



Analysis of diet composition and morphological characters of the little-known Peruvian bush anole *Polychrus peruvianus* (Noble, 1924) in a northern Peruvian dry forest

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Abstract.—Analyses of diet composition are an important element of studies focusing on biological diversity, ecology, and behavior of animals. *Polychrus peruvianus* was found to be a quite abundant lizard species in the northern Peruvian dry forest. However, our knowledge of the ecology of this species remains limited. Herein, we analyze the species dietary composition and the morphological features that may be related to the feeding behavior. Our results show that *P. peruvianus* is a semi-herbivorous food generalist, which also consumes faunistic prey. All age groups prefer mobile prey as sit-and-wait predators. However, during ontogenesis, plant material becomes the main component in the diet of adult specimens.

Keywords. Iguania, bite force, ontogenetic change, foraging strategy, stomach contents, food niche, feeding behavior, Marañón river

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Introduction

The study of diet and trophic relationships between a species and its environment is a central theme in ecology. Field and museum-based studies provide insights about feeding behavior, foraging strategies, and sexual or ontogenetic variation within species (Futuyama 1998; Clark 2002). According to their type of prey, lizards can be divided into different trophic categories: insectivorous, herbivorous, carnivorous, or omnivorous (Vitt and Pianka 2007). Some lizard species even show an ontogenetic shift in diet from carnivory to omnivory, or even to herbivory (Cooper and Vitt 2002; van Leeuwen et al. 2011). They can be food generalists that ingest a random sample of prey available (and also plant material), or specialists that select specific food items (Vitt and Caldwell 2013). Depending on a species' behavior to locate and capture prey, two basic foraging strategies are recognized: "sit-and-wait" and active foraging (Vitt and Caldwell 2013). "Sit-and-wait" foragers remain motionless and wait for mobile prey (e.g., spiders, beetles, dipterans, and butterflies) to pass through their field of vision (Anderson and Karasov 1988; Bergallo and Rocha 1994; Huey and Pianka 1981; Magnusson et al. 1985; Nagy et al. 1984; Pianka 1970; Pianka and Parker 1975; Toft 1985; Vitt

and Caldwell 2013). In contrast active foraging species normally prey on sedentary (e.g., insect larvae), clustered (e.g., termites), or hidden prey (e.g., scorpions) (Bergallo and Rocha 1994; Huey and Pianka 1981; Magnusson et al. 1985; Nagy et al. 1984; Vitt and Caldwell 2013). Especially based on morphological variation, there may exist differences in size or type of preferred prey between males and females (species with a distinct sexual size dimorphism) or between adults and juveniles (Pough 1973; Verrastro and Ely 2015; Vitt and Caldwell 2013). It is generally accepted that lizards with higher and broader heads are capable of producing stronger bite forces (Campos 2016; McBrayer and Corbin 2007; Miles et al. 2007) and are thus able to consume harder dietary items (Herrel et al. 2001a, b; Herrel 2007; Huyghe et al. 2009; Verwajen et al. 2002). Campos (2016) and Herrel et al. (2006) subdivided food items in "hard," "intermediate," and "soft" prey, the latter requiring the lowest bite forces. Knowledge of a species' diet as part of its natural history may be crucial for the implementation of conservation actions for a species and its environment (Greene 1994; Verrastro and Eli 2015).

Until a few years ago the polychrotid lizard *Polychrus peruvianus* (Squamata: Iguania) was only known from a few specimens, and sufficient data was lacking

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for a proper assessment of its conservation status. Consequently, it was listed as Data Deficient by the IUCN Red List of Threatened Species (Cisneros-Heredia 2010). Recent fieldwork (Koch et al. 2011) provided new insights into the distribution and ecology of the species and contributed to an updated assessment of its conservation status. Hence, the species is now listed as Vulnerable by the IUCN due to its relatively small extent of occurrence (~12,000 km²), the low number of known locations (<5), and a decline in the extent and quality of its habitat, due to logging, agricultural expansion, and hydroelectric dam constructions (Venegas et al. 2017). Nevertheless, during our intensive fieldwork in different inter-Andean dry forest regions in northern Peru, we could lately provide records of *P. peruvianus* for 12 of 28 surveyed localities in the departments of Amazonas and Cajamarca. As per the research permits, we collected up to six specimens per locality for preservation and examination, to further contribute to the knowledge of this scarcely known species. Surprisingly, the species seemed to be quite abundant in most surveyed regions, as we often found many more individuals than just the ones we were allowed to collect (Koch et al. 2011, 2018). The species is further known from the Zamora-Chinchipe province in southern Ecuador and Peruvian department of Piura at elevations of 400–1,750 m a.s.l. (Carrillo and Icochea 1995; Duellman 1979; Gorman et al. 1969; Koch et al. 2011; Noble 1924; Peters and Donoso-Barros 1970; Schlüter 2010; Torres-Carvajal et al. 2017; Yañez-Muñoz et al. 2006). *Polychrus peruvianus* is diurnal and highly arboreal, being almost exclusively found on trees or shrubs (Koch et al. 2011). Males and females show a conspicuous sexual dimorphism in coloration; females have lime green heads and a straight white stripe laterally between the axilla and the insertion of the hind limbs, whereas the heads of males are brownish and a white lateral stripe is lacking (Koch et al. 2011). The congeners *P. marmoratus* and *P. acutirostris* are known to feed on arthropods as well as plant material (Garda et al. 2012; Koski et al. 2016). However, the only available information regarding the diet of *P. peruvianus* derives from a single individual from Tingo in the Peruvian department of Amazonas, whose stomach contained several hymenoptera and a leaf fragment (Gorman et al. 1969).

