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What Do Co-Mimics eat? Trophic Ecology of *Ameerega pulchripecta* (Anura, Dendrobatidae) and *Allobates femoralis* (Anura, Aromobatidae) in Eastern Brazilian Amazonia

PATRICK R. SANCHES,[1,3,4] LUÃ E. SANTOS-GUERRA,[1] FILLIPE PEDROSO-SANTOS,[1] IGOR L. KAEFER,[2] AND CARLOS E. COSTA-CAMPOS[1]

[1]*Universidade Federal do Amapá, Departamento de Ciências Biológicas e da Saúde, Laboratório de Herpetologia, Campus Marco Zero do Equador, Macapá, Amapá, Brasil 68.903-419*
[2]*Programa de Pós-Graduação em Zoologia, Instituto de Ciências Biológicas, Universidade Federal do Amazonas, Manaus, Amazonas, Brasil*
[3]*Programa de Pós-graduação em Biodiversidade e Biotecnologia da Rede Bionorte, Universidade Federal do Amapá, Macapá, Brazil*

ABSTRACT.—Differentiation in resource use by sympatric species reduces competition and allows coexistence. Constraints imposed both by evolutionary history and current ecological interactions strongly influence the coexistence of distinct anuran species. In this context, we analyzed the dietary habits of two sympatric frogs in a Batesian mimicry system, *Ameerega pulchripecta* and *Allobates femoralis*, to assess potential resource overlap and competition between them. We explored the hypothesis that differences in feeding behavior and prey choice reflect these species' status as co-mimics in a Batesian system because toxicity in anurans is strongly related to diet. We obtained stomach contents by applying the stomach-flushing technique and data on prey availability through pitfall traps arranged along both sides of the trail where the sympatric species occur. We found that the toxic *A. pulchripecta* actively selects ants and mites as prey, while the nontoxic *A. femoralis* feeds opportunistically on beetles, ants, and other sedentary prey such as larval insects and adult spiders. Based on dissimilarity, diversity, electivity, and evenness analysis we concluded that the two frog species exhibited a significant difference in prey composition. We suggest that these differences found in the feeding habits are important to the syntopic coexistence of these two frog species in our study area.

Niches of sympatric species have long captured the interest of ecologists because competition and resource partitioning are among the pillars structuring ecological communities and ecosystem dynamics (Schoener, 1974; Putman, 1994). Among the three main dimensions of the niche (diet, space, and time), diet is by far the most studied in anurans (Solé and Rödder, 2010; Cortes-Gomez et al., 2015). Trophic interactions among sympatric anurans are associated with divergence in traits such as morphology, behavior, and physiology (Lima, 1998; Caldwell and Vitt, 1999; Solé and Rödder, 2010; Araújo et al., 2011). Evolutionary patterns of feeding behavior may play an important role in the coexistence of sympatric species in complex-structured communities (Toft, 1980, 1995; Wiens et al., 2010).

Terrestrial invertebrates are the main prey resource of anurans (Wells, 2007), and insects constitute a prominent component of their dietary intake (Solé and Rödder, 2010). Nonetheless, feeding habits can be partitioned into a dietary spectrum along two peaks determined by prey type and size: specialist predators and generalist feeders. The former are usually poisonous and aposematic species that concentrate on small alkaloid-containing prey such as ants. The latter are cryptic and nontoxic, consuming large prey according to environmental availability (Toft, 1980; Caldwell, 1996).

Ecological factors, such as interspecific competition, are usually thought to be the major force of ecological displacement among sympatric species of anurans (Losos, 2008; Sabagh et al., 2010; Solé and Rödder, 2010). However, feeding behavior may be related strongly to evolutionary patterns of morphological, behavioral, and physiological traits that could outweigh competition (Wiens et al., 2010; Toledo Moroti et al., 2021). In this sense, the use of resources may involve adaptive trends that evolved independently among Anura lineages, allowing for establishment of a complex trophic structure in anuran communities over time (Toft, 1980; Caldas et al., 2019). This may strongly influence the distribution of sympatric species and, ultimately, on the development of complex ecological relationships between species, such as mimicry.

Mimicry species converge in their local warning signals such that co-mimics occupy the same microhabitats (Lindström et al., 1997; Darst and Cummings, 2006). However, in the case of Batesian mimics only one species is noxious to predators, the model species (Bates, 1862). For anurans, this fact may imply that Batesian co-mimics segregate by diet, given that feeding behavior is strongly correlated to toxicity (Darst et al., 2005). The highest diversity of aposematic species is found in the neotropical Dendrobatidae, such as *Ameerega*, *Dendrobates*, *Oophaga*, and *Phyllobates*, which are highly toxic and have narrow diets composed mainly of ants (Mebs et al., 2010). Dendrobatids have been repeatedly suggested as unpalatable models in mimicry systems with edible mimics of their sister clade Aromobatidae, such as species in the genus *Allobates*, which are cryptic, nontoxic, and generalist feeders compared with species of Dendrobatidae (Darst and Cummings, 2006; Amézquita et al., 2017; Saporito and Grant, 2018).

