Different Evolutionary Causes of Clutch Size in the *Asaccus/Haemodracon* Cluster (Squamata: Gekkota: Phyllodactylidae)

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Abstract

Gekkota differ in their clutch sizes. This phenomenon is particularly evident in the variable double-egg clutches and practically invariant single-egg clutches. The clutch size developed from a selection of different life history characteristics. The reduction to a single egg is the most recent evolutionary adaptation of gecko's clutch size. In the Asaccus/Haemodracon cluster, both clutch sizes are known for geckos. The singleegg clutches developed convergently in the lineage and are (1) a generic feature (Asaccus) and (2) an intraspecific feature (Haemodracon). As biotic selection factors, possibly (1) predator-prey relationships and (2) food net patterns have contributed to the miniaturization of the invariant clutch size in the selected species. The regulated reproductive efforts have led to a reduction in adult mortality and an increase in the survival rate of offspring.

Key words: *Asaccus, Haemodracon,* different clutch sizes, natural selection factors, predator-prey system, food resources.

Introduction

As for the early reduction of the clutch sizes in the geckonid lineage and its subsequent fixation, the causal relationships to the lifehistory characteristics are largely unknown. The researchers recorded and analyzed the reproductive properties of species within two phyllodactylid sister genera *Asaccus* (Dixon and Anderson, 1973) and *Haemodracon* (Bauer, Good and Branch, 1997), in which the two known clutch-sizes of geckos occur. The aim of the present *Corresponding author: herbertroesler@aol.com investigation is to examine the basis of intraspecific reproductive characteristics, and to determine which morphological or ecological factors led to the development of the smallest possible clutch size in these related groups.

Material and methods

Two species of the genera *Asaccus* from Oman and *Haemodracon* from the Island of Socotra (Yemen) were made available for the present study of reproductive biology. The researchers examined specimens of *Asaccus caudivolvulus* (Arnold and Gardner, 1994) and *Asaccus montanus* (Gardner, 1994) each in the sex ratio 1/2 (male/female); *Haemodracon riebeckii* (Peters, 1882) in the sex ratio 3/5 (male/female) and *Haemodracon trachyrhinus* (Boulenger, 1899) in the sex ratio 3/3 (male/female). The species of both genera differ in size and body shape but share similar toe structures (Figures 1–6).

The reproductive data on both of the *Asaccus* species that were determined and logged were from 2008 to 2019, while the data on the two *Haemodracon* species were from 1999 to 2019.

The geckos were kept in pairs in terrariums of different sizes and were differently arranged according to the natural habitats. All couples were temporarily separated, and the sexes were housed individually. The geckos were mainly fed with various bred insects and their larvae (e.g. *Tenebrio molitor*, *Gryllus assimilis*, *Galleria mellonella*). Sporadically, they were also offered hand-captured spiders (non det.) and millipedes (non det.). In addition, several varieties of fruit porridge, yoghurt, and various vegetables were offered regularly. The foods were enriched with



Figure 1. Adult female of A. caudivolvulus. ©Herbert Rösler



Figure 2. Portrait of A. caudivolvulus. ©Konrad Kürbis



Figure 3. Ventral view of hind foot of A. caudivolvulus. ©Konrad Kürbis



Figure 4. Adult female of A. montanus. ©Herbert Rösler



Figure 5. Adult male of *H. riebeckii* and some toe details. ©Konrad Kürbis



Figure 6. Adult female of *H. trachyrhinus*. ©Herbert Rösler

mineral and vitamin supplements.

During the period of examination, all living adult geckos were measured and weighed several times, and the average values were calculated from the individual data. The size and weight of the eggs were recorded immediately after the oviposition, and the size and weight of the young animals were recorded on the day of hatching (Figures 7-11).

The following abbreviations are used:

SVL = snout-vent length

FM = female mass

EL = egg length

EW = egg width

CV = clutch volume

CM = clutch mass

JM = juvenile mass

All morphometric data are from living specimens. Their snout-vent length (distance between tip of snout and cloacal slit) and the egg size were measured with a digital caliper. The adult geckos were weighed with a laboratory scale, and the eggs and young specimens were weighed using a pharmaceutical analysis scale.

In terms of the clutch sizes, two categories were distinguished: invariant singleclutches and variable doubleegg clutches. The egg volume was egg calculated according to the formula: V = $4/3 \times \pi \times EL/2 \times EWh/2 \times EWv/2$ (EL = egg longitudinal axis, EWh = egg width axis horizontal, EWv = egg width axis vertical). The formula: clutch mass immediately after ovipositon/female live weight was used to calculate the relative clutch mass (CM/FM =RCM). Data analyses were carried out with multivariate statistics (analysis of variance [one-way ANOVA], principal components analysis [PCA]), and significant ranges were determined with the Mann-Whitney-U-Test. The normal distribution of the data on clutch size, clutch mass and mass of juveniles was checked with the Shapiro-Wilk test. A Spearman's rank correlation was used to test the relationships between female snout-vent length and clutch volume (SVL/CV), female mass and clutch mass (as RCM), as well as juvenile mass and female mass (JM/FM). Violin plots with embedded boxplots were generated for continuous morphometric characters to visualize the same plus the distribution frequency of the data. A hierarchical cluster analysis (CA) was performed to determine which taxa were the most similar morphologically and in terms of clutch-size based on the unweighted pair group method with arithmetic mean (UPGMA). For all the analyses, the statistics program PAST, Version 3.22 (Hammer 2010) was used.

Results

Reproduction-specific characteristics: *A. caudivolvulus*: female (n=2) SVL 68.0-69.0 mm (68.5 ± 0.50), mass 5.44-5.99 g (5.72 ± 0.28); male (n=1) SVL 69.0 mm, mass 5.89 g. *A. montanus*: female (n=2) SVL 37.0-39.0 mm

(38.0 \pm 1.00), mass 1.26–1.55 g (1.41 \pm 0.15); male (n=1) SVL 40.5 mm, mass 1.65 g.

H. riebeckii: female (n=5) SVL 106.0– 116.5 mm (110.7 \pm 4.0), mass 32.48–45.08 g (40.06 \pm 5.02); male (n=3) SVL 125.0– 128.5 mm (127.2 \pm 1.9), mass 57.30–59.14 g (58.35 \pm 0.95). *H. trachyrhinus*: female (n=3) SVL 40.0–43.0 mm (41.0 \pm 1.7), mass 1.62–3.09 g (2.43 \pm 0.75); male (n=3) SVL 40.0–41.0 mm (40.7 \pm 0.3), mass 2.01–2.34 g (2.00 \pm 0.17).