In the present study, we sought to describe the diet of populations of *Polychrus peruvianus* from the inter-Andean dry forest valley in northern Peru to provide information that may be relevant for the establishment of conservation criteria for this species. Therefore, we analyzed the trophic niche to reveal sexual differences and ontogenetic changes in diet composition, to define the foraging strategy, and to determine whether members of the species are food generalists or specialists. Furthermore, we performed morphological analyses in order to detect sexual dimorphism that may be related to differences in feeding behavior.

Material and Methods

In the framework of an intensive herpetological inventory in the inter-Andean dry forest valleys of the Marañón river and its tributaries we collected a total number of 64 individuals of *Polychrus peruvianus* (Koch et al. 2018). Most of these specimens were deposited in the collections of the Centro de Ornitología y Biodiversidad (CORBIDI), in Lima, Perú, and the Museo de Historia Natural de la Universidad Nacional de San Agustín (MUSA), in Arequipa, Perú. However, we were allowed to export 24 individuals (9 males, 10 females, 5 juveniles) for further examination and to add them to the collection of the Zoologisches Forschungsmuseum Alexander Koenig (ZFMK), in Bonn, Germany. The specimens housed in the ZFMK built the basis of the dietary analysis, presented herein. We detected these specimens between May 2008 and December 2009 at different localities during visual encounter surveys after nightfall, when they were sleeping on branches of trees and shrubs in heights between 1.5 m and 7.0 m above the ground (Koch et al. 2018). We collected one individual in May 2008 (ZFMK 88707), two in June 2008 (ZFMK 88708-09), four in July 2008 (ZFMK 88710-13), four in March 2009 (ZFMK 90817-20), two in April 2009 (ZFMK 90821-22), and eleven in December 2009 (ZFMK 90823-33). Exact localities of each specimen are given in the Appendix. We either captured the specimens by hand or by use of a fishing net and euthanized them by an injection of the veterinary anesthetic T61 the following morning, no later than 10 hours after their capture, to guarantee that the stomach contents were little digested and in good condition for identification. After fixation in 10% formalin for 24 to 48 hours, the specimens were preserved in 70% ethanol.

Sexes of the specimens were determined by coloration and/or by internal reproductive organs (testicles or ovaries) or by the presence of everted hemipenes. We categorized individuals with a snout-vent-length (SVL) of less than 100 mm as juveniles, since none of the dissected lizards up to this size had mature gonads.

Definition of head length, head width, and head height follows Meyers et al. (2002). Measurements of head (length, width, height), body (SVL, width) and tail length of the lizards and dimensions of prey items (length, width) were taken with a dial caliper (0 – 150 mm; to the nearest 0.01 mm) and weights of bodies, fat bodies, and stomachs were calculated with a digital weighing machine (Almasa® MT 7; max. 200 g; to the nearest 0.01 g). The bodies of the preserved specimens were opened ventrally and fat bodies and stomachs were removed and the latter were dissected.

Stomach contents were placed on a Petri dish and prey items were analyzed under a stereomicroscope and were verified to at least the level of order according to Bährmann (2011). Bergallo and Rocha (1994) and Cooper (1994) defined Formicidae, Isoptera, and larvae of Diptera

and Lepidoptera as “sedentary prey” and Araneae, Coleoptera, Diptera (adult), Hemiptera, Hymenoptera (excluding Formicidae), Lepidoptera (adult), Odonata, Orthoptera and Lithobiomorpha as “mobile prey.” Thus, in order to determine whether the lizard species is a sit-and-wait or active forager, we subclassified the orders Hemiptera into “Heteroptera” and “Other Hemiptera,” Hymenoptera into “Formicidae” and “Other Hymenoptera,” Lepidoptera into “adult Lepidoptera” and “Lepidoptera Larvae,” and likewise we subclassified Diptera into “adult Diptera” and “Diptera larvae.” Leaves, fibers, seeds and fruits were grouped together as “Plant material.” To identify the bite force food items were divided into three groups: hard prey, medium hard prey, and soft prey according to Campos (2016) and Herrel et al. (2006). Coleoptera, Hymenoptera, and plant material were considered as “hard prey,” Hemiptera, Formicidae, Isoptera, Odonata, Orthoptera, and Lithobiomorpha as “medium hard prey,” and Araneae, Diptera, Lepidoptera, and larvae as “soft prey.” All food items were quantified and measured.

The number of consumed items, the percentage, the frequency of occurrence (number of stomachs in which a given prey item was found), the percent by frequency, the volume, and the percent by volume for each prey category were estimated.

