SALAMANDRA **48**(3) | 125–132 | 30 October 2012 | ISSN 0036–3375

Intraspecific variation of morphology, colouration, pholidosis, and tail loss rate in a relic lacertid of South Africa, *Australolacerta rupicola* (Sauria: Lacertidae)

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Manuscript received: 9 February 2012

Abstract. Intraspecific variation in morphology, colouration, pholidosis, and tail loss rate of up to 80 specimens of the endemic Soutpansberg rock lizard *Australolacerta rupicola* were assessed from 2005 to 2007. These were analysed together with data from the type specimen and eleven additional specimens from an earlier study (1979–1985). In comparison with other lacertids, this species exhibits only a feeble sexual dichromatism. Analyses of morphometric characters show the existence of sexual size dimorphism, with females growing to greater snout–vent lengths and males having larger heads. Additionally, adult males have significantly more femoral pores than females. Compared to adults, juveniles have proportionally larger heads. The frequencies of regenerated tails did not show significant differences between the tested groups. All differences described are discussed in the light of the ecology of this species.

Key words. Squamata, endemism, Soutpansberg, ontogeny, pholidosis, sexual dimorphism.

Introduction

Following the discovery of *Australolacerta rupicola* (FitzSimons, 1933) by C. J. van der Horst along the shore of Lake Funduzi (Soutpansberg, South Africa) in July 1931, the type specimen remained the only record of this species for almost half a century. It was only rediscovered during an extensive survey of the reptiles and amphibians of the Transvaal Province by Jacobsen (1989). Subsequently, Kirchhof et al. (2010a, b, c) reported on the ecology of the species. Currently, the species is listed in the South African Red Data Book as restricted (Jacobsen 1988) and in the IUCN Red List as lower risk/near threatened (World Conservation Monitoring Centre 1996).

Morphology and size of a lizard are considered to be linked to several ecological aspects such as habitat (Butler & Losos 2002), foraging mode (Perry et al. 1990, Verwaijen & Van Damme 2007), thermoregulation (Carrascal & Díaz 1989), territoriality (Kaliontzopoulou et al. 2007), and sexual selection (Butler & Losos 2002). Body dimensions and pholidosis do not only vary between different species, but also intraspecifically, in sexual dimorphism (Fairbairn 1997) and ontogeny (Bischoff 1984, Monteiro et al. 1997).

Sexual dimorphism in size and shape is a common feature in lizard species and a result of different selective pressures on males versus females (Kaliontzopoulou et al. 2007). Accordingly, it is possible to gain deeper insight of these differences in the ecology of a species from observations of the lizards' lifestyle in its natural environment. Over the years 2005 to 2007, different ecological studies on *Australolacerta rupicola* were conducted (Kirchhof & Richter 2009, Kirchhof et al 2010a, b, c) and varying morphological parameters were measured subject to the particular study. Furthermore, measurements and pholidotic data acquired from the type specimen (FitzSimons 1933) as well as during the Transvaal survey (Jacobsen 1989) are available. The main goal of this article is to report on the morphology of the little-known lacertid *A. rupicola,* which is endemic to the Soutpansberg, by merging all existing data. We analyse intraspecific variations in colour, morphology, pholidosis, and tail loss rate and discuss the results in the light of the ecology of the species based on the available literature (FitzSimons 1933, Jacobsen 1988, Jacobsen 1989, Branch 1998, Kirchhof & Richter 2009, Kirchhof 2011, Kirchhof et al 2010a, b, c, 2011) and unpublished field observations by the authors.

