

Aspects of the ecology of the Arabian spiny-tailed lizard (*Uromastyx aegyptia microlepis* BLANFORD, 1875) at Mahazat as-Sayd protected area, Saudi Arabia

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Abstract. Burrows of semiadult to adult *Uromastyx aegyptia microlepis* at Mahazat as-Sayd Protected Area were between 300–530 cm long and 80–120 cm deep. Burrows are typically characterized by a perimeter wall around the burrow entrance, which consists of soil excavated by the animal occupying the burrow. These perimeter walls alter the thermal environment in the immediate vicinity of the burrow entrance and provide temporally and spatially different microhabitats to the lizard. Burrow entrance size is not linked to the size of the inhabitant. *Uromastyx* burrows lack passive wind-induced ventilation and diffusion is the main factor for the exchange of air in the burrow with atmospheric air. Therefore the burrows retain temperature as well as humidity very efficiently. Ambient humidity in the direct vicinity of the animal is between 4.0–98.4% rH in spring and 3.3–96.2% rH in summer. The ambient humidity fluctuates not only during the normal activity phases of the animals but also during the night, indicating movements within the burrow. Courtship behaviour, mating and signs of mating were observed in May. Hatchlings were observed in August and September, sitting in small bushes near burrow entrances of adult *Uromastyx*.

Key Words. Squamata, Sauria, Agamidae, *Uromastyx*, burrow morphology, morphology, home range, microclimate use, ecological observations, Saudi Arabia.

Introduction

The spiny-tailed lizards of the genus *Uromastyx* are inhabitants of the deserts and semi-deserts of North Africa, Arabia and the Middle East. Currently, 15 species are considered to be valid, of which 6 are known to occur on the Arabian Peninsula (WILMS et al. 2009a).

Uromastyx aegyptia (FORSKÅL, 1775) is by far the largest member of the genus, reaching a maximum body length of more than 700 mm and a weight of up to 2,500 g (Fig. 1). The Arabian Spiny-tailed Lizard (*Uromastyx a. microlepis* BLANFORD, 1875) lives in the deserts and semi-deserts of Arabia (Saudi Arabia, Yemen, Oman, United Arab Emirates, Qatar, Kuwait), in Jordania, Syria, Iraq and coastal Iran. Habitats show a marked seasonality regarding climatic parameters (temperature, humidity, precipitation) as well as regarding the availability of food. In contrast to the wide range of daily and annual fluctuations of air and soil temperatures, the temperatures within *Uromastyx* burrows are remarkably constant (WILMS & BÖHME 2007, and unpublished data). Therefore, these burrows are considered to play an important role as refuges in respect to thermo- and hydoregulation and as shelter from predators. *Uro-*

mastyx a. microlepis has a predilection for open habitats with hard, diggable substrates like coarse sand and gravel, and sparse vegetation (WILMS et al. 2009b). Mountainous areas and habitats with thick layers of stones, rocks or boulder are not suitable for *U. a. microlepis* (KEVORK & AL-UTHMAN 1972, ARNOLD 1980, AL-OGILY & HUSSAIN 1983). Population density in central Saudi Arabia is between 0.1 and 4 specimens per hectare (KORDGES 1998).

The primary production of *Uromastyx* habitats is quite low and exhibits strong seasonal and annual differences. Therefore, it is somewhat surprising that *Uromastyx aegyptia*, as all other species of the genus, is primarily herbivorous (MANDAVILLE 1965, KEVORK & AL-UTHMAN 1972, AL-OGILY & HUSSAIN 1983, BOUSKILA 1984 & 1987, ROBINSON 1995). Nevertheless, remains of beetles (Tenebrionidae, Carabidae), ants, grasshoppers and even scorpions are also found in the stomach contents as well as in fecal pellets of all age classes (KEVORK & AL-UTHMAN 1972, WILMS 2007, pers. obs.). However, the proportion of animal matter in the food is very low and was estimated to be only about 1–2% of total food intake.

The present paper analyzes the morphology of burrows of *U. a. microlepis*, the thermal and humidity environment

in the burrows as well as data on the animals' morphology. Beside this, observations on reproduction and co-inhabitation of burrows are presented.

This study was carried out on free ranging populations of *Uromastix aegyptia microlepis* in the Mahazat as-Sayd Protected Area, Saudi Arabia.

Material and methods

Study Site

All fieldwork was carried out within the boundaries of Mahazat as-Sayd Protected Area, Saudi Arabia, which has been protected since 1989 (Fig. 2). Mahazat as-Sayd (22° 15' N, 41° 50' E) is located in central-western Saudi Arabia, approximately 170 kilometers northeast of Taif. The reserve is Saudi Arabia's only completely fenced-in wildlife reserve and a reintroduction site for Houbara Bustards (*Chlamydotis undulata macqueenii*), Arabian Oryx (*Oryx leucoryx*) and Sand Gazelles (*Gazella subgutturosa*). Mahazat as-Sayd covers an area of 2244 km² and lies within one of the hottest regions of the world (MEIGS 1953). It is a hot and semi-arid to arid desert steppe habitat, typical of the central pla-

teau of the Arabian Peninsula, at elevations between 900 and 1050 m above sea level (LENAIN et al. 2004). The terrain of this area consists of flat gravel plains, known as regs, occasionally interdigitated by dry sandy wadis. More than 95% of the area are covered by sand and gravel. Air temperatures in Mahazat, as recorded in a standard weather shelter, often exceed 43°C during the summer, and occasionally reach 50°C (SEDDON 1996, SHOBRACK 1996, WILLIAMS et al. 1999). Rainfall averages ca. 100 mm per year (WILLIAMS et al. 1999) and typically occurs between March and May each year, but there are occasional important rain events at other times as well. There is no permanent source of water above ground level in Mahazat as-Sayd, but ephemeral pools exist for short periods after heavy rain (LENAIN et al. 2004).

