**SHORT COMMUNICATION**

**Burrowing star-nosed moles (**Condylura cristata**) are not hypoxia tolerant**

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**ABSTRACT**

Star-nosed moles (**Condylura cristata**) have an impressive diving performance and burrowing lifestyle, yet no ventilatory data are available for this or any other talpid mole species. We predicted that, like many other semi-aquatic and fossorial small mammals, star-nosed moles would exhibit: (i) a blunted (i.e. delayed or reduced) hypoxic ventilatory response, (ii) a reduced metabolic rate and (iii) a lowered body temperature (\(T_b\)) in hypoxia. We thus non-invasively measured these variables from wild-caught star-nosed moles exposed to normoxia (21% O\(_2\)) or acute graded hypoxia (21–6% O\(_2\)). Surprisingly, star-nosed moles did not exhibit a blunted HVR or decreased \(T_b\) in hypoxia, and only manifested a significant, albeit small (<8%), depression of metabolic rate at 6% O\(_2\) relative to normoxic controls. Unlike small rodents inhabiting similar niches, star-nosed moles are thus intolerant to hypoxia, which may reflect an evolutionary trade-off favouring the extreme sensory biology of this unusual insectivore.

**KEY WORDS:** Respirometry, Metabolism, Plethysmography, Hypoxic ventilatory response, Fossorial, Talpidae

**INTRODUCTION**

While most adult mammals are largely intolerant of hypoxia, a few species inhabit niches in which they acutely or chronically experience low O\(_2\) tensions (Boggs et al., 1984; Lacey and Patton, 2000; Roper et al., 2001; Shams et al., 2005). As environmental O\(_2\) decreases, aerobic metabolism is curtailed and cells struggle to generate the required ATP for homeostasis (Buck and Pamenter, 2006; Hochachka, 1986). To compensate, animals that exploit hypoxic environments have evolved a range of physiological, molecular and genetic adaptations (Dzial et al., 2015; Jiang et al., 2020). These specializations can be broadly categorized into mechanisms that decrease metabolic demand for O\(_2\), and mechanisms that increase the delivery of O\(_2\) to aerobic tissues. Metabolic rate suppression, wherein the body’s rate of O\(_2\) consumption (\(V_{O_2}\)) decreases in concert with environmental O\(_2\) availability, is an important strategy to mitigate the deleterious effects of hypoxia. The hypoxic metabolic response (HMR) may comprise various cellular and behavioural modifications; however, because the largest metabolic demand in small mammals is usually thermoregulation, downregulation of the body temperature (\(T_b\)) setpoint and reducing core \(T_b\) are often major components of the HMR (Tattersall and Milsom, 2009). Indeed, concurrent declines in \(V_{O_2}\) and \(T_b\) often occur in hypoxia-tolerant species (Frappell et al., 1992) and neonates (Teppema and Dahan, 2010) during hypoxic exposure. Comparatively, most terrestrial adult mammals are hypoxia intolerant and exhibit little to no HMR or change in \(T_b\) in hypoxia (Frappell et al., 1992).

Whereas most hypoxia-adapted mammals rely primarily on reducing \(V_{O_2}\) to tolerate low levels of environmental O\(_2\), most hypoxia-intolerant mammals instead increase O\(_2\) supply. Central to this latter strategy is the hypoxic ventilatory response (HVR), a reflexive increase in breathing (Frappell et al., 1992; Iturriaga et al., 2016; Pamenter and Powell, 2016; Powell et al., 1998). In hypoxia-intolerant species, this response typically manifests at environmental O\(_2\) levels as high as 18–15% (Arieli and Argar, 1979; Hemingway and Nahas, 1952). Comparatively, hypoxia-tolerant species exhibit a blunted HVR, and defer hyperventilating until environmental O\(_2\) tensions drop below 5–10% (Barros et al., 2004; Boggs et al., 1998; Frappell et al., 1994; Ivy et al., 2020; Tomasco et al., 2010).

