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Analysis of diet composition and morphological characters of the Peruvian lizard *Microlophus stolzmanni* (Squamata: Tropiduridae)

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Abstract

Analysis of diet composition and morphological characters of the Peruvian lizard *Microlophus stolzmanni* (Squamata: Tropiduridae). *Microlophus stolzmanni* is a diurnal lizard that is endemic to the dry forest of northern Peru. Little is known about the ecology of the species and the composition of its diet never has been studied. The stomach contents and morphological features related to feeding behavior are analyzed herein. *Microlophus stolzmanni* is a semi-herbivorous food generalist that also consumes animal items. All age groups prefer sedentary prey for which *M. stolzmanni* forages actively. As the lizard matures, plant material becomes a more important part of the diet.

Keywords: bite force, dry forest, feeding behavior, food niche, foraging strategy, Marañón River, ontogenetic change, stomach contents.

Resumo

Análise da composição da dieta e características morfológicas do lagarto peruano *Microlophus stolzmanni* (Squamata: Tropiduridae). *Microlophus stolzmanni* é um lagarto diurno endêmico da floresta seca do norte do Peru. Pouco se sabe sobre a ecologia da espécie, e a composição de sua dieta nunca havia sido estudada. Analisamos aqui o conteúdo estomacal e características morfológicas relacionadas ao comportamento de alimentação. *Microlophus stolzmanni* é um lagarto generalista semi-herbívoro que também consome animais. Todos os grupos etários preferem presas sedentárias, que capturam por meio de forrageio ativo. À medida que os lagartos atingem a maturidade, o material vegetal torna-se uma parte mais importante da dieta.

Palavras-chave: comportamento alimentar, conteúdo estomacal, estratégia de forrageio, floresta seca, força da mordida, mudança ontogenética, nicho alimentar, rio Marañón.

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Introduction

The genus *Microlophus* Duméril and Bibron, 1837 is a well-supported monophyletic group of 23 South American lizards characterized by apical disks on the hemipenes (Frost 1992, Harvey and Gutberlet 2000, Frost *et al.* 2001). These so-called "lava lizards" have a disjunct geographic distribution, unusual among terrestrial vertebrates (Benavides *et al.* 2007, 2009). Based on osteological characters, body scales, and skin folds, *Microlophus* is composed of two species groups: *M. occipitalis* and *M. peruvianus* groups (Dixon and Wright 1975, Frost 1992). The *M. peruvianus* Group contains two subgroups differing in their habitat preferences and feeding ecology. One group consists of three species that feed on crustaceans and algae in intertidal regions in Peru and Chile—*Microlophus atacamensis* (Donoso-Barros, 1960); *M. heterolepis* (Wiegmann, 1834); and *M. quadrivittatus* (Tschudi, 1845). The second group comprises seven species that feed on insects and terrestrial plants in dry terrestrial regions (i.e., valleys and deserts) in Ecuador, Peru, and Chile—*M. peruvianus* (Lesson, 1830); *M. tarapacensis* (Donoso-Barros, 1966); *M. theresiae* (Steindachner, 1901); *M. theresioides* (Donoso-Barros, 1966); *M. thoracicus* (Tschudi, 1845); *M. tigris* (Tschudi, 1845); and *M. yanezi* (Ortiz-Zapata, 1980) (Ortiz and Serey 1979, Ibáñez *et al.* 2015). The *M. occipitalis* Group contains two subgroups differing in distribution patterns. Ten species are endemic to the Galápagos Islands—*M. albemarlensis* (Baur, 1890); *M. barringtonensis* (Baur, 1892); *M. bivittatus* (Peters, 1871); *M. delanonis* (Baur, 1890); *M. duncanensis* (Baur, 1890); *M. grayii* (Bell, 1843); *M. habelii* (Steindachner, 1876); *M. indefatigabilis* (Baur, 1890); *M. jacobii* (Baur, 1892); and *M. pacificus* (Steindachner, 1876). The remaining three species occur in continental regions of Ecuador and Peru—*M. koepckeorum* (Mertens, 1956); *M. occipitalis* (Peters, 1871); and *M. stolzmanni* (Steindachner, 1891) (Dixon & Wright 1975, Frost 1992, Benavides 2007, 2009).

In an herpetological inventory of different inter-Andean dry-forest regions in northern Peru, *Microlophus stolzmanni* was abundant at most of the study sites (Koch *et al.* 2018). This species is endemic to northern Peru and occurs in the departments of Amazonas, Ancash, Cajamarca, La Libertad, Lambayeque, and Piura at elevations of 394–1952 m a.s.l. (Dixon and Wright 1975, Venegas *et al.* 2016, Koch *et al.* 2018). This diurnal, scansorial lizard is mostly commonly is found on the ground, but it also occurs on stones or rocks, tree trunks, or on branches of shrubs and cacti plants (Dixon and Wright 1975, Venegas *et al.* 2016). Adult males and females are sexually dimorphic in coloration and size. In females, the eyes and nostrils are framed in red and the ventral and lateral surfaces of the head are pigmented with gray, white, yellow, or orange. The throat is gray to brown, and the dorsum olive green with white dots. Females are distinctly smaller than males and have low dorsal crest (Figure 1). In contrast, the ventral part of the head of males is gray or cream-colored with oblique thin dark brown lines. The throat is pigmented with black and sometimes, some yellow. Dorsolaterally, the body bears two thin, parallel black lines. The males are bigger and more massive than the females, and have a pronounced dorsal crest (Figure 2).

