J. exp. Biol. 161, 533–536 (1991)
Printed in Great Britain © The Company of Biologists Limited 1991

SHORT COMMUNICATION

THE RELATIONSHIP BETWEEN BODY MASS AND VENTILATION RATE IN MAMMALS

By JAMES WORTHINGTON, IAIN S. YOUNG
AND JOHN D. ALTRINGHAM*
Department of Pure and Applied Biology, The University, Leeds, LS2 9JT

Accepted 5 August 1991

The resting, specific metabolic rate (rate per unit mass) and rate of oxygen consumption increase with decreasing body mass in mammals (see Schmidt-Nielson, 1984, for a review). Since lung volume is linearly related to body mass (Tenney and Remmers, 1963), the increased demand for oxygen in small mammals is met by an increase in ventilation rate, rather than by an increase in respiratory volume. The study most frequently cited which relates resting ventilation rate to body mass is that of Stahl (1967). In the course of completing an earlier project (Altringham and Young, 1991), we had reason to look at Stahl's paper in some detail, and identified a number of potential problems, which cast some doubt on the value of the results. Stahl used data from the literature in determining this relationship, and a study of the source material shows that the physiological state of the animals is very variable. The measurements are incidental to other studies, some animals are restrained, in others breathing was measured by invasive methods, and the variation in resting ventilation rate is often very large. No graph is provided, few raw data are included, and it is unclear what size range of mammals was investigated. We felt that it would be worthwhile to determine specifically the relationship between resting ventilation rate and body mass in as wide a size range of mammals as possible (tree shrew to elephant) using the same, non-invasive technique on all animals.

A VHS camcorder, powered by rechargeable batteries, was used to film respiratory movements of resting animals. Ventilation rates were determined by timing respiratory movements during playback of the tapes at normal or reduced speeds. To check the consistency of recording and playback, a stop-watch was filmed over a period of 50 min. The discrepancy on playback was never greater than ±1 s over the 50-min period.

The work was carried out largely on mammals at Chester Zoo, and a number of pets and laboratory mammals. All test animals were healthy adults, both males and females. Animals were filmed, with minimal disturbance, mainly when standing, but occasionally when sitting or lying upright. No significant differences

* To whom reprint requests should be addressed.

Key words: allometry, scaling, ventilation rate, mammals.

in breathing rates were seen between these different positions. Animals were not filmed for at least 15 min after exercise. However, the elephant was filmed during slow walking; when standing, elephants sway from foot to foot, making observation of breathing movements difficult. All animals were awake at the time of filming. Measurements were not taken immediately after feeding. Breathing was observed as movements of the chest and abdomen, or as water vapour in the breath condensing in the cool surrounding air. Ventilation rates were averaged over periods of 5–15 min.

All zoo animals were able to move between outside compounds and heated buildings, and it was assumed that they would choose to rest in locations that were within their thermal neutral zones. Thermal neutral zones of all but the smallest mammals will in any case be broad. Small domestic animals were filmed indoors at 19–24 °C.

The masses of the mammals were taken from Macdonald (1984), Owen-Smith (1988), Walker (1983) and Meinertzhagen (1938). These sources generally agreed with each other, but where they did not, a mean value was used.

Table 1 shows species, mass and breathing rate. N values represent total number of observations, on one or more individuals. In Fig. 1 the mass is plotted against breathing rate on logarithmic axes, and curve-fitted using a model 2 least-squares linear regression. The data can be described by the equation:

