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Ecology of a gecko assemblage (Phyllodactylidae: Squamata) from northern Peru

Janina AURICH*, Claudia KOCH and Wolfgang BÖHME

Zoologisches Forschungsmuseum Alexander Koenig, Adenauerallee 160, 53113 Bonn, Germany
*Corresponding author: J. Aurich, Email: janinaaurich@gmx.de

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Abstract. The ecology of four phyllodactylid geckos, three of them only recently discovered, viz. *Phyllopezus maranjonensis, Phyllodactylus delsolari, Phyllodactylus thompsoni* and *Phyllodactylus reissii,* was studied in a northern interandean basin of Peru. *P. maranjonensis* and *P. delsolari* were almost always encountered together and were exclusively found on rock faces; *P. thompsoni* was found in various microhabitats and coexisted with all three other species; *P. reissii* was rarely found and only in one locality on the walls of an abandoned house, coexisting solely with *P. thompsoni.* All species fed on arthropods with isopods, coleopterans and insect larvae dominating their diet, numerically. Stones and eggshells could be found in the stomachs of gravid *P. maranjonensis* females. Dietary niche breadth values for all species are well above 1 and similar. Dietary niche overlap among all species is low, except for *P. delsolari* and *P. reissii,* which might be associated with the low abundance of *P. reissii* in this area. Niche overlap among *P. maranjonensis* and *P. delsolari* was low and probably makes their coexistence possible, despite their remarkable size.

Key words: *Phyllodactylus delsolari, P. reissii, P. thompsoni, Phyllopezus maranjonensis,* equatorial dry forest, Marañon valley, microhabitat, natural history, sympatry, ecological relationship, niche overlap, diet.

Introduction

Peru has a high degree of biotic diversity due to its extreme topographic variation and its numerous ecosystems. According to Rodriguez (1996) only 60% of Peru's habitat has been herpetologically investigated. As study into previously neglected areas expands, the number of newly described species is increasing constantly. Three of the species which are the subject of this ecological study, *Phyllopezus maranjonensis* Koch, Venegas & Böhme 2006, *Phyllodactylus delsolari* and *Phyllodactylus thompsoni* Venegas, Townsend, Koch & Böhme 2008, have been recently described. They all occur in the Balsas region in a northern interandean basin along with their congener, *P. reissii,* which has been described by Peters in 1862. The latest analysis of phylogenetic relationships among gekkotan lizards revealed that the four geckos studied herein belong to the family Phyllodactylidae, a monophyletic trans-Atlantic gecko clade (Gamble et al. 2008).

Ecological and natural history studies are of great importance, as they can provide useful data on the evolution of important biological phenomena. Nonetheless, basic ecological and natural history data are lacking for most amphibians and reptiles and might never be accessible due to constant habitat and species loss all over the world (Vitt et al. 2003, Greene 1986 & Greene 1994). This justifies and makes ecological, behavioral and natural history studies more than necessary, to get a basic knowledge about species and to enable their conservation.

In this study the ecological relationship among the four gecko species *Phyllopezus maranjonensis, Phyllodactylus delsolari, Phyllodactylus thompsoni* and *Phyllodactylus reissii* is investigated and described. The three former species are so far known from the upper Marañon valley, from their type locality in the Balsas region (Koch 2006 & 2008, Koch et al. 2006 & Venegas et al. 2008) to 130 km upstream (Koch & Beraún 2011). *P. reissii* is known from southern Ecuador and north-western Peru (Dixon & Huey 1970) and inhabits various ecosystems like the coastal desert of Peru, the equatorial dry forest and the Pacific tropical forest (Dixon & Huey 1970, Jordán 2006).

The species *P. delsolari* and *P. reissii* can reach a similar, quite remarkable size (SVL: 81 mm and 75 mm; respectively) and *P. maranjonensis* even exceeds this size (SVL: 115 mm). It is currently the third largest gecko species of South America. According to Dixon & Huey (1970) sympatry among two *Phyllodactylus* species is sustainable if the size distribution differs markedly. Here, three large geckos are coexistent and a high competition among them is likely. A focused investigation of this unique ecological assemblage was expressed by Venegas et al. (2008).

