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RESEARCH ARTICLE

Morphology and burrowing energetics of semi-fossorial skinks (*Liopholis* spp.)

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ABSTRACT

Burrowing is an important form of locomotion in reptiles, but no study has examined the energetic cost of burrowing for reptiles. This is significant because burrowing is the most energetically expensive mode of locomotion undertaken by animals and many burrowing species therefore show specialisations for their subterranean lifestyle. We examined the effect of temperature and substrate characteristics (coarse sand or fine sand) on the net energetic cost of burrowing (NCOB) and burrowing rate in two species of the *Egernia* group of skinks (*Liopholis striata* and *Liopholis inornata*) compared with other burrowing animals. We further tested for morphological specialisations among burrowing species by comparing the relationship between body shape and retreat preference in *Egernia* group skinks. For *L. striata* and *L. inornata*, NCOB is 350 times more expensive than the predicted cost of pedestrian terrestrial locomotion. Temperature had a positive effect on burrowing rate for both species, and a negative effect on NCOB for *L. striata* but not *L. inornata.* Both NCOB and burrowing rate were independent of substrate type. Burrows constructed by skinks had a smaller cross-sectional area than those constructed by mammals of comparable mass, and NCOB of skinks was lower than that of mammals of similar mass. After accounting for body size, retreat preference was significantly correlated with body shape in *Egernia* group skinks. Species of *Egernia* group skinks that use burrows for retreats have narrower bodies and shorter front limbs than other species. We conclude that the morphological specialisations of burrowing skinks allow them to construct relatively narrow burrows, thereby reducing NCOB and the total cost of constructing their burrow retreats.

KEY WORDS: *Egernia*, Cost of burrowing, Morphometrics, Locomotion energetics, Metabolic rate

INTRODUCTION

Terrestrial locomotion, such as running, is more energetically expensive than flying or swimming for an animal of similar mass (Schmidt-Nielsen, 1972), but considerably less costly than travelling through a dense, cohesive medium such as soil (Vleck, 1979; Seymour et al., 1998). A specialised burrower such as the Namib Desert golden mole (*Eremitalpa granti namibensis*) expends 26 times more energy burrowing through loose sand (80 J m^{-1}) than running (3 J m^{-1}) on the surface of the sand, though the cost of 'swimming' through loose sand is less than a tenth of that expended by mammals that tunnel through compact soil (Seymour et al., 1998). A non-specialised burrower such as the spinifex hopping mouse (*Notomys alexis*), can expend 5000 times more energy burrowing than running (7.1 kJ m^{-1} compared with 1.2 J m^{-1}; White et al., 2006b). Despite the considerable energetic cost, burrowing has many benefits. These include food storage, access to underground food, a secure micro-environment free from predators and extreme environmental gradients (Robinson and Seely, 1980), nesting (Seymour and Ackerman, 1980), hibernation (Moberly, 1963) and enhanced acoustics to facilitate communication (Bennet-Clark, 1987).

Animals utilise a range of methods to burrow through soil, depending on soil characteristics (density, particle size and moisture content) and body morphology (limbed or limbless). Regardless of the method of burrowing, for animals that live and forage underground (fossorial species), the energy taken up must exceed the energy invested in burrowing. Fossorial mammals have therefore evolved ways to maximise burrowing capacities and efficiency and show convergent features that include reduction of hind-limbs, tail, eyes and external ears (Heffner and Heffner, 1990). Compared with mammals, burrowing reptiles tend to show different morphological features, such as limb reduction, body elongation and general size reduction (Wiens and Slingluff, 2001; Navas et al., 2004), strengthening of the cranium (Lee, 1998), shortening of the head and lower rostral angulation (Andrews et al., 1987; Barros et al., 2011), shortening of the tail (Shine and Wall, 2008) and streamlining of scales (Jackson and Reno, 1975). More specialised fossorial reptiles display reduction of both eyes and ears, fixation of the lower eyelid, a greater number of vertebrae and ribs associated with elongation of the body and atrophy of one lung (Bellairs, 1969).

The work required to excavate soil increases exponentially with body diameter, and fossorial animals therefore tend to be smaller than surface dwellers. Burrow size depends on animal morphology; bipedal animals such as birds construct significantly larger burrows than mammals to accommodate space for their beaks and feet to dig (White et al., 1978). Reptiles, however, tend to be more elongate than birds and mammals of a similar mass, so their burrows have a smaller cross-sectional area (White, 2005). Iguanas are more elongated than fossorial mammals of similar mass and construct smaller burrows (Rand and Dugan, 1983). The small cross-sectional area of burrows constructed by reptiles may therefore reduce their cost of burrowing, but this hypothesis remains untested. The hypothesis would be supported if reptiles are found to have lower burrowing costs than birds and mammals of similar mass.

Compared with fully fossorial species, semi-fossorial animals (facultative burrowers) use burrows as retreats and forage at the surface, or construct burrows only for nesting purposes (Seymour and Ackerman, 1980). Semi-fossorial animals construct less complex burrows than fully fossorial species, despite similar cross-sectional area (White, 2005), but their lack of structural adaptations for burrowing may require them to expend more energy per unit of cross-sectional area (White et al., 2006b).

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List of symbols and abbreviations

A_b	burrow cross-sectional area
DMR	digging metabolic rate
LDA	linear discriminant analysis
M_b	body mass
NCOB	net cost of burrowing
NCOT	net cost of pedestrian transport
RMR	resting metabolic rate
SVL	snout–vent length
$\dot{V}_{CO_2}$	rate of CO_2 production

Early work that considered the energetics of burrowing comprised either speculative accounts that featured no direct measurements (Grinnell, 1923; Tryon and Cunningham, 1968; Vaughan, 1974), or considered only basal metabolism and thermoregulatory costs (McNab, 1966). The first studies of burrowing energetics were conducted by Seymour (1973), who measured the metabolic rates of burrowing spadefoot toads (*Spea multiplicata*; prev. *Scaphiopus multiplicatus*) and Vleck (1979), who calculated the net energetic cost of burrowing (NCOB: the net energy cost of constructing a unit length of burrow, excluding maintenance costs associated with resting metabolism) of pocket gophers (*Thomomys bottae*). Since then, many studies of burrowing energetics have been conducted on a variety of burrowing mammals (e.g. Seymour et al., 1998; Ebensperger and Bozinovic, 2000a; Withers et al., 2000; White et al., 2006b), and have shown that the ambient air temperature (Luna and Antinuchi, 2007) and different substrate characteristics (Luna and Antinuchi, 2006; Zelová et al., 2010) can greatly affect the energetic cost of burrowing. For example, the cost of burrowing for mole rats (Bathyergidae) is up to 3.7 times higher when burrowing in dry sand relative to damp sand (Lovegrove, 1989) and burrowing metabolic rate is lowest for tuco-tucos *Ctenomys talarum* burrowing at ambient temperatures within their thermoneutral zone (Luna and Antinuchi, 2007).

To date, there have been no experimental studies of the cost of burrowing in reptiles. Burrowing is an important form of locomotion in reptiles (Lee, 1998) and one-third of Australian skinks are burrowing species that spend most of their lives underground (Wilson and Swan, 2013). The night skink (*Liopholis striata*) and the desert skink (*Liopholis inornata*) are nocturnal, semi-fossorial skinks from the genus *Liopholis* (previously *Egernia*; Gardner et al., 2008). In their natural habitat they are important bioturbators that modify the desert environment and produce burrows that provide shelter for other fauna including prickly geckos (*Heteronotia binoei*), knob-tailed geckos (*Nephrurus levis*) and king brown snakes (*Pseudechis australis*) (Pianka and Giles, 1982). These skinks occupy desert habitats ranging from sandy deserts to harder soils in *Acacia* deserts of Western Australia (Storr, 1978). Their burrows provide them with protection from surface sand temperatures that can exceed 40°C in the summer and from seasonal fires in spinifex grasslands (Wilson and Swan, 2013).

Adult *L. striata* ranges in size from 41 to 112 mm (snout–vent length; SVL) and construct elaborate burrow systems, with several interconnected openings (Pianka and Giles, 1982). The smaller *L. inornata* range in size from 32 to 84 mm (SVL) and construct simple U-shaped burrows roughly 30 cm deep (Storr, 1978). They live individually and often have two burrows 10–20 m apart (Pianka and Giles, 1982). The present study aimed to provide the first estimates of the NCOB in *L. striata* and *L. inornata* and examined the effect of temperature and substrate characteristics on burrowing energetics, testing the following four hypotheses: (1) because of their elongated body form, skinks will construct narrower burrows than other burrowing animals of similar mass (White, 2005) and will exhibit lower NCOB than a mammal of similar mass. (2) As fine sand is more cohesive than coarse sand, burrowing speed will be higher in coarse sand relative to fine sand (Zelová et al., 2010) and digging metabolic rate will be higher in fine sand than coarse sand (Luna and Antinuchi, 2006). NCOB incorporates costs associated with both shearing soil from the excavation face, and transporting soil away from the excavation face (Vleck, 1979). Changes in water content or state of compaction influence the soil density, cohesiveness, and shear strength (Collis-George, 1959). Thus, because the cost of shearing soil contributes to NCOB, NCOB should, all else being equal, increase with the cost of shearing soil (Vleck, 1979), so NCOB will be higher in fine sand compared with coarse sand. (3) The NCOB will be independent of ambient air temperature. This is because the NCOB reflects the mechanical cost of excavation, which should be independent over the range of temperature at which skinks burrow, and excludes maintenance costs (which are temperature dependent in ectotherms). (4) Species with preferences for burrow retreats will exhibit morphological specialisation for burrowing, such as elongated bodies and reduced limbs compared with non-burrowing species, because morphology contributes to burrowing efficiency.