All statistical tests were executed with the software OriginPro version 8.0724 (OriginLab, Northampton, Massachusetts, USA). Before comparisons, the Shapiro-Wilk-Test was used ($W \leq 0.966, p \leq 0.86$) to check if data were normally distributed and depending on the result parametric (*t*-test) or non-parametric (Mann-Whitney U-test) tests were used for data analysis.

For comparison of the head dimensions, regressions were performed for every dimension against SVL and a residual analysis was completed to avoid influence of different SVL values within the species. Similarly, for comparison of the weights, regressions were conducted on the weights of fat bodies and stomachs against body weight and residual analyses were completed to avoid influence of body weight values.

Prey items were subdivided according to the mean values of their size (very large, large, medium-sized, small, very small) to estimate the length and width of incomplete prey items for each order (see Supplement Table S1).

The length (L) and width (W) of the individual prey items were calculated for prey volume (V) with the formula for an ellipsoid according to Colli and Zamboni (1999):

$$V = \frac{4\pi}{3} \frac{L}{2} \left(\frac{W}{2}\right)^2$$

To quantify the diversity of prey used by the animals, niche breadth (B) was calculated using the Simpson-Index B (Simpson 1949):

$$B = 1 - \sum_{i=1}^s \frac{n_i(n_i-1)}{n(n-1)}$$

where n_i is the number of prey items in each category *i* (prey items of different orders and plant material) and *n* is the total number of prey items. Niche breadth values vary from 0 (no diversity, exclusive use of a single prey type, specialist) to 1 (highest diversity, prey items of all categories, generalist).

Additionally, the inverse of Simpson-Index B' was used to compare the values with other published data:

$$B' = 1 / \left(\sum_{i=1}^s \frac{n_i(n_i-1)}{n(n-1)} \right)$$

where niche breadth values (B') vary from 1 (no diversity, exclusive use of a single prey type, specialist) to *n* (highest diversity, prey items of all categories, generalist).

The Index of Relative Importance (IRI) was calculated for each prey category (i) in relation to the total food spectrum with the following formula:

$$IRI_i = PO_i(PI_i + PV_i)$$

where PO_i is the percent by frequency F% (100 x number of stomachs which contain the prey items *i*/total number of stomachs), PI_i is the percent by number N% (100 x number of prey items of each category *i*/total number of prey items), and PV_i is the percent by volume V% (100 x volume of prey items of each category *i*/total volume of prey items) of each prey category.

The Pianka-Index (Pianka 1974) was estimated to calculate niche overlap in the food spectrum of the different groups of examined animals (females, males, juveniles, adults):

$$O_{jk} = \frac{\sum_i^n P_{ij}P_{ik}}{\sqrt{\sum_i^n P_{ij}^2 \sum_i^n P_{ik}^2}}$$

where P_{ij} and P_{ik} represent the number of prey categories *i* used in the groups *j* and *k* to be compared. The value for niche overlap (O_{jk}) varies from 0 (no overlap, the compared groups have a completely different food spectrum) to 1 (complete overlap, the compared groups have the same food spectrum).

Results

Morphological analysis. There was no difference in SVL and weight of males and females (length: U-test, $U = 41, Z = -0.2858, p = 0.78$; weight: *t*-test, $t = -0.07, p = 0.94$; see Supplement Table S2). All head dimensions were positively correlated with the SVL (head length against SVL: $y = 0.262x + 1.783, R^2 = 0.854$; head width against SVL: $y = 0.157x - 0.076, R^2 = 0.831$; head height against SVL: $y = 0.130x + 2.204, R^2 = 0.684$). There were no differences between adults and juveniles for all the head dimensions' residuals (head length: *t*-test: $t = -0.44, p = 0.66$; head width: *t*-test: $t = 0.68, p = 0.50$; head height: *t*-test: $t = -1, p = 0.30$), but males showed longer, wider and higher heads than females (head length:

t-test: $t = -3.99$, $p = 0.0009$; head width: *t*-test: $t = -3$, $p = 0.006$; head height: *t*-test: $t = -4$, $p = 0.001$; see Supplement Table S2).

Fat bodies were found in 21 individuals (87.5%) of *P. peruvianus* (8 males, 10 females, 3 juveniles). Although there was no difference between adults and juveniles for fat body weight residuals (U-test: $U = 41$, $Z = 1.3568$, $p = 0.17$), females had heavier fat bodies than males (U-test: $U = 69$, $Z = 2.53229$, $p < 0.05$). Further, there was no difference between males and females for stomach weight residuals (*t*-test, $t = 0.79380$, $p = 0.44$), but juveniles had heavier stomachs than adults (*t*-test, $t = 4.46367$, $p = 0.03$) (see Supplement Table S2).

