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Push and bite: trade-offs between burrowing and biting in a burrowing skink (*Acontias percivali*)

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Trade-offs are thought to be important in constraining evolutionary divergence, as they may limit phenotypic diversification. Limbless animals that burrow head-first have been suggested to be evolutionarily constrained in the development of a large head size and sexual head shape dimorphism because of potential trade-offs associated with burrowing. Here we use an acontiine skink (*Acontias percivali*) to test for the existence of trade-offs between traits thought to be important in burrowing (speed and force). As head size dimorphism has been shown to be limited in acontiine lizards, thus suggesting constraints on head size and shape, we additionally explore the potential for trade-offs between burrowing and biting. Our data show that *A. percivali* uses a burrowing style different from those previously described for caecilians and amphisbaenians, which relies on the use of extensive lateral and dorsoventral head movements. Our data also show that animals use their entire bodies to generate force, as peak force was determined by total length only. Additionally, both bite force and the time needed to burrow into the substrate were principally determined by relative head width, suggesting a trade-off between biting and burrow speed. Performance data were indeed suggestive of a correlation between bite force and the time needed to burrow, but additional data are needed to confirm this pattern. In summary, our data suggests that trade-offs may exist, and may have been of crucial importance in shaping the evolution of head shape in *A. percivali*, and burrowing lizards more generally. © 2010 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2011, **102**, 91–99.

ADDITIONAL KEYWORDS: head shape – lizard – locomotion – performance.

INTRODUCTION

Phenotypic diversification has been suggested to be biased by trade-offs in the development or expression of phenotypic traits (Arnold, 1992; Schluter, 1996). Indeed, performance trade-offs are often thought of as imposing limits on phenotypic divergence, and occur when different and conflicting functional demands are imposed on the same phenotypic trait (Arnold, 1992; Vanhooydonck, Van Damme & Aerts, 2001; Levinton & Allen, 2005; Konuma & Chiba, 2007; but see Herrel *et al*., 2009). For example, in lizards, selection on burst locomotion capacity has been shown to trade off with endurance capacity (Vanhooydonck *et al*., 2001), as the demands on the locomotor muscles are conflicting in the expression of either fast- or slow-muscle fibre types (Bonine, Gleeson & Garland, 2005).

Limbless burrowing animals have been hypothesized to be constrained in the evolution of their body shape by limitations imposed on body diameter, as the work needed to compress soil increases exponentially

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*Corresponding author. E-mail: bieke.vanhooydonck@ua.ac.be with body diameter (Navas *et al*., 2004). However, in head-first burrowers, not only the diameter of the body but also that of the head can be expected to be constrained by a burrowing lifestyle, as it is the maximal diameter of the animal that will determine the energetic cost of burrowing. Consequently, it has been proposed and observed that at least in some groups of limbless head-first burrowers sexual dimorphism in head size may be limited because of the constraints imposed on the development of large heads in males (Heideman *et al*., 2008). Additionally, empirical data for the caecilian amphibian *Schistometopum thomense* show that males with bigger heads were slower in burrowing than females, suggesting a trade-off between head size and the ability to burrow fast (Teodecki *et al*., 1998; see also López, Martín & Barbosa, 1997). Although the ability to burrow fast into the soil is likely to be relevant as a predator escape strategy, wide heads may confer animals with a bite performance advantage. Indeed, in many vertebrates head width is a critical determinant of bite force capacity (Herrel *et al*., 1999, 2001; Herrel, De Grauw & Lemos-Espinal, 2001). Consequently, a trade-off between bite force and burrowing speed may result.