Materials and methods

From 2005 to 2007, individuals of *A. rupicola* were caught during different ecological studies (Kirchhof et al. 2010a, b, c). Six pitfall trap lines were set up along rocky slopes and rock outcrops that were known to harbour populations of *A. rupicola*. Additionally, when individuals were found during visual encounter surveys, they were caught by hand or using a noose. In total, 35 individuals were caught. Caudal autotomy was noted for all individuals and another 33 animals not captured but seen to have either whole, lost or regenerated tails. For the captured individuals, the following morphometric characters were measured using a digital calliper with an accuracy of 0.01 mm: snout–vent length (SVL): tip of snout to anal cleft*, tail length (TL): anal cleft to tip of tail*, head length (HL): tip of snout to posterior margin of parietals, head width (HW): where the head reaches its maximum width, and head height (HH): where the head reaches its maximum height. Additionally, the number of dorsal scale rows at midbody and the number femoral pores were counted. Measurements and counts were conducted on live specimens, which were then photographed to analyse colour patterns, marked on the legs using permanent markers of different colours to avoid pseudo-replications, and subsequently released at the exact site of their capture. Only two specimens (NMW 386832, NMW 386833) were euthanised under permit issued by the Department of Environmental Affairs (Limpopo Province; permit number CPM-005-00007) and dissected to establish their sexual maturity status. During the study period, no individual was measured twice.

In the first description of the species, FitzSimons (1933) provided data on SVL, TL, HL, HW, HH, number of dorsal scale rows around midbody, and number of femoral pores (among other parameters) for the female type specimen (TM 13989). Between 1979 and 1985, Jacobsen (1989) recorded SVL, TL, number of dorsal scale rows at midbody, and frequency of regenerated tails (among other parameters) for eleven individuals (five of these of unknown sex) of *A. rupicola*.

All data taken during these studies were combined for analyses. For the purpose of this study, minimum SVL for sexually mature adults was considered to be 33.00 mm, based on the dissected specimens that showed mature reproductive organs as well as on live specimens in which males already showed a broadened tail base due to the enlarged hemipenes.

Descriptive statistics (mean, standard deviation [SD], minimum, maximum) are provided independent of sex and age for the number of dorsal scale rows (n = 33) and the number of femoral pores per thigh (n = 19). Descriptive statistics are further provided for all morphometric parameters: SVL ($n_{\text{adults}} = 26$; $n_{♂} = 13$; $n_{♀} = 12$; $n_{\text{juveniles}} = 21$), original TL ($n_{\text{adults}} = 13$; $n_{♂} = 5$; $n_{♀} = 8$; $n_{\text{juveniles}} = 13$), HL, HW, HH ($n_{\text{adults}} = 12$; $n_{♂} = 5$; $n_{♀} = 5$; $n_{\text{juveniles}} = 5$). The percentage frequencies of regenerated tails are provided and analysed for a total of 80 individuals.

For further statistical analyses, the morphometric measurements were converted into non-dimensional dependent ratios: TL/SVL: relative tail length (T index) (only original tails)$^{*\#}$, HW/SVL: head index (HW index)$^{*\#}$, HL/SVL: relative head length (HL index)$^{*\#}$, and HH/SVL: relative head height (HH index)$^{*\#}$. A non-parametric statistical hypothesis test (Mann-Whitney-U-Test), which allows the use of small sample sizes, was employed to test for significant differences between males and females in the characters "number of dorsal scale rows at midbody" ($n_{♂} = 9$; $n_{♀} = 7$) and "number of femoral pores on each thigh" ($n_{♂} = 5$; $n_{♀} = 5$). The percentage of tail autotomy for the different sexes ($n_{♂} = 14$; $n_{♀} = 11$) and different stages of development ($n_{\text{juvenile}} = 25$; $n_{\text{adults}} = 55$) was tested for significance using the Kolmogorov-Smirnov-Test, which can be used for discrete variables in small sample sizes. Morphometric characters marked with * above were statistically tested for significance using the Mann-Whitney-U-Test to reveal potential sexual size dimorphism ($n_{\text{SVL}\,♂} = 13$; $n_{\text{SVL}\,♀} = 12$; $n_{\text{TL index}\,♂} = 5$; $n_{\text{TL index}\,♀} = 8$; $n_{\text{HW, HL, HH index}\,♂} = 7$; $n_{\text{HW, HL, HH index}\,♀} = 5$). This test was also used to assess possible age-related variations within different stages of development of morphometric characters marked with $^{\#}$ above ($n_{\text{TL index (juvenile)}} = 13$; $n_{\text{TL index (adult)}} = 13$; $n_{\text{HW, HL, HH index (juvenile)}} = 5$; $n_{\text{HW, HL, HH index (adult)}} = 12$). The level of significance was determined using exact significance [2* (1-tailed significance)] with a significance level of 5% ($p < 0.05$). All statistical analyses were performed using SPSS 17.0. Colouration of *A. rupicola* is described for juveniles and adults, and differences between ontogenetic stages and between males and females are presented. In total, data from a maximum of 80 different specimens of *A. rupicola* were analysed.

