

MAXIMUM OXYGEN CONSUMPTION DURING EXERCISE AND COLD EXPOSURE IN DEER MICE, *PEROMYSCUS MANICULATUS*

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Abstract. Convenient methods were developed for measuring maximum oxygen consumption ($\dot{V}_{O_2, \max}$) in untrained small mammals during treadmill exercise and cold exposure. Deer mice (*Peromyscus maniculatus*) were run once, for 6-min periods at velocities exceeding maximal aerobic running speed, while instantaneous oxygen consumption was measured. The $\dot{V}_{O_2, \max}$ during cold exposure was determined using high wind speeds to increase heat loss rates. During running, the kinetics of gas exchange were rapid and similar to those observed in larger mammals. Half-times of the \dot{V}_{O_2} and \dot{V}_{CO_2} on-responses were about 20 sec. The \dot{V}_{O_2} also increased rapidly during suddenly imposed cold stress, reaching $\dot{V}_{O_2, \max}$ within 1-1.5 min. Values of $\dot{V}_{O_2, \max}$ obtained during exercise were similar to the $\dot{V}_{O_2, \max}$ measured during cold exposure.

Carbon dioxide production	Maximal oxygen consumption
Cold exposure	Oxygen consumption
Exercise	Treadmill exercise

The purpose of this study (part of an investigation of altitudinal adaptation in deer mice, *Peromyscus maniculatus*) was, first, to develop and validate convenient and reproducible methods for measuring the maximum rate of oxygen consumption ($\dot{V}_{O_2, \max}$) during exercise and cold exposure; and second, to compare the $\dot{V}_{O_2, \max}$ induced by exercise with that elicited by cold exposure. An ancillary goal was to examine the transient gas-exchange responses of a small mammal subjected to suddenly imposed high aerobic demands.

Cold and exercise are commonly used to determine $\dot{V}_{O_2, \max}$ (e.g., Hart and Heroux, 1963; Pohl, 1965; Segrem and Hart, 1967a,b; Wunder, 1970; Rosenmann and Morrison, 1974; Lechner, 1978; Wickler, 1980; Seeherman *et al.*, 1981). However, both approaches have practical and interpretive disadvantages. Cold exposure is best suited to small mammals, since it is necessary to use an environment so cold that aerobic metabolism is insufficient to maintain constant body tempera-

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ture. In order to circumvent this limitation, researchers often artificially augment heat loss by means of pelage removal, ice-water baths (Feist and Rosenmann, 1975; Lechner, 1978), or highly conductive helium-oxygen atmospheres (Rosenmann and Morrison, 1974; Wickler, 1980). Exercise testing is applicable to a wide size range of animals, but the standard technique of gradually increasing running speed until $\dot{V}_{O_2\max}$ is attained requires long training periods. Training conditions and motives test animals, so that measured $\dot{V}_{O_2\max}$ may differ to an unknown extent from that of untrained individuals (Seeherman *et al.*, 1981). Because of these complications it is often difficult to make meaningful interspecific comparisons of $\dot{V}_{O_2\max}$, to compare $\dot{V}_{O_2\max}$ elicited by cold exposure with that attained during exercise, or to extrapolate from laboratory measurements to performance in field situations.

For the present study it was necessary to determine $\dot{V}_{O_2\max}$ with methods that avoided conditioning problems associated with exercise training regimes, and used cold exposure protocols as similar as possible to natural conditions. For exercise testing of deer mice it seemed reasonable to single utilize bouts of running at speeds above the maximum aerobic velocity. Several investigators (Margaria, 1976, Seeherman *et al.*, 1981) have established that \dot{V}_{O_2} increases with running speed until maximum aerobic velocity is exceeded; energy for further speed increases is supplied by anaerobic glycolysis. For cold exposure studies, a combination of moderate air temperature and high wind speeds was employed to produce high rates of heat loss. Both the exercise and cold exposure protocols were of relatively short duration and did not allow animals to attain a steady-state \dot{V}_{O_2} . Therefore, a new method for calculating instantaneous rates of gas exchange was used in order to resolve rapid changes in \dot{V}_{O_2} .

Materials and methods

Animals. Adult deer mice (*Peromyscus maniculatus*) were housed in groups of 4–6 in plastic cages (30 × 18 × 12 cm) in a 20–22 °C room kept on natural photoperiods. They were provided with laboratory mouse chow and water *ad libitum*, supplemented with fresh fruit or vegetables. The mice belonged to the nominal subspecies *sonoriensis* and *rufinus* (from eastern California, central Colorado, and northern Utah). Some individuals used in the study were wild-caught; the rest were from laboratory lines periodically outbred to wild-caught stock. All animals had been kept in the lab for at least six months prior to experiments.

