

Notes on the diet of *Anolis* lizards (Iguanidae: Dactyloinae) from Yasuní National Park in Amazonian Ecuador

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We briefly describe the diet of six species of lizards of the genus *Anolis* in the Yasuní National Park, located in the western part of the Amazon Rainforest. A total of 241 prey items found in the stomachs of the lizards were identified. We noted that Aranea and Hymenoptera were the most frequent diet categories used by the lizard community. In terms of prey volume, Hemiptera and insect larvae were the most representative prey. The description of the diet of *Anolis* provided by this study can be further combined with information related to their natural history, thus shedding light on ecological mechanisms that influence adaptation.

Key words: Amazon rain forest; *Anolis*; diet composition.

Anolis (Iguanidae: Dactyloinae) lizards represent the most diverse lizard clade traditionally recognized as a genus on the planet (UETZ *et al.*, 2022). Commonly referred to as anoles, they are widely distributed in the Caribbean, Central America, and northern South America (Losos, 1992; LOSOS & RICKLEFS, 2009) and despite being extensively studied in the Caribbean, information on mainland anoles, usually part of very large communities of insectivorous lizards (VITT *et al.*, 2002) is scarce. Diet is a pivotal part of reptile's natural history because it provides the energy for biological processes such as growth and reproduction (DUNHAM *et al.*, 1989). Previous studies have described the diet of species of *Anolis* from several localities within the Amazon Rain Forest (VITT *et al.*, 2002,

2003a, b).

Here we describe the diet of six species from a community of *Anolis* in one of the most biodiverse places on the planet located in the Western Amazon Forest, the Yasuní National Park (PNY) (BASS *et al.*, 2010), located in Orellana Province, Ecuador, on the southern bank of the Tiputini River. The *Anolis* community includes *A. fuscoauratus*, which forages in the lower strata of the forest and is a generalist. Its diet includes spiders, grasshoppers, larvae and cockroaches; in general, populations of this species have diversified diets, although some show a preference for the Orthoptera (VITT & DE LA TORRE, 1996; VITT *et al.*, 2003a). *Anolis ortonii* and *A. scypheus* are passive foragers, seeking for food in leaf litter and low vegetation. *Anolis ortonii*

diet includes grasshoppers, ants, insect larvae (caterpillars), and small beetles while *A. scypheus* diet includes spiders, orthoptera, cockroaches, insect larvae, isopods, and less frequently, small lizards (DUELLMAN, 1978; VITT & DE LA TORRE, 1996). *Anolis trachyderma* is also passive, semi-arboreal forager that also feeds on invertebrates in leaf litter; its diet includes spiders, grasshoppers, crickets, larvae, insect eggs, pupae, termites and cockroaches; also, it consumes its skin after molting. Spiders are the predominant items in the stomachs of this species (42% of the content volume) (ÁVILA-PIRES, 1995; VITT *et al.*, 2002). *Anolis transversalis* and *A. punctatus* are species that mostly inhabit the canopy. Their diet consists in ants, coleoptera, orthoptera, and also includes cockroaches, insect larvae and snails. Small vertebrates have also been reported in the diet of *A. punctatus*. (VITT & DE LA TORRE, 1996; VITT *et al.*, 2003b). The data on diet of *Anolis* provided in this study will contribute to our understanding of diet variation in anoles across the Amazon Basin.

MATERIALS AND METHODS

Sampling was carried out for 70 days during June, July, August, and September 2012 in Yasuní National Park, Orellana Province, Ecuador, on the southern bank of the Tiputini River (76° 24' 1.8" W; 0° 40' 16.7" S) at the Yasuní Scientific Station of Pontificia Universidad Católica del Ecuador. The main climatic characteristics of the PNY are high temperatures (24-27°C), high precipitation (~3200 mm annually) and high relative humidity (80-94%) (BASS *et al.*, 2010). The sampling period corresponds to the dry season, although BASS *et*

al. (2010) mentions that the site where the PNY is located is characterized by not having a severe dry season, that is, precipitation fluctuations during the year do not vary very much.

We searched for lizards in different forest strata using binoculars. Stomach contents were obtained from all captured lizards in the laboratory by introducing a ball-tipped dosing needle through the mouth up to the level of the stomach. Using a syringe attached to the needle, water was injected, and the needle was gently moved back and forth while the stomach was massaged until the lizard regurgitated. The obtained items were preserved in 95% alcohol for subsequent analysis. Prey items were identified with the help of a stereoscope using taxonomic keys for insects and arachnids (TRIPPLEHORN & JOHNSON, 2005; FOELIX, 1996). Most prey items were identified down to the taxonomic rank of order and some to family. All lizards were released back to their site of capture. Prey items that could not be identified due to various factors (e.g. advanced state of digestion) were placed in one category (no identifiable).

