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THERMAL BIOLOGY AND METABOLISM OF THE AMERICAN SHREW-MOLE, *NEUROTRICHUS GIBBSII*

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The American shrew-mole (*Neurotrichus gibbsii*) seems to occupy an ecological and evolutionary position intermediate to that of shrews and fully fossorial moles. However, because little is known regarding their physiology, we examined the metabolic rate and thermoregulatory competence of 6 shrew-moles exposed to ambient temperatures ranging from 3 to 34°C with flow-through respirometry. The basal rate of metabolism of *N. gibbsii* (3.94 ml O_2 g^{-1} h^{-1}; 77.90 J g^{-1} h^{-1}) was 2.32 times greater than predicted for similar-sized placental mammals and close to that of soricine shrews of comparable mass (10–12 g). Over the entire range of test temperatures, mean body temperature (38.4 ± 0.2°C *SE*) of this small semiterrestrial talpid was higher and more labile than that of other North American moles but within the range typical for north-temperate soricids. With declining ambient temperatures, shrew-moles exhibited gradual reductions in body temperature and minimal whole-body thermal conductance. In 2 instances, shrew-moles were observed to enter an apparent state of hypometabolism. Whether the observed reductions in body temperature and metabolic rate of *Neurotrichus* exposed to low ambient temperatures are adaptive energy-conservation mechanisms exhibited during periods of prolonged cool wet weather and food deficits in nature, or simply reflect an inability to proficiently thermoregulate after an extended fast, is currently unknown.

Key words: activity pattern, American shrew-mole, Insectivora, metabolism, *Neurotrichus,* thermal biology

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It is clear from classic anatomical (Reed 1951) and recent molecular studies (Stanhope et al. 1998) that shrews (Soricidae) and moles (Talpidae) share a common ancestry within the well-defined superfamily Soricoidea. Associated with soft loamy soils along the moist Pacific Coast from southwestern British Columbia to central California, the aptly named shrew-mole, *Neurotrichus gibbsii,* is the smallest North American mole (Dalquest and Orcutt 1942; Reed 1951). Long thought to be the most primitive North American talpid (Reed 1944, 1951), 2 recent phylogenetic analyses place shrew-moles between the more ancestral semiaquatic *Condylura* and the more derived fossorial moles, *Parascalops, Scalopus,* and *Scapanus* (Whidden 2000; Yates and Moore 1990). Despite their central placing within the Talpidae, shrew-moles possess physical features reminiscent of both soricids (small size, posteriorly directed pelage, and paired ampullary glands) and talpids (heavy dentition, large head, and modified front feet) and occupy an ecological niche overlapping that of both clades (Dalquest and Orcutt 1942; Terry 1981). For instance, although structurally less specialized for subterranean existence than other North American moles (Reed 1951), shrew-moles excavate extensive shallow underground galleries and maintain an appetite for earthworms and other soil

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invertebrates (Dalquest and Orcutt 1942; Racey 1929). However, shrew-moles are remarkably swift and agile on the forest floor, where they are thought to be in direct competition with shrews and small rodents for beetles, seeds, lichens, fungi, and other food resources (Dalquest and Orcutt 1942; Terry 1978).

Pioneering studies on the metabolism of mammals suggested that insectivores manifest an inherently high rate of mass-specific metabolism compared with other mammalian orders (Pearson 1947). Moreover, subsequent studies have revealed 3 distinct energetic tactics within the Soricoidea (McNab 1979, 1991; Sparti 1990), traits presumably radiating from the evolutionary history and ecological specializations intrinsic to each group. Soricines (red-toothed shrews), for example, are thought to have evolved in Holarctic regions (Vogel 1980). To compensate for the high rate of heat loss intrinsic to cool north-temperate environments, this subfamily of shrews typically exhibits body temperatures (T_b) and basal mass-specific rates of metabolism that are substantially above that predicted for other similar-sized eutherian mammals (McNab 1991; Vogel 1980). Apart from a few exceptions, red-toothed shrews are solitary and not known to enter torpor (McNab 1991). In contrast, the more southerly distributed white-toothed shrews (subfamily Crocidurinae) maintain a more sociable life style and commonly become torpid during cold weather or food restriction (McNab 1991; Sparti 1990). Presumably in conjunction with their paleotropical origins, crocidurines exhibit relatively low, moderately labile T_bs, and basal rates of metabolism only slightly higher than expected on the basis of mass (McNab 1991; Sparti 1990). Eurasian in origin (Whidden 2000), talpid moles are typically an order of magnitude larger in body mass than the shrews with which they coexist and are largely able to avoid temperature extremes because of their subterranean habits (McNab 1966, 1979). Hence, fossorial North American moles tend to exhibit T_bs intermediate to white- and red-toothed shrews, and rates of metabolism only modestly above those predicted on the basis of allometry (Contreras and McNab 1990; McNab 1979). To date, facultative daily torpor has not been demonstrated in any member of this lineage.