Star-nosed moles (**Condylura cristata** (Illiger 1811)) are small (40–60 g) non-hibernating fossorial mammals native to north-eastern North America, and are the only member of their subfamily (**Condylurinae**) within the family Talpidae (Hamilton, 1931; Petersen and Yates, 1980). They are distinguished by a mobile and highly mechanosensitive 22-tentacled snout that is used to search for invertebrate prey in both aquatic and subterranean settings (Catania and Kaas, 1996). Indeed, star-nosed moles are well adapted for underground life and dig extensive tunnel systems at depths of 3–60 cm in wet soils adjacent to wetlands and streams (Hickman, 1983; Rust, 1966). While gaseous measurements in star-nosed mole burrows are not available, soil moisture impedes gas exchange and exhibits an inverse relationship with O\(_2\) tension within coast mole (**Scapanus orarius**) tunnels (Schafer and Sadleir, 1979). As insectivores, the protein rich diet of *C. cristata* also contributes to a higher O\(_2\) requirement for energy metabolism (Campbell et al., 2000; Pearson, 1947; Stephenson and Racey, 1995). Importantly, star-nosed moles are also competent thermoregulators and maintain a high and stable \(T_b\) of ~38°C, despite the challenge of living, and especially swimming, in sub-zero temperatures (Campbell et al., 1999, 2000; McIntyre et al., 2002). This combination of lifestyle, diet and high \(T_b\) presumably culminate in a substantially greater energetic demand than expected for their size, which is twice that of other fossorial mole species (Campbell et al., 1999).

In addition to living underground, star-nosed moles are accomplished divers (McIntyre et al., 2002). Advanced diving capabilities have been linked with hypoxia tolerance owing to relatively long periods spent without breathing (Meir et al., 2009; Willmore and Storey, 1997). Although these traits do not universally correlate to hypoxia tolerance, given their burrowing lifestyle and diving capabilities, we hypothesized that star-nosed moles would exhibit physiological adaptations to resist severe hypoxia, as occurs in

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other subterranean and diving mammals. We predicted that this tolerance would be achieved in part through metabolic rate suppression, reduced thermogenesis and a blunted HVR.

MATeRIALS AND METhODS

Animals

Star-nosed moles (3 adults and 5 juveniles) of unknown sex were captured during June 2019 on private land in forested areas south of Saint-Anaclet-de-Lessard, Quebec, Canada, using Sherman and pitfall traps. Animals were housed at L’Université du Québec à Rimouski (22°C, 20.95% O2, 0.04% CO2, 50% humidity) with ambient lighting synchronized to the external photoperiod. The moles were housed individually in modified, interconnected chambers. The first chamber (61x41x22 cm) was used exclusively for feeding (to permit food consumption monitoring and facilitate daily cleaning) and was connected by ABS pipe (3.8 cm diameter) to a nesting chamber (16x16x9 cm) filled with dried grass and located within a container (73x50x30 cm) furnished with ~30 cm of top-soil for the animals to freely burrow. Animals were fed 7–10 large nightcrawlers (~30–40 g) every 12 h. Twenty-four hours after arriving at the animal facility, each unanesthetized mole was implanted with a RFID temperature transponder (Bio-Thermo, Destron Fearing, Langeskov, Denmark) via syringe along the back flank and given 48 h to recover before experimentation. The moles were not fasted prior to experimental trials and were allowed a minimum of 1 week between the normoxic and hypoxic experiments. Respective animal trials were performed at the same time of day to reduce confounding effects of individual circadian rhythms. All experimental procedures were approved by the University of Ottawa’s Animal Care Committee (protocol #2535) in consultation with the Animal Care Committee from L’Université du Québec à Rimouski, with animal trapping, husbandry and experimentation conducted in accordance with the Animals for Research Act and the Canadian Council on Animal Care.