Stomach contents. Table 1 shows the composition of the stomach content of *Polychrus peruvianus* for all specimens together and by sex/age classes. Altogether, 226 items were identified, representing 195 faunistic prey items ($N\% = 86.3\%$) and 31 pieces of plant material ($N\% = 13.7\%$), which were found in 21 stomachs ($F\% = 87.5\%$). The percent by volume of the plant material ($V\% = 75.25\%$) was three times higher than that of the faunistic prey items ($V\% = 24.75\%$). However, with respect to the IRI the latter (IRI = 9715.4) played a slightly more important role in the species' diet than plant material (IRI = 7784.6). Inorganic material (e.g., stones) was not found. In 19 stomachs of adult individuals 105 food items were found with a total volume of $V = 31651.8 \text{ mm}^3$, whereas 121 food items were found in five stomachs of juveniles, that had a total volume of $V = 5630.4 \text{ mm}^3$. In adults plant material was more important with an IRI = 9830.7 than faunistic prey items with an IRI = 7589.7, whereas in juveniles the latter played a far more important role in the diet with an IRI = 16989.9 than plant material with an IRI = 2408.1. In nine stomachs of male individuals 34 food items were found with a total volume of $V = 10994.0 \text{ mm}^3$, whereas 71 food items were found in 10 stomachs of female specimens with a total volume of $V = 20657.9 \text{ mm}^3$. In males plant material was more important with an IRI = 11387.0 than faunistic prey items with an IRI = 4793.1, whereas in females the latter played a slightly more important role in the diet with an IRI =

9900.6 than plant material with an IRI = 9089.5.

The most dominant faunistic prey category was the order Coleoptera with respect to the number of consumed items ($N = 76$, $N\% = 33.6\%$), the frequency in how many stomachs the category was found ($F = 14$, $F\% = 58.3\%$), the volume ($V = 2400.7 \text{ mm}^3$; $V\% = 6.4\%$), and the IRI (IRI = 2336.1). The second most important category was the suborder Heteroptera with respect to the frequency ($F = 9$, $F\% = 37.5$), the volume ($V = 1938.6 \text{ mm}^3$, $V\% = 5.2\%$), and the IRI (IRI = 642.4). However, the number of Heteroptera items ($N = 27$, $N\% = 12.0\%$) was slightly lower than that of the order Diptera ($N = 30$, $N\% = 13.3\%$) which ranked third in volume ($V = 1135.2 \text{ mm}^3$, $V\% = 3.0\%$) and fourth in IRI (IRI = 203.9) but only played an underpart with respect to the frequency ($F = 3$, $F\% = 12.5\%$). The order Orthoptera ranked third in frequency ($F = 7$, $F\% = 29.2\%$, together with Hymenoptera) and IRI (IRI = 219.4) and fourth with respect to the volume ($V = 993.2 \text{ mm}^3$, $V\% = 2.7\%$). On closer inspection of the IRI, the Coleoptera played a major role in the diet of adults (IRI = 1247.7), juveniles (IRI = 4656.6), and females (IRI = 2889.7), but only ranked fifth in the diet of males (IRI = 74.4). The second most important category in adults (IRI = 962.3) and females (IRI = 1648.7) was Heteroptera, which ranked third in males (IRI = 265.1) and fifth in juveniles (IRI = 475.7). The Lepidoptera larvae ranked third in adults (IRI = 270.6) and was even the most important prey category in males (IRI = 637.4), however it ranked only fifth in females (IRI = 121.3) and played an underpart in juveniles (IRI = 59.3). Important in the diet of juveniles were also the categories Diptera (rank 2, IRI = 1729.2), Hymenoptera (rank 3, IRI = 967.8), and Hemiptera (rank 6, IRI = 348.3), which only played an underpart in males and females. Orthoptera ranked third in females (IRI = 199.4) and fourth in adults (IRI = 134.4) as well as in juveniles (IRI = 808.4) (Table 2).

With regard to the food niche breadth, the Simpson-Index for the species was $B = 0.82$ and the inverse Simpson-Index was $B' = 5.65$. Values did not differ greatly between sexes (males: $B = 0.76$, $B' = 4.19$; females: $B = 0.82$, $B' = 5.63$), whereas juveniles had noticeably lower

Table 1. Composition of the stomach content (faunistic prey items (FP), plant material (PM)) of *Polychrus peruvianus*. Data were obtained by pooling stomachs of all specimens and by separating them according to sex/age classes. For each category the number (N), the percent by number (N%), the frequency (F), the percent by frequency (F%), the calculated volume (V [mm³]), the percent by volume (V%), and the Index of Relative Importance (IRI) are shown.

	Adults (n = 19)		Juveniles (n = 5)		Males (n = 9)		Females (n = 10)		Total (n = 24)	
	FP	PM	FP	PM	FP	PM	FP	PM	FP	PM
N	78	27	117	4	20	14	58	13	195	31
N%	74.3	25.7	96.7	3.3	58.8	41.2	81.7	18.3	86.3	13.7
F	16	17	5	4	6	8	10	9	21	21
F%	84.2	89.5	100.0	80.0	66.7	88.9	100.0	90.0	87.5	87.5
V [mm ³]	5014.2	26637.6	4121.7	1508.7	1437.2	9556.8	3577.0	17080.9	9257.2	28146.3
V%	15.8	84.2	73.2	26.8	13.1	86.9	17.3	82.7	24.75	75.25
IRI	7589.7	9830.7	16989.9	2408.1	4793.1	11387.0	9900.6	9089.5	9715.4	7784.6

Diet of *Polychrus peruvianus*

Table 2. Faunistic prey items of *Polychrus peruvianus*. For each category the number (N), the percent by number (N%), the frequency (F), the percent by frequency (F%), the calculated volume (V [mm³]), and the percent by volume (V%) are shown for all specimens of the species together. The Index of Relative Importance (IRI) of each prey category is given for adults, juveniles, males, and females separately and for all specimens together, respectively.