The speed by which an animal can burrow, however, is probably not the only relevant trait related to burrowing in limbless vertebrates. The maximal push force that can be generated is likely to be as important, as it may allow animals to penetrate a greater variety of soil types, and consequently to expand their resource base both in terms of potential habitat and potential dietary resources. Body cross-sectional area is expected to be related to the maximal burrowing force, as most limbless vertebrates are thought to burrow using the longitudinal axial musculature (but see O'Reilly, Ritter & Carrier, 1997). However, although a greater body diameter might indeed allow for an increase in the peak force that can be generated, it will probably impose high energetic costs and may constrain the speed by which animals can burrow into the soil. Yet, the presence of such a trade-off is critically dependent on the actual burrowing mechanism used. Unfortunately, little is known about the mechanics of burrowing in the majority of limbless vertebrates, rendering tests of the importance of constraints on the evolution of body shape difficult.

The first goal of our paper is to provide a qualitative description of burrowing in a legless skink (*Acontias percivali*) to gain insights into how limbless skinks burrow. This may provide insights into the traits that potentially affect an individual's burrowing capacity. Legless skinks of the subfamily Acontiinae appear well suited for this purpose, as they form part of a successful radiation that has evolved a wide range in body morphologies and has occupied a wide variety of habitats (Daniels *et al*., 2002, 2006; Heideman *et al*., 2008). Moreover, morphometric data suggest that the evolution of head size dimorphism is constrained in the group, suggesting a potential trade-off between burrowing and biting (Heideman *et al*., 2008). Secondly, we combine data on morphometrics and performance traits to directly test which traits strongly affect performance capacity. Finally, we test for the presence of trade-offs between three performance traits relevant to burrowing animals: bite force, maximal push force, and the time needed to burrow into the substrate.

MATERIAL AND METHODS

ANIMALS AND HUSBANDRY

Fourteen adult *A. percivali* of unknown sex were purchased from a commercial dealer and transported to the laboratory at the University of Antwerp. Animals were maintained individually in 2-litre containers filled with a mixture of potting soil and sand. The containers were placed in a temperature-controlled room (25 °C). Water was always available and animals were fed crickets and earthworms twice weekly.

MORPHOMETRICS

Before the onset of the performance trials individuals were weighed using a digital scale (accuracy 0.01 g; Ohaus), and head width, head height, and head length were measured using digital calipers (accuracy 0.01 mm; Mitutoyo). We were unable to reliably measure the head length of one individual. The total length was measured by stretching the animals along a ruler (accuracy 1 mm).

X-RAY SYNCHROTRON PROPAGATION PHASE-CONTRAST MICROTOMOGRAPHY

We used the ID19 beamlines of the European Synchrotron Radiation Facility (ESRF) to obtain data on *A. percevali* (Betz *et al*., 2007; Du Pasquier *et al*., 2007). We acquired tomographic data from one specimen (energy of 25 Kev, propagation distance of 900 mm, and voxel size of 14.93 μm) of unknown sex. Three-dimensional renderings were obtained after semi-automatic segmentation of the skeleton, using AVIZO v6.1 (Mercury Computer Systems, Chelmsford, MA, USA).

BITE FORCES

Bite forces were measured using an isometric Kistler force transducer (type 9203, range ± 500 N; Kistler, Switzerland) mounted on a purpose-built holder and