Stomach contents were stored in Eppendorf tubes containing 95% ethanol and deposited in the collection of Museo de Zoología (QCAZ) of Pontificia Universidad Católica del Ecuador, Quito, Ecuador.

Once the consumed prey were identified, the amount of prey ingested by each lizard was quantified. The volume (V) of each individual prey was calculated using the spheroid formula: $V = 4/3 \cdot P \cdot (\text{length}/2) \cdot (\text{width}/2)^2$.

Table 1: Diet composition of anole lizards from Yasuní National Park. For each prey taxon, the number (first line) and volume in % (second line) consumed by each species of *Anolis* is presented.

Prey item	<i>A. fuscoauratus</i>	<i>A. ortonii</i>	<i>A. transversalis</i>	<i>A. scypheus</i>	<i>A. trachyderma</i>	<i>A. punctatus</i>
Araneae	23 29.70	5 8.04	6 8.66	2 0.58	1 1.74	0 0
Blattodea	0 0.00	0 0.00	0 0.00	1 1.52	0 0.00	0 0.00
Coleoptera	17 9.63	4 4.26	6 20.19	2 3.43	0 0.00	1 0.27
Collembola	1 0.25	0 0.00	1 0.35	0 0.00	0 0.00	0 0.00
Diplopoda	2 0.50	0 0.00	0 0.00	1 0.87	0 0.00	0 0.00
Diptera	3 2.79	4 14.52	1 0.77	0 0.00	0 0.00	0 0.00
Exuviae	2 9.45	0 0.00	0 0.00	0 0.00	0 0.00	0 0.00
Hemiptera	12 22.23	6 35.99	10 42.13	2 10.31	0 0.00	2 46.96
Hymenoptera	9 5.47	8 6.63	11 7.35	4 11.39	0 0.00	1 0.48
Insect eggs	1 0.01	0 0.00	0 0.00	1 1.51	0 0.00	0 0.00
Isopoda	4 1.24	0 0.00	0 0.00	1 4.57	0 0.00	0 0.00
Isoptera	2 0.25	0 0.00	0 0.00	0 0.00	0 0.00	0 0.00
Larvae	11 11.63	2 9.76	3 11.40	7 61.56	1 41.45	0 0
Lizard scales	3 0.05	0 0.00	0 0.00	1 0.02	0 0.00	0 0.00
Orthoptera	14 6.05	1 20.81	5 9.16	3 4.21	2 56.82	3 52.29
Phasmatodea	1 0.74	0 0.00	0 0.00	0 0.00	0 0.00	0 0.00
Vegetal tissue	1 0.01	0 0.00	0 0.00	0 0.02	0 0.00	0 0.00
Total	115 100.00	30 100.00	43 100.00	26 100.00	4 100.00	7 100.00

RESULTS

A total of 91 individuals belonging to six species were captured and their stomach contents obtained: *Anolis fuscoauratus* (n = 46), *A. ortonii* (n = 12), *A. scypheus* (n = 16), *A. transversalis* (n = 12), *A. trachyderma* (n = 3) and *A. punctatus* (n = 2).

Out of 241 prey items observed in total, 16 were not identified. Eight lizards had no stomach contents. Plant tissue was found in three lizards, whereas lizard skin remains from molting were found in four individuals. Aranea was the most abundant prey item (n = 37), followed by Hymenoptera (n = 33), Hemiptera (n = 32),

Table 2: Total number (n) and average dimensions of prey (in mm) consumed by anole lizards from Yasuní National Park.

