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Activity profiles, habitat selection and seasonality of body weight in a population of Arabian Spiny-tailed Lizards (*Uromastyx aegyptia microlepis* Blanford, 1875; Sauria: Agamidae) in Saudi Arabia

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Abstract. A field study was carried out on the Arabian Spiny-tailed Lizard (*Uromastyx aegyptia microlepis*) in Saudi Arabia (Mahazat as-Sayd Protected Area) focusing on seasonal differences in activity, body condition and on parameters influencing selection of burrow sites in this large desert-dwelling lizard. *Uromastyx a. microlepis* is highly seasonal in respect to activity/visibility outside of its burrows which provide shelter against unfavorable climatic conditions. At Mahazat as-Sayd these lizards exhibit a bimodal activity in spring and summer while activity in autumn is unimodal with a peak at early afternoon, but the overall activity is generally low at this time of the year. More than 73 % of total observed yearly activity takes place in spring and early summer. Seasonal changes in availability of food result in differences of the animals' body condition, with a significant decrease of body-mass between spring / autumn and summer / autumn respectively. Selection of burrow sites is largely influenced by soil type and vegetation coverage.

Key Words. Reptilia; Sauria; Agamidae; *Uromastyx*; *Uromastyx aegyptia microlepis*; seasonality; habitat selection; activity; body condition; Mahazat as-Sayd Protected Area; 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. 2009). There is a considerable scientific interest regarding the taxonomy and phylogeny of these animals but ecological knowledge remains scarce and fragmentary with most studies focusing on *Uromastyx nigriventris* and *Uromastyx aegyptia* (Grenot & Loirat 1973; Grenot 1976; Bouskila 1986; Vernet et al. 1988; Cunningham 2000, 2001; Al-Hazmi 2002; Al-Johany 2003; Al-Hazmi et al. 2005). This is especially interesting, considering the ecological importance, prevalence and local abundance of these animals.

Uromastyx aegyptia (Forsskål, 1775) is by far the largest member of the genus, reaching a maximum body length of even more than 700 mm and a weight up to 2.500 g (Fig. 1). Taxonomically, three subspecies, *Uromastyx a. aegyptia* (Forsskål, 1775), *Uromastyx a. microlepis* Blanford, 1875 and *Uromastyx a. leptieni* Wilms & Böhme, 2001 are distinguised (Wilms et al. 2009). The present study focuses on the Arabian Spiny-tailed Lizard (*U. a. microlepis*) which lives in deserts and semideserts of Arabia (Saudi Arabia, Yemen, Oman, United Arab Emirates, Qatar, Kuwait), in Jordan, Syria, Iraq and coastal Iran. Habitats show a marked seasonality regarding climatic parameters (temperature, air humidity, precipitation) as well as regarding 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 & unpublished data). Therefore these burrows are considered to play an important role as refuges in respect to thermo- and hydroregulation and as shelter against predators. Burrows of *Uromastyx aegyptia* can be up to 1025 cm long and reach about 180 cm deep in the ground (Bouskila 1983, 1984), but are, at least at Mahazat as-Sayd, normally not longer than about 300–530 cm and 80–120 cm deep (own data).

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

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 seasonality of activity and body condition in this species which is induced by the aforementioned environmental variability. A second focus was put on the selection of habitat structures by *Uromastyx a. microlepis*. This study was carried out on free ranging populations of *Uromastyx aegyptia microlepis* at 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. Mahazat as-Sayd (22° 15' N, 41° 50' E) is located in central-western Saudi Arabia, approximately 170 kilometers north-east of Taif. The reserve is Saudi Arabia's only completely fenced wildlife reserve and is 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 km^2 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 plateau of the Arabian Peninsula. The elevation is between 900–1050 m above sea level (LENAIN et al. 2004). The terrain of this area consisted of flat gravel plains, known as regs, occasionally interdigitated by dry sandy wadis (Fig. 2). Over 95 % of the area is covered by sand and gravel. Air temperature in Mahazat, as recorded in a standard weather shelter, often exceed 43 °C during the summer, and occasionally reaches 50 °C (SEDDON 1996, SHOBRAK 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 with occasional important rain events at other times. 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 main study site was situated just south-east of the main gate to Mahazat as-Sayd (Al-Muwayh gate), covering an area of approx. 4 km^2 and was primarily used to assess habitat selection, while a second area nearby was chosen to establish a 60 km long transect for the evaluation of activity profiles.

The flat gravel plains in this part of the Arabian Desert are intersected by wadis and dominated by sparse vege-