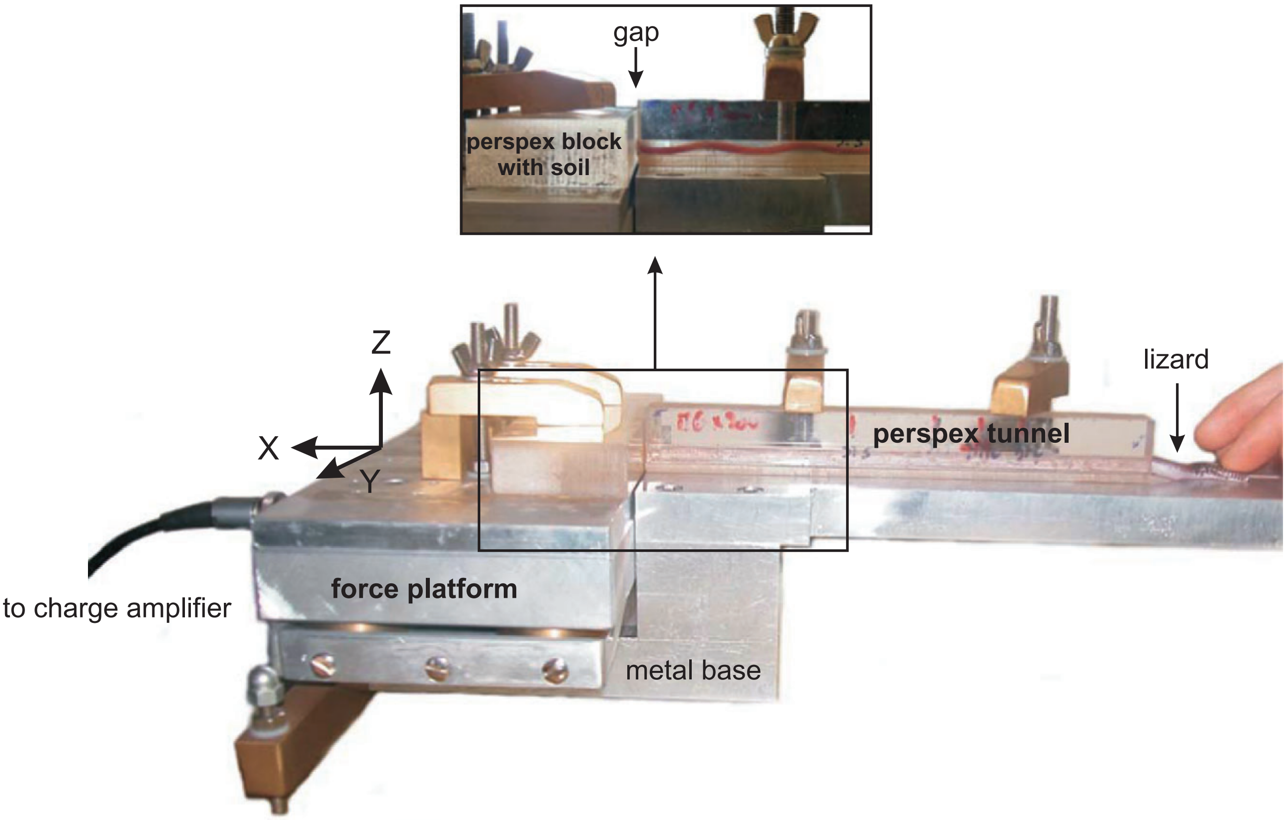

Figure 1. Photograph of the set-up used to measure burrowing forces. The lizard is positioned inside the perspex tunnel and pushes its head into the soil provided in the perspex block (see inset) inside a shallow tunnel of similar diameter. The Perspex block is mounted on the force plate. Note that the force plate is not in contact with the frame upon which the tunnel is mounted.

connected to a Kistler charge amplifier (type 5995A; see Herrel *et al*., 1999, for a more detailed description of the set-up). When the free end of the holder was placed between the jaws of the animal, prolonged and repeated biting resulted. The place at which the animals bit the plates was standardized for all animals. Gape angle (i.e. how far the animal needs to open its mouth) was standardized by moving the bite plates further apart for larger animals. Measurements were repeated five times for each animal, with an inter-trial interval of at least 30 min. The maximal value obtained during such a recording session was considered to be the maximal bite force for that individual.

PUSH FORCES

Push forces were measured using a modified version of the set-up described in O'Reilly *et al*. (1997). Measurements of push forces during burrowing were made using a custom piezoelectric force platform (Kistler Squirrel force plate, ± 0.1 N). The force platform was positioned on a custom-designed metal base (Fig. 1) and connected to a charge amplifier (Kistler Charge Amplifier type 9865). A Perspex block with 1 cm deep holes of different diameters was mounted on the force plate, level with the front edge (Fig. 1). One of the holes was loosely filled with soil from the container of the animal that was tested. A Perspex tunnel with a diameter similar to the maximal body diameter of the test animal was mounted on the metal base in front of (but not touching, see Fig. 1) the force plate, and aligned with the soil-filled hole in the Perspex block. First, a skink was introduced into the tunnel and allowed to move through it until reaching the soil-filled chamber. Next, the animal was stimulated to burrow into the soil by tapping the end of the tail sticking out of the tunnel, or by prodding the animal inside the tunnel with the blunt end of a thin wooden stick.

