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A 'mathematical' spider living on gravel plains of the Namib Desert

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In certain areas of the Namib gravel plains a new *Ariadna* sp. was discovered. It rims its vertical burrow with a stone circle, made on average of seven quartz stones. Some mathematical relationships between hole diameter, stone sizes and weight, and animal size were studied. A correlation was found, and stone selection by this spider postulated. Different hypotheses on the adaptive value of stone circle are suggested.

Keywords: *Ariadna* sp.; gravel plains; Namib Desert; mathematical relationships; animal size; stone circle; hole diameter ; spider ; Namibia

Bib: Namib; desert; DERU

Introduction

In September 1991, burrows of an apparently new species of Segestriidae, *Ariadna* sp. (Fig. 1) (P. Alicata, J. Henschel, pers. comm.), were discovered by us in certain areas of the gravel plains (Fig. 2) near Gobabeb, Namib Desert. The spider burrows are easily recognized because of their geometrical features: a stone ring that rims the circular entrance of the hole (Fig. 3).

Geometrical aptitudes are widespread among the araneomorph spiders: many of them build cobwebs, with complex modular patterns (Porter, 1906, Ades, 1986; Eberhard, 1986; Craig, 1987). Little is known about similar abilities in spiders which dig burrows in the soil. Some information, however, is available regarding trap-door mygalomorph spiders (Coyle, 1971; Murphy & Platnick, 1981). Their holes often emerge from the soil surface as a collar or a turret (Coyle, 1986); but, at present, no information exists on geometrical and numerically defined arrangements of habitat elements around the hole itself.

Material and methods

Numerous specimens of *Ariadna* sp. are present in certain areas around Gobabeb, —e.g. towards Mirabeb, about 10 km east from DERU, the Institute at which this investigation was conducted. The observations were made within an area of 2500 m^2, in which burrows with a great variability of hole diameters were observed. In order to

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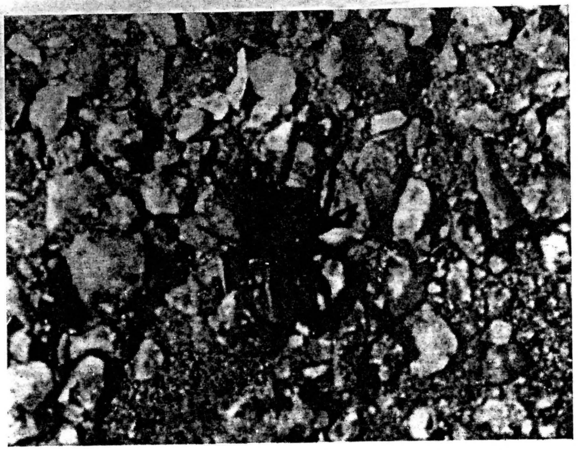

Figure 1. A specimen of *Ariadna* sp. in terrarium (× 2).

find out the number of stones used, their dimensions and the hole entrance diameters, we studied a sample of 27 burrows.

Burrows with stone circles that included a large stone, firmly fixed to the ground, were intentionally excluded from analysis. We measured the diameters of the holes and the number, weight and sizes of the stones around each. Moreover, we calculated mean and standard deviations of the stone weights and sizes for each burrow (Table 1).

Measurements were made of the following: (1) hole diameter (at entrance) (HD), (2) stones: (a) number (SN); (b) weight (SW); (c) size: (i) length (Le); (ii) width (Wi); (iii) height (He), (3) the animal's weight (AW).

Figure 2. A gravel plain area in the Central Namib Desert.

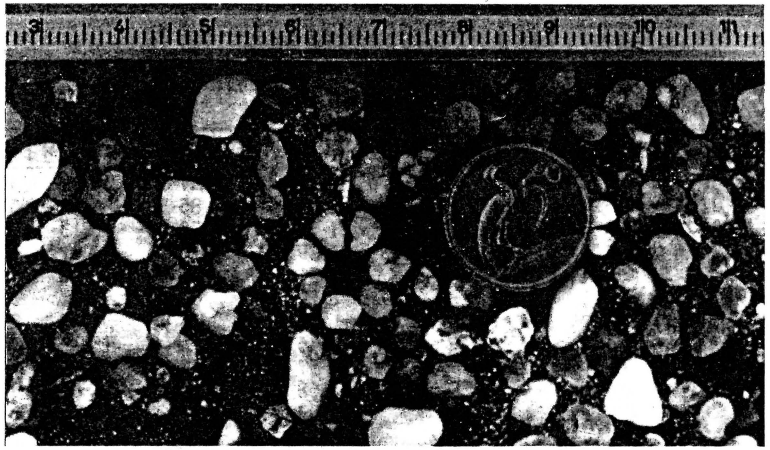

Figure 3. A typical seven-stone ring. The Namibian coin (5 cent) is used for scale.