Given the apparent intermediate ecological and evolutionary position of American shrew-moles within the Soricoidea, their physiology is of special systematic interest. We report on the metabolism, thermoregulatory competence, and whole-body thermal conductance of wild-caught *N. gibbsii* subjected to ambient temperatures ranging from 3 to 34°C. Limited information on the daily activity patterns of this species also is presented.

Materials and Methods

Nine American shrew-moles were captured in 1.4-1 tincan pitfall traps (932 trap-nights) buried in the ground at the University of British Columbia Animal Holding Facility (49°30′N, 123°10′W) in early autumn 1998. Dalquest and Orcutt (1942) reported live-trapping mortality for this species to reach 90%; thus, we checked traps at 3- to 4-h intervals to minimize fatalities.

Animals were housed individually at room temperature with a natural photoperiod in 38-1 plastic containers furnished with a wire-mesh cover, small nest box, water dish, and 10–15 cm of soil. Animals were supplied daily with a mixture of earthworms (*Lumbricus*), mealworms (*Tenebrio molitor*), and sow-bugs (*Oniscus asellus* and *Porcellio scaber*) equaling about 2–3 times their body mass. During their stay in captivity (<4 weeks), moles were cared for in accordance with the principles and guidelines of the Canadian Council on Animal Care with the consent of the University of British Columbia Committee on Animal Care.

Rates of oxygen consumption ($\dot{V}_{O_2}$) and carbon dioxide production ($\dot{V}_{CO_2}$) were measured using a negative pressure, open-flow respiratory system. After a 1-h fast, animals were placed in a 250-ml Plexiglas chamber furnished with 3–4 mm of dry sterilized soil to facilitate recurrence of low stable metabolic readings (Campbell et al. 1999). The metabolic chamber was fitted with inlet and outlet ports, and the interior was paint-

ed flat black. The respirometer was placed on a MAD-1 motion-activity detector (Sable Systems Inc., Henderson, Nevada) and installed in a controlled-temperature cabinet set to the desired test temperature. Dry CO_2-free air was drawn through the chamber via a combination pump-mass flowmeter at a rate of 500 ml/min (TR-SS1 gas analysis sub-sampler, Sable Systems Inc.). A sample of dry outlet gas (150 ml/min) was routed serially through carbon dioxide (Li-Cor model LI-6251, Lincoln, Nebraska) and oxygen analyzers (Applied Electrochemistry S-3A/I, Sunnyvale, California). Chamber ambient temperature (T_a), flow rate, relative animal movement, and fractional excurrent O_2 and CO_2 content were recorded every 5 s for 2 h using Datacan V data acquisition software (Sable Systems Inc.). At test temperatures >30°C, trials were shortened to 1 h to minimize risk of hyperthermia-induced mortality (Deavers and Hudson 1981). At least 48 h elapsed between successive trials for each shrew-mole.