Results

Colouration

Detailed descriptions of the general colour pattern of *A. rupicola* were given by FitzSimons (1933) based on the type specimen, and by Jacobsen (1989). However, with a greater sample size, especially of hatchlings and juveniles, which had not been previously recorded, a more complete description is now possible. In general, hatchlings and juveniles exhibit greater contrast between the dark brown background colour and the two bright yellow dorsolateral bands, which become paler with age and turn yellowish white. The stripes extend from the back of the head to the root of the tail. The sides of body and limbs are extensively speckled with clean, distinct, yellow spots in hatchlings. These spots become yellowish white and indistinct in adults, with the upper ones forming a broken lateral stripe running from the tip of the snout along the labials across the ear opening, continuing faintly towards the base of the tail. The sharply demarcated dorsolateral yellow stripes are separated from the broken stripes by the dark brown to black background colour.

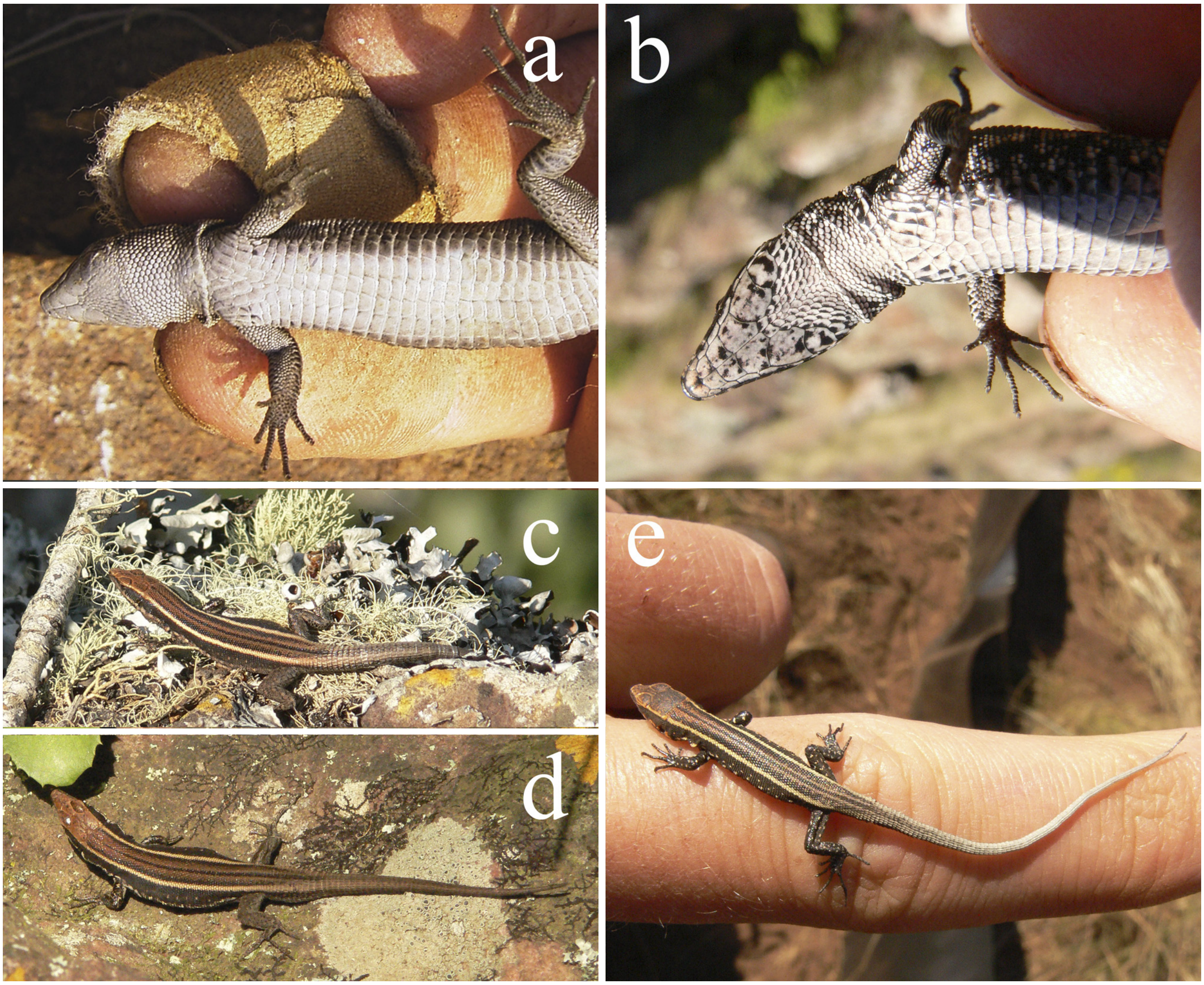

Figure 1. Colour patterns and habitus of *Australolacerta rupicola*. (a) ventral view of an adult female. The ventral, chin and gular scales are uniformly grey; (b) ventral view of an adult male. Note the extensive pattern on the ventral, chin and gular scales; (c) dorsal view of an adult female; (d) dorsal view of an adult male; (e) dorsal view of a juvenile. Note the long grey-white tail.

