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ORIGINAL PAPER

Similar burrow architecture of three arid-zone scorpion species implies similar ecological function

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Abstract Many animals reside in burrows that may serve as refuges from predators and adverse environmental conditions. Burrow design varies widely among and within taxa, and these structures are adaptive, fulfilling physiological (and other) functions. We examined the burrow architecture of three scorpion species of the family Scorpionidae: *Scorpio palmatus* from the Negev desert, Israel; *Opistophthalmus setifrons*, from the Central Highlands, Namibia; and *Opistophthalmus wahlbergii* from the Kalahari desert, Namibia. We hypothesized that burrow structure maintains temperature and soil moisture conditions optimal for the behavior and physiology of the scorpion. Casts of burrows, poured in situ with molten aluminum, were scanned in 3D to quantify burrow structure. Three architectural features were common to the burrows of all species: (1) a horizontal platform near the ground surface, long enough to accommodate the scorpion, located just below the entrance, 2–5 cm under the surface, which may provide a safe place where the scorpion can monitor the presence of potential prey, predators, and mates and where the scorpion warms up before foraging; (2) at least two bends that might deter incursion by predators and may reduce convective ventilation, thereby maintaining relatively high humidity and low temperature; and (3) an enlarged terminal chamber to a depth at which temperatures are almost constant (±2–4 °C). These common features among the burrows of three different species suggest that they are important for regulating the physical environment of their inhabitants and that burrows are part of scorpions' "extended physiology" (*sensu* Turner, Physiol Biochem Zool 74:798–822, 2000).

Keywords Burrows · Extended organism · Three-dimensional modeling · Scorpionidae · Temperature gradients

Introduction

Many animals, ranging in size from ants to aardvarks, inhabit burrows for all or most of their lives. Burrows are an extension of the burrower's physiology and therefore should be as subject to natural selection as conventional physiological organs (von Frisch 1974; Dawkins 1984; Hansell 1984; Turner 2000; Hansell 2007; Turner and Pinshow 2015). Such "organs of extended physiology" fulfill physiological (and other) functions that would otherwise require continuous investment of energy by the animal itself. These modified habitats vary enormously in architectural complexity (Meadows and Meadows 1991; Kinlaw 1999; Whitford and Kay 1999; Turner 2000,

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2001). Burrows can serve as refuges from adverse environmental conditions (Svendsen 1976; Reichman and Smith 1990) by providing a stable micro-climate, with the surrounding soil buffering residents from the vagaries of physical conditions that prevail above the ground surface.

In the present study, we examined the possible physiological functions of burrows built by scorpions. Many species of scorpions, in at least 10 families, construct burrows; these vary from temporary structures, occupied for less than 24 h, to semi-permanent structures, in which they spend most of their lives and more than 90 % of their time (Polis 1990). The form of scorpion burrows ranges from short runs or scrapes (e.g., Harington 1978; Robertson et al. 1982) to complex, spiral tunnels up to 3 m long, terminating a meter below the ground surface (our unpublished observations). However, most are simple tunnels, 15–30 cm deep, descending gradually from the surface at an angle of 20–40° (Williams 1966; Newlands 1972a; Eastwood 1978; Newlands 1978; Polis et al. 1986; Polis 1990; Prendini et al. 2003; Talal et al. 2015). Burrow structure and depth differ among species and depend on habitat and soil type, hardness, texture, and composition (Koch 1978; Lamoral 1978, 1979; Koch 1981; Prendini 2001, 2005; Hembree et al. 2012). The burrows of scorpions that inhabit mesic environments are often shallow and constructed beneath rocks, logs, or other surface debris (Smith 1966; Crawford and Riddle 1975; Eastwood 1978; Shivashankar 1992; Tare et al. 1993; Shivashankar 1994; Talal et al. 2015), whereas, in xeric environments, scorpion burrows are often deeper, more complex, and constructed in open ground (Koch 1978; Lamoral 1979; Polis et al. 1986; Talal et al. 2015). Some species are known to move along temperature gradients within their burrows to regulate body temperature (Hadley 1970b), and the tortuous architecture of some burrows may facilitate vertical movement within them (Polis 1990).

Burrows are central to the lives of many scorpions (Polis 1990). Various features of the burrow may assist the scorpion in meeting the physiological challenges of its environment. We hypothesized that burrow structure maintains temperature and soil moisture conditions optimal for the behavior and physiology of the scorpion. We tested the predictions that (1) burrow temperature at any depth is equal to that of the surrounding soil at that depth and (2) the terminal chamber of the burrow is located at a depth at which soil temperature is constant.

Materials and methods

Study species

The following three species of family Scorpionidae Latreille, 1802 were studied: *Scorpio palmatus* (Ehrenberg, 1828) in Israel and *Opistophthalmus setifrons* Lawrence, 1961 and *Opistophthalmus wahlbergii* (Thorell, 1876) in Namibia. The Middle Eastern and northern African genus *Scorpio* L., 1758 and the southern African genus *Opistophthalmus* C. L. Koch, 1837 are geographically separated relatives; *Opistophthalmus* is the basal clade of Scorpionidae, sister to a clade of three genera that includes *Scorpio* as its basal clade (Prendini et al. 2003). As such, some aspects of the ecology of these scorpions, including burrow architecture, may have been inherited from a common ancestor.

Scorpio palmatus, which has been extensively studied in Israel (e.g., Levy and Amitai 1980; Shachak and Brand 1983; Kotzman et al. 1989; Rutin 1996; Talal et al. 2015), inhabits brown-red sandy soils, loess, and alluvium (Levy and Amitai 1980). Burrows are always constructed in open ground and run parallel to the surface for approximately 10 cm before turning and descending at an angle of descent of 20–40° for 20–70 cm and terminating in an enlarged chamber (Levy and Amitai 1980; Talal et al. 2015). Depending on the species, *Opistophthalmus* construct burrows under stones or in open ground. These vary from shallow scrapes to elaborate, spiraling tunnels in substrates of different hardness and composition, from unconsolidated dune sand to compacted clay-rich soils (Lamoral 1979; Prendini et al. 2003). *Opistophthalmus setifrons* burrows are 15–20 cm deep (Lamoral 1979). Despite varying in depth and configuration, the burrows of different species of *Opistophthalmus* and *Scorpio* are readily identified by their typical oval-, reniform-, or crescent-shaped entrances. A tumulus of excavated soil is often present immediately in front of the entrances of occupied burrows.