The flat gravel plains in this part of the Arabian Desert are intersected by wadis and dominated by sparse vegetation of perennial grasses, including *Stipagrostis* spec., *Panicum turgidum* and *Lasiurus scindicus*, and small trees, mainly *Acacia* spec. (MANDEVILLE 1990).

The main study site was situated just southeast of the main gate to Mahazat as-Sayd (Al-Muwayh gate), covering an area of approx. 4 km². This study took place in spring, summer, and autumn of 2006 as well as spring and summer of 2007.



Figure 1. Adult *Uromastix aegyptia microlepis* at Mahazat as-Sayd, Saudi Arabia. Photo: T. WILMS.



Figure 2. Typical landscape at the study site in Mahazat as-Sayd, Saudi Arabia. Photo: T. WILMS.

Burrow morphology

The main study site was systematically scanned for *Uromastix* burrows by driving parallel transects (distances between transects ca. 50 meters). Each active burrow was marked with a flag (Fig. 3), and the following parameters were registered: Diameter of the perimeter wall, width of burrow entrance, height of burrow entrance, soil temperature on top of the perimeter wall, soil temperature just in front of the burrow entrance. Data of 194 active *Uromastix* burrows were registered. Burrows were considered as active (inhabited or visited) either if an *Uromastix* was observed directly or if fresh tracks were found near an open and clean burrow entrance. Otherwise, the burrow was classified as non-active (abandoned).



Figure 3. *Uromastix* burrow marked with a flag at the study site in Mahazat as-Sayd. Photo: T. WILMS.



Figure 4. *Uromastix a. microlepis* carrying a backpack with a radio transmitter and the “onboard” temperature and humidity data logger. Photo: T. WILMS.



Figure 5. *Uromastix* burrow with the typical perimeter wall made of excavated soil. The arrows indicate the position of the data loggers measuring soil temperatures. Photo: T. WILMS.

Microhabitat use

Air temperature and relative humidity were recorded in the direct vicinity of two *Uromastix a. microlepis* on 28 days each (summer, 20 July–16 August 2006; spring, 21 April–18 May 2007) using miniature data loggers (i-buttons, Dallas Semiconductors, Model 1923). In this study, the loggers stored temperature and relative humidity recordings every 20 minutes, resulting in 2048 temperature / humidity data-sets per respective season. The data loggers were attached as “onboard” data loggers (KERR et al. 2004) on the backpacks in the sacral region of the animals carrying the radio transmitters used for a separate study on the thermobiology of the species (Fig. 4).

Additionally, miniature data loggers (i-buttons, Dallas Semiconductors, Model 1921) were used to measure soil temperatures on 10 days (spring, two burrows, 16–21 May 2006) and 29 days (summer, one burrow, 13 August–10 September 2006) on top of the perimeter wall as well as just in front of the burrow entrance (Fig. 5). Data loggers were attached to strings, anchored to the ground using two nails (at least 10 cm from the logger) and covered with a thin layer of soil. Data loggers were calibrated in a water bath against a mercury-in-glass thermometer that had a calibration traceable to the National Institutes of Standards and Technology.

Animal morphology

At the main study site, *Uromastix* were trapped using snares placed into the entrance of active burrows. Trapping was carried out in spring 2006 (08 May–21 May), summer 2006: (15 July–01 August), autumn 2006 (20 October–11 November.), and spring 2007 (26 March–15 April). This trapping method has the advantage that a captured animal is still able to retreat into the burrow and therefore the risk of overheating and losing the animal is minimized. Captured *Uromastix* were marked with a passive integrated transponder (PIT) each, weighed, measured (total length,

tail length, head length and width, maximal tail width at fifth whorl and tail width between fourth and fifth whorls), and several scale counts (ventral scales between gular and inguinal folds, number of tail whorls, number of gular scales between mental scale and a line between the anterior margins of the ear openings, number of scales around fifth whorl, number of subdigital scales under left forth toe, number of preanofemoral pores, number of enlarged scales at the anterior margins of the ear openings on both sides, number of scale rows between supralabials, and enlarged subocular scales) were taken. Some specimens were implanted with temperature data loggers (i-buttons) and equipped with radio transmitters for a separate study on the thermobiology of *Uromastix a. microlepis* (WILMS et al. in prep.). The specimens were subsequently released at their original burrows.

Statistical data analyses

The Excel 2007 and RT4Win (HUO et al. 2006) statistical packages were used to run the analyses.

Results

Burrow morphology

Five *Uromastix* burrows inhabited by semiadult to adult specimens were excavated during the course of the present study. The burrows were between 300–530 cm long and 80–120 cm deep. None of the excavated as well as none of the additional 194 burrows investigated in the study area had more than one entrance. All excavated burrows entered the soil in a straight line for up to 1 m at a decline of about 30–45°. Farther down, the burrow in most cases turned to the left or right at an approximate right angle and then descended in the form of a spiral or in a zigzag line. In two cases we found blind side tunnels in the burrow.