In both adults and juveniles, the top of the head can be light brown with almost no dark speckles, but may also be extensively covered with blackish blotches with only a little light brown in between, giving it a dirty-looking appearance. The outer lateral edge of the parietal shields is slightly brightened and appears as an extension of the dorsolateral yellow stripes. Ventrally, the lizards are generally grey in both juveniles and adults. In adult females, a few small dark dots might appear on the gular scales and chin shields (Fig. 1a) whereas in adult males, the blackish body colour blends into the grey of the ventrals and/or the gular scales, which gives the sides of the belly and the throat a blotchy appearance (Fig. 1b). This seems to be the only sexual dimorphism in terms of colouration in *A. rupicola* (Fig. 1c, d) and does not change even during the breeding season beginning in September. The tail is very light grey in hatchlings and juveniles, sometimes almost whitish, and darkens with age, becoming brown dorsally (Fig. 1c, d, e). The subcaudals remain grey like the rest of the ventrals.

Pholidosis

Dorsal scales are generally smooth and only faintly keeled in few individuals. The number of dorsal scale rows around midbody ranged from 34 to 42 with a mean of 38 ± 2.3 and a mode of 36 (21.2%, n = 33) (Table 1). In the 16 specimens of known sex, the mean number of dorsal scale rows was 38 in both males and females, but with slightly different ranges (males: 34–40, n = 9; females 34–41, n = 7, p = 0.837) (Fig. 2). Femoral pores ranged from 14 to 19 per thigh ($\bar{x}$ = 16, SD = 1.5, n = 19) and were present in both sexes,

Table 1. Dorsal scale rows and femoral pores of male, female and combined data for *Australolacerta rupicola*.

		total	males	females
dorsal scale rows	n	33	9	7
	mean	37	38	38
	SD	2.3	1.9	2.5
	Min	34	34	34
	Max	42	40	41
femoral pores	n	19	5	5
	mean	16	18	16
	SD	1.5	0.8	1.1
	Min	14	17	15
	Max	19	19	17

Table 2. Percentage frequency of regenerated tails of *Australolacerta rupicola*.

