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Body oxygen stores, aerobic dive limits and diving behaviour of the star-nosed mole (*Condylura cristata*) and comparisons with non-aquatic talpids

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Summary

The dive performance, oxygen storage capacity and partitioning of body oxygen reserves of one of the world's smallest mammalian divers, the star-nosed mole *Condylura cristata*, were investigated. On the basis of 722 voluntary dives recorded from 18 captive star-nosed moles, the mean dive duration (9.2±0.2 s; mean ± S.E.M.) and maximum recorded dive time (47 s) of this insectivore were comparable with those of several substantially larger semi-aquatic endotherms. Total body O_2 stores of adult star-nosed moles (34.0 ml kg^{-1}) were 16.4 % higher than for similarly sized, strictly fossorial coast moles *Scapanus orarius* (29.2 ml kg^{-1}), with the greatest differences observed in lung and muscle O_2 storage capacity. The mean lung volume of *C. cristata* (8.09 ml 100 g^{-1}) was 1.81 times the predicted allometric value and exceeded that of coast moles by 65.4 % (P=0.0001). The overall mean myoglobin (Mb) concentration of skeletal muscles of adult star-nosed moles (13.57±0.40 mg g^{-1} wet tissue, N=7) was 19.5 % higher than for coast moles (11.36±0.34 mg g^{-1} wet tissue, N=10; P=0.0008) and 54.2 % higher than for American shrew-moles *Neurotrichus gibbsii* (8.8 mg g^{-1} wet tissue; N=2). The mean skeletal muscle Mb content of adult star-nosed moles was 91.1 % higher than for juveniles of this species (P<0.0001). On the basis of an average diving metabolic rate of 5.38±0.35 ml O_2 g^{-1} h^{-1} (N=11), the calculated aerobic dive limit (ADL) of star-nosed moles was 22.8 s for adults and 20.7 s for juveniles. Only 2.9 % of voluntary dives by adult and juvenile star-nosed moles exceeded their respective calculated ADLs, suggesting that star-nosed moles rarely exploit anaerobic metabolism while diving, a conclusion supported by the low buffering capacity of their skeletal muscles. We suggest that a high mass-specific O_2 storage capacity and relatively low metabolic cost of submergence are key contributors to the impressive dive performance of these diminutive insectivores.

Key words: aerobic dive limit, body oxygen store, diving behaviour, energetics, myoglobin, insectivore, star-nosed mole, *Condylura cristata*, coast mole, *Scapanus orarius*, lung volume.

Introduction

There is now a considerable body of literature supporting the conclusion that most endothermic divers sustain an oxygen-based metabolism under water (see Kooyman, 1989; Butler and Jones, 1997). In theory, aerobic diving results in enhanced foraging efficiency since disturbances in blood chemistry and obligate recovery times at the surface are minimized. However, most of the existing literature is based on studies of pinnipeds, seabirds and diving ducks. Relatively few studies have been conducted on small-bodied mammalian divers, including muskrat *Ondatra zibethicus* (MacArthur, 1990; MacArthur et al., 2001), platypus *Ornithorynchus anatinus* (Grant, 1984; Evans et al., 1994) and mink *Mustela vison* (Dunstone and O'Connor, 1979). With the exception of the European water shrew *Neomys fodiens* (Churchfield, 1985; Kohler, 1991), no published data exist on the voluntary dive performance of mammalian divers with adult body masses below 500 g. Virtually nothing is known of the oxygen storage capacity of these diminutive divers, nor of the relationship between their oxygen stores and their diving behaviour. Such studies are critical to confirm whether existing allometric models of vertebrate diving endurance (Boyd and Croxall, 1996; Schreer and Kovacs, 1997) can be extended to include the smallest endothermic divers.

One such animal is the star-nosed mole *Condylura cristata*. Of the seven species of North-American moles (Family Talpidae), only the star-nosed mole is semi-aquatic. This accomplished diver frequents tunnel systems excavated along the edges of streambeds and lakes and relies on aquatic insects and annelids for a substantial proportion of its diet (Hamilton, 1931; Rust, 1966). Despite its small size and presumed susceptibility to immersion hypothermia (MacArthur, 1989), this insectivore is reported to forage actively in near-freezing water during the frigid winter months (Merriam, 1884; Hamilton, 1931). In a preliminary study of the diving behaviour of six star-nosed moles, we observed dive durations that greatly exceeded predictions based on allometric theory (Schreer and Kovacs, 1997). The average dive times of these moles rivalled those of the mink (Dunstone and O'Connor,

1979), a semi-aquatic mustelid that is approximately 20 times larger than *Condylura cristata*. Given its small mass and inherently high basal metabolic rate, BMR (twice the mass-predicted value) (Campbell et al., 1999), and hence potentially high rate of O_2 utilization under water, the star-nosed mole presents an intriguing model for investigating mammalian dive endurance.

The purpose of this study was threefold. First, we wished to determine the extent of total body O_2 stores and estimate the diving metabolic rate (DMR) of star-nosed moles in order to derive the 'theoretical' aerobic dive limit (ADL) of this species. A second goal was to assess the correspondence, if any, between the calculated ADL and behavioural indices of the dive performance of star-nosed moles. Our final objective was to compare the oxygen storage capacity and potential for anaerobic metabolism in two talpids of similar mass and phylogenetic history: the semi-aquatic star-nosed mole and the strictly fossorial coast mole *Scapanus orarius*.

This comparison is relevant because both species are specialized for burrowing, and it is useful to know the extent to which diving has modified respiratory functions in the star-nosed mole. Since respiratory specializations for diving are potentially convergent with patterns seen in fossorial species, we hope that this study will shed light on the general mechanisms underlying hypoxia-tolerance in talpids. For example, previous studies have consistently demonstrated high muscle myoglobin (Mb) concentrations in divers (see Kooyman and Ponganis, 1998) and in non-diving, burrowing mammals such as the echidna *Tachyglossus aculeatus* (Hochachka et al., 1984) and the mole rat *Spalax ehrenbergi* (Widmer et al., 1997). It is conceivable that fossorial moles also exhibit enhanced oxygen stores, possibly to compensate for the low ambient O_2 tensions prevalent in closed-burrow systems (Schaefer and Sadleir, 1979). Are the tissue oxygen stores of star-nosed moles further enhanced by a dependence on diving? In addition to comparing the partitioning of body oxygen reserves, we assessed the potential for anaerobic metabolism from measurements of buffering capacity in the fore- and hindlimb muscles of the two mole species.

