Fasting metabolism and thermoregulatory competence of the star-nosed mole, *Condylura cristata* (Talpidae: Condylurinae)

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Abstract

Metabolic and body temperature (T_b) responses of star-nosed moles (*Condylura cristata*) exposed to air temperatures ranging from 0 to 33°C were investigated. The thermoneutral zone of this semi-aquatic mole extended from 24.5 to 33°C, over which its basal rate of metabolism averaged 2.25 ml O_2 g^{-1} h^{-1} (45.16 J g^{-1} h^{-1}). This rate of metabolism is higher than predicted for terrestrial forms, and substantially higher than for other moles examined to date. Minimum thermal conductance was nearly identical to that predicted for similar-sized eutherians and may represent a compromise between the need to dissipate heat while digging and foraging in subterranean burrows, and the need to conserve heat and avoid hypothermia during exposure to cold. *C. cristata* precisely regulated T_b (mean $\pm$ SE = 37.7 $\pm$ 0.05°C) over the entire range of test temperatures. Over three separate 24-h periods, T_b of a radio-implanted mole varied from 36.6 to 38.8°C, and generally tracked level of activity. No obvious circadian variation in T_b and activity was apparent, although cyclic 2–4 h intervals of activity punctuated by periods of inactivity lasting 3–5 h were routinely observed. We suggest that the elevated basal metabolic rate and relatively high T_b of star-nosed moles may reflect the semi-aquatic habits of this unique talpid. © 1999 Elsevier Science Inc. All rights reserved.

1. Introduction

The star-nosed mole (*Condylura cristata*), distinguished by its strange and conspicuous [22] fleshy-appendage proboscis, is the only member of the subfamily Condylurinae [29]. Unique among North American moles for its semi-aquatic habit and predilection for moist soils bordering on streams and lakes, the star-nosed mole is an adept burrower and excellent swimmer [13,14]. Direct observations of star-nosed moles indicate an active lifestyle, prompting speculation of a voracious appetite and 'high metabolism' [4,5,13,31,33]. Yet few data exist on even the most basic energetics of this curious invertebrativore. Indeed, information of this nature is limited to metabolic measurements obtained from two immature moles held at 27–28°C [37] and

from a single, restless 60-g specimen [28] that presumably was held at a similar air temperature.

The star-nosed mole ranges considerably farther north than any other North American talpid [29]. In fact, these animals have been observed tunneling through snow and even diving under ice during winter [13,26,33]. Moreover, analysis of stomach contents indicate that aquatic invertebrates are taken year round [13,30], and reportedly occur in the diet most frequently during winter. These observations imply a high level of thermoregulatory competence in this species, perhaps coupled with an elevated basal metabolic rate (BMR). Non-hibernating small mammals inhabiting cold environments, including semi-aquatic forms, often exhibit higher BMRs and lower heat transfer coefficients than predicted from allometry [9,18,34]. Though controversial, it has been speculated that these features are consistent with the high rates of thermogenesis and risks of hypothermia posed by chronic exposure to cold [8,32].

Like aquatic foraging, burrowing is considered one of the most energetically demanding activities engaged

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in by mammals [16,35]. However, the confined burrow environment impedes heat dissipation [19] and the inherently low gas permeability of soil may reduce oxygen availability and increase the risk of respiratory acidosis to fossorial mammals [2]. Consequently, an elevated BMR and reduced minimal thermal conductance (C_m) would not only increase the risk of hyperthermia in burrowing mammals [6,16,20,21], but may also aggravate disturbances of respiratory gases in burrow micro-environments [2]. Clearly, physiological phenotypes suited for subterranean life may be at variance with those compatible with a semi-aquatic existence. While much has been learned of the metabolic organization and thermal biology of fossorial and semi-aquatic rodents [6,9,18,20,21], data for comparable Insectivora [34] are scarce. The star-nosed mole manifests a clear propensity for both subterranean and aquatic environments and thus affords an ideal model for such investigation.