The two Asaccus species glued fertile eggs to both solid inorganic materials (glass, slate slabs) and organic material (wood, cardboard) (Figures 12-13). Mostly, they were placed hidden in crevices, but A. caudivolvulus also glued some eggs visibly to the top of stone slabs. In both Asaccus species, some of the unfertilized eggs were also glued, while others were deposited freely on the soil substrate. The two Haemodracon species always buried fertile eggs in the substrate (Figures 14–15), while unfertilized eggs were either buried glued to pieces of decoration or simply placed on the ground. In both of the Haemodracon species, the eggshells were adhesive, and all the eggs had densely-packed substrate incrustations.



Figure 7. Hatching of A. caudivolvulus. ©Herbert Rösler



Figure 8. Hatching of *H. riebeckii*. ©Herbert Rösler



Figure 9. Hatched juveniles of *H. riebeckii* independently burrow a narrow exit from the ground. ©Herbert Rösler



Figure 10. Hatchling of *H. riebeckii*, one week old. ©Herbert Rösler



Figure 11. Hatchling of H. trachyrhinus, two days old. ©Herbert Rösler



Figure 12. Fertilized egg of A. caudivolvulus four days after oviposition. ©Herbert Rösler



Figure 13. Eggs from two females of A. montanus, from the right egg hatchling hatched. ©Herbert Rösler



Figure 14. Nest pit for a clutch of *H. riebeckii*, vertically about 5 cm deep in the ground. ©Herbert Rösler



Figure 15. Nest pit for a clutch of *H. trachyrhinus*, vertically about 2 cm deep in the ground. ©Herbert Rösler

Data analysis of reproductive characteristics: The females of the four studied species differ considerably in morphological parameters. Significant differences between them were found to be in snout-vent lengths (ANOVA, F 460.3461, p < 0.01) but not in body weight (ANOVA, F 104.7094, p > 0.05). In the snout-vent length, H. trachyrhinus does not differ significantly from A. montanus, but in all other pairwise comparisons, the species differ significantly. In body weight, only H. riebeckii differs significantly from the other three species (see supplement).

The intraspecific reproductive data clutch size, clutch volume, clutch mass, and hatching weight were used for the interspecific comparison. The results observed were related to the snout-vent length and body weight of the females. The parameters of reproduction of the four species are summarized in Table 1.

The species differ significantly in clutch size. Only single-egg clutches were produced by *A. caudivolvulus* (n=79), *A. montanus* (n=59) and *H. trachyrhinus* (n=128). *H. riebeckii* produced a total of 346 clutches. About a third of these contained one egg (33.5 %), the remaining ones had two eggs (mean clutch size 1.66 ± 0.47).

The normal distribution of the intraspecific clutch volumes was examined. The clutch volume of A. caudivolvulus and H. trachyrhinus was normally distributed; non-normal distribution was found in A. montanus and in H. riebeckii. The volumes of both clutch-sizes were also not normally distributed (see supplement). In all four species, the clutch volume was correlated with the female snout-vent length (Spearman rank correlation: A. caudivolvulus rs 0.099, A. montanus rs 0.125, H. trachyrhinus rs 0.079, and H. riebeckii single-egg clutch rs 0.069, double-egg clutch rs 0.223). The lowest value of the SVL/CV index was found in H. riebeckii for the double-egg clutches, compared to the other three species with single-egg clutches. Significantly, in H. riebeckii, the volume of eggs from the single-egg clutch is almost exactly the same as that of a single egg from a double-egg clutch (Table 1). The clutch volumes of the four species are correlated with the snout-vent length and are distributed isometrically. Interspecifically, there is an increase in egg proportions with the snout-vent length decreasing (Figure 16). As for the clutch volume, all four species differ significantly in pairwise comparisons (ANOVA, F 1560.631, p < 0.01, see supplement).

For the calculation of the relative clutch mass, the clutch weights of the four species were verified for normal distribution. The clutch weights of A. caudivolvulus, A. montanus, H. trachyrhinus, and the weight of the doubleegg clutches of H. riebeckii were normally distributed. There was no normal distribution in the case of the single-egg clutches of H. riebeckii (see supplement). In all four species, the relative clutch mass was not correlated with the weight of the females (Spearman rank correlation: A. caudivolvulus rs -0.171, A. montanus rs -0.655, H. trachyrhinus rs -0.818, and the H. riebeckii single-egg clutch rs -0.698, double-egg clutch rs -0.644). The greatest energy effort (RCM) among the four species for the development of a clutch is for H. trachyrhinus and the lowest was for H. riebeckii. H. trachyrhinus, A.caudivolvulus, and A. montanus invest more in the production of a single-egg clutch than H. riebeckii in a double- egg clutch (Figure 17). The cost saving for the development of a single egg compared to two eggs is over 50 % for H. riebeckii (Table 1). In the relative clutch mass, the pairs of species differ partially significantly (ANOVA, F 107.8593, p < 0.01). A. montanus is not significantly different from A. caudivolvulus and H. trachyrhinus (see supplement).

For the calculation of the JM/FM index, the hatch weights of the four species were checked for normal distribution. In *A. caudivolvulus* and *A. montanus*, there was a normal distribution for the hatching weight, while the hatching weights of the young animals of *H. riebeckii* from doubleegg clutches and *H. trachyrhinus* were not normally distributed (see supplement).

species	clutch volum	e (mm ³)
	single egg clutch	double egg clutch
A. caudivolvulus	911.6±129.3 (n=32)	
	647.7-1256.0	
A. montanus	263.2±90.2 (n=27)	
	197.2-689.9	
H. riebeckii	2208.4±232.5 (n=89)	4352.5±414.5 (n=157)
	1552.8-2654.0	3065.2-5277.2
H. trachyrhinus	347.3±42.0 (n=59)	
	255.1-436.8	
	clutch ma	ss (g)
	single egg clutch	double egg clutch
A. caudivolvulus	0.8309±0.1552 (n=12)	
	0.5289-1.0056	
A. montanus	0.2251±0.0178 (n=4)	
	0.2117-0.2508	
H. riebeckii	2.1645±0.2919 (n=93)	4.3632±0.3674 (n=177)
	1.4425-2.5973	3.1528-5.3779
H. trachyrhinus	0.3315±0.0474 (n=52)	
	0.2041-0.4248	
	snout-vent length/o	elutch volume
	single egg clutch	double egg clutch
A. caudivolvulus	0.077±0.011 (n=32)	
	0.055-0.107	
A. montanus	0.154±0.027 (n=27)	
	0.054-0.193	
H. riebeckii	0.050±0.006 (n=89)	0.025±0.003 (n=157)
	0.041-0.072	0.021-0.036
H. trachyrhinus	0.117±0.015 (n=59)	
	0.092-0.157	
	relative cluto	ch mass
	single egg clutch	double egg clutch
A. caudivolvulus	0.147±0.027 (n=12)	
	0.097-0.185	
A. montanus	0.171±0.026 (n=4)	
	0.137-0.200	
H. riebeckii	0.052±0.007 (n=93)	0.107±0.015 (n=178)
	0.032-0.069	0.054-0.161
H. trachyrhinus	0.179±0.050 (n=52)	
	0 079-0 262	

