Maximum oxygen consumption and heat loss facilitation in small homeotherms by He-O₂

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ALTHOUGH ANIMALS IN NATURE spend the majority of their time resting or at low levels of activity, some functions critical for survival such as fighting, escaping, or predation greatly increase the energy demand. The maximum capability to increase metabolism is the main factor in limiting the intensity of such physical activity and, as well, sets the limit for cold tolerance. Evaluations of maximum oxygen uptake (Mₘₐₓ) in mammals have been made by cold exposure in air or water, by exercise on treadmills, by swimming, or by a combination of these. These methods may require extended training sessions for running (as long as 1 mo), cutting off the tail, and elimination of inept performers (32). Another serious reservation is that these procedures may directly modify the character under study. Exposures to subfreezing temperatures risk peripheral cold injury or lethal hypothermia (23). Removal of the natural insulation can increase metabolism greatly but, again, is traumatic and results in irreversible change.

To avoid such extreme cold exposure and the injuries reported during exercise (32, 16), we have developed the use of a helium-oxygen atmosphere to raise the heat output of small homeotherms to maximum levels at more modest ambient temperatures (Tₘ). The effect of He-O₂ in increasing metabolism has been known for some time (3, 36), and although once in some question its action is now generally ascribed to the increased thermal conductance of the gas (5, 25, 34). Since the insulative quality of fur or feathers depends on the slow transfer of heat through the enclosed air spaces, the substitution of a 4 times more conductive medium such as 80% He-20% O₂ should greatly facilitate heat transfer. However, the actual metabolic increases reported in small mammals are so much more modest, e.g., <25% in rats (34) or <50% in mice (3, 10), that the exact nature of the effect is still very much in question.

METHODS

Tests were conducted on two laboratory species, the white mouse and the white rat, previously assessed for Mₘₐₓ by various other procedures. Three further strains of Mus musculus, a hairless mutant (HRS/J), and feral house mice from 15,000 feet at Morococha, Peru and from Arkansas were also compared. In addition, measurements were made on wild species native to different habitats: arctic (Microtus oeconomus from Fairbanks), alpine (Calomys ducilla from 13,000 feet near Puno, Peru), and subtropical (Calomys callosus from San Joaquim, Beni Province, Bolivia), and the pygmy mouse Baiomys taylori. The final species was a small arctic bird, the redpoll (Acanthis flammea), also native to Fairbanks. We are indebted to Dr. Oliver P. Pearson and Dr Karl M. Johnson for the respective Calomys, to Dr. Hermann Pohl for the redpolls, and to Dr. John Sealander for the lowland Mus. These rodents were maintained in our animal facility at a neutral Tₘ of 20-24°C. Three to eight individuals of each type were tested at 735-750 torr.

O₂ consumption was measured in a closed-circuit manometric respirometer (28). Since the oxygen consumed by the animal is replaced by successive aliquots, the inert component maintains its concentration as established. The metabolic chambers of stainless steel were submerged in a thermostatted water-glycol bath. After a variable length of time (1-3 h) in which the metabolic rate in air was measured, the chambers were flushed with 5-6 times their volume of an 80% He-20% O₂ mixture from a proportioning gas mixing pump or from a gas tank. Use of the gas tanks with premixed He-O₂ reduced the purging time to only 2 min as compared with 7-9 min with the mixing pumps. To avoid temperature changes, the He-O₂ mixture was admitted through a submerged copper coil.
Food as apple, carrot, and sunflower seed was generally available during the tests. Regardless of the duration and temperature of the metabolic measurements, the animals were tested about 4 times a week, and generally 2 days were allowed between consecutive tests at high submaximal rates.

RESULTS

Immediately after the substitution of He-O₂ for air, O₂ consumption increased well above the resting levels in air, as shown in Fig. 1 for M. oeconomus. Of interest also is the suppression in He-O₂ of the metabolic cycles reflecting changes in activity or posture, an effect also seen at lower Tₐ in air. These relations are shown in Fig. 2 for a series of Tₐ between 26 and 7°C again for M. oeconomus. The respective values in air and in He-O₂ lie along two straight lines which extrapolate to the Tₜ at 39°C to fit the relations:

\[ M = C(Tₜ - Tₐ) = CΔT \]
\[ M = C^{He}ΔT \]

The constant C usually designated as the (minimum) conductance actually includes a component of evaporative/respiratory heat loss, but at these Tₐ below thermal neutrality this represents a constant (small) fraction of the thermal loss through the surface—a cost of “chemical” thermoregulation. Accordingly, C is a measure of the overall facility for heat loss from the body and will reflect changes in the properties of the insulative layers. In this example the substitution of He-O₂ increased conductance from 0.178 to 0.377 ml O₂ (g·h·°C)⁻¹, a factor of 2.12 (C^{He}/C).