Hypothesis 1 was tested by comparing the dimensions of burrows constructed by skinks with those constructed by other animals. Hypotheses 1–3 were tested by measuring the effects of soil characteristics and temperature on the burrowing energetics and NCOB for *L. striata* and *L. inornata*. Hypothesis 4 was tested by comparing morphometric measurements of *L. striata* and *L. inornata* with related skinks of the *Egernia* group (Gardner et al., 2008), which consists of seven genera (*Bellatorias*, *Corucia*, *Cyclodomorphus, Egernia*, *Liopholis*, *Lissolepis* and *Tiliqua*), to determine the relationship between size-independent body shape and retreat preferences.

RESULTS

Temperature and sand treatments

The mean ambient air temperatures were 22.6±0.7°C (mean±s.d.) and 35.3±0.4°C in the 23 and 35°C treatment, respectively. The mean sand temperature at 10 cm depth was lower than the ambient air temperature by 1.0°C (21.6±0.8°C) in the 23°C treatment while in the 35°C treatment, the sand temperature was lower by 3.0°C (32.2±1.3°C). Both temperature treatments showed significant differences between sand and air temperatures (paired *t*-test, t_{46}=8.64, P<0.001). The mean density of the coarse sand treatment was 1.57 ±0.02 g cm^{-3} and mean density of the fine sand treatment was 1.60 ±0.02 g cm^{-3} (Student's *t*-test, t_{30}=−3.68, P<0.001). Moisture content differed between sand treatments, where the coarse sand treatment contained 3.6±0.4% water and the fine sand treatment contained 5.4±1.4% water (Student's *t*-test, t_{35}=−6.52, P<0.001).

The effect of temperature and sand type on resting and burrowing metabolic rate

For *L. striata*, resting metabolic rate (RMR) and digging metabolic rate (DMR) was significantly positively affected by temperature (t_{14}=2.23, P=0.04; t_{14}=2.61, P=0.02, respectively). Sand treatments did not have a significant effect on RMR (t_{14}=0.33, P=0.74, Fig. 1A, filled symbols) or DMR (t_{14}=0.50, P=0.62, Fig. 1A, open symbols). For *L. inornata*, RMR was significantly positively affected by temperature (t_{12}=4.53, P=0.0007), but not significantly affected by sand treatments (t_{12}=0.30, P=0.77, Fig. 1B, filled symbols). DMR was not affected by temperature (t_{12}=1.83, P=0.09) or sand treatment (t_{12}=0.11, P=0.91, Fig. 1B, open

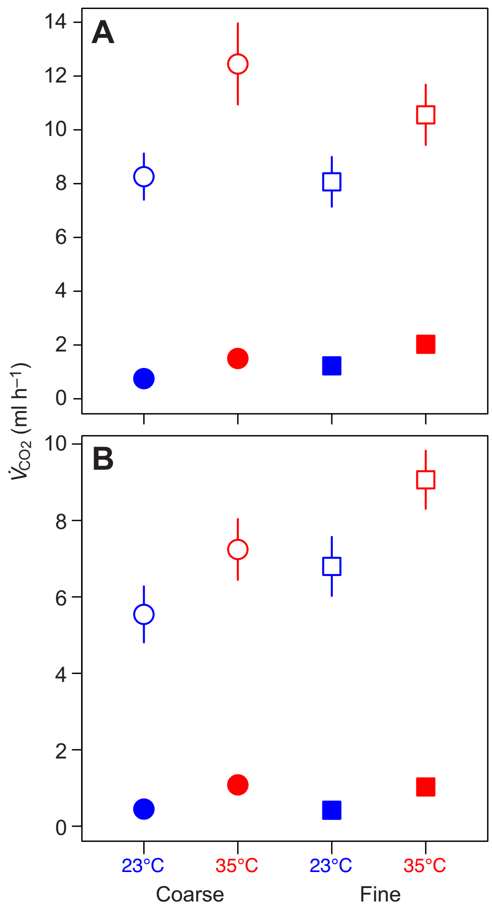

Fig. 1. Effect of sand type and temperature on resting and digging metabolic rates (RMR and DMR, respectively) in *Liopholis striata* and *Liopholis inornata*. The effect of sand type (coarse or fine) and temperature (23 or 35°C) on rates of CO_2 production ($\dot{V}_{CO_2}$, ml h^{-1}) during digging (DMR) and resting (RMR) for (A) *L. striata* and (B) *L. inornata*. Circles denote coarse sand, squares denote fine sand, blue symbols denote 23°C, red symbols denote 35°C, filled symbols denote RMR and open symbols denote DMR. Data are means±s.e. (N=6 for each treatment).

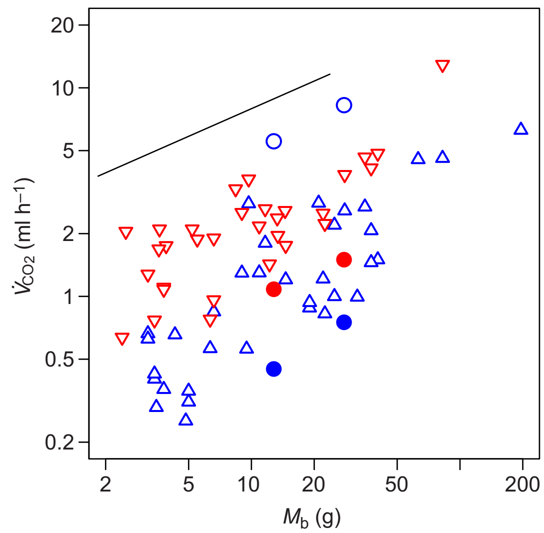

Fig. 2. Comparisons of resting and digging metabolic rates (RMR and DMR, respectively) in *L. striata* and *L. inornata* with RMR in other reptiles and DMR in a burrowing cockroach. The rates of CO_2 production ($\dot{V}_{CO_2}$, ml h^{-1}) during rest (RMR) are shown for *L. inornata* (body mass, M_b=12.8 g) and *L. striata* (M_b=27.8 g) at 23°C (filled blue symbols) and at 35°C (filled red circles). The RMR of other reptiles at 25°C (open blue triangles) and at 35°C (open red triangles) are shown for comparison (White et al., 2006a). The rates of CO_2 production during digging (DMR) are shown for *L. inornata* and *L. striata* digging through fine sand at 23°C (open blue circles). For comparison, the solid line shows the relationship between rate of CO_2 production during burrowing and body mass (M_b) for giant burrowing cockroach *Macropanesthia rhinoceros* (Xu et al., 2014). Data for metabolic rates (in mW) for burrowing cockroaches were converted to rate of CO_2 production assuming a respiratory quotient (RQ) of 1 (Xu et al., 2014); data for rates of O_2 consumption from White et al. (2006a) were converted to rates of CO_2 production assuming a RQ of 0.8.

symbols). There were no significant interactions between temperature and sand type (P>0.05 in all cases). Data for both *L. striata* and *L. inornata* are compared with resting metabolic rates of other reptiles (White et al., 2006a) and digging metabolic rates of giant burrowing cockroaches *Macropanesthia rhinoceros* (Xu et al., 2014) in Fig. 2.

The effect of temperature and sand type on burrowing rate and NCOB

The ambient air temperature had a positive effect on burrowing rate for both *L. striata* (t_{14}=6.45, P<0.0001, Fig. 3A) and *L. inornata* (t_{12}=3.25, P=0.007, Fig. 3C). Air temperature had a negative effect on the NCOB for *L. striata* (t_{14}=−3.97, P=0.001, Fig. 3B) but not for *L. inornata* (t_{12}=−1.25, P=0.24, Fig. 3D). There was no significant effect of sand treatments on burrowing rate for both species (*L. striata*, t_{14}=1.88, P=0.08; *L. inornata*, t_{12}=0.97, P=0.35). NCOB was not significantly affected by sand treatments (*L. striata*, t_{14}=−1.62, P=0.13; *L. inornata*, t_{14}=−0.72, P=0.48). Interactions between temperature and sand type were always non-significant (P>0.05 in all cases). The NCOB was negatively associated with burrowing rate for *L. striata* (t_{16}=−5.13, P<0.0001) but not *L. inornata* (t_{14}=−1.4, P=0.18).

Allometry of NCOB

Interspecific comparisons of the NCOB with body mass revealed, on average, that both skink species have lower mean NCOB (*L. striata*, 316±160 J m^{-1}; *L. inornata*, 188±58 J m^{-1}, averaged over all substrate types and temperatures) than burrow-constructing mammals of similar mass (Fig. 4), but higher than sand-swimming mammals that burrow through loose dry sand. The NCOB for both skink species was higher than the predicted net cost of pedestrian transport (NCOT) for runners and walkers by over two orders of magnitude (predicted NCOT of *L. striata*, 0.91 J m^{-1} and *L. inornata*, 0.54 J m^{-1}).