The diet of a congener, *Microlophus thoracicus,* consists of a great deal of plant material, as well as invertebrates, such as ants and insect larvae; this suggests that *M. thoracicus* is semi-herbivorous in contrast to the insectivorous species *M. peruvianus* and *M. occipitalis.* The head of *M. thoracicus* is higher and broader than those of the insectivorous congeners, thereby suggesting that *M. thoracicus* has a stronger bite force than do the insectivores (Pérez *et al.* 2015). Based on his observation that *M. stolzmanni* and *M. thoracicus* have similar cranial dimensions, Toyama (2016) predicted the species would have similar semi-herbivorous diets; however, the diet of *M. stolzmanni* has yet to be documented.

The following analysis of the diet in populations of *Microlophus stolzmanni* from the

Figure 1. Two different color patterns of female *Microlophus stolzmanni* with close-ups of the ventral part of the heads (top and middle) and coloration of a juvenile specimen (bottom) from Peru.

Figure 2. Two different color patterns of male *Microlophus stolzmanni* with close-ups of the ventral part of the heads from Peru.

inter-Andean dry-forest valleys in northern Peru was conducted to examine whether there are sexual differences and ontogenetic changes in the diet of this species. In addition, we describe the foraging strategy of the species, and determine whether *M. stolzmanni* is a food generalist or specialist. Morphological analyses were performed to explain differences in feeding behavior between age and sex groups.

Materials and Methods

Fieldwork

As part of an intensive herpetological inventory in the inter-Andean dry-forest valleys of the Marañón River and its tributaries, a total of 142 individuals of *Microlophus stolzmanni* was collected (Koch *et al.* 2018). Most of these lizards were deposited in the collections of the Centro de Ornitología y Biodiversidad (CORBIDI) in Lima, Peru, and the Museo de Historia Natural de la Universidad Nacional de San Agustín (MUSA) in Arequipa, Peru. However, CK was allowed to export 49 individuals (24 males, 14 females, 11 juveniles) for further examination and to add them to the collection of the Zoologisches Forschungsmuseum Alexander Koenig (ZFMK) in Bonn, Germany. These specimens were used for the dietary analysis. The lizards were collected in the course of different field surveys between July 2005 and October 2010 from various localities, and were encountered during visual surveys. During the day, individuals were found either basking in the sun on stones, stone walls, rocks, or logs until 17:30 hr or actively running around and searching for food on tracks or in low grass vegetation. Some lizards were found active until 23:00 hr. Nevertheless, after nightfall (~ 19:00 hr), most individuals were found sleeping or resting hidden under stones or logs, in holes of stone walls, or unhidden on trunks, shrubs, cacti plants, or on roofs (Koch *et al.* 2018). Of the lizards included in this analysis, most were collected during their active hours. Only four individuals (ZFMK 88722, 91778–91779, 91783) were collected while they were asleep; because these lizards were found within 3 hr after nightfall, they probably had not been asleep for a long. The other lizards collected by CK are, as follow: three in July 2005 (ZFMK 85021–85023); three in May 2008 (ZFMK 88715–88717); eight in July 2008 (ZFMK 88718–88725); eight in March 2009 (ZFMK 90839–90846); eight in April 2009 (ZFMK 90847–90854); three in December 2009 (ZFMK 90855–90857); 10 in January 2010 (ZFMK 91771–91780); and six in October 2010 (ZFMK 91781–91786). Collecting localities are given in Appendix I. The lizards were captured by hand, with a fishing net or a fishing rod with a loop of cord, or with a sling shot. The animals were euthanized by an injection of the veterinary anesthetic T61 the following morning, no more than 10 hr after their capture, to assure that the stomach contents were in the best possible condition for identification. After fixation in 10% formalin for 24–48 hr, the lizards were preserved in 70% ethanol.

Data Analysis

The sex of the lizards was determined by coloration, the internal reproductive organs (testicles or ovaries), or by the presence of everted hemipenes. Lizards lacking mature gonads and lacking the typical coloration of adults described above were considered to be juveniles.

Dial calipers (0–150 mm; to the nearest 0.01 mm) were used to measure snout–vent length (SVL), head length, head width, head height, body width, and tail length of each lizard, as well as to determine the length and width of prey items. Measurements of head length, head width, and head height are the same as those of Meyers *et al.* (2002). Stomachs and fat bodies were removed from the preserved specimens; the stomachs were dissected to remove the contents and examine them in a Petri dish under a stereomicroscope following the methodology of Bährmann (2011). Weights of lizards, stomachs, and fat bodies were determined with a digital weighing machine (Almasa® MT 7; max. 200 g; to the nearest 0.01 g). The food items were assigned to 14 prey categories; of these 13 were identified to order or family level and the 14th category was reserved for all undetermined taxa, including unidentifiable parts of athropods and plant material, which was not identified taxonomically, but noted as leaves, fibers, seeds and fruits. Contents of the stomach were categorized as either “sedentary” or “mobile” prey to define the foraging strategy of the lizards. In addition, the contents were identified as “soft,” “medium-hard,” or “hard” prey to analyze the bite force used by the lizard (explained in Beuttner and Koch 2019).