Prey category	N	N%	F	F%	V [mm ³]	V%	IRI				
							Adults	Juveniles	Males	Females	Total
Araneae	8	3.5	5	20.8	90.3	0.2	122.7	52.5	32.8	144.1	78.8
Coleoptera	76	33.6	14	58.3	2400.7	6.4	1247.7	4656.6	74.4	2889.7	2336.1
Diptera	30	13.3	3	12.5	1135.2	3.0	5.9	1729.2	0	16.5	203.9
Formicidae	5	2.2	4	16.7	8.3	0.02	60.3	18.3	32.8	84.8	37.2
Hemiptera	11	4.9	3	12.5	751.8	2.0	34.9	348.3	74.8	16.5	86.0
Heteroptera	27	12.0	9	37.5	1938.6	5.2	962.3	475.7	265.1	1648.7	642.4
Hymenoptera	10	4.4	7	29.2	633.4	1.7	71.7	967.8	40.4	99.5	178.5
Lepidoptera adult	1	0.4	1	4.2	191.7	0.5	0	84.6	0	0	4.0
Lepidoptera larvae	10	4.4	6	25.0	661.6	1.8	270.6	59.3	637.4	121.3	154.8
Lithobiomorpha	1	0.4	1	4.2	3.6	0.01	0	17.8	0	0	1.9
Odonata	1	0.4	1	4.2	63.5	0.2	0	39.1	0	0	2.6
Orthoptera	11	4.9	7	29.2	993.2	2.7	134.4	808.4	63.4	199.4	219.4
Undetermined	4	1.8	3	12.5	385.3	1.0	79.4	0	270.4	14.9	35.0

values than adults (adults: $B = 0.84$, $B' = 6.43$; juveniles: $B = 0.74$, $B' = 3.78$; Table 3).

The Pianka-Index (O_{jk}) showed highest niche overlap value between females and juveniles ($O_{jk} = 0.91$), whereas males and juveniles had the lowest overlap value ($O_{jk} = 0.74$). Adults and juveniles ($O_{jk} = 0.88$) showed almost a similar value for the overlap as males and females ($O_{jk} = 0.87$).

Foraging strategy. In 21 stomachs of *Polychrus peruvianus*, 191 faunistic prey items were determined with a total volume of $V = 8871.8 \text{ mm}^3$, of which 176 were assigned to the category mobile prey ($N\% = 92.15\%$) with a volume of $V = 8202.0 \text{ mm}^3$ ($V\% = 92.45\%$) and 15 ($N\% = 7.85\%$) belonged to sedentary prey with a volume of $V = 669.8 \text{ mm}^3$ ($V\% = 7.55\%$). Mobile prey was found in 19 stomachs ($F\% = 90.5\%$) and sedentary prey in 10 ($F\% = 47.6\%$). The IRI of mobile prey (IRI = 16701.6) was almost 23 times higher than the IRI of sedentary prey (IRI = 733.5). With respect to the different specimen groups (adults, juveniles, males, females) considerably higher values were examined for mobile prey than for sedentary prey (except for the same frequency with which mobile and sedentary prey were found in males). In adults the IRI for mobile prey was about 11 times higher than for sedentary prey and in juveniles it was even about 103 times higher. In adults the IRI value for mobile prey was about three times higher than for sedentary prey and in females it was even about 21 times higher (Table 4).

Bite force. Of the 226 food items found in the 24 stomachs of *Polychrus peruvianus* four faunistic prey items were not determined (Table 2). Hence, for the bite force

analyses 222 items remained, of which 117 were assigned to the category hard prey ($N\% = 52.7\%$) with a volume of $V = 31180.3 \text{ mm}^3$ ($V\% = 84.2\%$), 56 ($N\% = 25.2\%$) belonged to medium hard prey with a volume of $V = 3759.0 \text{ mm}^3$ ($V\% = 10.2\%$) and 49 ($N\% = 22.1\%$) belonged to soft prey with a volume of $V = 2078.8 \text{ mm}^3$ ($V\% = 10.2\%$). Hard prey items were found in 23 stomachs ($F\% = 95.8\%$), medium hard prey in 15 ($F\% = 62.5\%$) and soft prey in 13 stomachs ($F\% = 54.2\%$). The IRI of hard prey (IRI = 13122.7) was the highest, followed by the IRI of medium hard prey (IRI = 2211.2). With respect to the different specimen groups all examined values were considerably higher for hard prey than for medium hard prey or soft prey (except for the same frequency with which hard and medium hard prey was found in juveniles). In adults, the IRI for hard prey was about six times higher than for medium hard prey and 14 times higher than for soft prey. In juveniles, the IRI of hard prey was two times higher than for medium hard prey and three times higher than for soft prey. In females, the IRI for hard prey was four times higher than for medium hard prey and 15 times higher than for soft prey. In males, the IRI of hard prey was 12 times higher than the IRI for medium hard prey or soft prey (Table 5).