Here, we explore the hypothesis that differences in the feeding behavior and resource electivity between *Ameerega pulchripecta* (Silverstone, 1976) and *Allobates femoralis* (Boulenger, 1883) reflect their condition as co-mimics in a Batesian system (Amézquita et al., 2017; Saporito and Grant, 2018) and the divergent evolutionary pattern of feeding behavior in Dendrobatoidea, which includes Dendrobatidae and Aromobatidae as sister diverging lineages (Darst et al., 2005; Grant et al., 2006). We tested differences in prey composition based on size within prey category and predicted that *Ameerega pulchripecta* would consume more smaller chitinous prey categories, and that *Allobates femoralis* would show a greater variation in prey size. We next tested selectivity for prey items and predicted that both species would consume a large

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[4]Corresponding author. E-mail: patricksanchs@gmail.com
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FIG. 1. Map showing the location of Parque Natural Municipal do Cancão, Municipality of Serra do Navio, state of Amapá, Brazil (A) and sampling plot of the two frogs, (B) *Ameerega pulchripecta* and (C) *Allobates femoralis*.

amount of ants, but only *Ameerega pulchripecta* would select them. Further, we tested for feeding strategy differences between seasons, predicting that ants are a dominant prey for *Ameerega pulchripecta* and a common prey for *Allobates femoralis*, in support of the idea that both dendrobatids and aromobatids are myrmecophagous but only dendrobatids actively select ants to maintain alkaloid toxins.

MATERIALS AND METHODS

Study Area.—We conducted our study in the Parque Natural Municipal do Cancão (PNMC; 0.90083°N, 52.01347°W; DATUM = WGS84/SAD 69), Municipality of Serra do Navio, state of Amapá, Brazil (Fig. 1A). PNMC is an integral protection area of approximately 370 hectares dominated by primary forest, including upland rainforests, open areas, and treefall gaps. It has a humid tropical climate, typical of equatorial regions, with an average annual temperature ranging from 25.8° to 29.0°C sensu Köppen-Geiger (Alvares et al., 2013). Annual precipitation in this area is approximately 2,850 mm between February and May and monthly rainfall is about 400 mm on average.

Study Species.—*Ameerega pulchripecta* (snout–vent length = 24.37 ± 2.21 mm) and *Allobates femoralis* (snout–vent length = 27.26 ± 2.32 mm) are two small-sized frogs belonging, respectively, to the families Dendrobatidae and Aromobatidae (Grant et al., 2017). Whereas *Allobates femoralis* (Fig. 1C) occur in a wide range throughout the Amazon River basin, in Colombia, Ecuador, Peru, Bolivia, Brazil, French Guiana, Suriname, and Guyana (Frost, 2021), *Ameerega pulchripecta* (Fig. 1B) appears to have a distribution limited to the state of Amapá, northern Brazil (Silverstone, 1976; Costa-Campos et al., 2016; Frost, 2021). The species are remarkably similar in morphology, color pattern, and size, possibly comprising a Batesian mimicry system (Amézquita et al., 2017; Saporito and Grant, 2018; Fig. 1B, 1C). We sampled where *Allobates femoralis* is syntopic to *Ameerega pulchripecta* in the western portion of PNMC. Both species are diurnal and defend territories, and they also deposit terrestrial egg clutches and display parental care such as tadpole transportation. Individuals of both species can be found on the ground in and around fallen trunks and roots, sometimes elevated from the soil (Ringler et al., 2009; Costa-Campos et al., 2016).

Frog Sampling.—To capture seasonal variation in diet, we carried out the sampling in both dry (December) and wet (March to May) seasons, the latter coinciding with the Equatorial monsoon. We conducted four field surveys between March and December 2017, in the periods between 28 and 30 March, 20 and 22 April, 27 and 30 May, and between 07 and 11 December. We established all surveys during the nocturnal period for three consecutive nights, always starting early evening (1500 h) and lasting until 2100–2200 h. Sampling was conducted in a 650-m plot, where both target species occur syntopically (Fig. 1A). We located the specimens using visual and auditory search methods (Heyer et al., 1994). Each collected specimen was transported inside individual plastic bags for laboratory examination of stomach contents within 2 h after capture. We measured the snout–vent length (SVL) of specimens using a digital caliper (0.01-mm precision) and body mass using a portable scale (0.1-g precision).

Data Sampling.—In the laboratory, we retrieved prey items from stomachs of individuals through the stomach-flushing technique, a nonlethal method proposed by Solé et al. (2005). We stored all expelled prey items in plastic tubes filled with 70% ethanol to preclude continued digestion. After stomach-flushing treatment, we released frogs back to the original site of capture. We estimated prey availability using 10 pitfall traps with 500-mL volume arranged in both sides of the trail every

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60 m along the plot and within approximately 5 m of its margin (Fig. 1A). The pitfall traps contained alcohol at 70% and detergent and were sampled for 3 consecutive days of each campaign during the same period as frog sampling occurred. Stomach contents as well as the environment samples were analyzed under stereo microscopes and classified up to a minimum of order level with the aid of dichotomous keys (Rafael et al., 2012). Larval and embryonic (eggs) forms of insects (in this case Coleoptera and Diptera) were placed in apart from the adults. Ants were considered apart from other hymenopterans (such as wasps) and placed into the Formicidae family. Additionally, ants were analyzed in a more refined taxonomic scale and therefore placed into the level of genus as a means of compare qualitatively prey composition. Some noninsect invertebrates were difficult to identify in the level of order and therefore were placed into coarser taxonomic categories.