Equipment. Deer mice (N = 179) were exercised in a small enclosed treadmill constructed of Plexiglas with a fabric belt. The belt slid harmlessly under the animals if their running capabilities were exceeded, allowing safe experimentation at high speeds. All exercise tests took place at room temperature (22–26 °C), which is within or slightly below the thermal neutral zone for deer mice (unpublished data).

Cold exposure experiments were accomplished at moderate temperatures (0–5 °C) using a small airtight closed-loop wind tunnel to produce high rates of convective heat loss. Wind speed in the tunnel could be adjusted between 0 and 5 m/s by means of a rheostat. The tunnel assembly was placed in an environmental chamber which could control ambient temperature within 0.5 °C.

An open-circuit gas flow system was used for both experimental regimes. Flowrates of dry, CO₂-free air (800–1000 ml/min STPD for the wind tunnel and 1200 ml/min STPD for the treadmill) were maintained plus or minus 1% with Applied Materials AFC-550 mass flow controllers. Approximately 100 ml/min of the excurrent air from the chambers was diverted, dried, passed through a CO₂ sensor (Applied Electrochemistry CD-3A), passed through CO₂ absorbent, dried again, and passed through an oxygen sensor (Applied Electrochemistry S-3A). The gas analyzers were accurate to within 0.01% CO₂ and 0.001% O₂. The CO₂ sensor was calibrated every few days against a precision gas mixture, and both sensors were referenced immediately before and after runs against air diverted from upstream of the metabolism apparatus. During experiments, the concentration of O₂ in the chambers never fell below 20.4%, and CO₂ concentration never exceeded 0.55%. Response time of the system to events in the metabolism chambers was 30–40 sec. Data from the gas analyzers were recorded and displayed in real time by a microcomputer equipped with a precision analog-to-digital converter.

In order to detect rapid metabolic responses of the mice, instantaneous rates of oxygen consumption and carbon dioxide production (\dot{V}_{O_2} and \dot{V}_{CO_2} , ml/(g · min) STPD) were determined by the method of Bartholomew *et al.* (1981). Briefly, instantaneous rates were obtained by comparing observed rates of change of gas concentrations with predictions based on flowrate and known washout characteristics of the chamber. Accurate instantaneous calculations require rapid sampling, uniform gas mixing within the chamber, and high flowrates relative to the 'effective volume' of the flow system. Effective volume and washout characteristics were determined for each chamber and flowrate by decreasing chamber oxygen concentration below 20% and observing the time course of equilibration with ambient air (20.95% O₂). Values of effective volume obtained by this method (3900 ml for the wind tunnel and 1150 ml for the treadmill) were repeatable within 1–2%, indicating good mixing. In addition, the overall performance of the systems was tested by decreasing chamber oxygen concentration below 20%, and then drawing ambient air through the chamber while calculating instantaneous \dot{V}_{O_2} . In this situation actual \dot{V}_{O_2} was zero, and for both wind tunnel and treadmill the computed instantaneous \dot{V}_{O_2} closely approximated zero. Sampling of gas concentration occurred every 8–9 sec for treadmill experiments and every 20 sec for wind-tunnel work.

Protocol. The experimental procedure for exercise tests began when a mouse was placed in the treadmill and allowed to rest for 5–10 min. When the animal was quiet and \dot{V}_{O_2} had stabilized, the belt was quickly brought to a speed of 0.6–0.8

m/s (previously determined to be slightly above the maximum aerobic velocity for deer mice). This speed was maintained for 6 min, during which the treadmill assembly was shaken as needed to encourage the mouse to continue running. Most animals were unable to match belt velocity for more than 2–3 min; for the duration of the test they maintained somewhat reduced but still vigorous activity while the belt slid beneath them. On rare occasions, individuals were able to run as fast as 1 m/s for periods of up to 7–8 min. When the belt was stopped, almost all mice collapsed and lay prone for 1–3 min without moving. Data collection continued until the animal stood up and began to groom (usually 3–4 min post-run). The total duration of sampling for each animal averaged 15–20 min. Most mice were tested once, but a few randomly selected individuals were run twice, on successive days, in order to verify the reproducibility of \dot{V}_{O_2} measurements.