Burrows of *Uromastix aegyptia microlepis* are typically characterized by a perimeter wall around the burrow en-

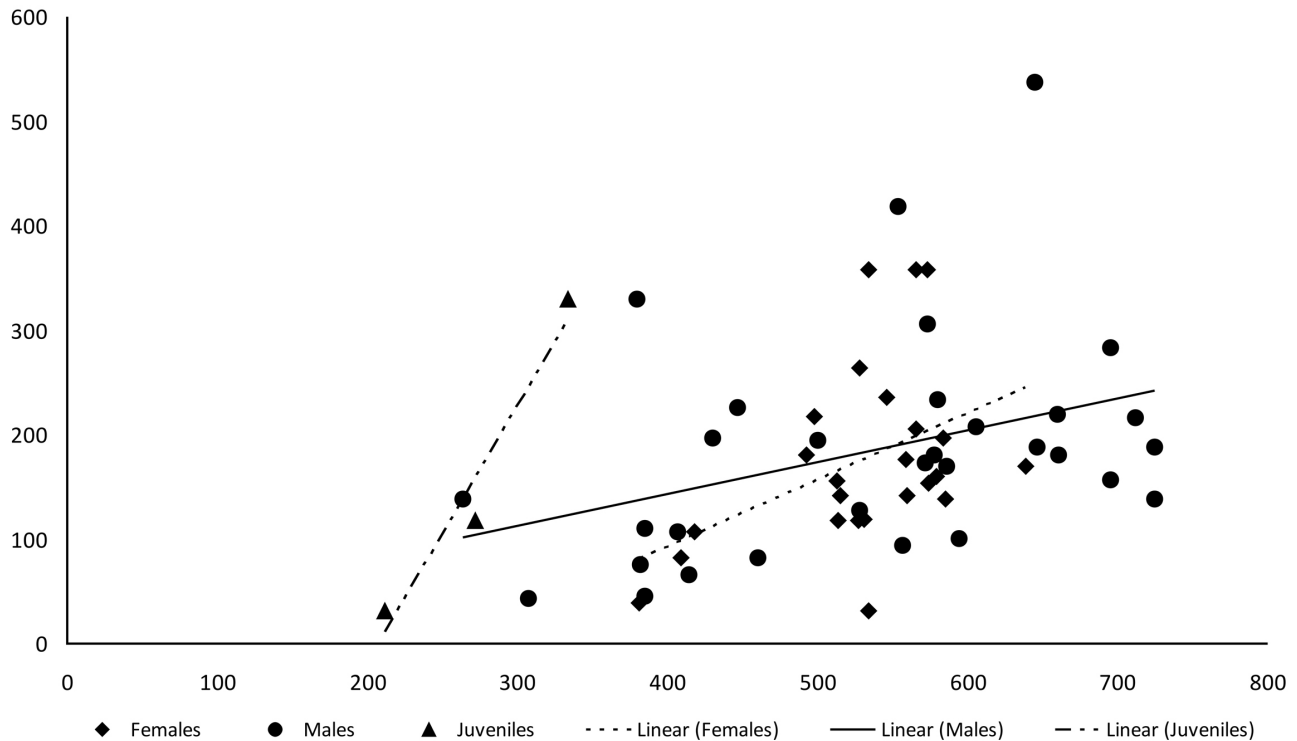


Figure 6. Total animal lengths (x-axis, in cm) plotted against approximated sizes of burrow entrances (y-axis, in cm²) with respective linear regressions. Regression equation and R² are as follows: Females: $y = 0.6371x - 161.9$; $R^2 = 0.1820$; Males: $y = 0.3069x + 20.146$; $R^2 = 0.1383$; Juveniles: $y = 2.4517x - 508.81$; $R^2 = 0.9485$.

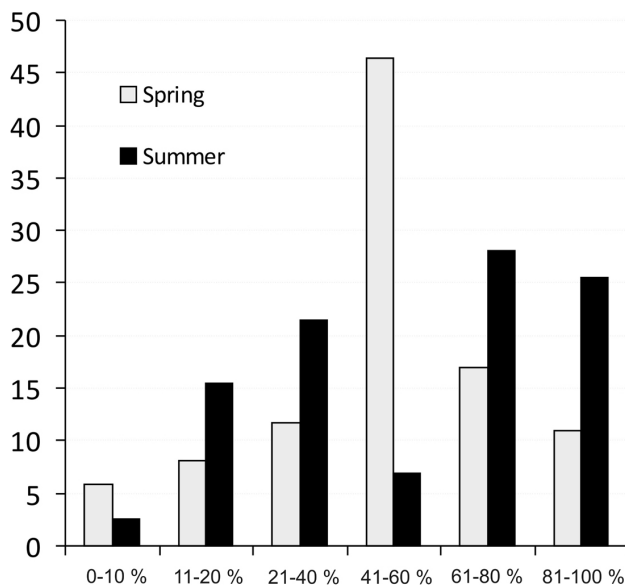


Figure 7. Microhabitat selection in respect to relative humidity for one *Uromastyx a. microlepis* per season during a period of 28 days each (spring 2007 and summer 2006). Frequencies of recorded selected relative humidity in defined intervals (total number of single humidity records: 4096).

trance, which consists of soil excavated by the animal inhabiting the burrow (Fig. 5). A total of 194 burrows were investigated in the study area regarding the presence and dimensions of the perimeter wall. Only three burrows, ac-

counting for 1.5% of all burrows examined, lacked this typical character. Diameters of perimeter walls were measured between the wall peaks and ranged from 35 to 210 cm (average: 120.96 ± 38.42). The burrow entrances were 7–60 cm wide (average: 22.35 ± 7.67) and 2–28 cm high (average: 9.61 ± 3.44). To check whether or not there was a correlation between the size of the animal inhabiting a specific burrow and burrow morphology, the size of each burrow entrance was calculated using an ellipse as approximation (size of burrow entrance in cm²: $A = \pi \cdot W/2 \cdot H/2$; W = width of entrance in cm, H = height of entrance in cm) and plotted against total animal length ($n = 31$ for males, $n = 24$ for females, $n = 3$ for juveniles).