Materials and methods

Animals

Thirty-one star-nosed moles (*Condylura cristata* Illiger) were live-trapped near Piney, Moose River, Rennie and Caddy Lake, Manitoba, Canada, between June 1997 and September 1999. Within 24 h of capture, moles were transported to the University of Manitoba Animal Holding Facility and held individually in a controlled-environment chamber maintained at 20±1 °C with a 12 h:12 h L:D photoperiod. Animal care procedures are described in detail by Campbell et al. (1999). Briefly, star-nosed moles were housed individually in large glass aquaria (88 cm×50 cm×60 cm) fitted with vertical Plexiglas partitions that divided each tank into aquatic and terrestrial compartments. The terrestrial section made up approximately three-quarters of the tank and was filled to a depth of 45 cm with sterilized soil in which the moles constructed extensive tunnel systems. On the aquatic side, a 24 cm deep pool of standing water was provided for the moles to swim and dive. Animals were maintained on a diet of earthworms *Lumbricus* spp., leeches *Nephelopsis obscura*, mealworms *Tenebrio molitor*, and a meat ration containing vitamins and a calcium supplement (Campbell et al., 1999). Of the 11 star-nosed moles from which morphometric and body O_2 stores data were collected, four were identified as juveniles on the basis of total body length (Simpson, 1923; Hamilton, 1931) and tooth wear characteristics (Hartman, 1995).

In May 1999, 11 adult coast moles (*Scapanus orarius* True) were live-trapped near Abbottsford, British Columbia, Canada, and immediately transported to the Department of Zoology, University of British Columbia. Holding conditions were identical to those adopted for the star-nosed mole, with the exception that coast moles were housed in large soil-filled plastic containers (46 cm×33 cm×38 cm) with no provision for swimming. The frozen carcasses of 11 additional coast moles were provided by a local mole trapper for muscle mass determinations. Muscle samples from two American shrew moles *Neurotrichus gibbsii* Baird, obtained as part of another, unrelated study (K. L. Campbell, unpublished data), were also analyzed for Mb content (see below). This study complied with University of Manitoba and University of British Columbia regulations governing animal research and at all times animals were cared for in strict accordance with Canadian Council on Animal Care guidelines.

Diving behaviour

Following 3 weeks acclimation to the animal holding facilities, 18 star-nosed moles were used in a study of voluntary diving behaviour. Dive trials were performed in a large fibreglass-lined plywood tank fitted with removable wooden and Plexiglas panels. The tank was provided with a dry resting platform (17.5 cm×68 cm), and the swimming/diving section (180 cm×68 cm×72 cm) was covered by a Plexiglas sheet except for an open swimming area immediately adjacent to the platform. The tank was filled to a depth of 61 cm with water at 3, 10, 20 or 30 °C. Of the 18 moles tested, only seven were exposed to all four water temperatures. For these individuals, trials were conducted in random order and on separate days. At the start of each 20 min trial, the mole was released onto the dry resting platform and allowed to move freely throughout the tank. The durations and frequencies of all diving, swimming, resting and grooming episodes were recorded on audiotape for subsequent analyses.

Diving respirometry

To estimate the metabolic cost of diving, a series of diving trials was conducted in a covered fibreglass tank (208 cm×55 cm×52 cm) filled to a depth of 44 cm with water. The animal was prevented from surfacing anywhere in the tank except in a 2.6 l Plexiglas metabolic chamber mounted on the Plexiglas tank cover. The chamber was similar in design to a larger version constructed for muskrats (MacArthur and

Krause, 1989). Air entered the chamber *via* a series of small holes bored in one of the walls near water level and was drawn by vacuum through the chamber *via* a ceiling exhaust port located at the opposite side of the structure. Gas mixing was facilitated by an electric fan installed in the chamber ceiling (MacArthur and Krause, 1989). The flow rate was maintained at 940 ml min^{-1} using a combination pump/mass flow meter (TR-SS1 gas analysis subsampler; Sable Systems Inc., Henderson, NV, USA). Excurrent air was drawn sequentially through a column of soda lime and a column of Drierite to eliminate CO_2 and H_2O vapour, respectively. A 250 ml subsample of dry, CO_2-free exhaust gas was drawn through the M-22 sensor of an Applied Electrochemistry S3-A oxygen analyser for determination of the fractional oxygen content of expired gas, F_{EO_2} (resolution 0.01 %). Air flow rate through the metabolic chamber (ml min^{-1}), F_{EO_2} and water temperature (°C) were recorded every 5 s using a Sable Systems Universal Interface and Datacan V data-acquisition software (Sable Systems Inc.).

Pretrial training sessions were conducted to familiarize animals with the diving tank and metabolic chamber. During training, the length of the tank available for diving was varied using removable Plexiglas partitions. Training runs were performed at an initial tank length of 90 cm, which was subsequently extended to 144 cm and, finally, to 191 cm. Prior to each trial, the water level was adjusted to the prescribed depth to ensure a constant gas volume in the metabolic chamber; water temperature was maintained at 30±0.5 °C. At this temperature, star-nosed moles exhibited maximal diving activity in the 20 min behavioural trials described above and were presumably under minimal thermal stress. Moles were weighed to the nearest 0.01 g approximately 10 min before the start of each trial.