	n	Individuals with regenerated tails	Percentage frequency
total	80	31	38.8%
adults	55	21	38.2%
adult males	14	9	64.3%
adult females	11	3	27.3%
juveniles	25	10	40.0%

with 42.1% of individuals having 15 pores on each thigh. However, judged by the eye they were larger and more developed in males, especially during the breeding season. Sexual dimorphism was present, with the mean number of femoral pores in males being 18 ± 0.8 (17–19, n = 5) and 16 ± 1.1 (15–17, n = 5) in females. This difference is statistically significant (Mann-Whitney-U-Test, p = 0.032) (Fig. 2).

Tail autotomy

In the present study, 31 of 80 (38.8%) individuals of all ages had regenerated tails (Table 2). When only adults were taken into consideration, caudal autotomy was present in 38.2% of the individuals (n = 55). The frequency of regenerated tails in adult males was 64.3% (n = 14) as opposed to 27.3% (n = 11) in adult females. However, the difference is not significant (Kolmogorov-Smirnov-Test, p = 0.368). Likewise, the proportion of regenerated tails in juveniles (40%, n = 25) was not significantly different from that in adults (Kolmogorov-Smirnov-Test, p = 1.000).

Morphometrics

The mean SVL for adults was 44.72 mm. Mean original tail length was 79.42 mm, which is 1.78 times longer than the mean SVL. Individuals with tails more than twice as long as SVL were also recorded (Table 3). The largest recorded in-

Table 3. Morphometric characters of *Australolacerta rupicola* (sample size (n), mean, standard deviation (SD), minimum (Min) and maximum (Max).

		SVL	orig. TL	HL	HW	HH	HW/SVL	HL/SVL	HH/SVL	TL/SVL
adult males	n	13	5	7	7	7	7	7	7	5
	mean [mm]	43.70	77.96	10.20	6.35	4.63	0.15	0.25	0.11	1.81
	SD [mm]	4.63	17.91	1.04	0.83	0.65	0.01	0.01	0.01	0.29
	Min [mm]	33.00	62.20	8.30	4.80	3.40	0.15	0.24	0.10	1.45
	Max [mm]	51.50	108.00	11.60	7.58	5.14	0.16	0.26	0.12	2.10
adult females	n	12	8	5	5	5	5	5	5	8
	mean [mm]	46.80	80.33	10.55	6.78	4.34	0.14	0.22	0.09	1.73
	SD [mm]	2.99	9.29	0.48	0.58	0.16	0.01	0.01	0	0.16
	Min [mm]	39.00	67.00	10.13	6.21	4.19	0.14	0.22	0.09	1.45
	Max [mm]	50.00	91.20	11.30	7.50	4.40	0.15	0.23	0.09	1.91
all adults	n	26	13	12	12	12	12	12	12	13
	mean [mm]	44.72	79.42	10.35	6.53	4.51	0.15	0.24	0.10	1.76
	SD [mm]	4.73	12.60	0.84	0.74	0.51	0.01	0.01	0.01	0.19
	Min [mm]	33.00	62.20	8.30	4.80	3.40	0.14	0.22	0.09	1.45
	Max [mm]	51.50	108.00	11.60	7.58	5.14	0.16	0.26	0.12	2.10
juveniles	n	21	13	5	5	5	5	5	5	13
	mean [mm]	24.62	44.42	6.71	3.81	2.72	0.16	0.29	0.12	1.89
	SD [mm]	4.02	8.22	0.38	0.31	0.25	0.00	0.01	0.01	0.13
	Min [mm]	20.05	35.00	6.20	3.60	2.41	0.16	0.27	0.11	1.71
	Max [mm]	31.05	65.00	7.25	4.35	2.98	0.16	0.30	0.13	2.09