All species of *Opistophthalmus* and *Scorpio* are solitary and cannibalistic, except when the young reside with the mother after parturition until dispersing from the natal burrow (Lamoral 1979; Shachak and Brand 1983). Short-distance dispersal of juvenile scorpions may result in dense, patchy populations in suitable habitats. Scorpionids can occupy a burrow for their entire life span, but dispersal information is deficient for many species. Burrows are excavated in the rainy season. *Scorpio palmatus* periodically leave old burrows and establish new ones throughout their lives depending on prey availability and population density (Shachak and Brand 1983). The burrow serves as the location for feeding and molting, while courtship, copulation, parturition, and maternal care also occur in the burrows of females (Prendini et al. 2003). Like other scorpionids, *Opistophthalmus* and *Scorpio* are "sit-and-wait" predators (McCormick and Polis 1990), emerging from their burrows to the entrances at dusk and remaining there, "doorkeeping," until passing prey comes within range, whereupon they dash out to seize it and then retreat down their burrows to consume it (Eastwood 1978; Shachak and Brand 1983; Kotzman et al. 1989).

Study sites

We studied burrows at three sites in 2014 and 2015. Between February and August 2014, we studied *S. palmatus* burrows in loess soil on the Sede Boqer Campus of Ben-Gurion University of the Negev (30° 51′ 17″ N, 34° 46′ 57″ E) in the Negev desert highlands, Israel. In May 2014, we studied *O. setifrons* burrows in sandy-loam soil of the thorn bush savanna (Eitel et al. 2002) at Cheetahview Research Farm (Farm Bergview 317; 20° 34′ 37.47″ S, 16° 53′ 22.76″ E) in the Central Highlands of the Otjiwarongo District, Namibia. In April 2015, we studied *O. wahlbergii* burrows at the crest and at the base of semi-consolidated red Kalahari sand dunes on Farm Bloukop 506 (25° 08′ 13.21″ S, 19° 53′ 34.72″ E) in the Mariental District, Namibia.

Burrow architecture

We cast 43 natural burrows with molten aluminum (30 of *S. palmatus*, 19 of *O. wahlbergii*, and four of *O. setifrons*). We followed the method of Tschinkel (2010), except that our kiln was heated with a gas burner rather than charcoal. Some linear measurements were made directly from the aluminum casts with a digital Vernier caliper (Absolute Digimatic 500–198 GL, Mitutoyo Corp., Aurora, IL). The shape of the aluminum casts was captured with a 3D laser scanner (NextEngine 3D scanner HD, Santa-Monica, CA; Supplementary material Appendix 1) and quantified using Rhinoceros 5 (Robert McNeel & Associates, Seattle, WA) and Geomagic Verify Viewer (3D Systems, Rock Hill, SC) software.

The height and width of burrow entrances were recorded in situ prior to casting, and the following metrics were recorded or calculated from each cast (following Hembree et al. 2012): depth from surface to bottom of the terminal chamber (*D*), length (*L*), and width (*W*) from entrance to terminal chamber; maximum and minimum tunnel height ($h_{\mathrm{min,\ max}}$) and width ($w_{\mathrm{min,\ max}}$); platform angle, length (l_p), and depth to first turn (d_p); terminal chamber height and width (h_tc, w_tc; Fig. 1); and burrow volume, entrance compass orientation, and burrow tunnel angle at five equally spaced intervals (a_1–a_5; Fig. 2). All angles were measured relative to the level ground surface, which served as the horizontal reference plane. A marker was used to indicate a horizontal plane relative to the burrow entrance. On the sand dune in the Kalahari, some burrows were not constructed on flat ground, but the marker allowed us to correctly orient the burrow model for analysis. Burrow complexity was calculated as the number of branches and terminal chambers, and burrow tortuosity by computing a line through the center and along the length of each burrow using Grasshopper in Rhinoceros 5, importing the line into MATLAB 2013a (MathWorks, Inc., Natick, MA), and calculating the Sum of Angles Metric by integrating total curvature and normalizing by the total length in three dimensions (Hart et al. 1999; Bullitt et al. 2003).

Scorpion identification and measurement

Before casting, the scorpion inhabiting each burrow was captured using a pitfall trap set in front of the entrance. Carapace length and width and total body length of each scorpion were measured with digital Vernier calipers, and the animal was