Table 1. Summary statistics of reproductive characteristics of A. caudivolvulus, A. montanus, H. riebeckii, and H.trachyrhinus.

juvenile mass/female mass





Figure 16. Comparisons of female SVL and CV in the *Asaccus/Haemodracon* cluster. Abbreviations: (1) = single egg clutch, (2) = double egg clutch.

The hatching weight of the young was only correlated with the weight of the females in one species (Spearman rank correlation: *A. caudivolvulus* rs 0.304). In the remaining three species, the hatching weight was not correlated with the weight of the females (Spearman rank correlation: *A. montanus* rs -0.005, *H. trachyrhinus* rs -0.321, *H. riebeckii* juveniles from single-egg clutches -0.357, juveniles from double-egg clutches -0.199). The JM/FM results largely correspond to the species-specific RCM values (Figure 18). The lightest juveniles were produced by *H. riebeckii* and the heaviest were produced by *H. trachyrhinus*.



Figure 17. Comparisons of RCM in the *Asaccus/* Haemodracon cluster. Abbreviations: (1) = single egg clutch, (2) = double egg clutch.

The young animals of all of the three species that produce single-egg clutches were relatively heavier (ANOVA, F 485.7438, p<0.01). Statistically, as expected, the JM/ FM index of the four species examined, hardly differed from the RCM values, however, there are significant differences between *H. trachyrhinus* and *A. montanus* (see supplement). In *H. riebeckii*, there is no significant difference in weight between the juveniles of the single-egg clutches (mean mass 1.3207±0.1779 g, n=31) and the doubleegg clutches (mean mass 1.3196±0.1689 g, n=187) (Man-Whitney-U-Test, z -0.0984,



Figure 18. Comparisons of JM and FM in the *Asaccus/ Haemodracon* cluster. Abbreviations: (1) = single egg clutch, (2) = double egg clutch.

p > 0.05). With successful hatching of the young animals of both clutch sizes (two vs one juvenile), the two indices JM/FM differ significantly (Whitney-U-Test, z -7.8941, p < 0.01). However, the ratio between the costs and the resulting benefits of both types of clutch sizes is assessed as neutral because *H. riebeckii* can only achieve the efficiency limit of reproduction through a proportional increase in energy expenditure.

A PCA was performed with six variables: female SVL (mm/Log10), FM (g/Log10), clutch size (one or two eggs/Log10), CV (mm³/Log10), CM (mg/Log10), and JM (mg/Log10). The PCA demonstrates that *A. montanus/H. trachyrhinus* and *A. caudivolvulus* as well as *H. riebeckii* occupy non-overlapping positions in morphospace among the collective ordination of the first two principal components (Figure 19). Principal component 1 accounts for 99.2 % of the variation and loads most heavily for FM, CV, CM and JM (Figure 20). Principal component 2 accounts for an additional 0.7 % of the variation and loads most heavily



Figure 19. PCA of the shape related reproduction specific data of four species from the *Asaccus/Haemodracon* cluster. Abbreviations: Hr = Haemodracon riebeckii, Ht = Haemodracon trachyrhinus, Ac = Asaccus caudivolvulus, Am = Asaccus montanus.

for FM, clutch size, and JM (Figure 21). Principal component 3 accounts for an additional 0.1% of the variation, respectively (Table 2). Although A. caudivolvulus, A. montanus and H. trachvrhinus do not differ significantly in clutch size, they do differ in several other characteristics. The ANOVAs of the data recovered four characters bearing statistically significant mean differences among them, illustrating that A. caudivolvulus has a significantly greater snout-vent length, and lesser RCM, SVL/CV, JM/FM than H. trachyrhinus; A. montanus has a significantly greater SVL/CV and lesser JM/FM than H. trachyrhinus respectively (see supplement). ANOVAs also demonstrated that H. riebeckii has significantly greater female SVL and FM than H. trachyrhinus, A. caudivolvulus, and A. montanus but significantly lesser RCM, SVL/CV, and JM/FM (see supplement).

The CA shows grouping compatible with PCA (Figure 22). *A. montanus* and *H. trachyrhinus* form a common cluster with a relatively small distance to *A. caudivolvulus* and were finally grouped with *H. riebeckii*.



Figure 20. PCA of *Asaccus/Haemodracon* cluster, bar plots loading scores of PC1.



clutch size

clutch volume

female mass

clutch mass

juvenile mass



0.6

0.4-0.3-

0.2-

0.0

-0.1

-0.3-

-0.5-

female SVL

Loading

Figure 22. Cluster analysis of the shape related reproduction specific data (1000 Bootstrap replicates) of four species from the *Asaccus/Haemodracon* cluster. Abbreviations: see Figure 19.