Cold exposure experiments began when a mouse was placed in the wind tunnel, which had previously been cooled to a temperature of 0–5 °C. The lid was closed and wind speed was quickly increased from about 0.5 to 4.5–5 m/s. Sampling began approximately 1–1.5 min after the tunnel had been sealed. Mice were left in the tunnel until instantaneous \dot{V}_{O_2} had first stabilized at high levels and then fallen unambiguously; in most cases this took 15–20 min but a few animals were able to keep \dot{V}_{O_2} high for 30 min or more.

Data analysis. Maximum rates of gas exchange (\dot{V}_{O_2} max and \dot{V}_{CO_2} max) were obtained for each mouse by instructing the computer to search for the highest rates as continuously averaged over various time intervals. For treadmill exercise tests, \dot{V}_{O_2} max and \dot{V}_{CO_2} max were calculated over intervals of 1, 2 and 5 min. In addition to computing the maximum values for individuals, a profile of the 'typical' 6-min run was assembled by superimposing and averaging the data from all mice (except the small number of animals which ran longer than 6 min).

Cold exposure experiments normally were of longer duration than exercise tests, so \dot{V}_{O_2} max and \dot{V}_{CO_2} max were calculated over longer averaging intervals (2, 5 and 8 min). Comparison of maximum gas exchange rates for individual mice during exercise and cold exposure was accomplished by matching the instantaneous values obtained during both protocols over 2- and 5-min intervals.

Results

During both treadmill and wind tunnel experiments, rates of gas exchange rapidly attained maximal levels after the sudden imposition of stress (either high belt speed or high wind speed, respectively). Figure 1 shows the oxygen consumption of a typical deer mouse in the wind tunnel. Approximately 1 min after the animal had been inserted, its instantaneous \dot{V}_{O_2} had reached a maximum of (in this case) about 0.22 ml/(g · min). High \dot{V}_{O_2} was maintained for about 8 min, whereupon

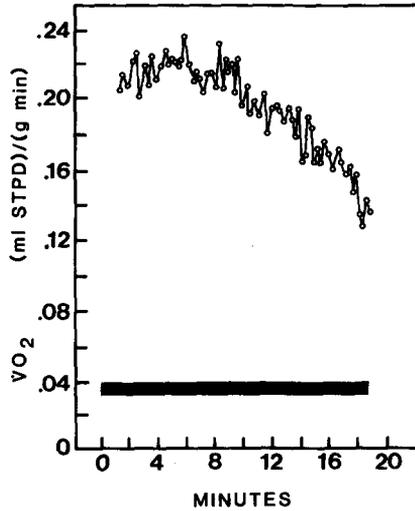


Fig. 1. Instantaneous oxygen consumption (\dot{V}_{O_2}) of a deer mouse subjected to combined high wind speed (4.5 m/s) and low ambient temperature (1 °C) in a wind tunnel. Black bar denotes the time the animal was within the wind tunnel; measurements began approximately one minute after the animal was inserted.

oxygen consumption began to decline rapidly as the animal became hypothermic. The \dot{V}_{CO_2} closely paralleled \dot{V}_{O_2} throughout all cold stress experiments (the respiratory quotient R was always between 0.9 and 1.08).

Figure 2 shows the response of a typical mouse in a treadmill experiment, and fig. 3 shows the summed and averaged responses of 175 animals. Pre-run \dot{V}_{O_2} was usually about $1.8 \times$ resting metabolism (probably due to moderate activity). Both

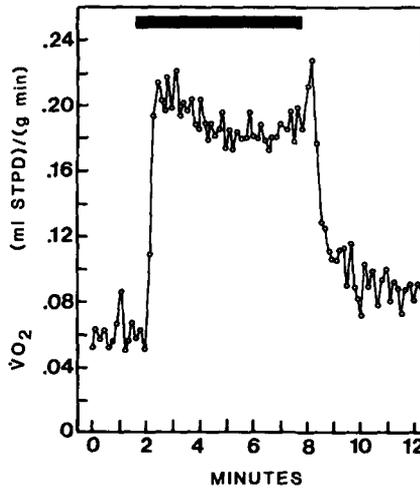


Fig. 2. Instantaneous oxygen consumption (\dot{V}_{O_2}) of a deer mouse run at 0.7 m/s on the treadmill. Black bar indicates the 6-min period of running.