In 1997, the duration of metabolic trials in water was limited to 8 min. However, as our preliminary findings indicated that the proportion of time spent diving increased with trial duration, aquatic trials were extended to 10 min in 1999. Animals gained access to the tank and metabolic chamber *via* a hinged door mounted on the tank cover. Both diving behaviour and activity in the metabolic chamber were closely monitored and recorded on a Sony tape recorder. Upon completion of the trial, a plunger mounted in the ceiling of the metabolic chamber was gently depressed, prompting eviction of the animal without interrupting gas analysis. This step facilitated measurement of the total oxygen consumed over a constant period of immersion (MacArthur and Krause, 1989). The animal was then permitted to leave the water and enter a dry nest box, at which point it was transferred to a large container of soil. All animals were fed immediately prior to metabolic testing. The mean rate of oxygen consumption ($\dot{V}_{O_2}$) was calculated for the entire run following equation 4a in Withers (1977). This value represents the combined costs of diving and surface swimming by the mole during the 8- or 10-min test period in water. For the purpose of calculating the ADL (see below), this mean $\dot{V}_{O_2}$ was assumed to approximate DMR. In most cases, moles swam continuously during each trial, alternating between diving and swimming at the surface. Unfortunately, given the short run time, we could not separate the costs of diving from those of surface swimming in these animals.

To obtain baseline metabolic measurements for intra- and interspecific comparisons, we measured the resting metabolic rate (RMR) of star-nosed moles at thermoneutrality in air. In this case, the metabolic chamber consisted of a modified 0.95 l paint can with a flat black interior that was fitted with inlet and outlet air ports and furnished with 3–4 mm of dry, sterilized soil. During each 1 h trial, the chamber was housed in a controlled-environment cabinet set at 30±0.5 °C. The lowest $\dot{V}_{O_2}$ maintained over at least a 3 min period of inactivity was taken as the RMR. The absence of motor activity was verified independently using a motion activity detector (MAD-1; Sable Systems Inc.) mounted directly beneath the metabolic chamber. Otherwise, the procedure for determining the $\dot{V}_{O_2}$ of resting animals in air was identical to that described for diving/swimming star-nosed moles.

Body oxygen stores

After completion of aquatic trials, 11 star-nosed moles were killed with an overdose of inhalant anaesthetic (Halothane; MTC Pharmaceuticals, Cambridge, Ontario, Canada) to assess the O_2 storage capacities of the blood, lungs and skeletal muscles. While moles were deeply anaesthetized, a blood sample was drawn by cardiac puncture for haemoglobin (Hb) and haematocrit (Hct) determinations (MacArthur, 1984b).

To obtain sufficient tissue for analyses, the entire heart and as much forelimb and hindlimb muscle as possible were harvested from freshly killed animals and immediately frozen at –70 °C. For all comparisons, care was taken to sample identical fore- and hindlimb muscles. Sub-samples (0.5 g) of pooled fore- or hindlimb muscles collected from each animal were subsequently analysed for Mb concentration following the procedure of Reynafarje (1963). Samples of skeletal muscle from coast moles and shrew moles were treated in an identical manner, with the exception that muscle from these species was freeze-clamped in liquid N_2 prior to freezing at –70 °C.

The lungs of star-nosed and coast moles were excised, and lung volume was determined gravimetrically (Weibel, 1970/71; MacArthur, 1990). For this purpose, the lungs were immersed in saline (0.9 mol l^{-1} NaCl) and inflated with humidified air at a constant pressure of 2.7 kPa. Final lung volume was corrected to standard temperature and pressure. Following removal of the internal organs, skin, eyes and brain, the eviscerated carcass was weighed, immersed in a detergent solution, and boiled for approximately 48 h to remove the remaining skeletal muscle. The mass of the dry skeleton was subsequently determined and subtracted from eviscerated carcass wet mass to derive total skeletal muscle mass.

The blood volumes (V_b; ml) of star-nosed and coast moles were estimated from the allometric equation:

$$V_b = 76M^{1.0},$$

where M is body mass (kg) (Prothero, 1980). Otherwise, the calculation of lung, blood and muscle O_2 stores followed

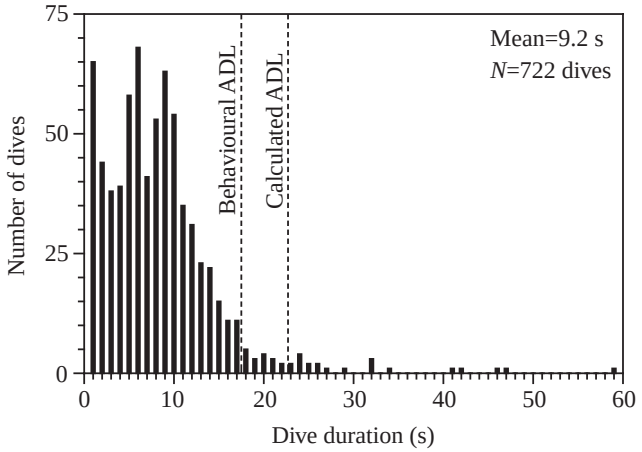

Fig. 1. Frequency distribution of all voluntary dive times recorded for 18 star-nosed moles tested in water at 3–30 °C. Vertical dashed lines denote behavioural and calculated aerobic dive limits (ADL; see Materials and methods for details).

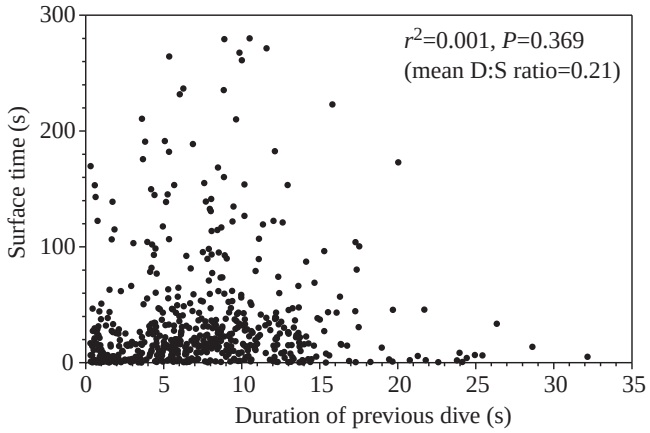

Fig. 2. The relationship between inter-dive surface period and the length of the preceding dive in 15 freely diving star-nosed moles tested in water at 3–30 °C. D:S ratio, dive:surface ratio.

conventional protocols (Lenfant et al., 1970; Kooyman, 1989; MacArthur et al., 2001). For star-nosed moles, the theoretical or 'calculated' ADL (s) was determined by dividing the total body oxygen stores (ml O_2, STPD) by the mean swimming/diving $\dot{V}_{O_2}$ (ml O_2 s^{-1}) obtained for each animal. Implicit in these calculations is the assumption that all oxygen reserves are fully exploited under water (Kooyman, 1989). We also determined the behavioural ADL, previously defined by Kooyman et al. (1983) and Burns and Castellini (1996) as the dive time exceeded by only 5 % of all voluntary dives.