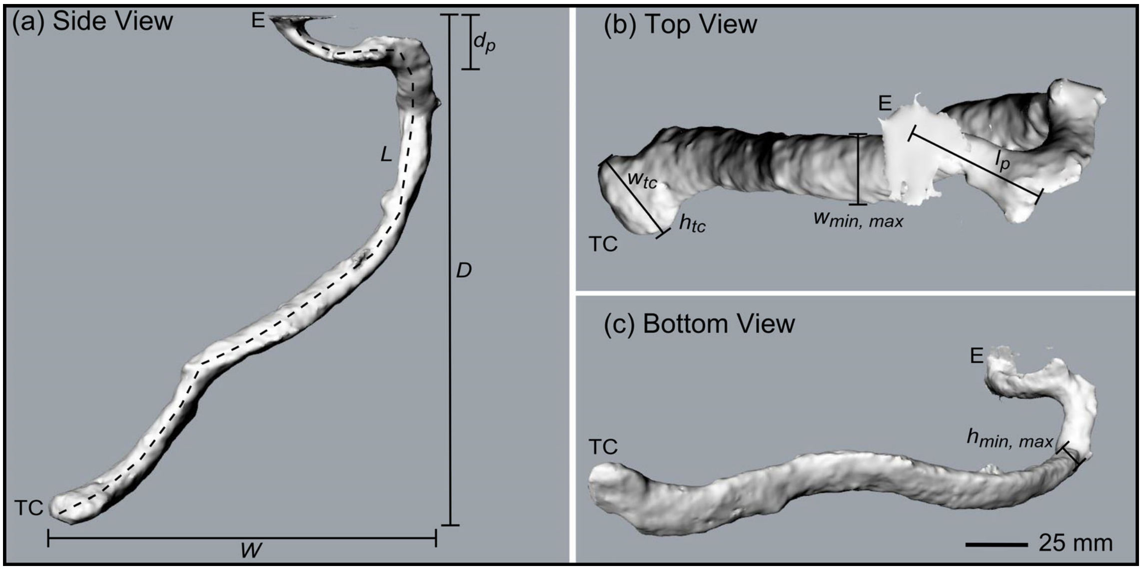

Fig. 1 Three-dimensional scan of an aluminum cast of a burrow of the scorpion *Scorpio palmatus* in the Negev desert highlands, Israel, in **a** side, **b** top, and **c** bottom views, illustrating burrow descriptor variables, total depth (*D*), length (*L*), and width (*W*) from entrance (*E*) to terminal chamber (TC); maximum and minimum tunnel height ($h_{\mathrm{min,\ max}}$) and width ($w_{\mathrm{min,\ max}}$); platform length (l_p) and depth (d_p) from entrance to first turn; and terminal chamber height (h_tc) and width (w_tc). Entrance height and width were measured with Vernier calipers before burrows were cast with molten aluminum

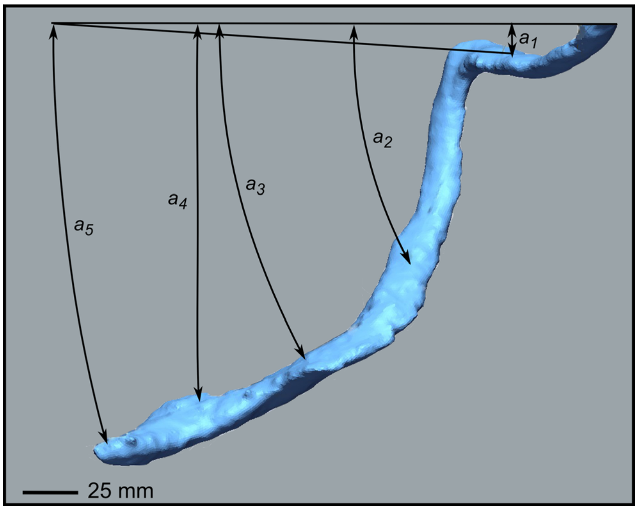

Fig. 2 Burrow tunnel angle measurements of a three-dimensional scan of an aluminum burrow cast of the scorpion *Scorpio palmatus* in the Negev desert highlands, Israel. Burrow tunnel angle, relative to ground level (horizontal), was measured at five evenly spaced intervals (a_1–a_5). See text for details

weighed to ±0.01 g with a digital scale (Israel Scout Pro SP202, Ohaus Corp., Pine Brook, NJ; Namibia PPS200, Pesola AG, Schindellegi, Switzerland). After identification by LP, voucher specimens of *S. palmatus* were deposited in the collection of the Mitrani Department of Desert Ecology, Ben-Gurion University of the Negev, Midreshet Ben-Gurion, Israel, and of the two *Opistophthalmus* species in the National Museum of Namibia, Windhoek. The sex of *S. palmatus* specimens was determined by examination of the pectines and genital aperture.

Soil temperature and moisture

We measured the daily fluctuation of temperature at the bottom, middle, and top of the burrow (within 5 cm from the entrance) by threading 45 standard wire gauge (SWG) Cu-constantan thermocouples (TCs) into three natural burrows of *S. palmatus* in Israel. The three TCs were glued to steel ball bearings (1.05 g, 6.34 mm diameter), ensuring that they could be carried to the bottom of a burrow. At the same time, a soil temperature profile was measured adjacent to the burrows with a single, vertical array of nine 30 SWG Cu-constantan TCs taking measurements at 5-cm intervals, from the ground surface (depth = 0 cm) to a depth of 40 cm. The TC array was inserted into a vertical hole, 1 cm in diameter, which was carefully refilled with soil and tamped firm. The replaced soil and TCs were allowed to equilibrate for at least 24 h with their surroundings before data were collected. We measured temperatures at 10-min intervals for 3 days in July/August 2014 using a data logger (CR23X Micrologger, Campbell Scientific, Logan, UT). We compared the temperature at the bottom of the burrow with the adjacent soil temperature profile to predict the depth of the burrow. We cast the burrows in aluminum after the 3 days of temperature measurement. Upon excavation, we confirmed the depths and the exact placement of the TCs to ensure that reliable comparisons could be made between burrow and soil temperature profiles.

All thermocouples were calibrated in a temperature-controlled, circulating water bath (ThermoHaake DC10 and V26, Karlsruhe, Germany) to ±0.1 °C against mercury-in-glass thermometers (Taylor Instrument Co., Rochester, NY; catalog numbers 21001 [−8–32 °C] and 21002 [25–55 °C]); the calibration accuracy of which was traceable to the US National Institute of Standards and Technology.