Species	n	Items per lizard	Prey length (mean ± SD)	Prey width (mean ± SD)
<i>A. fuscoauratus</i>	107	2.33	6.46 ± 3.39	2.28 ± 1.29
<i>A. ortonii</i>	30	2.50	5.73 ± 3.58	1.75 ± 0.83
<i>A. transversalis</i>	43	3.58	10.33 ± 4.46	3.16 ± 1.46
<i>A. scypheus</i>	26	1.63	9.60 ± 5.75	3.19 ± 2.22
<i>A. trachyderma</i>	4	1.33	9.19 ± 4.42	2.55 ± 0.93
<i>A. punctatus</i>	7	3.50	13.33 ± 7.61	3.14 ± 1.62

Orthoptera (n = 28), and insect larvae (n = 24). The least frequent consumed categories were: Collembola (n = 2 items), insect exuviae (n = 2), Isoptera (n = 2), Blattodea (n = 1) and Phasmidae (n = 1). Considering the volume of consumed prey, the most used category was Hemiptera (28.41%), followed by insect larvae (22.86%). Other categories that accounted for a considerable volume of the stomach contents were Orthoptera (12.02%), Aranea (11.76%), Coleoptera (10.53%) and Hymenoptera (7.05%), while the least consumed categories in terms of volume were Blattodea, Collembola, Diplopoda, Isopoda, Isoptera, Phasmidae and exuviae. A list of prey items and their dimension are showed in Table S1.

At the species level, a total of 115 items were found in the stomachs of *A. fuscoauratus*, mostly represented by Aranea, Hemiptera and insect larvae. Several small Orthoptera were found (n = 14) but their volume represented only 6.05%. A small amount of plant tissue was found in one individual (Table 1). Thirty prey items were found in the stomachs of *A. ortonii*, with Hymenoptera as the most consumed category (n = 8, representing 6.63% of the total ingested volume), followed by Hemiptera (n = 6), which represented the highest volume within this species

(35.99%). A total of 26 prey items were found in the stomach contents of *A. scypheus*, insect larvae being the most representative category. In one individual of *A. scypheus*, 19 Arthropoda eggs were found, and their volume represented 1.52% of the total stomach contents of that lizard.

In *A. transversalis* stomachs, 43 prey were found; Hymenoptera was the most representative category (n = 11 prey items), although it only represented 7.35% of the ingested volume, followed by Hemiptera (n = 10 prey items and 42.13% of the content volume). A considerable amount of Coleoptera and Aranea were found. Although few larvae were found (n = 3), their volume represented 11.4% of this species diet. In the case of *A. punctatus*, only seven prey items were obtained, mostly Orthoptera and Hemiptera. Similarly, due to the small number of individuals of *A. trachyderma* captured, only four prey items were obtained: two Orthoptera, one Aranea, and one insect larva (Table 1).

The species with the highest number of prey items observed per individual was *A. transversalis*, with an average of 3.58 prey items per lizard, followed by *A. punctatus* (3.50), *A. fuscoauratus* (2.33), *A. ortonii* (2.50), *A. scypheus* (1.63) and *A. trachyderma* (1.33) (Table 2). The highest average prey length was observed in *A. transversalis* and

Table 3: Average snout-vent length (in mm) of *Anolis* species from Yasuní National Park .

Species	Adult	Subadult	Adult	Subadult	Juveniles
	females	females	males	males	
<i>A. fuscoauratus</i>	44.57	42.15	42.48	40.48	38.10
<i>A. ortonii</i>	44.43	41.86	44.97	39.80	35.86
<i>A. transversalis</i>	80.18	70.04	77.55	65.39	59.99
<i>A. scypheus</i>	-	67.15	76.45	64.69	38.65
<i>A. trachyderma</i>	54.66	-	-	-	-
<i>A. punctatus</i>	76.50	-	-	73.17	-

A. punctatus, which are also the two largest species under study (Table 3).

DISCUSSION

Anolis lizards are primarily insectivorous (DIAL & ROUGHGARDEN, 1995) and consume a variety of arthropods, including arachnids, in large quantities. In the stomachs of the six *Anolis* species from the PNY, Hemiptera was the most consumed order of insects considering the prey volume. Hemiptera are insects that move readily in all forest strata (Tripplehorn & Johnson, 2005), hence this order of insects may be available as prey for all species, regardless of the stratum in which the lizards are foraging. In general, Aranea are the most observed category in stomach contents, followed by Hymenoptera, considering the number of prey. The small size of ants (Hymenoptera) makes lizards to consume large quantities of these animals to satisfy their nutritional requirements (MENÉNDEZ-GUERRERO *et al.*, 2020).

The presence of a high number of insects in the stomach contents of *Anolis* lizards may be attributed to fluctuations in insect availability throughout the year in tropical forests (WOLDA, 1992). This fluctuation may also affect the results of this study, as it was conducted between the months of June and September. Also, it is

important to note that the prey identification may be influenced by the digestive process. SCHOENER (1989) mentioned that less chitinous prey are digested quicker, which could explain the prevalence of chitinous prey, such as Hemiptera and Orthoptera, in the stomach contents of *Anolis* lizards.