Muscle buffering capacity

The buffering capacities of forelimb and hindlimb muscles were determined following the procedure of Castellini and Somero (1981). Briefly, a muscle sample (0.5 g) was homogenized in 0.9 mol l^{-1} NaCl and then titrated at 37 °C with 0.2 mol l^{-1} NaOH. The pH of the homogenate was determined using a Corning model 360 pH meter equipped with an ISFET electrode. Buffering capacity, measured in slykes, is defined as the amount of base required to raise the pH of 1 g of wet muscle from 6 to 7 (Van Slyke, 1922).

Statistical treatment of data

Two-sample comparisons of mean values were made using Student's or Welch's *t*-test or one-way analysis of variance (ANOVA) where appropriate. For interspecific comparisons of muscle variables, a split-plot design was employed (Steel, 1980). Regression lines were fitted by the method of least squares. Significance was set at the 5 % level and means are presented as ±1 S.E.M.

Results

Diving behaviour of star-nosed moles

There was no statistical difference between the dive times of juvenile and adult star-nosed moles (t=1.04, d.f.=720, P=0.30), so data for these cohorts were pooled. Exploratory dives tended to fall into one of two groups: those that were limited to depths less than 10 cm ('shallow dives') and those that involved exploration of the bottom of the tank at swimming depths of 50–60 cm ('deep dives'). Deep dives accounted for 11.5 % of all voluntary dives and averaged 11.6±0.6 s in duration. On the basis of a total of 722 voluntary dives in water at 3–30 °C (N=18 animals; n=65 trials), the overall mean dive time was 9.2±0.2 s (Fig. 1). The mean duration of the five longest exploratory dives was 13.2±0.8 s and the mean maximum dive time per trial was 17.7±1.4 s. The longest recorded exploratory dive by a freely diving star-nosed mole in this study was 47.0 s. However, one exceptional individual that briefly became disoriented in the tank dived for 58.8 s. For all animals combined, the mean diving frequency was 0.46±0.14 dives min^{-1} (range 0–0.95 dives min^{-1}).

The inter-dive surface interval of star-nosed moles averaged 34.0 s and the mean dive:surface ratio was 0.21±0.10. No relationship was observed between the inter-dive surface interval and the duration of the preceding dive (Fig. 2), suggesting that, in general, longer dives did not require extended periods of recovery at the surface. The dive:surface ratios of six individuals for which body O_2 stores data were also available ranged from 0.09 to 0.25 (Table 1).

Thermal influences on diving behaviour

Water temperature influenced both the duration ($F_{3,328}$=5.21, P=0.0016) and the frequency ($F_{3,24}$=3.82, P=0.02) of voluntary dives by star-nosed moles (Table 2). In fact, the mean dive duration of moles swimming in water at 30 °C exceeded that of the same individuals diving in water at 3 °C by 3.6 s, or 54.5 %. Least-squares regression analysis revealed a significant, albeit modest, positive correlation between water temperature and dive frequency (r^2=0.28, P=0.004). However, mean dive frequency only differed between trials conducted in water at 3 and 30 °C (P=0.006) (Table 2). Water temperature affected the dive:surface ratio

Table 1. *Intraspecific variability in voluntary dive times and calculated aerobic dive limits of eight captive star-nosed moles tested in water at 3-30 °C*

Animal	Cohort	Mass (g)	Duration of longest dive (s)[a]	Mean duration of five longest dives (s)[a]	Dive frequency (dives min^{-1})[a]	Dive:surface ratio[b]	Calculated ADL[c] (s)
M1/97	Adult	57.3	24.4	22.2	0.95	0.22	24.6
M3/97	Adult	52.2	16.9	14.4	0.42	0.18	25.8
M7/97	Adult	43.3	21.6	13.2	0.15	0.18	26.0
M2/98	Juvenile	53.1	17.5	13.3	0.20	0.16	21.0
M3/98	Juvenile	54.6	–	–	–	–	20.3
M5/99	Adult	53.4	3.1	–	0.15	–	19.4
M7/99	Adult	47.8	17.5	16.7	0.95	0.25	19.0
M8/99	Adult	50.2	15.6	11.9	0.85	0.09	21.7

[a]For each animal, values are means of trials in water at 3, 10, 20 and 30 °C (N=4 in all cases).
[b]Dive:surface ratio is the mean ratio of dive duration to the length of the subsequent recovery time at the surface.
[c]ADL, aerobic dive limit, total body O_2 stores (ml, STPD)/mean metabolic rate in water (ml O_2 g^{-1} h^{-1}); see text for details.

Table 2. *Influence of water temperature on voluntary diving behaviour of seven captive adult star-nosed moles*

	Water temperature (°C)			
	3	10	20	30
Total number of dives	44	76	102	107
Dive duration (s)	6.6±0.6[a]	7.2±0.4[a]	8.4±0.4[a]	10.2±0.9[b]
Dive frequency (dives min^{-1})	0.29±0.08[a]	0.57±0.11[a,b]	0.76±0.15[a,b]	0.84±0.14[b]
Dive:surface ratio	2.40±0.42[a,b]	0.61±0.09[a]	1.75±0.38[a,b]	3.45±1.03[b]
Duration of longest dive (s)	8.9±1.8[a]	13.4±2.0[a,b]	14.2±1.8[a,b]	18.0±1.9[b]

Values presented are means ± S.E.M.
Within each row, means sharing the same letter are not statistically different (P>0.05).