This paper is the first to report on the metabolic rate, thermal conductance and thermoregulatory performance of wild-caught star-nosed moles exposed to a range of ambient temperatures likely to be encountered by these animals in nature. Additional information on the daily activity and body temperature (T_b) patterns of these unusual invertebrativores also are presented.

2. Materials and methods

2.1. Study animals

A total of 12 star-nosed moles of both sexes were livetrapped 2 km north of Piney, Manitoba (49°06′ N, 95°59′ W), during June 1997/1998 and transported to the Animal Holding Facility, University of Manitoba. Animals were held at $20 \pm 1°C$ with a 12:12 light:dark photoperiod, and housed individually in rectangular plywood chambers ($88 \times 50 \times 60$ cm) filled with 45 cm of sterilized soil (ca. 60% peat moss, 20% sand and 20% potting soil mixture). The soil was moistened daily and chambers were covered with fine mesh netting, providing moles with dim, humid conditions approximating those of their natural habitat. Each container was attached via a length of ABS tubing (internal diameter, 4 cm) to a 40-l glass aquarium filled with 25 cm of water. Swimming tanks were covered with Plexiglas and fitted with removable ramps to allow easy access of moles to and from the water. Animals were maintained on a mixed ration of pork brain, beef heart, liver, kidney, hamburger, and canned cat food enriched with multivitamin and calcium supplements. Commercially purchased nightcrawlers (*Lumbricus* spp.), leeches (*Nephelopsis obscura*) and mealworms (*Tenebrio molitor*) also were provided daily. While in captivity, moles were cared for in accordance with the principles and guidelines of the Canadian Council on Animal Care and under the authorization of a University-approved animal research protocol.

2.2. Metabolic measurements

Resting rates of oxygen consumption ($\dot{V}_{O_2}$) and carbon dioxide production ($\dot{V}_{CO_2}$) were measured using a negative pressure, open-flow respirometry system. Animals were fasted for 4–8 h, weighed to the nearest 0.01 g, and transferred to a modified 0.95-l paint can fitted with inlet and outlet ports, that was installed in a temperature-controlled cabinet. The interior of the metabolic chamber was painted flat black to reduce radiative heat transfer and was furnished with 3–4 mm of dry, sterilized soil (see above). This latter provision increased the frequency and duration of stable metabolic readings from test animals. Dry CO_2-free room air was drawn through the chamber at a rate of 900 ± 10 ml min^{-1} (TR-SS1 gas analysis sub-sampler; Sable Systems Inc., Henderson, NV). A portion of the chamber exhaust gas (250 ml min^{-1}) was passed sequentially through a Drierite column, a Beckman LB-2 carbon dioxide analyzer, soda lime and Drierite trains, and an Applied Electrochemistry S3-A oxygen analyzer. Following a 30–45-min settling period, chamber ambient temperature (T_a), air flow rate, and fractional CO_2 and O_2 contents of chamber exhaust gas were recorded every 5 s for a period of 1–3 h, using Datacan V data acquisition software (Sable Systems Inc.). During metabolic trials conducted in 1998, animal activity was recorded at 5-s intervals with a MAD-1 motion/activity detector (Sable Systems Inc.). At test temperatures > 30°C (conducted in 1998 only) motor activity was virtually non-existent. Consequently, metabolic trials above 30°C were shortened to ≤ 1 h to reduce the risk of hyperthermia.

Resting $\dot{V}_{O_2}$ was calculated as the average of the three lowest steady-state values, each lasting at least 3–5 min. Use of the motion/activity detector aided identification of resting periods in the 1998 metabolic trials. $\dot{V}_{CO_2}$ (ml h^{-1}) was calculated by multiplying the fractional CO_2 content of excurrent gas by chamber flow rate, and V_{O_2} determined as:

$$\dot{V}_{O_2} \,(\text{ml g}^{-1}\,\text{h}^{-1})$$
$$= [(\dot{V}_e - \dot{V}_{CO_2}) \times (FiO_2 - FeO_2)/(1 - FiO_2)]/\text{body mass}$$

where $\dot{V}_e$ is the flow rate (ml h^{-1}) of dry excurrent gas and FiO_2 and FeO_2 are the fractional O_2 contents of inlet and outlet air streams, respectively. Body mass (g) represents the average value for each trial.