We measured three soil temperature profiles in situ for *O. wahlbergii* in Namibia, two at the crest of the dune and one at the base. Due to differences in available equipment, we used a different method than in Israel. Temperatures were measured with Thermochron® data loggers (iButton, Maxim Integrated Products, San Jose, CA), set to 8-bit precision (±0.5 °C), with manufacturer-supplied accuracy of ±1.5 °C. We performed three-point calibrations for all Thermochrons against one of the previously calibrated TCs (see above) and calculated correction factors for each. Five Thermochrons were wrapped in gauze and buried in the soil, one below the other, for each profile. We measured temperature every minute for 24 h at depths of 10, 30, 50, 70, and 100 cm below the surface, at the crest and base of the sand dune. We also prepared a separate temperature profile, recording soil temperatures on the crest of the dune at depths of 2, 10, 20, 40, and 80 cm every minute for 3 days. Thermochrons were allowed to equilibrate in the ground for more than 12 h before measurement commenced.

Gravimetric soil water content ($\omega = \frac{\text{wet}-\text{dry}}{\text{dry}}$) was calculated for nine *S. palmatus* burrows from the wet and dry masses of soil samples collected at burrow terminal chamber depth with a closed-sided bucket auger and weighed to ±0.0001 (Precisa 40SM–200A, Precisa Gravimetrics AG, Dietikon, Switzerland). Dry mass was measured after soil samples were dried to constant mass in an oven at 105 °C for 48 h. Gravimetric soil water content profiles, in 5-cm increments, were also measured at the burrow sites of *S. palmatus* in Israel (June and August 2014) and *O. wahlbergii* in Namibia (May 2015), weighed to ±0.01 using an electronic scale (Pesola PPS200).

Statistical analyses

Statistical analyses were performed using R (Core Team 2014). Log-transformed scorpion body length was compared among species using analysis of variance (ANOVA) and Tukey's post hoc test. We accounted for the effect of scorpion body size on burrow size by calculating the residuals from power function regressions for all burrow variables that were correlated to scorpion body length (D, $w_{\min}$, $h_{\max}$, $h_{\min}$). After testing for normal distribution of the measured variables (Shapiro-Wilk normality test, *shapiro.test* in R), we successfully normalized necessary variables with a log-transformation, and performed a multivariate analysis of covariance (MANCOVA) to identify which burrow features differed among species, with scorpion total body length as a covariate. We tested for differences in size and burrow features between sexes of *S. palmatus* with MANOVA and post hoc analysis with an ANOVA. Linear discriminant function analysis (DFA; *lda*, MASS package; Venables and Ripley 2002) was used to compare burrow structure among the three species. We used redundancy analysis (*rda*, vegan package of Oksanen et al. 2013) to model burrow characteristics (the response variables) as functions of soil water content (the explanatory variable). Significance was accepted at $p \leq 0.05$.

Results

Scorpion body length

The mean total body length of the *O. wahlbergii* specimens, captured before casting their burrows, did not differ significantly between the crest and base of the sand dune ($p = 0.313$). However, the captured specimens of *O. wahlbergii* were significantly smaller (37.9 ± 4.9 mm) than the specimens of *O. setifrons* (46.5 ± 12.1 mm) and *S. palmatus* (47.5 ± 6.7 mm; $F_{2,36} = 398.4$, $p < 0.001$) and were determined to be immature. The adult body length of *O. wahlbergii* is greater than that of the other two species (LP personal observations). There were no significant differences in body length between the sexes for *S. palmatus* (11 females, 10 males; $p = 0.944$).

Burrow architecture

Several features were common to the burrows of all three species: a platform, long enough to accommodate the scorpion, located just below the entrance, 2–5 cm under the surface (Table 1); at least two bends; and a terminal chamber wider than the burrow tunnel (Fig. 3). The platform descended more gradually (platform angle, 16.8 ± 12.6°) than the rest of the burrow (30.8 ± 15.4°) in all three species.

The depth and configuration of *O. wahlbergii* burrows did not differ significantly between the crest and base of the Kalahari sand dune ($p = 0.296$), except for the deepest two angles of the burrow ($F_{2,16} = 7.926$, Wilk's $\lambda = 0.502$, $p = 0.004$), and they were not included for further analysis. Burrows at the crest of the dune had a steeper angle of descent at the terminal chamber (a_5), whereas the second to last angle (a_4) was steeper at the base of the dune (Fig. S1). The data for these burrows were therefore pooled for analysis. Several features differed significantly among the burrows of the three species (Wilk's $\lambda = 0.001$, $F_{1,15} = 1045.865$, $p < 0.024$). The burrows of *O. wahlbergii* were significantly longer, but with narrower tunnels and longer, steeper entrance platforms. The burrows of *O. setifrons* were significantly more tortuous than those of the other two species, whereas the tortuosity of *S. palmatus* and *O. wahlbergii* burrows was not significantly different.

Discriminant function analysis distinguished burrows of the three species based on nine burrow shape variables (D, L, V, $h_{\max}$, $w_{\min}$, l_p, h_{tc}, tortuosity; Wilk's $\lambda = 0.036$, $\chi^2_{8,18} = 100.169$, $p < 0.001$) and correctly classified 98.1 % of the burrows. The burrows of *S. palmatus* were correctly identified in 96.7 % of the cases, those of *O. wahlbergii* in 94.4 %, and of *O. setifrons* in 100 %.