The present study should provide some insight into the complex ecological relationship among these four gecko species. Habitat and microhabitat are described and a quantitative dietary analysis is conducted. Niche breadth and niche overlap are calculated, to gain evidence on the extent of food competition among these four species.

Materials and Methods

The four gecko species were studied in the region of Balsas (6°49'S, 78°00'W), Peru during two time periods (03/26/2010 – 04/18/2010 and 05/20/2010 – 05/29/2010). Six localities around Balsas were selected, each of which was visited four times during the first field trip and two times during the second field trip. Temperature and humidity were measured each day at approximately 3 pm and at night at approximately 7 pm, before each night's field survey.

Due to the geckos' natural period of nocturnal activity, monitoring and collecting of specimens was conducted from after sunset (approx. 7 pm) until midnight or shortly after midnight (not later than 2 am). Headlights (Silva and Petzl) were used to locate animals on rock faces, walls, in crevices of rocks or walls and between shrubs. Geckos were caught manually by grabbing them between their head and forelegs.

Each specimen was sexed and measured with respect to its snout-vent length (SVL), head length, head width, forelimb length, hind limb length and tail length (tape measure, to 1mm). Total mass was taken with a precision spring balance (Pesola) to 0.5 g. For most captured lizards, data on surrounding habitat, microhabitat and vegetation, height on the rock surface and behavior before and during capture were recorded. Geckos not used for further analyses were marked by means of a waterproof marker and set free.

Animals used for dietary analysis were taken to the field station for euthanization and fixation. To guarantee that the stomach contents were little digested and in good condition for identification, specimens were killed the following morning, not later than 10 hours after their capture, by an injection of the veterinary anesthetic T61. To achieve the best possible fixation, 10% formalin was injected into the specimens' abdomen, tail and hind legs. They were then stored in 10% formalin for 24 to 48 hours, until they could be moved to 70% ethanol for preservation.

In the laboratory, the geckos' stomachs were removed and dissected. The percentage of empty stomachs within each species was determined. The contents of full stomachs were spread on a Petri dish and prey items of each stomach were separated and counted. Each prey item was identified to the level of order when possible. All items were grouped into 17 categories.

Prey items that were well preserved, were measured by length and width by means of a digital caliper. These data were used to calculate the volume of individual prey items with the formula for a prolate spheroid according to Lima et al. (2010):

$$V = 4/3\pi \,(\text{length}/2)(\text{width}/2)^2$$

To determine a size difference between the prey items eaten by the four different gecko species, a Kruskal-Wallis test was used with all variables ($P < 0.05$). A highly significant result allows a further stepwise discriminate analysis by means of a Mann-Whitney U test ($P < 0.05$). All statistical analyses were performed by PASW Statistics 18.

To quantify the resources used by each species, niche breadth was calculated using the inverse of Simpson's (1949) measure:

$$\beta = \frac{1}{\sum_{i=1}^{n} P_i^2}$$

where P is the proportional utilization of each prey type i for a total of n categories (Nentwig et al. 2009). Niche breadth values (β) vary from 1 (exclusive use of a single prey type, specialist) to n (even use of all prey, generalist).

Niche overlap was calculated using the similarity index (Pianka 1973) according to Montechiaro et al. 2011:

$$\frac{\sum_{i=1}^{n} P_{ij} P_{ik}}{\sqrt{\sum_{i=1}^{n} P_{ij}^2 \sum_{i=1}^{n} P_{ik}^2}}$$

where j and k represent the two species of which the overlap should be computed and P is the proportional utilization of each prey type i. Values for niche overlap vary from zero (no overlap) to one (complete overlap).

Voucher specimens of all lizards used in this study are stored in 70% ethanol and housed in the herpetology collections of the Zoologisches Forschungsmuseum Alexander Koenig (ZFMK) in Bonn, Germany and in the Centro de Ornitologia y Biodiversidad (CORBIDI) in Lima, Peru.