Data Analysis.—We estimated the length and width of all stomach items on each category to determine the volume of the prey items using the volume formula for ellipsoid bodies (Griffiths and Mylotte, 1987):

$$V = \frac{4}{3}\pi\left(\frac{l}{2}\right)x\left(\frac{w}{2}\right)^2$$

where V represents prey volume, l = item length, and w = item width

We applied the Index of Relative Importance (*IRI*) that indicates the importance of each category consumed from the percentage of number (*N*%), percentage of occurrence (*F*%) and percentage of volume (*V*%; Pinkas et al., 1971):

$$IRI = (N\% + V\%) + F\%$$

We measured trophic niche breadth of each species using the Levin's index (*B*) described by Pianka (1986):

$$B = 1/\sum_{i=1}^{n} p_{i^2}$$

where B = Levin's index (trophic niche breadth); i = prey category; n = number of categories; p_i = numerical or volumetric proportion of the category of prey i in the diet. Then, we calculated a standardized measure of Levin's index (L_{st}) described by Hurlbert (1978), which limits the value on a scale from 0 to 1 according to the following equation: $L_{st} = (B - 1)/(n - 1)$, where n represents the number of resources (prey species) registered and B represents the Levin's measure of niche breadth. Values closer to 0 were attributed to a more specialist diet, while values closer to 1 were considered as a more generalist diet (Krebs, 1989).

We used the absolute frequency of each prey category (N) and the absolute volume of each prey category (V) to compute the dietary overlap between *A. pulchripecta* and *A. femoralis* in the study area by applying Pianka's index, in which values range from 0 (no overlap) to 1 (complete overlap; Pianka, 1973). The Pianka's index was calculated using the formula

$$o_{jk} = \sum_{i}^{n} p_{ij}p_{ik}/\sqrt{\sum_{i}^{n} p_{ij}^2 \sum_{i}^{n} p_{ik}^2}$$

where p_{ij} (or p_{ik}) is the absolute frequency or volume of food item i in diet j (or k).

The electivity of prey was calculated using the Ivlev's electivity index (*IEI*; Krebs, 1999):

$$IEI = (r_i - n_i)/(r_i + n_i)$$

where r_i is the percentage of prey category i in diet, and n_i is the percentage of prey category i in the environment. The values of this index range from -1 to $+1$, with values near $+1$ indicating preference, values near -1 indicating rejection, and values near 0 indicating consumption in the same proportion as is present in the environment. Scorpiones, Chilopoda, Culicidae, larval Diptera, Embioptera, and Gastropoda were not found in pitfalls and, thus, were not included in the analysis. Analyses used to quantify amplitude of the ecological niche and niche overlap of the species were carried out in Ecosim program version 7.0 (Gotelli and Entsminger, 2001), with 1,000 randomizations.

To test whether diet composition differs between the two frog species, we performed a permutational multivariate analysis of variance (PERMANOVA) using Euclidean distance and 999 permutations (Anderson, 2001). Additionally, we performed a nonmetric multidimensional scaling (NMDS) analysis to reduce the dimensionality of species composition data to two axes of a multivariate ordination, allowing for a graphical evaluation of segregation between diet composition of frog species. To quantify and compare prey diversity, we used the Shannon Diversity Index (Magurran, 1988):

$$H' = -\sum p_i \ln p_i,$$

in which p_i is numeric proportion of prey i in total number of individuals of n prey categories.

Additionally, we calculated dietary evenness by using Pielou's evenness index using the diversity (H') and total richness (S) values (Ludwig and Reynolds, 1988). Evenness values range from 0 to 1, approaching 1 as prey proportions in the diet become equal:

$$J' = \frac{H'}{\ln(S)}$$

We compared diet diversity and evenness between the two frog species using ANOVA. Validation of assumptions of ANOVA were performed, including of normality of residuals. We were also interested in evaluating the relationship between body size and prey size, so we performed simple linear regressions between SVL and mean volume of prey.

To capture seasonal variation in feeding strategy we applied a graphical representation plotting prey-specific abundance (P_i) against frequency of occurrence (*F*%) of each prey category. The prey-specific abundance was calculated as $P_i = (\Sigma S_i/\Sigma S_{ti}) \times 100$, where S_i is the number of prey i and S_{ti} is the total number of prey items in those stomachs containing prey i (Amundsen et al., 1996). This procedure allowed for a graphical analysis of prey importance and the feeding strategy between seasons by visualizing the areas of the plot occupied by each prey category.

We plotted a predator–prey network graph based on the relative frequency of each prey item found per anuran species using the Program R package 'bipartite' (Dormann et al., 2009). All analyses were conducted using the *vegan* package (Oksanen et al., 2010) in R software v.4.0.2 (R Core Team, 2022). NMDS analyses were performed with the metaMDS function (arguments k = 2, trymax = 1,000).

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TABLE 1. Prey categories found in the stomachs of *Allobates femoralis* and *Ameerega pulchripecta* in Amapá state, northern Brazil. N = number of individuals registered (absolute number and %); F = frequency of occurrence of prey category (absolute number and %); V = volume occupied by prey item in the entire sample (in mm^3 and %); *IRI* = Index of Relative Importance.