The following variables were measured: the number of consumed items (N); the percent by number ($N_{\%}$); the frequency of occurrence (F, number of stomachs in which a given prey category was found); the percent by frequency ($F_{\%}$); the volume (V mm³); and the percent by volume ($V_{\%}$) for each prey category. The length and width of the individual prey item was used to calculate its volume (V) with the formula for an ellipsoid of Colli and Zamboni (1999). The data were pooled for all specimens and were subsequently separated by sex/age classes.

Every head dimension was regressed against SVL to compare head dimensions among lizard groups. A residual analysis was performed on these data to avoid the influence of different SVL values. Likewise, the weights of stomachs and fat bodies were regressed against body weight and a residual analysis conducted to avoid the influence of body weights. Before comparisons were made, we tested the normality of residuals with the Shapiro-Wilk-Test. Depending on the result, parametric (T-Test) or non-parametric (Mann-Whitney U-Test) tests were used to determine statistical differences between groups. All statistical tests were executed in OriginPro version 8.0724 (OriginLab, Northampton, MA, USA).

We used the dimensions of complete prey items as a reference to estimate the dimensions and calculate the volumes of fragmented prey items. Complete prey items of each prey category were categorized according to the mean values of their sizes (i.e., exceedingly large, large, medium-sized, small, minute; Appendix II). We calculated the niche breadth by using the (1) Simpson-Index B (Simpson 1949) to quantify the diversity of prey used by the animals, and (2) the inverse of the Simpson-Index B' to compare the values with other published data. Values for B vary from 0 (no diversity, exclusive use of a single prey type, specialist) to 1 (highest diversity, prey items of all categories, generalist), whereas values for B' vary from 1 (no diversity, exclusive use of a single prey type, specialist) to n (highest diversity, prey items of all categories, generalist). In addition, the Index of Relative Importance (IRI) of each prey category in relation to the total food spectrum was calculated (Pinkas 1971, Pinkas *et al.* 1971). Last, niche overlap (O_{jk}) in the food spectrum between the different groups (females, males, juveniles, adults) was estimated by the Pianka-Index (Pianka 1974). The values for O_{jk} vary from 0 (no overlap, groups compared have a completely different food spectra) to 1 (complete overlap, groups compared have the same food spectrum). All formulas used to calculate V, B, B', IRI, and O_{jk} are shown and explained in Beuttner and Koch (2019).

Results

Morphological Analysis

Female *Microlophus stolzmanni* are significantly smaller and lighter than males (Length: U-Test, U = 16, Z = -4,5846, $p = p < 0.001$; Appendix III). The head dimensions of all individuals are positively correlated with SVL (head length against SVL: $y = 0.2424x + 1.9509$, $R^2 = 0.955$; head width against SVL: $y = 0.1639x + 1.3293$, $R^2 = 0.967$; head height against SVL: $y = 0.1292x + 0.7496$, $R^2 = 0.9451$). Adults have significantly smaller head dimension residuals than do juveniles (T-Test; length: t = -3.64235; width: t = -4.95493; height: t = -1.89606; all $p < 0.05$), but there are no significant differences between males and females (T-Test; length: t = -1.11708, $p = 0.27$; width: t = -0.00822, $p = 0.99$; height: t = -0.27056, $p = 0.79$; Appendix III).

We found fat bodies in 38 individuals (77.6%) of *Microlophus stolzmanni* (22 males, 11 females, 5 juveniles). The residuals for the weights of stomachs and body fat do not differ among the groups (U-Test; fat body: $U_{female/male} = 223$, $U_{female/juvenile} = 102.5$, $U_{male/juvenile} = 159$, $U_{adult/juvenile} = 261.5$, all $p < 0.05$; stomach weight: $U_{female/male} = 190$, $U_{female/juvenile} = 68$, $U_{male/juvenile} = 92$, $U_{adult/juvenile} = 160$, all $p < 0.05$; Appendix III).

Stomach Contents

The composition of the stomach contents of the total sample of *Microlophus stolzmanni,* as well for specimens grouped by sex/age classes is summarized in Table 1. A total of 855 items, representing 802 prey items ($N_{\%}$ = 93.8%) and 49 pieces of plant material ($N_{\%}$ = 5.7%), and 4 stones ($N_{\%}$ = 0.5%) were identified. The plant material was almost exclusively comprised of entire seeds and leaves. We found prey items in 44 ($F_{\%}$ = 97.8%), plant material in 25 ($F_{\%}$ = 51.0%), and stones in 4 ($F_{\%}$ = 8.2%) stomachs. The percent by volume of the prey items ($V_{\%}$ = 59.5%) is slightly higher than that of the plant material ($V_{\%}$ = 40.3%), whereas that of the inorganic material is negligible ($V_{\%}$ = 0.2%). With respect to the IRI, the prey items (IRI = 14992.7) played the major role in the diet of *M. stolzmanni.* The IRI of plant material is 2555.8 and that of inorganic material an almost negligible 6.22. In 33 adult stomachs, we found 550 food items with a total volume of V = 27490.7 mm³, whereas 11 juvenile stomachs had 305 food items with a total volume of V = 778.4 mm³.