Results

<u>General Ecology</u>

All species were found active between 19.00 and midnight, at temperatures from 19.1 to 32.1 °C and humidity between 32 and 80%. One individual of *Phyllodactylus thompsoni* was observed active at 06.00, shortly after sunrise.

The two large geckos *Phyllopezus maranjonensis* (max SVL 115 mm) and *Phyllodactylus delsolari* (max SVL 81 mm) were encountered together in all localities. They were almost exclusively found on exposed rock faces. *P. maranjonensis* was usually observed in open spaces, without any surrounding vegetation, whereas *P. delsolari* was more often found near, or hidden beneath, vegetation. No *P. maranjonensis* were observed on the ground and only three *P. delsolari* were running over the ground when sighted. Both species have a similar color pattern with a grayish ground color and darker dorsal transverse bands, which makes them difficult to detect in their surroundings.

Geckos of both species were distributed over all heights of the rock faces (Fig. 1). A couple of individuals of *P. maranjonensis* were observed at heights above 4 m, where it was impossible to catch them. Animals of this species were generally observed individually, with no other specimens nearby. During the entire study period a total of 120 *P. maranjonensis* and 107 *P. delsolari* were observed in the investigated areas, indicating that both species were quite common and occurred in comparable abundance. In contrast, only 21 individuals of *Phyllodactylus reissii,* another large gecko (max SVL 75 mm) were found. They were observed almost exclusively in just one of the studied localities: an abandoned house, where they occupied its walls and hid in its crevices. They occurred together only with *P. thompsoni.* Three of the 19 *P. reissii* were found on a nearby coarse stone wall. Due to the height of the house walls, geckos of this species were not found more than 3 m above the ground.

Phyllodactylus thompsoni is the smallest (max SVL 42 mm) and most abundant species in this area (292 specimens observed). It was found in all localities, occurring alongside all other species. It is ubiquitous and was observed in different microhabitats: on rock faces, ground dwelling in sandy and rocky surroundings, between shrubs and grass, on tree and cactus trunks, on house and stone walls and in their crevices. More than half of the observed individuals (54.9 %) were running over the ground or sat at the base of rock faces, walls or tree trunks, less than 1 m off the ground (Fig. 1). With its grey-yellowish ground color and the dark blotches on its dorsum, *P. thompsoni* is difficult to see in its surroundings.

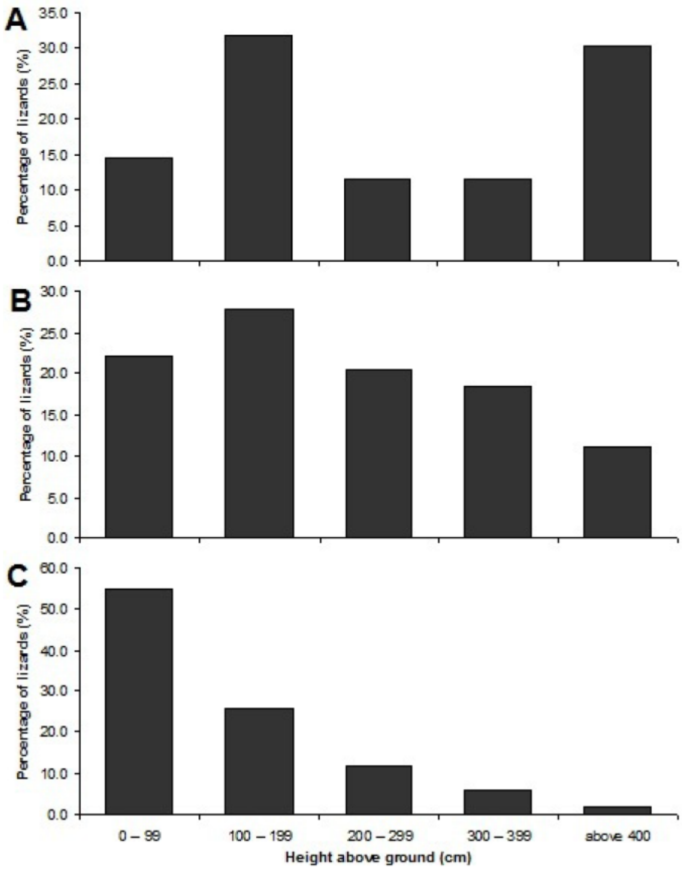

Figure 1. Height above ground when first sighted of **a)** *Phyllopezus maranjonensis,* **b)** *Phyllodactylus delsolari* and **c)** *Phyllodactylus thompsoni.*

