Balancing the competing requirements of saltatorial and fossorial specialisation: burrowing costs in the spinifex hopping mouse, *Notomys alexis*

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Summary

Semi-fossorial animals (burrowing surface foragers) need to balance the competing morphological requirements of terrestrial and burrowing locomotion. These species rarely show the same degree of claw, forelimb and pectoral girdle structural development that fully fossorial forms (burrowing subterranean foragers) do, but nevertheless invest considerable amounts of energy in burrow systems. The compromise between terrestrial and burrowing locomotion was investigated by measuring net costs of burrowing and pedestrian transport in the spinifex hopping mouse, *Notomys alexis*, a species that forages in open areas in arid environments and is adapted for saltatorial locomotion. The net cost of transport by burrowing of hopping mice was found to be more expensive than for specialised fossorial species, and burrows were estimated to represent an energy investment equivalent to the terrestrial locomotion expected to be incurred in 17–100 days. A phylogenetically independent-contrasts approach revealed that morphological specialisation for burrowing was associated with low maximum running speeds in fossorial mammals and, for non-fossorial rodents and marsupials, maximum running speed was positively correlated with an index of habitat structure that ranged from arboreal to open desert. The high terrestrial speeds attainable by this semi-fossorial species by saltatory locomotion apparently outweigh the energetic savings that would be associated with burrowing specialisation.

Key words: cost of transport, burrowing, saltation, energetics, maximum running speed, hopping mouse, *Notomys alexis*.

Introduction

Burrowing provides animals with access to subterranean food resources and provides protection both from predation and from extremes of temperature and humidity that may be encountered on the surface. However, despite the fact that a substantial proportion of mammals construct burrows and spend at least some time underground, little is known about the energetic cost of obtaining access to this environment. At present, the only published measurements of burrowing costs that are available for mammals (see White, 2001) are for wholly fossorial species (those that live and forage almost entirely beneath the surface and rarely, if ever, leave their burrows). Fossorial animals show a variety of convergent morphological specialisations that are thought to complement one another to optimise burrowing capacities and efficiency (Nevo, 1979). However, many burrowing animals are semi-fossorial (surface foraging burrowers) and most of these do not show such extreme specialisations. The burrow refuges constructed by semi-fossorial species are far less complex and extensive than the large systems constructed by fossorial animals despite a similar cross-sectional area (White, 2005), and are therefore likely to represent a far less substantial energetic investment, because the energetic cost of burrow construction is proportional to burrow length (Vleck, 1979). It might therefore be reasonably hypothesized that selective pressure to reduce burrow construction costs is weaker for semi-fossorial than fossorial species, because the amounts of energy invested in the systems differ.

This study assesses the net costs of transport by burrowing and running in the spinifex hopping mouse, *Notomys alexis*, an Australian murid rodent, the first semi-fossorial (burrowing, but surface-foraging) mammal for which the net cost of transport by burrowing has been measured. We hypothesise that semi-fossorial species are indeed less specialised for burrowing than fossorial ones, and that they will therefore show relatively inefficient and energetically costly burrowing. This hypothesis is tested by comparing burrowing costs between this species, which is adapted to saltation, and fossorial species that are adapted to burrowing.

Materials and methods
Study species

Eleven adult spinifex hopping mice *Notomys alexis* Thomas 1922 (Rodentia: Muridae) (6 male, 5 female, mass 33.0±3.6 g, mean ± s.d.) were obtained from a captive colony maintained by the Department of Anatomical Sciences at the University of Adelaide. Mice were housed either individually or in single sex groups of three in an air-conditioned animal housing facility at the North Terrace campus of the University of Adelaide at a temperature of 22–26°C and maintained on an *ad libitum* diet of mixed grains, supplemented with fresh fruit. Mice were housed with recycled paper cat litter substrate that was disturbed and turned over extensively during the night, and therefore appeared to provide suitable burrowing exercise. Water was available at all times. All animals maintained body mass under these conditions.

Resting oxygen consumption

The rate of oxygen consumption ($\dot{V}_{O_2}$, ml min^{-1}) of resting, postabsorptive (fasted for 6+ h), non-reproductive mice was measured during daylight hours using positive-pressure, open-flow respirometry, according to standard techniques (Withers, 2001). Air drawn from outside was pumped through a pressure regulator and a series of absorbent tubes (Drierite^{TM}, self-indicating soda lime, and Drierite) to provide a dry, CO_2-free air stream. This air stream was then split four ways to provide a single reference stream and three animal streams. Each of the animal streams passed through a 0–1 l min^{-1} mass-flow controller (Sierra Instruments Mass-Trak model# 810C-DR-13, Monterey, CA, USA; calibrated with a Brooks Vol-U-Meter, Hatfield, PA, USA) at a rate of 500–750 ml min^{-1}, 1 m of temperature equilibration tubing, a 765 ml animal chamber and a respirometry multiplexer that sequentially selected each of the four streams for a user-specified period (usually 10 min). A subsample of the multiplexer outflow was passed through a small U-tube containing absorbents (Drierite–Ascarite^{TM}–Drierite or Drierite only, see below) and into an Oxzilla^{TM} dual absolute and differential oxygen analyser (Sable Systems, Las Vegas, NV, USA), calibrated with outside air (0.2095 O_2). The temperature equilibration tubing and respirometry chamber were contained within a constant temperature cabinet stable to ±1°C, the temperature of which was measured with a precision mercury thermometer (ambient temperature, T_a, °C). The voltage output of the oxygen analyser was connected to a PC-compatible computer *via* a Sable Systems Universal Interface analogue/digital converter. Sable Systems DATACAN V5.2 data acquisition software sampled the analyser output at a rate of 3 Hz and averaged three samples to generate each recorded point.

Measurements of resting $\dot{V}_{O_2}$ were obtained at T_a ranging from 5–36°C. Animals were observed in the respirometer and periods of inactivity were noted; data were accepted if $\dot{V}_{O_2}$ remained low and stable for 5 min. The thermoneutral zone was defined as the T_a range over which $\dot{V}_{O_2}$ was independent of T_a, which could easily be discerned on visual inspection (e.g.
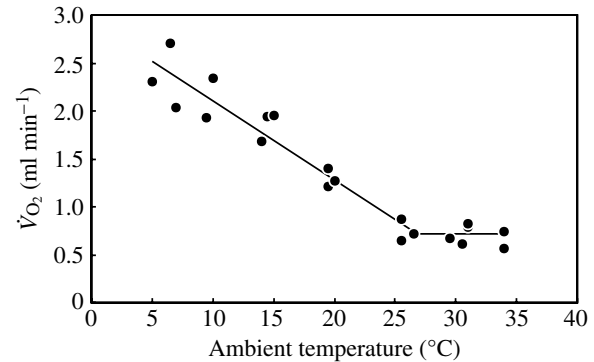

Fig. 1. Effect of ambient temperature on resting rate of oxygen consumption ($\dot{V}_{O_2}$, ml min^{-1}) for a single male hopping mouse, *Notomys alexis* (body mass=28.1 g). N=21. Below 26.8°C, $\dot{V}_{O_2}$=2.93–0.082T_a; above 26.8°C, $\dot{V}_{O_2}$=0.72.