Burrow dimensions and allometry

The mean burrow cross-sectional area constructed by *L. striata* was 5.3±1.4 cm^2 and 2.6±0.7 cm^2 for *L. inornata*. The body width of *L. striata*, on average took up 51% of their constructed burrow space. The body width of *L. inornata* took up 56% of the space of their constructed burrow. Video recordings showed skinks would often turn around halfway along a completed burrow and rest in a C shape, with their head and tail end towards the entrance, taking up all the space in the burrow.

Interspecific comparisons of burrow cross-sectional area (A_b) with body mass (M_b) revealed allometric scaling for all animals (Fig. 5). Three specific groups were distinguished from the grouped data; birds (A_b=5.46$M_b^{0.62}$, r^2=0.84), reptiles (A_b=0.46$M_b^{0.74}$, r^2=0.99) and vermiforms (A_b=0.39$M_b^{0.63}$, r^2=0.99). Reptiles (excluding tortoises) constructed relatively narrower burrows but still within the variation of the grouped data (Tukey's HSD, P=0.02). Vermiforms constructed significantly smaller burrows (Tukey's HSD, P<0.0001) and birds

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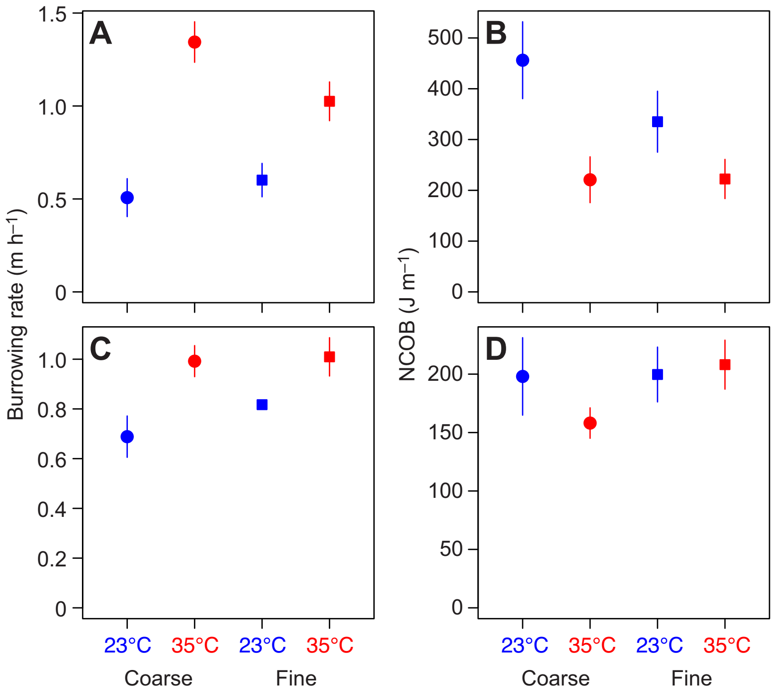

Fig. 3. Effect of sand type and temperature on burrowing rate and net cost of burrowing (NCOB) in *L. striata* and *L. inornata*. The effect of sand type (coarse or fine) and temperature (23 or 35°C) on burrowing rate (m h^{-1}) and NCOB (J m^{-1}) for (A,B) *L. striata* and (C,D) *L. inornata*. Circles denote coarse sand, squares denote fine sand, blue symbols denote 23°C and red symbols denote 35°C. Data are means±s.e. (*N*=6 for each treatment).

constructed significantly larger burrows than the overall grouped animals of similar mass (Tukey's HSD, $P<0.0001$).

Morphometrics

Linear discriminant analysis (LDA) revealed distinct separations for all retreat groups [hollow logs/rock crevices, hollow logs/burrows, burrows, vegetation (under scrub, grass or bush) and trees (arboreal), Fig. 6] and Wilk's lambda for size-corrected residual values revealed nine body morphology variables were significantly different among retreat preferences ($F_{4,19}$=5.26, $P<0.0001$): hindfoot length, head length, pelvis height, tail width, body width, head width, upper hind leg length, upper foreleg length, and lower foreleg length (supplementary material Table S2). The first discriminant function (LD1) reduced total variance by 67% and was positively loaded for body width and head length (loading value >1) while negatively loaded for pelvis height, upper hindleg length and hindfoot length. Tree species were loaded negatively, revealing longer hind leg (upper hindleg length and hindfoot length) and pelvic height, whereas vegetation species were loaded positively, with larger heads and bodies, and smaller limbs (Fig. 6).

The second discriminant function (LD2) accounted for 20% of the total variation (supplementary material Table S2) and loaded positively for lower foreleg length, upper hindleg length and head width, but was negatively loaded for upper foreleg length, tail width and body width (Fig. 6). The second function loaded burrowing species positively, revealing longer upper hindleg, shorter upper foreleg, and narrower body width and tail width. Species living in hollow logs and rock crevices showed the opposite traits, with longer upper foreleg length, wider body width and tail width and shorter upper hindleg and head width.

The value of λ>1 indicates that species traits are more similar than expected under Brownian motion (Cooper et al., 2010; Münkemüller et al., 2012). Our value of λ was high (1.42), and significantly different from zero (likelihood ratio test $P<0.0001$), suggesting that related species are more similar to one another than they are to unrelated species.

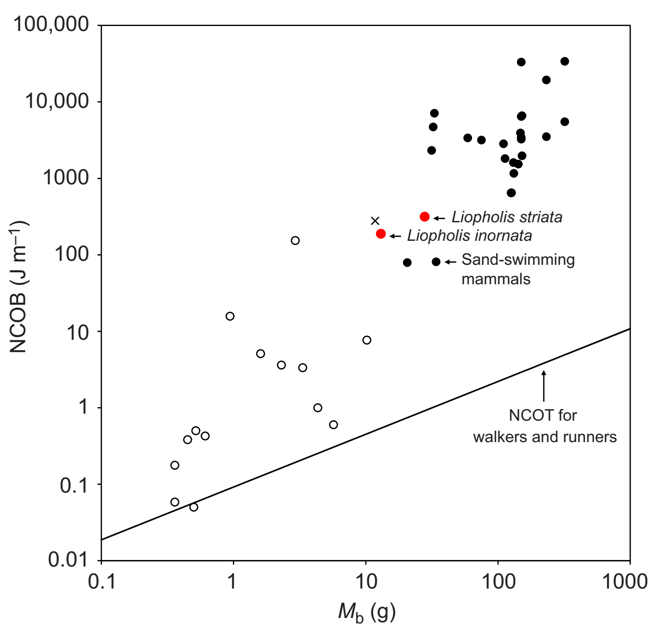

Fig. 4. Comparison of the average net cost of burrowing (NCOB) of *L. striata* and *L. inornata* with other species. The NCOB (J m^{-1}) for *L. inornata* (body mass M_b=12.8 g) and *L. striata* (M_b=27.8 g) is shown (filled red circles) in comparison to other taxonomic groups which were categorised into the following: invertebrates (open circles), mammals (filled circles) and amphibian (×). For comparison, the solid line shows the relationship between net cost of transport (NCOT) and M_b (NCOT=0.092$M_b^{0.69}$) for walkers and runners from a wide range of animals from Full et al. (1990). Burrowing data are from published studies presented in supplementary material Table S3.

DISCUSSION

Metabolic rate

RMRs of both *L. striata* and *L. inornata* are toward the lower range of measurements of other reptiles at similar temperatures (Fig. 2). *L. striata* and *L. inornata* are both desert-adapted species, and arid

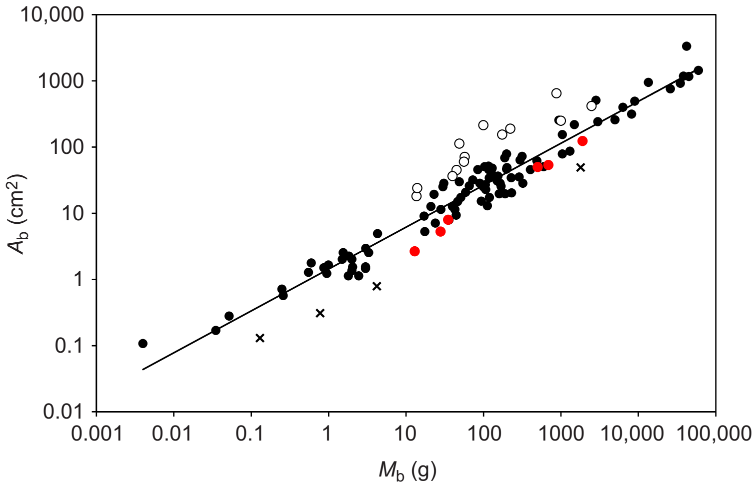

Fig. 5. Interspecific relationship between burrow cross-sectional area (A_b, cm^2) and body mass (M_b, g). Grouped data (filled circles) include mammals, fish, amphibians and invertebrates, while birds (open circles), reptiles (red circles) and vermiform species (×) were separated. The regression line represents an allometric slope of 0.64 (A_b=1.37$M_b^{0.64}$, r^2=0.96) for grouped data. Data are from published studies presented in supplementary material Table S4.

species are often shown to have lower metabolic rates than related non-arid species (e.g. McNab and Morrison, 1963; Lovegrove, 1986; Lighton et al., 2001; Tieleman et al., 2003). There is, however, no association between field metabolic rate and aridity for free-living reptiles (Nagy et al., 1999) and we are not aware of any broad-scale tests for an association between RMR and aridity in reptiles. Thus, although the low RMRs of *L. striata* and *L. inornata* are consistent with the hypothesis that species from arid environments have low RMR, this hypothesis remains to be verified for reptiles more generally.