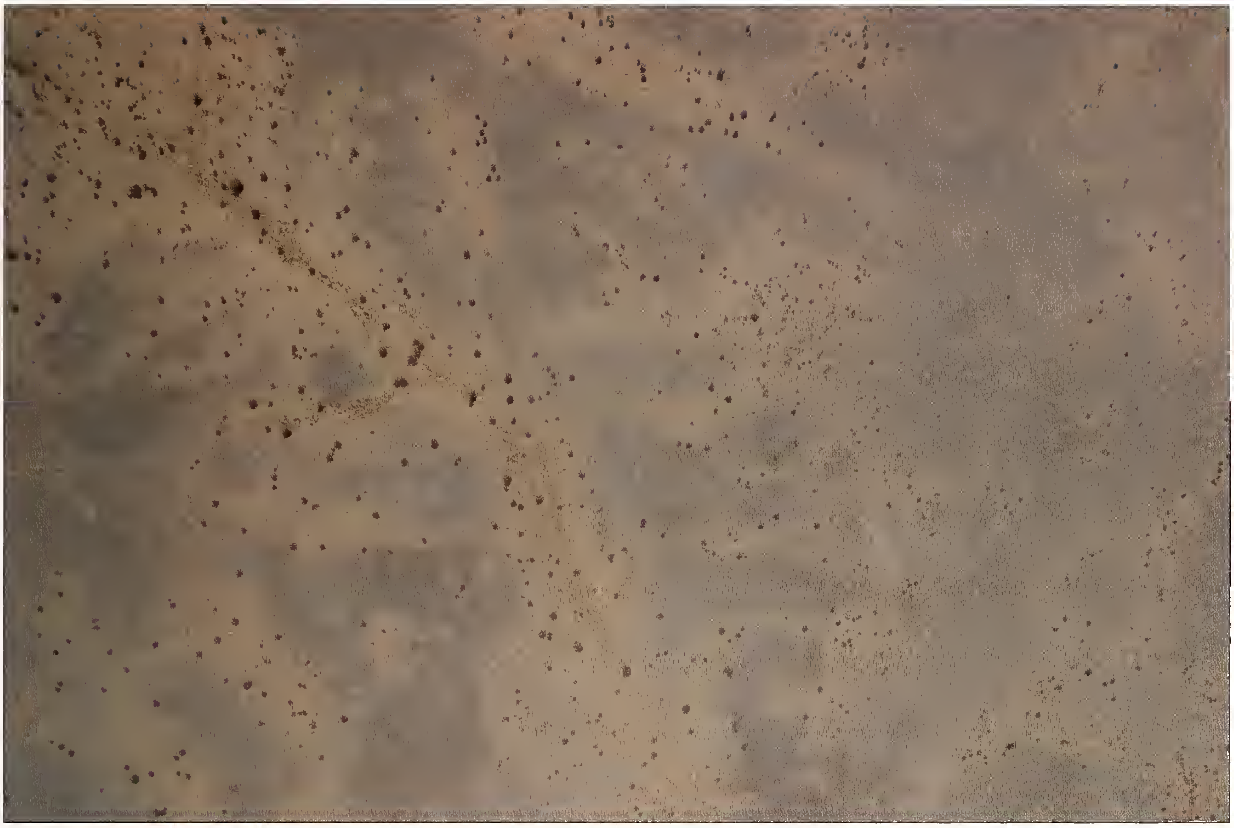

Fig. 2. Aerial view on the study site at Mahazat as-Sayd Protected Area showing reg formation with interdigitating sandy wadis. Photo: T. WILMS.

tation of perennial grasses, including *Stipagrostis* spec., *Panicum turgidum* and *Lasiurus scindicus*, and small trees, mainly *Acacia* spec. (MANDEVILLE 1990).

This study took place in spring, summer and autumn 2006 as well as spring and summer 2007.

Methods applied to assess activity profiles

To assess the differences in seasonal activity of the Spiny-tailed Lizards a transect was defined within an *Uromastyx* colony. The length of this transect was 60 km and it was driven with a 4 WD vehicle eight times per season (equals 480 km each) with an average speed of 40 km/h. These transects were driven only on sunny and calm days. As a result of this protocol the covered time per season was 12 hours (7 am–7 pm). The transect was driven in the following seasons: Summer 2006 (28th July–04th August), autumn 2006 (26th October–17th November), spring 2007 (30th March–06th April) and early summer 2007 (27th June–01st July).

The following data were registered by two persons (each concentrating on the area on either side of the transect): Presence of specimens (time), size class [juveniles (total length < 200 mm), subadults (total length 200–400 mm), adults (total length > 400 mm)], distance of specimen from respective burrow, animal behaviour (e.g. basking, shading, feeding), coloration (dark grey, bright yellow) and habitat (e.g. soil type, vegetation). To estimate the thermal environment of the observed specimens physical models were used to measure operative temperatures (T_e) in different microhabitats in summer 2006 and spring 2007 (HERTZ et al. 1993, SHINE & KEARNEY 2001). Hollow copper cylinders (230 mm long, 78 mm diameter, 0.6 mm wall thickness) were used as models. Miniature data loggers (i-buttons, Dallas Semiconductors, Model 1921) were placed in the model lumen to record T_e. 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. To mimic the reflectance of a cold (grey colored) *Uromastyx* the model was covered with grey duct tape. Temperatures measured with the tape covered copper model followed the body temperatures of a dead *Uromastyx* better than temperatures measured with the uncovered model. Duct tape covered models were calibrated against dead as well as live *Uromastyx* under the original climate in the field (data will be published elsewhere).

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

Methods applied to assess habitat selection

The main study site was in spring 2006 systematically scanned for *Uromastyx* burrows by driving parallel transects (distances between transects ca. 50 meter). Each active burrow was marked with a flag (Fig. 3) and the following parameters were registered: Orientation of burrow entrance (N, NE, E, SE, S, SW, W, NW), soil type (fine sand, coarse sand, clay sand, sand/gravel mixture, fine gravel, medium gravel, coarse gravel, rock/sand mixture, rock), slope, vegetation coverage (0 %, < 5 %, < 15 %, < 25 %), distance to next *Acacia*. A total of 206 active *Uromastyx* burrows were registered. Burrows were considered as active (inhabited or visited) either if an *Uromastyx* was observed directly or if fresh tracks were found near the opened and clean burrow entrances. Otherwise, the burrow was classified as non-active (abandoned).

To assess habitat selection 80 burrows out of the 206 registered ones were selected randomly and tested against 80 additional random localities within the boundaries of the study site, for which the same parameters as for the active burrows were collected. $\chi 2$ analyses were performed to assess differences between burrow locations and randomly placed locations.

Methods applied to assess seasonality of body weight

At the main study site *Uromastyx* were trapped using snares put into the entrance of active burrows. Trapping was carried out in spring 2006 (08th May–2nd June), summer 2006 (15th July–01st August), autumn 2006 (20th October–11th November.) and spring 2007 (26th March–15th 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 loosing the animal is minimized. Captured *Uromastyx* were marked with a passive integrated transponder (PIT), weighted, measured (total length, tail length, head length and width) and several scale counts 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 *Uromastyx a. microlepis* (WILMS et al. in prep.). The specimens were subsequently released at their original burrow.

To assess seasonality of body condition, a body-mass-index (bmi) was calculated for each animal using the following quotient: *bmi = weight (g) / total length (cm)*. Only data of adult specimens (total length > 400 mm) were included in the analysis (n=62).

Statistical analyses of ecological data

The Excel 2000 and SPSS (15.0) statistical packages were used to run the analyses. $\chi 2$ analyses have been selected to evaluate activity data as well as data on habitat selection. To uncover differences in body-mass-indices Mann-Whitney *U*-test and Kruskal-Wallis statistical test were applied.