Character	PC 1	PC 2	PC 3
female SVL	0.19644	-0.14617	0.66372
FM	0.60663	0.48465	-0.13301
clutch size	0.090664	0.54657	-0.16253
CV	0.45268	-0.033226	0.5446
СМ	0.47943	-0.091452	-0.2907
JM	0.38784	-0.65996	-0.36643

Table 2. Statistics of principal component analysis scores for the reproductive characters of *A. caudivolvulus*, *A. montanus*,

 H. riebeckii, and *H. trachyrhinus*.

Discussion

Clutch sizes in the Asaccus/Haemodracon cluster: Asaccus and Haemodracon are sister genera of the family Phyllodactylidae (Gamble et al. 2008, 2012, 2015, Pyron et al. 2013). Both genera are distributed allopatrically in the Near East (Bauer et al. 1997, Sindaco and Jeremčenko 2008). It is believed that the common ancestor of the Asaccus/Haemodracon cluster lived in the Eocene further west in East Africa. although this hypothesis requires further studies (Arnold and Gardner 1994, Carranza et al., 2016, Simó-Riudalbas et al. 2018). According to (Tamar et al. 2019), Asaccus and Haemodracon separated in the middle Eocene about 42-48 Ma on the Arabian Peninsula. The speciation in Asaccus began earlier than in Haemodracon. According to the molecular mtDNA and nDNA data, the oldest Asaccus branch occurred in the Oligocene (ca. 24.6 Ma) and the youngest in the Pliocene (approx. 4 Ma), but the family tree reconstruction of Asaccus does not yet consider all species of the genus (Carranza et al. 2016). Socotra separated from the Arabian Peninsula 30-17,6 Ma ago (Autin et al. 2013). The in-situ speciation of *Haemodracon* took place in the middle Miocene about 15.5 Ma ago (Tamar et al. 2019).

In the *Asaccus/Haemodracon* cluster, both clutch sizes known from Geckos are represented (Rösler 2020). the researchers hypothetically assumed a production of double-egg clutches in the *Asaccus/ Haemodracon* ancestor and that *H. riebeckii* is the only species from the cluster which retained the plesiotypic clutch size. According to the speciation sequences in the Asaccus/ Haemodracon cluster, the clutch sizes were modified convergently. Infragenerically, the Asaccus ancestor developed single-egg clutches earlier and independently from the intraspecific H. trachyrhinus which developed these later. The alternative hypothesis, which is based on a clutch-size reduction to a single egg already secondarily acquired by the common ancestor, would mean that the diversification of the clutch size did not take place at a staggered time in the Asaccus/Haemodracon cluster, but H. riebeckii may have decreased the egg size again in order to increase the number of eggs to two. In view of the generally low tendency of clutch enlargement of single-egg producing geckos, this conversion process seems unrealistic (Rösler 2020).

The two *Asaccus* species used in this study, *A. caudivolvulus* and *A. montanus*, produced only single-egg clutches. A literature search revealed that the clutches of *A. andersoni*, *A. gallagheri*, *A. granularis*, *A. kurdistanensis*, *A. platyrhynchus* and *A. tangestanensis* also contained only a single egg (Arnold and Gardner 1994, Leptien *et al.* 1994, Torki and Sharifi 2007, Parsa *et al.* 2009, Torki 2010, Torki *et al.* 2011a, b, Gardner 2013). If the reduction of the left oviduct is a generic feature of *Asaccus*, it can be assumed that all other species of the genus, for which the clutch size is not yet known, also lay singleegg clutches only (Carranza *et al.* 2016). *Haemodracon* belongs to a larger number of genera in which a combination of invariable clutch sizes (single-egg and double-egg clutches) occurs (Rösler 2020).

Reduction of clutch size depending on snout-vent length and body weight: Numerous authors describe a variability of the clutch sizes of lizards of different development lines correlated with the snoutvent length (Fitch 1970, 1985, Tinkle et al. 1970, Turner 1977, Vitt and Congdon 1978, James and Shine 1988, Henle 1991, Shine and Greer 1991, Thompson and Pianka 2001, Du et al. 2005, Galdino and Van Sluys 2011, Kiefer et al. 2008, Winck and Rocha 2012). The ability to adjust the number of eggs and the egg size to the body size is necessary for the development of invariant clutch sizes. A prerequisite for the historical assessment of the correlation of the two parameters is that the current conditions correspond to those that were decisive for the evolution of invariant clutch sizes. This study can only speculate on whether the evolutionary reduction of snout-vent length correlated with an increase in maternal stress was the driving force, which led to the development of the invariant clutch size of two eggs in the Gekkota. However, fossil records from the Cretaceous to the late Neogen (97-5.3 Ma) support the early predisposition of small body sizes in them (Daza et al. 2014 and references cited therein). Some recent gecko species belong to the smallest landdwelling vertebrata, e.g. Sphaerodactylus ariasae, adult snout-vent length 17.9 mm, mass 0.14 g (Hedges and Thomas 2001) and S. parthenopion adult snout-vent length 17– 18 mm, mass 0.15 g (Thomas 1965, Mc Lean 1985).

From a linear order of snout-vent lengths of the geckos combined with their clutch sizes, however, it is clear that the reduction of the clutch size to a single egg cannot be explained by morphometric modifications only (Rösler 2020), if phylogenetic inertia is excluded as the cause. The latter means that the reduction of the clutch size to a minimum of one egg was acquired by a small ancestor and was then maintained by the descendants independently of an evolutionary increase in snout-vent length ('bottlenecking' hypothesis, Shine and Greer 1991, Kratochvil and Kubiska 2007). The authors do not have any valid information on the snout-vent length of the Asaccus/ Haemodracon ancestor. The snout-vent length of recent Asaccus-species (unsexed) varies between 33.6 mm (A. arnoldi) and 70.7 mm (A. gardneri) (Carranza et al. 2016, Simo-Riudalbas et al. 2018) and the mean generic SVL is $56.98 \pm 11.41 \text{ mm}$ (n=19), close to the mean of 57.55 mm calculated for recent geckos (species n=1115, Meiri 2008). The SVL of both Haemodracon species may have been influenced by the 'island effect' (Mertens 1934, Case 1978, Pregill 1986, Meiri 2007, 2008, Tamar et al. 2019). Of the Haemodracon species (unsexed), H. riebeckii reaches a maximum SVL of 140

mm (Peters 1882) and probably deviates much more from the size of the Asaccus/ Haemodracon ancestor than the smaller H. trachyrhinus with a snout-vent length with a maximum size of 50 mm (Boulenger 1899). Numerous gecko species with snout-vent length <40 mm from the genera *Cnemaspis*, Ebenavia, Lygodactylus, Matoatoa and Phelsuma are able to produce double egg clutches (Spawls et al. 2002, Branch 2005, Glaw and Vences 2007, Hallmann 2008, Grismer et al. 2014). Adult females of A. montanus and H. trachyrhinus correspond to this size range, but due to their robust physique, they are proportionally much heavier compared to the females of many other small gecko species (e.g., Ebenavia inunguis 0.55 g, Lygodactylus conraui 0.75 g, *Matoatoa brevipes* 0.75 g, own data). Despite this special type of body constitution, A. montanus and H. trachyrhinus produce only single-egg clutches instead of double-egg clutches, but this contradicts with the clutch size of many even smaller and lighter gecko species from which this would be expected. The small reproduction-specific differences (e.g., index SVL/CV, cost-benefit ratio) between the two species do not result from

the clutch size, but in the dimorphic character of female snout-vent length and female mass. This study provisionally excludes the bottleneck hypothesis (as seen above) for the development of single-egg clutches in the *Asaccus/Haemodracon* cluster. Instead, the authors assume that the diversification of the clutch size was not triggered in connection with possible evolutionary changes in body size and weight either in the common ancestral form or the ancestors of both genera, but other biotic selection factors were found to be responsible for this.

