	7	8.1–15.3 (mean 11.4)	Approx. 160‡	393±80‡ (Approx. 500‡)	Nagel (1991) ($T_a=22^\circ\text{C}$)

Values are means ± s.d.

Highest single values are given in parentheses.

Maximal breathing rates of *S. etruscus* were provoked by physical stimulation.

The data were obtained from ECG recordings using foot electrodes or from thorax displacement measurements using a laser autofocus system (*).

†Thorax movements recorded using a strain gauge; ‡body plethysmography.

Approximate values are estimated from a plotted data range.

Discussion

Resting heart rate and circulatory oxygen transport capacity

The mean resting heart rate of 835 min⁻¹ in *S. etruscus* at a T_a of 22 °C is higher than the resting heart rates of other small shrews. This resting heart rate is lower than the range of 1000–1300 min⁻¹ reported by Weibel *et al.* (1971) for lightly anaesthetized *S. etruscus* and also lower than the resting rate of 960 min⁻¹ reported by Oron and Mandelberg (1985) for awake individuals of this species, which indicates that the present method was appropriate for inducing resting conditions. The ambient temperature of 22 °C that we used is the mean temperature that *S. etruscus* encounters when resting in its nest within the stone walls of the vineyards around Banyuls-sur-Mer (Fons, 1975).

As has been extensively discussed by Vornanen (1992), small mammals such as shrews have considerably lower resting and maximal heart rates than predicted from their body mass using allometric relationships. Under basal conditions, i.e. at the thermoneutral ambient temperature of 35 °C, the Etruscan shrew consumes 100 ml O₂ kg⁻¹ min⁻¹, while at an ambient temperature of 22 °C it consumes 267 ml O₂ kg⁻¹ min⁻¹ (Fons and Sicart, 1976), or 67 times as much as a resting human at this temperature. Heart rate differs between these two mammals by only a factor of 12 (835 min⁻¹ in *S. etruscus* compared with 70 min⁻¹ in man). Since:

relative circulatory oxygen transport rate =

$$f_H(V_s/M_b)Ca-vO_2, \quad (1)$$

where V_s is stroke volume, M_b is body mass and $Ca-vO_2$ is the arterio-venous difference in oxygen content of the blood, the remaining factor of 5.6 must be attributable to a larger V_s and/or a larger $Ca-vO_2$ in the shrew than in man.

Literature data are available on $Ca-vO_2$ and V_s , which allow a quantitative investigation of such differences. In a previous study (Bartels *et al.* 1979), we investigated the oxygen-binding properties of the blood of *Suncus etruscus*, from which data $Ca-vO_2$ can be deduced. This blood is characterized by a large oxygen capacity (0.242 ml O₂ ml⁻¹ blood) and a low oxygen

affinity (P_{50} at 37 °C=35.2 mmHg; 1 mmHg=0.133 kPa). At a mixed venous PO_2 of 40 mmHg, which is typical for normothermic resting mammals, the Etruscan shrew can unload 0.092 ml O₂ ml⁻¹ blood, which is approximately 1.8 times more than that released from human blood under the same conditions (0.05 ml O₂ ml⁻¹ blood). At a mixed venous PO_2 of 30 mmHg, a level corresponding to moderate work, this factor increases to 2.7. So, if a factor of 1.8–2.7 may be contributed by a higher $Ca-vO_2$ in the shrew than in man, another factor of 2–3 must be accounted for by a higher relative stroke volume (see equation 1) in the shrew in order to obtain the required factor of 5.6. In our previous study, we found that the relative heart mass of *S. etruscus* is three times that of man (Bartels *et al.* 1979). It is also twice as high as that expected from the interspecific allometric relationship between heart mass and body mass (Prothero, 1979). Since it seems reasonable to assume an approximately proportional relationship between heart mass and stroke volume (Holt *et al.* 1968), a factor of 3 is likely to exist between the relative stroke volumes of the shrew and human. In the 2.4 g shrew, this corresponds to a stroke volume of 8.3 µl, representing nearly 30 % of the mean heart mass of *S. etruscus* (Bartels *et al.* 1979). This percentage of the organ mass represents maximal stroke volume in larger mammals such as humans and, according to Holt *et al.* (1968), is likely to represent the upper limit of the stroke volume in the Etruscan shrew as well.

