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Evolution of fossorial locomotion in the transition from tetrapod to snake-like in lizards

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Research

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Dramatic evolutionary transitions in morphology are often assumed to be adaptive in a new habitat. However, these assumptions are rarely tested because such tests require intermediate forms, which are often extinct. In vertebrates, the evolution of an elongate, limbless body is generally hypothesized to facilitate locomotion in fossorial and/or cluttered habitats. However, these hypotheses remain untested because few studies examine the locomotion of species ranging in body form from tetrapod to snake-like. Here, we address these functional hypotheses by testing whether trade-offs exist between locomotion in surface, fossorial and cluttered habitats in Australian *Lerista* lizards, which include multiple intermediate forms. We found that snake-like species penetrated sand substrates faster than more lizard-like species, representing the first direct support of the adaptation to fossoriality hypothesis. By contrast, body form did not affect surface locomotion or locomotion through cluttered leaf litter. Furthermore, all species with hindlimbs used them during both fossorial and surface locomotion. We found no evidence of a trade-off between fossorial and surface locomotion. This may be either because *Lerista* employed kinematic strategies that took advantage of both axial- and limb-based propulsion. This may have led to the differential occupation of their habitat, facilitating diversification of intermediate forms.

1. Background

The tree of life is filled with dramatic evolutionary transitions such as the invasion of land by plants and animals [1–3], the evolution of powered flight in insects and vertebrates [4,5], the re-invasion of marine habitats by whales [6,7], and the evolution of snake-like body forms in fossorial and/or cluttered habitats [8–11]. These transitions are characterized by major shifts in phenotype and ecology, as organisms adapt and radiate into novel adaptive zones [12,13]. However, the absence of extant intermediate forms [14] hampers our understanding of these transitions. While many intermediate forms exist in the fossil record [15], how they function can be inferred only indirectly [16]. Furthermore, the selective pressures that led to the transitions changed as the clades subsequently radiated [13,17,18].

A snake-like form has evolved dozens of times across most major vertebrate lineages, and this transition involves the elongation of the body and the reduction of the limbs [9,19,20]. The prevailing hypotheses for the evolution of this body form are that it is an adaptation for fossoriality and/or inhabiting cluttered habitats because such bodies experience less drag and can fit through narrower gaps than limbed forms [10,21–23]. Although snake-like forms are often correlated with locomotion through fossorial or cluttered habitats [21,24], it remains unknown whether snake-like forms are better at fossorial locomotion or moving through cluttered habitats than tetrapodal forms.

Snake-like forms have evolved independently at least 25 times in squamates (lizards, amphisbaenians and snakes), as two ecomorphs: a short-tailed fossorial morph and a long-tailed surface-dweller that lives in cluttered habitats

[8,24]. Some of these lineages have many extant intermediate forms [25–30], allowing tests of functional hypotheses about the origin of snake-like forms directly. The Australian skink genus *Lerista* contains species belonging to 12 forms, ranging from pentadactyl to limbless [29,31–33]. Most *Lerista* are semi-fossorial—swimming through loose sand and inhabiting *Acacia* leaf litter mats that lie atop the sand [34]. The shed leaves that comprise the litter mats are stiff and slender [35] and interdigitate to form small crawl spaces. Thus, *Lerista* uses both fossorial and cluttered habitats and have intermediate tail lengths, allowing testing of both hypotheses about the evolution of snake-like forms [33,36].

Here, we test both the fossoriality and the cluttered habitat hypotheses using 12 species of *Lerista*, representing nearly the full range of extant body forms (electronic supplementary material, table S1). If a snake-like form is an adaptation for fossoriality or cluttered habitats in *Lerista*, then we expect that more snake-like species will achieve greater velocities while moving through a sand substrate or leaf litter, respectively, than more lizard-like species. A corollary of this prediction is that more lizard-like species should achieve higher velocities during surface locomotion than more snake-like species [37,38], resulting in a performance trade-off between surface and fossorial locomotion that is related to body form (figure 1). We also test the hypothesis that *Lerista* partition their habitat in relation to their body form. Multiple species of *Lerista* that differ in body form can be found in sympatry, often under the same *Acacia* bush [39,40]. Some evidence suggests that more snake-like and smaller species tend to occupy the periphery of leaf litter mats, where the litter is shallower [40], and inhabit less compacted sands [41]. If body form is related to habitat preferences, this may lend further support to hypotheses of snake-like forms being adaptations for particular habitats.