Overall, there were no significant differences in burrow features between sexes of *S. palmatus* ($F_{1,19} = 1.35$,

Table 1 Mean ± SD measurements of burrows of three scorpion species, *Scorpio palmatus* in the Negev desert, Israel; *Opistophthalmus wahlbergii* in the Kalahari desert, Namibia; and *Opistophthalmus setifrons* in the Central Highlands, Namibia: total depth (D), length (L), and width (W) from entrance (E) to terminal chamber (TC); maximum and minimum tunnel height ($h_{\min}$, $h_{\max}$) and width ($w_{\min}$, $w_{\max}$); entrance (E) height and width; platform angle (a_p), length (l_p), and depth from entrance to first turn (d_p); and terminal chamber height (h_{tc}) and width (w_{tc})

	S. palmatus $n = 30$	*O. wahlbergii* $n = 19$	*O. setifrons* $n = 4$
D (mm)	172.7 ± 42.4	270.6 ± 58.1	194.9 ± 30.8
L (mm)	335.5 ± 75.0	627.8 ± 162.0	404.3 ± 40.7
W (mm)	201.7 ± 50.9	262.7 ± 73.4	194.2 ± 75.1
$h_{\min}$ (mm)	16.4 ± 3.3	7.2 ± 1.6	10.3 ± 1.7
$h_{\max}$ (mm)	32.5 ± 8.4	13.7 ± 2.2	19.5 ± 2.9
$w_{\min}$ (mm)	16.3 ± 3.0	16.4 ± 3.3	20.0 ± 4.5
$w_{\max}$ (mm)	30.4 ± 5.3	32.5 ± 8.4	41.8 ± 9.6
E height (mm)	25.3 ± 4.7	11.8 ± 2.0	12.3 ± 1.9
E width (mm)	20.7 ± 2.8	25.3 ± 4.7	21.7 ± 2.9
a_p (°)	10.6 ± 7.4	23.5 ± 5.7	13.6 ± 3.9
l_p (mm)	66.9 ± 16.7	110.0 ± 50.7	70.0 ± 22.1
d_p (mm)	22.8 ± 9.8	47.4 ± 22.6	29.7 ± 7.7
h_{tc} (mm)	29.6 ± 8.7	12.7 ± 2.2	17.5 ± 4.4
w_{tc} (mm)	28.7 ± 6.2	29.6 ± 8.7	39.8 ± 10.2

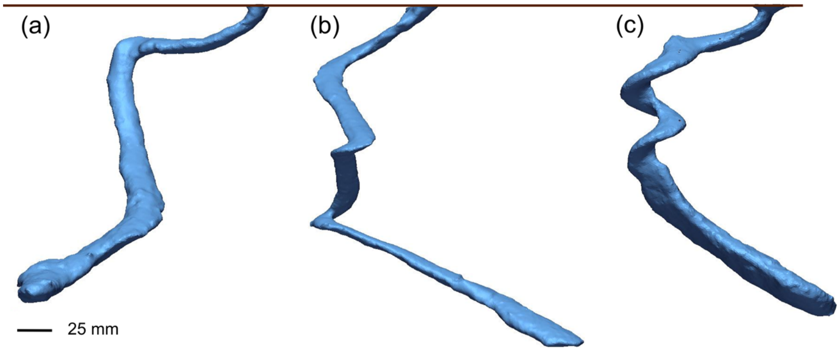

Fig. 3 Three-dimensional scans of aluminum casts of burrows of three scorpion species, **a** *Scorpio palmatus* in the Negev desert highlands, Israel; **b** *Opistophthalmus wahlbergii* in the Kalahari desert, Namibia; and **c** *Opistophthalmus setifrons* in the Central Highlands, Namibia

$p = 0.60$), except for females that had wider terminal chambers ($F_{1,19} = 7.99$, $p = 0.011$).

Soil temperature and moisture

Soil and burrow temperatures at the same depth were similar (Fig. 4a, b). Due to the close similarity between temperatures in the soil and the burrow, it was possible to predict burrow depths based on temperatures measured within them. For example, burrows that we predicted to be 23, 12, and 14 cm deep, based on comparisons between temperatures measured at the bottom of the burrows and in the adjacent soil, were measured from the aluminum casts to be 22.5, 12, and 13.8 cm deep.