To estimate the rate of heat exchange between the body and environment, coefficients of whole-body thermal conductance were calculated as [22]: conductance $= \dot{V}_{O_2}/(T_b - T_a)$.

We used a continuous two-phase regression model [27] to statistically calculate the lower critical temperature from metabolic data, and to derive the inflection point in the relationship of thermal conductance to T_a [3].

2.3. Body temperature

Initial attempts to record rectal temperatures were abandoned, owing to difficulties encountered in restraining these remarkably agile animals. We subsequently discovered that moles were easily restrained if provided access to a blind-ending, 3-cm diameter tunnel cut in a foam block. Immediately following metabolic testing, moles were allowed access to the tunnel and T_b determined with a copper-constantan thermocouple lubricated with mineral oil and inserted 1.5–2.0 cm into the rectum. The temperature probe was connected to a model BAT-12 thermocouple thermometer.

A limited number of abdominal T_b recordings were obtained from a single mole implanted with a 1.3-g model X–M transmitter (Mini-Mitter Inc., Sunriver, OR). Transmitter calibration and implantation procedures are described elsewhere [10,19]. Star-nosed moles are highly prone to anesthesia-induced mortality, [1] and this study, and we found it best to anesthetize each mole in stages, as recommended by Catania (personal communication). Briefly, the animal was weighed to the nearest 0.01 g, allowed access to the foam tunnel, and injected with Ketamine hydrochloride (ca. 35 mg kg^{-1} i.p.). Within 5–10 min, a second intraperitoneal injection (ca. 25 mg kg^{-1}) was administered to establish a deep plane of anesthesia. Additional small doses (5–10 mg kg^{-1}) were given as needed to maintain a surgical plane of anesthesia (Catania, in litt.). The sterilized transmitter was implanted into the abdominal cavity and the midline abdominal incision promptly closed. Metabolic measurements were initiated 1 week following surgery.

2.4. Daily activity and T_b patterns

Three 24-h activity and T_b recordings were obtained from the single radio-implanted mole. The animal was housed in a 38-l plastic container placed on the MAD-1 motion/activity detector. The container was furnished with a screen cover, 8 cm of soil, a small nest box, and a water dish. T_b was recorded at 10-min intervals on analog tape using an automated recording system similar to that described by Dyck and MacArthur [10]. Activity was monitored at 15-s intervals for the duration of the trial. Several additional 24–48-h activity recordings were obtained from two non-instrumented moles. For all trials, moles were held at $20 \pm 1°C$ with a 12:12 light:dark photoperiod. Food and water were provided ad libitum.
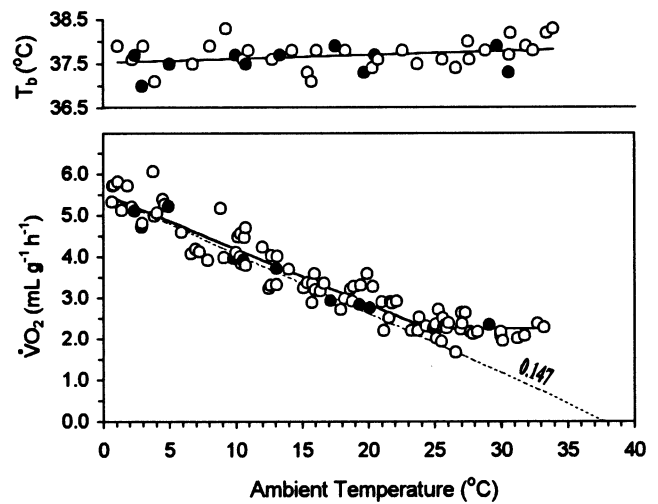

Fig. 1. The relationship of body temperature (T_b) and resting metabolic rate to air temperature in 12 fasted star-nosed moles, *Condylura cristata*. For $\dot{V}_{O_2}$ data, the solid line was fitted using a continuous two-phase linear regression model [27]. The dashed regression line was derived by forcing the regression of $\dot{V}_{O_2}$ on T_a to intersect the abscissa at mean T_b (37.7°C). The slope of this regression (0.147 ml g^{-1} h^{-1}°C^{-1} O$_2$) represents the minimal thermal conductance below thermoneutrality [22]. (●) $\dot{V}_{O_2}$ and telemetered T_b recordings for a single radio-implanted mole (see text).