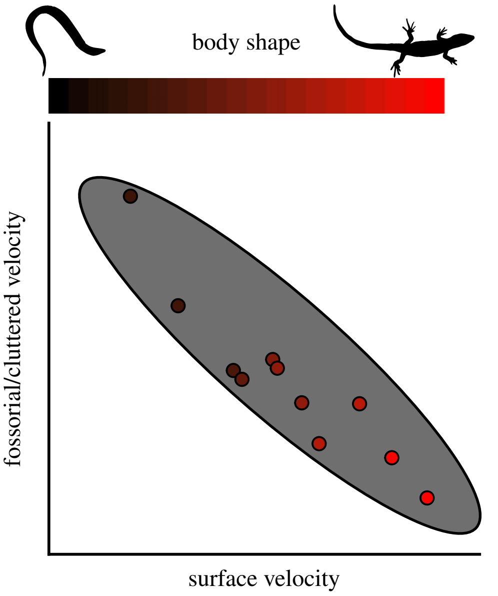

Figure 1. Theoretical predictions of the hypothesis that a snake-like form is an adaptation for fossoriality or moving in cluttered habitats. The colour of the dots indicates body form. Snake-like species should be better locomotors in fossorial or cluttered habitats, but worse surface locomotors, than lizard-like species, resulting in a performance trade-off related to body shape. (Online version in colour.)

2. Methods

(a) Specimen and microhabitat data collection

We sampled 102 adult and subadult specimens belonging to 12 species of *Lerista*, including 8 of the 12 evolved body forms (electronic supplementary material, tables S1 and S2). We sampled nine species in October–December 2014 in coastal Western Australia, and three species were laboratory specimens at the University of Adelaide. We collected lizards by hand while raking *Acacia* leaf litter [40,42]. We measured the depth of leaf litter where each animal was captured, the area of each leaf litter mat, and the relative distance each animal was from the trunk of the *Acacia* (electronic supplementary material, methods). We measured head length, snout–vent length, body width, tail length, fore- and hindlimb lengths, and counted the number of digits on the fore- and hindlimbs [33]. We only collected data from specimens with original tails or long, regenerated tails. We vouchered two specimens of each species at the Western Australian Museum and released the rest at the site of capture.

(b) Locomotion trials

We painted points on animals along their dorsal midline using non-toxic white paint at the level of the occiput, pectoral girdle, mid-body, pelvic girdle, cloaca and mid-tail. In the laboratory, we kept lizards in an incubator at 33°C prior to trials. In the field, we conducted trials when the ambient temperature was 30–33°C between 1200 and 1700 h, the preferred temperature of *Lerista* [43]. We conducted surface locomotion trials on approximately 5 mm deep mixed particle sand and sand-penetrating trials in approximately 25 mm deep coarse and fine sand ([44]; electronic supplementary material, methods). We also did trials with animals moving into approximately 25 mm deep *Acacia* leaf litter for lizards we caught in the field (electronic supplementary material, figures S2–4).

We recorded at least two good locomotor trials per individual per treatment from dorsal view at 240 Hz and a 518 × 384-pixel resolution using a Casio Exilim Ex-ZR1000 camera (Tokyo, Japan). We measured sand-penetrating force in the coarse and fine substrates with a custom-built tunnel attached to a Kistler Type 9203 uniaxial piezoelectric force transducer (Kistler Instrumente, Winterthur, Switzerland) [45,46] (electronic supplementary material, methods). We filled the tunnel with approximately 50 mm of the substrate, coaxing the animal to move into the sand while being careful not to push the animal to avoid erroneous force readings. We measured body temperature following each trial using a Raytek MT6 infrared thermometer (Santa Cruz, CA, USA).

(c) Quantifying locomotion

We digitized painted points using DLTdv5 [46] in MatLab 2016A (Mathworks, Natick, MA, USA) to get their *xy* coordinates in each video frame. For surface locomotion trials, we digitized the mid-body point. For sand-penetrating and leaf litter locomotion trials, we digitized the pelvic point, allowing us to track locomotion from the moment the tip of the snout penetrated the substrate to when the pelvic point disappeared into the substrate. We converted pixels to metres and frames to time, and calculated the cumulative distance moved for each frame [44]. We fitted a quintic spline with the Curve Fitting toolbox in MatLab to the cumulative distance and time data [44,47]. We used the first derivative of the spline, representing frame-by-frame velocity, and calculated average velocity from the moment of penetration of the substrate until the pelvic point disappeared. We tallied whether each specimen used its hindlimbs during each mode of locomotion. We then calculated the proportion of individuals that used their hindlimbs for each species (electronic supplementary material, table S3).