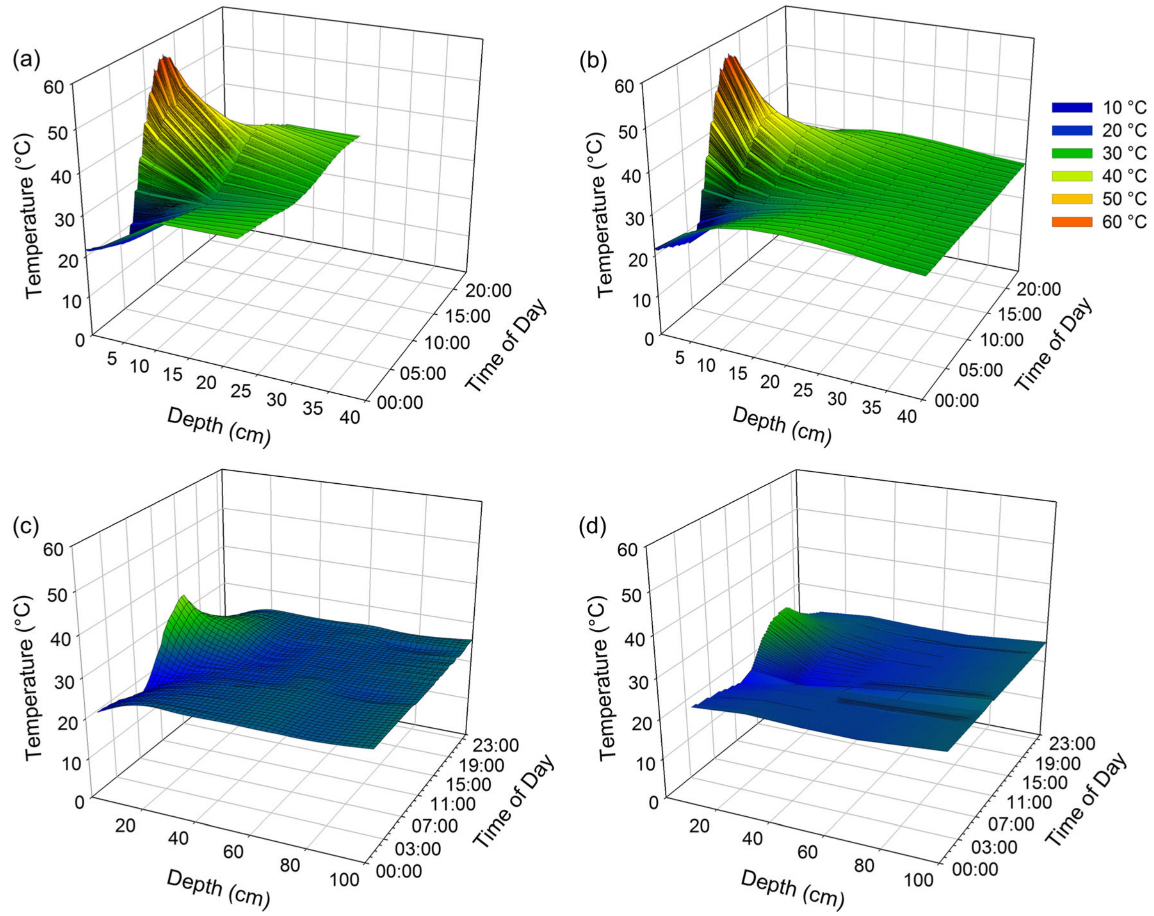

Fig. 4 Soil temperature profiles with increasing depth recorded in **a**, **b** the Negev desert highlands, Israel, and **c**, **d** the Kalahari desert, Namibia. Temperatures were recorded simultaneously for 24 h in August 2014 at **a** three locations in burrows of the scorpion *Scorpio maurus* at the entrance (2 cm deep), in the middle (11 cm deep), and at the bottom (22.5 cm deep) and **b** in an adjacent profile at 5-cm intervals from 0 to 40 cm deep in soil, 10 cm from the burrow. Temperatures in the burrows closely matched those of the surrounding soil, allowing the depth of burrows to be predicted from the temperatures within them. Mean soil temperature in burrows of the scorpion *Opistophthalmus wahlbergii* on **c** the crest and **d** at the base of a sand dune was recorded during 3 days in April 2015

The daily fluctuation of soil temperature varied with depth. At the burrow sites of *S. palmatus*, soil temperature fluctuated by 0.9 ± 0.6 and 3.1 ± 0.2 °C at depths of 40 and 20 cm, respectively (Fig. 4b). At the average depth of the entrance platform, 2 cm below the surface, the temperature cycled through a daily range of 24.0 ± 1.1 °C, from a mean maximum of 42.8 ± 0.8 °C to a mean minimum of 18.8 ± 0.9 °C. At sunset, temperatures at the entrance platform and the average burrow depth were within 4 °C of each other (platform 28.5 ± 1 °C, terminal chamber 32.1 ± 0.3 °C; Fig. 4a).

At the burrow sites of *O. wahlbergii* in Namibia, the daily fluctuation of soil temperature 30 cm below the surface was 2 °C on the crest of the sand dune (Fig. 4c) and 4.4 °C at its base (Fig. 5d). Temperatures were almost stable, with only a 1 °C fluctuation, at 50-cm depth on the crest of the sand dune (24.11 ± 0.44 °C; Fig. 4c) and at 70-cm depth at its base (23.35 ± 0.32 °C; Fig. 4d). The daily temperature range at 2-cm depth on the crest of the dune was 11.7 ± 7.2 °C.

The volume, length, and entrance size of *S. palmatus* burrows decreased with increasing soil water content ($F_{1,7} = 7.24$, $p = 0.03$; Fig. 5). Soil water content was greater in the Kalahari sand than in the loess soil in Israel and greater at the base of the sand dune than at the crest (Fig. 6).

Discussion

Despite belonging to two genera, occurring at three geographically separate locations, and being constructed in substrates of different hardness and composition, the burrows of the three scorpionid species studied had several remarkably similar features, including a horizontal to shallowly angled platform just below the entrance and near the surface, at least two bends, and an enlarged terminal chamber where it is dark, relatively cool, and damp.

Burrow entrance platform

Entrance platforms of similar length to those in the burrows of *S. palmatus* are apparently also present in the burrows of two *Scorpio* taxa occurring in Turkey (Çolak and Karataş 2013) and Iran (Navidpour et al. 2015). Similar entrance platforms, described as “short tunnels” or “straight entrance runs” descending at an angle of 25–30° and preceding the spiral section of the burrow, are also present in the burrows of several species in the Australian genus *Urodacus* (Koch 1978; Shorthouse and Marples 1980; White 2001).

The ubiquity of the entrance platform in five scorpionid taxa and several urodacids suggests that it might serve an important behavioral and/or physiological function. The entrance platform may provide a safe place for doorkeeping close to the burrow entrance where the scorpion can detect subtle air currents; substrate-borne vibrations; and/or pheromones of potential prey, predators, and mates (Brownell and Farley 1979; Krapf 1986, 1988; Brownell and van Hemmen 2001; Mineo and Del Claro 2006), especially on moonlit nights when there is a greater risk of predation by vertebrate predators (Skutelsky 1996). In addition, the platform, which typically has a higher temperature than the terminal chamber, might provide a safe place for the scorpion to warm up before foraging.

Burrow tortuosity

The ubiquitous presence of bends and spirals in the burrows of the three scorpionid species studied, as well as in the burrows of other species of Scorpionidae, Urodacidae, and the distantly related chactoid genus, *Anuroctonus* Pocock, 1893 (Williams 1966; Newlands 1972a; Koch 1978; Shorthouse and Marples 1980; Prendini et al. 2003; Prendini 2005), suggests another important, common function. Polis (1990)