Forces were recorded during a 60-s recording session at 1000 Hz, and three trials were performed for each individual, with at least 1 h between trials. A recording session typically included between ten and 15 pushes of varying magnitude (Fig. 2A). Forces were recorded in three dimensions, and, as burrowing

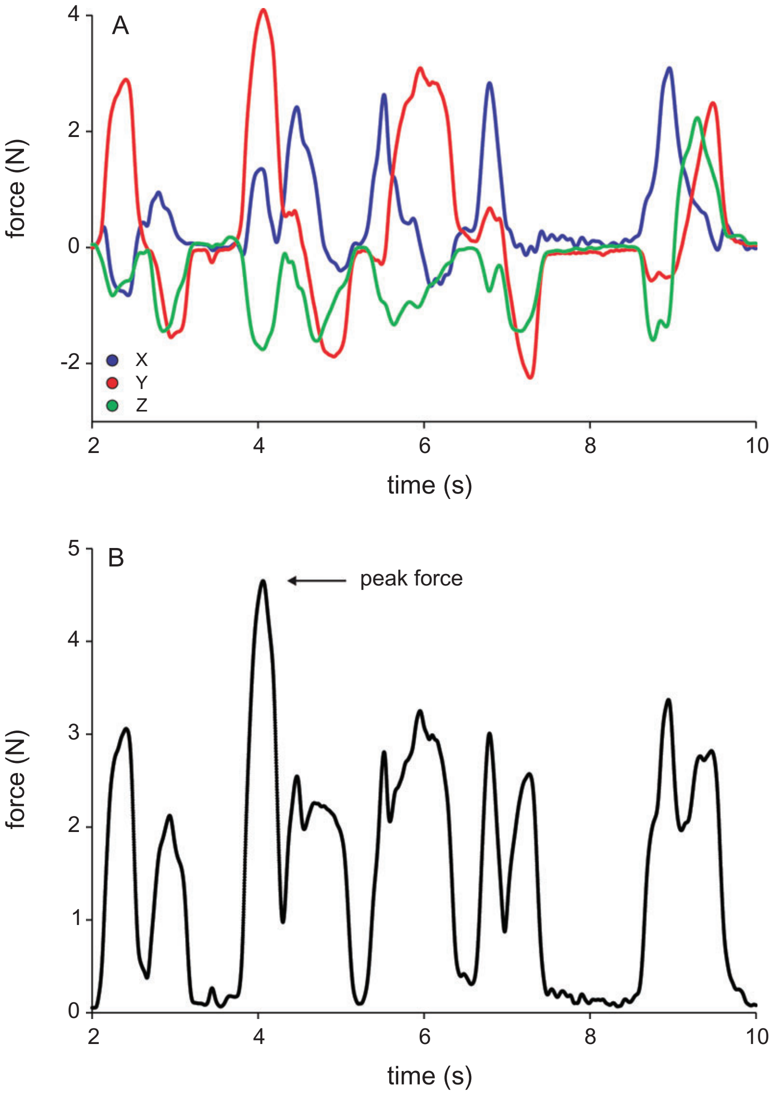

Figure 2. A, representative force profile of an *Acontias percivali* pushing on the force plate during the first 10 s of a 60-s trial. Note how the force profile consists of significant *x* (blue online/black in print), *y* (red/dark grey), and *z* (green/pale grey) components. B, the forces in three dimensions were combined and the resultant force was calculated. As an indicator of maximal pushing force the peak resultant force was extracted from each trial. Only the highest push force across all trials was used in the analyses.

in *A. percevali* was characterized by complex three-dimensional movements, we chose to combine the individual forces into the resultant force (Fig. 2B) using BIOWARE (Kistler). For each individual we then extracted the highest peak resultant force across all trials as an indicator of that animal's maximal push force.