Prey category	N	N%	F	F%	V(mm^3)	V%	*IRI*
Allobates femoralis							
Araenae	10	6.25	9	17.65	57.1	6.21	30.10
Scorpiones	1	0.63	1	1.96	8.08	0.88	3.46
Chilopoda	3	1.88	3	5.88	60.8	6.61	14.37
Coleoptera	47	29.38	18	35.29	301.881	32.82	97.48
Larval Coleoptera	3	1.88	3	5.88	35.3	3.84	11.60
Diptera	4	2.50	4	7.84	8.0	0.87	11.21
Culicidae eggs	18	11.25	2	3.92	0.3	0.03	15.20
Larval Diptera	10	6.25	2	3.92	206.1	22.40	32.57
Hemiptera	3	1.88	3	5.88	41.4	4.50	12.25
Formicidae	41	25.63	25	49.02	87.4	9.50	84.15
Isoptera	16	10.00	4	7.84	68.1	7.40	25.24
Orthoptera	2	1.25	2	3.92	40.4	4.39	9.56
Collembola	1	0.63	1	1.96	5.1	0.55	3.14
Gastropoda	1	0.63	1	1.96	0.004	0.0004	2.59
Ameerega pulchripecta							
Acari	109	11.65	48	65.75	47.99	4.03	81.43
Araneae	11	1.18	9	12.33	22.15	1.86	15.37
Coleoptera	73	7.80	42	57.53	145.80	12.25	77.58
Collembola	2	0.21	2	2.74	0.32	0.03	2.98
Diptera	4	0.43	3	4.11	4.48	0.38	4.91
Embioptera	1	0.11	1	1.37	0.53	0.04	1.52
Hemiptera	5	0.53	5	6.85	39.38	3.31	10.69
Hymenoptera	5	0.53	4	5.48	1.15	0.10	6.11
Formicidae	670	71.58	69	94.52	655.02	55.03	221.13
Isoptera	27	2.88	5	6.85	106.17	8.92	18.65
Larval Coleoptera	5	0.53	5	6.85	30.30	2.55	9.93
Larval Diptera	22	2.35	14	19.18	134.36	11.29	32.82
Orthoptera	1	0.11	1	1.37	2.11	0.18	1.65
Zoraptera	1	0.11	1	1.37	0.50	0.04	1.52

RESULTS

A total of 1,096 items were retrieved from the stomachs of *Ameerega pulchripecta* (N = 936, retrieved stomachs = 90) and *Allobates femoralis* (N = 160, retrieved stomachs = 54). We identified 18 prey categories at the levels of Class, Subclass, Order, and Family, comprising terrestrial invertebrates and including embryonic (eggs), larval, and adult stages (Table 1). In addition to these prey items, we also found vegetal matter ($N_{A.pulchripecta} = 2$; $N_{A.femoralis} = 1$) and stones ($N_{A.pulchripecta} = 1$) in some stomachs.

Diet Composition.—We collected stomach contents of 90 specimens of *Ameerega pulchripecta* for dietary analysis (69 adult males and 21 adult females). Out of the 90 stomachs retrieved, 17 were empty (19%). We identified 14 prey categories in the diet of *Ameerega pulchripecta* to the level of Order or Family (for ants), in which the most important in terms of number and frequency were Formicidae and Acari. As well, Coleoptera (larval and adult), Isoptera, larval Diptera, and Hemiptera were highly represented (Table 1). The most important prey item according to Index of Relative Importance (*IRI*) was Formicidae (*IRI* = 221.13), followed by Acari (*IRI* = 81.43) and Coleoptera (*IRI* = 77.58). The variation in SVL of *Ameerega pulchripecta* did not explain the variation in mean prey volume ($r^2 = 0.02$, $P = 0.22$).

We collected stomach contents of 54 individuals of *Allobates femoralis*, including 32 males and 22 females. Fifty-one out of 54 (94%) *Allobates femoralis* individuals contained identifiable prey in their stomachs. Most prey items were arthropods, and one Mollusca was also observed. We classified prey items into 14 taxonomic categories for *Allobates femoralis* to the levels of Class, Subclass, Order, or Family (for ants). In terms of number, frequency, and volume, Coleoptera and Formicidae were found to represent the major components of the diet of *Allobates femoralis* (Table 1). Eggs of Culicidae and larval forms of Coleoptera and Diptera were also consumed and representative in terms of number and volume, but occurred sporadically. Adult Coleoptera (*IRI* = 97.48) and Formicidae (*IRI* = 84.15) were the most important items in the diet of *Allobates femoralis*. We found no relationship between the variation in SVL and mean prey volume in *Allobates femoralis* ($r^2 = 0.015$, $P = 0.38$).

The two species shared 10 prey categories: Araneae, Coleoptera (larval and adult), Collembola, Diptera (larval and adult), Hemiptera, Formicidae, Isoptera, and Orthoptera. Exclusive prey categories in the diet of *Ameerega pulchripecta* were Acari, Hymenoptera (wasps), Embioptera, and Zoraptera. Exclusive items in the diet of *Allobates femoralis* were Scorpiones, Chilopoda, Culicidae (eggs), and Gastropoda. With regard to the richness of ants in the diet of the two species, we found 711 ants from 34 genera (Fig. 2). Of these, 23 belonged to the subfamily Myrmicinae. We identified 30 ant genera in the diet of *Ameerega pulchripecta*, of which the most abundant were *Solenopsis* (15.7%), followed by *Ochetomyrmex* (11.4%) and *Carebara* (8.97%). We found less ant diversity in the diet of *Allobates femoralis*, which consumed 11 genera with *Pheidole* (38.1%) making up the largest proportion followed by *Crematogaster* (21.4%) and *Solenopsis* (9.5%).

Comparing the two sympatric frog species, *Allobates femoralis* was found to have a broader niche breadth ($L_{st} = 0.34$) compared with *Ameerega pulchripecta* ($L_{st} = 0.07$). In terms of evenness of abundance among prey categories, *Allobates femoralis* had a more even diet ($J' = 0.78$) compared with *Ameerega pulchripecta* ($J' = 0.4$; $F_{1,91} = 5.25$, $P = 0.01$; Fig. 3). Niche overlap was 67% according to Pianka's index ($O_{jk} = 0.67$). However, diet composition