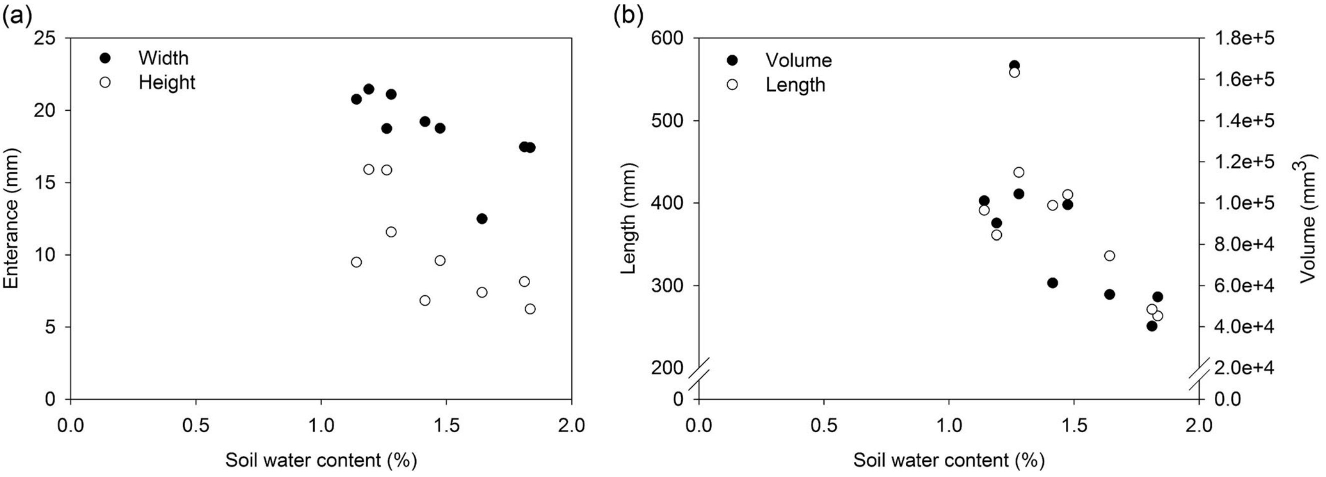

Fig. 5 Relationship between burrow characteristics and soil water content (%) at the depth of the terminal chamber of the burrow of the scorpion *Scorpio palmatus* in the Negev desert highlands, Israel. Burrow volume, length, and entrance size decreased with increasing soil water content ($p = 0.03$)

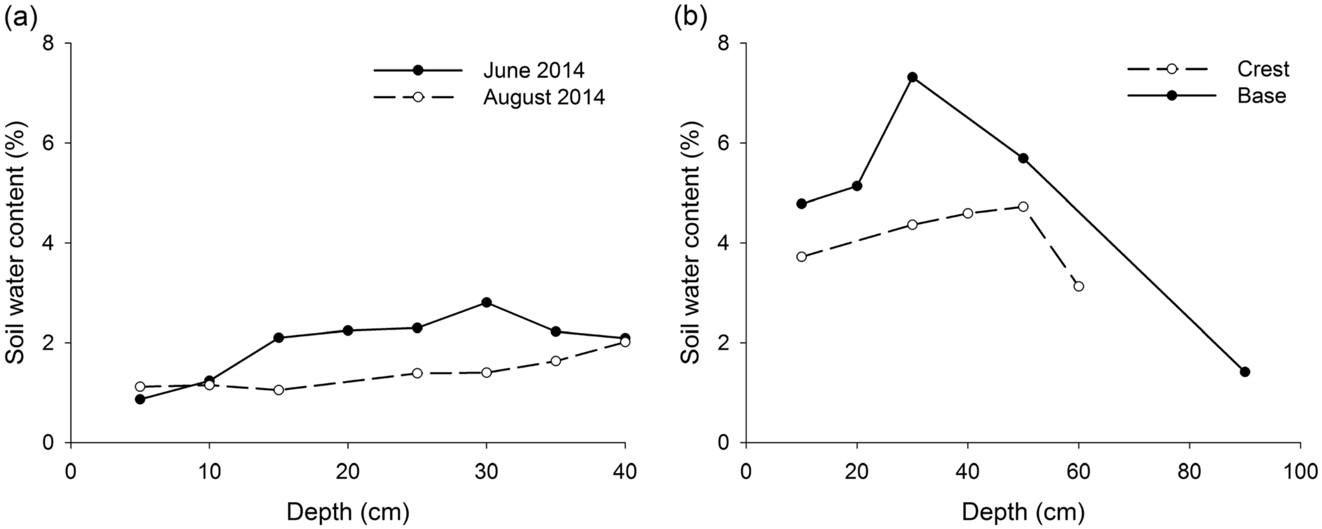

Fig. 6 Gravimetric soil water content (%) profiles with increasing depth in burrows of two scorpion species, **a** *Scorpio palmatus* in the Negev desert, Israel, in June and August 2014, and **b** *Opistophthalmus wahlbergii* at the crest and base of a sand dune in the Kalahari desert, Namibia, in May 2015

hypothesized that tortuosity may attenuate the angles of ascent and descent, facilitating vertical movement in burrows that are required to be deep enough to reach optimal temperature and humidity. This is not necessarily the case since some species of the scorpionoid family Hormuridae Laurie, 1896, e.g., the African *Cheloctonus jonesii* Pocock, 1892; Indian *Liocheles nigripes* (Pocock, 1897); and at least two species of the Australian genus *Hormurus* Thorell, 1876 (Tilak 1970; Newlands 1972a; Harington 1978; Monod et al. 2013) construct simple, vertical burrows descending 70–90° from the horizontal to 15–30 cm (i.e., to a similar depth as the burrows of *S. palmatus*, *O. setifrons*, and *O. wahlbergii*), without any twists and turns. Thus, some species are capable of climbing vertically, so tortuosity may serve other functions as well.

Shorthouse and Marples (1980) hypothesized that tortuous, spiral burrows reduce the risk of antagonism or cannibalism by reducing the possibility of encounters between scorpions from neighboring burrows. The same hypothesis was presented by Martin and Bennett (1977) when investigating helical burrows of a Miocene beaver, *Palaeocastor fossor* Leidy, 1869, at high densities. This hypothesis leads to the prediction that burrows in dense populations are more tortuous than those in sparse populations. The abovementioned hormurid scorpions, which construct simple, vertical burrows, occur in similar densities to *O. wahlbergii* and *S. palmatus*, i.e., up to four burrows per square meter in *C. jonesii* (Harington 1978). Further study is necessary to confirm or refute the hypothesis of Shorthouse and Marples (1980), but according to the calculations of Meyer (1999), the chance a straight section of a burrow would intersect another burrow is low (5–8 %).