Additional information on the features and dimensions of the holes was obtained by making gypsum casts of the burrows. This was done by pouring a mixture of gypsum into the burrows, excavating the casts once set, and taking measurements with a calliper. Since we never happened to see *Ariadna* specimens out of their holes, we excavated five burrows, taking five specimens, each from a medium-sized burrow having a stone number ranging from 5 to 9. All the spiders were weighed and the parameters (no. of stones in circle, their weight, plus the diameter of the hole entrance) of their burrows measured.

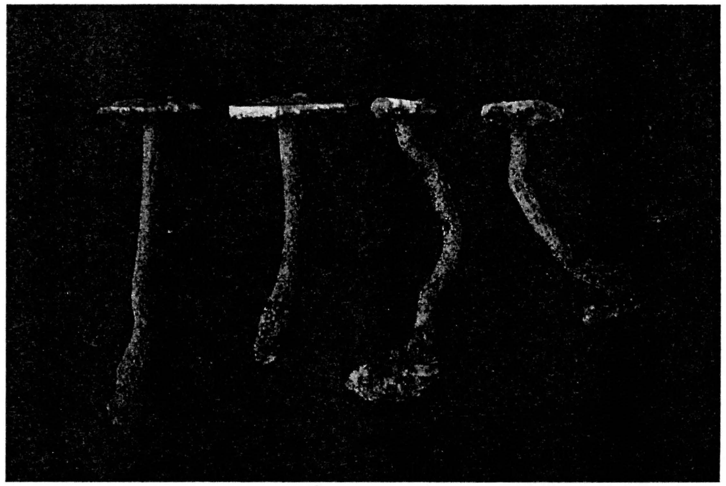

Figure 4. Some gypsum casts of *Ariadna* sp. burrows, scale bar = 3 cm.

Table 1. *Parameters relative to burrows and stones in their circles. The four values of stone weight, length, width and height are respectively the minimum value, maximum value, mean and standard deviation. The hole entrance diameters, stone length, width, and height are reported in mm 10^{-1}, the stone weights in g 10^{-2}*

Hole	*n* of stones	Hole diameter	Weight of stones	Length	Width	Height
1	6	54	16·17	57·00	38·20	32·00
			30·84	85·30	60·30	57·00
			21·51	72·77	52·13	45·95
			5·29	9·26	8.67	10·38
2	7	44	4·41	44·00	28·20	18·00
			8·77	61·20	50·10	34·20
			6·51	51·34	37·08	28·47
			1·46	6·02	18·11	5·35
3	6	55	6·57	42·10	38·20	24·00
			18·68	89·00	51·00	42·20
			12·03	63·68	44·48	31·85
			5·25	15·69	5·92	7·14
4	7	42	1·94	32·20	24·00	16·00
			6·65	49·10	44·10	24·40
			3·77	41·11	31·50	21·11
			1·73	5·83	6·64	3·09
5	8	42	4·62	45·40	28·30	21·00
			24·37	75·00	61·20	46·40
			8·61	54·56	40·32	30·19
			6·52	9·48	9·69	8·47
6	7	69	8·90	57·20	38·00	27·30
			41·60	100·00	64·10	58·20
			22·12	82·20	53·78	39·97
			10·30	16·51	9·07	11·89
7	8	38	1·36	35·00	24·10	13·00
			8·88	61·00	46·00	31·00
			4·45	47·43	4·09	24·19
			2·40	8·31	7·07	5·19
8	8	62	5·27	57·10	44·10	30·00
			18·57	78·00	66·00	44·00
			13·78	67·95	55·95	36·14
			4·49	6·76	8·29	4·00
9	7	37	4·05	38·00	30·00	23·00
			9·27	65·20	50·20	35·00
			6·85	50·17	39·10	28·76
			1·75	8·82	6·24	4·64
10	9	67	3·29	41·00	34·20	21·20
			17·36	70·00	60·00	44·10
			10·86	57·19	45·73	32·07
			4·62	10·95	8·44	7·64
11	8	51	1·46	27·00	24·30	13·40
			7·92	66·40	42·00	40·00
			4·60	46·02	33·24	23·74
			2·31	12·94	6·67	7·91
12	8	32	0·99	26·00	19·00	15·00
			4·63	51·30	37·20	26·20
			2·46	35·84	32·44	21·05
			1·35	9·50	8·73	4·05
13	5	41	3·28	34·00	31·20	20·30
			21·90	86·20	62·00	38·40
			9·61	57·84	46·24	30·04
			7·28	19·34	11·19	7·65