$$f = 0.84M^{-0.26},$$

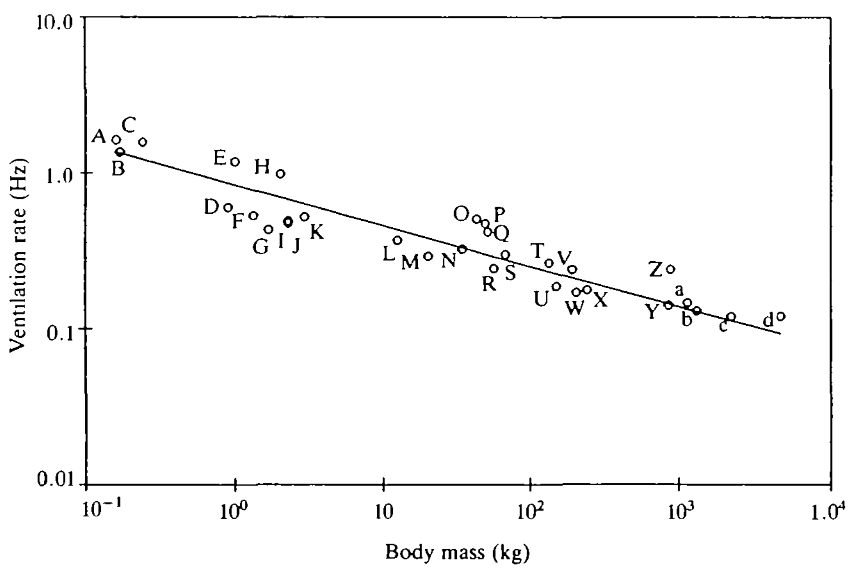

Fig. 1. Mass plotted against breathing rate on logarithmic axes for all data. Data are fitted to a straight line by least-squares regression; 95 % confidence limits on the slope = ±0.03, r^2=0.87. The letters beside each point refer to the identifying letters in Table 1.

Table 1. *Species, masses and ventilation rates*

Species	Mass (kg)	Reference	Ventilation frequency (Hz)
A. *Tupaia glis* (mixed) common tree shrew	0.16	1,2	1.623±0.102 (10)
B. *Rattus* spp. (female) laboratory rat	0.17	5	1.357±0.203 (7)
C. *Rattus* spp. (female) pet rat	0.24	5	1.570±0.092 (3)
D. *Suricatta suricata* (mixed) slender tailed meerkat	0.90	1,2	0.603±0.112 (5)
E. *Cavies porcellus* (mixed) domestic guinea pig	1.00	2	1.176±0.154 (6)
F. *Cercopithecus talopoin* (male) talopoin monkey	1.33	1,2	0.536±0.089 (4)
G. *Mungos mungo* (mixed) banded mongoose	1.67	1,2	0.435±0.052 (7)
H. *Oryctolagus cuniculus* (mixed) rabbit	2.00	1,2	0.983±0.162 (14)
I. *Lemur fulius albifrons* (male) white-fronted lemur	2.25	1	0.493±0.003 (4)
J. *Lemur fulius albifrons* (female) white-fronted lemur	2.25	1	0.479±0.060 (4)
K. *Lemur catta* (mixed) ring tailed lemur	2.90	1	0.525±0.036 (7)
L. *Canus familiaris* (male) mongrel	12.5	5	0.372±0.037 (4)
M. *Hystrix cristata* (mixed) crested porcupine	20.0	1,2	0.295±0.030 (8)
N. *Canis familiaris* (female) german shepherd	34.0	5	0.327±0.070 (4)
O. *Canis familiaris* (male) german shepherd	43.0	5	0.511±0.131 (10)
P. *Hydrochoerus hydrochaeris* (male) capybara	49.5	1,2	0.477±0.026 (4)
Q. *Hydrochoerus hydrochaeris* (female) capybara	51.5	1,2	0.424±0.009 (4)
R. *Pan troglodytes* (female) common chimpanzee	56.5	2	0.246±0.037 (5)
S. *Pan troglodytes* (male) common chimpanzee	68.0	2	0.303±0.016 (4)
T. *Panthera tigris altaica* (female) siberian tiger	134	2	0.266±0.062 (12)
U. *Panthera leo* (female) african lion	151	1,2,4	0.188±0.044 (6)
V. *Panthera leo* (male) african lion	193	1,2,4	0.242±0.007 (3)
W. *Oryx dammah* (mixed) scimitar-horned oryx	204	1	0.171±0.016 (5)
X. *Panthera tigris altaica* (male) siberian tiger	242	2	0.178±0.058 (6)
Y. *Bos taurus* (female) ankole cattle	875	3	0.243±0.068 (6)
Z. *Giraffa camelopardis* (female) giraffe	852	1,3	0.142±0.009 (8)
a. *Diceros bicornis* (male) black rhinoceros	1142	1,2,3,4	0.148±0.023 (9)
b. *Giraffa camelopardis* (male) giraffe	1310	1,3	0.131±0.010 (4)
c. *Hippotamus aquaticas* (male) hippopotamus	2205	1,3,4	0.120±0.033 (3)
d. *Elephas maximas* (male) asian elephant	4667	2,3	0.120±0.020 (8)