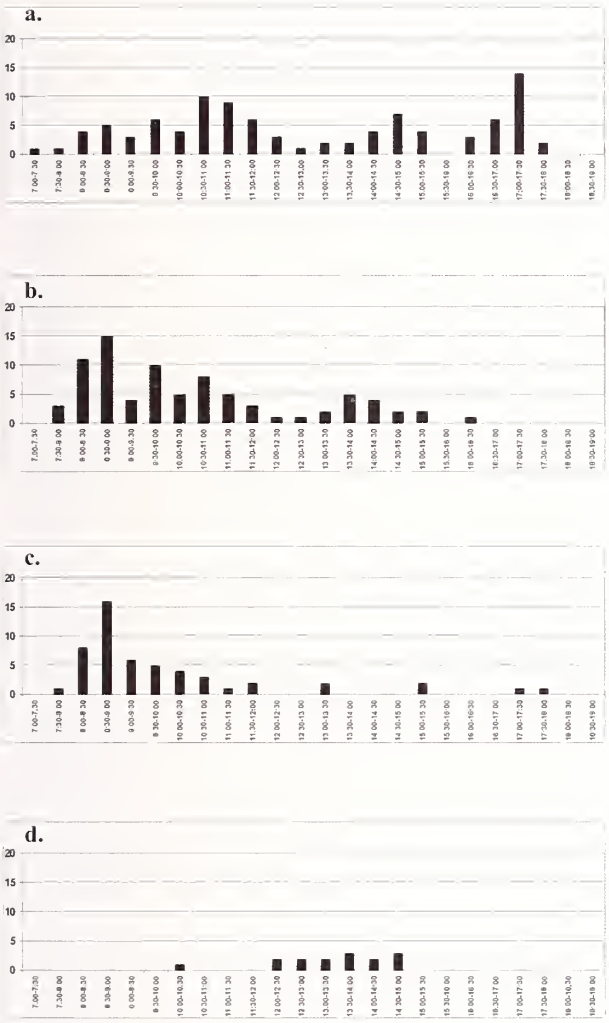

Fig. 4. Visibility profiles of *Uromastyx aegyptia microlepis* at Mahazat as-Sayd at different seasons; **a.** Spring; **b.** Early Summer; **c.** Summer; **d.** Autumn.

RESULTS

Activity structures

A total of 245 *Uromastyx* were sighted while driving the transects. The absolute numbers for the respective seasons are: 97 (spring), 82 (early summer), 52 (summer), 14 (autumn). This is equivalent to 39.59 % (spring), 33.46 % (early summer), 21.22 % (summer) and 5.71 % (autumn) of total observed presence above ground. There is a very restricted activity during winter (deduced from own data on body temperatures, data not shown; BOUSKILA 1986, AL-HAZMI et al. 2005). These observations show that *Uromastyx a. microlepis* is highly seasonal at Mahazat as-Sayd ($\chi_2 = 65.74$, $P < 0.01$, $df = 3$), with a maximum visibility from spring to early summer.

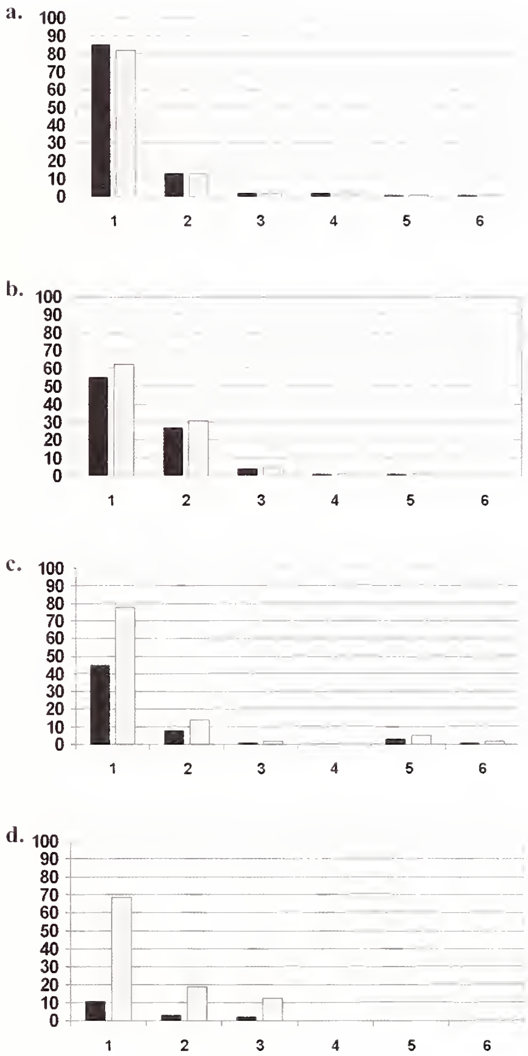

Fig. 5. Distribution of different behavioral activities as absolute numbers (black bars) and as percentage of total observations (grey bars) at different seasons; **a.** Spring; **b.** Early Summer; **c.** Summer; **d.** Autumn.
Behavior: **1.** Basking near burrow entrance; **2.** Animal far away from burrow entrance; **3.** Shading under *Acacia* tree; **4.** Feeding; **5.** Basking on a bush; **6.** Basking on a stone.

Profiles of daily visibility were produced for every season by adding up the specimens observed within respective intervals of 30 minutes (Fig. 4). The diagrams show, that *U. a. microlepis* exhibits a bimodal rhythm in spring and early summer with two relatively high visibility peaks in spring (at morning from 10:30–11:00 hrs respectively afternoon from 17:00–17:30 hrs) but only one pronounced peak in early summer (at morning from 8:30–9:00 hrs), followed by a greatly reduced but nevertheless clearly visible peak at early afternoon (13:30–14:00 hrs). The profiles for spring and early summer exhibit a period with a significantly reduced visibility during the hottest time of

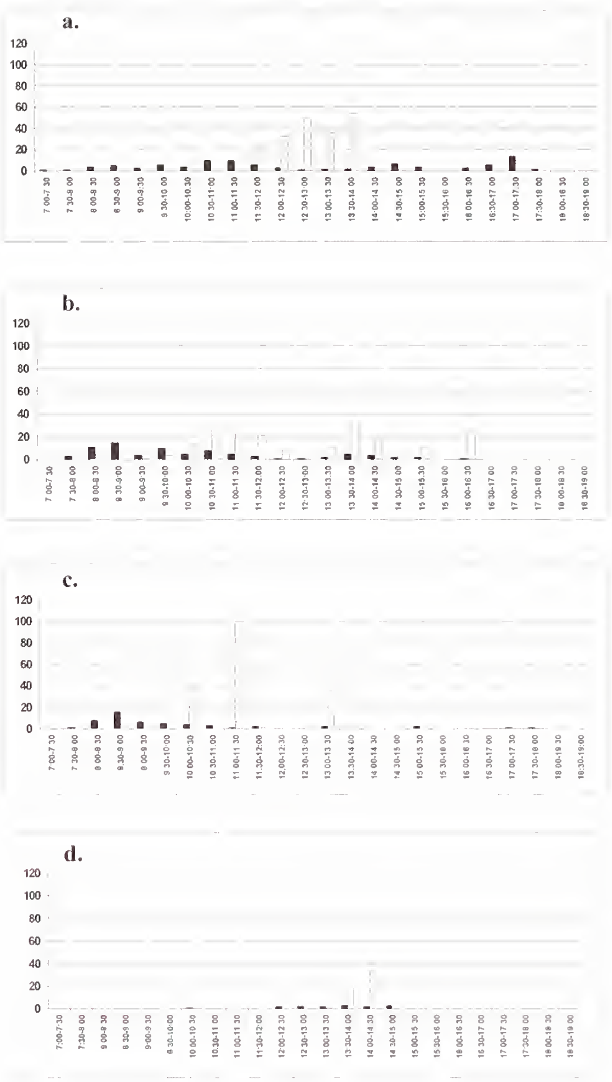

Fig. 6. Profiles showing the number of visible specimens (black bars) as well as average distances (in meters) of all observed specimens within each respective interval of 30 minutes (grey bars); **a.** Spring; **b.** Early Summer; **c.** Summer; **d.** Autumn.