(d) Statistical analysis

We conducted all statistical analyses while taking phylogeny into account using R v. 3.5.2 [48]. We ln-transformed all morphometric measurements prior to analysis. We only included one trial with the highest maximum velocity or force for each individual on each substrate to calculate species mean performance (electronic supplementary material, methods).

We reduced the dimensionality of our data using a phylogenetic principal component analysis (pPCA) on the trait correlation matrix while accounting for phylogenetic signal as λ [49] using 'phytools' [50]. The pPCA included ln-transformed linear morphometric measurements and digit counts. The first two pPCs together explained 84% of variance (electronic supplementary material, table S4; figure 2). All variables loaded strongly positively on pPC-1. On pPC-2, limb variables loaded strongly positively while head length, SVL, body width, and tail length loaded strongly negatively. We used pPC-2 in subsequent analyses because species with low scores were more snake-like, while those with high scores were more lizard-like. For *L. labialis* and *L. praepedita*, we could only sample one specimen. To ensure that the specimens we collected were typical of each species, we ran a pPCA with a dataset supplemented with additional specimens of *L. labialis* and *L. praepedita* (eight each) from the Western Australian Museum. We then compared pPC scores each specimen to the supplemented specimens, confirming that our singletons were representative of each species (electronic supplementary material, figure S5).

We tested our hypotheses using phylogenetic generalized least-squares (PGLS) multiple regression, as implemented in 'phylolm' [51] while estimating phylogenetic signal of the residuals [52]. To test whether surface and fossorial/cluttered habitat performance were related to body form and size, we used regressions with each measure of performance as the response and pPC-2 and ln-mass as explanatory variables. We did the same with the other locomotor and habitat variables. Further, we regressed average sand-penetrating and leaf litter locomotor velocity on average surface locomotor velocity to test for the predicted trade-off between them. Our analyses included 12 species, except for leaf litter locomotion and habitat, which had 9 and 8 species, respectively. We reduced all regressions to the minimum adequate model [53].

3. Results

We found that more snake-like species moved at higher average velocities than more lizard-like species in both coarse (slope = −0.148 ± 0.039, $p = 0.004$, $R^2_{\text{adj}} = 0.587$) and fine (slope = −0.109 ± 0.038, $p = 0.019$, $R^2_{\text{adj}} = 0.450$) substrates (figure 3; and electronic supplementary material, table S5), lending the first functional support to the adaptation for fossoriality hypothesis. We found no relationship between body form and velocity during locomotion in leaf litter or surface locomotion (electronic supplementary material, table S5). We also found no relationship between velocity during surface locomotion and sand-penetration or moving through leaf litter (electronic supplementary material, table S6). Taken together, these results lend support to the fossoriality hypothesis and not the cluttered habitat hypothesis in *Lerista* but without the expected performance trade-off. Body mass did not affect any of these modes of locomotion (electronic supplementary material, table S5). However, we did find that larger species produced more force during sand-penetration into coarse (slope = 1. 652 ± 0.346, $p = 0.001$, $R^2_{\text{adj}} = 0.665$) and fine substrates (slope = 1.657 ± 0.461, $p = 0.005$, $R^2_{\text{adj}} = 0.520$; electronic supplementary material, table S7 and figure S6), but body form and sand-penetration force were unrelated (electronic supplementary material, table S7). In considering locomotor kinematics, we found that more lizard-like species used their hindlimbs more frequently during sand-penetration and moving into leaf litter but not during surface locomotion (electronic supplementary material, table S8 and figure S7). Body mass did not affect limb use (electronic supplementary material, table S8).

We found evidence to suggest that *Lerista* species partitioned the leaf litter habitat according to body form. More