Linear regression and the coefficient of determination (R^2) were calculated for males, females and juveniles separately to gain some information about the “goodness of fit” of the model (Fig. 6). Both coefficients of determination for males and females are relatively low ($R^2 = 0.1383$ for males; $R^2 = 0.182$ for females), while R^2 for the juveniles 0.9485 is quite high (as a result of the low sample size!). On the basis of the respective values of R ($R = 0.372$ for males; $R = 0.427$ for females; $R = 0.974$ for juveniles), the correlation for males and females are “weak” respectively “modest”, while for juveniles the correlation is “very strong”. Nevertheless, the correlations are statistically significant for males and females ($R = 0.372$, $df = 29$, $P = 0.05$ for males; $R = 0.427$, $df = 22$, $P = 0.05$ for females) but not for juveniles ($R = 0.974$, $df = 1$, $P > 0.05$). The coefficient of determination is a measure of the proportion of the variability in one variable (e.g., burrow entrance size) that is accounted for by variability in another (e.g., total animal length) (FOWLER et al. 2006). Giv-

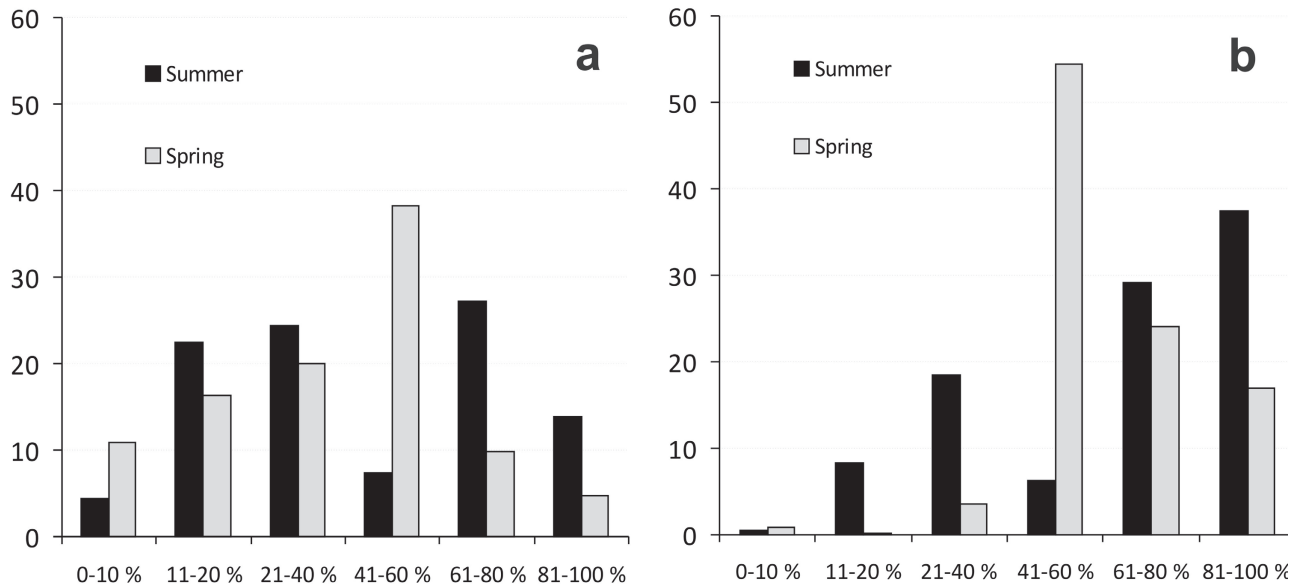


Figure 8. Same datasets as in Figure 7 separated for day- and nighttime respectively. a: daytime; b: nighttime.