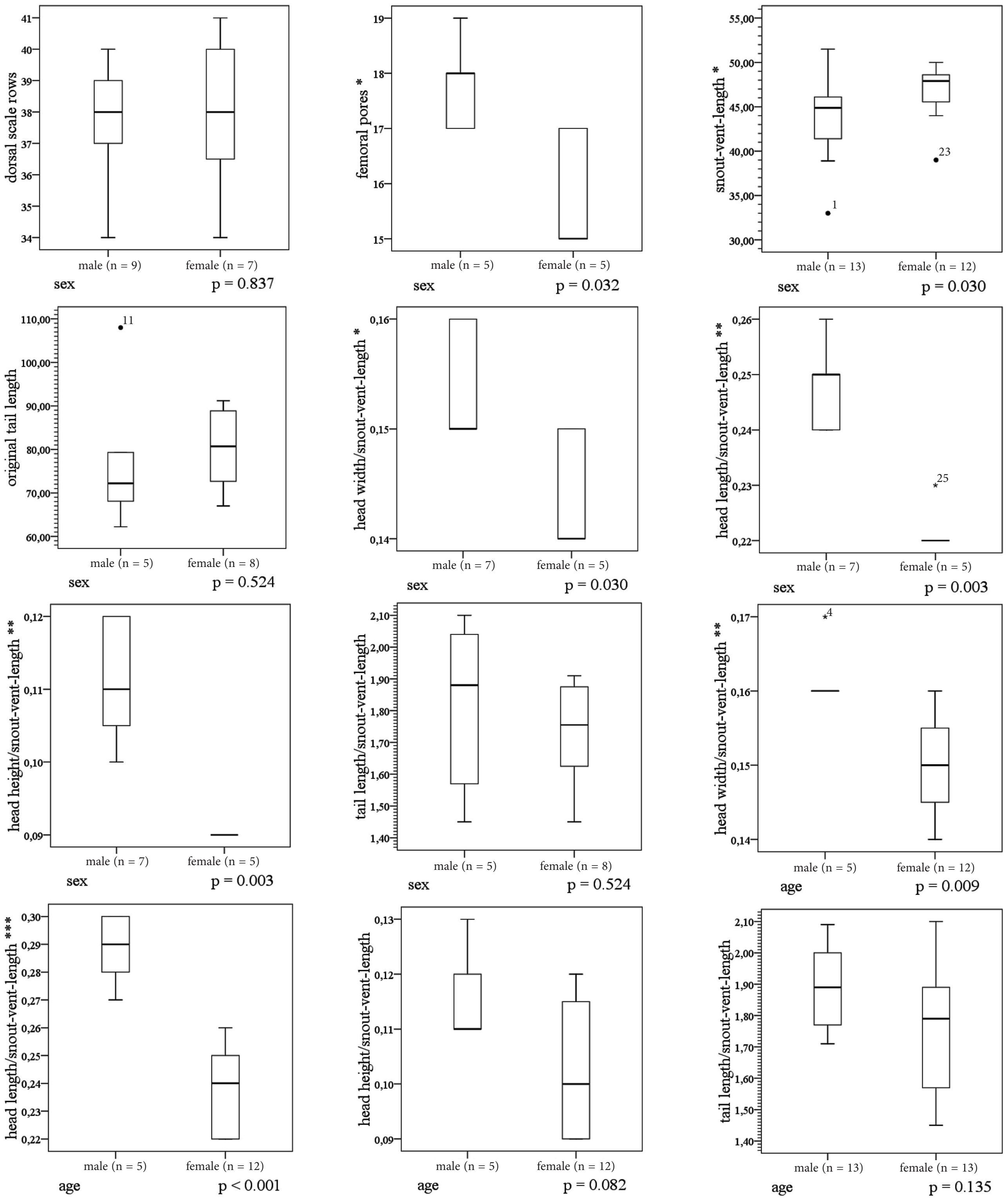

Figure 2. Box and whisker plots of all analysed morphometric characters as well as the number of dorsal scale rows and femoral pores providing the p-values and levels of significance (* = significant with $p < 0.05$, ** = significant with $p < 0.01$, *** = highly significant with $p < 0.001$), rounded to nearest three decimals. The figure shows the median (—), the interquartile with 50 % of the recorded values (▭), minimum and maximum values (⊤⊥), outliers (●) that are between 1.5 and 3 box-lengths distant from the upper or lower edge of the box, and extreme values (+) that are more than 3 box lengths from the upper or lower edge of the box.