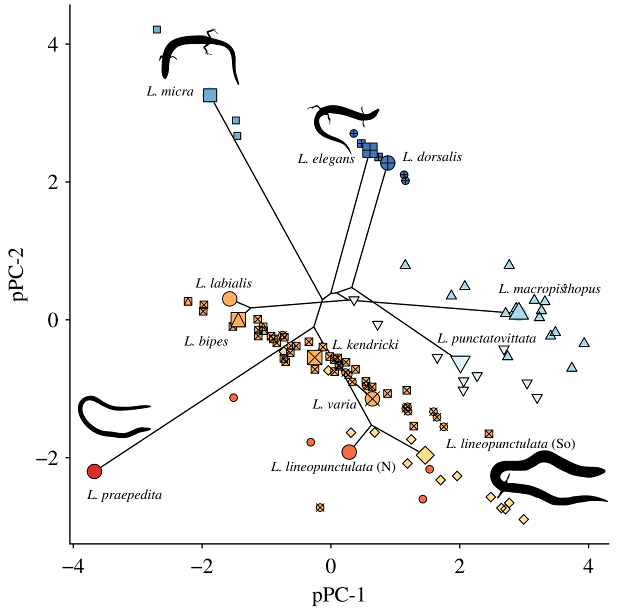

Figure 2. Phylomorphospace of *Lerista* characterized by pPC-1 and pPC-2. Colours indicate digit configuration, with warmer colours representing species with more digits and cooler colours representing species with fewer. Larger symbols are pPC scores of species means and smaller symbols are for individuals. 'So' and 'N' differentiate the southern and northern populations of *L. lineopunctulata*, respectively. (Online version in colour.)

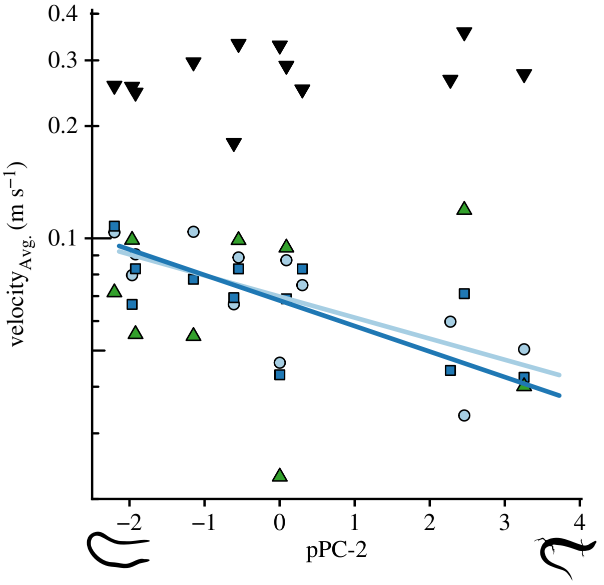

Figure 3. Relationship between pPC-2 and average velocity during surface locomotion (black, inverted triangles, $n = 12$), sand-penetration in coarse (light blue circles, $n = 12$) and fine sand (dark blue squares, $n = 12$), and in leaf litter (green triangles, $n = 9$). Lines are only shown for significant PGLS slopes and correspond to symbol colours. (Online version in colour.)

snake-like species tended to occupy smaller leaf litter mats than more lizard-like species (slope = 6.285 ± 1.956, $p = 0.034$, $R^2_{\mathrm{adj}} = 0.481$). More snake-like species also tended to occupy peripheral parts of the leaf litter mat (slope = −0.042 ± 0.016, $p = 0.034$, $R^2_{\mathrm{adj}} = 0.481$). We found no effect of body form on leaf litter depth, nor of body mass on any of the habitat variables (electronic supplementary material, table S9).

4. Discussion

(a) Snake-like body forms are an adaptation for fossoriality

We are the first to empirically test the hypotheses that a snake-like form is an adaptation for fossoriality and for locomotion in cluttered habitats [24,54]. We found strong support for the adaptation for fossoriality hypothesis but not for the cluttered habitat hypothesis. This is exemplified by more snake-like species of *Lerista* achieving higher velocities when sand-swimming but not when moving in litter composed of stiff leaves (figure 3). These findings add an additional line of evidence to support the hypothesis that snakes themselves may have evolved from a fossorial ancestor [54–56]. However, this hypothesis is not easily testable in snakes because of the lack of extant intermediate forms, which are numerous in *Lerista* skinks [33].

That body form did not affect the velocity of moving in leaf litter was surprising because a narrow, limbless body should facilitate negotiation of tight spaces [10,21]. However, this lack of support for the cluttered habitat hypothesis may be related to the tail. Despite strong correlations between elongate lizards with exceptionally long tails and cluttered habitats [8,24], there is considerable variation in relative tail length among snake-like species, and *Lerista* has an intermediate tail length ([25,36]; electronic supplementary material, table S2). Intermediate tail lengths may result from a balance between sand-swimming and moving through cluttered habitats. It is unknown whether the tail contributes to propulsion during sand-swimming in *Lerista*. While increasing total length improves the cost of transport during sand-swimming, this benefit diminishes at greater total lengths and incurs greater drag [23,57]. Simultaneously, the tail can provide points of static friction to push against features in a cluttered habitat [22,58,59]. However, consistent with our results, other work on semi-fossorial skinks, including *Lerista*, with intermediate tail lengths suggested that the tail exerted negligible propulsive forces [39,60,61].