Fig. 1). For each mouse, basal metabolic rate (BMR) was calculated as average $\dot{V}_{O_2}$ within the thermoneutral zone.

Exercise oxygen consumption

A negative pressure respirometry system was used to measure $\dot{V}_{O_2}$ of active animals while running or burrowing. Air was drawn with a Reciprocator piston pump (Selby Scientific, Clayton, Victoria, Australia) through a running chamber or a burrowing tube (see below) and a 0–10 l min^{-1} mass-flow meter (Sierra Instruments Top-Trak model# 822-13-OV1-PV1-V1 calibrated with a Brooks Vol-U-Meter). A subsample of this air was then passed through a small U-tube containing only Drierite (for running and burrowing net cost of transport) or Drierite–Ascarite–Drierite (for maximum exercise metabolic rate $\dot{V}_{O_2max}$) and into a Sable Systems Oxzilla^{TM} dual absolute and differential oxygen analyser, calibrated with outside air (0.2095 O_2) connected to a PC-compatible computer *via* a Sable Systems Universal Interface analogue/digital converter. Sable Systems DATACAN V5.2 data acquisition software sampled the analyser output at a rate of 3 Hz and averaged three samples to generate each recorded point.

To determine the maximum exercise metabolic rate of mice ($\dot{V}_{O_2max}$, ml min^{-1}), air was drawn at a rate of 5–6 l min^{-1} through a 1.8 l running chamber resting on a motorised treadmill at speeds of 5–60 m min^{-1}. Starting at the lower speeds, mice were run until $\dot{V}_{O_2}$ stabilised, at which time treadmill speed was increased in intervals of 10–20 m min^{-1}. Each speed was maintained until $\dot{V}_{O_2}$ was stable, at which time speed was again increased. This was continued until further increases in speed no longer resulted in increased $\dot{V}_{O_2}$ (Fig. 2). This procedure was then repeated on several non-consecutive days to provide data for a wide range of speeds. $\dot{V}_{O_2max}$ was calculated as the average of the stable plateau $\dot{V}_{O_2}$ (Fig. 2). The procedure was again repeated on several non-consecutive days to determine net cost of transport of pedestrian locomotion (NCOT$_p$, J m^{-1}), which was calculated by multiplying the slope of the line relating $\dot{V}_{O_2}$ (ml min^{-1}) and speed (m min^{-1}) by the energy equivalent of 1 ml of O_2 (20.5 J) (Withers, 1992),
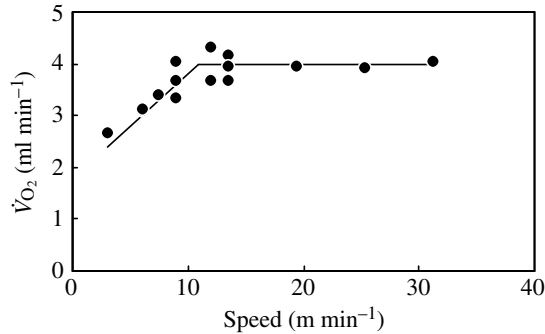
Fig. 2. Relationship between metabolic rate ($\dot{V}_{O_2}$, ml min^{-1}) and speed (m min^{-1}) for a single male hopping mouse (body mass=31.5 g). The break-point of the regression relating $\dot{V}_{O_2}$ and speed is equal to maximum aerobic speed (U_{max}, m min^{-1}). At slower speeds, the slope of the line relating $\dot{V}_{O_2}$ and speed is equal to the net O_2 cost of transport (ml O_2 m^{-1}). Average $\dot{V}_{O_2}$ at speeds greater than U_{max} is equal to maximum metabolic rate ($\dot{V}_{O_2max}$, ml min^{-1}). N=12. Below 21.8 m min^{-1}, $\dot{V}_{O_2}$=1.80+0.100U, where U is speed; above 21.8 m min^{-1}, $\dot{V}_{O_2}$=3.98.

Fig. 4. Example trace of a typical burrowing trial (female mouse, 36.1 g, excurrent airflow rate=1.6 l min^{-1}). The mouse was placed in the chamber at the point indicated on the graph. It then explored the chamber and scratched at the soil for ~3 min, rested for ~1 min and burrowed for ~35 min. The washout after the mouse was placed in the chamber suggests an equilibration time of approximately 5 min. F_{O_2}, fractional oxygen concentration.

assuming a respiratory quotient (RQ) of 0.8, which minimises error in the estimated rate of energy use when RQ is unknown (Koteja, 1996).

To determine the net cost of transport by burrowing (NCOT$_b$, J m^{-1}), mice were placed in a chamber similar to that used by Vleck, who made the first measurements of burrowing energetics of a mammal (Vleck, 1979). The chamber consisted of a 40 cm long clear acrylic tube (11 cm i.d.) filled with soil to a distance of ~35 cm from the terminal end (Fig. 3). A 10 cm diameter PVC T-junction was fixed to the open end of the tube. The animal could be placed in the chamber through the threaded lid on the end branch, and the spoil fell through wire mesh on the lower branch (Fig. 3). Prior to being placed in the tube, soil (80:20 v/v sand and loam mix) was moistened until it was cohesive enough to stick together when squeezed by hand. This soil type is similar to the sandy soil in which hopping mice construct natural burrows (Lee et al., 1984). The
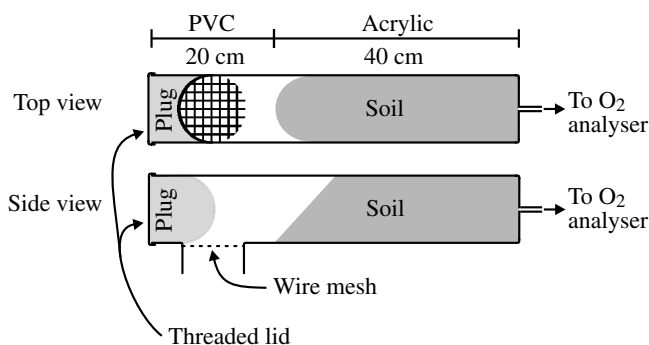
total mass of moist soil averaged 5.1±0.6 kg, and density averaged 1.5 g cm^{-3} (means ± s.d.).