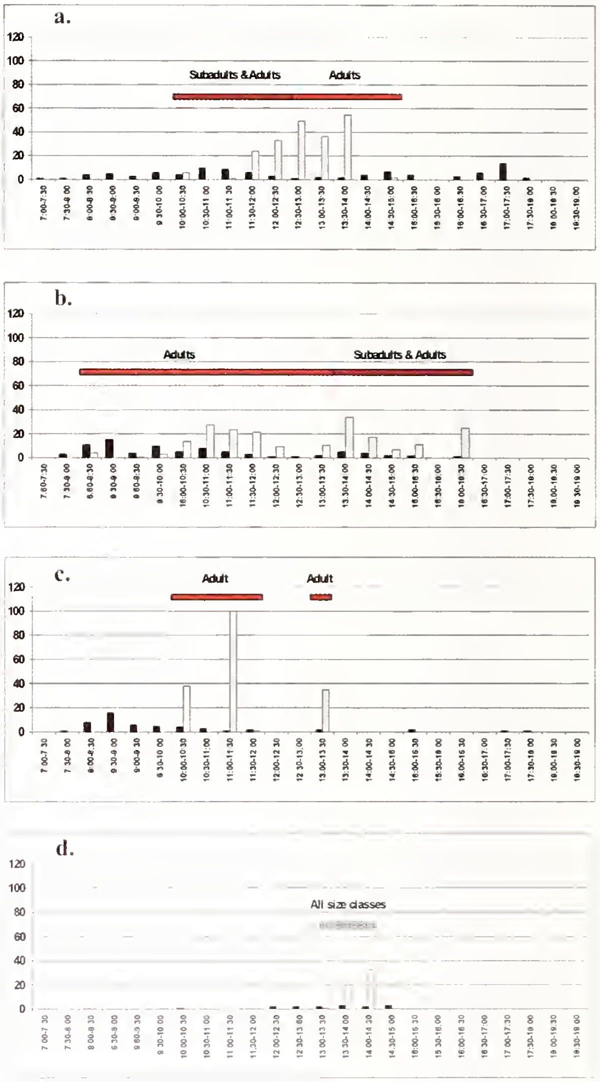

Fig. 7. Profiles showing the number of visible specimens (black bars) as well as the average distances (in meters) from the burrows (grey bars). Vertical bars indicate size class of active specimens. **a.** Spring; **b.** Early Summer; **c.** Summer; **d.** Autumn.

the day (12:30–14:00 hrs in spring; 12:00–13:30 hrs in early summer). The profile for the summer season shows principally also a bimodal visibility rhythm with the highest visibility between 8:30 hrs and 9:00 hrs followed by a rapid decrease of visibility. After 12:00 hrs specimens were seen only occasionally (two specimens between 13:00–13:30 hrs, three specimens between 15:00–15:30 hrs, one specimen at 17:26 hrs and one specimen at 17:34 hrs); but nevertheless some specimens were still visible. The comparison of the profiles from spring, early summer and summer show an obvious trend of reduction of afternoon visibility and a shift of the first visibility peak from late morning to early morning, which is possibly related to the increase of maximum day temperature. The visibility profile for autumn is unimodal and shows an overall very restricted level of visibility with a maximum occurring between 12:00 hrs and 15:00 hrs, then the warmest time of the day.

These visibility profiles were produced regardless of the type of observed activity, thus counting a visible specimen as being active. Figure 5 shows the distribution of the different activities like basking, shading, feeding and specimens being far outside of their respective burrow for all four observation periods as absolute numbers (black bars) as well as percentages thereof (grey bars). Calculation of χ^2 statistics showed that the observed seasonal differences are significant for the categories "basking near burrow entrance" ($\chi_2 = 57.451$, $P < 0.01$, df = 5) and "animal far outside of its burrow" ($\chi_2 = 24.000$, $P < 0.01$, df = 5), while differences in the other four categories were not significant. As a consequence, diagrams showing the number of visible animals as well as the average distance of specimens from their burrows during each 30 minute interval were created (Fig. 6).

Temperatures in spring are relatively mild, resulting in a prolonged time the lizards have to spend basking near the burrow entrance to reach their preferred body temperatures. After having reached the preferred body temperature some animals start leaving the direct vicinity of their own burrow. From 12:30–14:00 hrs presence of specimens is greatly reduced, but those animals still present exhibit a high degree of activity indicated by the long distance from their respective burrow (Fig. 6a). Evaluating the activity data in respect to animal size revealed, that from 12:07 hrs until 14:41 hrs only large adults were seen far outside of their burrows (Fig. 7a). Obviously temperatures during midday are even in spring high enough to force the juveniles and subadults under ground, seeking shelter in their burrows as thermal refuges and therefore accounts for the relatively low number of active specimens. In early summer average as well as absolute temperatures are higher than during spring, thus the basking period near the burrow entrance on early morning is shorter; thus resulting in an earlier start of "far from the burrow activity" (Fig. 6b). Obviously temperatures at morning are already too high to allow activity of juveniles and subadults away from their burrows because of the risk of overheating. From 8:28 hrs until 14:00 hrs only adults have been seen active. After 14:12 hrs also subadults started "far from the burrow activity" (Fig. 7b). In summer visibility of *Uromastyx* was generally greatly reduced. There was no observed activity of juveniles and subadults and only five adult specimens have been seen active during the period between 10:12–11:40 hrs and at 13:08 hrs and 13:25 hrs (Fig. 6c & 7c). In autumn visibility and activity is greatly reduced due to the low temperatures. Activity was observed for all size classes only during early afternoon (Fig. 6d & 7d).

Habitat selection

Of the five registered parameters at burrow locations three proved to show significant deviations between observed and expected frequencies. These are: orientation of burrow entrances ($P < 0.01$), soil type ($P < 0.01$), and vegetation coverage ($P < 0.01$). The slope of the area around burrow entrances as well as the distances of burrow entrances to next *Acacia* were not significantly different compared to circumstances at random locations (data not shown).