Reduction of the clutch size depending on the body shape: Morphological adaptations to the habitat can contribute to the reduction of reproductive investments, including the number of eggs (Vitt 1981). In the *Asaccus/Haemodracon* cluster, there are species with two different body shapes represented. The *Asaccus caudivulus* and both *Haemodracon* species have a voluminous-cylindrical trunk (abdomen more or less flattened) largely common in geckos. In *A. montanus*, the trunk shape is asymmetrical and dorsoventrally compressed, and the body is about three times as wide as height.

Kratochvil and Frynta (2005) found that in the hard-shelled eggs of geckos, the egg length/egg width index (EL/EW) is correlated with the SVL. The EL tends to increase with the SVL decreasing. The researchers have determined some egg proportions of different small-growing gecko species (SVL <40 mm) and compared them with the species of the Asaccus/Haemodracon cluster. The index EL/EW is for the single-egg clutch species Gonatodes fuscus 1.19 ± 0.03 (n= 9), Sphaerodactylus ruibali 1.26±0.04 (n=16), Sphaerodactylus torrei 1.28±0.06 (n=43) and for the double-egg clutch species E. inunguis 1.06±0.12 (n=23), Hemidactylus adensis 1.11±0.06 (n=14), Lepidodactylus planicaudus 1.35±0.10 (n=28), and Matoatoa brevipes 1.38±0.17 (n=6). According to the variation range of these species, the eggs of both Haemodracon species have similar egg parameters (H. riebeckii 1.25±0.07, H. trachyrhinus 1.22±0.07).

The *Asaccus* species with voluminous physique also produce more spherical to oval eggs (e.g., index EL/EW *A. caudivolvulus* 1.31, *A. kurdistanensis* 1.20, *A. nasrullahi* 1.15), while those with the dorsoventral flattened physique produce more elliptical eggs (e.g., Index EL/EW at *A. montanus* 1.58, *A. gallagheri* 1.50) (Leptien *et al.* 1994, Torki and Sharifi 2007, Torki *et al.* 2010, this study).

Regarding the cause for the infrageneric development of single-egg clutches, the study provisionally excludes a direct connection with the different body shapes Asaccus species. Probably, more of flattened body shapes developed in them only after speciation in new microhabitats, later than the previously fixed clutch size. If the volume of hard-shelled gecko eggs increases, an increase in the length of the egg is expected (Werner 1989). The hypothesis of the limited width of the pelvic aperture (Sinervo and Licht 1991a, b, Kratochvil and Frynta 2005, 2006) does not seem to account for the significantly larger egg length in relation to the egg width of some Asaccus species; however, an adaptive compromise in which the egg shape adapted to the body shape serves to produce larger offspring.

Possible reduction of the clutch size depending on the climate: Meiri et al. (2020 and references cited therein) find that due to short seasonal activity periods, combined with abundant resources. lizards produce at higher latitudes and in highly seasonal regions few clutches with relatively many eggs. On the other hand, longer reproductive periods in tropical and subtropical habitats support increased clutch production in lizards, correlated with a lower number of eggs (Tinkle et al. 1970, Andrews and Rand 1974, James and Shine 1988).

The climatic influence on clutch sizes of recent gecko species is weaker compared to other Squamata (Rösler 2020). *Gymnodactylus* is a genus common in the equatorial zone, in which the two

known clutch sizes of geckos occur. Colli et al. (2003) discuss the interrelationships between climate, food supply, reproductive periodicity, and the clutch size of two species of this genus. Gymnodactylus unpredictable amarali produces in environments cyclically double-egg clutches and G. geckoides produce in predictable environments acyclical single-egg clutches. The reproductive cycle of Homonota darwini, which is common in the southern hemisphere to reach up to 45°S, is significantly dependent on climatic conditions. In this species, vitellogenesis up to ovulation can extend to twelve months, and it produces singleegg clutches without exception, usually in a two-year cycle (Ibargüengoytía and Casalins 2007). The form of reproduction is an adaptation to boreal climates, and the survival of the species would be impossible without a low mortality in both parents and their offspring (Williams 1966, Hirshfield and Tinkle 1975, Henle 1990b).

Globally, a pronounced warming trend occurred in the Canozoic, culminating with a climate optimum on the border between the Paleocene and Eocene. After that, temperatures continued to decline throughout the Eocene (Zachos et al. 2001). Jacobs et al. 2010; and references cited therein) used macrofossils from the middle Eocene of Tanzania to conclude on forest types in an open landscape, such as those found in seasonally dry and warm climates. The authors suspect that the climatic conditions under which the Asaccus/Haemodracon ancestor lived were such, that even with strong seasonality, sufficient time was available for several clutches in one reproductive period (Meiri 2019). The early ancestral forms of Asaccus and Haemodracon were exposed to interregional climate changes. Changes in the Indian monsoon system occurred in middle and late Miocene and reached into North Africa (De Menocal 1995, Gupta and Thomas 2003, Gupta et al. 2004). Since the period, in which H. trachyrhinus changed to produce only single eggs instead of two eggs, cannot be defined more precisely, no environment-related conclusions on the

development of the single egg-clutch type are possible. Climatic factors for another life-history feature, the size diversification in the in-situ speciation of *Haemodracon*, are largely excluded by Garcia-Porta *et al.* (2016). Recently, a molecular diversification of both *Haemodracon* species during the Pleistocene was found (Tamar *et al.* 2019), but this did not affect the intraspecific clutch size.

According to the study's hypothesis, a convergently acquired ability to produce single-egg clutches the in Asaccus/ Haemodracon cluster does not correspond to epochal climatic processes. Even with a theoretically assumed regional cooling or regional contrasts (Ethiopian-Yemeni plateau to coastal lowlands) in different phases of evolution, the reduction of two eggs to a single egg would not have been directly caused by the climate (reduction of reproduction time) but may be correlated with the associated changes in other biotic factors.