In adults and juveniles, the prey items constituted the major part of the diet with an IRIs of 14911.0 and 19840.0, respectively. Plant material is less important in adults (IRI = 3539.4), and almost negligible in juveniles (IRI = 6.1).

In 22 stomachs of male *Microlophus stolzmanni,* 347 food items with a total volume (V) 24026.6 mm³ was found, whereas and in the stomachs of 12 females, 203 food items with a total volume 3464.2 mm³ was found. Prey items are more important in both males and females, with IRIs of 13738.1 and 16873.0, respectively; in contrast, plant material accounts for IRIs of 4527.4 and 1758.1, respectively. Inorganic material is almost negligible in all groups, with IRIs of 6.6 in adults, 0.3 in juveniles, 6.6 in males, and 9.4 in females.

The most important prey category is Formicidae with respect to the number of consumed items (N = 462, $N_{\%}$ = 54.0%), the number of stomachs which contained the category (F = 31, $F_{\%}$ = 68.9%), and the IRI 4002.5, whereas formicids rank fourth in the volume (V = 1147.6 mm³; $V_{\%}$ = 4.1%). The prey having the greatest volume is lepidopteran larvae (V = 5076.9 mm³; $V_{\%}$ = 18.0%); these rank second in frequency (F = 15, $F_{\%}$ = 33.3) and IRI (758.6) and third in number of consumed items (N = 41, $N_{\%}$ = 4.8%). Adult Lepidoptera rank second in volume (V = 3453.6 mm³; $V_{\%}$ = 12.2%), third in IRI (398.6), and fourth in number of consumed items (N = 35, $N_{\%}$ = 4.1%). Isopterans are second in number of consumed items (N = 157, $N_{\%}$ = 18.4%), whereas coleopterans rank third in frequency (F = 14, $F_{\%}$ = 31.1%) and Heteroptera ranks third in volume (V = 2922.8 mm³; $V_{\%}$ = 10.3%).

On closer inspection of the IRI values, Formicidae is the most important prey category in the diet of all groups: adults, 3150.5; juveniles, 6721.7; males, 1317.4; and females, 7696.5 (Table 2). Lepidopteran larvae are the second most important category in adults with an IRI of 755.7; males, 720.2; and females, 390.9; however, they rank third in juveniles with an IRI of 618.1. In juveniles, adult Lepidoptera ranked second with an IRI of 952.6, whereas this prey ranks fourth in all other groups with the following IRI values: adults, 321.2; males, 321.6; and females, 191.5. Isoptera ranks third in adults (IRI = 397.0) and males (IRI = 678.9), and also is of some importance in the diet of juveniles (IRI = 274.3); Isoptera is least significant in females, which have an IRI of 23.3. The third most important prey category in females is Heteroptera (IRI = 344.2), which ranked fifth in adults (IRI = 201.2), as well as in males (IRI = 247.3), and is almost insignificant in the diet of juveniles (IRI = 17.5). The order Araneae is of some importance in the diet of juveniles (IRI = 460.4; Table 2).

With regard to the food niche breadth, the Simpson-Index for the species is B = 0.64 and the inverse Simpson-Index is B' = 2.79. Males have the highest values (B = 0.74, B' = 3.87) and females the lowest (B = 0.27, B' = 1.37). Furthermore, there is a significant difference between adults (B = 0.71, B' = 3.44) in contrast to juveniles (B = 0.41, B' = 1.71; Table 3).

The Pianka-Index (O_{jk}) indicated that the highest niche overlap value is between females and juveniles (O_{jk} = 1.00), whereas males and females had the lowest overlap value (O_{jk} = 0.80). Adults and juveniles have the second highest overlap value (O_{jk} = 0.95) and males and juveniles rank third in food niche overlap (O_{jk} = 0.83).

Table 1. Composition of the stomach content (prey items (PI), plant material (PM) and inorganic material (IM)) of *Microlophus stolzmanni*. The data were pooled for all specimens and were subsequently separated by 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* = 34)			Juveniles (*N* = 11)			Males (*N* = 22)			Females (*N* = 12)			Total (*N* = 45)		
	PI	**PM**	**IM**	**PI**	**PM**	**IM**	**PI**	**PM**	**IM**	**PI**	**PM**	**IM**	**PI**	**PM**	**IM**
N	499	48	3	303	1	1	304	41	2	195	7	1	802	49	4
$N_{\%}$	90.7	8.7	0.6	99.4	0.3	0.3	87.6	11.8	0.6	96.1	3.4	0.5	93.8	5.7	0.5
F	33	24	3	11	1	1	21	18	2	12	7	1	44	25	4
$F_{\%}$	97.1	70.6	8.8	100.0	9.1	9.1	95.5	81.8	9.1	100.0	58.3	8.3	97.8	55.6	8.9
V (mm³)	16048.6	11382.8	59.4	771.0	2.6	4.7	13531.1	10458.3	37.3	2517.5	924.5	22.2	16819.6	11382.8	64.1
$V_{\%}$	58.4	41.4	0.2	99.1	0.3	0.6	56.3	43.5	0.2	72.7	26.7	0.6	59.5	40.3	0.2
IRI	14477.6	3539.4	6.6	19840.0	6.1	0.3	13738.1	4527.4	6.6	16873.0	1758.1	9.4	14992.7	2555.8	6.2