Diet

For the stomach analyses, 21 specimens were used for each of the species *Phyllopezus maranjonensis, Phyllodactylus delsolari* and *Phyllodactylus thompsoni* and only 8 of the species *Phyllodactylus reissii*. The stomach content observation showed that 23.8% of the examined *P. maranjonensis*, 14.3% of *P. delsolari*, and 9.5% of *P. thompsoni* had empty stomachs, whereas all *P. reissii* contained prey items. The diet of these four species is exclusively composed of arthropods, although some other material was found in the stomachs. Stones and eggshells were present in 3 stomachs of *Phyllopezus maranjonensis* and 2 stomachs contained plant material, matter which was also found in one stomach of *Phyllodactylus thompsoni*. Shed skin, which was consumed by the geckos after molting, was found in one stomach of each *P. maranjonensis* and *P. thompsoni* and in two stomachs of *P. delsolari*. None of the stomachs of *P. reissii* contained material other than arthropods.

A total of 68 objects were found in the stomachs of *Phyllopezus maranjonensis*, whereas only 46 of those were prey items (the others were stones, egg shells etc.). The number of prey items per stomach varied between one and 14, with an average of 3.2 (1SD: 3.4). Numerically, isopods accounted for the largest part of the diet of *P. maranjonensis* with 19.1%, followed by the coleopterans with 11.76%. Since one gecko swallowed 16 small stones, they actually accounted for the majority (26.5%) of the diet, but were not further considered in the evaluation (Tab. 1).

Due to advanced digestion, only 43.5% of the prey items of *P. maranjonensis* could be measured for width and length. These averaged 4.5 mm (1SD: 2.1) (2.0 to 8.5 mm) in width, 11.4 mm (1SD: 10.2) (4.4 to 52.2 mm) in length and 185.4 mm^3 (1SD: 274.5) (10.7 to 1119.5 mm^3) in volume. As it was not possible to measure more prey items and calculate their volume, no volumetric analyses were performed.

The stomachs of *Phyllodactylus delsolari* contained 45 prey items in total. The number of prey items in each stomach varied from 1 to 6 and averaged 2.5 (1SD: 1.5). Coleopterans dominated the diet of *P. delsolari* numerically by 35.6%, followed by lepidopterans and orthopterans each with

Table 1. Diet of 16 *P. maranjonensis*, 18 *P. delsolari*, 19 *P. thompsoni* and 8 *P. reissii* from Balsas, Peru. No: Number of prey items in each category; %No: Number of prey items in each category, divided by the total number of prey items, multiplied by 100; Freq: Number of lizards that ate a particular prey type. Skin, vegetative material, stones, egg shells, etc. were combined in category "Other".