DMRs of *L. striata* and *L. inornata* at 23°C are around 24–40% lower than the DMR of similarly sized giant burrowing cockroaches *Macropanesthia rhinoceros* measured at 25°C (Fig. 2). DMR increased with temperature in both *L. striata* (Q_{10}=1.28) and *L. inornata* (Q_{10}=1.29), revealing weak temperature dependence relative to those observed for physiological traits in other species (values of Q_{10} typically fall between 2 and 3; Withers, 1992). For example, the temperature dependence of DMR of the *Liopholis* species considered in the present study is lower than that of a related habitat generalist, *Liopholis whitii* (Bellamy, 2006), which has a Q_{10} of 1.6 for metabolic rate during activity (Huey and Bennett, 1987).

Energetic cost of burrowing

Digging is an energetically demanding process, resulting in skinks expending 350 times more energy moving the same distance than the predicted cost of terrestrial locomotion (Fig. 4). Both *Liopholis* skinks have a similar NCOB to spadefoot toads (*Spea multiplicata*) (Seymour, 1973) and expend less energy per unit distance than a mammal of similar mass (Fig. 4). Although among-species variation in NCOB is positively correlated with body mass, there is considerable variation in the NCOB that is not explained by mass (Fig. 4). Differences in air temperature have been shown to affect the NCOB of ectotherms; as temperature increases, the NCOB of scorpions (*Urodacus yaschenkoi*) decreases (White, 2001), as is also generally the case for *Liopholis* skinks in the present study, although the effect of temperature is not significant for *L. inornata* (Fig. 3). This trend was also not observed in *S. multiplicata* (Seymour, 1973).

NCOB is also dependent on the physical and chemical properties of the substrate through which animals burrow (Collis-George, 1959; Vleck, 1979; Zelová et al., 2010). In the present study, the NCOB was not affected by substrate for either species (Fig. 3B,D). Similarities in the NCOB between coarse and fine sand may be due

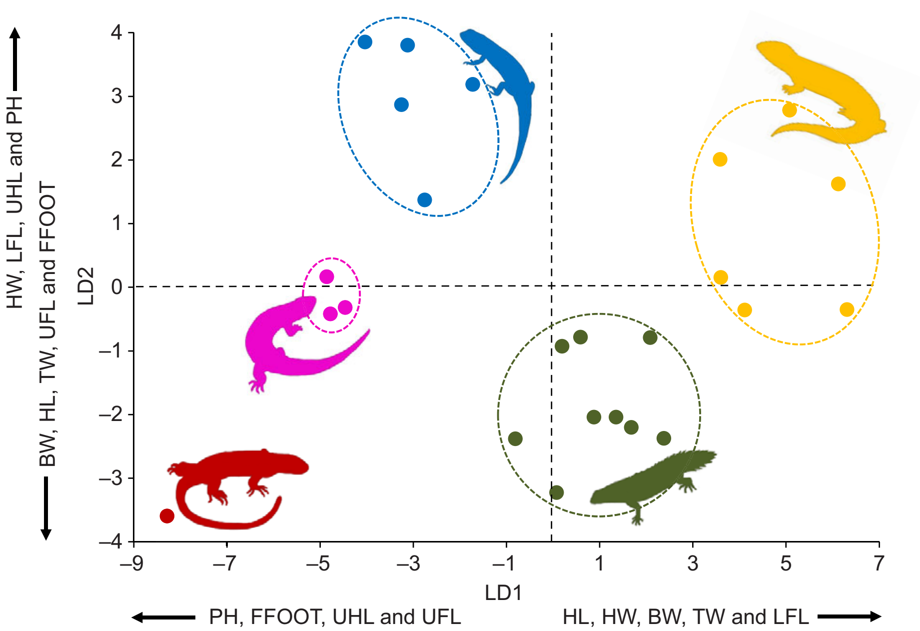

Fig. 6. Linear discriminant function 1 (LD1) and 2 (LD2) for size-corrected residual morphometric dimensions. Dashed circles represent outer regions of each retreat group and arrows represent loading direction of morphology variables. Retreat preferences and a representative skink for each group represented by the following colours and silhouette image, respectively: burrow retreats (blue, *Liopholis striata*), vegetation retreats (yellow, *Tiliqua scincoides*), hollow logs/rock crevices (green, *Egernia depressa*), hollow logs/burrow retreats (pink, *Bellatorias major*) and trees (red, *Corucia zebrata*). HL, head length; HW, head width; BW, body width; PH, pelvic height; TW, tail width; LFL, lower forelimb; UFL, upper forelimb; UHL, upper hindlimb; FFOOT, forefoot.

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to small differences in density (difference of 0.03 g cm^{-3}) and moisture content (difference of 1.79%) relative to other studies. The densities of the 'hard' and 'soft' soil treatments employed by Luna and Antinuchi (2006), for example, differed in density by 0.61 g cm^{-3}, and they found that the NCOB was significantly higher in the 'hard' soil treatment compared with the 'soft' soil treatment. Similarly, Vleck (1979) used a variety of substrates from fine sand (1.37 g cm^{-3}) to clay (1.84 g cm^{-3}) and observed that burrowing energetics were highest in clay substrates and were lowest in gravelly sand substrates. The 'dry' and 'damp' sand treatments utilised by Lovegrove (1989) had moisture contents of 0% and 7.9%, respectively, and resulted in the NCOB being highest when burrowing in dry sand relative to damp sand. Finally, sand-swimming mammals expended less energy to 'swim' through loose un-compacted sand than both burrowing mammals and skinks. Since dry loose sand has similar properties to a fluid (Shimada et al., 2009), it is likely that adopting a swimming type of locomotion (e.g. undulatory) in this environment will reduce the energy expenditure during excavation. An example can be seen in sand-swimming lizards, where they have been observed transitioning from quadrupedal locomotion at the surface to undulatory locomotion when submerged in the sand (Maladen et al., 2009; Sharpe et al., 2013).

Burrowing rate

The average burrowing rate of the *Liopholis* skinks increased at higher air temperature (Fig. 3A,C), as has previously been shown for scorpions (White, 2001). Sand treatment did not significantly affect the burrowing speed in *Liopholis* skinks; however, other studies have shown that different substrate characteristics affect burrowing speed (Lovegrove, 1989; Luna and Antinuchi, 2006; Zelová et al., 2010). The relationship between the energy expenditure during locomotion and locomotory speed has been well documented (Taylor et al., 1970; Full et al., 1990; Seymour et al., 1998). All show a rapid decline in the cost of transport as speed increases. Although total power output increases approximately linearly with speed (Margaria et al., 1963; Heglund et al., 1982), the energy expended to move a given distance decreases non-linearly as speed increases. *Liopholis* skinks also follow this pattern, where the NCOB decreases with increasing burrowing rate, although the relationship is not significant for *L. inornata*. Irrespective of the medium travelled through, it seems the cost of transport per unit distance is more efficient at higher speed. However, if an animal travels outside its range of preferred speed without changing gait, then the cost of transport tends to increase (e.g. Hoyt and Taylor, 1981). It is therefore likely that the NCOB will not decrease indefinitely as speed increases, but animals presumably avoid burrowing at speeds that would require the use of anaerobic metabolism (Seymour, 1973) and avoid speeds that are high enough to cause an increase in NCOB. Thus, selecting a burrowing speed that avoids anaerobic metabolism and minimises NCOB allows burrowing animals to tunnel economically.

Adaptations for burrowing in semi-fossorial skinks

The size of a burrow is fundamentally dictated by the body shape and method of burrowing employed by the animal that constructed it. Elongated animals (e.g. marine worms, eels) construct narrower burrows compared with globular animals (e.g. birds) of similar body mass (White, 2005). The advantage of smaller, narrower bodies is that animals can expend less energy excavating burrows, because the energetic cost of burrowing is proportional to the amount of substrate removed (Vleck, 1981). Animals with spherical body shapes are therefore required to undertake more work per unit distance to excavate their wider burrows. Fossorial mammals minimise the cost of burrow construction by developing shorter and stronger limbs (Nevo, 1979) to increase power output and reduce the quantity of soil that must be excavated to burrow a given distance. Fossorial mammals in general are also smaller than semi-fossorial mammals (White, 2003). Fossorial reptiles like lizards and snakes generally have elongated bodies and reduced limbs to reduce energy expenditure during burrowing, and by increasing muscle mass and muscle cross-sectional area longitudinally they are able to do so without sacrificing power (Navas et al., 2004). Both *Liopholis* skinks examined in the present study constructed smaller burrows than the predicted burrow cross-sectional area, on the basis of their body mass (Fig. 5), but were within the variation observed in the grouped data.