(b) Absence of a performance trade-off and the persistence of intermediate forms

The persistence of intermediate forms with reduced limbs in *Lerista* and other lizards suggests that these intermediate forms are not transitory, but altogether different optima on the fitness landscape [8,25,62]. In *Lerista*, the intermediate forms comprise the majority of species diversity, having evolved and diversified multiples times [29,33]. However, it has long been a mystery why these forms persist and how their phenotype might be adaptive.

Contrary to predictions (figure 1), we showed a definitive lack of trade-off between fossorial and surface locomotion, and other aspects of the phenotype of the intermediate forms may be the reason for this. The lack of a trade-off in *Lerista* results from a relatively high surface locomotor speed that is independent of body form (figure 3). There has long been an appreciation that the transition to snake-like body form involves a dramatic shift in locomotion from limb-based to axial propulsion [21,22,63]. We found that even species with highly reduced limbs used them during both surface and fossorial locomotion (electronic supplementary material, figure S7 and table S8), and so intermediate species may run fast by effectively combining axial and limbed propulsion.

Intermediate species of *Lerista* are physically larger than the diminutive snake-like and lizard-like species [33]. This may contribute to higher surface locomotor velocities and help explain their persistence, eliminating any possible trade-off. Although we found no relationship between sand-penetration force and body form, there was a strong positive relationship with body mass (electronic supplementary material, figure S6). Since the diameter is an important predictor of how much force is needed to penetrate a substrate [57,64], the large intermediate species require more force to penetrate sand but also produce that required force. By contrast, small pentadactyl species do not produce much force for sand-swimming and are likely further hindered by their limbs. However, work on amphisbaenians shows that some sand-penetration forces are exerted vertically and laterally as well as in the direction of travel [65,66], so it would be interesting to quantify these forces in sand-swimming lizards as well.

Being large and powerful may also allow the intermediate species to gain access to niches unavailable to diminutive species. More snake-like species occupied the periphery of smaller leaf litter mats (electronic supplementary material, table S9). These positions probably contain less compacted sand, which is easier to penetrate [41,67]. Indeed, these different microhabitat usages are mirrored by differences in diet. More snake-like species ate a greater proportion of termites, which are small and fossorial, while intermediate species fed more on other invertebrates that tended to be larger [40]. Lizard-like species, like *L. elegans*, fed on various arthropods that were not fossorial [40], suggesting that they may themselves spend less time under the substrate. These lines of evidence show that the different species of *Lerista* fill different niches, reflected by microhabitat use, diet and locomotor capacities, allowing persistence and coexistence.

(c) Diversity of snake-like forms

The hypothesis that a snake-like form is an adaptation for fossoriality is fundamentally a hypothesis about locomotor performance, and we offer the first such evidence in support of it. Snake-like species of *Lerista* are better sand-swimmers than more lizard-like ones. We also present data germane to understanding why intermediate forms between lizard- and snake-like persist and coexist. Species of *Lerista* are divergent in body size, microhabitat use, and diet. However, *Lerista* is but one of several clades with a range of body forms from lizard- to snake-like [8,25]. Recently, we showed that snake-like body shapes exhibit imperfect convergence (*sensu* [68]), with historical contingency likely playing an important role in how snake-like bodies evolved in each clade [25]. Likewise, the evolution of sand-swimming is likely historically contingent as short-bodied, robustly limbed lizards like *Scincus scincus* and *Uma scoparia* are capable of exhibiting similar levels of sand-penetrating performance [69,70]. However, these differences in evolutionary history remain largely unexplored in terms of organismal function and niche-use, which may have profound functional implications in how each lineage interacts with the environment.

Ethics. D. Stefoni of Western Australia Department of Parks and Wildlife issued our collecting permits for Western Australia (licence SF009969 and CE004562). We conducted this study under Clark University IACUC approval (Protocol 017R).

Data accessibility. The dataset analysed in this article is available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.5hqbzkh2x [71].

Authors' contributions. G.M. and P.J.B. conceived and designed the study and wrote the manuscript. G.M. collected and analysed the data. Both authors gave final approval for publication.

Competing interests. We declare we have no competing interests.

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