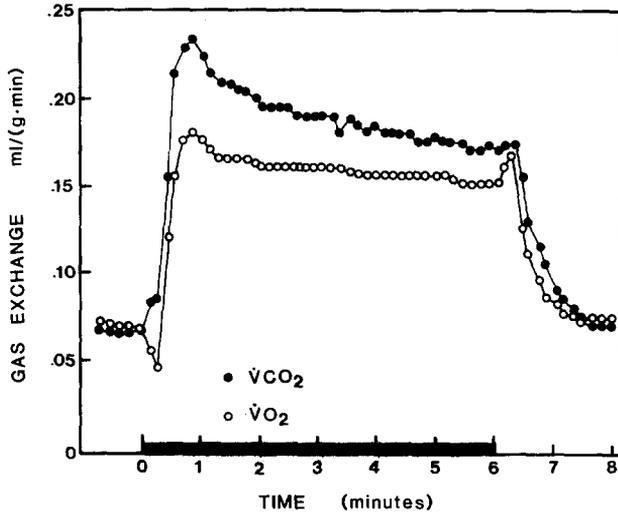


Fig. 3. Summed and averaged instantaneous oxygen consumption (\dot{V}_{O_2}) and carbon dioxide production (\dot{V}_{CO_2}) of 175 deer mice run for 6 min on the treadmill. Black bar indicates running time.

\dot{V}_{O_2} and \dot{V}_{CO_2} increased rapidly when the belt was started. Mice usually attained maximal gas exchange rates within 30–40 sec after beginning to run, and the half-times for the \dot{V}_{O_2} and \dot{V}_{CO_2} on-responses were roughly 20 sec. The highest \dot{V}_{O_2} and \dot{V}_{CO_2} values occurred in a brief (approximately 1 min) peak near the start of a run; a second, very short (15–20 sec) peak in \dot{V}_{O_2} was often seen immediately after the belt was stopped. The small decline in \dot{V}_{O_2} at the start of runs (fig. 3) was unexpected, and initially was thought to be an artifact of the animal's position change as the belt began to move. However, the decrease was apparently real, since (a) its occurrence was independent of mouse position, and (b) a similar drop was not observed in \dot{V}_{CO_2} .

The respiratory quotient of mice in the treadmill was between 0.8 and 1.0 prior to the onset of exercise. However, \dot{V}_{CO_2} quickly exceeded \dot{V}_{O_2} after the belt was started, and R remained between 1.125–1.35 until the mice stopped running. When the belt was stopped, both \dot{V}_{O_2} and \dot{V}_{CO_2} declined immediately, but the rate of decrease was slower than the rate of increase at the start of runs. Also, \dot{V}_{O_2} usually remained at about 0.075 ml/(g·min), or about $2 \times$ resting metabolism, for several minutes post-run, even though the mice were quiet and temperatures were approximately thermoneutral. Repeat runs on the same mice yielded similar \dot{V}_{O_2} max values (mean difference between runs was 4.5%, $N = 15$).

For both exercise and cold exposure, the instantaneous gas exchange calculations yielded significantly higher \dot{V}_{O_2} and \dot{V}_{CO_2} than computed from traditional steady-state equations (e.g., Hill, 1972). As expected, higher mean values were obtained from shorter averaging intervals, although differences were not large (table 1). Individuals varied by as much as 30% in the values of \dot{V}_{O_2} max obtained for

TABLE 1

Comparison of maximal oxygen consumption and carbon dioxide production ($\dot{V}_{O_2,max}$ and $\dot{V}_{CO_2,max}$, respectively; ml/(g · min) STPD) obtained during treadmill exercise and cold exposure, as averaged over different time intervals (see Materials and Methods for exact procedures).

Averaging interval (min)	Exercise			Cold exposure			Ratio $\frac{\dot{V}_{O_2,max, cold}}{\dot{V}_{O_2,max, run}}$
	$\dot{V}_{O_2,max}$ (SD)	$\dot{V}_{CO_2,max}$ (SD)	N	$\dot{V}_{O_2,max}$ (SD)	$\dot{V}_{CO_2,max}$ (SD)	N	
1	0.1767 (0.0226)	0.2353 (0.0302)	179	—	—	—	—
2	0.1718 (0.0220)	0.2245 (0.0286)	179	0.1743 (0.0224)	0.1860 (0.0274)	172	0.986
5	0.1649 (0.0213)	0.2187 (0.0279)	179	0.1716 (0.0230)	0.1786 (0.0263)	172	0.961
8	—	—	—	0.1689 (0.0230)	0.1733 (0.0255)	172	—

equal averaging intervals in exercise and cold exposure (fig. 4). Nevertheless, mean values from all animals were quite similar for the two types of stress (table 1). Overall, cold exposure elicited $\dot{V}_{O_2,max}$ 2-3% higher than obtained from exercise.