Orientation of burrow entrances: χ_2 analysis revealed a significant deviation of the observed distribution of burrow entrance directions from the expected distribution of burrow entrance directions ($\chi_2 = 30.27$; $P < 0.01$; df =7). The highest deviation from the expected value exists for burrow entrances directed to south-west and south-east (Fig. 8).

Selected soil type at burrow location: Nine different soil types were found at the 80 randomly selected locations within the study area (fine sand, coarse sand, clay sand, sand/gravel mixture, fine gravel, medium gravel, coarse gravel, rock/sand mixture, rock). χ_2 analysis of observed frequencies of selected soil types at burrow locations and of soil types at randomly placed locations within the study

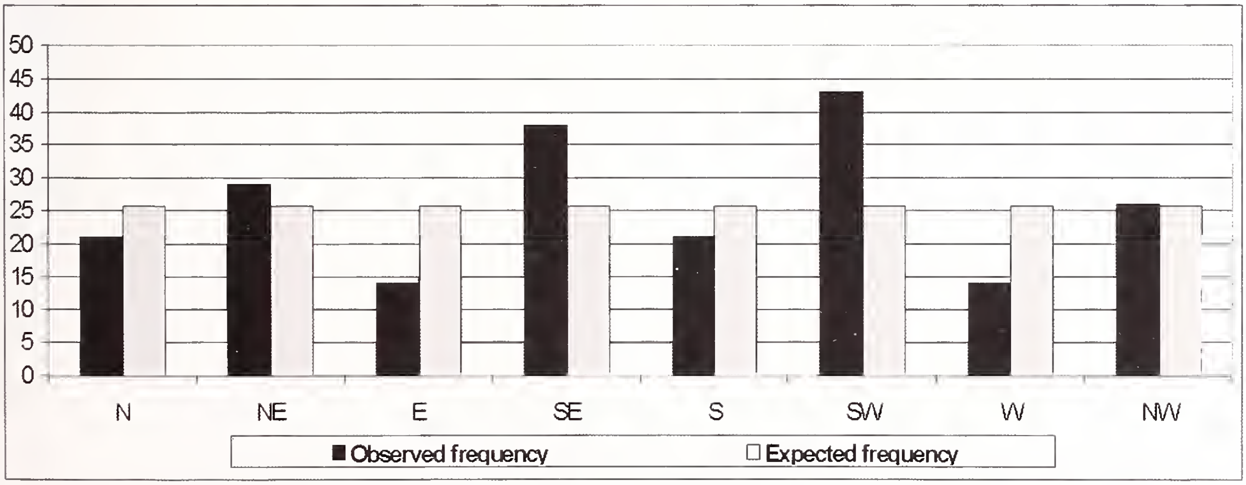

Fig. 8. Observed and expected frequencies of *Uromastyx* burrow entrance directions at Mahazat as-Sayd.

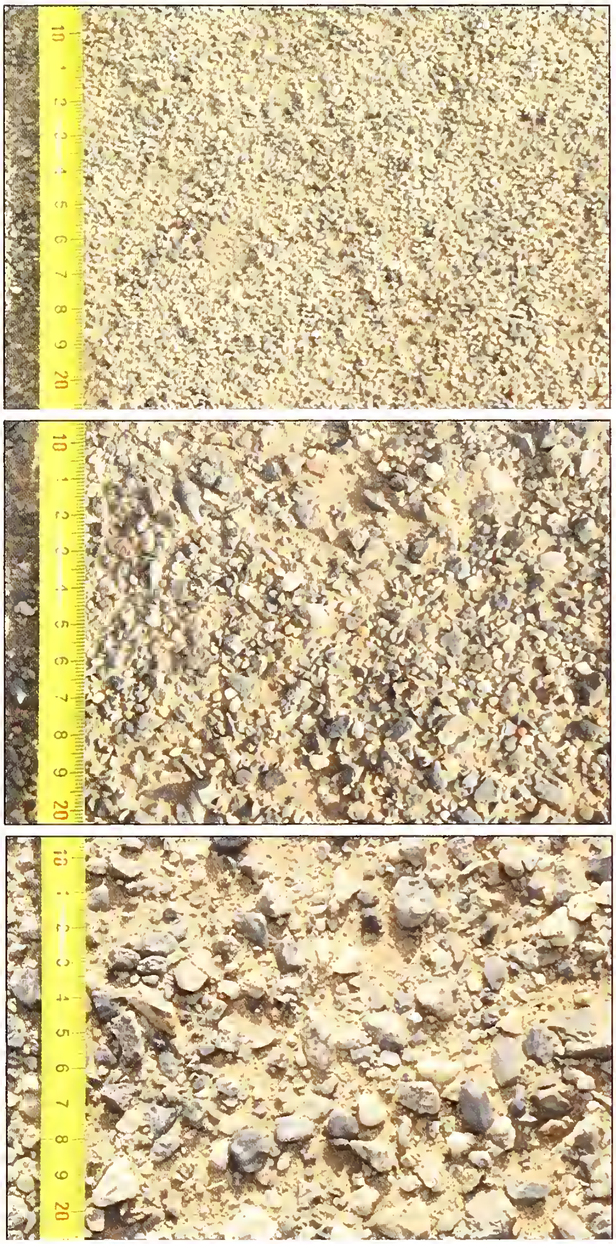

Fig. 9. Selected soil types at *Uromastyx* burrow locations **a.** coarse sand; **b.** fine gravel; **c.** medium gravel.

Fig. 10. Vegetation coverage estimated within a radius of five meters around entrances; **a.** 0 %; **b.** < 5 %; **c.** < 15 %; **d.** < 25 %.

area revealed significant differences ($\chi_2 = 40.30$; $P < 0.01$; df = 8). All but one of the randomly selected *Uromastyx* burrows were located at places with medium gravel, fine gravel and coarse sand (Fig. 9). The only exceptional burrow was found between black rocks. Occasionally the original soil type in the vicinity of *Uromastyx* burrows was covered by a thin layer of drifting sand, which did not interfere with the physical properties of the under laying soil. In such cases only the main substrate was considered for the statistical analysis. Sandy soil was therefore defined as loose deep sand.

Selected vegetation coverage at burrow location: Vegetation coverage was estimated within a radius of five meters around the burrow entrances respectively around the randomly selected locations (0 %, < 5 %, < 15 %, < 25 %; Fig. 10). χ_2 analysis revealed a significant difference between vegetation coverage frequency at burrow locations and at randomly placed locations (χ_2 = 49.40; P < 0.01; df = 3). The data show that *Uromastyx* avoid area with 0 % coverage but show a preference for areas with < 5 % vegetation coverage. For places with < 15 % and < 25 % vegetation coverage no differences between observed and expected frequencies were evident.