Whole-body plethysmography and respirometry

A single unrestrained mole was placed in a transparent 450 ml Plexiglas chamber connected in parallel to an identical (empty) reference chamber and closely monitored throughout each experimental trial. Experiments were performed at 22°C, to which animals were habituated prior to experimentation. The animal chamber was sealed and ventilated by positive pressure with gas mixtures set to the desired fractional gas composition by calibrated chamber was sealed and ventilated by positive pressure with gas experimental trial. Experiments were performed at 22°C, to which (empty) reference chamber and closely monitored throughout each 450 ml Plexiglas chamber connected in parallel to an identical experimental trial. The chamber temperature was recorded every 2 s by a custom-built thermocouple.

Before each trial, the O2 and CO2 analyzers were calibrated using 100% N2 and compressed air (20.95% O2, 0.04% CO2, balance N2). For the final 5 min of each O2 exposure, incurred humidity and fractional O2 (FiO2) and CO2 (FiCO2) concentrations were measured by bypassing the experimental chamber and diverting air flow directly to the gas analyzers. Stable 30 s measurements of recent gas concentrations and relative humidity (%) were then used as baselines for metabolic rate calculations (see below). In the hypoxia trials, incurred gas concentrations were then changed to the desired O2 level before returning airflow to the experimental chamber.

Animal ventilation causes pressure fluctuations because of changes in humidity and temperature between inspired and expired air that can be measured relative to a reference chamber to noninvasively monitor breathing (Jacky, 1978). We employed a differential pressure transducer (DP103-18, Validyne, Northridge, CA, USA) connected between the two chambers to amplify and continuously monitor this signal. Before each trial, the transducer was calibrated by injecting/withdrawing 6 known volumes of air (0.1, 0.2, 0.3, 0.4, 0.5, and 0.6 ml) 10 times into the experimental chamber at a rate similar to the breathing rate of the test subjects.

Data collection and analysis

Because experiments were conducted in random order and not all star-nosed moles were tolerant to 6% O2, sample size varied between the normoxic (n=7) and hypoxic (n=6–8) exposures. For the hypoxic dataset, two juvenile animals appeared to become distressed while in 6% O2 and were immediately transferred to normoxia; hence only data to 9% O2 were included for these individuals. Ventilatory and metabolic data were collected using LabChart software and analyzed in PowerLab (AD Instruments, Colorado Springs, CO, USA). Respiratory gas concentrations and pressure deflections were sampled at 1000 Hz. The 10 min interval between 20 and 30 mins of each gas exposure was analyzed to calculate mean excursion fractional O2 (FiO2) and CO2 (FiCO2) concentrations and ventilatory parameters.

\[ V_{O2} = \frac{\text{ml min}^{-1} \text{ kg}^{-1}} {\text{kg}} \] was calculated using equation 10.6 in Lighton (2008):

\[ \dot{V}_{O2} = \text{FR}[\text{FiO2} - \text{FeO2}] - \text{FR}[\text{FiCO2} - \text{FeCO2}] / (1 - \text{FeO2}). \] (1)

The rate of CO2 production \( V_{CO2} \) (ml min\(^{-1} \) kg\(^{-1} \)) was calculated using equation 10.7 from the same source:

\[ \dot{V}_{CO2} = \text{FR}[\text{FeCO2} - \text{FiCO2}] - \text{FR}[\text{FeO2} - \text{FiO2}] / (1 - \text{FeCO2}). \] (2)

The resulting \( \dot{V}_{O2} \) and \( \dot{V}_{CO2} \) values were divided by animal body mass for mass-specific comparisons. The respiratory exchange ratio (RER) was calculated as the ratio of \( \dot{V}_{CO2}/\dot{V}_{O2} \). The O2 extraction efficiency (EO2, %) was calculated as: \( (\text{FiO2} - \text{FeO2}) / \text{FiO2}) \times 100\% \).