Burrow time

Individuals were induced to burrow into a compacted substrate (i.e. a mixture of potting soil and sand) and the time needed to burrow into the substrate until the animals were completely covered was recorded. The substrate was compacted to a similar degree for all trials to get comparable data on burrowing time for all individuals. As lizards often had difficulty in starting a burrow, or would burrow along the sides of the container, we pre-made a 3 cm deep burrow, with the width proportional to the individual's diameter, into which the head of the animal was placed. This resulted in immediate and directed burrowing in all individuals. Three trials with at least 1 h between trials were performed, and the shortest time needed to burrow into the soil was retained as an individual's minimal burrowing time (note that the faster the animals burrow into the soil, the lower the time). Burrow time, push-force and bite-force trials were performed on different days with 1 day in between successive performance trials. Two individuals had died prior to the onset of the burrowing experiments, so data on time needed to burrow into the soil are missing for these two animals.

ANALYSES

Data were $\log_{10}$-transformed before analysis to confirm assumptions of normality and homoscedascity. Multiple stepwise regressions were used with each of the three performance traits as dependent, and all morphometric data, including total length, as independent variables to investigate which variables best explained the observed variation in performance. As head length was missing for one individual, multiple regressions analyses are based on 13 individuals. Next, regression analyses were run of the performance variables against total length. Unstandardized residuals were extracted if a significant relationship between total length and the performance variable was found. We then used Pearson correlations to test for trade-offs among the different (relative) performance variables. All analyses were performed using SPSS v15.

RESULTS

BURROWING

Analyses of burrowing trials using our force-plate data indicate that while pushing into the soil, high forces are generated in all directions (Fig. 2A). Moreover, there appears to be no fixed temporal sequence of the observed force peaks. Specifically, in 28% of the trials forces peaked first in the x direction, in 50% forces peaked first in the y direction, and in 22% of the trials forces peaked first in the z direction. Moreover, the magnitude of the forces was not uniformly highest in either one of the directions, despite a dominance of high force peaks in the lateral (y) direction ($x = 7\%$, $y = 60\%$, $z = 33\%$). The temporal separation of the force peaks in the different directions resulted in double-humped force peaks in the resultant force profile, with peak forces reaching almost 5 N (Fig. 2B). These data indicate a complex burrowing behaviour characterized by complex three-dimensional head movements involving significant lateral and dorsoventral movements, implicating the action of both the laterally positioned longissimus and the dorsal spinalis–semispinalis systems (see Fig. 5) during burrowing.

MORPHOLOGICAL DETERMINANTS OF PERFORMANCE

A multiple regression model indicated that push force was best predicted by differences in total length ($r = 0.88$; $P < 0.001$; Fig. 3A), with bigger individuals