Behavioural adaptations such as utilising a sit-and-wait foraging strategy from the safety of a burrow may allow energy conservation and reduce the risk of predation. Active foraging lizards have daily rates of energy expenditure about 1.3–1.5 times greater than sit-and-wait lizards in the same habitats, however the net food gain is about 1.3–2.1 times greater for foraging lizards (Huey and Pianka, 1981). Both *Liopholis* skink species use a sit-and-wait strategy where they sit inside the entrance of their burrows and wait for prey that pass by (Pianka and Giles, 1982), although some *L. striata* are occasionally seen foraging at night. Sociality in subterranean animals has been shown to facilitate the partitioning of burrowing workload among multiple individuals, thereby reducing each individual's total energy cost (Hansell, 1993; Ebensperger and Bozinovic, 2000b). Sociality allows the construction of complex multi-entrance burrows, which provide protection from predators (Rand and Dugan, 1983) and, for endotherms, provides a greater ability to thermoregulate (Yahav and Buffenstein, 1991; Kauffman et al., 2003). Given their higher individual energy costs, solitary species tend to be more efficient diggers than social species, as compared in two African mole rats (Bathyergidae, Rodentia). Solitary *Heliophobius argenteocinereus* expend less energy digging over a given distance than communal-living *Fukomys mechowii*, but *F. mechowii* shares the workload of burrow construction in a cooperative group (Zelová et al., 2010). Most *Egernia* group skinks, including the semi-fossorial skinks, show some degree of social communal living among closely related kin (Pianka and Giles, 1982; McAlpin et al., 2011; Fenner et al., 2012), which, in combination with the relatively low NCOB afforded by an elongate body form, may contribute to minimising the individual cost of burrow construction.

Morphological specialisations for burrowing

The relationship between body shape and habitat specialisation has been well studied (Vitt et al., 1997; Thompson and Withers, 2005; Grizante et al., 2012). Some studies have shown no relationship between morphology and habitat preference in lizards (Jaksić et al., 1980). Others found anti-predator escape (distance a lizard moved away from potential predator) was correlated with body shape [particularly body width and pelvic dimensions (Schulte et al., 2004)]. *Egernia* skinks occupy a wide range of habitats (Chapple, 2003) and show diverse body shapes, from very elongated, short-limbed *Cyclodomorphus* species to the large, heavy built *Tiliqua* (Wilson and Swan, 2013). Divergence of body shapes in the *Egernia* skinks relating to retreat preferences seems to be conserved and dependent on phylogeny (λ=1.42) as related species have similar retreat preferences (supplementary material Fig. S1). However, morphological differences between

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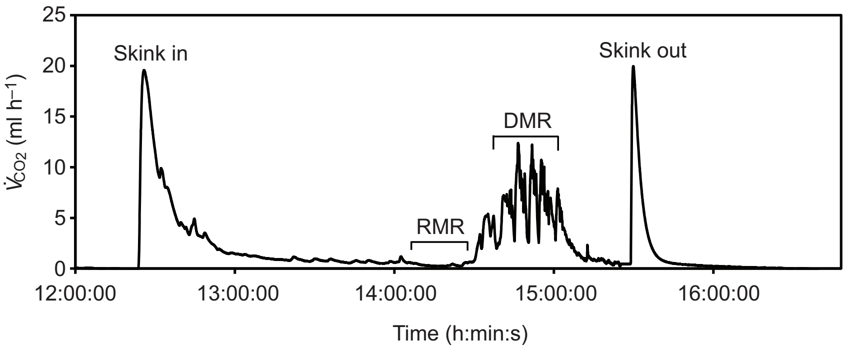

Fig. 7. Resting and digging metabolic rates (RMR and DMR, respectively) for *L. inornata*. Example data trace showing rate of CO_2 production ($\dot{V}_{CO_2}$, ml h^{-1}) during rest (RMR) and digging (DMR) for *L. inornata* (M_b=15.7 g). Treatment conditions are as follows: coarse sand (sand density: 1.6 g cm^{-3}, sand moisture: 3.8%) at 35°C with flow rate at 300 ml min^{-1}. DMR was defined by the spike in CO_2 production (verified by video recording). During digging, the animal placed its head on the sand and angled its body so one of the front limbs was in front of the head. A forefoot was then used to shovel the sand away with about 5–11 strokes before switching to the other side. Between switches, the animal rested for 0.5–3 s.

retreat preferences have been observed at a sub-species level (e.g. cranial differences in *Egernia depressa*; Doughty et al., 2011; Hollenshead, 2011).

LDA revealed distinct separation between rock crevices, hollow logs and burrow retreat groups. Burrowing species have narrower bodies, smaller heads, hindfoot and upper forelimb, and longer upper hindlimbs (Fig. 6). Similar specialisations for burrowing as those observed in the present study for *Egernia* group skinks have also been identified in Australian *Ctenophorus* (Agamidae) and *Varanus* (Varanidae), where burrowing representatives of all three groups have wider heads and longer, narrower bodies than their non-burrowing relatives (Thompson and Withers, 2005; Thompson et al., 2008). There is no consistent association between burrowing and limb dimensions; however, burrowing skinks and varanids have relatively long upper hindlimbs, while burrowing skinks and agamids have relatively short upper forelimbs. Shorter forelimbs for both skinks and agamids may allow them to increase their power output during excavation as they tend to burrow head first with their front limbs. However, the benefits of burrowing with shorter limbs can only be properly examined though biomechanical and kinematic studies.

In conclusion, digging requires a high level of specialisation to ensure that the benefits of burrowing outweigh the cost of a burrowing lifestyle. Locomotion via burrowing has been shown to greatly affect energy expenditure in various animals. The present study has provided the first estimates of the energy expenditure of burrowing in skinks and reveals that the semi-fossorial skinks, *L. striata* and *L. inornata* exhibit specialisation towards a subterranean lifestyle. These features include a relatively low NCOB compared with other tunnel-constructing species, low temperature dependence of metabolic rate during burrowing, construction of narrower burrows than mammals, and exhibition of morphological traits such as narrower bodies and smaller limbs compared with other *Egernia* group species. Future research on the energetic cost of burrowing in specialised fossorial reptiles (e.g. *Lerista*, *Amphisbaenia* and *Serpentes*) should be compared with the measurements of semi-fossorial reptiles obtained in the present study, to verify whether fossorial species expend less energy on burrow excavation than semi-fossorial reptiles, and establish the causality of why fully fossorial reptiles show convergence towards legless, elongated bodies and lower metabolic rate.

MATERIALS AND METHODS

Animal collection and maintenance

Six *Liopholis striata* (formerly *Egernia striata* Sternfeld 1919) (mean±s.d. SVL and mass of 93.6±3.4 mm and 27.8±3.7 g, respectively) were collected from the goldfields region of Western Australia (Government of Western Australia Department of Environment and Conservation Licence SF008358) in October 2011. Six *Liopholis inornata* (formerly *Egernia inornata* Rosén 1905) (mean±s.d. SVL and mass of 76.4±3.5 mm and 12.8±1.3 g, respectively) were collected from Big Desert State Forest, Victoria (Victoria Department of Sustainability and Environment Permit 10005993) in October 2011. Skinks were housed individually in white plastic tubs (60×40×26 cm) which contained sand (25–30 mm deep) (Ki-carma®, Ormeau, Australia) in a temperature-controlled room (20±5°C). Each tub was maintained under two linear fluorescent bulbs with a 12 h:12 h light:dark photoperiod cycle; one bulb emitted only visible radiation (Crompton Lighting, Padstow, NSW, Australia) and the other bulb emitted visible, ultraviolet-A (320–400 nm) and ultraviolet-B (290–320 nm) radiation (Repti Glo 10.0, Exo Terra®, Rolf C. Hagen Inc., Montreal, QC, Canada). Skinks were provided with two black plastic refuges: one refuge was situated at one end of the tub directly under a 50 W halogen lamp (Crompton Lighting, Padstow, NSW, Australia) that heated the top of the refuge to 35±2°C, the inside of the refuge to 30±2°C, and the far end of the tub to 25±2°C for 8 h in the middle of the 12 h light cycle; the second refuge was positioned at the other end of the tub away from the halogen lamp with a wet sponge positioned on top to maintain a mean relative humidity of 60% in the tub.

Skinks were given access to water at all times and were maintained on a diet of finely processed raw food that consisted of 50% vegetables (butternut pumpkin, green beans and rocket), 40% meat (turkey mince) and 10% fruit (strawberries). This food mix was supplemented with a reptile-specific multi-vitamin (Herptivite™, Rep-Cal, Los Gatos, CA, USA) and calcium powder (phosphorus-free calcium with vitamin D_3 Ultrafine, Rep-Cal) at the recommended dose of 15 ml of each supplement per 1 kg of food. *L. striata* were given 2.5 ml and *L. inornata* were given 1.2 ml of this food and supplement mix once or twice a week. Faeces were removed and water was replaced twice a week; the sand was replaced every six months. All skinks were handled in accordance with the Queensland Department of Environment and Resource Management Scientific Purposes Permit WISP10698712 and the University of Queensland Animal Ethics Approval Certificate SBS/288/11/ARC.