Diet category	Gecko species											
	P. maranjonensis			*P. delsolari*			*P. thompsoni*			*P. reissii*		
	No	%No	Freq	No	%No	Freq	No	%No	Freq	No	%No	Freq
Crustacea												
Isopoda	13	19.12	2	1	2.22	1	2	5.13	2	1	5	1
Myriapoda												
Chilopoda	4	5.88	4	1	2.22	1	1	2.56	1	-	-	-
Arachnida												
Araneae	7	10.29	6	2	4.44	2	2	5.13	2	3	15	3
Scorpiones	1	1.47	1	2	4.44	2	-	-	-	1	5	1
Acari	-	-	-	1	2.22	1	-	-	-	-	-	-
Insecta												
Formicidae	1	1.47	1	-	-	-	4	10.26	1	-	-	-
Other Hymenoptera	-	-	-	1	2.22	1	-	-	-	1	5	1
Coleoptera	8	11.76	7	16	35.56	10	1	2.56	1	8	40	4
Isoptera	1	1.47	1	-	-	-	-	-	-	-	-	-
Heteroptera	1	1.47	1	2	4.44	2	-	-	-	-	-	-
Auchenorrhyncha	1	1.47	1	-	-	-	8	20.51	5	-	-	-
Diptera	-	-	-	1	2.22	1	1	2.56	1	-	-	-
Lepidoptera	3	4.41	3	5	11.11	3	2	5.13	2	1	5	1
Orthoptera	4	5.88	4	5	11.11	5	4	10.26	4	3	15	3
All insect larvae	1	1.47	1	4	8.89	3	9	23.08	6	2	10	2
Unidentified arthropods	1	1.47	1	2	4.44	2	3	7.69	3	-	-	-
Other	22	32.35	6	2	4.44	2	2	5.13	2	-	-	-
Total	68	100.0		45	100.0		39	100.0		20	100.0	
Niche breadth		6.98			5.86			7.41			4.44	

11.11% (Tab. 1). Twenty prey items (44.4%) were measured by width and length and their volume was estimated. They averaged 8.9 mm (1SD: 7.3) (2.5 to 31.5 mm) in length, 2.1 mm (1SD: 0.8) (1.1 to 3.6 mm) in width and 28.6 mm³ (1SD: 30.5) (2.0 to 105.2 mm³) in volume. One captured *Phyllodactylus delsolari* disgorged a complete, recently consumed prey item, identified as a centipede (Chilopoda), of the genus *Scolopendra* (Fig. 2) which measured approximately 6 cm in length.

The stomachs of *Phyllodactylus reissii* held 20 prey items in total. Prey item number per stomach varied between 1 and 6, with an average of 2.5 (1SD: 1.8). Numerically, coleopterans dominated the diet of *P. reissii*. This prey category contributed 40% to this species' diet (Tab. 1). Eight prey items (40 %) could be measured by width and length and averaged 14.3 mm (1SD: 8.8) (2.5 to 28.5 mm) in length, 3.9 mm (1SD: 2.3) (1.0 to 8.3 mm) in width and 201.5 mm³ (1SD: 242.5) (1.3 to 707.0 mm³) in volume.

Thirty-nine prey items were counted in the stomachs of *Phyllodactylus thompsoni*. The number of items per stomach varied between 1 and 5 and averaged 2.2 (1SD: 1.2). Insect larvae (not divided by order) accounted for the largest part of this species with 23.08 %, followed by Auchenorrhyncha with 20.51% (Tab. 1). It was possible to measure 16 prey items (41%) which averaged 6.1 mm (1SD: 5.3) (1.2 to 19.9 mm) in length, 1.4 mm (1SD: 0.6) (0.4 to 2.4 mm) in width and 9.2 mm³ (1SD: 10.4) (0.1 to 35.2 mm³) in volume.

Numerical niche breadth for all four gecko species is similar (Tab. 1) and suggests that none of them is a specialist. *Phyllodactylus reissii* had the lowest niche breadth with a value of 4.44 and used 8 of 15 prey categories (excluding "Other" from Tab. 1). The other three species used the categories more evenly. *Phyllopezus maranjonensis* and *Phyllodactylus delsolari* exploit all categories except for 3 each (Acari, other Hymenoptera, Diptera and Formicidae, Isoptera, Auchenorrhnycha, respectively) and their niche breadth values are 6.98 and 5.86, respectively. *Phyllodactylus thompsoni* had the highest niche breadth with a value of 7.41 and used 10 of 15 categories.

Niche overlap between the four species is relatively low, except between *P. delsolari* and *P. reissii* with a high overlap value of 0.95. The lowest niche overlap value of 0.28 is between *P. maranjonensis* and *P. thompsoni*. Overlap values for all other species combinations vary from 0.30 to 0.48 (Tab. 2).