3. Results

Based on the relationship between resting metabolic rate and T_a of fasted animals (Fig. 1), the lower critical temperature of the star-nosed mole was calculated to be 24.5°C. This is reasonably close to the inflection point (25.4°C) derived for the relationship between whole-body thermal conductance and T_a (Fig. 2). Although an upper critical temperature could not be clearly delineated, T_b, $\dot{V}_{O_2}$ and thermal conductance all increased slightly at $T_a = 33°C$ (Figs. 1 and 2), suggesting that
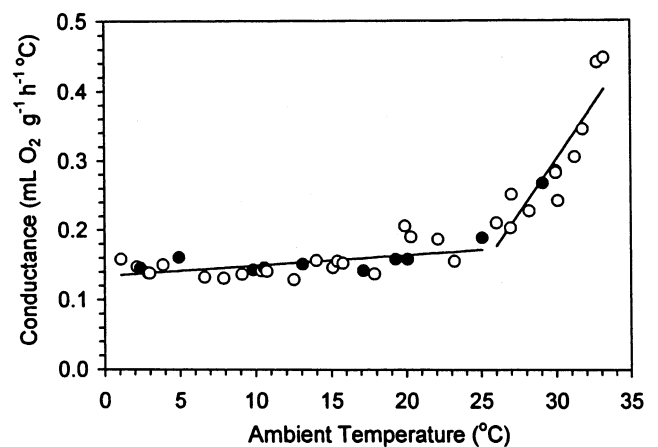

Fig. 2. Whole-body thermal conductance of fasted star-nosed moles in relation to air temperature. Regression lines were fitted using a continuous two-phase, straight-line regression model [27]. Closed circles denote values obtained from the radio-implanted mole (see text).
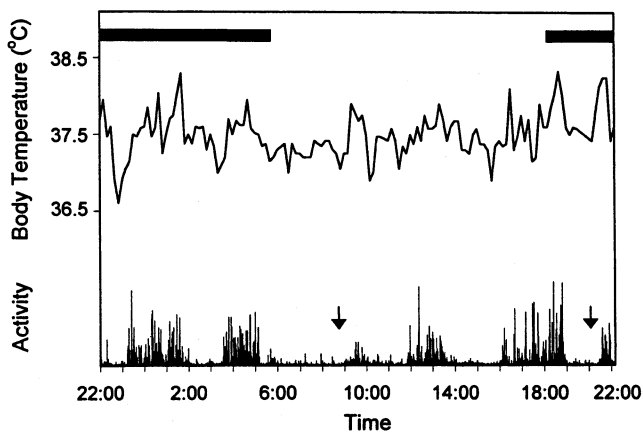
Fig. 3. Daily variation in telemetered abdominal temperature and motor activity of a radio-implanted star-nosed mole held at an air temperature of 20°C. Amplitude of the activity trace denotes relative level of movement detected by an activity/motion sensor (see text for details). The solid bars indicate hours of darkness. Arrows indicate times fresh food and water were placed in the animal chamber.