Experimental treatments

To determine whether temperature and substrate characteristics affect the NCOB, each skink was individually subjected to an environment with two variables: air temperature (23 and 35°C) and substrate characteristics (coarse sand and fine sand), which were presented in a full factorial combination.

Sand characteristics

Two grades of commercial sand were used to produce sand treatments that varied in particle size distribution. Washed fine sand (Joint Fill fine graded sand, Cement Australia Pty Ltd, Darra, QLD, Australia) consisting of >95% silica dioxide sand and <5% mineral and organic impurities (particle size: 0.06–0.25 mm) and washed coarse sand (Easy mix Tiler's coarse sand, River Sands Pty Ltd, Carbrook, Australia) consisting of <1% silt (particle size: 0.5–1.5 mm).

Sand bulk density (compacted) was measured as weight of soil per cubic centimetre (g cm^{-3}), and the moisture content (%) of sand during burrowing trials was regulated by adding measured amounts of water to dry sand until a standard consistency was achieved (damp enough to be moulded by hand; White, 2001; White et al., 2006b). The coarse sand treatment consisted of a mixture of 70% coarse sand and 30% fine sand, because coarse sand alone

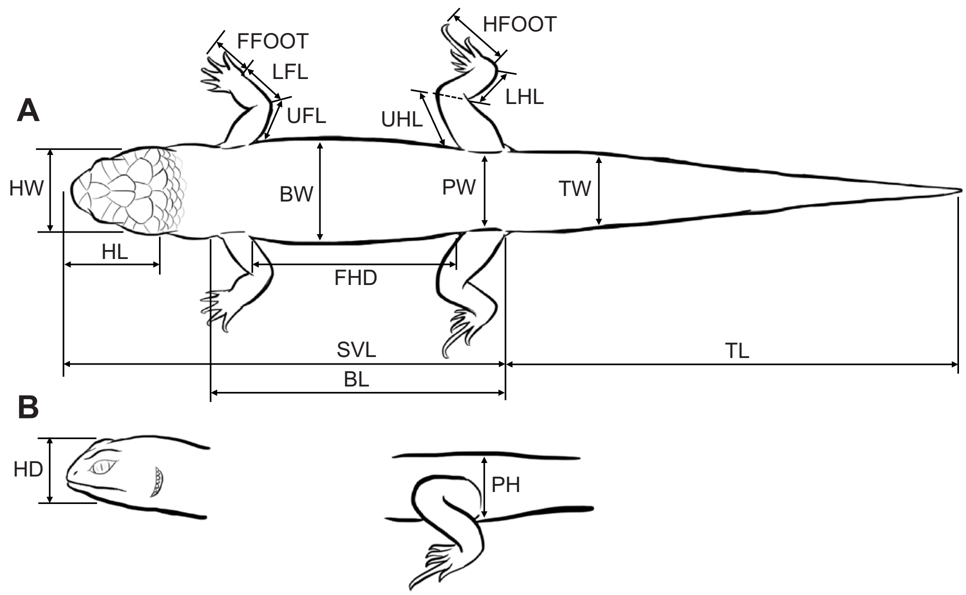

Fig. 8. Morphometric measurements used for analysis. (A) Dorsal and (B) lateral view of a skink's body plan showing measurements recorded. Snout–vent length (SVL), tip of snout to anterior end of cloaca; tail length (TL), anterior end of cloaca to tip of tail; tail width (TW), widest portion of the tail; head length (HL), ventral measurement from tip of the snout to the end of the external ear; head width (HW), widest portion of the head anterior to the ear; head depth (HD), highest position of the head to the bottom of the lower jaw; body width (BW), widest portion of mid-body; body length (BL), posterior of the neck to the anterior end of cloaca; pelvic width (PW), width of body immediately anterior to hind legs; pelvis height (PH), highest position of the body immediately anterior to the hind legs to the lowest position; fore-hind limb distance (FHD), distance between the insertion of the forelimb to the insertion of the hind leg; upper foreleg length (UFL), from insertion of foreleg into body to elbow; lower foreleg length (LFL), from elbow to proximal end of manus; forefoot length (FFOOT), from proximal end of manus to proximal end of the longest finger (3rd); upper hind leg length (UHL), from insertion of hind leg into body to knee; lower hind leg length (LHL), from knee to proximal end of foot; hindfoot length (HFOOT), from proximal end of foot to proximal end of longest toe (4th toe). Image based on *Liopholis striata*.

would not bind at all without the addition of some fine sand. The fine sand treatment consisted of 100% fine sand. Soil temperature during burrowing trials was measured 10 cm under the surface of the sand using a type K thermocouple (QM1538 Digitech®, www.jaycar.com.au).

Respirometry

Positive pressure flow-through respirometry (Lighton, 2008) was used to measure resting metabolic rate (RMR) and digging metabolic rate (DMR) as the rate of CO_2 production ($\dot{V}_{CO_2}$, ml h^{-1}). A gas analyser sub-sampler pump (SS-3, Sable Systems International, Las Vegas, NV, USA) was used to pump outside air scrubbed of CO_2 (using soda lime, Chem-Supply, Adelaide, Australia) and water vapour (using Drierite, W. A. Hammond Drierite Co. Ltd, Xenia, OH, USA) to a mass flow controller (GFC17, Aalborg Instruments & Controls Inc., Orangeburg, NY, USA) that regulated flow rate to a nominal value of 400 ml min^{-1} (for *L. striata*) or 300 ml min^{-1} (for *L. inornata*). The mass flow controller was calibrated using a NIST-traceable bubble film flow meter (1-10-500 ml, Bubble-O-Meter, Dublin, OH, USA). After passing through the mass flow controller, air was pushed through a respirometry chamber, which was a 2 l airtight clear polypropylene container (111×111×283 mm) holding 1.2 l of sand. After the respirometry chamber, air was rescrubbed of water vapour (using Drierite) before passing through an infrared CO_2 gas analyser (LI-820, LI-COR® Biosciences Inc., Lincoln, NE, USA). The fractional concentration of CO_2 in the ex-current air ($F\text{E}_{CO_2}$) was recorded at a frequency of 1 Hz using Li-Cor software (LI-820 software version 2.0). The CO_2 analyser was calibrated with dry CO_2-free air and a certified gas mix (0.386±0.008% CO_2 in N_2, BOC Gases, Wetherill Park, Australia).

Resting and burrowing metabolic rate measurements

Each skink was fasted for 3–4 days prior to measurement to ensure a post-absorptive state (Secor, 2009). The background fractional CO_2 concentration of the ex-current air from the respirometry chamber was measured for a minimum of 2 h prior to the introduction of the animal. Before the skink was placed in the chamber, body mass was measured to 0.1 g using a digital scale (Mettler Toledo XS4001S Precision Balance, Port Melbourne, Victoria, Australia). Each individual was measured once for each treatment for approximately 5–7 h beginning around dusk, with the average resting $\dot{V}_{CO_2}$ recorded for approximately 5 min when $\dot{V}_{CO_2}$ was low and stable (e.g. Fig. 7). We refer to this measurement as resting metabolic rate (RMR) rather than standard metabolic rate because animals were measured during the active phase of their circadian cycle. The average DMR was taken over a 5 min period of consistent burrowing (e.g. Fig. 7). During the experiment, skink activities were filmed using an infrared (IR) camera (R-IR-60A, Airtight Security Plus, Rockville, Maryland) and recorded using GeoConcept Multiviewer 1.0 software (GeoConcept, Bagneux, France). The respirometry chamber was housed in a temperature control cabinet (ERI140, ProSciTech, Thuringowa, Australia) that regulated the air treatment temperatures at ±1°C. Average burrow dimensions (length, width and height) were measured to the nearest mm with a digital vernier caliper (Part no: 2351, Kincrome® Australia Pty Ltd., Victoria, Australia) at the conclusion of the burrowing trial. The respirometry chamber was angled at approximately 10 deg, which generally allowed the skinks to burrow at the top, making it easier to measure burrow parameters.

Mean $\dot{V}_{CO_2}$ (converted to ml h^{-1}) was calculated following Withers (2001):

$$\dot{V}_{CO_2} = \frac{(\dot{V}_i \times F\text{E}_{CO_2})}{(1 + ((1/\text{RER}) - 1) \times F\text{E}_{CO_2})}, \quad (1)$$

where $\dot{V}_{CO_2}$ is rate of CO_2 production (ml CO_2 min^{-1}), $\dot{V}_i$ is rate of incurrent airflow (ml min^{-1}), $F\text{E}_{CO_2}$ is ex-current fraction of CO_2 and RER is respiratory exchange ratio, which was assumed to be 0.8. Rate of burrowing energy expenditure (J h^{-1}) was calculated by subtracting resting $\dot{V}_{CO_2}$ from burrowing $\dot{V}_{CO_2}$ and multiplying by the energy equivalent of 1 ml CO_2 production (25.6 J; Withers, 1992). The NCOB (J m^{-1}) was determined by dividing rate of energy expenditure by burrowing rate (m h^{-1}).