Table 1. *(cont.)*

Hole	*n* of stones	Hole diameter	Weight of stones	Length	Width	Height
14	7	73	11·16	54·30	42·00	33·30
			37·23	94·00	72·00	57·30
			25·19	76·51	59·90	43·36
			10·92	14·90	11·04	9·13
15	7	45	2·72	37·00	22·30	21·00
			7·91	74·20	47·10	28·30
			4·95	50·96	35·90	24·84
			1·81	11·76	8·56	2·46
16	6	47	1·65	31·20	20·30	19·20
			7·15	51·00	38·20	31·00
			4·17	40·18	30·50	25·07
			2·17	8·24	6·98	4·28
17	6	40	5·20	45·00	33·00	26·10
			25·26	90.00	44.00	45.40
			9·98	57·27	37·92	31·72
			7·63	17·13	4·24	7·10
18	5	64	16·26	62·00	53·10	36·40
			39·39	108·00	69·20	49·10
			24·91	80·08	59·96	43·76
			8·87	18·71	7·21	4·93
19	7	46	0·47	31·20	17·10	10·30
			4·76	48·00	37·10	29·00
			3·16	39·99	27·44	21·01
			1·56	10·02	6·92	5·64
20	7	57	3·20	38·00	23·40	25·00
			15·47	75·00	46·40	32·20
			7·78	53·36	39·50	28·54
			3·93	14·17	8·07	2·41
21	7	40	2·40	38·20	20·00	18·10
			15·46	59·00	50·00	47·20
			7·35	44·23	37·04	29·73
			4·45	11·18	9·02	9·78
22	7	46	1·25	32·10	22·20	19·00
			8·76	58·30	46·00	31·00
			4·90	48·93	32·14	24·07
			3·00	8·90	8·38	4·51
23	7	18	0·10	13·10	11·40	8·00
			1·10	25·00	23·30	18·00
			0·42	18·13	15·54	11·84
			0·35	4·34	4·74	3·78
24	6	56	10·17	61·20	43·10	31·00
			30·41	95·30	68·00	58·30
			18·98	72·97	51·33	40·92
			6·93	12·41	10·12	9·40
25	5	38	5·57	46·00	30·30	29·20
			17·11	90·20	73·10	37·90
			10·12	59·48	43·14	32·22
			4·39	17·68	17·04	3·40
26	7	46	8·02	50·00	32·20	20·40
			125·61	173·10	96·20	63·10
			27·63	75·74	51·80	37·37
			43·27	43·65	20·52	13·38
27	5	54	8·70	51·10	42·00	27·20
			22·88	162·00	61·10	41·40
			15·18	83·84	49·78	32·92
			5·31	44·45	7·26	5·69

Results

Features of the burrows

The diameter of the entrance holes of the burrows was very variable, with a range of 5·5 mm (from 1·8 mm to 7·3 mm in the sample examined. The sample distribution of frequency is unimodal. The mode lies between 3·5 mm and 4·5 mm (37·0% of the burrows). The diameters varied from 4·5 mm to 6·5 mm in 44.4% of cases; their values were under 3·5 mm or over 6·5 mm in only 18·5% of the burrows. Burrows are dug vertically and assume the aspect of a rectilinear tube. When the substratum is less easily penetrable, the tunnel has an irregular course (Fig. 4).

The use of gypsum casts showed that the hole diameter is more or less constant along the upper part of the burrow and usually enlarges near its base. The dilated distal tract (or 'bulb') occupies about one-third of the tunnel length.

Stone and spider features

The data related to hole diameter, stone numbers, weights and sizes are recorded in Table 1. The number of the stones surrounding the entrances of the holes sampled ranged from 5 to 9 (average, 6·8; Standard Deviation, 1·05). According to the frequency sample distribution, the modal class corresponds to number 7: this distribution is almost symmetrical, as is also shown by the percentage values (Table 2).