At temperatures below the thermoneutral zone, heat production more than doubled in He-O₂ until at about 6°C (in this species) a limit was reached, indicating maximum metabolic capability for temperature regulation (M_max). In fact, at 1°C in He-O₂ the maximum heat production could only be maintained for approximately 5 min, and longer exposure under these conditions resulted in decreased O₂ consumption and hypothermia. Exposure to lower temperatures in He-O₂ did not seem to modify their maximum response, but the highest rates were held for a shorter time. The quotient, M_max/C, provides an estimate of the maximum temperature differential tolerable by the animal, in this case -70°C. This has been shown graphically by extrapolation of M = CΔT to the value M_max = 12.5 ml O₂ (g·h)⁻¹ at -31°C. It may be noted that we have observed limiting values of cold tolerance of this species (neutral acclimation) at -25 to -30°C (unpublished observations).

A somewhat lower ratio was observed in white rats (Fig. 3). Maximum rates in He-O₂ were attained within 6–10 min at -3°C. Exposure at -10°C in He-O₂ resulted in reduced O₂ consumption and hypothermia.

The effects of He-O₂ on highland house mice and white mice are shown in Fig. 4. The ratio C^{He}/C was 2.3 in the house mice as compared to 2.1 in white mice and M_max was 24% higher, 13.8 vs. 11.1 ml O₂ (g·h)⁻¹. In lowland
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FIG. 4. Oxygen consumption of feral house mice (circles) and of white mice (squares) in air (open symbols) and in He-O₂ (solid symbols) as a function of Tₘ.

FIG. 5. Oxygen consumption of hairless mice in air (open symbols) and in He-O₂ (solid symbols) as a function of Tₘ. Reference curves compare function for normal mice.

In feral house mice the M_max was intermediate at 12.3 mlO₂ (g·h)⁻¹.

To gain insight into the relation between the surface insulation and the effects of He-O₂, hairless mice were also tested (Fig. 5). The ratio of the thermal conductance in air of hairless versus normal mice was 1.9, close to a previously reported ratio of 2.2 for these strains (29). However, in He-O₂, the conductance ratio hairless versus normal was only 1.3 due to the much smaller response of the hairless mice to helium (Cₘ/ₘ = 1.40). M_max in hairless mice was 13% higher than in the normal white mice (12.5 vs. 11.1 mlO₂ (g·h)⁻¹) but still 10% lower than in the feral mice. Similarly, the metabolic expansivity of the hairless mice (10.5 mlO₂ (g·h)⁻¹) lay between those of the two other strains. M_max/M_min ratios were 6.3 in both the white and the hairless mice as compared with 7.2–7.3 in both feral groups.

Results of He-O₂ exposure in Calomys ducilla, a highland species, and Calomys callousus, a tropical species, are shown in Fig. 6. M_max of 14 mlO₂ (g·h)⁻¹ was found in the 16-g C. ducilla and 6.8 mlO₂ (g·h)⁻¹ in the 3 times larger C. callousus.

Redpolls (Acanthis flammea) were treated in a similar way to the rodents with the exception of a wooden perch in the cages and an aluminum cover to maintain a dark environment and so diminish spontaneous activity. O₂ consumption values in air and in He-O₂ are shown in Fig. 7. The highest ratio, Cₘ/ₘ = 2.6, was observed in the redpoll and a M_max of 21.8 mlO₂ (g·h)⁻¹ was elicited at -5°C.

Table 1 summarizes the thermogenetic effects of He-O₂ in the experimental species, the temperatures at which M_max was elicited in He-O₂, the extrapolated air temperatures for these rates, and the thermal conductance values in relation to the He-O₂ atmosphere and to the animal's surface area. In general, M_max in the rodent species was obtained in He-O₂ at 13–30°C warmer temperatures than expected in air, but in the hairless mice the difference was only 7°C. In contrast, a 70°C warmer temperature for M_max elicitation in He-O₂ was estimated for the redpolls.
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DISCUSSION

A comparison of our data on $M_{\text{max}}$ of mice, rats, and of the pygmy mouse with reported values for the same species but obtained with different methodologies is shown in Table 2. Our values for white mice are equal or higher than reported figures from mice kept at neutral or warm temperatures but are 8% lower than from cold-acclimated mice (12). Similarly in white rats, $M_{\text{max}}$ values in He-02 are the same or higher than reported capabilities in normal mice (12). In Baiomys, 18% higher $M_{\text{max}}$ was obtained in He-O$_2$ than the maximum values reported with cold exposure (20).

Published data for the rest of our wild species seem to be unavailable, but some values have been reported in related species. In 18-g Microtus arvalis a ratio $M_{\text{max}}/M_{\text{min}}$ 5.5 has been reported in treadmill studies (21). Our value for 32-g Microtus oeconomus was 5.2.