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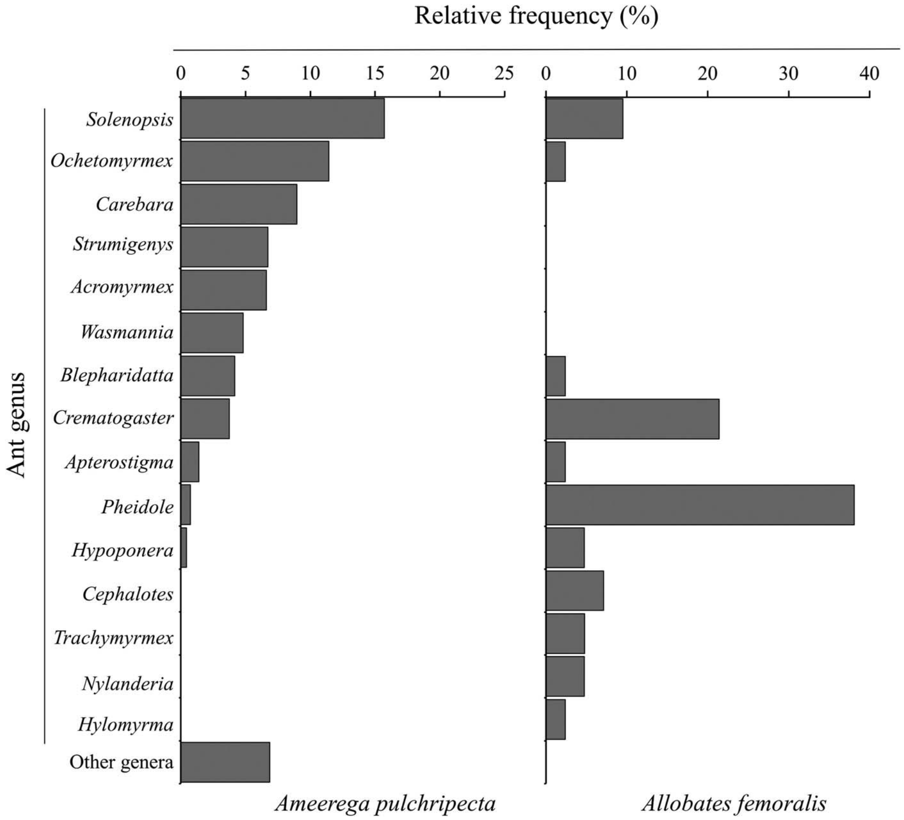

FIG. 2. Ant genera composition between *Ameerega pulchripecta* and *Allobates femoralis* in the municipality of Serra do Navio, Amapá, Brazil. Bars represent the relative frequency (%) of each genus.

significantly differed between the two frogs ($F = 30.73$, df $= 117$, $P = 0.001$; Fig. 4) and *Allobates femoralis* had a more diverse diet ($H' = 2.18$) than *Ameerega pulchripecta* ($H' = 1.06$; $F_{1,91} = 8.53$, $P = 0.0004$).

Electivity.—In the leaf litter, where both species live and forage, the most abundant invertebrate taxa were Collembola (34.9%), Coleoptera (33.5%), and Formicidae (17.4%). In the diet of *Ameerega pulchripecta*, the highest Ivlev's electivity indices

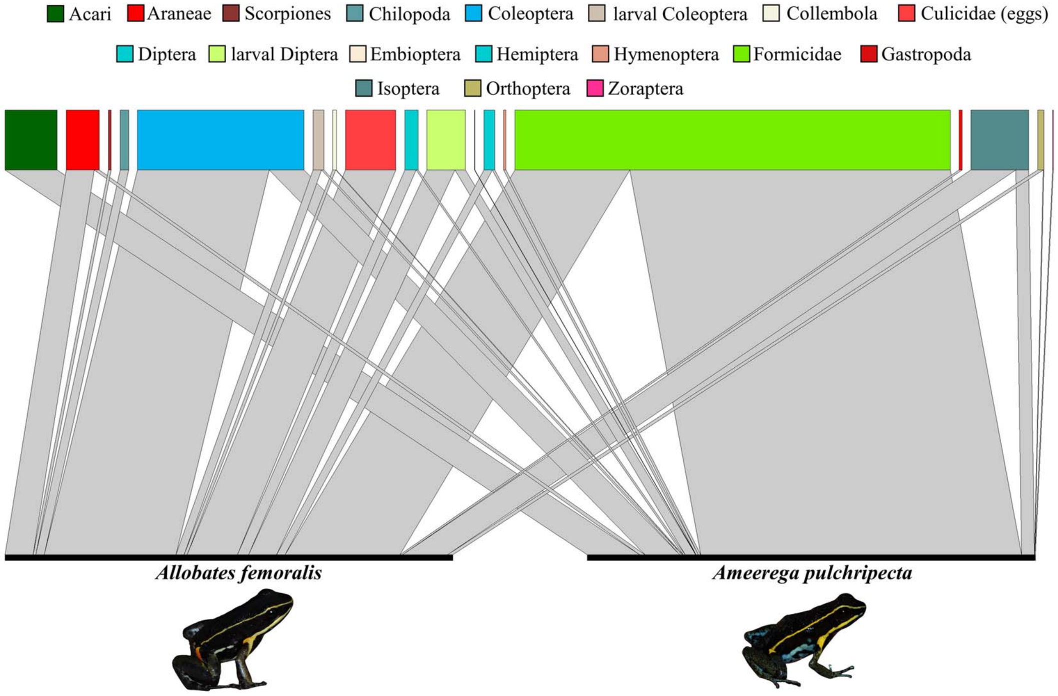

FIG. 3. Network of interactions between prey and the two frog predators, *Allobates femoralis* and *Ameerega pulchripecta*, in Serra do Navio municipality, Amapá, Brazil. The gray bar width represents the number of interactions observed per species and prey categories (i.e., the relative frequency each prey category consumed). The corresponding colored bar represents the proportion of each prey category in the diet of both species.

