

## The allometric scaling of aerobic power in adult humans, across the physiological range

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Oxygen consumption varies greatly among exercising humans, largely due to differences in body size. Scaling enables the comparison of those data across individuals of widely variable size, or the prediction of values for mass ranges in which data are limited. However, in humans, the nature of that relationship is still debated (linear *versus* non-linear) because it can be modified by changes in metabolic rate or the presence of uncontrolled covariates. Indeed, the effect of variations in exercise intensity remains unknown, and has yet to be investigated using an appropriately large, but otherwise homogeneous, sample covering a wide mass range. Therefore, it remained uncertain whether or not independent scaling models were required for basal and exercising states of different intensity within the same exercise mode, and this was the focus of the current investigation.

The relationship between absolute oxygen consumption and body mass was evaluated in 68 men (mass range: 56.0-109.8 kg) matched for age (range: 23-34 y), subcutaneous adiposity and height-to-mass proportionality to minimise inter-individual variability in the dependent variable. On three separate days, participants were tested under four states: day 1: basal (supine, rest) and standing rest; day 2: steady-state walking; and day 3: maximal exercise (running). Data were collected using open-circuit respirometry. Basal and standing data were collected over a 70-min period: 60-min supine (basal) in a low-stimulus, normothermic environment (~23°C; ~50% relative humidity), following a 12-h fast (07:00 h; Bowes *et al.*, 2015), and was immediately followed by a 10-min standing stage. Steady-state walking (4.8 km.h<sup>-1</sup>, 0% gradient) was performed on a treadmill (15 min). Data were collected during the last 5 min of standing and walking. Peak aerobic power (oxygen consumption) was measured using a ramped treadmill protocol to volitional fatigue, with peak data recorded and analysed. Three scaling models were independently applied to the four resulting datasets (least-squares regression): two linear models (isometric [ $y=ax$ ] and first-order polynomial with positive intercept [ $y=ax+c$ ]) and one non-linear model (power [ $y=ax^b$ ]). A non-linear relationship was adopted if the assumptions of linearity were not met for the untransformed data, or the regression did not pass through the origin. Analysis of covariance was used to compare the three scaling models.

Within each dataset, oxygen consumption data were found to scale non-linearly, with a power model (mass<sup>exp</sup>) providing superior relationships and yielding the following (raw) scaling exponents: basal: 0.55 ± 0.05 (mean ± SEM); standing: 0.66 ± 0.09; steady-state walking: 0.88 ± 0.06; and maximal exercise: 0.81 ± 0.08. The exponents were equivalent within the resting, and also within the exercising states ( $P>0.05$ ). However, the basal exponent differed significantly from both walking and running ( $P<0.05$ ).

To the best of our knowledge, these observations represent the first evaluation of scaling oxygen consumption data against body mass across the complete range of human metabolic activity, and within a large sample of homogeneous individuals with widely varying body mass. Three novel outcomes arose. Firstly, non-linear (allometric) scaling provided the best description of the relationship between oxygen consumption and body mass across the entire physiological range. Secondly, the scaling exponent increased significantly from the basal state to both of the exercising conditions. It is suggested that the mechanism responsible for this was an increase in the proportion of metabolically active tissues as metabolic rate increased, contributing to a higher demand for oxygen. Thirdly, differences between the exercising exponents were not apparent. Since the lighter intensity was mild, this final outcome implies that exercise of all intensities can be scaled using a power function and a common exponent (0.81-0.88).

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