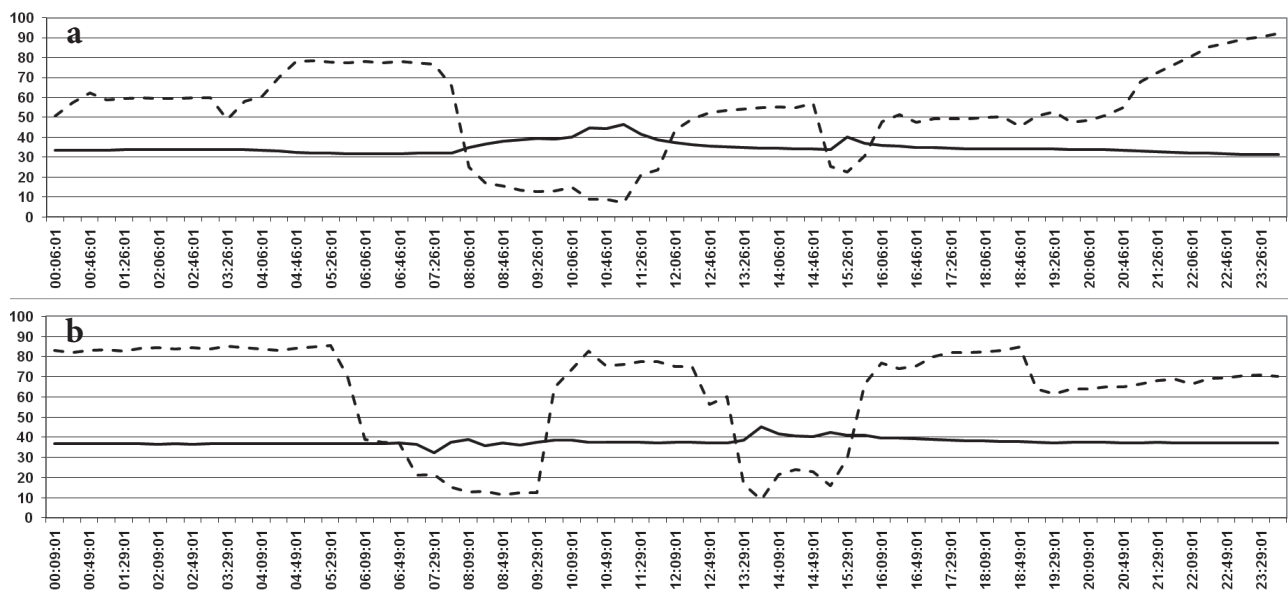


Figure 9. Representative temperature and humidity profiles for one day each in spring and summer; x-axis: time (hrs); y-axis: temperature (°C) and humidity (% r.H.); solid line: temperature; dashed line: relative humidity; a: Spring; b: Summer.

en the respective values of R ($R = 0.372 = 37.2\%$ for males; $R = 0.427 = 42.7\%$ for females) it follows in both cases that some 60% of variability of the burrow entrance size is not explained by variation in total body length. The selection of a particular burrow is therefore without any doubt also strongly influenced by factors other than animal size alone.

Microhabitat use

Humidity of air in the direct vicinity of the animals was between 4.0–98.4% rH in spring and 3.3–96.2% rH in summer. Despite this overall similarity of the humidity ranges in both seasons, pronounced spatial differences in the se-

lection of areas with different humidity levels were recognized (Fig. 7). Evaluation of the differences in microhabitat selection in respect to the time of the day (nighttime versus daytime) revealed that the differences in the selection of areas with different humidity levels at daytime were not ($\chi^2 = 846.33$, NS, $df = 1033$; Fig. 8a), while the differences during nighttime were highly significant ($\chi^2 = 4739.44$, $P < 0.001$, $df = 1013$; Fig. 8b). Movements resulting in changes in the environmental humidity available to the animals did not only occur during the normal activity phases of this diurnal species (e.g., moving into and out of the burrow), but also in 82% of nights in summer and 89% of nights in spring (Fig. 9). Air temperatures within undisturbed (not excavated) burrows were measured in the direct vicinity of

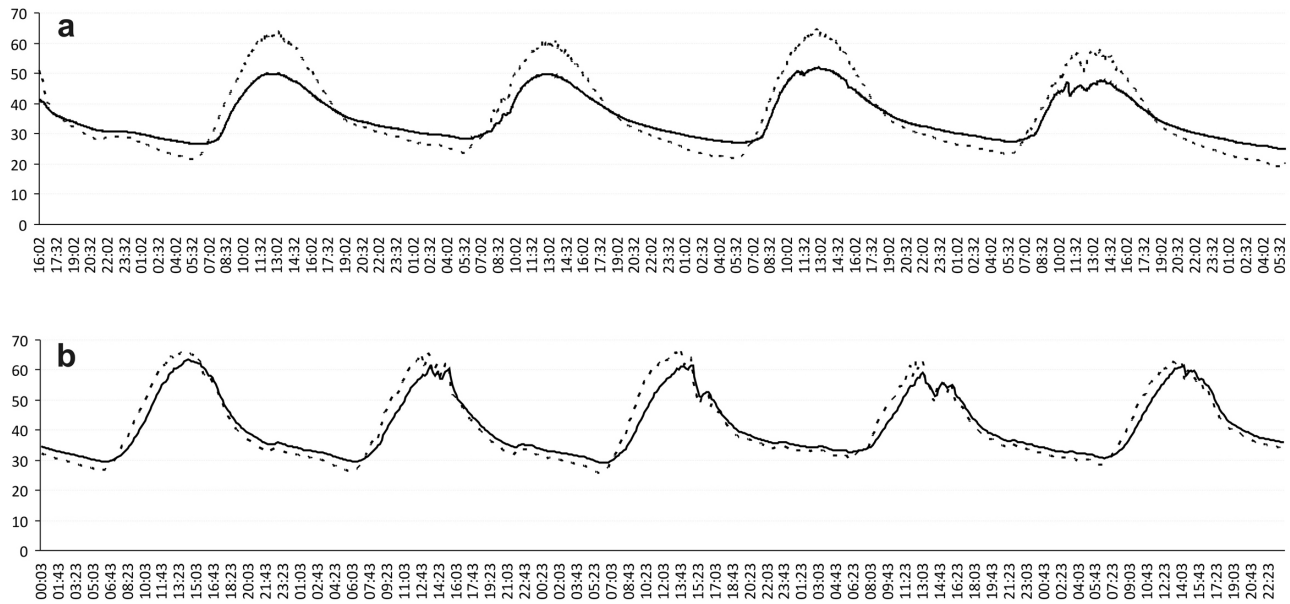


Figure 10. Representative profiles of soil temperatures on different days (soil temperature just in front of the burrow entrance and on top of the perimeter wall) in spring and summer; x-axis: time (hrs); y-axis: temperature ($^{\circ}\text{C}$); solid line: soil temperature in front of the burrow entrance; dashed line: soil temperature on top of the perimeter wall. a: Spring; b: Summer.

the animal using “onboard” data loggers. In spring, temperatures ranged between 30.05 and 36.97°C (average $33.59 \pm 1.36^{\circ}\text{C}$), in summer, the respective values were 35.72 and 40.47°C (average $37.07 \pm 0.51^{\circ}\text{C}$).