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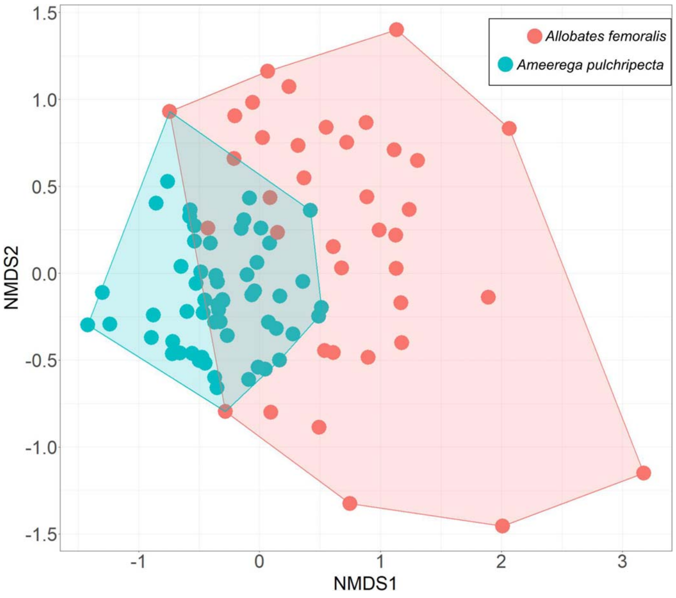

FIG. 4. Relationship between the two axes generated after nonmetric multidimensional scaling (NMDS) ordination, summarizing 118 sampled stomachs. Red circles represent samples of *Allobates femoralis*. Blue circles represent samples of *Ameerega pulchripecta*.

were observed for Acari, Hymenoptera (wasps) and Formicidae while the lowest were observed for Collembola, Orthoptera, and Hemiptera. Prey such as Araneae and larval Coleoptera were consumed in proportions similar to those found in the environment. The highest electivity by *Allobates femoralis* was for larval Coleoptera and Araneae (Fig. 5). Prey categories such as Diptera, Coleoptera, and Formicidae were consumed in the same proportion as they occurred, and some prey categories such as Acari, Collembola, Hymenoptera and Orthoptera had negative values of electivity, indicating rejection (Fig. 5).

Seasonal Variation in Feeding Strategy.—Ants were a dominant prey type in the diet of *Ameerega pulchripecta* in both wet and dry season as indicated by their position in the right upper corner of the graphs (Fig. 6). Most prey types were rare and present only in the wet season (Fig. 6A). *Ameerega pulchripecta* consumed only four prey types in the dry season, during which Coleoptera and Acari remained constant, but not dominant, items (Fig. 6B). The absence of any prey type in the lower right corner of the graphs indicates no between-phenotype component to the niche width nor within-phenotype component to any prey type. Thus, no specialization in prey type among individuals was observed. These findings support the concept that *Ameerega pulchripecta* is an ant-specialist.

The contrary was observed for *Allobates femoralis* as a result of the absence of any prey type in the upper right corner of the graphs for both seasons. Thus, there were no dominant prey. Formicidae and Coleoptera were common prey types in both seasons. However, the graphs indicate a high between-phenotype component to prey types among seasons. In the wet season, larval and adult Diptera, Culicidae eggs, and Isoptera were positioned in the left upper corner, indicating a high between-phenotype component (Fig. 6C). Thus, there was variation in resource use among individuals for these types of prey. The same was observed in the dry season only for Culicidae eggs (Fig. 6D). These results indicate a tendency for dietary generalization in *Allobates femoralis*.

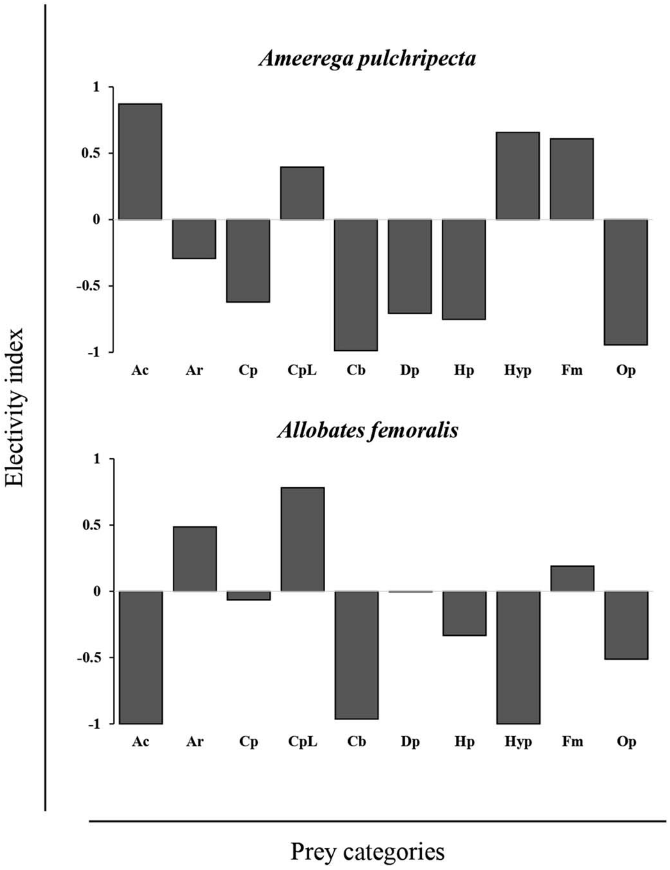

FIG. 5. Ivlev's Electivity Index for each prey category by *Allobates femoralis* and *Ameerega pulchripecta* in Serra do Navio municipality, Amapá, Brazil. Abbreviations: Acari (Ac), Aranae (Ar), Coleoptera (Cp), larval Coleoptera (CpL), Collembola (Cb), Diptera (Dp), Hemiptera (Hp), Hymenoptera (Hyp), Formicidae (Fm), Orthoptera (Op).