To calculate tidal volume (V\(_T\), ml kg\(^{-1}\)) and respiratory frequency (f\(_R\), breaths min\(^{-1}\)) five breathing intervals were selected from within the same 10 min period used for metabolic rate calculations,
with each interval consisting of a minimum of 10 consecutive and clearly defined pressure oscillations, each of which was counted as one breath. The Drorbaugh and Fenn equation:

\[ V_T = \frac{[P_m V_{cal} T_A (P_B - P_C)]}{[P_{cal} (T_A (P_B - P_C) - T_C (P_B - P_A))]}, \]

was used to calculate \( V_T \) (Drorbaugh and Fenn, 1955). \( P_m \) (measured in volts) is the pressure deflection corresponding to the expired breaths. The average cyclic maximum and minimum deflections were taken from each breathing interval. The difference represented the average total pressure deflection of a breath, \( P_m \), while \( P_{cal} \) (volts) and \( V_{cal} \) (µl) are the pressure deflection and volume of a known calibrated volume, respectively. The average cyclic maximum and minimum deflection of each calibration set was plotted against the injected volume to create a linear relationship. The point on this line representing 0.2 ml was chosen as \( P_{cal} \) and \( V_{cal} \). \( T_A \) and \( T_C \) are the animal body and chamber temperature (K), respectively, each recorded at the end of the 10 min period. \( P_B \) is the barometric pressure (mmHg) as measured by the O2 analyzer. \( P_A \) (mmHg) is the vapour pressure of water at the animal’s \( T_A \) and \( P_C \) is the partial pressure of water vapour (mmHg) in the incident gas stream. \( P_{cal} \) was calculated using the relative humidity (%) of excurrent air, \( T_B \) (°C), and barometric pressure (mmHg). \( P_C \) was determined from relative humidity (%) of incident air, chamber temperature (°C), and barometric pressure (mmHg). Minute ventilation (\( \dot{V}_{E} \), ml min\(^{-1}\) kg\(^{-1}\)) was calculated as the product of \( f_{R} \) and \( V_T \). The air convection requirement of \( O_2 \) and \( CO_2 \) (ACRO2 and ACRCO2, respectively) were calculated as the quotient of \( \dot{V}_{E} \) and \( V_{O_2} \) or \( V_{CO_2} \), respectively.

**Statistical analysis**

Statistical analysis was performed using commercial software (Prism v. 8.4.2, GraphPad Software Inc., CA, USA). All values are presented as mean±1 s.e.m, where \( P<0.05 \) was the threshold for significance. Owing to the wide variance, sphericity was not assumed but was corrected for using a Geisser–Greenhouse correction. Statistical significance was evaluated using a mixed-effects model analysis (REML) to test for interactions between two independent variables: normoxia and \( O_2 \) level (20.95, 15, 12, 9, 6 and 20.95% \( O_2 \)). Tukey’s and Sidák’s multiple comparisons tests were performed on each dependent variable to determine significance. Respirometry and ventilatory data were qualitatively similar whether mass-corrected or not mass-corrected, and so data are presented normalized to body mass, where appropriate. Adult and juvenile data were pooled as no differences were found across \( O_2 \) conditions/time points for any of the evaluated parameters (Table S1).

**RESULTS AND DISCUSSION**

**Star-nosed moles have a high lethal threshold to hypoxia**

Star-nosed moles possess large spade-like forepaws and, like fossorial rodents, are morphologically specialized to exploit the subterranean niche. It is thus somewhat surprising that, despite their long evolutionary history of fossoriality (Petersen and Yates, 1980), the lethal hypoxic threshold for this species appears to be near 6% \( O_2 \), which is comparable to mice and humans (Milroy, 2018; Zhang et al., 2004). By contrast, the lethal hypoxic threshold of fossorial and subterranean rodents typically spans 0–3% \( O_2 \) (Ivy et al., 2020; Park et al., 2017).