Table 3. Diversity in the dietary spectrum of *Polychrus peruvianus*. The Simpson-Index (B), the inverse Simpson-Index (B'), and the number of consumed prey categories (S, including plant material) are given for adults, juveniles, males, and females separately and for all specimens together, respectively.

	Adults	Juveniles	Males	Females	Total
B	0.84	0.74	0.76	0.82	0.82
B'	6.43	3.78	4.19	5.63	5.65
S	10	13	9	10	13

Table 4. Mobile (MP) and sedentary prey (SP) items in the stomach content of *Polychrus peruvianus* for all specimens together and by sex/age classes. The number of items (N), the percent by number (N%), the frequency (F), the percent by frequency (F%), the calculated volume (V [mm³]), the percent by volume (V%) and the Index of Relative Importance (IRI) are shown.

	Adults (n = 16)		Juveniles (n = 5)		Males (n = 6)		Females (n = 10)		Total (n = 21)	
	FP	PM	FP	PM	FP	PM	FP	PM	FP	PM
N	65	13	115	2	13	7	52	6	176	15
N%	83.3	16.7	98.3	1.7	65.0	35.0	89.7	10.3	92.15	7.85
F	14	8	5	2	4	4	10	4	19	10
F%	87.5	50.0	100.0	40.0	66.7	66.7	100.0	40.0	90.5	47.6
V [mm ³]	4469.8	544.4	3996.3	125.5	1274.4	162.8	3195.5	381.6	8202.0	669.8
V%	89.1	10.9	97.0	3.0	88.7	11.3	89.3	10.7	92.45	7.55
IRI	15091.7	1376.2	19524.7	190.1	10244.7	3088.6	17898.9	840.5	16701.6	733.5

Discussion

This is the first detailed study of the diet of *Polychrus peruvianus*, based on specimens collected in the dry forest of northern Peru. Findings suggest that *P. peruvianus* is a semi-herbivorous food generalist, which also consumes faunistic prey. All age groups prefer mobile prey as sit-and-wait predators. However, during ontogenesis, plant material becomes the main component in the diet of adult specimens.

Although in *Polychrus acutirostris*, *P. gutturosus*, *P. jacquelineae*, *P. liogaster*, and *P. marmoratus* a sexual size difference with females growing larger than males is stated (Avila-Pires 1995; Garda et al. 2012; Koch et al. 2011), this was not observed in our specimens of *P. peruvianus* examined herein. Nevertheless, a relatively small number of specimens was analyzed and a larger sample size would allow a more reliable estimation whether a sexual size dimorphism exists in this species. No significant differences between most specimen groups in fat body weight and stomach weight in proportion to body weight were observed. It can be assumed that the examined specimens had a similar nutritional state, except for females of *P. peruvianus*, who were in a better nutritional state with heavier fat bodies in proportion to body weight. Juveniles of *P. peruvianus* proved to have heavier stomachs than adults in proportion to body weight. This coincides with the fact that distinctly more prey items were found in juvenile stomachs of this spe-

cies as compared to adults. Additionally, in juveniles the percent by volume of faunistic prey items (V% = 73.2 %), which are usually heavier, was much higher as compared to plant material (V% = 26.8 %), whereas stomachs of both adult sexes contained a significantly higher percent by volume of plant material as compared to faunistic prey items (86.9 % vs. 13.1 % in males, 82.7 % vs. 17.3 % in females). This observation further suggests that *P. peruvianus* has a semi-herbivorous dietary spectrum, as was also observed in the congeners *P. acutirostris* and *P. marmoratus* (Avila-Pires 1995; Garda et al. 2012; Vanzolini 1983). In adult specimens of *P. peruvianus*, plant material plays a greater role (IRI = 9830.7) in the dietary spectrum than faunistic prey items (IRI = 7589.7). Nevertheless, the importance of plant material is much lower in the diet of juveniles (IRI = 2408.1) compared to adults (IRI = 9830.7). Many lizard species undergo an ontogenetic diet shift from eating insects as a juvenile to an herbivorous or semi-herbivorous diet as an adult (i.e., Cooper and Vitt 2002; Dessem 1985; Estes and Williams 1984; van Leeuwen et al. 2011). This is explained by the fact that juvenile lizards need more animal protein for their growth and development (Johnson and Lillywhite 1979; Mayhew 1963). Furthermore, juveniles are less efficient at digesting plant material than older lizards, until they acquire the intestinal flora that degrades cellulose (Troyer 1982).

With a relatively high value for the Simpson-Index (B = 0.82) *Polychrus peruvianus* can be considered as a food

Table 5. Hard (H), medium hard (M) and soft prey (S) items in the stomach content of *Polychrus peruvianus* for all specimens together and by sex/age classes. The number of items (N), the percent by number (N%), the frequency (F), the percent by frequency (F%), the calculated volume (V [mm³]), the percent by volume (V%) and the Index of Relative Importance (IRI) are shown.