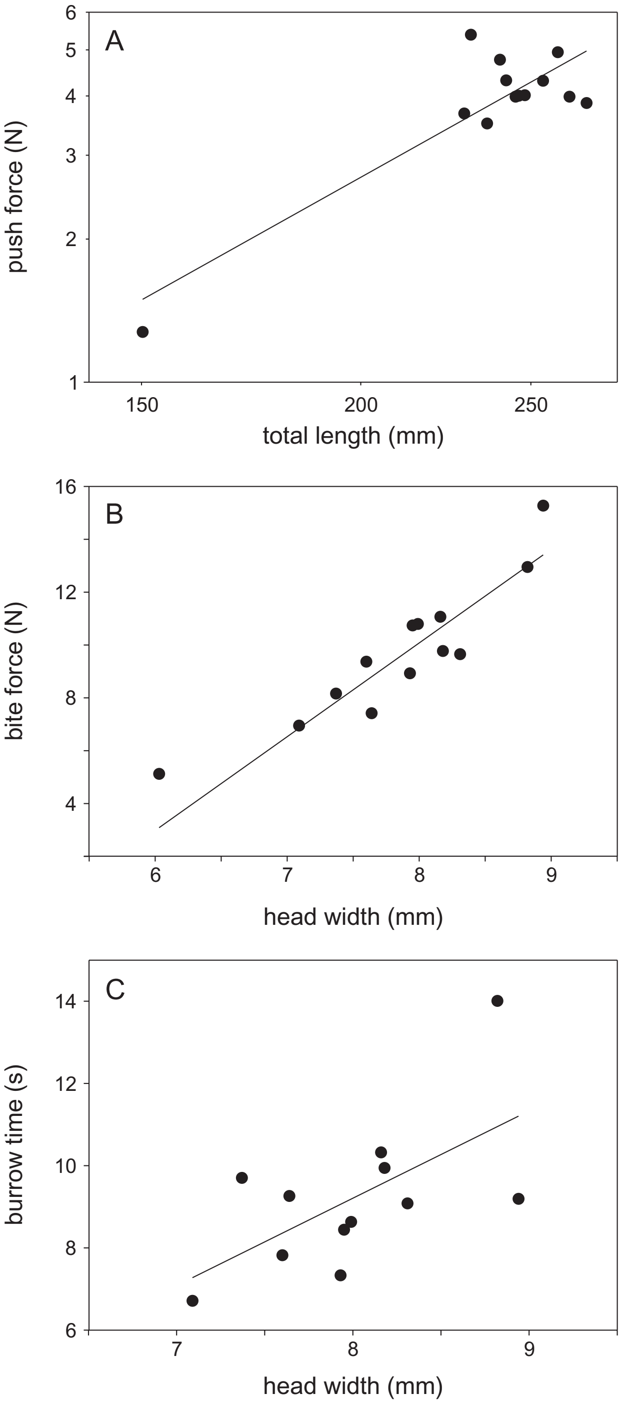

Figure 3. Graphs illustrating the correlations between morphology and performance. A, the maximal push force is significantly predicted by total length ($r = 0.88$; $P < 0.001$). B, the bite force is best predicted by the total length (not shown) and head width of an individual ($r = 0.97$; $P < 0.001$). C, the time needed to burrow into the soil is only predicted by the head width ($r = 0.64$; $P = 0.03$).

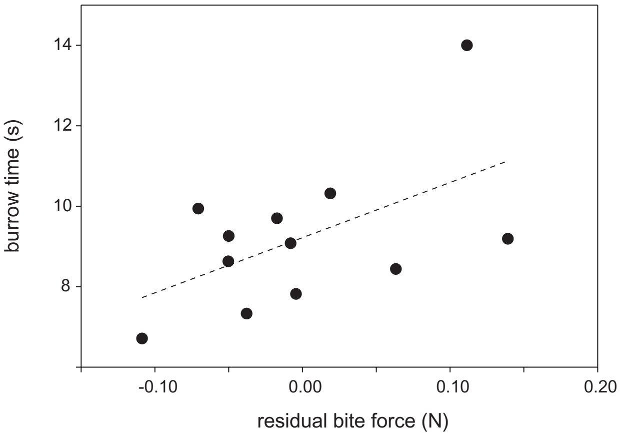

Figure 4. Graph illustrating the correlation between residual bite force and burrowing time. Although the correlation is not significant, a distinct trend ($r = 0.55$; $P = 0.06$) is present, suggesting that individuals with greater relative bite forces need more time to burrow into the soil.

generating higher push forces. Bite force, on the other hand, was significantly predicted by both total length and head width ($r = 0.97$; $P < 0.001$; Fig. 3B), both positively related to bite force (total length, $\beta = 0.53$; head width, $\beta = 0.52$). Thus, individuals that are bigger and that have relatively wider heads are stronger biters. Finally, burrowing time was significantly and positively associated with head width ($r = 0.64$; $P = 0.03$; Fig. 3C), indicating that individuals with wider heads needed more time to burrow into the soil.