Animals were monitored throughout burrowing trials, and periods of burrowing were noted. When animals were within a tunnel, however, they could not be observed continuously, and burrowing behaviour was identified by observing the animal's behaviour when it returned to the burrow entrance, and whether it was depositing spoil at the entrance. Only periods when the animal appeared to be burrowing continuously were used in the subsequent analysis. Equilibration time for the burrowing system was estimated at around 5 min from examination of experimental traces (e.g. Fig. 4) and was considerably less than the time spent burrowing during a typical trial (burrowing duration=27±16 min, mean ± s.d.). It was not possible to use instantaneous correction methods (e.g. Bartholomew et al., 1981) to resolve temporal changes in $\dot{V}_{O_2}$ during burrowing in detail (e.g. fluctuations in Fig. 4), because the excavation of soil alters the washout characteristics of the system, and precludes calculation of a washout constant. Burrowing mouse $\dot{V}_{O_2}$ ($\dot{V}_{O_2b}$) was determined by subtracting soil $\dot{V}_{O_2}$ from the combined $\dot{V}_{O_2b}$ of mouse and soil. Soil $\dot{V}_{O_2}$ (0.09±0.05 ml O_2 min^{-1}) averaged only 2% of burrowing mouse $\dot{V}_{O_2}$. Burrowing speed (U_b, m min^{-1}) was calculated by dividing distance burrowed by total time spent burrowing and NCOT$_b$ was then determined by subtracting resting $\dot{V}_{O_2}$ at burrowing T_a from $\dot{V}_{O_2b}$ and dividing this value by U_b. NCOT$_b$ was also calculated by multiplying the slope of the line relating $\dot{V}_{O_2b}$ and U_b by the energy equivalent of 1 ml of O_2 assuming a respiratory quotient (RQ) of 0.8. $\dot{V}_{O_2b}$ measurements were made at T_a=20–22°C.

Phylogenetic comparative analysis

Phylogenetic ANCOVA was used to compare BMR and $\dot{V}_{O_2b}$ between fossorial and semi-fossorial species. Phylogenetic ANCOVA was undertaken using the PDTREE, PDSIMUL and PDANOVA modules of the PDAP suite of

Fig. 3. Diagrammatic representation of the chamber used for measurement of burrowing $\dot{V}_{O_2}$. The plug functioned both to reduce the airspace in the chamber and to prevent spoil from collecting within the chamber.
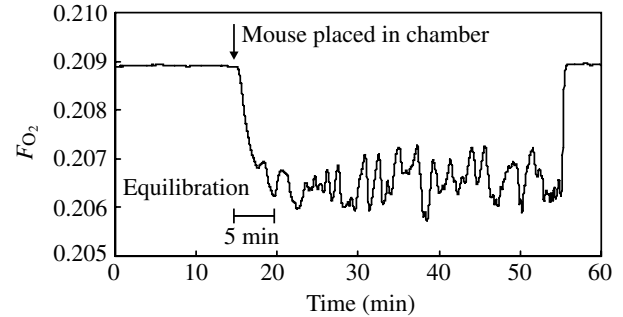
programs (Garland et al., 1993; Garland et al., 1999; Garland and Ives, 2000) and White's burrowing mammal phylogeny (White, 2003), which was trimmed to include only species for which BMR and $\dot{V}_{O2b}$ data were available. A gradual Brownian model of evolution, with limits, was used for all evolutionary simulations conducted for phylogenetic ANCOVA. For each comparison 10 000 simulations were used, and data were constrained using the 'throw out' algorithm, which restarts any simulation in which characters move outside specified limits. The minimum mass of simulated node and tip species was 1 g. This is 1.5 orders of magnitude smaller than the smallest species in the current data set (*Heterocephalus glaber*, 31.5 g) and similar to the minimum used in other studies, under the assumption that the smallest extant or extinct mammal probably weighed no less than 1–2 g (Garland et al., 1993). The maximum permitted mass was 3 kg. This is an order of magnitude larger than the largest species in the current data set (*Thomomys talpoides*, 300 g), but within the mass range of extant burrowing mammals (Woolnough and Steele, 2001). Minimum permitted BMR and $\dot{V}_{O2b}$ were each 1.5 orders of magnitude smaller than the smallest in the data set; maximum BMR and $\dot{V}_{O2b}$ were each one order of magnitude larger than the largest in the data set. The starting mean and variance of each evolutionary simulation was set to be the same as those for the tip species in the analysis (i.e., there was assumed to be no directional evolutionary trend in body mass M_b, BMR or $\dot{V}_{O2b}$). The correlations between mass and BMR, and mass and $\dot{V}_{O2b}$ of the simulated data, were also identical to that of the input data. Phylogenetic ANCOVA was undertaken following a test for homogeneity of regression slopes (ANOVA mass×BMR and mass×$\dot{V}_{O2b}$ interaction). Mass, BMR and $\dot{V}_{O2b}$ were log-transformed prior to analysis.

For phylogenetically informed (PI) regression, Felsenstein's phylogenetically independent contrasts were calculated (Felsenstein, 1985) using the PDTREE module of the PDAP suite. PI regression slopes were calculated by producing a scatter plot of the standardised contrasts for $\log\dot{V}_{O2b}$ and $\log M_b$ and computing a linear least squares regression constrained to pass through the origin. A phylogentically informed regression equation was then mapped back onto the original data by constraining a line with this slope to pass through the bivariate mean estimated by independent contrasts (e.g. Garland et al., 1993).

Phylogenetic ANCOVA was also used to compare maximum running speeds (MRS, m s^{-1}) between fossorial and non-fossorial species. In this case, phylogenetic ANCOVA was undertaken using the PDAP:PDTREE module of Mesquite (Maddison and Maddison, 2004; Midford et al., 2005) and the PDTREE, PDSIMUL and PDANOVA modules of the PDAP suite of programs (Garland et al., 1993; Garland et al., 1999; Garland and Ives, 2000). Data for marsupials, eulipotyphlan insectivores and rodents were considered in the analysis, and were compiled from published sources (Garland, 1983a; Djawdan and Garland, 1988; Garland et al., 1988; Iriarte-Díaz, 2002). Non-fossorial species with highly specialised habits and limb morphologies were excluded from the analysis (i.e.

Erithizon, *Didelphis* and *Bradypus*) (Iriarte-Díaz, 2002). A phylogenetic tree including all species for which data were available was constructed as a composite of several published trees (Murphy et al., 2001; Grenyer and Purvis, 2003; Cardillo et al., 2004; Lovegrove, 2004), with branch lengths assigned according to Pagel's arbitrary method (Pagel, 1992). This tree included five trifurcating polytomies, so five degrees of freedom were subtracted for tests of significance (Purvis and Garland, 1993). As above, 10 000 simulations of a gradual Brownian motion model of evolution with limits were used. In this case, the smallest species was 0.9 orders of magnitude larger than the minimum permitted M_b of 1 g, and the minimum permitted logMRS was thus set at 0.9 orders of magnitude lower than the smallest MRS in the data set. Upper limits for M_b and MRS were set one order of magnitude larger than the largest values in the data set. The starting mean and variance of each evolutionary simulation was set to be the same as those for the tip species in the analysis, as was the correlation between mass and MRS of the simulated data. Both M_b and MRS were log-transformed for analysis. Phylogenetic regression of logMRS on $\log M_b$ was undertaken using the same procedure as for phylogenetic regression of $\log\dot{V}_{O2b}$ on $\log M_b$.