	Adults (n = 19)			Juveniles (n = 5)			Males (n = 9)			Females (n = 10)			Total (n = 24)		
	H	M	S	H	M	S	H	M	S	H	M	S	H	M	S
N	50	35	16	67	21	33	17	7	7	33	28	9	117	56	49
N%	49.5	34.7	15.8	55.37	17.4	27.3	54.8	22.6	22.6	47.1	40.0	12.9	52.7	25.2	22.1
F	18	11	10	5	5	3	8	3	4	10	8	6	23	15	13
F%	94.7	57.9	52.6	100.0	100.0	60.0	88.9	33.3	44.4	100.0	80.0	60.0	95.8	62.5	54.2
V [mm ³]	28644.8	1994.4	627.3	2535.6	1643.4	1451.5	9722.7	740	163.6	18922	1254.5	463.8	31180.3	3759	2078.8
V%	91.6	6.4	2.0	45.0	29.2	25.8	91.5	7.0	1.5	91.7	6.1	2.3	84.2	10.2	5.6
IRI	13369.3	2375.6	939.4	10040.9	4654.3	3183.1	13007.6	984.8	1072.0	13881.8	3686.2	906.2	13122.7	2211.2	1499.8

generalist with a great diversity in consumed food items. The congener *P. acutirostris* has a lower value ($B = 0.67$; calculated with the data of Garda et al. 2012) and thus shows a lower diversity in the dietary spectrum. Adult *P. peruvianus* exhibit the greatest diversity ($B = 0.84$), whereas juveniles show the lowest diversity ($B = 0.74$).

The niche overlap in the dietary spectrum of the different subgroups of *P. peruvianus* is relatively high with all values for $O_{jk} \geq 0.74$. The highest overlap in the food niches exists between juveniles and females ($O_{jk} = 0.91$), whereas the niches of the juveniles and males show the lowest overlap values ($O_{jk} = 0.74$). One reason for this could be that male specimens have higher and wider heads, which enable them to consume larger prey items (Pough 1973). Additionally, their head dimensions allow them to produce higher bite forces (Campos 2016; McBrayer and Corbin 2007; Miles et al. 2007), whereby they are able to feed on harder dietary items (Herrel et al. 2001a, b; Herrel 2007; Huyghe et al. 2009; Verwajen et al. 2002). Thus, male specimens are able to consume a greater diversity of food items. In fact, females have as well larger heads than juveniles, but the difference is smaller than between males and juveniles. “Hard prey” items are the preferred category in the spectrum of consumed food in all subgroups of *P. peruvianus*, although the percent by volume in juveniles is only half as high as in adults, indicating that juveniles are less able to consume a broad spectrum of hard prey items. Plant material also belongs to hard prey and as already mentioned is consumed to a lesser amount by the juveniles.

The most important faunistic prey categories in the diet of all subgroups represent mainly mobile insects which are capable of flying (Coleoptera, Heteroptera, Diptera, and Orthoptera) and are thus easily accessible for arboreal animals (Hogue 1993) such as *P. peruvianus*. Almost no sedentary prey items were found (e.g. larvae, ants, and termites) in the stomachs of this species. A similar preference for mobile, volant, or arboreal prey was observed for the congener *P. acutirostris* (Garda et al. 2012). Mobile prey is preferred by sedentary species with a sit-and-wait foraging strategy (Anderson and Karasov 1988; Bergallo and Rocha 1994; Huey and Pianka 1981; Magnusson et al. 1985; Nagy et al. 1984; Pianka 1970; Pianka and Parker 1975; Toft 1985). Thus, it can be assumed that *P. peruvianus* is a sit-and-wait predator, which lives up in trees and mainly preys on mobile species that are able to fly or climb trees. This coincides with the general assumption that sedentary or hidden prey types are relatively unavailable to iguanian lizards (Vitt and Pianka 2005). Our observed great diversity in the dietary spectrum coincides with the general observation that sit-and-wait predators consume a wide variety of prey types as they spend a larger amount of time motionless, whereas actively foraging species can be more selective (Bergallo and Rocha 1994).

Although *Polychrus peruvianus* seems to be quite abundant in many localities studied herein the popula-

tion size and exact distribution range of the species has never been determined. Most surveyed localities are facing multiple and complex threats due to logging, agriculture and narcotics plantations, mining, and several planned hydroelectric projects that will lead to flooding of vast portions of the species' habitat (Koch et al. 2013). These threats, together with the enormous lack of knowledge that still exists about the biodiversity of the region, and no protected area has so far been designated in the inter-Andean dry forest, highlight the urgent priority for conservation and research activities in this area. It is likely that populations of *P. peruvianus* and many other endemic species will decline in the near future without further knowledge on their natural history and activities to protect their habitat.