this T_a was close to the upper limit of thermoneutrality. Based on all measurements above 24.5°C ($n = 25$), the BMR ($\pm$ SE) of *C. cristata* was estimated to be 2.25 ± 0.05 ml O_2 g^{-1} h^{-1}, or 45.16 J g^{-1} h^{-1}. Assuming an average body mass of 49.0 g, this value is 199.3% that predicted for a similar-sized eutherian, $\dot{V}_{O_2} = 3.45$ Mass$^{-0.287}$ [23]. Body temperature was closely regulated over the entire range of test temperatures (Fig. 1), averaging 37.7 ± 0.05°C ($n = 42$). Below thermoneutrality, $\dot{V}_{O_2}$v increased as a linear function of air temperature: $\dot{V}_{O_2} = 5.534 - 0.134 T_a$ (slope significantly different from zero, $P < 0.0001$, $n = 71$, $r^2 = 0.88$). The C_m derived by forcing the least-squares regression of $\dot{V}_{O_2}$ on T_a to intersect the abscissa at 37.7°C [22] was 0.147 ml O_2 g^{-1} h^{-1}°C^{-1} (Fig. 1), whereas that obtained by averaging all values of conductance below thermoneutrality (Fig. 2) was 0.151 ml O_2 g^{-1} h^{-1}°C^{-1}. Both estimates of C_m were nearly identical to that predicted from allometry, 0.145 ml O_2 g^{-1} h^{-1}°C^{-1} [25].

Activity patterns were distinctly cyclical in all moles tested. In nearly all cases, persistent 2–4 h blocks of activity were punctuated by periods of rest lasting 3–5 h (Fig. 3). This activity pattern corresponded closely to the approximate 4-h wake/sleep cycle previously reported for *C. cristata* and *Scalopus aquaticus* [1]. Abdominal T_b of the radio-implanted mole averaged 37.5–37.8°C over three 24-h periods, with a maximal daily amplitude of 2.2°C (range, 36.6–38.8°C). Generally, T_b fluctuated with level of activity, attaining peak values following bursts of motor activity. While the highest T_bs and most intense periods of activity were recorded during the hours of darkness, no obvious circadian variation in T_b and activity was apparent (Fig. 3).

4. Discussion

The star-nosed mole is the only semi-aquatic mole found in the Western Hemisphere, and with the exception of the diminutive shrew-mole (*Neurotrichus gibbsii*), is the least fossorial of the North American talpids [3,13]. Functionally blind, star-nosed moles rely primarily on their specialized and thinly keratinized nasal rays [4,5] to probe the moist surfaces of stream beds, lake bottoms and shallow tunnels for earthworms and aquatic invertebrates [13]. Given this species' epigeal nature, delicate nose, and early divergence [38] from the main talpid line, 30–49 mya [39], it is tempting to speculate that *C. cristata* may have progressed directly from a primitive ancestral cursorial morph to its current semi-aquatic form. Anatomical evidence, however, suggests *Condylura* passed through a specialized fossorial phase in its evolutionary development [11].

It has long been recognized that burrowing endotherms often exhibit low BMRs, reduced T_bs, and relatively high thermal conductance coefficients, compared to their terrestrial counterparts [16,20]. However, at body masses less than ca. 60 g, fossorial mammals tend to have BMRs slightly higher than expected [6,21]. Moreover, minimal thermal conductances of small fossorial mammals that are < 1 kg or inhabit cool burrows (< 20°C) are typically close to those predicted from allometry [6,21]. Our results indicate that the basal $\dot{V}_{O_2}$ of star-nosed moles (2.25 ml O_2 g^{-1} h^{-1}) is nearly twice the mass-predicted estimate for a comparable-sized eutherian, 1.13 ml O_2 g^{-1} h^{-1} [23]. This basal $\dot{V}_{O_2}$ is also considerably higher than values reported for other moles of comparable size, including the eastern mole, *Scalopus aquaticus*, 1.41 ml O_2 g^{-1} h^{-1} [21], the broad-footed mole, *Scapanus latimanus*, 1.25 ml O_2 g^{-1} h^{-1} [6], the coast mole, *Scapanus orarius* (1.02 ml O_2 g^{-1} h^{-1}, [15], and the larger Townsend's mole, *Scapanus townsendii*, 0.82 ml O_2 g^{-1} h^{-1} [15]. Star-nosed moles also maintain a deep T_b that is ca. 0.6–1.7°C higher than those reported, [1,6,21] Campbell unpublished data, for these more evolutionarily derived fossorial talpids [38]. It is noteworthy that the estimated lower critical temperature of star-nosed moles is at least 1.5°C lower than for other moles tested to date [6,21]. However, this finding is not surprising, since an elevated BMR should theoretically extend the lower limit of the species' thermoneutral zone [32].