Table 2. *Percentage distribution of number of stones surrounding the holes sampled*

n of stones	% distribution
5	14·8
6	18·5
7	44·4
8	18·5
9	3·7

Arithmetic mean (M), standard deviation (S.D.) and coefficient of variation (V = s/m) of the three stone sizes are given in Table 3.

In Table 4, the data relative to the five specimens of *Ariadna*, including their weights, are shown.

Table 3. *Parameters relative to the stone sizes of the entire sample*

	Length	Width	Height
M (arithmetic mean)	55·77	39·66	30·01
S.D.	15·50	12·85	7·86
V (coefficient of variation)	27·80	32·40	26·19

Statistical analysis

We made a statistical analysis of the sizes of the stones bordering the hole and of their dimensions. We also considered the relation between stone size and hole diameter and, finally, the relation between spider weight and hole diameter. All the statistical methods used follow Zar (1974).

Table 4. *Measures relative to the five specimens collected and related hole and stone parameters (weights in g, diameters in mm)*

Weight of animal	*n* of stones	Hole diameter	Weight of stones
0·0565	5	6·4	1·2455
0·0469	7	5·7	0·4958
0·0369	8	5·1	0·3705
0·0452	8	6·2	1·1018
0·0720	9	6·7	0·9771

Length vs. *width of stones*

The ratio between length and width was almost regular (mean, 1·36; Standard Deviation, 0·1259). The coefficient of correlation between the two dimensions was very high ($r = 0{\cdot}94$); the t_r test is extremely significant. The regression line is characterized by the following parameters: $a = -0{\cdot}0196$ and $b = 1{\cdot}4156$. In Table 5 the result of this comparison can be seen. The goodness of fit of the regression line was tested by the analysis of variance ($p << 0{\cdot}001$).

Table 5. *Statistical comparisons. M = arithmetic mean of ratio; S.D. = standard deviation of ratio; min = minimum value of ratio; max = maximum value of ratio; r = coefficient of correlation; a = intercept of regression line; b = angular coefficient of regression line; F = statistical test*

	Comparison	M	S.D.	min	max	*r*	*a*	*b*	*F*
A	Length *vs.* Width	1·36	0·1259	1·10	1·68	0·94	−0·0196	1·4156	*p* << *0·001*
B	Width *vs.* Height	1·37	0·1058	1·13	1·55	0·95	0·0329	1·2538	*p* << *0·001*
C	Width *vs.* Hole diameter	0·87	0·1480	0·65	1·14	0·78	0·0879	0·6754	*p* << *0·001*

Width vs. *height of stones*

We obtained an almost regular ratio of width to height (M = 1·37; S.D. = 0·1058). The correlation between the two dimensions is very high ($r = 0{\cdot}95$), the t_r test results being extremely significant. The regression line has an intercept $a = 0{\cdot}0329$ and an angular coefficient $b = 1{\cdot}2538$. The analysis of variance also gave an extremely significant result ($p << 0{\cdot}001$). All data are given in Table 5.

Width of stones vs. *hole diameters*

The ratio between width of stones and diameters of holes is quite constant, even though it shows a greater variability than the other ratios. The mean ratio among the 27 burrows was M = 0·87, S.D. = 0·1480. The correlation coefficient was $r = 0{\cdot}78$; the t_r test was extremely significant. Regression line coefficients are $a = 0{\cdot}0879$ and $b = 0{\cdot}6754$ (Table 5); the analysis of variance confirms the extreme significance of the regression ($p << 0{\cdot}001$).

Hole diameters vs. *spider weights*

The scanty sample size did not allow us to carry out suitable statistical analysis. Nevertheless, we studied the pair-wise relationship between various parameters. Only the relationship between hole diameter and animal weight was significantly correlated; the coefficient of correlation was $r = 0{\cdot}88$ ($p < 0{\cdot}05$). The regression line parameters are $a = 0{\cdot}390$, $b = 4{\cdot}117$; the regression significance ($F = 10{\cdot}17$) reaches a probability level of 0·05).