Maximal heart rate and circulatory oxygen transport capacity

Our method of physically stimulating the animals led to a mean heart rate of almost 1100 min⁻¹, exceeding the mean maximal heart rates recorded in slightly larger shrew species after injection of isoproterenol or exposure to cold (Vornanen, 1992; Nagel, 1991). The highest single value recorded of 1511 min⁻¹ is the highest heart rate ever reported in an endotherm. It exceeds the highest values given so far for small shrews (Vornanen, 1992), small bats (Kallen, 1977) and small hummingbirds (Berger *et al.* 1979) by approximately

200 min⁻¹. Our recordings show that, at this heart rate, the beginning of the P wave of the *S. etruscus* ECG occurs immediately after the end of the T wave (T–P segment approaches 0 ms, see Fig. 3), i.e. atrial excitation directly follows repolarisation of the ventricles. It is, therefore, most likely that, at least in this individual, no higher heart rate could be achieved. The measured mean maximal heart rate of *S. etruscus* of 1093 min⁻¹ and the highest single value of 1511 min⁻¹ are 1.3 and 1.8 times the mean resting rate of this species, respectively. These results correspond well with observations in other small shrews that also show a relatively small factorial increase in heart rate (Table 1).

What is the maximal circulatory oxygen transport rate that can be achieved by the smallest mammal? The oxygen-binding curve of *S. etruscus* blood shows that a reduction in mixed venous P_{O_2} to 20 mmHg, as may occur under maximal work conditions, results in 80% oxygen desaturation of the blood, corresponding to a $Ca-v_{O_2}$ of 0.194 ml O₂ ml⁻¹ blood (Bartels *et al.* 1979). Using this $Ca-v_{O_2}$, the estimated maximal relative stroke volume of 8.3 μl 2.4 g⁻¹ (=3.46 μl g⁻¹) and a measured heart rate of 1093–1511 min⁻¹, a maximal circulatory oxygen transport rate of 730–1010 ml O₂ kg⁻¹ min⁻¹ can be calculated for an Etruscan shrew.

This range for the maximal circulatory oxygen transport rate corresponds fairly well with experimentally obtained oxygen consumption rates. The maximal rate of oxygen consumption of *S. etruscus* (obtained during exposure to cold, 12 °C) reported by Fons and Sicart (1976) was almost 400 ml O₂ kg⁻¹ min⁻¹. Gehr *et al.* (1980) measured values up to 570 ml O₂ kg⁻¹ min⁻¹ at an ambient temperature of 25 °C. An extreme oxygen consumption rate of 1000 ml O₂ kg⁻¹ min⁻¹ has been reported by Weibel *et al.* (1971) for *S. etruscus*. This leads to the conclusion that the above estimates of maximal $Ca-v_{O_2}$ and stroke volume appear to be consistent with maximal O₂ consumption values in the literature.

Resting respiratory rate and ventilatory oxygen transport

The resting respiratory rate of 661 min⁻¹ for *S. etruscus* that we measured at a T_a of 22 °C (Table 2) is much higher than the range 200–300 min⁻¹ reported by Weibel *et al.* (1971) for lightly anaesthetized Etruscan shrews. The average respiratory rate is approximately four times higher than in the fourfold larger *Crociodura russula* at rest at a T_a of 22 °C (Nagel, 1991). Even higher values have been reported by Morrison *et al.* (1959) for *Sorex cinereus* (ambient temperature not given). For resting conditions at the thermoneutral ambient temperature for *S. etruscus* of 35 °C, a respiratory frequency of 256 min⁻¹ can be calculated for a 2.4 g individual using an interspecific allometric relationship between respiratory rate and body mass (Stahl, 1967). If this value is multiplied by a factor of 2.7, to account for the elevated metabolic rate at 22 °C compared with 35 °C (Fons and Sicart, 1976), a respiratory rate of 688 min⁻¹ is predicted, which is not significantly different from the value measured by us. Compared with humans with a mean resting respiratory rate of 14 min⁻¹, the recorded rate in *S. etruscus* is 47 times higher.

The relative ventilatory oxygen transport rate is given by:

$$\text{relative ventilatory oxygen transport rate} = f_v(V_T/M_b)C_{in-exO_2}, \quad (2)$$

where V_T is the tidal volume and C_{in-exO_2} is the oxygen extraction from the inhaled air.

Since respiratory rate alone accounts for a factor of 47 of the 67-fold higher oxygen transport rate in the shrew compared with man, the product of relative tidal volume and oxygen extraction must be only 1.4 times higher in the shrew than in man. This is in accordance with allometric results which show that neither relative tidal volume (Stahl, 1967) nor oxygen extraction per breath (Calder, 1984) depends significantly on body size in mammals.