Foraging Strategy

The 41 stomachs of *Microlophus stolzmanni* contained 776 prey items with a total volume of V = 15413.8 mm³. One hundred and ten prey items were assigned to the mobile prey category ($N_{\%}$ = 14.2%) with a volume of V = 7025.0 mm³ ($V_{\%}$ = 45.6%), whereas 666 ($N_{\%}$ = 85.8%) were classified as sedentary prey with a volume of V = 8388.8 mm³ ($V_{\%}$ = 54.4%). We found mobile prey in 34 stomachs ($F_{\%}$ = 82.3%) and sedentary prey in 38 ($F_{\%}$ = 92.7%). The IRI of sedentary prey (12997.4) is 2.6 times higher than the IRI of mobile prey (4955.9). The different lizard groups (i.e., adults, juveniles, males, females) have considerably higher values for sedentary prey items than for mobile prey. Moreover, sedentary prey items appear the most frequently in the stomachs in all groups. The volume of consumed sedentary prey items is slightly higher in all groups than the volume of mobile prey, except for females which consume a slightly higher volume of mobile prey than sedentary prey. The IRI for sedentary prey is between 2.5 and 3 times higher than for mobile prey for all specimen groups (Table 4).

Bite Force

We identified 825 prey items and plant material in 45 stomachs of *Microlophus stolzmanni.* Of these, 67 were categorized as hard prey ($N_{\%}$ = 8.1%) with a volume of V = 11860.8 mm³ ($V_{\%}$ = 44.3%), 644 ($N_{\%}$ = 78.1%) as medium-hard prey with a volume of V = 6115.1 mm³ ($V_{\%}$ = 22.8%), and 114 ($N_{\%}$ = 13.8%) as soft prey with a volume of V = 8820.7 ($V_{\%}$ = 32.92%). Hard prey items were present in 32 stomachs ($F_{\%}$ = 71.1%), medium-hard prey in 33 ($F_{\%}$ = 73.3%), and soft prey in 29 stomachs ($F_{\%}$ = 64.4%). The IRI of medium-hard prey (3725.1) is the highest, followed by the IRI of hard prey (3725.1). All groups of lizards consumed greater numbers of medium-hard prey items than either hard or soft prey.

Table 2. Prey items of *Microlophus stolzmanni*. For each category the number (N), the percent by number ($N_{\%}$), the frequency (F), the percent by frequency ($F_{\%}$), the calculated volume (V; mm^3), 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. (*Please note: the volume of the order Orthoptera could not be calculated, as no entire prey items of this category were found to calculate the mean value).

							IRI				
Prey category	***N***	***N*$_{\%}$**	***F***	***F*$_{\%}$**	**V (mm^3)**	**V$_{\%}$**	**Adults**	**Juveniles**	**Males**	**Females**	**Total**
Araneae	20	2.3	13	28.9	133.0	0.5	37.5	460.4	19.4	97.7	81.2
Coleoptera	16	1.9	**14**	31.1	389.3	1.4	113.9	110.4	146.2	53.8	101.1
Diptera adult	12	1.4	2	4.4	17.2	0.1	0.6	51.5	1.4	0	6.5
Diptera larvae	6	0.7	4	8.9	140.0	0.5	12.4	4.4	27.6	0	10.7
Formicidae	**462**	54.0	**31**	68.9	1147.6	4.1	**3150.5**	**6721.7**	**1317.4**	**7696.5**	**4002.5**
Hemiptera	4	0.5	2	4.4	17.4	0.1	1.1	19.6	2.7	0	2.4
Hymenoptera	2	0.2	2	4.4	88.6	0.3	0.8	79.8	1.8	0	2.4
Heteroptera	18	2.1	6	13.3	**2922.8**	10.3	201.2	17.5	247.3	**344.2**	166.0
Isoptera	**157**	18.4	6	13.3	2024.3	7.2	**397.0**	274.3	**678.9**	23.3	340.2
Lepidoptera adult	35	4.1	11	24.4	**3453.6**	12.2	321.2	**952.6**	321.6	191.5	**398.6**
Lepidoptera larvae	**41**	4.8	**15**	33.3	**5076.9**	18.0	**755.7**	**618.1**	**720.2**	**390.9**	**758.6**
Orthoptera	2	0.2	2	4.4	-*	-	2.1	0	0	16.5	1.0
Lithobiomorpha	1	0.1	1	2.2	3.0	0.01	0	6.5	0	0	0.3
Undetermined prey items	26	3.0	14	31.1	1405.8	5.0	241.2	562.5	191.2	698.3	249.2

Table 3. Diversity in the dietary spectrum of *Microlophus stolzmanni*. 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	0.71	0.41	0.74	0.27	0.64
B'	3.44	1.71	3.87	1.37	2.79
S	13	13	12	9	14

There are no great differences in the numbers of hard or soft prey items consumed, except in juveniles, which consumed conspicuously more soft prey than hard prey items. In females, all prey items appeared in the stomachs with the same frequency. In males and in adults, hard prey items are encountered more frequently than soft prey items. In contrast, in juveniles the frequency of soft prey is the higher than that of hard prey items. In males and adults, hard prey items have a greater volume than does medium-hard prey. In females, the volume of medium-hard prey is higher than that of soft prey. In juveniles, the volume of soft prey is higher than that of hard prey. The IRI for medium-hard prey is higher in all groups than that of soft prey; however, in juveniles, the IRI is lowest in for hard prey (Table 5).