Comparative data for NCOB and body mass were compiled from the literature for a variety of vertebrate and invertebrate studies (supplementary material Table S3). Species were grouped taxonomically (mammals, reptiles, amphibians and invertebrates), and the effects of temperature and substrate were examined. Data for NCOB were compared with the predicted scaling relationship for the net cost of pedestrian transport (NCOT) of runners and walkers from Full et al. (1990).

Burrow dimensions

The average burrow cross-sectional area (A_b, cm^2) for *L. striata* and *L. inornata* was calculated based on an ellipse shape: $A_b = \pi\alpha\beta$, where α is half of the burrow width and β is half of the burrow height. Additionally the proportion (%) of body width space taken up within the burrow (burrow width) was compared with the total burrow width. For comparisons between burrow dimensions with other animals, published measurements of burrow cross-sectional area were obtained from White (2005), supplemented with additional studies (supplementary material Table S4). If multiple values were available, the average burrow dimension was calculated and when body mass was not stated, an appropriate mass was obtained from multiple published sources. Data were $\log_{10}$ transformed and classified into the following groups: grouped data (mammals, fish, amphibians and invertebrates), birds, reptiles, and vermiforms (worm-like shape). Scaling exponents of burrow area with mass (g) from each group were calculated by linear regression.

Morphometrics

Body proportions of skink species from the *Egernia* group were compared with *L. striata* and *L. inornata*. A digital vernier caliper (Part no: 2351, Kincrome® Australia Pty Ltd., Victoria, Australia) or one metre ruler (for larger specimens) was used to measure 17 body variables to 0.01 mm or 1 mm (tail length), respectively (Fig. 8). Measurements were taken from seven live species (81 individuals) kept at the University of Queensland and 24 ethanol-preserved species (121 individuals) from the Queensland Museum. The mean of each morphological variable was calculated for each species. Furthermore, species were grouped into five different retreat preferences: hollow logs/rock crevices, hollow logs/burrows, burrows, vegetation (under scrub, grass or bush) and trees (arboreal) based on the retreat with which they are most commonly associated in published accounts (supplementary material Table S1). Although tail length has been shown to be significantly associated with retreat type in the literature (Kohlsdorf et al., 2001; Bickel and Losos, 2002; Schulte et al., 2004; Velasco and Herrel, 2007), this association was not considered in the present study because a large number of museum specimens had missing or regenerated tails.

Statistical analysis

The effect of temperature and substrate characteristics

Analyses were performed in R 3.0.1 (R Development Core Team, 2013). An independent student's *t*-test was used to test the null hypothesis that sand density and moisture do not differ between treatments and a paired *t*-test was used to determine if sand temperature was significantly different from the ambient air temperature. The effect of air temperature (23 or 35°C) and substrate characteristics (coarse or fine) on the NCOB and burrowing rate for *L. striata* and *L. inornata* were analysed using linear mixed effects models in the R 'nlme' package (Pinheiro et al., 2013) with sand and temperature as fixed effects and individual identity as a random effect to account for repeated measurements of each individual. Two individual *L. striata* were repeated twice in the experiment. Means±s.d. are presented, α was set at 0.05 for all statistical tests.

Burrow allometry

Analysis of covariance (ANCOVA) was used to test for differences in burrow cross-sectional area among species [grouped data (mammals, fish, amphibians and invertebrates), birds, reptiles, and vermiforms] with mass as a fixed continuous predictor.

Morphometrics: linear discriminant analysis

Linear discriminant analysis (LDA) was used to calculate a set of weightings which allowed each pre-determined group to be distinguished. Morphology data were $\log_{10}$ transformed and corrected for size by obtaining residuals from body length for each morphology variable using linear models prior to LDA. A forwards stepwise model using greedy.wilks function from the 'klaR' package (Weihs et al., 2005) was performed to extract significant variables depending on the Wilk's lambda criterion. The results were used for the following discriminant function analysis by the lda function from 'MASS' package (Venables and Ripley, 2002). Phylogenetic signal was also calculated using LDA scores to determine if related species resemble one another using (Pagel, 1999) lambda (λ).

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Competing interests

The authors declare no competing or financial interests.

Author contributions

N.C.W., C.R.W. and M.R.K. designed the study. N.C.W. collected the data. N.C.W., C.J.C. and C.R.W. analysed the data. M.R.K., L.A.A. and C.R.W. collected the animals. L.A.A. and N.C.W. maintained the animals. N.C.W. wrote the paper, and all authors contributed to data interpretation and the final version of the paper.

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Supplementary material

Supplementary material available online at
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Table S1. List of *Egernia* group species used for morphometric analysis showing number of individuals per species measured (alive: The University of Queensland, preserved: Queensland Museum) with retreat types from cited references.

Scientific name	Number		Retreat type	References*
	Alive	Preserved		
Non-Australian out-group				
Corucia zebrata (Gray, 1856)		1	Trees	3
Cyclodomorphus				
Cyclodomorphus casuarinae (Duméril and Bibron)		3	Vegetation	1
Cyclodomorphus gerrardii (Gray, 1845)	7	3	Vegetation	1
Bellatorias				
Bellatorias frerei (Günther, 1897)	4	10	Hollow logs/ burrows	1, 2
Bellatorias major (Gray, 1845)		10	Hollow logs/ burrows	1, 2, 4
Egernia				
Egernia cunninghami (Gray, 1832)	20	10	Hollow logs/rocks	1, 2
Egernia depressa (Günther, 1875)		1	Hollow logs/rocks	1, 2
Egernia hosmeri (Kinghorn, 1955)		7	Hollow logs/rocks	1, 2
Egernia kingii (Gray, 1838)		1	Burrows	1, 2
Egernia mcpheei (Wells & Wellington, 1984)		2	Hollow logs/rocks	1, 2
Egernia napoleonis (Gray, 1838)		1	Hollow logs/rocks	1, 2
Egernia richardi (Peters, 1869)		5	Hollow logs/rocks	1, 2
Egernia rugosa (De Vis, 1888)		5	Hollow logs/ burrows	1, 2
Egernia saxatilis (Cogger, 1960)		2	Hollow logs/rocks	1, 2
Egernia stokesii (Gray, 1845)		8	Hollow logs/rocks	1, 2
Egernia striolata (Peters, 1870)	13	10	Hollow logs/rocks	1, 2
Liopholis				
Liopholis inornata (Rosén, 1905)	12	3	Burrows	1, 5
Liopholis modesta (Storr, 1968)		10	Burrows	1, 2, 6
Liopholis striata (Sternfeld, 1919)	6	2	Burrows	1, 5
Liopholis whitii (Lacépède, 1804)		10	Burrows	1, 2, 6
Tiliqua				
Tiliqua nigrolutea (Quoy & Gaimard, 1824)		2	Vegetation	1, 7
Tiliqua occipitalis (Peters, 1863)		2	Vegetation	1
Tiliqua rugosa (Gray, 1825)		6	Vegetation	1, 8
Tiliqua scincoides (White, 1790)	19	7	Vegetation	1

* Reference listed: 1 –Wilson and Swan (2013), 2 – Chapple (2003), 3 – Hagen and Bull (2011), 4 – Klingenböck et al. (2000), 5 – Pianka and Giles (1982), 6 – Chapple et al. (2008), 7 – Sass et al. (2007) and 8 – Kerr et al. (2003).

Table S2. Eigenvalue coefficients of linear discriminants for size-free residual morphometric measurements based on stepwise discriminant analysis.

Variables	LD1	LD2	LD3	LD4
Proportion of variance (%)	67.24	19.73	12.04	0.99
Cumulative proportion (%)	67.24	86.97	99.01	100
Morphometrics				
Hindfoot	-1.57	-0.19	-1.03	1.24
Head length	1.69	-0.89	0.71	-0.33
Pelvic height	-3.11	0.07	0.78	-1.04
Tail width	0.63	-1.53	1.89	0.00
Body width	1.81	-0.88	-0.10	0.20
Head width	0.13	1.57	-1.60	1.45
Upper hindlimb	-2.05	2.98	1.90	-0.55
Upper forelimb	-0.08	-6.66	0.46	-1.85
Lower forelimb	0.82	3.86	-2.25	1.76

Table S3. The net cost of burrowing on a variety of different taxa with available data on temperature and substrate type. *N/A indicates data not stated in study.