Ventilation frequency is given as mean±S.E. (*N*).

References: 1, Macdonald (1984); 2, Walker (1983); 3, Owen-Smith (1988); 4, Meinertzhagen (1938); 5, recorded mass for the individuals used.

where f is breathing rate (Hz) and M is body mass (kg). The results are similar to those determined by Stahl ($f=0.89M^{-0.26}$).

Kleiber (1932) showed that resting metabolic rate in mammals is proportional to $M^{0.75}$. Recent literature has attempted to explain deviations from this relationship on taxonomic and ecological grounds (Hayssen and Lacy, 1985; McNab, 1986; Elgar and Harvey, 1987). It was not our aim to enter this controversy, and we have not analysed our data for taxonomic effects. Assuming a relationship of $M^{0.75}$, specific resting metabolic rate is proportional to $M^{-0.25}$. The empirical relationship between resting ventilation rate and body mass can be explained if changes in oxygen demand associated with variation in specific resting metabolic rate are met by changes in ventilation rate alone. This suggests that lung volume scales linearly with body mass, as observed by Tenney and Remmers (1963), and that gas exchange is linearly related to lung volume.

We would like to thank Chester Zoo for their co-operation and assistance, Chris Smith for technical assistance and Professor R. McNeill Alexander for reading the manuscript.

References

ALTRINGHAM, J. D. AND YOUNG, I. S. (1991). Power output and the frequency of oscillatory work in mammalian diaphragm muscle: the effects of animal size. *J. exp. Biol.* **157**, 381–389.
ELGAR, M. A. AND HARVEY, P. H. (1987). Basal metabolic rates in mammals: allometry, phylogeny and ecology. *Funct. Ecology* **1**, 25–36.
HAYSSEN, V. AND LACY, R. C. (1985). Basal metabolic rates in mammals: taxonomic differences in the allometry of BMR and body mass. *Comp. Biochem. Physiol.* **81**, 741–754.
KLEIBER, M. (1932). Body size and metabolism. *Hilgardia* **6**, 315–353.
MACDONALD, D. (1984). *Encyclopaedia of Mammals.* London: Allen & Unwin.
MCNAB, B. K. (1986). The influence of food habits on the energetics of eutherian mammals. *Ecol. Monog.* **56**, 1–19.
MEINERTZHAGEN, R. (1938). Some weights and measurements of large mammals. *Proc. zool. Soc., Lond.* A **1938**, 433–439.
OWEN-SMITH, R. N. (1988). *Megaherbivores: the Influence of Very Large Body Size on Ecology.* Cambridge: Cambridge University Press.
SCHMIDT-NIELSEN, K. (1984). *Scaling; Why is Animal Size so Important?* Cambridge: Cambridge University Press.
STAHL, W. R. (1967). Scaling of respiratory variables. *J. appl. Physiol.* **22**, 453–460.
TENNEY, S. M. AND REMMERS, J. E. (1963). Comparative, quantitative morphology of the mammalian lung: diffusing area. *Nature* **197**, 54–56.
WALKER, E. P. (1983). *Mammals of the World*, 4th edn. London: John Hopkins University Press.