Discussion

This first detailed study of the diet of *Microlophus stolzmanni* is based on lizards collected in the dry forest of northern Peru. Our findings suggest that *M. stolzmanni* is a semi-herbivorous food generalist that also consumes animal items. All age groups prefer sedentary prey and *M. stolzmanni* can be considered to actively forage. However, as the lizard matures, plant material becomes more prevalent in the diet.

Male *Microlophus stolzmanni* are significantly larger than females, as has been observed in

Table 4. Mobile (MP) and sedentary prey (SP) items in the stomach content of *Microlophus stolzmanni* 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* = 33)		Juveniles (*N* = 11)		Males (*N* = 21)		Females (*N* = 12)		Total (*N* = 44)	
	MP	**SP**	**MP**	**SP**	**MP**	**SP**	**MP**	**SP**	**MP**	**SP**
N	63	417	147	249	49	240	14	177	110	666
$N_{\%}$	13.1	86.9	15.9	84.1	17.0	83.0	7.3	92.7	14.2	85.8
F	22	28	9	11	14	17	9	10	34	38
$F_{\%}$	64.7	82.4	81.8	100.0	63.6	77.3	75.0	83.3	82.9	92.7
V (mm³)	6694.0	8051.4	331.0	337.4	5741.8	7143.4	952.2	908.0	7025.0	8388.8
$V_{\%}$	45.4	54.6	49.5	50.5	44.6	55.4	51.2	48.8	45.6	54.4
IRI	3786.7	11651.1	5350.8	13460.1	3914.7	10701.0	4388.9	11790.2	4955.9	12997.4

congeners, such as *M. atacamensis* and *M. occipitalis* (Watkins 1996, Vidal *et al.* 2002).

In the absence of significant differences in stomach weight and fat body weight in proportion to body weight among our defined groups of *Microlophus stolzmanni,* we assume that all members of our sample had a similar nutritional state. We observed a high percent by volume of both prey items ($V_{\%}$ = 59.5%) and plant material ($V_{\%}$ = 40.3%). This confirms Toyama's (2016) assumption of a semi-herbivorous dietary spectrum in *M. stolzmanni,* based on his investigations of the head dimensions of the species. However, animal items are more prevalent in the diet of adults (IRI = 14477.6) than plant material (IRI = 3539.4), and plant material is relatively unimportant to juveniles (IRI = 6.1). Thus, juveniles are insectivorous and adults are semi-herbivorous. This ontogenetic diet shift occurs in many lizard species that consume insects as juveniles and become herbivorous or semi-herbivorous as adults (e.g., Estes and Williams 1984, Dessem 1985, Cooper and Vitt 2002, van Leeuwen *et al.* 2011). Troyer (1982) observed that juvenile lizards lack the intestinal cellulose-degrading microflora that enables adult lizards to digest plant material. Moreover, juvenile lizards require animal protein to promote growth and development (Mayhew 1963, Johnson and Lillywhite 1979). Toyama (2016) assumed that the congener of *M. stolzmanni*—*M. thoracicus*—also has a semi-herbivorous diet, because the heads of both species are significantly higher and wider than those of the insectivorous species, *M. peruvianus* and *M. occipitalis.*

Having found only an insignificant amount of inorganic material in the stomachs of *Microlophus stolzmanni,* we assume that its consumption was unintentional.

With a value of B = 0.64 for the Simpson-Index, *Microlophus stolzmanni* can be considered as a food generalist characterized by consumption of a great diversity food items. However, given inverse Simpson-Index of B' = 2.79, the diversity is lower than those of *M. thoracicus* (B' = 6.97) and *M. tigris* (B' = 4.33) (Pérez *et al.* 2015) and

Table 5. Hard (H), medium-hard (M) and soft prey (S) items in the stomach content of *Microlophus stolzmanni* 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; mm^3), the percent by volume ($V_{\%}$) and the Index of Relative Importance (IRI) are shown.

	Adults (*N* = 34)			Juveniles (*N* = 11)			Males (*N* = 22)			Females (*N* = 12)			Total (*N* = 45)		
	H	**M**	**S**	**H**	**M**	**S**	**H**	**M**	**S**	**H**	**M**	**S**	**H**	**M**	**S**
N	61	404	63	6	240	51	51	229	50	10	175	13	67	644	114
N%	11.6	76.5	11.9	2.0	80.8	17.1	15.5	69.4	15.2	5.1	88.4	6.6	8.1	78.1	13.8
F	28	24	14	4	9	10	20	15	11	9	9	9	32	33	29
***F*%**	82.4	70.6	41.2	36.4	81.8	90.9	90.9	68.2	50.0	75.0	75.0	75.0	71.1	73.3	64.4
V (mm^3)	11773.6	5853.4	8501	89.7	261.7	319.7	10825.6	4487.1	8030.7	948	1366.3	470.3	11860.8	6115.1	8820.7
V%	45.1	22.4	32.5	13.4	39.0	47.6	46.4	19.2	34.4	34.0	49.1	17.0	44.3	22.8	32.9
IRI	4662.4	6982.4	1831	559.7	9801.8	5891.6	5620.9	6042.0	2477.7	2932.1	10308.7	1759.2	3725.1	7397.9	3011.8

nearly the same as the dietary spectrum of *M. peruvianus* (B' = 2.97; Quispitúpac and Pérez 2009).