Finally, for non-fossorial species, MRS was related to habitat type, scored according to the classification of Garland et al. (Garland et al., 1988). Habitats were ranked on an ordinal scale: 3=open country, e.g. deserts; 2=terrestrial, but habitat less open than in 3; 1=intermediate between terrestrial and arboreal; 0=arboreal. Standardised contrasts of logMRS, habitat type, and $\log M_b$ were calculated using the PDAP:PDTREE module of Mesquite (Maddison and Maddison, 2004; Midford et al., 2005) and residuals of the positivised relationships of logMRS on $\log M_b$ and habitat type on $\log M_b$ were calculated. The relationship between MRS and habitat type residuals was then assessed by correlation through the origin.

Results

Eleven hopping mice were measured, but some did not burrow or run sufficiently long to obtain reliable data. The mean (± s.d.) BMR of hopping mice was 0.67±0.06 ml O$_2$ min^{-1} (*N*=11), $\dot{V}_{O2max}$ was 4.2±0.6 ml min^{-1} (*N*=11) and $\dot{V}_{O2b}$ was 3.7±0.6 ml min^{-1} (*N*=6). $\dot{V}_{O2b}$ represented a 5.5-fold elevation above BMR and averaged 89% of $\dot{V}_{O2max}$.

U_b was 0.0074±0.0008 m min^{-1} (*N*=6) and ranged from 0.0057 to 0.0088 m min^{-1}. When calculated by subtracting resting $\dot{V}_{O2}$ at burrowing T_a from $\dot{V}_{O2b}$ and dividing this value by U_b, NCOT$_b$ was 7.1±0.9 kJ m^{-1} (*N*=6). $\dot{V}_{O2b}$ was positively correlated with U_b, but not significantly (r=0.75, t_4=2.29, P=0.08), so NCOT$_b$ estimated from the slope of $\dot{V}_{O2b}$ on U_b was not significantly different from zero (NCOT$_b$=11.1 kJ m^{-1}, 95% CI: –2.3, 24.6), and the value for NCOT$_b$ estimated by this method was not used in the subsequent analysis and discussion. NCOT$_p$ was 1.26±0.36 J m^{-1} (*N*=7) and was not significantly different from that predicted by allometry (t_6=1.65, P=0.15, allometric prediction=1.03 J m^{-1}: Fig. 5).
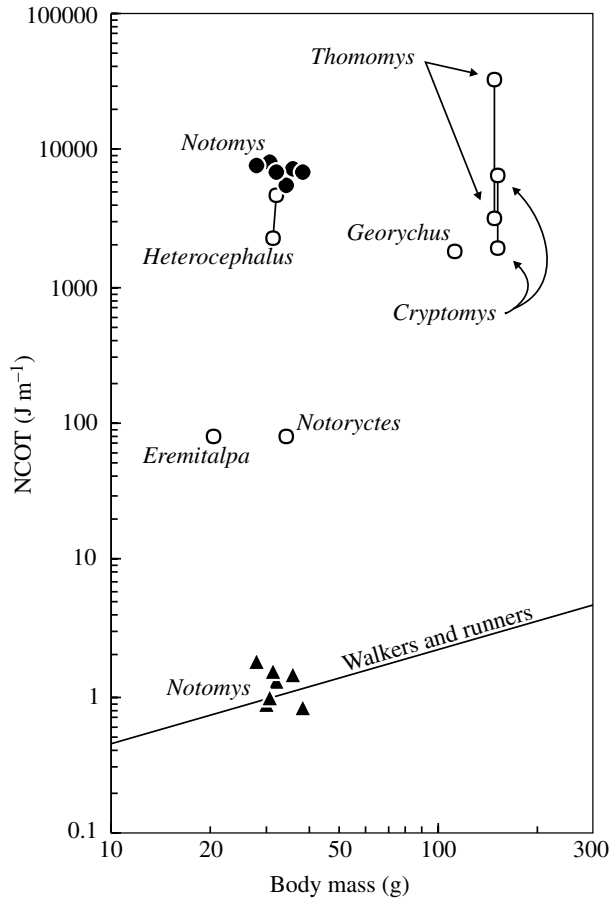
Fig. 5. Relationship between body mass and net cost of pedestrian (filled triangles, $NCOT_p$) and burrowing (filled circles, $NCOT_b$) transport for individual hopping mice, *Notomys alexis*. Unfilled symbols are mean $NCOT_b$ measurements for a variety of burrowing mammals taken from the literature (Vleck, 1979; Du Toit et al., 1985; Lovegrove, 1989; Seymour et al., 1998; Withers et al., 2000). Regression line shows $NCOT_p$ for walkers and runners derived from (Full et al., 1990) and incorporates data from mammals, birds, reptiles, amphibians, myriapods, crustaceans and insects.

BMR was not significantly different between fossorial and semi-fossorial species (phylogenetic ANCOVA $F_{2,4}=0.95$, $P=0.46$). $\dot{V}_{O2b}$ of semi-fossorial species was significantly higher than that of fossorial ones (phylogenetic ANCOVA $F_{2,4}=42.5$, $P=0.008$, Fig. 6).

MRS of fossorial species was significantly lower than that of non-fossorial species (phylogenetic ANCOVA $F_{1,58}=35.9$, $P=0.0006$, Fig. 7). MRS was significantly positively correlated with habitat type ($r=0.47$, $t_{53}=4.09$, $P=0.0001$, Fig. 8).

Discussion

Many of the convergent morphological specialisations observed among fully fossorial species, e.g. structural developments of claws, forelimbs and pectoral girdle (Nevo, 1979), are not shared with semi-fossorial species. As these specialisations are thought to increase burrowing energy
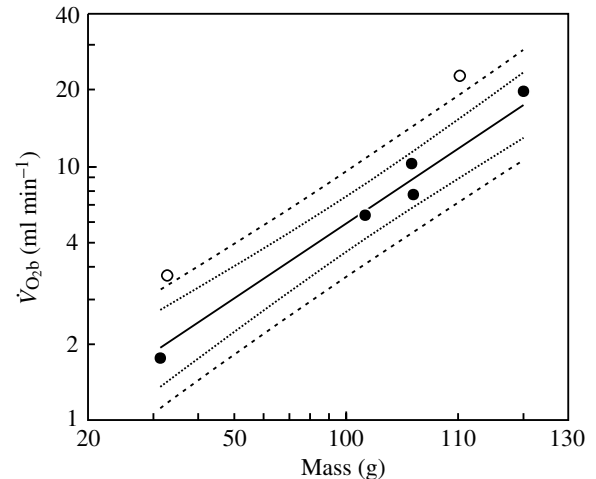