CORRELATIONS AMONG PERFORMANCE TRAITS

Although none of the performance traits were significantly related to one another (residual bite force versus residual push force, $r = 0.30$, $P = 0.30$; residual push force versus burrowing time, $r = 0.02$, $P = 0.96$), a distinct trend existed for individuals with relatively greater bite forces to be associated with longer burrowing times ($r = 0.58$; $P = 0.06$; see Fig. 4).

DISCUSSION

BURROWING IN ACONTIINE SKINKS

Burrowing in *A. percivali* differs markedly from burrowing in the other groups of head-first burrowers that have been studied previously, such as caecilians, amphisbaenids, and uropeltid snakes (see O'Reilly *et al.*, 1997; Herrel & Measey, 2010). In contrast to caecilians that use whole-body hydrostatic pressure to generate principally forward-directed forces to create burrows (O'Reilly *et al.*, 1997), our data for *A. percivali* show that they do not use a hydrostatic mechanism, as high forces are exerted in all three dimensions during burrowing. Moreover, *A. percivali* does not exhibit the skin-vertebral independence thought to be crucial in the internal concertina locomotion typical of caecilians (von Schnurbein, 1935; Gaymer, 1971; Gans, 1973). Yet, the force profiles observed here are also different from those predicted and observed for amphisbaenians, where burrowing is achieved by an initial penetration phase, followed by a soil compression phase in either dorsal or lateral direction (Gans, 1986; Navas *et al.*, 2004). Rather, *A. percevali* bent their heads predominantly in the lateral direction and did not display an initial forward-directed penetration phase (Fig. 2A).

Given the dominance of side-to-side and dorsoventral head movements used to compact the soil and create a tunnel, we predict that animals mainly recruit the dorsally positioned semispinalis–spinalis system and the laterally positioned longissumus dorsi complex. Indeed, Figure 5 illustrates the well-developed neural arches that serve as the origin, and the expanded occipital area of the skull that serves as the insertion, for the dorsal muscles responsible for head lifting, and the longissimus cervicocapitis complex that is likely to be responsible for side-to-side head movements (see Herrel & De Vree, 1999). Unfortunately, comparative data are scarce, making it hard to judge whether these muscles are actually better developed in burrowing relative to surface-dwelling species.

MORPHOLOGICAL DETERMINANTS OF PERFORMANCE

In contrast to our initial prediction, the maximal push force generated by an individual was not determined by its body diameter. Rather, the total length of the individual was the principal determinant of maximal push force. These results strongly suggest that animals not only generate forces by using the cervical components of the spinalis and longissimus groups, but rather are able to transfer forces from the entire muscle group to the head. Although the exact mechanism of force generation and transmission needs to be studied, this observation does suggest that animals may circumvent potential burrow-force trade-offs by recruiting muscles lying along the long axis of the body.

Time needed to burrow and bite force were, however, determined by the same sets of traits: the (relative) head width of an individual was a significant predictor of both bite force and the time needed to burrow into the soil. This result is not unexpected for bite force as lateral bulging of the external jaw adductors is prominent in *A. percevali*, similar to what has been observed for other lizards (see Fig. 5; Herrel *et al.*, 2007; Huyghe *et al.*, 2009). Additionally, burrowing time was also positively correlated with head width, thus skinks with wider heads took more