Possible reduction of the clutch size depending on the predator-prey relationship: A reduction in the number of eggs contributes in general to an increase in the hatchling size of the young animals, reducing the risk of predation and mortality (Andrews and Rand 1974, Fitch 1985, Henle 1990a, Meiri 2019). It is well known that a size-dependent mortality exerts a strong selection pressure in lizards (Lacertidae see Kramer 1946, Diplodactylidae and Gekkonidae see Henle 1988, 1990b, 1991), which can be buffered by an increase in the SVL of the young. In the assessment of the life-history characteristics of the Squamata, Vitt (1981), Tinkle and Dunham (1986) and Henle (1988, 1990a) agree that grounddwelling lizards are exposed to greater predation pressure compared to tree- or rockdwelling species.

In the hatchlings of *A. caudivolvulus*, the mass is 9.9 % of that of the mother's, and in the *A. montanus*, the mass is10.8 %, while in *H. trachyrhinus*, it is11.8 %. With a similar single-egg fixed clutch size, the newly

hatched young e.g., of *Aristelliger georgensis* 3.3 % (n=2) and *Aristelliger lar* 3.4 % (n=4) are relatively lighter, but in the SVLs, they are significantly larger than the *Asaccus* and *Haemodracon* hatchlings. Based on the low RCM values, similar ratios can be expected for *Thecadactylus rapicauda* (Vitt and Zani 1997). The interspecific differences show that the risk of being eaten is lower for the young of larger species than it is for smaller species. Small species are forced to produce larger young to reduce the number of potential predators.

If predator-prey relationships are assumed to be a possible trigger mechanism for the development of single-egg clutches in the *Asaccus/Haemodracon* cluster, then the clutch size must be interpreted interspecifically, as (1) an optimal adjustment of the reproduction performance, based on the available abdominal volume of the mother, and (2) as an increase in the hatchling size of the young, which should serve to reduce size-dependent mortality.

The Irano-Arab Asaccus species have a largely montane distribution (Hadschar Mountains, Zagros Mountains) and are saxicolous (Rösler 1995, Gardner 2013, Šmid et al. 2014, Carranza et al. 2016, 2018). The present study depends on assumptions about their former way of life. A terrestrial Asaccus ancestor may have been forced to move to vertical rock surfaces due to increased predation pressure. The new locomotor requirements could then have had a counterproductive effect on pregnancy with two large eggs in the females and led to a reduction in the clutch size. The one-sided oviduct loss in Asaccus may be a consequence of this development. A left-sided regression or reduction of the paired organ is typical of Squamata (Blackburn 1998). A single egg follicle or mature egg was always found in the right oviduct of Ptenopus garrulus (Hibbits et al. 2005, Goldberg 2008). Furthermore, the researchers believe that the Asaccus ancestor already glued its eggs. The risk of predation during the search and preparation of a suitable egg storage site on the ground is greater than when laying eggs in natural crevices and cavities of vertical rock formations. However, females require less energetic cost for gluing compared to burying the eggs. The pregnant female is not forced to leave her residential area in search of a site with suitable nesting conditions to bury her eggs. Furthermore, optimal nest sites for burying eggs can be difficult to find in natural habitats.

Two characteristics presumably found in the ancestor of the Asaccus/Haemodracon, namely the production of double-egg clutches and the burial of eggs, have been preserved in the genus Haemodracon. Tamar et al. (2019) assume that the Haemodracon ancestor lived on vertical surfaces. If this hypothesis is correct, H. riebeckii has retained the original way of life (as rock- and tree-dweller) while *H. trachyrhinus* has developed into a soil dweller. As a possible scenario for the stability vs reduction of the clutch size in Haemodracon, the researchers suggest that a very strong increase in body size in H. riebeckii interacted with the growth of the egg size which explains why the resulting larger young animals could only be caught by fewer predators. This would eliminate the selection pressure to reduce the number of eggs from two to one in favour of lower mortality. H. trachyrhinus, in which the extent of diversification of the body size is likely to be less than in its sister species (Meiri 2007, 2008), was faced with an increased number of potentially dangerous predatory arthropods by entering a free ecological niche. Under island conditions, taxa usually increase the speed of change and adjustment, and in the context of low predation pressure, they quickly colonize ecological niches which were not present in their area of origin (Schluter 2000, Harmon et al. 2008, Losos and Ricklefs 2009, Tamar et al. 2019). Starting from an oligocene insular isolation of the Haemodracon ancestor and the later sympatric or allopatric Miocene speciation, the start-up effect of a fast ecological incorporation is eliminated. From a common micro-habitat (rocks, caves, crevices and cliffs) H. riebeckii with the increasing body size may have pushed the sister species H.

trachyrhinus into a horizontal microhabitat (areas with low vegetation, shrub areas) (Tamar *et al.* 2019).

The population dynamics and demographics of small soil geckos are affected by a disproportionately high mortality rate in juveniles, and this ultimately would lead to the extinction of the species. In general, the number of potentially dangerous predatory arthropods on juveniles of ground-dwelling lizards with small SVL is increased (McCormick and Polis 1982, Bauer 1990, Reyes-Olivares et al. 2020, Valdez 2020). The invertebrate fauna of Socotra is rich in species (Wranik 2000, 2003). Among them are also numerous predatory arthropods dangerous for lizards, e.g. Araneae, Scolopendridae. The researchers found that Socotra's most dangerous predator for terrestrial lizards to be Scolopendra valida occurring synoptically with *H. trachyrhinus*. The centipede is able to overwhelm and eat adult skinks (Hakaria simonyi). A strong selection pressure caused by predation-related mortality may have provoked an increase in the SVL of juveniles in H. trachyrhinus, which subsequently led to a reduction in the number of eggs in order to produce larger eggs and offspring.

Possible reduction of the clutch size depending on prey acquisition strategies and food resources: Ecological niche models have different food web structures (Williams and Martinez 2000, Woodward and Hildrew 2002). Various studies on resource use patterns have shown that animals normally have a proportionality of body size and prey size (Warren and Lawton 1987, Fisher and Dickman 1993, Moen and Wiens 2009, Alcantara et al. 2019). Cocilio et al. (2016) described the ontogenetic variation of the food composition of Homonota fasciata. The food spectrum of the adult specimens included fourteen different species of arthropods, compared to only five of juveniles. Transformations of prey acquisition strategies, changes in activity patterns and new micro-habitats are closely linked to changes in food resources. Niche diversity, coupled with specifically and

ontogenetically different dietary preferences, can, in a limited or absence of supply of size-specifically adapted prey species in certain habitats, force animals to produce larger young, which provides a better chance of survival in the interspecific competition for small food animals.