Fig. 6. Relationship between rate of oxygen consumption during burrowing ($\dot{V}_{O2b}$) and body mass for fossorial (filled circles) and semi-fossorial (open circles) mammals. Solid line is the phylogenetically correct regression relating $\dot{V}_{O2b}$ to mass for fossorial species ($\dot{V}_{O2b}=0.065M_b^{0.98\pm0.06}$, where the mass exponent is mean ± s.e.). Inner dotted lines represent the 95% confidence interval of this regression; outer broken lines represent the 95% prediction interval. Data sources are provided in Table 1.

efficiency, it might be reasonably expected that $NCOT_b$ for semi-fossorial species would be higher than that of fossorial species. Indeed, $NCOT_b$ of hopping mice is significantly higher than that of the similarly sized (31.5 g) naked mole-rat *Heterocephalus glaber* ($t_5=13.3$, $P<0.0001$) and, when normalised to burrow cross-sectional area, hopping mouse $NCOT_b$ is three- to tenfold higher than that of other mammals burrowing through similar substrates (Table 1). This suggests
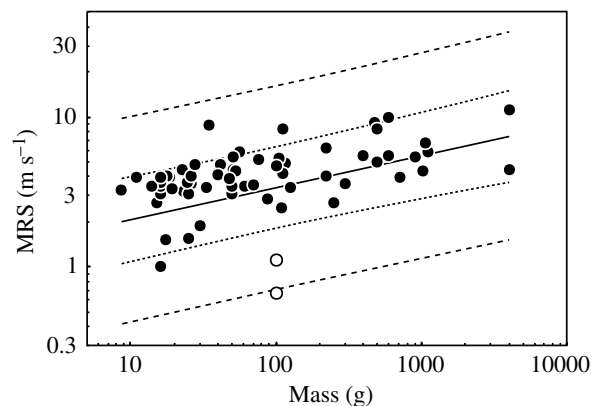
Fig. 7. Relationship between maximum running speed (MRS) and body mass for fossorial (filled circles) and semi-fossorial (open circles) mammals. Solid line is the phylogenetically correct regression relating MRS to mass for fossorial species (equation: $MRS=1.27M_b^{0.21\pm0.04}$, where the mass exponent is mean ± s.e.). Inner dotted lines represent the 95% confidence interval of this regression; outer broken lines represent the 95% prediction interval. Data sources are provided in Materials and methods.

Fig. 8. Correlation between residual contrasts in maximum running speed (MRS) and habitat type for non-fossorial rodents and marsupials. Habitat type was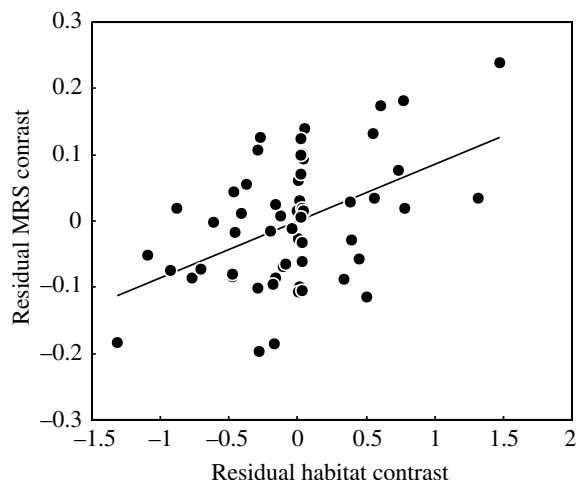 scored according to Garland et al. (Garland et al., 1988): 3=open country, e.g. deserts; 2=terrestrial, but habitat less open than in 3; 1=intermediate between terrestrial and arboreal; 0=arboreal.

that semi-fossorial species burrow less efficiently than fossorial species, but insufficient data are available for formal significance of any model parameters in a phylogenetic ANCOVA model comparing $NCOT_b$ of fossorial and semi-fossorial species. However, semi-fossorial hopping mice and degus, *Octodon degus*, were found to have significantly higher $\dot{V}_{O_2b}$ than fossorial burrowing species (Fig. 6). This difference, which is not a consequence of differences in BMR [fossorial and semi-fossorial mammals were found to have similar BMR in both the present study, and in the larger data set analysed elsewhere (White, 2003)], further suggests that the high $NCOT_b$ of hopping mice is real. The high $NCOT_b$ and $\dot{V}_{O_2b}$ of semi-fossorial species supports the notion that the morphological specialisations observed in fossorial species are indeed adaptive and reduce the energetic cost of burrowing.

To evaluate the possible benefits of specialisation for terrestrial rather than burrowing locomotion for hopping mice, it is informative to estimate the total cost of burrow construction and compare this with an estimate of the total energy used by a species of this size for terrestrial locomotion. Hopping mice commence burrow construction by excavating a sloping section to a depth of 70 to 150 cm (Lee et al., 1984). They then construct a system of horizontal tunnels and chambers from the bottom of the sloping tunnel. Finally, vertical shafts are excavated upward from the horizontal tunnels and the spoil generated by these diggings is used to backfill the sloping tunnels. A generalised system such as this may comprise five vertical tunnels and about 11 m of horizontal tunnel and is usually occupied by 5–8 adults and young of one or two litters (Lee et al., 1984). All adults assist in burrow construction and maintenance. For simplicity, it is assumed that each of five founding adults is responsible for construction of one sloping tunnel to a depth of 1.1 m, one vertical tunnel, and 2.2 m of horizontal tunnel. No data are available on the declination angle of the sloping tunnel, so data for a related species, *Notomys mitchellii*, are used (40°) (Nowak, 1999). The total cost of burrow construction can then be estimated from $NCOT_b$, estimates of burrow cross-sectional area (13 cm^2) (White, 2005), soil density (1.6 g cm^{-3}) (Vleck, 1979; Du Toit et al., 1985; Lovegrove, 1989), and a model that incorporates $NCOT_b$ (the cost of excavating from a cohesive soil face) together with the additional costs of working against distance and gravity to move spoil to the surface (see Appendix). The model estimates a total construction cost of 55.5 kJ per mouse. Assuming that each mouse burrows at a speed similar to that observed in the burrowing chamber, burrow construction would take approximately 11.2 h. Based on $NCOT_p$ and an allometric prediction of daily movement distance for a mammal of its body size (413 m) (Garland,

Table 1. *Net cost of transport by burrowing and metabolic rate measurements for a selection of mammalian fossorial and semi-fossorial species*

| | Mass (g) | | $NCOT_b$ | | MR (ml O$_2$ min^{-1}) | | |
	Burrowing	Basal	(kJ m^{-1})	(J g$^{-0.67}$ m^{-1})	Burrowing	Basal	Reference
Heterocephalus glaber	31.5	32.0	2.3	230	1.76	0.34	1, 2, 3
Notomys alexis*	33.0	33.0	7.1	684	3.70	0.67	This study
Georychus capensis	113.0	195.0	1.8	76	6.42	1.93	4, 5
Thomomys bottae	150.0	143.0	6.4	224	10.3	2.00	6
Cryptomys damarensis	152.1	138.0	2.0	68	7.68	1.31	3, 7, 8, 9
Octodon degus*	203.0	193.0			22.6	2.84	10, 11, 12
Thomomys talpoides	300.0	106.8			19.6	2.37	13, 14, 15

$NCOT_b$, net cost of transport by burrowing; MR, metabolic rate.