Prey size distribution differs significantly among those four species (Kruskal-Wallis Test, P = 0.000), with larger species eating larger prey, except for *P. maranjonensis* and *P. reissii* (Mann-Whitney U Test, Z = -0.203, P = 0.839), where prey size is not significantly different. However, prey items eaten by *P. maranjonensis* are significantly larger than those consumed by *P. delsolari* (Mann-Whitney U Test, Z = 3.400, P = 0.001) and *P. thompsoni* (Mann-Whitney U Test, Z = -4.521, P = 0.000). *P. thompsoni* consumed significantly smaller prey than *P. delsolari* (Mann-Whitney U Test, Z = -2.395, P = 0.017) and *P. reissii* (Mann-Whitney U Test, Z = -2.817, P = 0.005). Although *P. delsolari* and *P. reissii* are similar in size, the latter consumed significantly larger prey (Mann-Whitney U Test, Z = -2.111, P = 0.035).

Discussion

As already known for *Phyllodactylus reissii*, its primary habitat is formed by arid, tropical scrub regions in the west of the Andes and cacti-dominated regions in northern interandean basins of Peru (Goldberg 2007, Dixon & Huey 1970). Balsas is situated in a northern interandean valley of Peru and represents the described habitat. The other three investigated species *Phyllopezus maranjonensis, Phyllodactylus delsolari* and *P. thompsoni* were found in parts of the upper Marañon valley, from Balsas to 130 km upstream. This arid cacti-dominated land is part of the equatorial dry forest and can be considered as the primary habitat of these three geckos.

Apart from *Phyllopezus maranjonensis* and *Phyllodactylus delsolari,* the four studied species apparently choose different kinds of microhabitat. Whereas *P. thompsoni* was found in various microhabitats, the other species seem to specialize on one microhabitat. Although Carrillo de Espinoza (1990) and Schlueter (2002) noted that *P. reissii* occupies various vertical microhabitats like tree and cactus trunks, house walls and rock faces, the species could almost always be found on house walls in this area. *P. maranjonensis* was exclusively found on rock faces as well as *P. delsolari* in general. Although both are large species, they were almost always coexisting in all localities.

According to two characterizations by Dixon & Huey (1970), sympatry among two *Phyllodactylus* species is rather unlikely if those two species do not differ markedly in size or arboreality. Although *Phyllopezus maranjonensis* comes from

Figure 2. *Scolopendra* sp. disgorged by *P. delsolari* after its capture.

Table 2. Dietary niche overlap among the four species.

Species	*P. delsolari*	*P. thompsoni*	*P. reissii*
P. maranjonensis	0.435	0.276	0.483
P. delsolari	-	0.368	0.947
P. thompsoni	-	-	0.301

another genus, coexistence with *Phyllodactylus delsolari* seems exceptional, since they do not conform to either of the characterizations, and intense competition must be present.

Despite the ecological similarity of these two species, coexistence probably becomes possible due to differences in their diet. First, *P. maranjonensis* consumes significantly larger prey than *P. delsolari,* and second, they seem to prefer different prey categories, since their dietary overlap is relatively low (0.435). Both species are hardly specialized concerning their prey and exploit a lot of different prey categories within the arthropods. According to Pianka & Pianka (1976) species with more generalized requirements tend to have higher niche overlaps, accompanied by higher reproduction success than more specialized species.

This statement seems to be confirmed by the gecko assemblage of the Balsas region. Both, *Phyllopezus maranjonensis* and *Phyllodactylus delsolari,* have a relatively high niche breadth concerning their diet (6.98 and 5.86, respectively), but a specialization on one microhabitat is apparent. Both species are quite abundant in the area, but not as abundant as *Phyllodactylus thompsoni*. This species is the one with the most generalized requirements, which is obvious by its high dietary niche breadth (7.41) and the equal use of various microhabitats. In contrast, *Phyllodactylus reissii* was the least abundant species with the most specialized requirements, apparent by its low dietary niche breadth (4.44) and its microhabitat specialization.