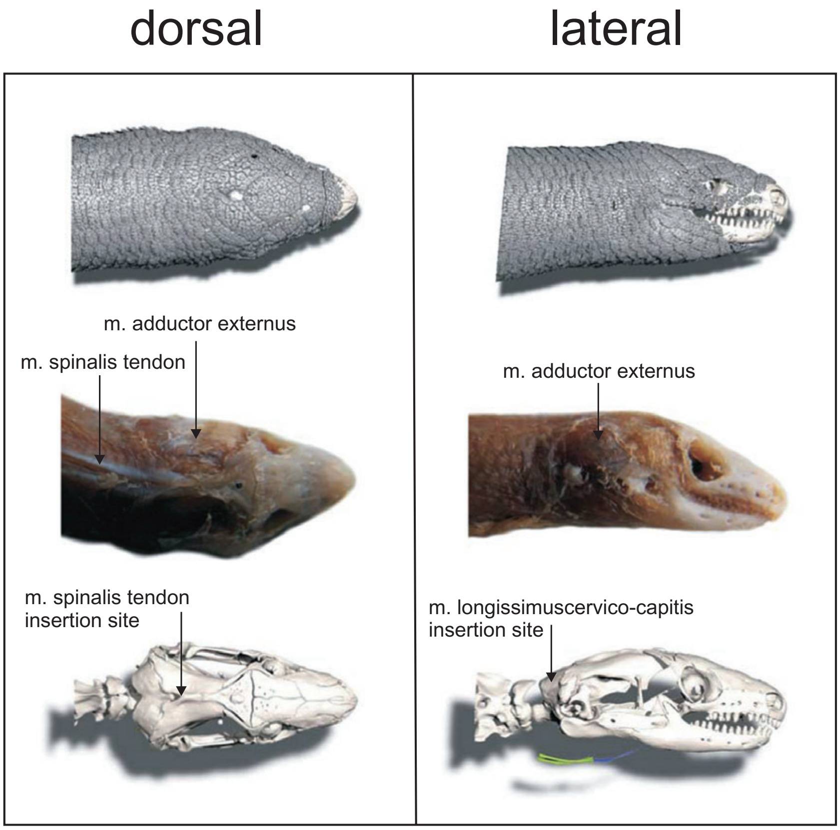

Figure 5. Photographs of the head of an *Acontias percivali* in dorsal (left) and lateral (right) view. The top pictures illustrate the external view of the head. The middle set are of the same individual, but with the skin removed to illustrate the well-developed external adductor and dorsal cervical muscles. Below a dorsal and lateral view of the skull is shown based on computed tomography images. Note the elongate head shape, and well-developed attachment sites of the longissimus and spinalis–semispinalis muscle complexes.

time to burrow into the soil. Moreover, head width was the only variable to explain a significant proportion of the observed variation in time needed to burrow, suggesting that head width imposes a strong constraint on burrowing speed. Navas *et al.*'s (2004) findings suggest the forces needed to penetrate and compact the soil increases disproportionately with the widest diameter of the animal. As head width is decoupled from burrowing force-generating capacity, even small increases in head width will have a large impact on burrowing speed. Given that bite force and time needed to burrow are both determined positively by head width, a trade-off between burrow speed and bite force is expected. Note, however, this reasoning is only valid if such a trade-off is caused by head width and not by an intrinsic performance trade-off in the muscular system related to burrowing.

TRADE-OFFS

Our data provide support for the suggestion that the evolution of head shape is constrained in lizards and other head-first burrowers (Teodecki *et al.*, 1998; Navas *et al.*, 2004; Heideman *et al.*, 2008). Moreover, our data are suggestive of a performance trade-off between bite force and burrow speed. Although the correlation between these two parameters was not significant ($P = 0.06$), this was probably caused by our relatively small sample size of individuals for which both performance traits could be measured (note that two of the smallest individuals died before burrowing times could be measured, thus reducing our sample size). The fact that both performance traits are principally determined by (relative) head width suggests that this trend is the reflection of a biologically significant pattern. Although additional data needs to be collected, head shape evolution in head-first limbless burrowers may principally be determined by the outcome of conflicting sexual and natural selection pressures. As both bite force and burrowing time increase for individuals with relatively wider heads, selection for higher bite force, relevant in intrasexual competition (Lailvaux *et al.*, 2004; Huyghe *et al.*, 2005; Lappin & Husak, 2005; Husak, Lappin & Van

Den Bussche, 2009), will come at the cost of an increased burrowing time, a trait potentially crucial for the survival of an individual. Future studies testing for the actual survival advantage of increased burrowing speed are clearly needed to test for the evolutionary significance of the trends observed here. Moreover, similar data for additional groups of limbless head-first burrowers would be especially insightful in testing the generality of the patterns observed here.

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