dividual of *A. rupicola* was a male with a SVL of 51.50 mm and an original tail of 108.00 mm in length (Jacobsen 1989). Mean head length in adults was 10.35 mm; mean head width 6.53 mm, and mean head height 4.51 mm. The Mann-Whitney-U-Test confirms that on average female SVL ($\bar{x}_{\text{SVL (♀)}} = 46.8$ mm) was significantly larger than that of males ($\bar{x}_{\text{SVL (♂)}} = 43.7$ mm) ($p = 0.030$) (Fig. 2). In addition to sexual dimorphism in SVL, significant differences in relative head width (HW index), relative head length (HL index) and relative head height (HH index) were also manifest between the sexes. Males had proportionately wider heads ($\bar{x}_{\text{HW index (♂)}} = 0.15$) in relation to SVL than females ($\bar{x}_{\text{HL index (♀)}} = 0.14$, $p = 0.030$) as well as proportionately longer ($\bar{x}_{\text{HL index (♂)}} = 0.25$, $\bar{x}_{\text{HL index (♀)}} = 0.22$, $p = 0.003$) and higher heads ($\bar{x}_{\text{HH index (♂)}} = 0.11$, $\bar{x}_{\text{HH index (♀)}} = 0.09$, $p = 0.003$). The T index was also higher in males, but the difference is not significant.

The smallest hatchlings measured 20.00 mm SVL ($n = 21$) and their mean SVL was 24.62 mm. Mean original tail length in juveniles was 44.42 mm ($n = 13$), and accordingly, $\bar{x}_{\text{T index (juv.)}}$ was 1.89, which is longer than in adults but not significantly so ($p = 0.135$) (Fig. 2). The heads of juveniles were significantly wider and in relation to SVL longer than those of adults ($\bar{x}_{\text{HW index (juv.)}} = 0.16$, $\bar{x}_{\text{HW index (ad.)}} = 0.15$, $p = 0.009$; $\bar{x}_{\text{HL index (juv.)}} = 0.29$, $\bar{x}_{\text{HL index (ad.)}} = 0.24$, $p < 0.001$). On average the head fits 3.7 times into SVL, as compared to 4.3 times in adults. Juveniles also had proportionately higher heads (HH index) than adults, but the difference is not significant ($p = 0.082$) (Fig. 2).

Discussion

The results of the analysis of intraspecific variations within *A. rupicola* reveal the existence of sexual dimorphism and ontogenetic differences, even though sample sizes for some tests were relatively small. Females were significantly larger than males, while males had significantly larger heads in proportion to SVL and displayed slightly stronger ventral patterns. Juveniles had significantly longer and wider heads in proportion to SVL than adults and were more colourful with whitish grey tails. The data also reveal that the female type specimen (TM 13989), which was referred to as half-grown in the original description (SVL 49.0 mm; FitzSimons 1933), is actually a fully grown, relatively large individual.