Since the number of observed *P. reissii* is so low, all calculated values and analyses are rather vague. Nonetheless, some conclusions can be made. The low abundance of *P. reissii* in the Balsas region might result from dietary similarities with *Phyllodactylus delsolari* and *Phyllopezus maranjonensis.* Niche overlap with the former species is high, almost complete (0.947), and prey size distribution does not differ significantly with respect to latter species and *P. reissii.* Thus, this species is probably not able to compete with the other large species in the Balsas region.

The ecological relationship among *Phyllodactylus thompsoni* and the three large geckos conforms to both characterizations by Dixon & Huey (1970) (see above). Additionally, dietary niche overlap between *P. thompsoni* and the other species is relatively low and prey size distribution differs significantly, with *P. thompsoni* eating smaller prey than all others. All these factors make coexistence of *P. thompsoni* with each of the large species feasible.

Pianka & Pianka (1976) stated that apparently species with specialized feeding habits tend to have empty stomachs more often than generalized feeders. Despite the general feeding habits of *Phyllopezus maranjonensis,* the percentage of individuals that ran on empty seems rather high (23.8% of 21). Even so, this value is just slightly higher than the average of 21.2% which was estimated by Huey et al. (2001) for nocturnal geckos. In general, geckos seem to have empty stomachs more often than other lizard groups including Agamidae and Iguanidae (Huey et al. 2001). Within the Gekkota nocturnal species tend to have empty stomachs more often than diurnal species. The studied *Phyllodactylus* species are withal low with respect to the average calculated by Huey et al. (2001) for nocturnal geckos, with 14.3 (*P. delsolari*), 9.5 (*P. thompsoni*) and 0% (*P. reissii*) empty stomachs.

The centipedes of the genus *Scolopendra* (Fig. 3) and scorpions (Fig. 4) found in the stomachs of all four studied gecko species were quite striking (Tab. 1). *Scolopendra* uses its venom claws to catch, anaesthetize and euthanize its prey. Scorpions possess a venomous spine at the end of their metasoma which they utilize to kill large prey. Consuming these animals seems rather unlikely, but they have been found in the stomachs of other squamates like *Crotalus lepidus klauberi* (Holycross et al. 2002), *Sistrurus catenatus* (Holycross & MacKessy 2002), *Ptenopus garrulous* (Hibbitts et al. 2005), *Tropidurus plica* (Vitt 1991) and *Amphibolurus inermis* (Pianka 1971), as well.

Figure 3. *Scolopendra* sp. found in the stomach of a female *P. maranjonensis* (7x magnification).

Figure 4. Claw of a scorpion contained in the stomach of a female *P. delsolari* (20x magnification).

Also striking were stones and eggshells found in the stomachs of three gravid *Phyllopezus maranjonensis*. Consuming eggshells might be reasonable, since geckos are the only squamates that produce calciferous eggs (Kluge 1987). Thus, eating eggshells might help the gravid females synthesizing the shells of its own eggs but as sample size was low, no valid conclusions can be made and the intake of those objects was merely accidental along with arthropod prey.

A recent paper on the diet of *Phyllodactylus reissii* from Tumbes (Jordán 2006) shows that feeding habits of both populations, the one from Tumbes and the one from Balsas, are comparable. In Tumbes, 6 prey categories were identified in the diet of *P. reissii,* in the present study 8. Nonetheless, the Tumbes population had a higher niche breadth (5.73) than the one from Balsas (4.44). In both study areas, coleopterans dominated the diet, although blattopterans accounted for an even larger part of the diet of *P. reissii* from Tumbes. No blattopterans could be identified in the diet of any of the studied species from Balsas. Mean prey number eaten by *P. reissii* from Tumbes was higher, whereas *P. reissii* from Balsas consumed larger prey on average.

Another study on a gecko community, including the species *Phyllodactylus microphyllus, P. kofordi* and *P. reissii* at Bayovar, Peru (Huey 1979) shows that those species feed exlusively on arthropod prey, with *P. reissii* consuming the largest and *P. kofordi* the smallest prey. The three species differ significantly in microhabitat associations, with *P. kofordi* being the least arboreal one, occurring generally on leaf litter beneath shrubs and trees.

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