For each trial, $\dot{V}O_2$ was determined following Campbell et al. (1999). The respiratory exchange ratio (RER) of test animals was then calculated and used to convert $\dot{V}O_2$ into units of heat production (J g^{-1} h^{-1}; hereafter termed metabolic rate, MR) as: $MR = [16.218 + 4.716(RER)] \times \dot{V}O_2$. This formula is based on the assumptions that catabolism of carbohydrates and lipids liberated 20.93 and 19.55 J of heat per milliliter of O_2 consumed, respectively (Jungas et al. 1992: 438, table 17), and that amino acid oxidation was negligible. All fasted resting MRs, gauged by traces of minimal animal activity, were then calculated as the average of the 3 lowest steady-state rates of oxygen consumption and metabolic heat production lasting a minimum of 3 min in each case. Animals were weighed to the nearest 0.01 g before and after each trial, and the mean mass was used for mass-specific metabolic measurements.

Immediately before and after experimentation, shrew-moles were allowed access to a blind-ended tunnel (2-cm diameter) carved into a block of foam, and T_b was determined within 15–30 s using a lubricated copper-constantan thermocouple wire inserted 1.5 cm into the rectum. In several cases, difficulty inserting the probe precluded obtaining accurate readings; those measurements were subsequently discarded. To estimate the rate of heat exchange between the body and environment (McNab 1980), coefficients of whole-body thermal conductance (C) were calculated for all test temperatures as: $C = \dot{V}O_2/(T_b - T_a)$.

The relationship between $\dot{V}O_2$ and T_a was evaluated, and the boundaries of the thermoneutral zone were calculated, by modifying the 2-phase straight-line regression model advocated by Nickerson et al. (1989) to a 3-phase regression model. A continuous 2-phase regression model was used to assess the relationship between C and T_a, and the calculated inflection point between the 2 linear regressions was used as a 2nd estimate of the lower critical temperature. Calculations were performed using the regression and solver functions of Microsoft Excel (version 5.0). All values are presented as $\bar{X} \pm 1$ *SE*.

Activity traces were obtained from 3 shrew-moles held at room temperature and under a natural photoperiod in late August ($n = 2$) and early October ($n = 1$) 1998. For each recording, holding containers were placed on the motion-activity detector, and T_a and relative activity level were recorded at 15-s intervals for ≤48 h. Food and water were provided ad libitum.

Results

Trap-related mortality was 33%, because 1 mole perished in the trap, and 2 individuals taken together died of unknown causes within 24 h of capture. Metabolic and T_b data were obtained from 6 shrew-moles ranging in mass from 10.8 to 12.9 g ($\bar{X}$ = 11.8 g) at ambient temperatures ranging from 2.8 to 33.8°C (Fig. 1). Based on the relationship between $\dot{V}O_2$ and T_a, the calculated thermoneutral zone of *N. gibbsii* was 24.9–32.0°C. That estimate of the lower critical temperature was nearly identical to that derived (25.0°C) from the relationship between whole-body thermal conductance and T_a (Fig. 1). Within thermoneutrality, the metabolic rate of fasted, inactive shrew-moles averaged 3.94 ± 0.04 ml O_2 g^{-1} h^{-1} or 77.90 ± 0.73 J g^{-1} h^{-1} ($n = 18$). Over the entire range of test temperatures, RER averaged 0.752, confirming that shrew-moles were predominantly metabolizing lipids. Below thermoneutrality, resting rates of oxygen consumption varied inversely with T_a as: $\dot{V}O_2 = 8.280 - 0.175\ T_a$ (slope significantly different from zero, $r^2 = 0.92$, $n = 32$, *P*

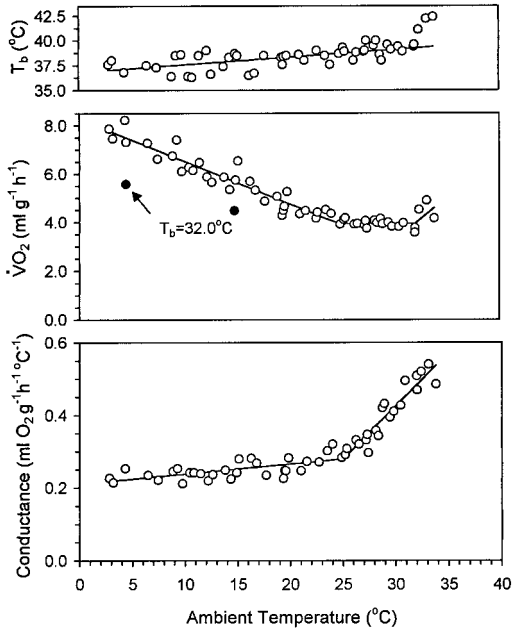

Fig. 1.—Body temperature, rate of metabolism, and whole-body thermal conductance of 6 fasted American shrew-moles, *Neurotrichus gibbsii*, in relation to air temperature. Closed circles denote instances when shrew-moles seemed to enter a state of hypometabolism.