($F_{3,24}$=4.12, P=0.02), but mean values were significantly different only for animals tested in water at 10 and 30 °C. Maximum dive duration also appeared to increase with water temperature ($F_{3,24}$=3.79, P=0.02), although only the mean values for water at 3 and 30 °C differed significantly (P<0.05) (Table 2).

Metabolic rates and aerobic dive limits of star-nosed moles

The metabolic costs of surface swimming/diving were obtained for 11 star-nosed moles (two juveniles, nine adults), all of which adapted well to the aquatic respirometry system. Too few data were obtained from juveniles for statistical comparisons with adults, so the metabolic data for both cohorts were pooled. In 22 trials, these moles made a total of 519 dives and spent 0–51 % (mean 20.3±3.8 %) of each 8- or 10-min test session actively diving. We observed no statistical relationship between mean $\dot{V}_{O_2}$ in water and either the percentage of time spent diving (Fig. 3A) or dive frequency (Fig. 3B) in the 11 moles tested. The mean $\dot{V}_{O_2}$ of these moles in water was 5.38±0.35 ml O_2 g^{-1} h^{-1}, which is 2.1 times greater than the mean RMR recorded for the same individuals in air (2.56±0.01 ml O_2 g^{-1} h^{-1}).

Assuming that the total body O_2 stores of star-nosed moles are 34.0 ml O_2 STPD kg^{-1} (Table 3), that all these stores are exploited under water and that their diving metabolic rate is 5.38 ml O_2 g^{-1} h^{-1}, then the calculated ADL of adult moles is 22.8 s. This value exceeds that derived for juvenile star-nosed moles by only 2.1 s, or 10.2 % (P=0.178) (Table 3). For all animals combined, the proportion of voluntary dives exceeding the calculated ADL was only 2.9 % (Fig. 1). In adults, 2.8 % of all voluntary dives exceeded the calculated ADL; for juveniles, the corresponding figure was 3.6 %. The mean behavioural ADL determined for adults and juveniles combined was 17.5 s (N=18 moles).

Partitioning of body O_2 stores in star-nosed moles and coast moles

Hct, blood Hb content and blood O_2 capacity were not statistically different in the three groups tested (P>0.05) (Table 4). However, significant intra- and interspecific differences were observed in lung and muscle O_2 stores. The mass-specific lung capacity of adult star-nosed moles was 16.3 % less than in juveniles of this species (P=0.015), but was 65.4 % greater than for adult coast moles (P=0.0001) (Table 3). The lungs accounted for 45.6 and 35.9 % of the total body O_2 stores of adult and juvenile star-nosed moles, respectively, compared with only 24.5 % for adult coast moles (Table 3). While total

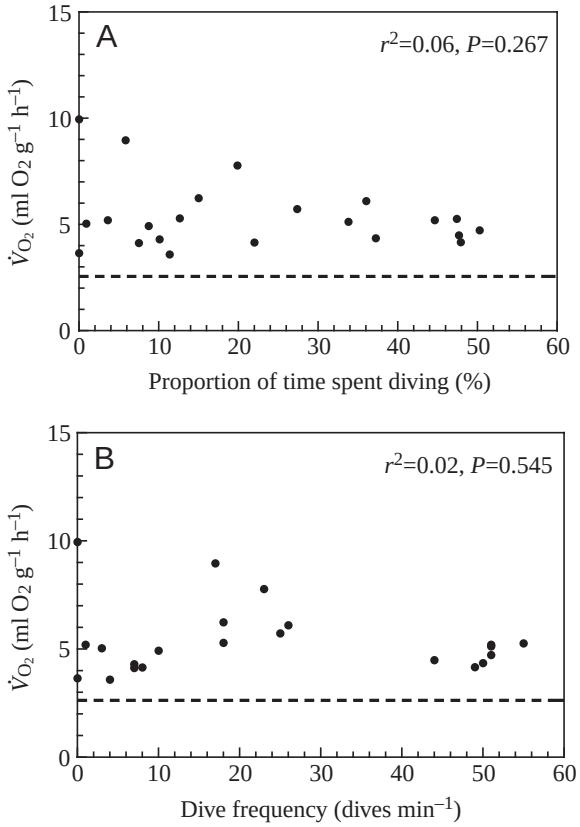

Fig. 3. Relationship between the mean $\dot{V}_{O_2}$ of star-nosed moles in water (N=11 animals) and (A) the percentage of time spent diving and (B) the dive frequency during 8- and 10-min immersion trials in water at 30 °C. Dashed lines denote the mean resting $\dot{V}_{O_2}$ of the same individuals in air (2.56 ml O_2 g^{-1} h^{-1}).

body O_2 stores were statistically similar for all groups (P>0.05), adult star-nosed moles exhibited the highest overall total O_2 storage capacity, with the lung and muscle reserves contributing most to the observed intra- and interspecific differences (Table 3). Differences in mean skeletal muscle Mb concentration between adult (13.57±0.40 mg g^{-1} wet tissue) and juvenile (7.10±0.42 mg g^{-1} wet tissue) star-nosed moles were highly significant (P<0.0001). Mean muscle Mb content also differed between adults of both mole species (P=0.0008) (Table 4). Adult star-nosed moles possessed a slightly lower percentage of skeletal muscle mass (41.75±1.2 % of digesta-free body mass, N=11) than coast moles (43.45±1.4 %, N=11), but a mass-specific muscle O_2 storage capacity that was 19.5 % higher.