*Species are semi-fossorial, the remainder are fossorial.

All digging measurements were obtained in damp sand or sandy loam. $NCOT_b$ data are presented as whole animal measurements (J m^{-1}) and normalised to burrow cross-sectional area ($\propto M_b^{2/3}$) (Vleck, 1979).

References: 1 (McNab, 1966); 2 (Withers and Jarvis, 1980); 3 (Lovegrove, 1989); 4 (Du Toit et al., 1985); 5 (Lovegrove, 1987); 6 (Vleck, 1979); 7 (Lovegrove, 1986); 8 (Lovegrove, 1988); 9 (Bennett et al., 1992); 10 (Bozinovic and Novoa, 1997); 11 (Ebensperger and Bozinovic, 2000); 12 (Arends and McNab, 2001); 13 (Bradley et al., 1974); 14 (Gettinger, 1975); 15 (Andersen and Macmahon, 1981).

1983b), it is possible to estimate a daily terrestrial movement cost of 519 J, which is less than 1% of the estimated daily energy expenditure of this species (64 kJ) (Nagy et al., 1999). However, voluntarily running deer and laboratory mice move several kilometres per day and movement costs are between 2.7 and 7.5% of daily energy expenditure (Koteja et al., 1999; Chappell et al., 2004), which suggests that a daily movement distance of 413 m for hopping mice may be an underestimate. Despite taking less than 12 h, burrow construction requires a similar amount of energy to that expended during the terrestrial locomotion expected to occur in 17–100 days (assuming either a daily movement distance of 413 m or a daily movement cost of 5% of daily energy expenditure).

Because of the apparently high cost of burrow construction relative to terrestrial locomotion, it therefore seems reasonable to ask why hopping mice are specialised for saltation rather than burrowing locomotion. Firstly, burrow construction represents an investment over a short period, and this investment is likely to be small when compared to total energy turnover throughout the period of burrow use. For example, assuming that a burrow is used for 6 months, the cost of construction represents only 0.5% of total estimated energy turnover (64 kJ day^{-1}) (Nagy et al., 1999). Furthermore, the ecological consequences associated with fossorial specialisation are likely to be detrimental for hopping mice. Although the energetic costs of terrestrial locomotion of specialised burrowers (*Eremitalpa granti namibensis* and *Notoryctes caurinus*) are similar to allometric predictions (Seymour et al., 1998; Withers et al., 2000), maximum running speeds of fossorial moles (*Talpa europaea* and *Scalopus aquaticus*) are significantly lower than those of non-fossorial species (Fig. 7). Hopping mice forage in open areas in arid environments (Garland et al., 1988), so their capacity to escape predation is probably related to maximum running speed, and species from open habitats have higher maximum running speeds than species from less open habitats (Fig. 8). Specialisation for burrowing is likely to occur at the expense of running speed, and is therefore likely to have a negative effect on overall fitness. For animals that can avoid predation within a closed burrow system, however, the energetic advantages of burrowing specialisation are clear: a 65.2 g pocket gopher invests only 193 kJ in the construction of a labyrinth of feeding tunnels 52.5 m in length, whereas a 33.0 g hopping mouse constructing a system of similar length would expend 552 kJ, calculated using a modified version of the model described elsewhere (White, 2001), together with published data (Vleck, 1979; Vleck, 1981).

Appendix
A model for calculation of the cost of burrow construction for semi-fossorial mammals

When measured for short lengths of tunnel, burrowing net cost of transport (NCOT$_b$) accounts only for the cost of removing soil from the undisturbed face and moving along a relatively short length of horizontal tunnel. This measurement therefore neglects the additional costs of pulling soil along a longer tunnel, raising soil to the surface, and moving the animal's own body mass between the workface and the surface. The following model is an expanded revision of that presented in the literature (White, 2001), which considered only a simple, blind ending tunnel. The model is based largely on the burrow systems of *Notomys alexis* (Lee et al., 1984), but is generally applicable to semi-fossorial species and can be used to estimate the total cost of burrow construction for any system that is constructed in three stages: (1) excavation of a sloping section of known declination to a given depth, (2) construction of a blind-ending horizontal tunnel from the end of the sloping tunnel, (3) construction of a vertical shaft excavated upward from the junction of the horizontal and sloping tunnels – spoil generated by this excavation is used to backfill the sloping tunnel. The total cost of construction (E_{TOT}, in J) is equal to the sum of the costs of constructing the individual components. Thus $E_{TOT}=E_{sloping}+E_{horizontal}+E_{vertical}$.

Sloping tunnel

The model assumes that the energy cost of constructing the sloping component of the system ($E_{sloping}$, J) can be calculated using the equation: $E_{sloping}=E_e+E_{sh}+E_{sv}+E_{ah}+E_{av}$, where E_e=cost of removing soil from the undisturbed face (cost of excavation), E_{sh}=cost of moving soil horizontally to the burrow entrance, E_{sv}=cost of moving soil vertically to the burrow entrance, E_{ah}=cost of moving the animal horizontally to the burrow entrance and E_{av}=cost of moving the animal vertically to the burrow entrance.

If no significant effect of total excavation length on net cost of transport by burrowing (NCOT$_b$, J m^{-1}) can be detected, it can be assumed that NCOT$_b$ multiplied by the distance burrowed provides a reasonable estimate of E_e (J). Therefore, given that d is burrow depth (m), and θ is the angle at which the burrow descends relative to horizontal,

$$E_e = \text{NCOT}_b(d/\sin\theta) . \qquad (A1)$$

The energy cost of moving soil horizontally to the burrow surface (E_{sh}, J) can be calculated as the product of the mass of soil moved (M_s, g), the mean horizontal distance through which it must be moved ($\frac{1}{2}l_h$, m), and the energy cost of pushing 1 g of soil 1 m [k, J g^{-1} m^{-1} (after Vleck, 1979)]. M_s is equal to $A_b\rho(d/\sin\theta)$, where A_b=burrow cross sectional area (m^2) and ρ=soil bulk density (g m^{-3}); l_h is equal to $d/\tan\theta$,

$$E_{sh} = \tfrac{1}{2}kM_s(d/\tan\theta) . \qquad (A2)$$

Evaluation of k requires knowledge of the shear strength and cohesion between the loose spoil pushed by the animal and the undisturbed compact soil over which it is dragged. Alternatively, it may be assumed that the animal effectively carries spoil to the surface (i.e. the cost of overcoming friction while dragging the soil is similar to the energy required to carry the soil; the influence of this assumption on the estimation E_{TOT} is discussed below). In this case it may be further assumed that the cost of moving 1 g of load a distance of 1 m is equal to the cost of moving 1 g of body mass 1 m, as has been shown for mammals (Taylor et al., 1980), a hermit crab (Herreid and Full,