Male and female *Microlophus stolzmanni* have the greatest disparity in food diversity of all of the groups; the diet of males is more diverse (B = 0.74) than that of females (B = 0.27). Accordingly, only male *M. stolzmanni* are food generalists, whereas females have a more specialized diet. The diet of juveniles is more diverse (B = 0.41) than that of females, but much lower than that of males. Therefore, juveniles, like females are not food generalists. The niche overlap in the dietary spectra of the various groups of *M. stolzmanni* is comparatively high with all values for $O_{jk} \geq 0.8$. The "medium-hard prey" category is preferred by all groups of *M. stolzmanni;* however, as measured by percent by volume, "hard prey" is greater in adults, males, and in all specimens together. These observations may reflect our placement of plant material in the category of hard prey. Plant material was counted as one item when found in the same stomach, thereby accounting for the relatively low number of hard prey items. Male *M. stolzmanni* have a greater diversity of food items than do females and juveniles because the higher and wider heads of males enable them to produce a higher bite force (McBrayer and Corbin 2007, Miles *et al.* 2007, Toyama 2016) and thus consume larger and harder dietary items (Herrel *et al.* 2001a,b, Verwaijen *et al.* 2002, Herrel 2007, Huyghe *et al.* 2009). Females also have larger heads than juveniles, but the difference is far less pronounced than that between males and juveniles. Other factors also may influence dietary variation among the groups, such as seasonal variation in temperature or differing microhabitat usage (Paulissen 1988, Griffiths *et al.* 1996). Furthermore, hard food items do not decompose as rapidly as soft items. Some lizards were euthanized as many as 10 hr after capture. The longer the time before euthanization, the higher the probability that soft items may have decomposed such that it might seem that there was a greater proportion of hard items. However, most lizards were euthanized more quickly.

All *M. stolzmanni* examined mainly contained clumped, colony-building (e.g., Formicidae and Isoptera) or sedentary prey (e.g., Lepidoptera larvae), with mobile prey being less frequent. Sedentary or clumped prey usually is consumed by active foragers (Pianka 1970, Pianka and Parker 1975, Huey and Pianka 1981, Nagy *et al.* 1984, Magnusson *et al.* 1985, Toft 1985, Anderson and Karasov 1988, Bergallo and Rocha 1994). Thus, *M. stolzmanni* should be considered to be an active forager, which is consistent with our field observations of several lizards actively foraging on the ground by day.

Recently we analyzed the diet of the arboreal lizard *Polychrus peruvianus* (Beuttner and Koch 2019) from primarily the same Peruvian localities from which we collected *M. stolzmanni.* Although both species have access to the same food resources, we found differences in the niche breadth values of both species. *Polychrus peruvianus* (B' = 5.65) has a much more diverse diet than *M. stolzmanni* (B' = 2.79). This is consistent with Bergallo and Rocha's (1994) observation that actively foraging species can be more selective in food choice, resulting in lower food diversity. In contrast, sit-and-wait predators, such as *P. peruvianus,* spend more time motionless and consume a wide variety of prey types, depending on what passes by (Vitt and Caldwell 2013).

Microlophus stolzmanni is considered as Least Concern by the IUCN Red List of Threatened Species (Venegas *et al.* 2016) and was found in high densities in most surveyed localities of the inter-Andean dry-forest valleys in northern Peru. Nevertheless, as Beuttner and Koch (2019) and Koch *et al.* (2013) pointed out, most of these surveyed localities face multiple, complex threats that may lead to habitat loss or fragmentation. To our knowledge, *M. stolzmanni* does not occur in any protected area, and there is limited information in the literature about natural history, distribution and population sizes of the species. Thus, we cannot assess the effect of potential habitat threats that might lead to a populational decline of the species.

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Appendix I. *Specimens examined.*