Soil temperatures as measured with i-buttons in spring of 2006 ranged between 19.3 and 64.4°C on top of the perimeter wall (T_{pw}) and between 24.6 and 56.8°C in front of the burrow entrance (T_{be}). The respective values for the summer of 2006 were between 23.0 and 67.6°C on top of the perimeter wall (T_{pw}) and between 24.3 and 66.0°C in front of the burrow entrance (T_{be}).

Typical temperature profiles for both seasons are shown in Fig. 10. Spring T_{pw} were higher than T_{be} between 6:53–7:20 hrs and 17:17–18:30 hrs, depending on the respective day. On two days, both temperatures were identical until 12:21 and 11:36 hrs, respectively. Temperature profiles for the rest of those two days were similar to profiles of the remaining eight days. In summer, T_{pw} were higher than T_{be} between 6:53–7:33 hrs and 11:33–17:33 hrs, depending on the respective day. Time ratios between $(T_{be} > T_{pw}) : (T_{be} < T_{pw})$ were 1.27:1 in spring and 2.52:1 in summer, which means that in spring, during 56% of the day, the temperature just in front of the burrow entrance is higher than the temperature on the perimeter wall. In summer, the picture is even more extreme, with T_{be} being higher than T_{pw} during 71% of the day. The situation changes drastically when considering only the time from 6:00 to 19:00 hrs. During this period of time in spring, $(T_{be} > T_{pw}) : (T_{be} < T_{pw})$ is 1:4.30, which means that T_{be} is higher than T_{pw} for only 18.9% of this time. In summer, the respective data are 1:1.07 and 48.3%. The arithmetic mean (\pm SD) of all differences between T_{be} and T_{pw} between 6:00 and 19:00 hrs with $T_{be} > T_{pw}$ in spring is $1.86 \pm 1.64^{\circ}\text{C}$ and $2.1 \pm 1.32^{\circ}\text{C}$ in summer, the respective mean of all differences between T_{be} and T_{pw} with $T_{be} < T_{pw}$ in spring is $7.34 \pm 4.33^{\circ}\text{C}$ and in summer $4.32 \pm 2.53^{\circ}\text{C}$.

Morphology

Within the sample of 74 specimens caught at the study site and subsequently examined in detail, the sex ratio of males to females was 1.50:1, with only 5.4% of the animals being juveniles. Males generally grow larger than females [Independent t-Test, Random Permutation: $t = 2.411$, $\alpha = 0.0099$ (one-tailed), 50 000 Permutations] with a maximum total length of 725 mm (females: 639 mm). There is also a significant difference in body weight between adult males and females [Independent t-Test, Random Permutation: $t = 2.103$, $\alpha = 0.0135$ (one-tailed), 50 000 Permutations], with adult males (total length > 400 mm) ranging between 350 and 2350 g (mean: 1285 g), while adult females (total length > 400 mm) range between 500 and 1750 g (mean: 1022 g). Fig. 11 shows total lengths of juvenile, male and female *Uromastix aegyptia microlepis* plotted against weight.

The morphological data are as follows: 147–227 scales between gular and inguinal folds, 38–57 gular scales. 5–8 scales on both sides between supralabial and enlarged subocular scale. 4–7 enlarged scales on the anterior margin of the ear openings, 30–48 scales around the fifth whorl. 20–23 tail whorls. 17–22 scales beneath fourth left toe. 15–25 preanofemoral pores on either side (one female had a very low number of 8 preanofemoral pores on either side).

Discussion

Burrow morphology

There is no correlation between animal size and size of the burrow entrance or the diameter of the perimeter wall (this study). These results imply that burrows are not dug by a particular specimen and then continuously used, but that animals change the burrows they use from time to time.

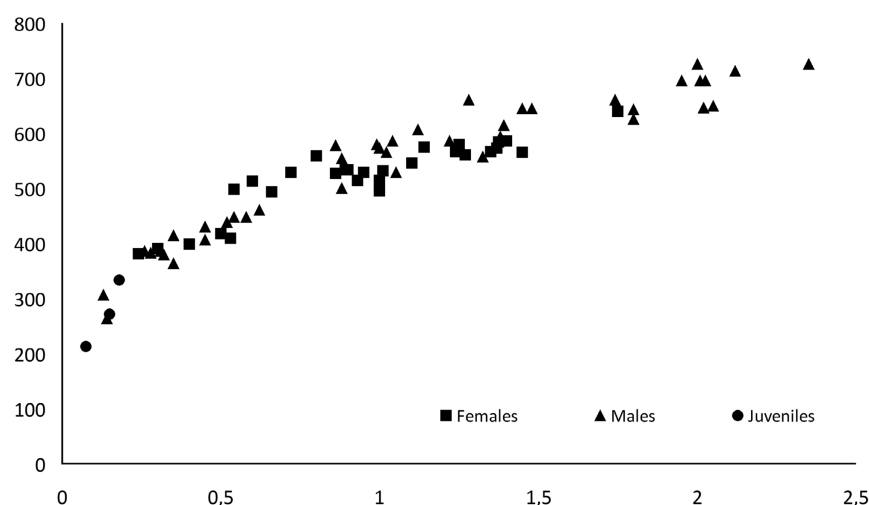


Figure 11. Scatter plot of weight (in kg; x-axis) against total length (in mm; y-axis) of male, female and juvenile *Uromastyx aegyptia microlepis* from Mahazat as-Sayd.