Species	Temperature (°C)	Soil type	Mass (g)	Net Cost of Transport (J m^{-1})	References
Invertebrates					
Emerita portoricensis	N/A	Wet sand	0.50	0.05	(Ansell and Trueman, 1973)
Donax incarnatus	N/A	Wet sand	0.52	0.5	(Ansell and Trueman, 1973)
Sipunculus nudus	N/A	Wet sand	3.33	3.33	(Trueman and Foster-Smith, 1976)
Nephtys cirrosa	12	Wet sand	0.45	0.38	(Trevor, 1978)
Nereis diversicolor	12	Wet sand	0.61	0.43	(Trevor, 1978)
Arenicola marina	12	Wet sand	10.20	7.65	(Trevor, 1978)
Bullia digitalis	15	Wet sand	4.34	1	(Brown, 1979)
Polyphysia crassa	4	mud	1.60	5.08	(Hunter and Elder, 1989)
Priapulus caudatus	4	mud	2.30	3.61	(Hunter and Elder, 1989)
Tylos granulatus	15	Wet sand	5.70	0.6	(Brown and Trueman, 1996)
Urodacus yaschenkoi		Sand	2.93	153.61	(White, 2001)
Gryllotalpa monanka	19-21	loam sand	0.94	15.73	(White et al., 2008)
Cirriformia moorei	11	Gelatin	0.36	0.06	(Dorgan et al., 2011)
	11	Sediment	0.36	0.18	
Fossorial mammals					
Cryptomys damarensis	27	Dry	152.1	1967.5	(Lovegrove, 1989)
	27	Damp	152.1	6583.52	
Heterocephalus glaber	27	Dry	31.5	2319.82	(Lovegrove, 1989)
	27	Damp	32.3	4701.65	
Georychus capensis	22	Loose sand	113	1814.39	(Du Toit et al., 1985)
Thomomys bottae	23	Fine sand	150	3250	(Vleck, 1979)
	23	Clay	150	33100	
	23	Sand loam	150	6430	
	23	Gravel	150	3420	
Thomomys talpoides	N/A	Damp clay	75	3160	(Lovegrove, 1989)
Scapanus townsendii	N/A	Damp clay	148	3920	(Lovegrove, 1989)
Scapanus orarius	N/A	Damp clay	59	3380	(Lovegrove, 1989)
Eremitalpa namibensis	23 – 28.5	Loose sand	20.62	78.96	(Seymour et al., 1998)
Fukomys mechowii	25	Hard soil	320	33800	*(Zelová et al., 2010)*
	25	Soft soil	320	5500	
Heliophobius argenteocinereus	25	Hard soil	232	19300	*(Zelová et al., 2010)*
	25	Soft soil	232	3500	
Ctenomys talarum	15	Soft soil	131.6	1162.87	*(Luna and Antinuchi, 2007)*
	25	Soft soil	126.4	647	
	35	Soft soil	142.4	1532	
Ctenomys talarum	24	Soft soil (sandy loam)	125	643.29	*(Luna and Antinuchi, 2006)*
Ctenomys talarum	24	Hard soil (gravely sand)	130	1604.62	
Semi-fossorial mammal					
Notomys alexis	26.8	sand-loam	33	7100	(White et al., 2006)
Marsupial					
Notoryctes caurinus	15 – 30	Loose dry soil	34	81	(Withers et al., 2000)
Amphibian					
Scaphiopus hammondii		soil	11.75	278.22	(Seymour, 1973)
Reptiles					
Liopholis striata			27.9	296.03	this study
Liopholis inornata			13	204.68	this study

Table S4. Additional data of burrow cross-sectional area and body mass from a range of animals not listed from White (2005).

Species	Common name	Mass (g)	A_b (cm^2)	References
Mammals				
Dasypus novemcinctus	Nine-banded armadillos	6350	397.76	(Sawyer et al., 2012)
Lemmus lemmus	Norwegian lemming	100	25.13	(Eriksson, 2011)
Mus musculus	House mouse	30	25.13	(Eriksson, 2011)
Orycteropus afer	Aardvark	60000	1431.68	(Whittington-Jones, 2007)
Otomys sloggetti robertsi	African ice rat	130	48	(Hinze et al., 2006)
Spermophilus brunneus	Idaho ground squirrel	120	17.3	(Yensen et al., 1991)
Birds				
Alcedo spp.	Kingfishers	45	45	(Heneberg, 2012)
Apteryx australis mantelli	North Island brown kiwi	2500	415.47	(Potter, 1989)
Bulweria bulwerii	Bulwer's petrel	100	213.63	(Ramos et al., 1997; Rodríguez et al., 2013)
Calonectris diomedea	Cory's shearwater	877	647.97	(Zino, 1971; Ramos et al., 1997)
Merops apiaster	European Bee-eater	56	60	(Heneberg, 2012)
Oceanodroma castro	Band-rump storm petrol	49	112.31	(Ramos et al., 1997)
Pseudopodoces humilis	Tibetan ground tit	40	36.31	(Ke and Lu, 2009)
Puffinus assimilis	Little shear water	223	188.5	(Ramos et al., 1997; Booth et al., 2000)
Riparia riparia	Sand Martin	14	24	(Heneberg, 2012)
Reptiles				
Liopholis inornata	Desert skink	12.92	3.37	this study
Liopholis slateri	Slater's skink	35	7.96	(Fenner et al., 2012)
Liopholis striata	Night skink	27.82	6.72	this study
Sphenodon guntheri	Brother's island tuatara	500	50	(Cree et al., 1991)
Invertebrate				
Upogebia pugettensis	Blue mud shrimp	5.3	2.84	(Thompson and Pritchard, 1969)
Callianassa subterranea		2.45	1.130972	(James et al., 1990; Astall et al., 1997)
Callianassa tyrrhena		4.3017	4.908734	(Dworschak, 1998; Dworschak, 2001)
Calocaris macandreae		1.55	2.010618	(Nash et al., 1984; Astall et al., 1997)
Jaxea nocturna		0.95	1.227184	(Nickell and Atkinson, 1995; Astall et al., 1997)
Solenopis invicta	Fire ant	0.004	0.107521	(Gravish et al., 2013; Tschinkel, 2013)
Upogebia deltaura		6.75	4.154753	(Astall et al., 1997; Hall-Spencer and Atkinson, 1999)
Upogebia pusilla		1.505	2.010618	(Dworschak, 1983; Astall et al., 1997)
Upogebia stellata		1.8	1.130972	(Nickell and Atkinson, 1995; Astall et al., 1997)
Anguilla japonica	Japanese eel	1800	49.02	(Okamura et al., 2002; Aoyama et al., 2005)

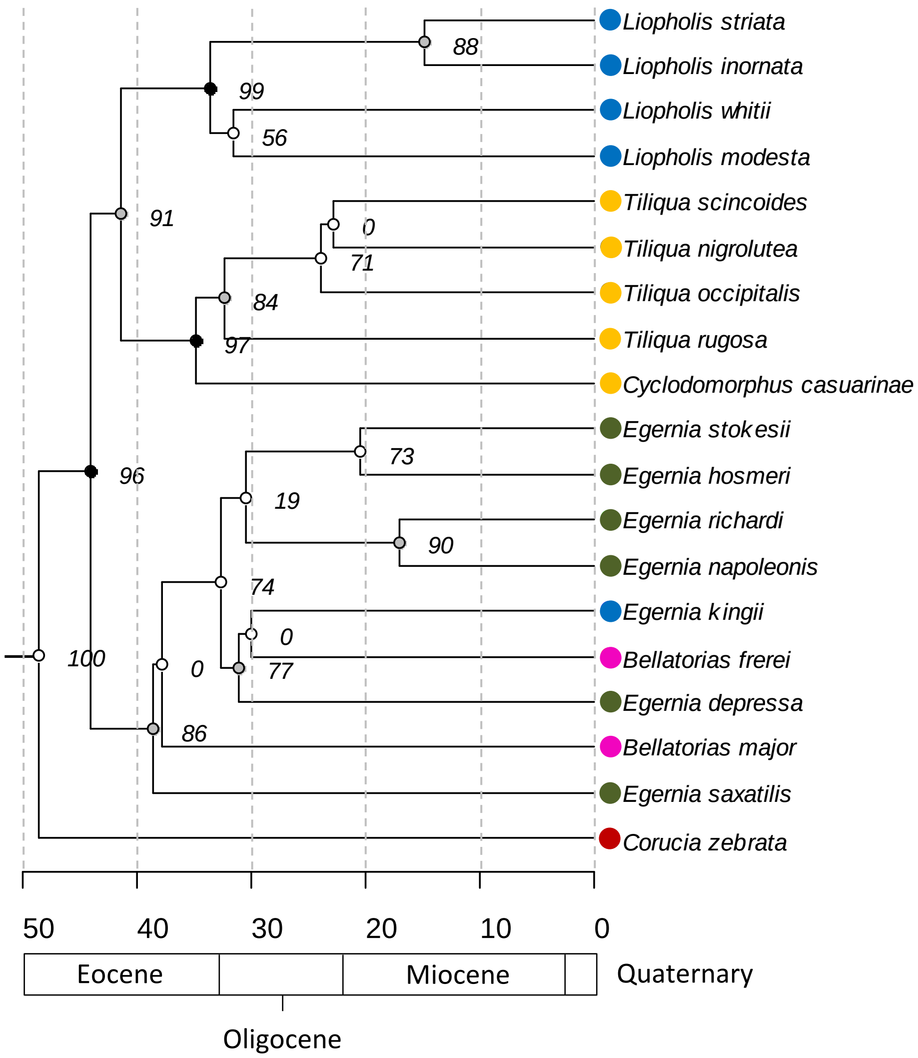

Figure S1. Phylogeny for 19 species of *Egernia* group skinks used for this study based on time calibrated Maximum Likelihood estimates of squamate phylogeny by Pyron and Burbrink (2014). Strength of ancestral state nodes were represented by shaded circles (> 95 = black, 75 – 95 = grey, < 75 = white). Time scale in millions of years before the present (mya). Retreat preferences represented by the following coloured circles: Burrow retreats (blue), Vegetation retreats (yellow), Hollow logs/rock crevices (green), Hollow logs/ burrow retreats (pink) and trees (red).

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