1986) and several species of ant (Lighton et al., 1987; Bartholomew et al., 1988; Duncan and Lighton, 1994), although this is not always the case (Maloiy et al., 1986; Kram, 1996). Assuming that the costs of moving equivalent load and body masses are equal, k can be evaluated by multiplying the net cost of pedestrian transport ($NCOT_p$, J m^{-1}) by the ratio of total soil mass to animal mass (M_s/M_a). E_{sh} can therefore be estimated using the equation:

$$E_{sh} = \tfrac{1}{2}(d/\tan\theta) \, (M_s/M_a)NCOT_p \, . \tag{A3}$$

The energy cost of working against gravity to raise the soil excavated during construction of an angled burrow to the surface (E_{sv}, J) can be calculated as the product of the mass of soil removed (M_s, g), the mean depth through which it must be moved ($\tfrac{1}{2}d$, m), and the amount of mechanical work necessary to move a load against gravity (g, 9.8×10^{-3} J g^{-1}·m^{-1}) divided by the efficiency with which metabolic work is done against gravity (α):

$$E_{sv} = \tfrac{1}{2}dM_s(g/\alpha) \tag{A4}$$

(after Vleck, 1981, eqn 2).

The energy cost of the horizontal component of motion along the length of the tunnel (E_{ah}, J) depends upon the total horizontal distance travelled and the net cost of pedestrian transport ($NCOT_p$). In turn, the total horizontal distance travelled depends on the number of trips the animal makes to the surface to deposit spoil (n_t), which is determined by the maximum load size that the animal can move. The burrow is therefore excavated in portions equal in size to l/n_t, of which the horizontal component is equal to l/n_t or $d/(n_t\tan\theta)$. Following excavation of a segment, the animal must travel to the surface and return to the excavation face, such that each newly excavated segment is traversed twice following excavation and twice more following excavation of each new segment. The total distance travelled is therefore equal to $2\Sigma(1, 2, \ldots, n_t-1, n_t)d/(n_t\tan\theta)$ and the cost of the horizontal component of motion along the burrow can be determined with the equation:

$$E_{ah} = NCOT_p2\Sigma(1, 2, \ldots, n_t-1, n_t)d \, / \, n_t\tan\theta \, . \tag{A5}$$

Calculation of the cost of vertical movement (E_{av}, J) along the length of the burrow follows a similar pattern. In this case, $NCOT_p$ is replaced with the energetic cost of raising the animal's mass vertically minus the gravitational potential energy that can be harnessed and used to reduce the cost of moving down an incline. If we let β equal the efficiency with which gravitational potential energy is harnessed to reduce the energetic cost of descent, then:

$$E_{av} = [M_a(g/\alpha)\Sigma(1, 2, \ldots, n_t-1, n_t)d/n_t] -$$
$$[M_a(g\beta)\Sigma(1, 2, \ldots, n_t-1, n_t)d/n_t] =$$
$$M_ag[(1/\alpha) - \beta]\Sigma(1, 2, \ldots, n_t-1, n_t)d/n_t \, . \tag{A6}$$

Horizontal tunnel

Calculation of the cost of construction of a horizontal tunnel of length l at the end of the sloping tunnel follows a similar

logic to that described above. Again, $E_{horizontal}=E_e+E_{sh}+E_{sv}+E_{ah}+E_{av}$.

Following Eqn A1 above, E_e is equal to the distance that must be excavated (l, m) multiplied by $NCOT_b$:

$$E_e = lNCOT_b \, . \tag{A7}$$

Again, E_{sh} is equal to the mean distance through which the soil must be moved multiplied by M_s and the ratio of soil to animal mass. In this case however, the soil must also be moved through the sloping tunnel to be deposited on the surface, thus:

$$E_{sh} = [(\tfrac{1}{2}d/\tan\theta) + l] \, (M_{sn}/M_a)NCOT_p \, . \tag{A8}$$

Because this section of tunnel is horizontal, mean depth is equal to d, so E_{sv} can be calculated by modifying Eqn A4:

$$E_{sv} = dM_s(g/\alpha) \, . \tag{A9}$$

The animal must now travel to the surface and return to the excavation face through the sloping section of tunnel, as well as the horizontal section. It must traverse the sloping section twice following excavation of each new segment, in addition to traversing each excavated horizontal segment twice.

$$E_{ah} = NCOT_p2\Sigma(1, 2, \ldots, n_t-1, n_t) \, (d/n_t\tan\theta) +$$
$$2n_t(d/\tan\theta)NCOT_p = 2NCOT_p[\Sigma(1, 2, \ldots, n_t-1, n_t)$$
$$(d/n_t\tan\theta) + (n_td/\tan\theta)] \, . \tag{A10}$$

Because this section of burrow is horizontal, the only vertical component to movement is travel to the surface to deposit spoil: excavation has no vertical component, therefore:

$$E_{av} = M_ag[(1/\alpha) - \beta]n_td \, . \tag{A11}$$

Vertical tunnel

Construction of the vertical tunnel follows a slightly different pattern because spoil is not deposited on the surface, but is used to backfill the sloping tunnel. Again, $E_{vertical}=E_e+E_{sh}+E_{sv}+E_{ah}+E_{av}$. Excavation costs are determined in an analogous manner as for the sloping and horizontal sections, and assume that the cost of excavating in an upward direction is similar to the cost of excavating horizontally or down:

$$E_e = dNCOT_b \, . \tag{A12}$$

Because the excavated soil falls from the excavation face and then must be transported to the plug, it must be moved to a mean horizontal distance of $\tfrac{1}{2}d\cos\theta$ from the entrance and must therefore be moved a mean horizontal distance of $(d/\tan\theta-\tfrac{1}{2}d\sin\theta)$, thus:

$$E_{sh} = (d/\tan\theta - \tfrac{1}{2}d\sin\theta) \, (M_s/M_a)NCOT_p \, . \tag{A13}$$