In addition, mean skeletal muscle Mb levels of both star-nosed and coast moles were substantially higher than mean values obtained for the semi-fossorial shrew mole *Neurotrichus gibbsii* (8.8 mg g^{-1} wet tissue, N=2). With exception of the shrew mole, the Mb content of the forelimb swimming and digging muscles tended to exceed levels in the hindlimb muscles and ventricles of all moles tested. However, only in adult star-nosed and coast moles were these differences statistically significant (P<0.0001) (Table 5). A split-plot model revealed a significant effect of both age ($F_{1,9}$=109.15, P<0.0001) and muscle site ($F_{1,9}$=19.35, P=0.0017) on Mb concentration, but there was no evidence of interaction effects between these variables in either adult or juvenile star-nosed moles ($F_{1,9}$=0.79, P=0.398). Interspecific comparisons of mean skeletal muscle Mb content yielded statistically significant differences between the forelimb (P=0.0001) and hindlimb (P<0.0001) for adult star-nosed moles and coast moles (Table 5). A split-plot analysis revealed significant differences in mean Mb content between species ($F_{1,14}$=6.76, P=0.021) and limb sites ($F_{1,14}$=15.99, P=0.0013), with no evidence of interaction between these variables ($F_{1,14}$=0.2, P=0.66).

Muscle buffering capacity of star-nosed moles and coast moles

Muscle buffering capacities tended to be highest in adult star-nosed moles, but only the hindlimb value for this species was statistically different from that of adult coast moles (P=0.038) (Table 5).

Discussion

Comparisons of star-nosed moles with other mammalian divers

It is widely acknowledged that the breath-hold endurance of vertebrate divers depends critically on the parsimonious use of

Table 3. *Oxygen storage capacities of the lungs, blood and skeletal muscles of star-nosed moles (*Condylura cristata*) and coast moles (*Scapanus orarius*)*

		Oxygen stores (ml O_2 STPD kg^{-1})					Calculated aerobic dive limit[a]
Species	N	Lungs	Arterial blood	Venous blood	Muscle	Total	(s)
C. cristata							
Juveniles	2	14.1	5.0	7.5	4.3	30.9	20.7
Adults	6	12.2	5.6	8.7	7.5	34.0	22.8
Adult *S. orarius*	7	7.3	5.9	9.3	6.7	29.2	–

[a]Calculated for a 50 g animal assuming a diving metabolic rate of 5.38 ml O_2 g^{-1} h^{-1} (see text for details).

Table 4. *Comparisons of lung, blood and muscle characteristics of star-nosed moles (*Condylura cristata*) and coast moles (*Scapanus orarius*)*

Variable	Star-nosed mole		Coast mole	Difference (adult *C. cristata* – adult *S. orarius*)
	Juvenile	Adult	Adult	
Body mass (g)	48.6±3.3 (4)	50.9±1.7 (7)	64.1±3.1 (11)	–13.2†
Total lung capacity (ml STPD 100 g^{-1})	9.7±0.4 (3)	8.1±0.3 (6)*	4.9±0.4 (7)	+3.2†
Haematocrit (%)	49.9±4.6 (2)	50.5±2.6 (8)	46.8±2.0 (11)	+3.8
Haemoglobin content (g 100 ml^{-1})	15.5±0.4 (2)	17.2±1.3 (7)	17.4±0.8 (11)	–0.25
Blood O_2 capacity (vol %)	20.8±0.5 (2)	23.0±1.7 (7)	23.4±1.1 (11)	–0.34
Skeletal muscle myoglobin content (mg g^{-1} wet tissue)[a]	7.1±0.4 (2)	13.6±0.4 (7)*	11.4±0.3 (11)	+2.2†

[a]Mean for forelimb and hindlimb muscles.
*Adult–juvenile differences are significant (P<0.05).
†Interspecific differences are significant (P<0.05).
Values are means ± S.E.M. (N).

Table 5. *Myoglobin concentrations and buffering capacities of skeletal muscles of star-nosed moles (*Condylura cristata*) and coast moles (*Scapanus orarius*)*

Variable	Tissue	Star-nosed mole		Coast mole	Difference (adult *C. cristata* – adult *S. orarius*)
		Juveniles	Adults	Adults	
Myoglobin content (mg g^{-1} wet tissue)	Heart	7.74±0.46 (4)	8.91±0.38 (6)	9.24±0.28 (7)	–0.3
	Forelimb	8.33±0.83 (4)	14.39±0.52 (7)*	12.10±0.25 (10)	+2.3†
	Hindlimb	5.86±0.16 (4)	12.75±0.43 (7)*	10.61±0.56 (10)	+2.1†
Buffering capacity, β[a] (Slykes)	Forelimb	43.65±2.54 (4)	44.12±2.96 (6)	37.33±2.10 (10)	+6.8
	Hindlimb	43.18±1.25 (4)	48.01±4.26 (6)	38.94±1.77 (10)	+9.1†

[a]1 slyke=μmoles of base required to titrate the pH of 1 g of wet muscle by 1 pH unit.
*Adult – juvenile differences are significant (P<0.05).
†Interspecific differences are significant (P<0.05).
Values are means ± S.E.M. (N).

limited 'on-board' stores of oxygen. Allometry predicts that, while total body oxygen stores scale close to unity, the rate of O_2 consumption scales to approximately the 0.75 power of mass (Schmidt-Nielsen, 1985; Hudson and Jones, 1986; de Leeuw, 1996). Furthermore, in small-bodied endotherms, the cost of diving is exacerbated because drag increases with mass-specific surface area (de Leeuw, 1996), and air trapped in the fur or feathers can generate positive buoyancy. Therefore, relative to their O_2 stores, larger divers should have lower mass-specific metabolic rates than their smaller counterparts. It is not surprising, then, that the diving capacities of endothermic divers tend to increase with body mass (Schreer and Kovacs, 1997).