Discussion

Table 2 illustrates the high frequency of 7-stone rings, as well as the symmetry of distribution around the modal class. The distribution of hole diameters is, of course, strongly influenced by size. The sample includes few of the smallest burrows. This scarcity may be due to a number of factors; for example, it could depend on the real difficulty in locating very small holes on the gravel plains, or on a particular phase of the yet unknown life-cycle of the species. Length and height are respectively, the most and the least variable of the three dimensions of the stones. Nevertheless, the coefficient of variation of width is the greatest. With regard to the pair-wise comparisons of the stone dimensions, the ratios Le/Wi and Wi/He are almost coincident.

The pattern of arrangement of stones around the burrow entrance appears to be unique among Araneida. After building a vertical tube inside the forestal soil of Sierra Nevada (California), the mygalomorph *Atypoides riversi* arranges oblong leaves radially around the burrow entrance. The leaves are placed with their major axes lined up along the radii of the circular hole (Coyle, 1986). It is probable that the leaves are in contact with silk threads, and that they link up with the cobweb that covers the circular wall of the tunnel. Unlike *Ariadna* sp. however, this spider does not appear to employ any numerical rule in the construction of its burrows. Our segestriid spider utilizes a consistent number of stones (the mean is 7). This may denote a capability for exploiting the entire circumference of an almost continuous stone ring. *Ariadna* almost always seems to select quartz stones. The weight of the stones used is probably related to the spider's size and ability to carry the stones to the hole from the place when they are found.

The regularity in the number and proportions of stones used by the spiders, and the relationship between their sizes and the diameters of the holes, suggests that these animals choose suitable stones for their burrows. It is difficult to explain the physical and mathematical characteristic of ring stones on the basis of random stone-taking. Spiders have somehow to select between the numerous stones scattered in their habitat. Nevertheless, active selection has neither been directly observed nor, as yet, been experimentally proved to occur.

We do not know yet the function of stone rings. Different hypotheses can be formulated; but we realise that, as often happens for biological phenomena, a multi-function hypothesis is also possible.

(a) Predatory function

The stone ring could perhaps attract prey or facilitate the detection of prey by the spider waiting inside its burrow. For example, it could convey information about prey position, as in the case of other spiders (Masters *et al.*, 1986). On the other hand, other segestriid spiders, such *Segestria florentina*, obtain information about the proximity and direction of passing prey by means of radiating silk lines arranged around the entrances to their holes (Bristowe, 1958; Hansell, 1984); Gertsch (1949) reported that *Ariadna*

bicolor connects the inner silk lining of its burrow with a series of heavy silk lines (two dozen or more) that radiate outward and are supported by little silken piers (one near the hole entrance and the other far away). Consequently, when prey stumbles against a line, the spider is suddenly informed of its presence.

(b) Strengthening the burrow and making it impervious

The ring could perhaps help to strengthen the top of the burrow and to prevent the entry of wind-blown sand or débris.

(c) Anti-predatory function

The stone ring might be a way of reducing predatory risk. The evenly lighted circle around the burrow's entrance could make this appear like, a black stone or a shaded area. On the other hand, spider holes may simulate the little black stones that are scattered over the gravel plain. The characteristic alternation of light and dark areas on the gravel ground complicates the detection of real burrows by predators.

Other hypotheses, such as thermo-hygric and ventilation functions, appear to be less probable on account of the flatness of the stone rings.

Summary

A new species of segestriid spider, *Ariadna* sp., has been discovered in certain areas of gravel in the Namib Desert. It excavates a vertical, cylindrical burrow, lined internally with silk. The bottom of the burrow appears to be enlarged. Moreover, the spider arranges a ring of shallow quartz stones around the edge of the circular entrance hole.

The number of stones is usually 7, ranging from 5 to 9 in a sample of 27 burrows. In addition, the stones of each ring are similar in size, shape and colour. Furthermore, they are placed radially to the major axis.

Proportional relationships occur between the length, width and height of the stones utilized by the spiders, and between the sizes of stones and the diameters of the holes. It is difficult to explain these regularities on the basis of a random stone-collecting. Nevertheless, it remains to be ascertained whether the selection of stones is active or passive.

The stone ring of *Ariadna* may have a predatory function. The quartz stones could inform the spider in ambush about the presence of prey. Since the burrow is lined with silk, each stone could convey vibrations caused by the movements of potential prey near to or over the ring. Other hypotheses regarding the function of the stone ring (for example, strengthening or making the top of the burrow impervious or an antipredatory function) could also be formulated.