The \dot{V}_{O_2} values obtained from the longest averaging intervals (5 min for running and 8 min for cold exposure) were 0.165-0.17 ml/(g · min), about the same as observed in other *Peromyscus* species (Segrem and Hart, 1967a,b; Wickler, 1980). The basal rate of oxygen consumption for the deer mice in the present study (unpublished data) was about 0.025-0.03 ml/(g · min); hence, the factorial aerobic scope for both exercise and cold exposure was approximately 6.5. Similar aerobic scopes have been reported for a number of other small mammals (Wunder, 1970; Pasquis *et al.*, 1970; Lechner, 1978).

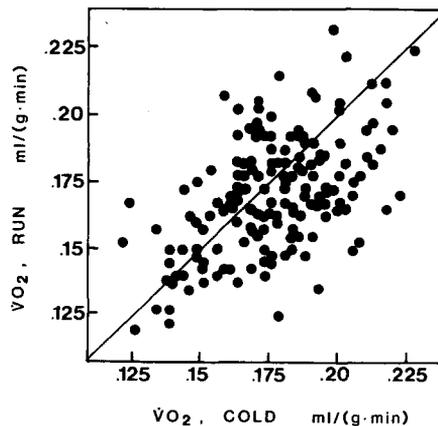


Fig. 4. Relationship of $\dot{V}_{O_2,max}$ during running and cold exposure, both averaged over 2-min intervals.

Discussion

Methodology. By using relatively short episodes of high-speed running in conjunction with instantaneous gas-exchange calculations, it was possible to measure maximum oxygen consumption during exercise in untrained animals. This approach differs from the standard practice of running animals repeatedly at gradually increasing speeds until an unambiguous $\dot{V}_{O_2\max}$ is attained (*e.g.*, Seeherman *et al.*, 1981). Assessment of whether the observed oxygen consumption was actually $\dot{V}_{O_2\max}$ was based on several lines of evidence: (1) In preliminary experiments, the maximum aerobic running speed was determined to be about 0.5 m/s, and during $\dot{V}_{O_2\max}$ measurements the mice were run at 0.6–0.8 m/s. (2) Most animals could not maintain belt velocity for more than 2–3 min, even though they struggled vigorously for the duration of the 6-min run. (3) The respiratory quotient during running was substantially greater than 1.0, indicating considerable anaerobic metabolism. (4) Almost all animals collapsed after the belt was stopped, and most individuals remained immobile for several minutes. (5) Despite this immobility, \dot{V}_{O_2} usually remained elevated above basal levels for several minutes post-run, indicating the presence of oxygen debt. Additionally, the measurements of $\dot{V}_{O_2\max}$ obtained by this method were quite reproducible for repeated runs on the same individuals.

Attainment of $\dot{V}_{O_2\max}$ during cold exposure was usually obvious. The \dot{V}_{O_2} invariably jumped to high levels at the start of experiments, and then remained high and constant until the mice became noticeably hypothermic. At the conclusion of experimental runs all animals were shivering violently, had rapidly declining \dot{V}_{O_2} values and often had lost coordination to the point of being unable to walk. Unlike exercise, cold exposure did not elicit R values substantially greater than 1.0 or other indications of significant anaerobic metabolism. Similar findings were reported by Seeherman *et al.* (1981).

An important observation was that instantaneous \dot{V}_{O_2} during cold exposure was usually 10–20% higher than the highest value calculated with standard 'steady-state' \dot{V}_{O_2} equations (*e.g.*, Hill, 1972), even when averaged over 8-min intervals. Evidently the animals became hypothermic, with concomitant decline of \dot{V}_{O_2} , before the concentration of O_2 in the chamber (and hence the calculated 'steady-state' \dot{V}_{O_2}) had time to reach equilibrium. A similar effect could have influenced the results of other investigators using cold exposure to elicit $\dot{V}_{O_2\max}$ in small mammals, particularly when protocols producing rapid hypothermia were employed, such as ice-water baths (*e.g.*, Feist and Rosenmann, 1975; Seeherman *et al.*, 1981).