Despite these theoretical limitations, the maximum dive time recorded for freely diving star-nosed moles (47 s) exceeded the predicted maximum dive duration (32.3 s; $1.62M^{0.37}$) of Schreer and Kovacs (1997) by 45.5 %. In an earlier study of this species, Hickman (1984) reported a maximum dive time of 19 s, but noted that one individual survived 2 min of forced submergence. By comparison, Calder (1969) reported a maximum dive time of only 37.9 s in a single American water shrew (*Sorex palustris*) subjected to a forced dive. The average dive time of star-nosed moles (9.2 s) was comparable with that of the considerably larger mink (9.9 s, mass 850 g) (Dunstone and O'Connor, 1979) but shorter than the mean time recorded for freely diving juvenile muskrats (19 s, mass 254–360 g) (MacArthur et al., 2001). Few other empirical studies of diving behaviour exist for small-bodied, endothermic divers. Mean voluntary dive times are available for adult platypus (28 s, mass 900–1500 g) (Evans et al., 1994), European water shrews (3–6 s, mass 10–20 g) (Ruthardt and Schröpfer, 1985) and one 14 g American water shrew (5.7 s) (McIntyre, 2000). It is noteworthy that the duration and frequency of voluntary dives by star-nosed moles were strongly influenced by water temperatures that are routinely encountered by this species in nature. MacArthur (1984a) reported a similar finding for muskrats, and both studies suggest that thermoregulatory constraints affect dive performance in small-bodied endotherms.

The question remains, then, how does one account for the exceptional dive performance of the star-nosed mole? Potential factors contributing to the enhanced dive endurance of this

species could include a strong dependence on anaerobic pathways during diving, a relatively low rate of oxygen depletion under water or higher-than-expected O_2 reserves.

The absence of correlation between muscle buffering capacity and muscle Mb content suggests that variation in Mb content, and hence muscle aerobic capacity, is not matched by compensatory adjustments in the anaerobic potential of these muscles. Without adequate buffering capacity, even muscles possessing large glycogen deposits cannot function anaerobically for extended periods, because falling pH inhibits enzyme function and impedes further glycolytic activity (Castellini and Somero, 1981). The low buffering capacity of the skeletal muscles of star-nosed moles suggests little dependence on anaerobic metabolism while diving. This conclusion is supported by behavioural observations indicating that only 2.9 % of all voluntary dives exceeded the calculated ADL, a finding that may reflect the adoption of an aerobic diving schedule to maximize underwater search time and, hence, optimize foraging efficiency (Butler and Jones, 1997).

Conventional estimates of DMR are often assumed to be approximately twice the BMR or RMR of the species in question (Burns and Castellini, 1996). Consistent with this assumption, the estimated DMR of star-nosed moles ($5.38\,ml\,O_2\,g^{-1}\,h^{-1}$) was 2.10×RMR (present study) and 2.39×BMR ($2.25\,ml\,O_2\,g^{-1}\,h^{-1}$) (Campbell et al., 1999). However, these ratios are lower than that reported for muskrats (2.73×BMR) (MacArthur and Krause, 1989). Moreover, the mean metabolic cost of surface swimming/diving of star-nosed moles was low compared with the mean value reported for mink ($6.54\,ml\,O_2\,g^{-1}\,h^{-1}$) (Stephenson et al., 1988), suggesting that these insectivores display a relatively low mass-specific cost of submergence. Star-nosed moles, like muskrats, are strongly positively buoyant (mean specific gravity of moles 0.826±0.008, N=8) (McIntyre, 2000), a factor that may contribute to the two- to threefold increase in the estimated cost of diving by these species. Marine birds that are almost neutrally buoyant, such as the Humboldt penguin *Spheniscus humboldti*, exhibit little change in $\dot{V}_{O_2}$ during voluntary diving (Butler and Woakes, 1984).

That body oxygen stores are often elevated in vertebrate divers appears well established (Butler and Jones, 1997; Kooyman and Ponganis, 1998). Consistent with this trend, we found that the mean Hct of adult star-nosed moles (50.5 %) was similar to that of platypus (52 %) (Parer and Metcalfe, 1967), but exceeded mean values reported for muskrat (39.1–46.8 %) (MacArthur et al., 2001) and beaver *Castor canadensis* (42.1 %) (Kitts et al., 1958). Combining lung, blood and muscle estimates, the mass-specific body O_2 stores of adult star-nosed moles ($34.0\,ml\,kg^{-1}$) (Table 3) exceed those estimated for platypus ($25\,ml\,O_2\,kg^{-1}$) (Evans et al., 1994), but fall within the range of values reported by MacArthur et al. (2001) for summer- and winter-acclimatized muskrats (30.2 and $38.8\,ml\,O_2\,kg^{-1}$, respectively). A causal link between oxygen storage capacity and dive endurance is often assumed in interspecific comparisons (Kooyman, 1989; Butler and Jones, 1997), and our findings suggest that the exceptional diving ability of *Condylura cristata* may be attributed, at least in part, to elevated body O_2 stores.

Comparisons of star-nosed moles with other fossorial mammals

A major objective of this study was to compare the O_2 storage capacities of star-nosed moles and coast moles. The rationale for this comparison is the premise that several hypoxia-driven respiratory adaptations are potentially convergent in burrowers and divers, and it is informative to know the extent to which a reliance on diving has modified the O_2 storage capacity of star-nosed moles. In making this comparison, we recognize that the phylogeny and evolutionary history of this family is not fully resolved and remains contentious. For instance, some workers have suggested that moles adopted fossorial habits following a period of aquatic adaptation (Campbell, 1939; Whidden, 1999), while others have rejected this view, concluding instead that semi-fossorial and fossorial forms evolved directly from an ambulatory ancestor, without passing through a semi-aquatic phase (Reed, 1951; Hickman, 1984). However, it is important to stress that both *Condylura cristata* and the more recently derived *Scapanus orarius* passed through a specialized fossorial phase in their evolutionary development (Grand et al., 1998), with the ancestral *Condylura cristata* either reverting towards or subsequently acquiring a semi-aquatic habit.