Seasonality of body weight

Morphometric data of 62 adult specimens (total length > 400 mm) caught in spring 2006, summer 2006, autumn 2006 and spring 2007 were used to calculate body-mass-indices (bmi). Bmi in spring 2006 was 1.1961–3.2414 (2.4348 +/ 0.6033), in summer 2006 it was 1.1057–3.1269 (2.2172 +/- 0.6146), in autumn 2006 it was 0.8454–2.2981 (1.4972+/-0.4257) and in spring 2007 it was 1.1872–2.8921 (1.9828 +/- 0.4901). Kruskal-Wallis statistics were performed to test data for significances (Fig. 11), which revealed that bmi differs significantly in respect to season (P < 0.001; Fig. 11 a) but not regarding to the sex of the respective specimens (P < 0,189. Fig. 11 b). To check if between seasons bmi differences are statistically significant, data for all four seasons were pair wise tested using Mann-Whitney *U*-test. These tests show, that differences between spring 2006 and autumn 2006 were highly significant (P < 0.001) as well as for summer 2006 and autumn 2006 (P < 0.004). All other pairs showed no significances.

To further evaluate the relationship of bmi between spring 2006 and autumn 2006 respectively summer 2006 and autumn 2006 Mann-Whitney *U*-tests were performed on data for males and females separately. As result, differences for males were significant between spring 2006 and autumn 2006 (P < 0.001) but not for females while between summer 2006 and autumn 2006 differences were significant for females (P < 0.016) but not for males. After Fowler et al. (1998) Mann-Whitney *U*-test may be used with very low sampling units, but in that case there must be no overlap of observations between the two samples to reject H_0. This precondition of the test was met by the dataset for females with values for summer being 1.81–2.74 and for autumn 1.08–1.43, while it was not met by the dataset for males with values for spring being 1.99–3.24 and for autumn 0.85–2.30. Therefore we reject H_0 only for the females' dataset.

a.) Season: 1 = spring 2006; 2 = summer 2006; 3 = autumn 2006; 4 = spring 2007

	season	N	Mean Rank
bmi	1	12	44,08
	2	10	37,40
	3	12	15,67
	4	28	30,79
	Total	62	

Test Statistics(a,b)

	bmi
Chi-Square	16,193
df	3
Asymp. Sig.	,001

a Kruskal Wallis Test

b Grouping Variable: season

b.) Sex: 1 = male; 2 = female

	sex	N	Mean Rank
bmi	1	36	34,06
	2	26	27,96
	Total	62	

Test Statistics(a,b)

	bmi
Chi-Square	1,722
df	1
Asymp. Sig.	,189

a Kruskal Wallis Test

b Grouping Variable: sex

Fig. 11. Kruskal-Wallis test statistics testing body-mass-index data for significance regarding season (Fig. 11a) and sex (Fig. 11b).

DISCUSSION

Activity structures

As has been shown in this study *Uromastyx aegyptia microlepis* is highly seasonal, with this seasonality not being restricted to behavioral means of avoidance of temporarily unsuitable microenvironments but also to changes in the physical constitution of the animals (changes of bmi). The evaluation of thermoregulation in this species is not the primary objective of the present paper and will be discussed elsewhere (Wilms et al. in prep.). Nevertheless, the observed seasonality accounts to some degree to interactions between the thermal environment and the lizard and is therefore here briefly discussed.

Differences in temporal patterns of activity, the use of space, and body temperature relationships are not independent. Many lizards behaviorally regulate body temperatures by shuttling between sun and shade or hot and cold microenvironments to alter heat flux, by modifying posture to alter surface areas exposed to heat sources or sinks, and by regulating activity times (Huey 1974, Pianka 1986). These are well accepted paradigms of reptile ecology and especially true for extreme habitats like those inhabited by the studied *Uromastyx* at Mahazat as-Sayd.

The visibility profiles of *Uromastyx* at Mahazat as-Sayd show a bimodal structure in spring, early summer and to a lesser degree in summer combined with a general decrease of visibility from spring to summer. Visibility structure changes from a bimodal to an unimodal rhythm from summer to autumn reflecting changes in the availability of suitable thermal microhabitats. The visibility profile for autumn shows an overall very restricted level of visibility with a maximum occurring between 12.00 hrs and 15.00 hrs, then the hottest time of the day.

These results are in good accordance with the observations of Al-Hazmi et al. (2005) made in central Saudi Arabia (Al-Gassim region), with two activity peaks in spring (April) and summer (July) (9.00–11.00 hrs and 15.00–17.00 hrs in spring, 7.00–10.00 hrs and 16.00–18.00 hrs in summer) and only a single activity peak in autumn (mid October) (11.00–13.00 hrs). In this study observations were also conducted in early spring (February) showing that the animals have only one daily activity period in this season (11.00–15.00 hrs). After Bouskila (1986) the period with the highest activity is from March to September in a population of *Uromastyx a. aegyptia* in Israel, while from October to February only 70 % of the observed *Uromastyx* burrows showed signs of activity. The lowest levels of activity were recorded from December to Mid-February, were all observations of active specimens were made on clear and sunny days only.

In another study conducted by Al-Johany (2003) near Riyadh (Thumama; King Khalid Wildlife Research Center) an unimodal activity structure was observed in spring (May) starting between 9.00 and 10.00 hrs and ending around one hour before sunset. Summer activity (August) was found to be bimodal with one activity period starting 8.00–9.00 hrs until midday and another period from 15.00–16.00 hrs until sunset (18.30 hrs). We suggest, that the different spring activity profiles established in the present study compared with the result of Al-Johany (2003) might be explained by the different methodology used to assess activity. While in the present study a transect method was applied Al-Johany (2003) observed the animals from a hiding place within the study area, which probably lead to biased results by overestimating activity during midday by observing single actively roaming specimens. As has been shown in the present study, few specimens are visible above ground during midday but some of these show an extraordinary high activity by walking far from their respective burrow. All observed specimens being active during the hottest period of the day were adult. Adult *Uromastyx a. microlepis* have a body mass of up to 2.500 g and have therefore a higher thermal inertia than smaller conspecifics. This property is reducing the risk of overheating for large specimens and allows them a prolonged activity phase under unsuitable thermal conditions compared to smaller specimens.