DISCUSSION

The diet of the poison frog *Ameerega pulchripecta* was composed mainly of ants and mites (82% of total items), resulting in a narrow niche breadth. These results are in line with the few investigations on diet of the genus *Ameerega*, carried out in different biomes (Biavati et al., 2004; Forti et al., 2011; Luiz et al., 2015, Pacheco et al., 2020). Ants and mites are considered the main sources of alkaloid toxins for frogs and their abundance in the diet of poison frogs can be explained by selectivity toward these prey categories (Simon and Toft, 1991; Toft, 1995). As such, our findings further demonstrate that species able to sequester and maintain alkaloids as defense also actively select ants and mites as prey. Moreover, *Ameerega pulchripecta* showed wide variability in the ant genera consumed, including fire ants of the genus *Solenopsis* and *Ochetomyrmex*, which are potentially rich sources of alkaloids (e.g., Weldon et al., 2013), as well as arboreal ants from the genus *Crematogaster* and *Gnamptogenys* (Wilson, 1976), and fossorial ants of the genus *Acanthostichus* (Baccaro et al., 2015). These observations reinforce an active myrmecophagous behavior into different microhabitats that these ants inhabit.

Ameerega pulchripecta seemed to avoid soft-bodied prey, given the poor representation of spiders, dipterans, hemipterans, and orthopterans in their diet. It should be noted that soft-bodied invertebrates possess less chitinous body parts and, therefore, are likely rapidly digested in the digestive tract compared

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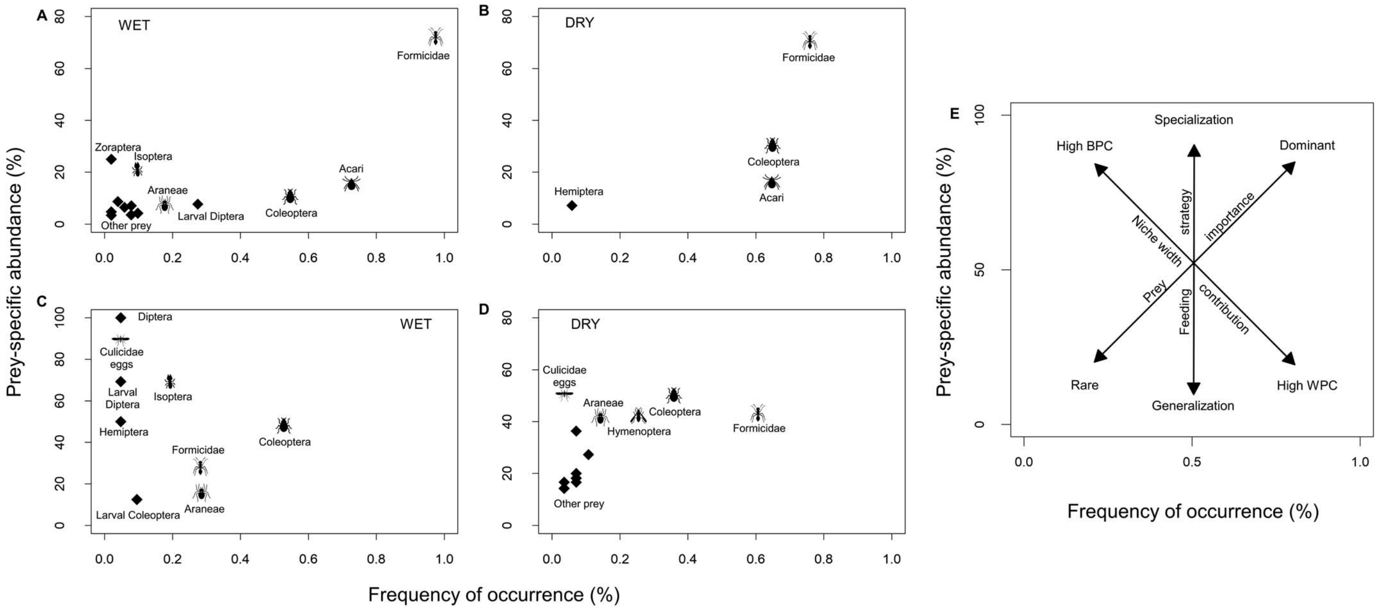

FIG. 6. Feeding strategy of *Allobates femoralis* (A, B) and *Ameerega pulchripecta* (C, D) in Serra do Navio municipality, Amapá, Brazil, according to prey-specific abundance (%) and frequency of occurrence (%) of each prey category in the wet (A, C) and dry (B, D) seasons, and diagram for feeding strategy interpretation considering prey importance (rare to dominant), niche width contribution (BPC = between-phenotype component; WPC = within-phenotype component) and feeding strategy (E; based on Amundsen et al., 1996).

with highly chitinous prey such as ants and mites (Gabor and Jaeger, 1995; Vignoli et al., 2006; Lunghi et al., 2022). In the wet season, our results indicated that *Ameerega pulchripecta* had a broader diet, with abundance of larval insects and termites, whereas in the dry season they ate mainly ants, mites, and beetles. A previous study found a similar pattern for *Dendrobates tinctorius*, supporting the idea that increased diet diversity of poison frogs in the wet season is attributable to increased arthropod diversity during this period (Born et al., 2010; Moskowitz et al., 2018). In contrast to *Ameerega pulchripecta*, however, *Allobates femoralis* still had a diverse diet in the dry season, lending further support to the conclusion that it is a generalist species.