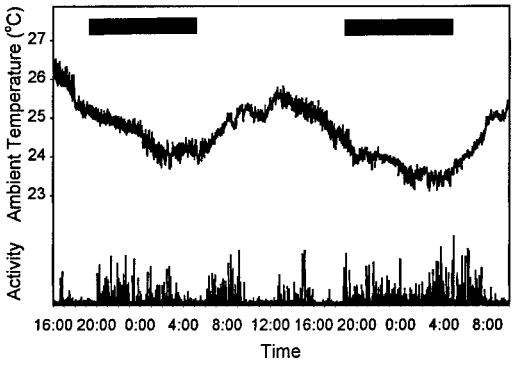

Fig. 2.—Ambient room temperature and corresponding 48-h activity rhythm trace for a single American shrew-mole, August 1998. Activity has no scale; amplitude denotes the relative level of movement detected; solid bars denote hours of darkness.

< 0.0001). On 2 occasions (values not included in regression analysis), shrew-moles seemed to enter a state of hypometabolism (Fig. 1). In these cases, metabolic heat production was 21.2 and 27.8% below that expected from the calculated relationship between T_a and MR below thermoneutrality ($MR = 163.36 - 3.48\ T_a$, slope significantly different from zero, $r^2 = 0.89$, $n = 32$, $P < 0.0001$). An accurate T_b reading was obtained only in one of those metabolic runs ($T_a = 4.4$°C); that animal exhibited a 6.8°C drop in core temperature within 45 min of commencing the trial.

Before metabolic testing, the body temperature of *N. gibbsii* averaged 38.7 ± 0.1°C ($n = 43$). After trials, mean body temperature (38.4 ± 0.2°C, $n = 50$) was found to be moderately labile and dependent on T_a (Fig. 1). After omitting values of T_b for T_as above 32°C and the aberrant value obtained at 4.4°C, T_b varied in linear fashion with ambient temperature according to the regression: $T_b = 36.80 + 0.076T_a$ (slope significantly different from zero, $r^2 = 0.43$, $n = 46$, $P < 0.0001$). Similarly, a significant relationship was found between minimal C and T_a below thermoneutrality: $C = 0.210 + 0.0028T_a$ ($r^2 = 0.57$, $n = 30$, $P < 0.0001$; Fig. 1). Consequently, whole-body thermal conductance estimated at the lower critical temperature (0.280 ml O_2 g^{-1} h^{-1} °C^{-1}) was 28.5% higher than that calculated at the lowest test temperature of 2.8°C (0.218 ml O_2 g^{-1} h^{-1} °C^{-1}). Those values of minimal thermal conductance were 96% and 75%, respectively, of those predicted for placental mammals of comparable mass ($C = 1.0M^{-0.50}$; McNab and Morrison 1963).

Similar to the observations of Dalquest and Orcutt (1942), our animals did not exhibit cyclic patterns of activity. Rather, intermittent intervals of activity followed by rest periods of irregular duration often were apparent (Fig. 2). The single 48-h activity trace obtained in October revealed little dichotomy in nocturnal–diurnal activity of *N. gibbsii*. However, activity patterns obtained from 2 captive specimens in late August suggested that, at least during that time of year, shrew-moles may exhibit more intense

activity throughout the night than during daylight (Fig. 2). That finding was in accordance with our live-trapping data (all 9 specimens were caught between 2300 and 0700 h), which suggested surface activity of this species to be primarily nocturnal.