Operative temperatures (T_e) for observation periods in spring 2007 and summer 2006 are available from three different microhabitats (sandy plain, gravel plain and 40 cm deep in the entrance of an *Uromastyx* burrow). There is only a slight difference regarding T_e (average of all days with observations) between spring and summer with al-

Table 1. Operative temperatures of three different microhabitats in spring and summer in Mahazat as-Sayd (only temperatures between 07.00 hrs and 19.00 hrs were used for calculation).

	$T_{e\ (min,\ spring)}$	$T_{e\ (min,\ summer)}$	$T_{e\ (max,\ spring)}$	$T_{e\ (max,\ summer)}$	average $T_{e\ (spring)}$	average $T_{e\ (summer)}$
Sandy plain	27.8 °C	27.6 °C	54.4 °C	55.5 °C	45.3 °C	47.2 °C
Gravel plain	28.8 °C	28.4 °C	53.3 °C	54.8 °C	44.6 °C	46.4 °C
Burrow entrance	29.8 °C	35.1 °C	39.4 °C	38.1 °C	36.7 °C	37.2 °C

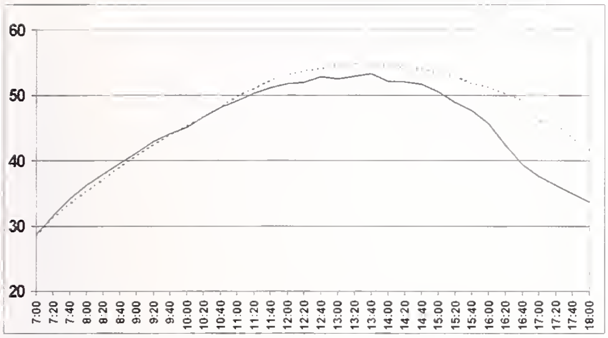

Fig. 12. Profiles of T_e in gravel plain in spring (solid line) and summer (dashed line).

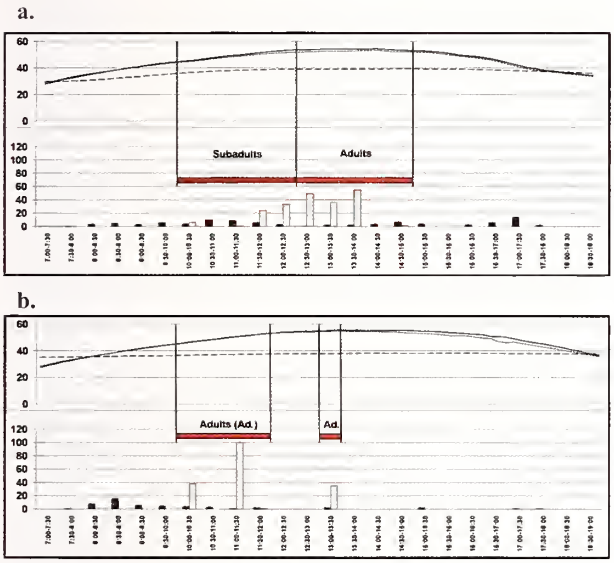

Fig. 13. Estimation of *Uromastyx* T_b based on average T_e; **a.** Spring; **b.** Summer; – – – T_e burrow entrance (approx. 40 cm deep); - - - -T_e gravel plain; ——T_e sandy plain

most identical minimum values but slightly higher maxima at summer (Tab. 1). The main observed differences lie in the temperatures of the *Uromastyx* burrow entrance and in the profiles of T_e in spring and summer (for the profile of T_e in the gravel plain see Fig. 12). During spring, temperatures in the entrance of the burrow differ between 7.00 hrs and 19.00 hrs about ten degrees centigrade while in summer this variation accounts only to three degrees. The profiles of mean $T_{e\ \text{gravel plain}}$ in spring and summer are quite similar until 10.40 hrs. After that time T_e rises faster in summer and reaches a higher maximum than in spring. Afternoon T_e in summer remains significantly higher until sunset (see Fig. 12).

Based on the combined visibility/activity profiles and the mean T_e for the respective seasons, body temperatures (T_b) for the first specimens seen outside of their burrows are estimated to be around 30–31 °C in spring and 33 °C in summer (because all specimens observed on the transects have been found in a gravel or in a mixed gravel/sandy microhabitat we suppose that T_b is within the range of $T_{e\ \text{sandy plain}}$ and $T_{e\ \text{gravel plain}}$). T_b estimates for specimens observed active far from their burrows are 44–52 °C for subadults and 48–54 °C for adults in spring and 47–55 °C for adults in summer (only adult specimens have been observed during summer).These temperature ranges were deduced using the actual measurements of T_e for each observed specimen (Fig. 13 gives an approximated visualization of these data!). These estimates are based on operative temperatures which reflect the interactions between biophysical and to some degree morphological factors influencing T_b of an ectotherm but lacking physiological (and behavioral) control (Hertz et al. 1993) and therefore overestimate T_b, at least in the upper temperature range. The experimentally established critical maximum temperature (CT_{Max}) is 51°C for this taxon (Al-Johany 2003) and temperatures of 55 °C are lethal within 4–5 hours (El-Gohary & Ashour 1975), therefore it is suggested that *Uromastyx aegyptia microlepis* is able to control T_b by physiological and behavioral control mechanisms at least at high temperatures (data on T_b control based on semi continuous T_b measurements will be published elsewhere). It has to be pointed out, that preferred body temperatures change in respect to season, food composition and amount, hormonal status and other physiological traits and that therefore critical temperatures might also be subject to seasonal changes (Phillips & Harlow 1981, Wood 1989, Seebacher & Franklin 2005, Tracy et al. 2005).

Time windows during which operative temperatures in spring and summer would allow activity on a gravel plain far from the burrows were estimated for adult and subadult *Uromastyx* (Fig. 14) using the above listed T_b estimates (spring data of subadults were used to estimate time window during summer). The resulting diagrams show, that estimated time windows for subadults are considerably longer in spring and in summer compared to actually observed activity. In spring estimated time window is ca. four hours (ca. two hours at morning and two hours at afternoon), while observed activity is restricted to the morning totaling to ca. two hours. In summer estimated time window is ca. 3.5 hrs during two periods, one late morning and the other late afternoon, while observed activity was zero. For the adults, the estimated time window in spring is approximately 4.5 hrs and the period of observed activity is with ca. 4 hrs almost identical, while the estimated activity window for summer is about 6.5 hrs with the observed activity is only about two hours. The differences between the estimated and observed activity phases may be explained by the costs associated with thermoregulation, by other needs adversely influencing above ground activity like the necessity to maintain an adequate water balance and the seasonally different avail-