This controversy notwithstanding, our findings indicate that the mass-specific O_2 stores of the star-nosed mole are 16.4 % greater than those of the coast mole ($29.2\,ml\,kg^{-1}$). Interestingly, this difference is due mainly to interspecific variation in lung and muscle, rather than blood, O_2 reserves (see below). The blood O_2-carrying capacity of star-nosed moles (20.8–23.0 vol %) (Table 4) is relatively high, but comparable with those of other vertebrate divers including muskrat (20.6–24.1 vol %) (MacArthur et al., 2001) and platypus (23.0 vol %) (Grant, 1984). Similarly, the blood O_2-carrying capacity of coast moles (23.4 vol %) (Table 4), Townsend's moles *Scapanus townsendii* (22.7 vol %) (Pedersen, 1963) and the European mole *Talpa europaea* (23.3 vol %) (Quilliam et al., 1971) is, as in other highly fossorial species including mole rats (20.2 vol %) (Ar et al., 1977) and valley pocket gophers *Thomomys bottae* (22.8 vol %) (Lechner, 1976), elevated relative to that of non-burrowing terrestrial mammals. These findings underscore the significance of this O_2 storage compartment in vertebrates that routinely encounter hypoxia associated with diving or burrowing.

The skeletal muscle Mb concentration of the strictly fossorial coast mole ($1.14\,g\,100\,g^{-1}$) was comparable with that of another burrowing mammal, the echidna ($1.26\,g\,100\,g^{-1}$) (Hochachka et al., 1984), but substantially higher than for the semi-fossorial American shrew-mole ($0.88\,g\,100\,g^{-1}$) (present study). This finding supports the argument that elevated muscle Mb concentrations are often associated with mammals highly specialized for a subterranean existence (Widmer et al., 1997). However, muscle Mb concentration has also been shown to be

a strong correlate of dive performance in mammalian divers (Kooyman and Ponganis, 1998; Ponganis et al., 1999). The relatively high Mb levels observed in *Condylura cristata* (1.36 g 100 g^{-1}) (Table 4) are consistent with values recorded for other semi-aquatic mammals, including platypus (1.43 g 100 g^{-1}) (Evans et al., 1994), beaver (1.2 g 100 g^{-1}) (McKean and Carlton, 1977) and seasonally acclimatized muskrats (1.21–1.38 g 100 g^{-1}) (MacArthur et al., 2001). The tendency for the muscle Mb levels of star-nosed moles to exceed those of other subterranean mammals examined to date, including fossorial and semi-fossorial talpids, is noteworthy. It suggests that the adoption of a semi-aquatic lifestyle by this unique mole may have selected for enhanced muscle Mb levels, beyond those dictated by strictly fossorial habits.

Intraspecific variation in muscle myoglobin content

Skeletal muscle Mb concentration varied with age and sampling site in star-nosed moles. Confirming earlier studies, our results suggest that significant ontogenetic changes occur in muscle Mb levels. For instance, Ponganis et al. (1999) reported Mb levels for pre- and post-molt emperor penguin *Aptenodytes forsteri* chicks that were only 24–31 % of adult values, whereas MacArthur et al. (2001) found that the muscle Mb concentrations of juvenile muskrat cohorts varied closely with mass, ranging from 30.2 to 77.8 % of adult values. Noren et al. (2001) recently reported age-dependant differences in muscle Mb concentration for a variety of diving marine endotherms, including the king penguin *Aptenodytes patagonicus*, the bottlenose dolphin *Tursiops truncatus* and the striped dolphin *Stenella coeruleoalba*, in which juvenile Mb values were 25, 57 and 68 % of adult values, respectively. Consistent with these trends, we found that the mean muscle Mb concentration of juvenile star-nosed moles was only 52.3 % of that measured in adults. Not surprisingly, the tendency for forelimb Mb levels to greatly exceed hindlimb values in *Condylura cristata* and *Scapanus orarius* is reversed from the trend generally observed in muskrats (MacArthur, 1990; MacArthur et al., 2001). Whereas the forelimb muscles of moles are the primary locomotor swimming and digging muscles, as reflected by their large relative mass, the hindlimbs of muskrats are the primary propulsive organs under water (Fish, 1982).

Why a large lung volume in the star-nosed mole?

As noted above, differential partitioning of O_2 stores was evident in the two talpid species examined. Of particular interest was our finding that the average lung volume of adult star-nosed moles (4.12 ml or 8.09 ml STPD 100 g^{-1}) was 1.81 times greater than the value predicted from allometry (2.28 ml) (Stahl, 1967). By comparison, the mean lung volume of coast moles (3.14 ml or 4.89 ml STPD 100 g^{-1}) conformed to standard allometric predictions. Lung O_2 provides a large potential reserve in shallow-water divers (Snyder, 1983) and contributed significantly to the total O_2 storage capacity of star-nosed moles (Table 3). That this substantial reserve of O_2 may be effectively exploited under water is supported by the observation that stripped Hbs of star-nosed moles from the same study population demonstrate exceptionally high oxygen-binding affinities (K. L. Campbell and R. E. Weber, unpublished data). The large lung volume of this species may also provide positive buoyancy during surface swimming, thus reducing the trunk surface area exposed to water and potentially minimizing the metabolic cost of aquatic thermoregulation. The sea otter *Enhydra lutris* also exhibits an exceptionally large lung volume that Costa and Kooyman (1984) suggest facilitates floating at sea between periodic thermogenic bouts of activity.

Concluding remarks

The results of this study reveal that, like the coast mole, the star-nosed mole exhibits a large mass-specific blood O_2 reserve. Whether this finding reflects convergence arising from diving- or burrowing-induced hypoxia, or instead is a trait conserved through lineage, is currently unknown. Star-nosed moles, however, possess more substantive lung and muscle Mb reserves, resulting in a greater total oxygen storage capacity, than for coast moles. We suggest that the additional need to attenuate heat loss associated with a semi-aquatic existence, perhaps combined with a need to augment O_2 reserves for diving, may account for the exceptionally large lung volume and elevated Mb concentration observed in star-nosed moles. These traits, coupled with a high blood O_2 storage capacity and a relatively low metabolic cost of underwater swimming, are probably key factors contributing to the impressive dive performance of this peculiar mammal.

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