**Star-nosed moles have a weak HMR and do not alter thermogenesis in acute hypoxia**

We found no pronounced metabolic or thermoregulatory responses to hypoxia in this species (Tables S2 and S3). Specifically, \( V_{O_2} \) was not strongly affected by hypoxia, decreasing only in 6% \( O_2 \) (by 7.4% relative to normoxia; \( P=0.0308, F_{5,62}=3.855 \), Fig. 1A). By contrast, \( V_{CO_2} \) was unchanged (\( P=0.4468, F_{5,62}=1.438 \), Fig. 1B). This finding is consistent with a recent genome-wide analysis of five subterranean species, which suggested that numerous positively selected genes of star-nosed moles are linked to the maintenance of a high energy supply (Jiang et al., 2020).

A minimal HMR is commonly observed in hypoxia-intolerant and non-fossorial small mammals (Frappell et al., 1992). Conversely, hypoxia-tolerant mammals manifest a more robust HMR that ranges from a 48% to an 85% reduction in \( V_{O_2} \) (Frappell et al., 1992; Guppy and Withers, 1999; Ivy et al., 2020), and is typically initiated at much higher \( O_2 \) tensions (~18–10% \( O_2 \)) than hypoxia-intolerant species (Devereaux and Pamenter, 2020; Ivy et al., 2020; Walsh et al., 1996). By contrast, the \( V_{O_2} \) of star-nosed moles was only significantly below the normoxic control at 6% \( O_2 \), but was not significantly lower than that observed during other hypoxia steps (Fig. 1A).

Thermogenesis is an energetically expensive process, particularly in small mammals (Ballesteros et al., 2018); thus, reducing thermogenesis is a common strategy of metabolic rate suppression in hypoxia-tolerant species. Consistent with results from hypoxia-intolerant species (Frappell et al., 1992), we did not observe a drop in \( T_B \) in hypoxia (\( P=0.999, F_{5,62}=0.6243 \), Fig. 1D). Conversely, strategies to markedly lower \( T_B \) and reduce overall \( O_2 \) consumption have been observed in many hypoxia-tolerant species (Houlaian et al., 2018; Ilacqua et al., 2017; Mortola and Feher, 1998; Nilsson and Renshaw, 2004; Wood and Gonzales, 1996).

Although there was little to no change in both metabolic rate and \( T_B \) with hypoxia, the RER increased from ~0.8 in normoxia trials to ~1.0 in all hypoxia exposures, but only reached significance at 6% \( O_2 \) (\( P=0.0011, F_{5,62}=15.09 \), Fig. 1C). This shift is indicative of a metabolic fuel switch from lipids/proteins to carbohydrates. Such a shift is consistent with an upregulation of anaerobic carbohydrate breakdown during acute hypoxia to sustain cellular function.

Increased reliance on anaerobic pathways typically results in the accumulation of acidic end products in metabolically active tissues, the clearance of which requires \( O_2 \) (Coffman, 1963; Lewis et al., 2007; Maxime et al., 2000; Plambech et al., 2013; Svendsen et al., 2012). Indeed, the observed shift in RER was rapidly reversed following reoxygenation via a sharp increase in \( V_{O_2} \) (Fig. 1A), which is consistent with the accumulation of an \( O_2 \) debt in hypoxia. Adaptive mechanisms that prevent the formation of an \( O_2 \) debt, such as use of alternative energy pathways or enhanced pH buffering, are common in hypoxia-tolerant species (Jackson et al., 1996; Park et al., 2017).