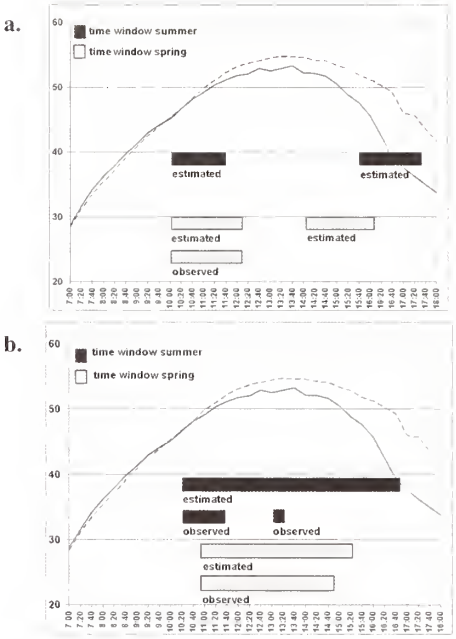

Fig. 14. Estimated time windows during which operative temperatures in spring (solid line) and summer (dashed line) would allow activity on a gravel plain far from the burrows for adult and subadult *Uromastyx*; **a.** for Subadults; **b.** for Adults.

ability of food sources. We suggest that the high activity in adults during spring is associated with reproduction; in this case the benefits of successful reproduction may outweigh the costs of thermoregulation.

Habitat selection

There is only one published study on habitat selection of *Uromastyx aegyptia* (Bouskila 1986). This study was carried out on the nominotypic subspecies (*Uromastyx a. aegyptia*) in southern Israel (near Hazeva Field Study Center, Arava) and focused on the following habitat parameters: habitat topography, soil type, distance to *Acacia* trees and orientation of burrow entrance.

Selected soil type at burrow location: After Bouskila (1986) *Uromastyx aegyptia* significantly prefers reg soil and avoids dry water courses, loose saline soil and sandy reg. This result is in accordance with the present study were medium gravel, fine gravel and coarse sand on the surface was significantly preferred. All of these three mentioned soil types can be subsumed as reg soil. Reg soil is characterized by a layer of closely packed stones over a layer of fine sediment several centimeters to meters thick (Breed et al. 1997). We suggest that this preference for reg soils is mainly because of the physical properties of this layer of fine sediments, providing a stable underground for the lizards to dig their burrows. Sandy soil [loose deep sand in old water courses (wadis) or sandy reg] might be disadvantageous to dig burrows in, because of its low stability and in the case of sandy reg because of the drifty sand being blown into the burrow entrance.

Orientation of burrow entrances: Bouskila (1986) did not find any evidence for a preference of specific orientation of the burrow entrances, which was principally confirmed by Al-Ogily & Hussain (1983) for *Uromastyx* burrows in the Riyadh Region. However these authors report a slightly higher number of burrow entrances oriented to the northeast. In the present study χ^2 analysis revealed a significant deviation of the observed distribution of burrow entrance directions from the expected distribution of burrow entrance directions, with the highest deviation from the expected value exists for burrow entrances directed to south-west and south-east (Fig. 8). One reason for this observation could be the prevailing wind direction, which is NE at 0–30° N. Unfortunately this suggestion can not be tested with actual data of wind directions in Mahazat as-Sayd because of a malfunctioning weather station during this study.

Selected vegetation coverage at burrow location: Vegetation coverage at burrow locations revealed to be significantly different compared to vegetation coverage frequency at randomly placed locations. Visibility/activity profiles of the present study are likely to explain this observed preference, because of the generally very high percentage of specimens seen in direct vicinity of their burrow entrance. Having a food source directly available near the retreat entrance may lower ecological stress for the lizards due to the supposedly relative low costs associated with foraging. Based on these observations it seems obvious, that for *Uromastyx a. microlepis* at least some vegetation in the vicinity is essential for the selection of a burrow location. One main difference between the results of the present study and those of Bouskila (1986) is the failure to demonstrate a significant relationship between burrow location and distribution of *Acacia* trees. In his study Bouskila found a significant correlation in the distance between *Uromastyx* burrow respectively random locations and the nearest *Acacia* tree. His medians of the distances were 21 m (burrow – *Acacia*) respectively 28 m (random location – *Acacia*). In the present study both medians are considerably lower (14.5 m) and even the median of all 206 registered burrows is comparably low (14.0 m). These findings raise again the question of the importance of *Acacia* for *Uromastyx* in Mahazat as-Sayd. We take our data as a high availability of *Acacia* for the lizards in Mahazat as-Sayd which we consider as a strong factor minimizing the need of an active selection of burrow locations in this particular respect. Nevertheless we regard *Acacia* trees as very important for the survival of *Uromastyx* providing food and opportunities for thermoregulation (Fig. 15).

Fig. 15. Adult *Uromastyx* thermoregulating under an *Acacia* at Mahazat as-Sayd. Photo: T. Wilms.

Alternatively a second hypothesis explaining the "observed selection of locations" may be that *Uromastyx* is in fact a seed disperser and actively vegetates the area near the burrow entrance. The occurrence of seed dispersal through reptiles is well demonstrated (Godínez-Álvarez 2004, Valido & Olesen 2007). Spiny-tailed lizards defecate regularly near their own burrow which can be proven by the abundances of fecal pellets, and these pellets contain regularly seeds of different plant species. In Mahazat as-Sayd they consist in summer to a high degree of undigested seeds of *Acacia*. Al-Hazmi (2002) evaluated the amount of seeds in the stomach of 40 *Uromastyx a. microlepis* per season (spring, summer, autumn, winter) totaling 6.7 % (spring), 40 % (summer) and 48.2 % (autumn) of total organic matter, thus representing a significant portion of the total food intake. In winter no food at all was found in the stomachs. Therefore a study testing the effects of an intestinal passage on the germination of desert plant seeds and a possible impact of *Uromastyx* on the vegetation coverage would be highly beneficial to understand the ecology of the species and this desert community.

Seasonality of body weight

Seasonal changes in body weight of an *Uromastyx* species (*U. nigriventris*; nomenclature after Wilms et al. 2009) had already been evaluated by Grenot (1976) and Vernet et al. (1988). In this species changes in body conditions are quite pronounced and associated with seasonal differences in food availability, which is also related to rainfall distribution. Extracellular and intracellular fluid volumes vary widely during the year (Vernet et al. 1988). This is also the case in *U. a. microlepis* with significant differences in body mass indices between seasons and with marked differences in extracellular water in the body cavity (observation made during implantation of data loggers). This difference in seasonal body weight is most likely as in *Uromastyx nigriventris*, also attributed to the seasonality of food availability.

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