Discussion

Perhaps because of the difficulty involved in obtaining and maintaining live shrew-moles (Dalquest and Orcutt 1942; Racey 1929), information pertaining to the energy requirements of these elusive mammals is negligible, and limited primarily to anecdotal observations from only a few live specimens (Reed 1944; Terry 1978). The enormous appetite of captive shrew-moles (a 10-g individual was observed to consume 1.4 times its body mass in 12 h; Dalquest and Orcutt 1942) suggested that that members of this species may exhibit a high metabolic intensity. Our results support this notion, because the basal $\dot{V}O_2$ of *N. gibbsii* (3.94 ml O_2 g^{-1} h^{-1}) was found to be 2.32 times that predicted for similar-sized eutherian mammals based on McNab's (1988) all-mammal allometric equation ($\dot{V}O_2 = 3.45M^{-0.287}$).

Associated with a limited insulative capacity and a large gradient for heat loss, red-toothed shrews typically exhibit an impressive thermogenic capacity (McNab 1991; Merritt 1995; Vogel 1980). These diminutive endotherms are thought to have acquired this trait through selection pressures favoring the expression of a high, precisely regulated T_b, an elevated basal rate of metabolism, and a standard to low thermal conductance in response to seasonally cool environments (McNab 1991; Merritt 1995). The paleotropically derived white-toothed shrews, including those inhabiting temperate regions of Europe and Asia, exhibit a different suite of thermal-metabolic adaptations. These include a slightly elevated minimal thermal conductance, a depressed, labile T_b, and a relatively low thermogenic capacity (Sparti 1990; Vogel 1980). Members of this group also exhibit standard rates of metabolism and a penchant to enter spontaneous torpor (McNab 1991). Similar to the warm, reasonably uniform thermal environments regularly encountered by many crocidurines (Sparti 1990), microclimates commonly inhabited by fossorial mammals are relatively stable and buffered against temperature extremes (McNab 1966, 1979). Although metabolic depression is not known to occur in any fossorial North American mole, these animals typically exhibit T_bs that are moderately depressed and rates of metabolism close to or slightly higher than those expected for terrestrial forms based on mass-specific estimates (Contreras and McNab 1990; Kenagy and Vleck 1982; McNab 1979).

Our results clearly indicate that American shrew-moles embody a metabolic intensity substantially above that found in both fully fossorial talpids and crocidurine shrews but comparable to that of north-temperate soricine shrews (Fig. 3). Mean rectal temperatures of *N. gibbsii* (38.4 ± 0.2°C) also are moderately above those recorded for fossorial moles (36.0–37.1°C; K. L. Campbell, in litt.; Contreras and McNab 1990; McNab 1979) and white-toothed shrews (34.5–35.7°C; Sparti 1990), but are similar (although considerably more labile) than those maintained by red-toothed shrews (38.0–38.7°C; Deavers and Hudson 1981; Merritt 1995; Vogel 1980).

Examinations on the allometry of metabolism to body mass have demonstrated that several groups of small mammals exhibit basal rates of metabolism that scale with a different exponent than the Kleiber relationship for eutherian mammals (McNab 1983, 1988). This scaling pattern has been proposed to be related to the ability of these small animals to regulate T_b and maintain homeothermy at subthermoneutral temperatures. Species with basal rates of metabolism above the theoretical boundary curve for endothermy, such as most soricine shrews, are able to maintain a high relatively constant T_b (McNab 1983). However,

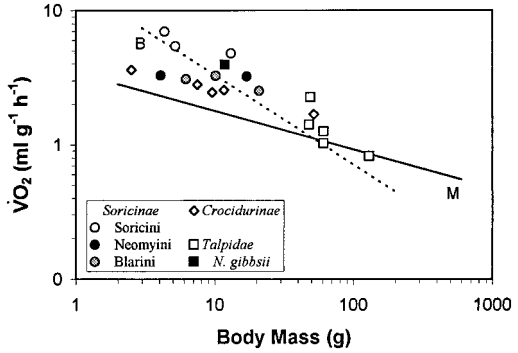

Fig. 3.—Relationship between basal rate of metabolism and body mass in soricid shrews and talpid moles. M and B denote the all-mammal scaling relation of McNab (1988) and the boundary curve for continuous endothermy (McNab 1983), respectively. Note that in relation to the all-mammal curve, *Neurotrichus gibbsii* exhibits a basal $\dot{V}O_2$ substantially above that generally found for talpids and crocidurines but similar to that of soricines. Data are from Campbell et al. (1999), Contreras and McNab (1990), Deavers and Hudson (1981), Kenagy and Vleck (1982), McNab (1991), Merritt (1995), Platt (1974), and Sparti (1990) except for *N. gibbsii* (this study) and *Sorex palustris* (*n* = 2; I. W. McIntyre et al., in litt.).