A more plausible explanation for the tight switchback bends and spirals observed in the burrows of scorpionids and urodacids is that they serve as protection against predators, from both those that enter the burrows, such as centipedes or lizards, and those that excavate scorpions from their burrows, such as mongooses, honey badgers, hyenas, and monitor lizards (Koch 1970; King and Green 1979; Polis et al. 1981; Shivashankar 1994; Avenant and Nel 1997; Begg et al. 2003; De Vries et al. 2011). It costs less energy for predators to excavate scorpions from soft soils. However, the cost of excavation may increase disproportionately the deeper and more tortuous the burrow, as sand caves in and the tunnel becomes increasingly harder to follow.

Yet, another possible explanation for tortuous burrows is that the twists and turns serve to reduce temperature change and drying by wind-induced gas exchange. Scorpions typically have very low rates of evaporative water loss through their cuticle (Hadley 1970a; Toolson and Hadley 1977; Hadley 1990). Some burrowing scorpions have higher rates of water loss than epigean species (Gefen and Ar 2004), hinting at the potential importance of the burrow for maintaining water balance. Tortuous burrows are typically found in more open areas, e.g., on plains and sand dunes (Koch 1978), and are likely more exposed to wind and eddies in the turbulent boundary layer (Stull 1988; Turner and Pinshow 2015). Thus, tortuous burrows may be an adaptation to minimize convective ventilation and sustain high relative humidity in the burrow, thereby reducing the evaporative water loss of its occupant, but this has yet to be tested.

Other animals have tortuous burrows, such as the gopher tortoise, *Gopherus polyphemus* Daudin, 1802, which may add twists to its burrow to decrease the chance of collapse relative to a straight tunnel (Kinlaw and Grasmueck 2012). *Varanus panoptes* (Storr, 1980), a burrowing varanid lizard, has a highly tortuous, helical segment leading to the nest in its nesting burrow (Doody et al. 2015). The entrance of the burrow is plugged with soil, indicating that the tortuosity is not related to maintaining consistent temperature or humidity by limiting air circulation. The helical segment requires greater energy expenditure than a straight burrow of the same incline (Meyer 1999); thus, there is an adaptive function that is yet to be described (Doody et al. 2015).

Soil moisture

Burrow architecture may also depend upon prevailing soil moisture, with burrows in moist soils having higher humidity, and less need for energetically expensive modifications, such as tortuosity, to reduce wind-induced gas exchange. Consistent with this hypothesis, the length and volume of *S. palmatus* burrows decreased with increasing soil moisture in the present study. Newlands (1972a, b) and Lamoral (1979) noted increased depth and tortuosity in the burrows of *Opistophthalmus* species inhabiting softer, sandier substrates, supporting the hypotheses that deeper burrows are required to reach optimal temperature and humidity in dry, sandy soils. It also would cost less energy for scorpions to excavate deeper burrows in loose, sandy soils. We found evidence to support this in the present study; burrows of immature *O. wahlbergii* in semi-consolidated Kalahari sand were longer and deeper than burrows of adult *O. setifrons* and *S. palmatus* in harder, more compacted soils. The relationship of burrow structure to soil moisture could also be correlated with soil hardness, as harder, clay-rich soils have the potential for greater moisture retention.

Soil temperature

The daily fluctuation of burrow temperatures closely followed that in the surrounding soil recorded at the same depth, allowing us to predict the depth of burrows based on the temperatures measured in their terminal chambers. Soil temperature is therefore a good proxy for burrow temperature at the same depth. Contrary to our predictions, however, burrows were not deep enough to reach the iso-thermocline. Burrow depth may therefore be a trade-off between optimizing thermal conditions and the energy required for burrow excavation. *Scorpio palmatus* burrows reached an average depth of 17 cm, where the range of daily temperature was about 3 °C, rather than 45 cm, where the soil temperature was constant throughout the day. *Opistophthalmus wahlbergii* burrows reached an average depth of 27 cm, where the daily temperature fluctuation was 2–4 °C, rather than 70 cm or more, where daily temperatures fluctuated less than 1 °C. Burrow depth differs among populations of *S. palmatus* (Abdel-Nabi et al. 2004), but dimensions very similar to those reported in the present study were also reported for two *Scorpio* taxa occurring in Turkey (Çolak and Karataş 2013) and Iran (Navidpour et al. 2015). Differences in burrow depth within and among species appear to be driven by differences in their local soil temperature profiles.

Conclusions

The striking architectural similarity among the burrows of three scorpion species suggests that their common features are important for managing the scorpions' physical environment, making the burrows part of the scorpions' "extended physiology" (*sensu* Turner 2000). Our results have led us to hypothesize that (1) the entrance platform may provide a safe place for doorkeeping, especially on moonlit nights, and for thermoregulation; (2) burrow tortuosity may reduce the risk of predation and may reduce desiccation by wind-induced gas exchange; and (3) burrow architecture may change in response to soil composition, hardness, and moisture, which are interrelated. Although many questions remain unanswered concerning the burrow environment and the natural history of burrowing scorpions in general, it seems clear that an understanding of burrowing scorpion ecology requires an understanding of burrow architecture. The stereotypical features observed in the burrow architecture of the three scorpionid species investigated have been shaped by natural selection over millions of years and may be similarly important to other burrowing scorpion species around the world.

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Authors' contributions AMA, EM, JST, and BP conceived, designed, and performed the experiments. AMA analyzed the data. LP identified the scorpions. AMA and BP wrote the manuscript and JST and LP edited the manuscript.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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