As noted earlier, several aquatic mammalian species appear to be endowed with an intrinsically high BMR [9,18]. For example, the sea otter (*Enhydra lutris*), coypus (*Myocastor coypus*) and platypus (*Ornithorhynchus anatinus*) all exhibit BMRs that are substantially greater than those of other closely related members of their respective lineages [7,9,12]. Like *C. cristata* with which it shares a largely sympatric range and semi-aquatic habits, the northern water shrew

(*Sorex palustris*) also demonstrates a higher basal $\dot{V}_{O_2}$ (I.W. McIntyre, R.A. MacArthur and K.L. Campbell, unpublished data) than non-aquatic insectivores, *Blarina brevicauda* [8,24] and *N. gibbsii* [3], of similar size. The adaptive value of an elevated BMR for semi-aquatic existence has been questioned by several investigators [18]. For instance, a chronically elevated BMR dictates a high rate of heat production at all ambient temperatures, and compounds the risk of hyperthermia during activity on land [18,19]. The latter problem would seem especially acute for a semi-aquatic species that is also fossorial, and therefore challenged by the high metabolic heat loads associated with digging [16,35]. Indeed, variation in T_b of the radio-implanted mole appeared to track bursts of motor activity in the soil (Fig. 3).

Direct observations of star-nosed moles engaged in foraging activity indicated that during tunnel excavation, these animals frequently use their noses to probe newly exposed earth in search of prey [5]. Though speculative, it is possible that the relatively large surface area, high vascularity, and remarkably thin (5–6 μm) epidermis of the nasal rays [4] afford a proficient heat shunt while foraging in moist soils, thereby retarding the accumulation of excess metabolic heat. However, these same morphological features are also conducive to heat loss during excursions in cold water. Heat loss from the fleshy nose appendages may also account, at least in part, for our finding that minimal thermal conductance is unremarkable in *C. cristata*, despite the fact that the dense pelage of this species provides an effective waterproof boundary in the aquatic medium, [14] personal observation.

Considering their large surface area-to-volume ratio and the exceptional thermal conductivity of water compared to air, it is not surprising that most small-bodied, semi-aquatic mammals are unable to maintain core T_b while immersed, and tend to cool rapidly in the aquatic medium [18], but see [12,36] for exceptions. Cold acclimation in shrews is accompanied by an elevation of BMR and maximal heat-producing capabilities [8]. Thus, adoption of an elevated BMR, perhaps in conjunction with brown fat thermogenesis, unpublished data [17], may serve to accelerate the rate of rewarming following immersion of star-nosed moles, and may even increase the duration and overall efficiency of foraging bouts. Furthermore, maintenance of an elevated T_b by this species would reduce the risk of immersion hypothermia substantially.

In summary, results of this study reveal that star-nosed moles exhibit a high T_b, an elevated BMR, a broad thermoneutral zone, but a similar C_m, compared to other fossorial talpids examined to date. The observed C_m of *C. cristata* likely reflects a compromise between the need to dissipate excess metabolic heat while surface foraging, and the need to conserve heat

during exposure to cold. We suggest that the highly modified nose of this mole provides a major avenue of heat loss in both air and water. Adoption of a relatively high, stable T_b and elevated BMR by this species may augment thermogenesis at sub-thermoneutral air temperatures while lowering risks of hypothermia. These factors, in combination with a reduction in the lower critical temperature, may in part explain the successful invasion of star-nosed moles into more northern regions than those tolerated by other North American talpids. These physiological attributes may also compensate for the high rates of heat loss presumably experienced by these animals during aquatic excursions. Clearly, additional data on the thermoregulatory performance and metabolic responses of these animals in water are required to more accurately delineate this physiological phenotype.

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