The Asaccus/Haemodracon complex includes species of different microhabitats and activity patterns. The two Asaccus species are saxicolous, H. riebeckii saxicolous and arboricolous and H. trachyrhinus terricolous; the first three species are cathemeral and the latter nocturnal (Rösler and Wranik 2005, Gardner 2013, Tamar et al. 2019). All four species are insectivore (Weber 1960, Torki and Sharifi 2007, Torki et al. 2010, 2011a, Martin et al. 2017). Only H. riebeckii is additionally frugivorous and herbivorous (Rösler and Wranik 2007). Furthermore, all four species are cannibalistic and differ in their preying strategies. H. trachyrhinus is a more active forager when seeking food (Schätti and Desvoignes 1999, Martin et al. 2017), while the other three species use a sit-and-wait strategy. The average energyproduction cost per clutch (based on RCM values) for the sit-and-wait predators is higher (25%) than that of the search hunters (18%)as measured by Dunham et al. (1988) and is not detectable in the Asaccus/Haemodracon complex (see also Vitt and Congdon 1978). H. trachyrhinus has an effort of 18 %, A. montanus 17 %, A. caudivolvulus 15 % and H. riebeckii 11 %.

Interspecifically, contrasting trophic niches can be assumed in Asaccus and Haemodracon. The researchers assume that Asaccus sp. and H. riebeckii are dependent on a high percentage of food introduced via the air (Torki and Sharifi 2007, Torki et al. 2011b and own observations). A. montanus can catch prey up to the size of ant maids (myrmeleontid, wing lengths >40 mm, B.M. Zwanzig personal communication). The food composition of H. riebeckii and H. trachyrhinus (Martin et al. 2017) differs according to the different habitats and hunting strategies. Normally, the larger young ones eat large prey species, but also do not despise the tiny species of arthropods. The smaller young ones are dependent on a size-specific adapted and sufficiently large prey potential. The proportion of the available prey is extended by the size of the young of *H. riebeckii* and is being more limited in *H. trachyrhinus*. In addition to the intraspecific predation-related mortality, *H. trachyrhinus* may also have been forced to develop individual large eggs if the death rate of the too small juveniles increased as a result of too few adequate prey potentials in its microhabitat.

Reproductive-specific effects of clutch-size

reduction: *Haemodracon riebeckii* is the only species of the *Asaccus/Haemodracon* complex with a variable clutch size, wherein the percentage of double-egg clutches produced in the course of an egg-laying season predominates (as seen above).

If the abdominal volume of the female is assumed as a limiting factor for the maximum clutch volume (Shine 1992), then more abdominal space is available in the vitellogenesis of one instead of two eggs. A theoretically resulting possible egg enlargement did not occur in H. riebeckii. The average of the egg volume from singleegg clutches is 2212±228 (n=96), while in the eggs from the double-egg clutches, it is 2175 ± 259 (n=337). The volumes of the eggs of both clutch sizes do not differ significantly (Mann-Whitney-U-Test, z -1.8933, p >0.05). This means that in the vitellogenesis of an egg (whether in the right or left oviduct), no unilaterally disproportionate expansion of the oviduct occurs, which corresponds to the results in other gecko species (Kubička and Kratochvil 2009, Weiser et al. 2012 and references cited therein).

In the species of the genus *Tarentola* from the Canary Islands and the Cape Verde Islands, alternating clutch sizes are also found (Nettmann and Rykena 1985, Hielen 1993). The researchers collected and statistically analyzed reproduction data from *T. nicolauensis* in captivity and found that 47.1 % of the clutches contained a single egg (mean clutch size 1.27 ± 0.45 , n=51). The volume of the eggs from single-egg clutches is 1339 ± 196 (n=26) while in the eggs from double-egg clutches, it is 1039 ± 139 (n=24). The egg volume of both clutch sizes differs significantly (Mann-Whitney-U-Test, z -4.6902, p < 0.01). Similar results apply to *Tarentola angustimentalis*, *T. delalandii* and *T. rudis* (Hielen 1991, Rösler 2020).

Tarentola nicolauensis is scansorial and lives on gravel plains with granular substrate (Wranik and Rösler 2007). The eggs from the single-egg clutches of T. nicolauensis are larger and heavier than those of H. riebeckii. The reason for the positive allometric enlargement of the eggs of single-egg clutches in T. nicolauensis could be intraspecific competition. Larger juveniles are able to build food territories faster and to be more effective in resource competition (Nettmann and Rykena 1985). The tendency to enlarge single eggs could be a stage of development, which ultimately results in the relative increase in costs in the development process of invariant single-egg clutches in geckos (see below). The affine egg dimensions in both clutch sizes of H. riebeckii, on the other hand, are conservative. Lower intraspecific competition may have reduced intraspecific selection pressure to produce larger eggs and juveniles, or the egg conformity of the two types of clutches is fixed in the way of life as rock- and tree-dwellers (Andrews and Rand 1974, Shine et al. 1998, Schwarz and Meiri 2017, Meiri et al. 2020).

In the evolutionary process of reduction from two eggs to a single egg per clutch, geckos have applied different strategies, their results can be interpreted by comparing the egg dimensions proportional to the SVL, RCM, or other parameters. For the time being, the eggs from single-egg clutches are placed interspecifically into two weight classes. A small group of specialized arboricol taxa miniaturized the total clutch mass (as seen above Aristelliger and Thecadactylus), probably like the Dactyloidae for reasons of reducing the physical reproduction stress of females in difficult habitats (Kratochvil and Kubička 2007 and references cited therein). The opposite strategy, an increase in total

clutch mass combined with the development of single-egg clutches, includes the second, larger group of gekkonid taxa. This strategy compensates for a lower reproduction rate by more competitive offspring. This work concludes that the growth limitation of the egg size in the double-egg clutches of geckos is primarily regulated by the maximum available abdominal volume of the female and secondly by the pelvic opening, while for the proportionally larger eggs from the single-egg clutches, mainly, the width of the pelvic passage is the decisive factor.