Short-term responses. Previous studies of transient metabolic responses at the onset and termination of exercise have utilized large animals wearing small-volume, high-flowrate masks. There is little comparable data for small mammals, which are usually studied in relatively large-volume metabolism chambers with mixing

characteristics that greatly slow system response time. However, use of instantaneous gas exchange calculations allows much higher resolution of transient events than is possible with standard methods.

The short-term metabolic responses of deer mice to suddenly-imposed heavy exercise were similar to those reported for larger mammals such as dogs (Cerretelli *et al.*, 1964; Marconi *et al.*, 1982) and humans (Cerretelli *et al.*, 1977, 1979; Whipp and Wasserman, 1972; Hagberg *et al.*, 1980). The kinetics of oxygen uptake were rapid, and there was little oxygen deficit at the onset of exercise. Mice attained \dot{V}_{O_2} max within 35–40 sec after beginning to run, and carbon dioxide production increased with equal rapidity. After the cessation of running, both \dot{V}_{O_2} and \dot{V}_{CO_2} declined rapidly, but the presence of oxygen debt was indicated by post-run \dot{V}_{O_2} values substantially above basal levels despite inactivity and thermoneutral ambient temperatures. It was not possible to determine the size of the oxygen debt, since the mice recovered quickly and resumed locomotory activity (grooming or exploring) within 3–4 min after they stopped running. Most animals showed a fairly rapid initial decline in \dot{V}_{O_2} lasting about 1 min, which was followed by a more gradual decrease (figs. 2, 3).

Mice also responded remarkably quickly to the imposition of cold stress. There was a lag of 1–1.5 min between the insertion of the animal into the wind tunnel and the first measurements of \dot{V}_{O_2} , but in almost all cases the animals had attained \dot{V}_{O_2} max within this interval. Assuming that the response time of \dot{V}_{O_2} to increased oxygen demand by the tissues is the same in sudden cold exposure as in exercise (30–40 sec), the mice must have detected the cold environment and increased metabolic heat production to maximal rates in 1 min or less.

Comparison of cold exposure and exercise. There is conflicting evidence as to whether \dot{V}_{O_2} max differs during exercise, cold exposure, or combinations of the two. Early studies of small mammals (Hart and Heroux, 1955, 1963) indicated that \dot{V}_{O_2} max in cold was similar to \dot{V}_{O_2} max during exercise. Segrem and Hart (1967a,b) found that the \dot{V}_{O_2} max of winter-acclimated *Peromyscus* during cold exposure was substantially larger than in exercise. They attributed the difference to the recruitment of the additional metabolic machinery of nonshivering thermogenesis during cold exposure. Similarly, Wunder (1970) demonstrated that in chipmunks (*Eutamias merriami*) a somewhat higher \dot{V}_{O_2} max could be elicited during running at low temperatures than in warm conditions, and that in cold environments \dot{V}_{O_2} max was attained at lower velocities. Interestingly, several investigators have suggested that small mammals acclimatized to cold have higher \dot{V}_{O_2} max in both cold stress and exercise (Segrem and Hart, 1967b; Pasquis *et al.*, 1970). Results from the present study are somewhat equivocal, in that deer mice showed considerable individual variation – some animals had substantially higher \dot{V}_{O_2} max when running than during cold exposure, while for others the reverse was true (fig. 4). Nevertheless, on average the responses to the two stresses were quite similar, with a slight tendency for higher \dot{V}_{O_2} max during cold exposure.

In a recent paper, Seeherman *et al.* (1981) suggested that maximum rates of oxygen consumption in mammals are 15–20% lower during cold exposure than during sustained exercise. This study included several species within a size range of 7 g to 100 kg. Seeherman *et al.*'s results are at variance with the present study and most previous work. The differences may be related to the particular species examined or to variation in measurement techniques (as discussed above), but are most likely a result of the vigorous training and conditioning regime (up to eight weeks per animal) necessary for the Seeherman study. The long training period may have increased the animals' abilities to perform heavy exercise without producing a similar change in the ability to generate metabolic heat during cold exposure.

These potential complications must be taken into account when comparing \dot{V}_{O_2} max data from different studies. They should also be considered when designing experimental protocols. The choice between trained and untrained animals is largely dependent on the purpose of a particular study. For example, highly trained and conditioned animals might be desirable for an investigation of the absolute limits of the gas transport system. Alternatively, if one were interested in the performance capabilities of free-living animals, it would be more appropriate to utilize untrained, freshly-captured specimens. For the latter purpose, the techniques described in this paper should be applicable to most small animals.

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