In lacertids, males usually grow larger than females (Kaliontzopoulou et al. 2007) but exceptions exist, as for example in *Iberolacerta monticola* (see Salvador 1984), *Lacerta agilis* (see Bischoff 1984), *Psammodromus hispanicus* (see Salvador 1981) and *Podarcis muralis* (see Gruschwitz & Böhme 1986). The longer SVL of *A. rupicola* females in this study in combination with their shorter heads should result from increased trunk length, although this parameter was not measured. Sexual dimorphism favouring trunk length in females has been suggested to impart a fecundity advantage by facilitating more space for eggs (Braña 1996). The only published data regarding fecundity and clutch size for *A. rupicola* report one gravid female containing two eggs (Jacobsen 1989) as well as two females with three and four eggs, respectively (Kirchhof & Richter 2009). In species where males are often involved in fights, sexual selection may favour larger males (Olsson et al. 2002). Especially in territorial species, males are often engaged in intrasexual conflicts (Butler & Losos 2002). The behaviour of male *A. rupicola* individuals observed in the field during ecological studies (Kirchhof & Richter 2009, Kirchhof et al 2010a, b, c) was not aggressive towards conspecific males. The only observed expression of aggressive behaviour was restricted to one incident of an individual being chased out of a hiding place that was already occupied by another individual (Kirchhof, unpubl. data). These observations do not attest to strong territoriality of *A. rupicola* and support the results of smaller SVL in male *A. rupicola*. However, a larger head in males is a feature typical of most species of the family (see Böhme 1981, 1984, 1986), even for those with females that grow larger, e.g. *Zootoca vivipara*. For the latter species it has been shown that the ability to grasp females during mating activities was enhanced with increased head dimensions (HL, HL and HW) and affected a male's reproductive success (Gvozdík & Van Damme 2003). Future studies could address this question for *A. rupicola*.

Sexual dimorphism may also evolve as a result of intersexual competition for resources like food (Verwaijen et al. 2002, Kaliontzopoulou et al. 2007), which would become apparent in the utilization of different microhabitats and/or differences in foraging mode/prey selection (Perry et al. 1990). The studies on microhabitat selection and the foraging mode of *A. rupicola* were conducted independent of sex, but the results do not reveal any striking indications for sex-related differences (Kirchhof et al. 2010b). Hence, we propose that fecundity selection is likely to explain the sexual dimorphism in *A. rupicola*, but information on habitat use and foraging mode of the different sexes, as well as mating behaviour of *A. rupicola*, would be required to test this hypothesis. Apart from sexual dichromatism and sexual size dimorphism, sexual dimorphism was also apparent in femoral pore counts, with males having significantly more pores than females, a fact that is also known for most other lacertid species (e.g., Böhme 1981, 1984, 1986).

In many species of lacertids, the juveniles have larger heads relative to their SVL than the adults (e.g., Böhme 1981, 1984, 1986). Juveniles of *A. rupicola* showed the same ontogenetic pattern. The smaller body dimensions of the juveniles might facilitate the exploitation of a different trophic niche, as has been shown for other lacertids (Verwaijen et al. 2002). The larger head in relation to body size usually helps with catching relatively larger and therefore energetically more favourable prey (Herrel & Gibb 2006). Both assumptions are supported by the fact that the juveniles of *A. rupicola* inhabit different habitats than the adults (Kirchhof et al. 2010a), the reason for which could be the exploitation of different prey sources.

Frequencies of tail autotomy may vary between different populations (Luiselli et al. 2005) and different sexes (Jaksić & Busack 1984, Bringsøe 1986). This is because tail loss might be the result of either high predation pressure (Luiselli et al. 2005) or intraspecific fights especially in territorial species (Jaksić & Busack 1984, Bringsøe 1986). Although the number of individuals with regenerated tails in this study is higher in males than in females, the p-value is not significant ($p = 0.368$). This supports the assumption that *A. rupicola* males rarely engage in intraspecific territorial conflicts. However, the increased regeneration rates observed in males could have been due to greater activity during the breeding season, when they search for mating partners and consequently run a higher risk of encountering predators.

Acknowledgements

The Studienstiftung des Deutschen Volkes (Germany) and the Prof.-Hellriegel-Institut (Bernburg, Germany) provided part of the financial framework for this study, thank you very much. For issuing the collecting permit (permit number CPM-005-00007), we thank the Department of Environmental Affairs of Limpopo Province. We are very grateful to Ian and Retha Gaigher from the Lajuma Research Station, who provided knowledge, moral support and accommodation. Michael Krämer, Jabu Linden and Norbert Hahn were of major help on field trips. Special thanks go to René Lesnik for lending a hand. Two anonymous reviewers and John Measey greatly improved the manuscript.

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