Since star-nosed moles were not fasted prior to experimentation and have a protein-rich insectivorous diet (Campbell et al., 2000), it is also possible that the observed metabolic fuel switch to primarily carbohydrates in hypoxia may have resulted in the accumulation of protein-based substrates. Increased \( V_{O_2} \) upon reoxygenation may indicate a return to protein-based metabolism, which is more \( O_2 \) intensive. Importantly, this possibility accounts for the simultaneously elevated \( V_{O_2} \) and normoxic-level RER (~0.7) following hypoxia, whereas an \( O_2 \) debt would more likely coincide with an RER below normoxic levels (Kaminsky et al., 1990; Takala, 1997).
Star-nosed moles do not have a blunted HVR

Most adult mammals increase ventilation in hypoxia (FrapPELL et al., 1992; POWell et al., 1998); however, the hypoxic threshold at which this response is initiated tends to be strongly blunted in hypoxia-tolerant species (Devereum and Pamenter, 2020; Ivy et al., 2020; Tomasco et al., 2010). By contrast, star-nosed moles exhibited a robust HVR that was not blunted, in that both $V_{\text{R}}$ and ACRO$_2$ were significantly increased in 15% O$_2$. This activation threshold is inconsistent with observations from other subterranean and hypoxia-tolerant species. Instead, it is similar to that of non-fossorial species such as dogs, rats and rabbits, where the HVR is initiated at 15–16% O$_2$ (Cao et al., 1992; Holloway and Heath, 1984; Sokolowska and Pokorski, 2006). Notably, both these variables continued to increase with progressively deeper hypoxia, with $V_{\text{R}}$ increasing by 167% in 6% O$_2$ ($P<0.0001$, $F_{5,62}=53.15$, Fig. 2B) and ACRO$_2$ increasing by 341% at this same gas tension ($P<0.0001$, $F_{5,62}=41.13$, Fig. 2D).

In addition to $V_{\text{R}}$, $V_T$ also increased in acute hypoxia, reaching significance in 12% O$_2$ and peaking at 53% over baseline in 6% O$_2$ ($P=0.0048$, $F_{5,62}=6.948$, Fig. 2C). Accordingly, $V_E$ was also elevated in 12% O$_2$ and progressively increased to a maximum of 320% above baseline in 6% O$_2$ ($P<0.0001$, $F_{5,62}=51.57$, Fig. 2A). ACRCO$_2$ increased by 247% over this same interval ($P<0.0001$, $F_{5,62}=25.62$, Fig. 2E). Of the total increase in $V_T$ at 6% O$_2$ (the most severe level of hypoxia tolerated), 63.5% was attributable to the increase in $V_{\text{R}}$ and 36.5% to the increase in $V_T$. Although breathing more deeply requires greater energy expenditure, increasing $V_T$ increases non-dead space ventilation, thereby maximizing the gas exchange of each breath (Tenney and Boggs, 2011; Vitalis and Milsom, 1986). Relying predominantly on $V_{\text{R}}$ to increase O$_2$ supply, as observed here, is a less efficient strategy as it results in a high degree of dead-space ventilation. The HVR of non-hypoxia-tolerant species are predominantly mediated by increases in $V_{\text{R}}$ (Izumizaki et al., 2004; Morris and Gozal, 2004), whereas hypoxia-adapted species tend to increase $V_T$ (Boggs et al., 1984; Devereum and Pamenter, 2020).

Interestingly, E$_{O_2}$ was also significantly elevated by 12% O$_2$ and reached a maximum 240% increase in 6% O$_2$ ($P<0.0001$, $F_{5,62}=69.54$, Fig. 2F). E$_{O_2}$ is the fraction of inhaled O$_2$ that is absorbed into the body and is an indirect indicator of mechanisms that promote O$_2$ supply during hypoxia, such as increases in blood O$_2$ affinity (Ar et al., 1977; Johansen et al., 1976), gas diffusion, hematocrit, and/or cardiac output. The nearly 3.5-fold increase in E$_{O_2}$ suggests that compensatory mechanisms are robustly activated in star-nosed moles during hypoxia. While the blood O$_2$ affinity of C. cristata (22.5 mmHg at 36°C) is generally slightly lower than that of fully fossorial moles (Campbell et al., 2010; Quilliam et al., 1971), it is markedly higher than similarly sized non-subterranean mammals. Consistent with genome analysis revealing an enrichment of genes for respiratory gas exchange (Jiang et al.,...
2020), star-nosed moles also exhibit an enlarged lung volume, high blood hematocrit (∼50%) and blood carrying capacity, and elevated muscle myoglobin content relative to fossorial moles (McIntyre et al., 2002). These traits align with the observed increase in EO2 and presumably are important for extending dive durations of this species. Finally, and unlike non-talpid subterranean lineages, star-nosed moles do not have expanded families of hypoxia-related genes relative to non-subterranean species (Jiang et al., 2020), supporting our finding that their metabolic and ventilatory responses are more in line with those of hypoxia-intolerant species.