small-bodied mammals exhibiting basal rates of metabolism below this curve, as is found in many crocidurine shrews, are unable to maintain a large temperature differential with the environment for extended periods (McNab 1983).

Thermoregulatory heat production of shrew-moles at 2.8°C was slightly less than twice that observed at thermoneutrality (Fig. 1), suggesting that *Neurotrichus* may possess a relatively low thermogenic capacity in relation to soricines (Merritt 1995). Therefore, despite the finding that *N. gibbsii* lies above the minimal boundary curve for endothermy (Fig. 3), it is not surprising that fasted shrew-moles exhibited progressive reductions in T_b at all subthermoneutral temperatures (Fig. 1). Endotherms that experience discernible reductions in T_b in response to cold stress commonly exhibit an appreciable diminution in metabolic rate and minimal thermal conductance (McNab 1980). Although virtually nothing is known of the foraging habits and microclimate of shrew-moles in nature, analysis of our live-trapping data suggests that surface activity by *N. gibbsii* is restricted primarily to periods after nightfall when ambient temperatures are at their lowest. Shrew-moles conceivably tolerate modest reductions in T_b while foraging in cool thermal conditions, thus deferring much of the thermogenic response until after returning to their nesting chambers.

Although little is known of the conspecific social organization of shrew-moles, individuals are routinely trapped in the same runways (Dalquest and Orcutt 1942; this study), prompting speculation that members of this species may be gregarious. Fully fossorial moles and soricine shrews inhabiting north-temperate regions are highly territorial in nature, but crocidurines are not (Vogel 1980). In fact, many white-toothed shrews are thought to conserve energy in winter through huddling and communal nesting (McNab 1991). The possibility that *Neurotrichus* actively rewarm or conserve energy by huddling cannot be overlooked and is in need of study.

Most species of crocidurine shrews are known to exhibit spontaneous torpor (McNab 1991; Sparti 1990). This trait may be associated with the relatively low thermogenic capacity and labile T_b inherent to members of this group (Vogel 1980). These physiological traits seem to be shared by *N. gibbsii*, and in fact 2 shrew-moles seemed to enter a state of hypometabolism (Fig. 1). Within 45 min of initiating metabolic testing, the MR of 1 individual held at a T_a of 4.4°C declined to 72.2% of the value predicted for this test temperature, whereas T_b immediately after metabolic testing was only 32.0°C. However, because both metabolic trials were terminated soon after the onset of the hypometabolic state because of animal-welfare considerations, it is plausible that both T_b and MR may have declined further with continued exposure to these conditions.

Although food was removed 1 h before testing, the time of last feeding before the initiation of metabolic trials was unknown. Hence, the depressed metabolism observed in the 2 aforementioned shrew-moles possibly simply reflected an inability to proficiently thermoregulate after an extended fast, rather than the onset of facultative torpor. Conversely, because all study animals were collected in early autumn, it is conceivable that when confronted with short-term food shortages and thermally inclement surroundings, *Neurotrichus* may be predisposed to enter a state of reversible torpor. It is noteworthy that both shrew-moles that entered the hypometabolic state were active and appeared healthy within several minutes of concluding metabolic measurements, suggesting that the hypothermic–hypometabolic condition had little adverse long-term effects on these individuals. Thus, the possibility that shrew-moles occasionally use torpor as an energy conservation tactic during winter in northwestern coastal regions, when periods of cool wet weather may limit available food supplies and aboveground foraging opportunities, cannot readily be discounted and requires further investigation.

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