Notably, larval forms of Coleoptera and Diptera and adult termites were represented in small proportions, which may indicate opportunistic ingestion during the wet season. Previous research in Cerrado indicated that some *Ameerega* ingest a considerable proportion of termites (Biavati et al., 2004; Forti et al., 2011; Pacheco et al., 2020). An explanation could be that termites have high levels of carbohydrates, making them nutritionally profitable to frogs (Redford and Dorea, 1984; Marconi et al., 2002). The absence of these prey in *Ameerega pulchripecta* in the dry season may result from behavioral differences that are not observed in *Allobates femoralis*, which have a similar prey diversity between seasons. During periods of less reproductive activity, such as in the dry season, individuals may change their prey choice as nutritional demand for highly energetically-dense food decreases (Moskowitz et al., 2022).

The trophic niche of the mimic *Allobates femoralis* was broader—they exhibited more evenness of abundance in the overall set of prey consumed. In contrast to *Ameerega pulchripecta*, *Allobates femoralis* avoided mites. They consumed ants in similar proportions as those available in the leaf litter (Toft, 1980, 1995). Formicidae accounted for 25% of prey consumed by *Allobates femoralis*, corroborating similar results by Juncá and Eterovick (2007), Simões et al. (2010), and Astwood-Romero et al. (2016), who reported high proportions of ants from the stomachs of *Allobates hodli* and *Allobates marchesianus* in Amazonia, and *Allobates cepedai* and *Allobates juanii* in the slopes of eastern Colombia. However, our results indicated that ants are not actively selected by *Allobates femoralis*. No species of Aromobatidae are known to possess alkaloid toxins and, so far, all diet studies underscore the status of this clade as generalists (Juncá and Eterovick, 2007; Grant et al., 2017). Additionally, ant genera recognized in the diet of *Allobates femoralis* were widely distributed and locally abundant ants, namely *Pheidole* and *Crematogaster* (Wilson, 1976; Baccaro et al., 2015). Thus, the idea that myrmecophagy in this nontoxic species is opportunistic, but potentially a plesiomorphic trait of basal dendrobatoids, was reinforced (Toft, 1995).

Members of the order Coleoptera were important food items consumed by *Allobates femoralis*, as has been reported in previous studies of other congeneric species (Juncá and Eterovick, 2007; Astwood-Romero et al., 2016). However, *Allobates femoralis* ingested beetles in proportions not significantly different from those in the leaf litter, reinforcing its status as a generalist feeder. Coleoptera seems to be a common and easy prey for ground-dwelling anurans, especially in the Neotropics, most probably because of the abundance and wide range of habitats of beetles (Rafael et al., 2012). Additionally, beetles are a major protein source compared with other invertebrate taxa and a are more palatable and less aggressive prey (Anderson and Smith, 1998). Among the contents recognized from the stomachs of *Allobates femoralis*, we observed uncommon prey such as Culicidae (mosquito) eggs and Gastropoda (snails), both never reported in the diet of *Allobates* before. Snails and mosquito eggs were taken occasionally and probably opportunistically. In particular, mosquito eggs were found on two occasions and we hypothesize that they could have been ingested together with an adult female carrying the eggs. Although rare, consumption of insect eggs has already been reported in anurans (Das and Coe, 1994; Teles et al., 2018).

Our research underscores the importance of including resource availability for better inference of species foraging habits. Considering prey consumption along with prey availability pointed to food preferences of certain prey orders by

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the two frog species. However, prey selection results should be interpreted cautiously on account of biases of the sampling method employed toward certain types of invertebrates. Isoptera and larval Diptera, for example, were consumed in large numbers by the frog species. However, these prey were not represented in samples from the frog habitat. Another bias is the differential digestion rate for soft- and hard-bodied prey producing a lower detectability of some prey taxa in our sampling. Springtails (Collembola), for instance, appeared as a dominant potential prey present on the forest floor. However, they were not present in the frog stomachs, perhaps because of a more rapid digestion rate for collembolans, which poison frogs do not appear to reject as prey (Simon and Toft, 1991; Biavati et al., 2004).

Our results showed that differences between toxic and nontoxic species are significantly correlated with divergences in dietary specialization (Darst et al., 2005, 2006). We demonstrated that morphology did not affect individual prey choice in *Ameerega pulchripecta* and *Allobates femoralis*. Therefore, volumetric differences in prey composition are driven by the differences in prey selection between the two species. As suggested by Daly et al. (1994) and others, ant-specialization associated with alkaloid-based chemical defenses is a derived trait in poison frogs, whereas basal nontoxic groups exhibit a generalist opportunistic feeding behavior (Toft, 1995; Santos et al., 2003). Our findings agree well with the repeated association of these traits among dendrobatids across the Neotropical region (Mebs et al., 2010; Forti et al., 2011; Lima and Eterovick, 2013; Pacheco et al., 2020).

We amplify the discussion about the necessity of accessing the supply of environmental resources. Dietary overlap values did not detect differences in diet composition between *Allobates femoralis* and *Ameerega pulchripecta* on the basis of a major, biologically significant difference such as differential prey choice. On the other hand, composition (dis)similarity, diet diversity, and evenness indices were useful in summarizing detailed differences regarding the diet between the two frog species. *Allobates femoralis* comprises a complex of diurnal frogs believed to be Batesian mimics of sympatric poisonous species of the genus *Ameerega* (Amézquita et al., 2017; Saporito and Grant, 2018). Therefore, this study reveals important divergence in feeding habits of *Allobates femoralis* and *Ameerega pulchripecta*, reinforcing their status as Batesian mimics.

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