**Conclusions**

Our results refute or a priori prediction that star-nosed moles are strongly hypoxia tolerant. Specifically, their relatively high lethal hypoxic (6% O2) and HVR thresholds (12–15% O2), the minimal HMR, and lack of Tb reduction in hypoxia are more similar to the phenotype of hypoxia-intolerant and non-fossorial mammals, and starkly contrast with the physiological responses of hypoxia-tolerant rodents.

Whereas metabolic depression and reduced thermogenesis are often key contributors to hypoxia tolerance, such responses may be maladaptive for star-nosed moles owing to their unusual biology
and feeding behaviour. For example, the distribution of star-nosed moles is substantially further north than other North American talpids, which, coupled with their semi-aquatic habitats and an inability to exploit facultative torpor, has presumably selected for a high metabolic intensity and stable $T_b$ (Campbell et al., 1999). Indeed, consistent with results of previous studies (Campbell et al., 2000), our captive moles consumed more than their body mass per day.

Unlike hypoxia-tolerant rodents, star-nosed moles are voracious predators and meet their high energy requirements by actively searching both their invertebrate-dense tunnel systems and adjacent underwater areas (Hamilton, 1931). Further, the elaborate nose in the star-nosed mole has undergone strong directional selection for speed—capable of >10 prey searches per second—allowing the moles to consume hundreds of prey per minute (Catania and Remple, 2005). The likely consequence of their ‘hard-wired’ high metabolic intensity lifestyle and extreme sensory motor specialization for speed is a high continual supply of oxygen. Thus, despite exploiting shallow burrow systems constructed in muddy soils with limited gas exchange, star-nosed moles exhibit a relative hypoxia-intolerant phenotype, which is presumably mitigated by behavioural and respiratory adaptations for semi-aquatic and feeding behaviour. For example, the distribution of star-nosed moles is substantially further north than other North American talpids, which, coupled with their semi-aquatic habitats and an inability to exploit facultative torpor, has presumably selected for a high metabolic intensity and stable $T_b$ (Campbell et al., 1999). Indeed, consistent with results of previous studies (Campbell et al., 2000), our captive moles consumed more than their body mass per day.

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**Table S1.** Metabolic and ventilatory responses of juvenile vs. adult star-nosed moles to acute hypoxia. Mean ± S.E.M. and p-values of Sidak’s multiple comparison test between adult and juvenile star-nosed moles, with sample sizes for each presented in parentheses.

Click here to download Table S1

**Table S2.** Metabolic and ventilatory comparisons of star-nosed moles during normoxia and hypoxia trials. Mean ± S.E.M. and p-values of Sidak’s multiple comparison test between normoxic and hypoxic protocols for pooled adult and juvenile data, with sample sizes presented in parentheses.

Click here to download Table S2

**Table S3.** Metabolic and ventilatory timecourse comparisons of star-nosed moles during normoxia and hypoxia trials. Mean ± S.E.M. and p-values of Tukey’s multiple comparison between time points within the normoxic and hypoxic protocols for pooled adult and juvenile data, with sample sizes presented in parentheses.

Click here to download Table S3