Because the excavated soil falls from the excavation face and then must be transported to the plug, it must be moved from the burrow floor to a mean vertical distance of $\tfrac{1}{2}d\sin\theta$ from the surface, and must therefore be moved a mean distance of $(d-\tfrac{1}{2}d\sin\theta)$ against gravity, thus:

$$E_{sv} = (d - \tfrac{1}{2}d\sin\theta)M_s(g/\alpha) \, . \tag{A14}$$

Assuming again that this portion of the burrow is excavated in segments appropriately sized for the animal to carry, the
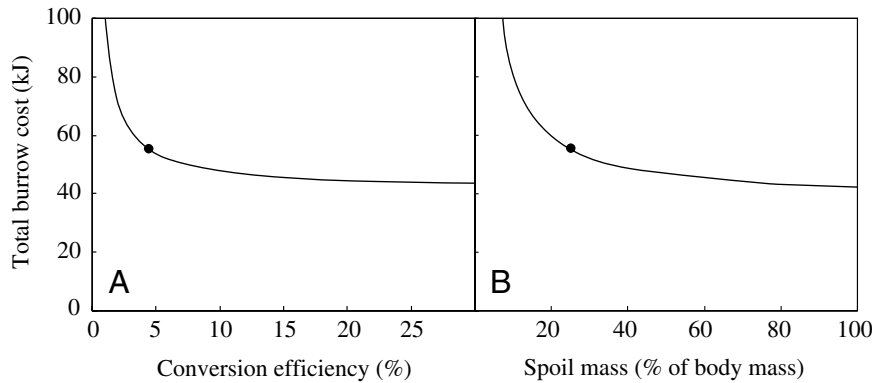
Fig. A1. (A) Effect of efficiency of conversion of metabolic energy to mechanical work against gravity and (B) mass of spoil (expressed as % of body mass) carried in each trip to the surface on total burrow construction cost for *Notomys alexis*. Filled symbol represents spoil mass used in model calculations (4.4% and 25% for conversion efficiency and spoil mass, respectively; total burrow cost=55.5 kJ).

burrow is excavated in segments of which the horizontal component is equal to $(d/\tan\theta - \frac{1}{2}d\sin\theta)/n_t$, and by substitution into Eqn A5:

$$E_{ah} = NCOT_p 2\Sigma(1, 2, \ldots, n_t-1, n_t)$$
$$[(d/\tan\theta) - (\tfrac{1}{2}d\sin\theta)] / n_t . \quad (A15)$$

Similarly, excavation occurs in segments with a vertical component of d/n_t, but spoil must also be deposited in segments with a vertical component of $(d-\frac{1}{2}d\sin\theta)/n_t$, so by substitution into Eqn A6, and assuming that backfilled segments are the same size as excavated ones,

$$E_{av} = M_a g[(1/\alpha) - \beta]\Sigma(1, 2, \ldots, n_t-1, n_t)$$
$$[d + (d - \tfrac{1}{2}d\sin\theta)] / n_t . \quad (A16)$$

Evaluation of assumptions

To calculate the total cost of burrow construction, knowledge of a number of burrow parameters and energetic constants is required. The number of trips required to construct a burrow requires knowledge of the amount of soil transported by the animal on each trip to the surface. Fig. A1B shows the effect of mass of spoil (expressed as % of body mass) carried

Table A1. *Total energetic cost of burrow construction for Notomys alexis partitioned into that associated with excavation, moving spoil horizontally and vertically, and moving the animal's mass horizontally and vertically, for each of the three tunnel components of the burrow system (sloping, horizontal and vertical)*

	E_e	E_{sh}	E_{sv}	E_{ah}	E_{av}	% of total
Sloping	12.2	0.09	0.44	1.43	3.50	**32**
Horizontal	15.7	0.21	1.12	3.66	4.48	**45**
Vertical	7.83	0.08	0.38	0.67	3.78	**23**
% of total	**64**	**0.7**	**3.5**	**10**	**21**	

E_e, energetic cost of excavation; E_{sh}, E_{sv} (kJ), cost of moving spoil horizontally and vertically, respectively; E_{ah}, E_{av} (kJ), cost of moving the animal's mass horizontally and vertically, respectively.

The percentage contributions of each of the five energetic and three tunnel components to the total burrow cost of 55.5 kJ are summed in bold type in the lower row and far right column, respectively.

in each trip to the surface on total burrow construction cost for *Notomys alexis*. Burrow construction costs rise dramatically below about 25% of body mass, but decrease little above 25%. As such, 25% was selected as the appropriate spoil mass for model calculations.

The efficiency with which metabolic energy can be transferred to useful mechanical work against gravity (α) has been estimated to be in the range of 4.4–63% (Cavagna et al., 1963; Taylor et al., 1972; Full and Tullis, 1990). Within this range, α has little effect on the total cost of burrow construction (Fig. A1A). Nevertheless, a conservative position was adopted for model calculations and an efficiency of 4.4% was used. Although the efficiency with which gravitational potential energy can be harnessed to reduce the cost of moving downhill has been estimated to be as high as 92% (Taylor et al., 1972), reducing this value has a minor effect on total burrow construction costs (total cost estimated with efficiencies of 0% and 92% differ by less than 1%). Gravitational potential energy harnessing efficiency was therefore conservatively estimated at 0% for model calculations.

Finally, estimation of burrow construction cost by the method described above involves the untested assumption that the cost of overcoming friction when dragging spoil horizontally (E_{sh}) is similar to the energy required to carry a load of equivalent mass. To evaluate the influence that this assumption has on estimation of E_{TOT}, we partitioned each of $E_{sloping}$, $E_{horizontal}$ and $E_{vertical}$ into E_e, E_{sh}, E_{sv}, E_{ah} and E_{av} (Table A1). Surprisingly, the cost of moving spoil amounts to only 4.2% of E_{TOT}, and E_{sh} amounts to less than 1% (Table A1). Thus, the high apparent cost of burrow system construction for *Notomys alexis* does not arise as a consequence of this assumption. Instead, the high E_{TOT} arises largely as a consequence of high $NCOT_b$, as the cost of removing soil from the undisturbed face (E_e) represents 64% of E_{TOT} (Table A1).

List of symbols and abbreviations

A	cross-sectional area (m^2)
BMR	basal metabolic rate
d	depth (m)
E	energy (J)
g	cost of moving 1 g a distance of 1 m against gravity (9.8×10^{-3} J g^{-1} m^{-1})

k	mass- and distance-specific cost (J g^{-1} m^{-1})
l	length (m)
M	mass (g)
M_b	body mass
MRS	maximum running speed
NCOT$_b$	net cost of transport by burrowing (J m^{-1})
NCOT$_p$	net cost of pedestrian transport (J m^{-1})
n	number
PI	phylogenetically informed
RQ	respiratory quotient
T_a	ambient temperature
U	speed
$\dot{V}_{O_2}$	metabolic rate (ml min^{-1})
α	efficiency of conversion of metabolic energy to work against gravity
β	efficiency of harnessing gravitational potential energy
θ	angle of burrow declination
ρ	soil density (g m^{-3})

Subscripts:

a	animal
b	burrow
e	excavation
h	in horizontal plane
s	soil
t	trips to surface
TOT	total
v	in vertical plane

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