This hypothesis is supported by capture data. In the course of the study, 5 animals were caught two times in the same burrow, two different animals were found in 5 burrows, and 3 different animals were caught in one burrow. All other captures were single captures where an animal was caught in a burrow where no other animal was captured (42 specimens). This means that 21.66% of all captured specimens moved from one burrow to another during the course of the present study.

One main question about burrow morphology, viz. the function of the perimeter wall, is still open. A possible explanation could be related to the rare, but nevertheless heavy and unpredictable rain events. On 11 April 2007, heavy rain fell in Mahazat as-Sayd, flooding large areas within a few minutes (Fig. 12). It was observed that the perimeter walls functioned as dams, preventing the burrows from being flooded. Beside this, the perimeter wall obviously plays a role in altering the microclimate in the vicinity of the burrow entrance (see following paragraph).

Microhabitat use

Temperatures within *Uromastyx a. microlepis* burrows are relatively constant, with the temperatures laying well within the thermal range of the species, and therefore providing shelter from the unfavorable thermal conditions in the surrounding habitat.

In contrast to many burrows and burrow systems dug, e.g., by rodents, *Uromastyx* burrows are characterized by only a single entrance, lacking a passive wind-induced ventilation as is known for example from the burrows of Prairie Dogs, *Cynomys ludovicianus* (VOGEL et al. 1973). It has been shown that *Uromastyx* burrows stabilize temperature as well as humidity very efficiently (AL-OGILY & HUSSAIN 1983, WILMS & BÖHME 2007, this study), which is presumably correlated with the aforementioned lack of ventilation. Therefore, we consider diffusion to be the main factor for the exchange of air in the burrow with atmospheric air. Estimates of maximum burrow lengths through which diffu-

sion could facilitate an adequate gas exchange are possible by applying Fick's law if the oxygen consumption rate and the biomass of the animal are known (VOGEL et al. 1973).

There are no data concerning oxygen and carbon dioxide concentrations in *Uromastyx* burrows available, therefore data from a burrowing rodent, the Valley Pocket Gopher, *Thomomys bottae* (Rodentia, Geomyidae), were used as a model for the environment within an *Uromastyx* burrow (CHAPMAN & BENNETT 1975). The normal oxygen and carbon dioxide concentration in air is 20.95 and 0.04%, respectively. In the burrows of *Thomomys bottae*, oxygen concentrations between 6–21% have been found and carbon dioxide concentrations between 0.6–3.8%. We consider these values as being within the range in a *Uromastyx* burrow. The resting oxygen consumption rate of *Uromastyx a. microlepis* is 0.0394 ml/g/h at 25°C and 0.0677 ml/g/h at 30°C (ZARI 1991). Therefore, a medium-sized animal with a mass of 1000 g would need 39.4 ml/h O₂ at 25°C and 67.7 ml/h O₂ at 30°C (Q/t). Under the assumption of a diffusion constant (D) of 0.2 cm²/sec, a burrow cross-section (A) of 300 cm² and an oxygen concentration of 6% by volume at the burrow end [resulting in a gradient, Δu , of 0.21–0.06].

$$\text{Fick's Law } dQ = -DA \times \frac{\delta u}{\delta x} dt$$

may be approximated for present purposes as:

$$x = DAA\Delta u/Q/t \text{ (VOGEL et al. 1973)}$$

Maximum burrow length meeting the respiratory requirement of an *Uromastyx a. microlepis* with a mass of 1000 g alone by diffusion is therefore estimated to be 478.58 cm (30°C, $\Delta u=15$) and 822.33 cm (25°C, $\Delta u=15$). These theoretically established burrow lengths fall well within the observed range for this species (300–530 cm, this study; up to 1025 cm, BOUSKILA 1983 & 1984).

A study on ventilation and breathing pattern of *Uromastyx aegyptia microlepis* revealed that breathing frequency decreases with higher CO₂ concentrations, while tidal volume and overall ventilation increases. After high

CO₂ concentrations were removed, the animals showed an immediate increase in breathing frequency and changes in breathing pattern that consisted of an immediate and pronounced use of gular pumping (post-hypercapnic hyperpnea; KLEIN et al. 2002). Due to the post-hypercapnic hyperpnea, a CO₂ washout from blood, lungs and upper airways is achieved. Based on these results, *Uromastix aegyptia microlepis* responds to different CO₂ concentrations, which leads to the conclusion that this species (like other reptilian species) possesses receptors that enable it to detect different levels of CO₂. Humidity in the direct vicinity of both *Uromastix* carrying “onboard” data loggers during the present study changed – partly drastically – in 82% of nights in summer and 89% of nights in spring (Fig. 9). It is assumed that soil moisture is responsible for maintaining high burrow vapor pressures, which under the influence of diffusion creates a humidity gradient from burrow entrance to burrow end. Changes in humidity near the animals are therefore explicable by *Uromastix* relocating within the burrow. This behavior could be related to the avoidance of high CO₂ concentrations (low O₂ concentrations) towards the end of the burrow or to the active selection of areas with different humidity levels at different times of the year.