The single-egg-producing species of the *Asaccus/Haemodracon* complex belong to the group of egg-enlargement strategists. Interspecifically, subtle differences can be observed within this group, which are noticeable in the correlation of egg volume and egg mass to the female size and female weight. *A. montanus* produces eggs that are relatively larger than *H. trachyrhinus;* intraspecifically reversed, the eggs of the former are relatively lighter than the latter, but how to explain this discrepancy?

It is assumed that both species have adjusted the resource investment per clutch in an equilibrium ratio (used maternal resource to offspring fitness). Cox and Calsbeek (2009) have experimentally shown that the locomotor abilities (endurance, speed) of productive (gravid) Anolis females measurably deteriorate compared to unproductive ones, even if they only carry a single small egg. This effect increases exponentially with an increase in egg proportions. Compared to the tree- and branch-dwelling Anolis species with low RCMs (0.051-0.128, medium 0.074±0.024, n=10) (Andrews and Rand 1974, Ramirez-Batista and Vitt 1997, Ramirez-Batista 2003, Vitt and Zani 2005, Johnson et al. 2010), the rock-dwelling Anolis montanus has enlarged its eggs but is inferior in direct proportional comparison to H. trachyrhinus in the RCM (Table 1). A. montanus and H. trachyrhinus are scansorial and have morphologically similar toe structures (Gamble et al. 2012) but inhabit various ecological niches. A plausible explanation for the inter-specific differing RCMs would be a relation to ecological parameters. In addition to predation intensity and food availability (as seen above), staying on vertical surfaces correlated with the fitness of pregnant females could allow a regulated increase in egg size, while in gravid females on horizontal surfaces, it depends on other parameters (e.g., pelvis passage). The theory, however, has a caveat. It cannot be applied to geckos in general. Relatively higher RCM values can also reach small-growing rock-living species (e.g., Pristurus cf. rupestris 0.217±0.020, n=14) and comparatively larger ground-dwelling can also reach relatively lower values (e.g., *Homonota horrida* 0.124±0.022, n=5). Probably, several mutually influencing factors are responsible for the interspecific differences in the modification of the relative clutch mass.

Conclusion

To sum up, this work concludes that the Asaccus/Haemodracon ancestor produced double-egg clutches and the species of both genera reduced their clutches convergently to a single egg. The aim of the present study is to investigate which earlier selective forces led to the development of single-egg clutches. In the comparison of ancestral and derived reproductive traits, the researchers reconstructed relationships have with predation risk and food acquisition as biotic selection factors for the allometries of clutch size. This work concludes that Asaccus and Haemodracon possibly independently developed single-egg clutches for various reasons. The authors are aware that the analysis only considers part of the functional feedbacks for the evolutionarily eligible miniaturized clutch size in the Asaccus/ Haemodracon cluster, but they do believe it will offer approaches for further research into the developmental phenomenon of invariant single-egg clutches within the Gekkota.

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Supplement

Summary of statistics of the normal distribution tests of *Asaccus/Haemodracon* cluster. Shaded cells are those characters bearing significantly different means p < 0.05.

character, species	W	р			
clutch volume					
A. caudivolvulus	0.97687	0.70489			
A. montanus	0.49373	0.00000			
H. riebeckii (single egg clutch)	0.96665	0.02173			
H. riebeckii (double egg clutch)	0.96263	0.00030			
H. trachyrhinus	0.98914	0.87775			
clutch mass					
A. caudivolvulus	0.91213	0.22715			
A. montanus	0.95091	0.74763			
H. riebeckii (single egg clutch)	0.94816	0.00129			
H. riebeckii (double egg clutch)	0.98756	0.12079			
H. trachyrhinus	0.97156	0.18974			
hatchling weight					
A. caudivolvulus	0.97956	0.89861			
A. montanus	0.96201	0.18488			
H. riebeckii (single egg clutch)	0.96467	0.38547			
H. riebeckii (double egg clutch)	0.97379	0.00138			
H. trachyrhinus	0.94535	0.00577			

Summary of statistics of Tukey HSD results for the reproductive characters of Asaccus/Haemodracon cluster.

snout-vent length					
	H. riebeckii	H. trachyrhinus	A. caudivolvulus	A. montanus	
H. riebeckii	-	** p<0.01	** p<0.01	** p<0.01	e
H. trachyrhinus	0.0010053	-	** p<0.01	insignificant	ey D rrfen
A. caudivolvulus	0.0010053	0.0010053	-	** p<0.01	Tuk HSI infe
A. montanus	0.0010053	0.6923274	0.0010053	-	
		Tukey HS	SD p-value		
female mass					-
	H. riebeckii	H. trachyrhinus	A. caudivolvulus	A. montanus	
H. riebeckii	-	** p<0.01	** p<0.01	** p<0.01	Se
H. trachyrhinus	0.0010053	-	insignificant	insignificant	.ey D rrfeno
A. caudivolvulus	0.0010053	0.7234100	-	insignificant	Tuk HSI infe
A. montanus	0.0010053	0.8999947	0.6725777	-	
		Tukey HS	SD p-value		
snout-vent length/	clutch volume				-
	H. riebeckii	H. trachyrhinus	A. caudivolvulus	A. montanus	
H. riebeckii	-	** p<0.01	** p<0.01	** p<0.01	Se
H. trachyrhinus	0.0010053	-	** p<0.01	** p<0.01	cey D srfeno
A. caudivolvulus	0.0010053	0.0010053	-	** p<0.01	Tuk HSI infe
A. montanus	0.0010053	0.0010053	0.0010053	-	

_		Tukey HSD p-value			_
relative clutch mass					
	H. riebeckii	H. trachyrhinus	A. caudivolvulus	A. montanus	
H. riebeckii	-	** p<0.01	** p<0.01	** p<0.01	e
H. trachyrhinus	0.0010053	-	** p<0.01	insignificant	ey Tfen
A. caudivolvulus	0.0010053	0.0011277	-	insignificant	Tuk HSI infe
A. montanus	0.0010053	0.8999947	0.3742620	-	
_		Tukey HS	SD p-value		_
juvenile mass/female mass					
	H. riebeckii	H. trachyrhinus	A. caudivolvulus	A. montanus	
H. riebeckii	-	** p<0.01	** p<0.01	** p<0.01	e
H. trachyrhinus	0.0010053	-	** p<0.01	* p<0.05	cey D srfen
A. caudivolvulus	0.0010053	0.0010053	-	insignificant	Tuk HS infe
A. montanus	0.0010053	0.0269861	0.3279569	-	
Tukey HSD p-value					