Microlophus stolzmanni: PERU. Amazonas: Bagua: **Bagua Grande:** ZFMK 88723 (05°47'33.3" S, 78°23'04.9" W, 568 m a.s.l.); **Bagua Chica:** ZFMK 88724, 88725 (05°38'06.9" S, 78°32'27.7" W, 500 m a.s.l.); Utcubamba: **Cumba:** ZFMK 90855, 90856 (05°56'14.6" S, 78°39'50.4" W, 465 m a.s.l.); Chachapoyas: **Balsas:** ZFMK 90847 (06°50'20.7" S, 78°01'23.3" W, 859 m a.s.l.); ZFMK 90848 (06°50'54.3" S, 78°00'01.5" W, 1065 m a.s.l.); Quebrada Honda / Llusca: ZFMK 85021–85023 (06°49'11" S, 78°00'12" W, 900 m a.s.l.). Cajamarca: Jaén: **Santa Rosa de la Yunga:** ZFMK 88718 (05°26'23.9" S, 78°33'16.7" W, 1273 m a.s.l.); ZFMK 88719, 88720 (05°26'17.3" S, 78°33'12.7" W, 1280 m a.s.l.); **Bellavista:** ZFMK 88715 (05°38'02.9" S, 78°38'08.1" W, 447 m a.s.l.); ZFMK 90845 (05°37'27.6" S, 78°38'49.5" W, 434 m a.s.l.); ZFMK 90846 (05°30'29.0" S, 78°30'23.6" W, 444 m a.s.l.); **Gotas de Agua:** ZFMK 88716, 88717 (05°41'08.9" S, 78°45'22.5" W, 660 m a.s.l.); **Pucará:** ZFMK 88721, 90839–90841 (06°02'23.0" S, 79°07'59.4" W, 901 m a.s.l.); ZFMK 88722 (06°01'59.2" S, 79°07'27.7" W, 966 m a.s.l.); ZFMK 90842, 90843 (06°02'37.1" S, 79°08'15.5" W, 965 m a.s.l.); ZFMK 90844 (06°03'36.1" S, 79°03'16.4" W, 949 m a.s.l.); Cutervo: **Across from Cumba:** ZFMK 90857 (05°54'24.1" S, 78°39'50.4" W, 465 m a.s.l.); Celendín: **Chacanto:** ZFMK 90850 (06°50'59.0" S, 78°02'14.6" W, 1087 m a.s.l.); ZFMK 90849 (06°51'08.9" S, 78°01'58.2" W, 992 m a.s.l.); ZFMK 90851 (06°51'14.1" S, 78°01'40.1" W, 969 m a.s.l.). La Libertad: Bambamarca: **Calemar:** ZFMK 91784–91786 (07°32' S, 77°43' W, 1108–1340 m a.s.l.); Bolívar: **San Vicente / Pusac:** ZFMK 90852–90854 (06°59' S, 77°55' W, 1449–1596 m a.s.l.); Cajabamba: **Santa Rosa (Marcamachay):** ZFMK 91781, 91782 (07°22'06.1" S, 77°53'33.8" W, 1185 m a.s.l.); ZFMK 91783 (07°22'03.9" S, 77°53'54.5" W, 1235 m a.s.l.); Pataz: **Chagual:** ZFMK 91771, 91772 (07°50' S, 77°38' W, 1239–1363 m a.s.l.); **Vijus:** ZFMK 91773–91777 (07°43' S, 77°39' W, 1290–1408 m a.s.l.); **Pias:** ZFMK 91778 (07°53'55.3" S, 77°33'55.5" W, 1937 m a.s.l.); ZFMK 91779 (07°53'47.7" S, 77°34'29.2" W, 1883 m a.s.l.); ZFMK 91780 (07°53'41.0" S, 77°33'58.3" W, 1952 m a.s.l.).

Appendix II. *Mean values of prey-item sizes to estimate the length and width of incomplete prey items for each prey taxon. Taxa represented by only complete items are not listed.*

Prey taxon	Size	Body length (mm)	Body width (mm)
Araneae	exceedingly large	5.0	2.6
	medium	3.6	1.9
	small	1.9	1.2
	minute	0.9	0.5
Coleoptera	exceedingly large	16.4	10.9
	large	12.8	3.7
	medium	4.7	2.9
	small	2.3	0.9
Formicidae	exceedingly large	8.9	2.7
	large	6.8	2.3
	medium	4.0	0.9
	small	2.3	0.6
	minute	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
Isoptera	medium	6.4	2.0
	small	3.9	1.1
Lepidoptera Larve	large	29.9	4.9
	medium	14.2	3.2
	small	10.0	1.3
	minute	3.7	0.9
Orthoptera	large	17.4	4.5
	medium	13.1	3.2

Appendix III. *Measurements (range/±SD) of* Microlophus stolzmanni. *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
$N_{specimens}/N_{fat\ bodies}$	14/11	24/22	11/5	49/38
Snout–vent length (mm)	52–100	66–138	27–56	27–138
	65.1 ± 10.3	97.2 ± 18.2	40.6 ± 8.8	75.3 ± 27.3
Body weight (g)	14–33	15–40	7–12	7–40
	18.6 ± 4.5	25.5 ± 5.7	9.9 ± 2.1	20.0 ± 7.8
Head length (mm)	5–36	9–99	1–5	1–99
	10.6 ± 7.4	38.3 ± 22.8	2.8 ± 1.4	22.4 ± 22.8
Head width (mm)	15–26	19–35	9–15	9–35
	17.0 ± 2.7	26.0 ± 3.7	11.7 ± 2.3	20.2 ± 6.8
Head height (mm)	9–20	12–23	6–11	6–23
	11.7 ± 2.4	17.4 ± 2.8	8.1 ± 1.3	13.7 ± 4.6
Fat body weight (g)	0.01–0.4	0.01–1.1	0.01–0.01	0.01–1.1
	0.11 ± 0.13	0.13 ± 0.24	0.01 ± 0.00	0.11 ± 0.20
Fat body weight (%)	0.1–4.1	0.03–1.1	0.2–0.9	0.03–4.1
	0.91 ± 1.10	0.22 ± 0.27	0.49 ± 0.31	0.46 ± 0.70
Stomach weight (g)	0.1–0.8	0.2–2.8	0.01–0.3	0.01–2.8
	0.34 ± 0.21	1.07 ± 0.66	0.12 ± 0.08	0.65 ± 0.63
Stomach weight (%)	1.0–8.3	1.1–8.6	0.9–7.6	0.9–8.6
	3.64 ± 2.10	3.04 ± 1.62	4.22 ± 2.30	3.48 ± 1.99