We are very grateful to the Ministry of Wildlife, Conservation and Tourism of Namibia for the permission to carry out this research in the Namib-Naukluft Park. We also thank the staff of DERU, and the staff of DRFN, very much for their co-operation. Prof J.L. Cloudsley-Thompson kindly commented on the manuscript. The research grant was made available by the Italian Ministry of Scientific Research.

References

Ades, C. (1986). A construcao da teia geométrica como programa comportamental. *Ciencia Cult*, **38**: 760–775.

Bristowe, W.S. (1958). *The World of Spiders*. London: Collins. 304 pp.

Coyle, F.A. (1971). Systematics and natural history of the mygalomorph spider genus *Antrodiaetus* and related genera (Araneae: Antrodiaetidae). *Bulletin of Museum of Comparative Zoology*, **141**: 269–402.
Coyle, F.A. (1986). The role of silk in prey capture by nonaraneomorph spiders. In: Shear, W.A. (Ed.), *Spiders. Webs, behavior, and evolution*, pp. 269–305. Stanford, CA: Stanford University Press. 492 pp.
Craig, C.L. (1987). The ecological and evolutionary interdependence between web architecture and web silk spun by orb web weaving spiders. *Biological Journal of Linnean Society*, **30**: 135–162.
Eberhard, W.G. (1986). Effects of orb-web geometry on prey interception and retention. In: Shear, W.A. (Ed.), *Spiders. Webs, behavior, and evolution*, pp. 70–100. Stanford, CA. Stanford University Press. 492pp.
Gertsch, W.J. (1949). *American Spiders*. Toronto, New York, London: D Van Nostrand Company Inc. 285 pp.
Hansell, M.H. (1984). *Animal Architecture and Building Behaviour*. London and New York: Longman. 324 pp.
Masters, W.M., Markl, H.S. & Moffat, A.J.M. (1986). Transmission of vibration in a spider's web. In: Shear, W.A. (Ed.), *Spiders. Webs, behavior, and evolution*, pp. 49–69. Stanford, CA: Stanford University Press. 492 pp.
Murphy, J & Platnick, N.I. (1981). On *Liphistius desultor* Schiodte (Araneae, Liphistiidae). *Bulletin American Museum Natural History*, **170**: 46–56.
Porter, J.P. (1906). The habits, instincts, and mental powers of spiders, genera *Argiope* and *Epeira*. *American Journal of Psychology*, **17**: 306–357.
Zar, J.H. (1974). *Biostatistical Analysis*. London and New York: Englewood Cliffs, Prentice Hall. 520 pp.

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The ecology of *Agama yemenesis* Klausewitz (Lacertilia: Agamidae) in south-western Arabia

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A field study of the ecology of *Agama yemenensis* was carried out in Dalaghan National Park near Abha, Saudi Arabia. This lizard occurs in rocky areas of the highland in the south-west of Arabia. Emergence time, basking, thermoregulation and activity period have been determined. The body temperature of active lizards in the field is 29°C, while the selected temperatures in a thermal gradient during the day and night were 32·2°C and 26·5°C, respectively. Lizards depend on a sit-and-wait strategy, and spend little time feeding on the ground. They feed mainly on ants which are very abundant in their habitat. Seeds, leaflets, twigs and other plant materials are also an important part of their diet.

Keywords: *Agama yemenensis*; lizard; Arabia; ecology; thermoregulation; feeding

Introduction

Agama yemenensis Klausewitz is commonly seen on rocks and boulders in South-western Arabia. When warm, it is conspicuous due to its bright blue colour. Little is known of its ecology, behaviour or natural history. Field studies of the herpetofauna of this part of Arabia are limited. Farage & Banaja (1980) surveyed the amphibians and reptiles and provided information on the distribution of some species of the herpetofauna. Al-Khalili & Nader (1984) published a checklist of the terrestrial vertebrates of the Asir National Park and its surroundings. *A. yemenensis* and *A. adramitana* occur in close proximity in Asir National Park and the surrounding area. The two species have similar features and it is not easy to recognize them in the field. Until recently, they were considered to be subspecies of the *A. cynogaster* complex which occurs in north-eastern Africa and south-western Arabia. Arnold (1980), however, suggested that the two merit species status, based on a number of criteria which distinguish them.

Materials and methods

This study was carried out at Dalaghan National Park, 30 km SE of Abha, Saudi Arabia, during the summers of 1989 and 1990. Field observations were made on the

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