Anolis lizards are known to forage passively (VITT & ZANI, 1996), meaning they do not expend energy searching for food, but rather feed on nearby prey. Passive foragers typically feed on prey that are constantly in motion, such as flying insects, including Hemiptera, Orthoptera, and Coleoptera. However, Isoptera (termites) and Hymenoptera (ants) are social insects that live in colonies and are potential prey for active foragers, such as certain types of anurans, specifically Dendrobatidae and Bufonidae (MENÉNDEZ-GUERRERO *et al.*, 2020). The type of foraging may help to explain the low percentage of Isoptera found in the stomachs of these lizards (HUEY & PIANKA, 1981). However, another possible explanation is based on the hardness of the Isoptera body, as they have a non-chitinous body (TRIPPLEHORN & JOHNSON, 2005). It is possible that these insects were digested before the stomach content was washed out. On the other hand, a substantial number and volume of

Hymenoptera were discovered, which contradicts the notion that social insects are not a significant component of the diet for species with passive foraging behaviour.

A study on the ecology of *A. fuscoauratus* (VITT *et al.*, 2003a) carried out at six sites in the Amazon Forest (Cuyabeno, Curuá-Una, Rodonia, Solimoes River, Juruá River and Itúxi River) presented results that differ from this study. First, several types of prey were found, such as Mantidae, Neuroptera, Dermaptera, Lepidoptera, Pseudoscorpiones and Mollusca, which were not observed in the stomachs of *Anolis* from the PNY. Aranea are widespread in Cuyabeno and Curuá-Una, as well as in this study (PNY). Nevertheless, the results obtained by VITT *et al.* (2003a) cover the sum of prey from the six locations, which widens the evaluated trophic niche. A similar study on the ecology of *A. transversalis* and *A. punctatus* (VITT *et al.*, 2003b) showed certain similarities in diet with PNY lizards. At the six sites where the study by VITT *et al.* (2003b) was conducted, Hymenoptera and Coleoptera were the numerically predominant prey, while Coleoptera, Hymenoptera and Blattodea were volumetrically dominant in *A. transversalis*. In the PNY, it was observed that Hymenoptera and Hemiptera were the most abundant prey, followed by Coleoptera and Aranae; however, the volumetrically dominant prey item was Hemiptera. With respect to *A. punctatus*, the two studies show that Orthoptera and Hemiptera are an important part of the diet. However, VITT *et al.* (2003b) mentioned that Hymenoptera were the most important prey item both numerically and

volumetrically. Morphological observations revealed that larger species tended to feed on larger prey (VITT & ZANI, 1996), a finding that was confirmed in this study.

VITT & DE LA TORRE (1996) mentioned in a study conducted in Cuyabeno that *A. ortonii* fed mainly on Orthoptera, Hymenoptera and insect larvae. In the PNY, it was observed that Hymenoptera are indeed the most common prey, but also Hemiptera are a very common and quantitatively dominant prey for this *Anolis* species. It has been observed that Diptera, Aranae and Coleoptera are also common. *Anolis ortonii* was mostly observed near station buildings where there were also abundant Hymenoptera attracted by food waste products of human consumption. VITT & DE LA TORRE (1996) also mentioned that the most common prey of *A. scypheus* was Aranea, Orthoptera, Blattodea and larvae. In line with these findings, larvae were the most consumed and most common prey for *A. scypheus* in the PNY. However, in contrast to the data reported by VITT & DE LA TORRE (1996), Hymenoptera were the second most consumed category in the PNY, both in terms of quantity and total number of preys items.

Three types of prey were observed in *A. trachyderma*: Orthoptera, a larva and an arachnid. VITT & DE LA TORRE (1996) mentioned that Arachnida and Orthoptera constituted an important part of the diet of this species. In this study *A. punctatus* and *A. trachyderma* could be considered the species with higher levels of specialization in their diets, which is not in agreement with VITT *et al.* (2002). However, our results may be affected by the small number of samples. In a study on amphibians, PAR-

MELEE (1998) mentioned that the breadth of trophic niches is directly related to the number of individuals examined.

Overall, this data provide insights on the diet of *Anolis*, which is composed mainly by Aranae, Himenoptera and Hemiptera. Also, the data from this study suggest the absence of specialist species in terms of both the volume, number, and type of prey, in line with findings from previous studies on the diet of species of this genus (VITT & ZANI, 1996; VITT *et al.*, 2002, 2003a, b).

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