If we attribute the factor of 1.4 to the relative tidal volume alone, a value of 10 ml kg⁻¹ can be calculated for the shrew compared with a mean of 7.1 ml kg⁻¹ in resting man. This may be a reasonable value for the shrew at 22 °C (13 °C below thermoneutrality) in view of the value of 7.7 ml kg⁻¹ calculated allometrically for the mean mammalian tidal volume under resting and thermoneutral conditions (Stahl, 1967). For a 2.4 g shrew, a tidal volume of 24 μl is thus predicted, corresponding to 24% of the mean lung volume of approximately 100 μl for *S. etruscus* (measured from animals ventilated using a small syringe and a tracheal catheter under open chest conditions). The latter value is in accordance with the range of 80–130 μl reported by Gehr *et al.* (1980) for the lung volume of *S. etruscus*, and is in good agreement with the value of 90 μl expected from the interspecific allometric relationship for a mammal of 2.4 g body mass (Stahl, 1967).

Maximal respiratory rate and ventilatory oxygen transport capacity

The mean maximal respiratory rate of 758 min⁻¹ in *S. etruscus*, recorded during physical stimulation, is 1.15 times its mean resting rate at 22 °C, and the highest single value of 894 min⁻¹ represents 1.35 times the mean resting rate at this T_a . In contrast to maximal heart rate, we do not have suitable criteria to determine whether the maximal breathing rates obtained from our experiments represent the highest rates possible. Indeed, some doubt is justified since Morrison *et al.* (1959) recorded higher rates than these for *Sorex cinereus*, which is approximately 1 g heavier than *Suncus etruscus*. Therefore, only a rough estimate of the maximal ventilatory oxygen transport rate can be given. As no data on maximal tidal volume are available for the shrew or for mammals in general, and since a systematic dependency on body size is not very likely, we assume a maximal tidal volume of 40% of the lung volume, the value reported for working humans (Astrand and Rodahl, 1977). This gives a value of 52 μl in the shrew, based on the maximal lung volume reported by Gehr *et al.* (1980). Oxygen extraction per breath is expected to be independent of body size and, therefore, we take the value of 50 ml O₂ l⁻¹ air measured for humans (Calder, 1984). These approximations and the respiratory rates given above lead to an estimated maximal ventilatory oxygen transport rate of 720–970 ml O₂ kg⁻¹ min⁻¹ in the Etruscan shrew.

Aerobic scope and oxygen flow-rate limitation

From the maximal oxygen consumption rate of 1000 ml O₂ kg⁻¹ min⁻¹ reported by Weibel *et al.* (1971) and the minimal resting oxygen consumption rate at a *T_a* of 35 °C of 100 ml O₂ kg⁻¹ min⁻¹ (Fons and Sicart, 1976), a factorial aerobic scope of 10 can be calculated for *S. etruscus*. Aerobic scopes of 10 are normally found in mammals (Taylor *et al.* 1981), while if small mammals (<900 g) are considered separately, values of 6–7 are more usual (Lechner, 1978). A range of 7–10 for the smallest mammal is consistent with the maximal convective oxygen transport rates estimated by us, 730–1010 ml O₂ kg⁻¹ min⁻¹ for the circulatory and 720–970 ml O₂ kg⁻¹ min⁻¹ for the ventilatory oxygen transport system. Both rates seem to limit the oxygen consumption of the shrew to a similar degree.

In this context, it is of interest to investigate the extent to which the diffusion capacity of the lung is rate-limiting for oxygen transport in the smallest mammal. Gehr *et al.* (1980) determined morphometrically a mean specific oxygen diffusion capacity of 11 ml O₂ kg⁻¹ min⁻¹ mmHg⁻¹ and a maximal value of 15 ml O₂ kg⁻¹ min⁻¹ mmHg⁻¹ for *S. etruscus*. Assuming a rather large mean maximal *P*_{O₂} difference of 50–70 mmHg between alveolar gas and lung capillaries (which is appropriate for heavily working humans; Meyer, 1982), the maximal diffusion capacity leads to a maximal diffusional oxygen flow of 750–1050 ml O₂ kg⁻¹ min⁻¹. This means that, in contrast to larger mammals where the morphometrically determined diffusion capacity of the lung generally exceeds the functional diffusion capacity required for maximal aerobic performance (Gehr *et al.* 1981), in the Etruscan shrew maximal oxygen consumption is limited by the structurally determined diffusional oxygen transport capacity as well as by the circulatory and ventilatory oxygen transport capacity. All three capacities seem to match at this lowest end of the mammalian body size range, i.e. the concept of symmorphosis (Taylor and Weibel, 1981) is realized in a perfect way in the smallest mammal.

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