Measurements revealed that soil temperature distribution differs spatially and temporally around the burrow entrance. During daytime (6:00 to 19:00 hrs), soil temperatures directly in front of the burrow entrance (T_{be}) were in 80.1% (spring) respectively 51.7% (summer) of the time lower than soil temperatures on top of the perimeter wall (T_{pw}). It is noteworthy that the arithmetic means between 6:00 and 19:00 hrs of all differences ($T_{be} - T_{pw}$) with $T_{be} > T_{pw}$ is generally lower ($1.86 \pm 1.64^{\circ}\text{C}$ in spring; $2.10 \pm 1.32^{\circ}\text{C}$ in summer) than the respective mean of all differences ($T_{pw} - T_{be}$) with $T_{be} < T_{pw}$ ($7.34 \pm 4.33^{\circ}\text{C}$ in spring; $4.32 \pm 2.53^{\circ}\text{C}$ in summer). This means that there is a relatively steep thermal gradient between the area in front of the burrow entrance and the top of the perimeter wall if $T_{be} < T_{pw}$, and a

quite shallow thermal gradient between both places if $T_{be} > T_{pw}$. Generally T_{be} is lower than T_{pw} during most of the day in spring and from morning until midday in summer (Fig. 10). In contrast to that, T_{be} is higher than T_{pw} mainly in the late afternoon and early night hours, minimizing the cooling effect of the night. The perimeter walls around entrances of *Uromastix* burrows create different thermal environments, which have temporally and spatially different properties and therefore presumably prolong the time window that could be used by the thermoregulating animal.

Morphology

In a study on *Uromastix aegyptia leptieni*, a sexual size dimorphism was found, with adult males reaching greater total lengths and higher weights compared to females (WILMS & BÖHME 2007). This is likewise the case in the Arabian subspecies, *U. a. microlepis*.

We consider the sex ratio in the sample of the current study to be biased and therefore not reflecting the true sex ratio in the whole population. The sex ratio in the current sample was 1.50:1 (males:females), which means that 50% more males were caught than females. WILMS & BÖHME (2007) established a sex ratio of 1:1.43 (males:females) for a population of *U. a. leptieni* in Abu Dhabi (UAE).

Most morphological data taken from the sample from Mahazat as-Sayd specimens are within the range established for this taxon in a previous study (WILMS et al. 2009a).

Differences were found in the number of ventrals where 2 specimens had slightly fewer (147 & 148 scales) and 5 specimens had more ventral scales (194, 195, 198, 226, 227 scales, respectively) than were known for this taxon (149–193). Beside this, the maximum number of preanofemoral pores is slightly larger (max. 25 pores in Mahazat as-Sayd animals vs. max. 21 pores after WILMS et al. 2009a). It is re-



Figure 12. Mahazat as-Sayd during heavy rain (11th April 2007). Photo: N. LUTZMANN.



Figure 13. *Uromastix a. microlepis* female caught on 15th May 2006, showing signs of mating bites on the nape of the neck. Immediately before capture, this animal was observed in nuptial interaction with an adult male. Photo: T. WILMS.

markable that one adult female (TL: 515 mm, weight: 930 g) had only 8 preanofemoral pores on either side.

Since *U. a. microlepis* is the subspecies with the smallest scales (and therefore the highest scale counts) within the *U. aegyptia* clade, these findings do not interfere with previously established differential diagnoses.

Miscellaneous ecological observations

Reproduction

Courtship behavior, mating and signs of mating (bite marks in the nape of females) were observed on 15 May 2006 (Fig. 13). The first hatchling was caught on 04 August 2006 in a pitfall trap (weight 13.77 g). Hatchlings were observed in August and September, sitting in small bushes near burrow entrances of adult *Uromastix*. In a single case, a hatchling was seen fleeing in a burrow inhabited by an adult. While excavating *Uromastix* burrows, 16 empty eggshells were found in a small side chamber of one burrow. These were without any doubt *Uromastix* eggs.

Co-inhabiting animals

Uromastix burrows play an important role as refuges for a variety of different animals. At Mahazat as-Sayd, the main species co-inhabiting *Uromastix* burrows are without any doubt the carabid beetle *Anthia* (*Termophilum*) *duodecimguttata* and the gekkonid lizard *Ptyodactylus hasselquisti*. *Anthia* were found in more than 60% of the investigated *Uromastix* burrows, while *Ptyodactylus hasselquisti* were found in more than 30% of burrows. Both species can easily be observed in the early morning or late afternoon, sitting in the burrow entrance. Normally, only a single adult *Ptyodactylus* was seen in one burrow, while *Anthia* can form aggregations of up to 30 individuals. It is noteworthy that the *Ptyodactylus hasselquisti* living in *Uromastix* burrows were observed regularly walking on the ground hunting for food at night. This is especially interesting, because this species is not ground-dwelling but saxicolous. Beside the aforementioned co-inhabiting species, the following species were regularly found in *Uromastix* burrows: the gekkonid lizard *Bunopus tuberculatus*, the varanid lizard *Varanus griseus*, and the scorpions *Androctonus crassicauda* and *Leiurus quinquestriatus*.

It is well known that Dunn's Larks (*Eremalauda dunni*), Bar-tailed Desert Larks (*Ammomanes cincturus*), Black-crowned Finchlarks (*Eremopterix nigriceps*), and Hoopoe Larks (*Alaemon alaudipes*) use *Uromastix* burrows as thermal refuges during hot summer days in the Arabian Desert (WILLIAMS et al. 1999, CUNNINGHAM 2000). The first observation of this behavior was made in Mahazat as-Sayd (WILLIAMS et al. 1999) and this behavior is easily observed there. Two lacertid lizards, *Acanthodactylus opheodurus* and *Mesalina* cf. *rubropunctata*, were observed seeking shelter in an *Uromastix* burrow. We take these observations as exceptional, because both species normally dig their own small burrows.

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