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APPENDIX

Examined specimens

Polychrus peruvianus: AMAZONAS: Bagua: **Bagua Grande**: ZFMK 88712, 88713 (05°47'33.7"S, 78°23'04.9"W, 570 m a.s.l.); Utcubamba: **Cumba**: ZFMK 90830–90833 (05°56'S, 78°39'W, 450–500 m a.s.l.); **Zapatalgo/Chiñuña**: ZFMK 90823–90825 (06°04'S, 78°29'W, 900–1,030 m a.s.l.); **Puerto Malleta**: ZFMK 90826–90828 (06°03'S, 78°36'W, 480–510 m a.s.l.); CAJAMARCA: Jaén: **Santa Rosa de la Yunga**: ZFMK 88710 (05°26'S, 78°33'W, 1,250–1,300 m a.s.l.); **Bellavista**: ZFMK 88707 (05°39'49.8"S, 78°40'13.9"W, 411 m a.s.l.); ZFMK 90818, 90819 (05°38'06.6"S, 78°39'36.2"W, 405 m a.s.l.); ZFMK 90820 (05°34'35.7"S, 78°38'10.8"W, 700 m a.s.l.); **Gotas de Agua**: ZFMK 88708 (05°41'S, 78°46'W); **Perico**: ZFMK 88709 (05°21'16.5"S, 78°47'30.6"W, 443 m a.s.l.); ZFMK 90822, 90821 (05°21'S, 78°47'W, 460–720 m a.s.l.); **Pucará**: ZFMK 88711, 90817, (06°02'S, 79°07'W, 900–930 m a.s.l.); Cutervo: **Across from Puerto Malleta**: ZFMK 90829 (06°04'24.5"S, 78°36'47.8"W, 535 m a.s.l.).

Supplementary material

Supplementary Table S1. Mean values of prey item sizes to estimate the length and width of incomplete prey items for each order. Orders of which only complete prey items were found are not listed.

Order	Size	Body length [mm]	Body width [mm]
Araneae	large	5.0	2.6
	medium	3.6	1.9
	small	1.9	1.2
	very small	0.9	0.5
Coleoptera	very large	16.4	10.9
	large	12.8	3.7
	medium	4.7	2.9
	small	2.3	0.9
Formicidae	very large	8.9	2.7
	large	6.8	2.3
	medium	4.0	0.9
	small	2.3	0.6
	very small	1.6	0.4
Heteroptera	large	11.6	6.3
	medium	8.9	5.1
	small	4.8	2.3
Hymenoptera	medium	9.5	3.9
	small	8.1	2.7
Lepidoptera Larve	large	29.9	4.9
	medium	14.2	3.2
	small	10.0	1.3
	very small	3.7	0.9
Orthoptera	large	17.4	4.5
	medium	13.1	3.2

Diet of *Polychrus peruvianus*

Supplementary Table S2. Measurements of *Polychrus peruvianus*: Snout-vent-length [mm], body width [mm], body weight [g], head length [mm], head width [mm], head height [mm], fat body weight [g], percental fat body weight [%], stomach weight [g], and percental stomach weight [%] of females, males, juveniles and all animals together (total). Shown is the range, the mean value (\bar{x}) and the standard deviation (SD).

		Females	Males	Juveniles	Total
n_{specimens} / n_{fat bodies}		10/10	9/8	5/3	24/21
Snout-Vent-Length [mm]	Range	106-138	116-135	74-96	74-138
	$\bar{x} \pm \text{SD}$	123.4 \pm 11.6	127.0 \pm 6.4	90.4 \pm 8.4	117.9 \pm 17.0
Body weight [g]	Range	24-68	30-57	9-20	9-68
	$\bar{x} \pm \text{SD}$	40.1 \pm 12.1	40.4 \pm 8.9	14.7 \pm 3.6	34.9 \pm 14.2
Head length [mm]	Range	29-37	34-40	21-28	21-37
	$\bar{x} \pm \text{SD}$	32.8 \pm 2.9	36.6 \pm 1.8	25.3 \pm 2.5	32.7 \pm 4.8
Head width [mm]	Range	16-21	18-24	12-15	12-24
	$\pm \text{SD}$	18.7 \pm 1.5	20.8 \pm 1.6	13.9 \pm 1.0	18.5 \pm 2.9
Head height [mm]	Range	15-19	18-23	12-16	12-23
	$\bar{x} \pm \text{SD}$	17.2 \pm 1.5	20.0 \pm 1.5	14.0 \pm 1.5	17.6 \pm 2.7
Fat body weight [g]	Range	0.01-1.3	0.01-0.3	0.01-0.1	0.01-1.3
	$\bar{x} \pm \text{SD}$	0.53 \pm 0.38	0.114 \pm 0.09	0.03 \pm 0.03	0.30 \pm 0.35
Fat body weight [%]	Range	0.04-2.6	0.03-1.0	0.08-0.4	0.03-2.6
	$\bar{x} \pm \text{SD}$	1.25 \pm 0.77	0.30 \pm 0.28	0.20 \pm 0.15	0.74 \pm 0.75
Stomach weight [g]	Range	0.9-1.9	0.6-2.6	0.5-1.7	0.5-2.6
	$\bar{x} \pm \text{SD}$	1.37 \pm 0.24	1.35 \pm 0.57	1.01 \pm 0.45	1.29 \pm 0.46
Stomach weight [%]	Range	2.1-5.7	2.0-4.9	4.3-9.9	2.0-9.9
	$\bar{x} \pm \text{SD}$	3.66 \pm 1.01	3.28 \pm 0.95	6.60 \pm 1.97	4.13 \pm 1.79