In summer birds, exposure of house sparrows to −30 to −65°C resulted in $M_{\text{max}}$ of 15 mLO$_2$ (g·h)$^{-1}$ and $M_{\text{max}}/M_{\text{min}}$ of 3.3 (14). In the goldfinch, exposure to 0°C after removing the feathers gave $M_{\text{max}}$ of 18.9 mLO$_2$ (g·h)$^{-1}$ and $M_{\text{max}}/M_{\text{min}}$ of 4.2 (8). By comparison $M_{\text{max}}$ of summer redpolls in He-O$_2$ was 21.8 mLO$_2$ (g·h)$^{-1}$ with a $M_{\text{max}}/M_{\text{min}}$ ratio of 5.6.

In previous studies of white mice and rats, considerably smaller effects of He have been reported (34, 36). Examination shows that those measurements, sometimes on groups of animals rather than individuals, gave reference values in air which clearly include a considerable activity component which is then suppressed under the cooling influence of the He (compare Fig. 1). Nor will measurements made within the thermoneutral zone show as large an increase in metabolism with He-O$_2$.

Free/forced convection and radiation present major routes for heat loss from bare skin with little or no involvement of simple conduction. Convective heat transfer in He-O$_2$ as compared with air has been described by Ep-\textit{peron et al. (5)}, in relation to the ratios of their thermal conductivities, densities, specific heats, and viscosities, together representing a ratio of $2.1$. A somewhat larger value has been calculated for conductive-convective effects (7).

By contrast to bare skin, conductive heat transfer should be of greater importance through fur (13), and a facilitation of conduction which is then suppressed under the cooling influence of the He (compare Fig. 1). Nor will measurements made within the thermoneutral zone show as large an increase in metabolism with He-O$_2$.

TABLE 2. Comparison of maximum metabolism and $M_{\text{max}}/M_{\text{min}}$ ratios obtained with different techniques

<table>
<thead>
<tr>
<th>Species</th>
<th>Weight, g</th>
<th>$M_{\text{max}}$, ml O$_2$ (g·h)$^{-1}$</th>
<th>$M_{\text{max}}/M_{\text{min}}$</th>
<th>Reference and Technique</th>
</tr>
</thead>
<tbody>
<tr>
<td>\textit{Mus musculus} albino</td>
<td>18.5</td>
<td>10.75</td>
<td>3.5</td>
<td>(8) Cold water wetting</td>
</tr>
<tr>
<td></td>
<td>26.5</td>
<td>10.10</td>
<td>5.2</td>
<td>(13) Run 6 m/min at 2°C</td>
</tr>
<tr>
<td></td>
<td>26.7</td>
<td>12.15</td>
<td>6.5</td>
<td>(12) Run 5 m/min at −10°C</td>
</tr>
<tr>
<td></td>
<td>33.0</td>
<td>10.50</td>
<td>4.2</td>
<td>(32) Run 23 m/min at −10°C</td>
</tr>
<tr>
<td></td>
<td>34.0</td>
<td>9.30</td>
<td>6.3</td>
<td>(32) Run 19 m/min at −3°C</td>
</tr>
</tbody>
</table>

| Wild, lowland | 33.4 | c | 7.40 | (18) Noradrenaline, 1.7 mg/kg |
|Wild, lowland | 29.5 | n | 11.10 | 6.3 |

| Wild, highland | 21.0 | n | 12.50 | 6.3 |
|Wild, highland | 17.3 | n | 13.80 | 7.3 |
|Wild, lowland | 17.0 | n | 12.30 | 7.2 |

| \textit{Rattus norvegicus} albino | 380 w | 3.20 | 2.7 | (19) Cold exposure at −35°C |
|                   | 385 | 2.76 | 2.7 | (4) Cold exposure down to −33°C |
|                   | 290 | 4.85 | 3.3 | (27) Swim with 2% load |
|                   | 115 | 4.81 | 3.6 | (3) Cold water wetting |
|                   | 300* w | 3.20 | 2.7 | (17) Run at 0°C or rest at −35°C |
|                   | 300* c | 5.05 | 4.2 | (17) Run at −30°C or rest at −45°C |
|                   | 286 | 4.90 | 3.1 | (32) Run 35 m/min at 6°C |
|                   | 334 | c | 5.40 | (32) Run 27–37 m/min at −3°C |
|                   | 253 | n | 5.20 | 4.9 |
|                   | 371 | c | (∼5.53) | (∼5.0) |

| \textit{Baionmys taylori} | 7.3 | n | 10.40 | 5.3 |
|                   | 6.9 | n | 12.30 | 4.3 |

* Assumed. † Acclimation: cold, warm, neutral, $T_A$. ‡ This study.


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