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Interindividual patterns of resource use in three subtropical Atlantic Forest frogs

VÍTOR CARVALHO-ROCHA,[1,2]* BENEDITO CORTÊS LOPES[1] AND SELVINO NECKEL-OLIVEIRA[1]

[1]*Departamento de Ecologia e Zoologia, Universidade Federal de Santa Catarina, Florianópolis, Brazil, and* [2]*Vítor Carvalho-Rocha, 88040-900 Florianópolis - SC, Bairro Córrego Grande, Brazil (E-mail: vc87rox@gmail.com)*

Abstract Studies with disparate taxa suggest that generalist populations are composed of relatively specialist individuals that use a narrow part of a population's resource pool. Models based on optimum diet theory (ODT) can be used to predict different patterns of variation in resource use among individuals. In this work, we investigated the diet and measured the degree of individual specialization of three anuran species, *Hypsiboas leptolineatus*, *Pseudis cardosoi* and *Scinax granulatus*, from the Atlantic Forest of southern Brazil. The study is based on gut content obtained using a stomach-flushing technique. Additionally, we tested for a correlation between the individuals' diet and morphological variation. Furthermore, we applied methods based on network theory to investigate patterns of resource use among individuals of each species. All three study species showed generalized diets and significant values of individual specialization. However, we did not find any correlation between diet and morphology, indicating that diet variation is not a consequence of morphological trade-offs. The individual-resource networks of *H. leptolineatus* and *S. granulatus* showed a nested pattern. This result indicates the presence of individuals with more diverse diets than others, and the diets of the more specialist individuals are a predictable subset of the diets of the more generalist ones. The individual-resource network of *P. cardosoi* did not show a distinct pattern, diverging from what was predicted by optimal diet theory-based models. Although nested or modular patterns are commonly found in individual-resource networks, our results indicate that they are not ubiquitous and that random patterns can also be found.

Key words: individual specialization, nestedness, network theory, niche overlap, optimum diet theory.

INTRODUCTION

Ecological studies have long neglected variation in resource use among individuals within populations. However, there is increasing evidence that individual-level variation regarding resource use is a widespread phenomenon, and has important ecological and evolutionary implications at both population and community levels (Bolnick *et al.* 2003, 2011; Hughes *et al.* 2008; Araújo *et al.* 2011). Therefore, generalist populations may comprise relatively specialist individuals that explore only a subset of the population resource base (Bolnick *et al.* 2007; Araújo *et al.* 2009; Snowberg *et al.* 2015). This individual specialization (IS) occurs even after accounting for age, sex and morphological differences among individuals (Bolnick *et al.* 2003; Araújo *et al.* 2011).

Studies have used optimal diet theory (ODT) as a theoretical framework to understand niche variation among individuals (Schoener 1971; Stephens & Krebs 1987; Bolnick *et al.* 2003). ODT predicts that individuals rank prey according to their energetic value per handling time, maximizing energy gain. If there are functional trade-offs associated with trait variation in an individual that leads to differences in prey capture and handling efficiency, the rank of the prey should differ among individuals (Bolnick *et al.* 2003; Svanbäck & Bolnick 2005; Tinker *et al.* 2007). Trade-offs constrain an individual's efficiency at capturing alternative prey, which prevents the use of all available resources and can be based on biomechanical, cognitive and/or physiological factors (Afik & Karasov 1995; Sanz-Aguilar *et al.* 2015; Snowberg *et al.* 2015). For example, Svanbäck and Eklöv (2003) showed that there is a functional trade-off between body form and performance in different habitats in individuals of the Eurasian perch (*Perca fluviatilis*) from a Swedish lake.

Extrinsic factors not related to variation among individuals can also lead to IS (Araújo *et al.* 2011). For example, an increase in prey availability during the warm-wet season in the Brazilian Cerrado increased interindividual diet variation in males of the gracile mouse opossum (*Gracilinanus microtarsus*) (Martins *et al.* 2008). High-density populations of sea otters (*Enhydra lutris*) from the northeast Pacific also showed higher values of interindividual diet

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*Corresponding author.

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variation compared to low-density populations (Newsome *et al.* 2015). On the other hand, the presence of a predator can reduce prey densities and concentrate the prey in restricted areas. In turn, this reduces the ecological opportunities of individuals of a prey, which lowers the values of interindividual diet variation (Araújo *et al.* 2014).

Individual specialization is pervasive in many disparate taxa (Araújo *et al.* 2011), and network analysis has been proved to be useful to describe patterns of resource use among individuals (e.g. Araújo *et al.* 2010; Pires *et al.* 2011; Polidori *et al.* 2013). Araújo *et al.* (2008, 2010) proposed a network-based approach to identify relationships among individuals and their resource use. By analysing the individual-resource network structure, such as average density of connections, nestedness and modularity, the degree and emergent patterns of the relationship among individuals and resource use can be identified (Pires *et al.* 2011; Tinker *et al.* 2012). Thus, predictions of different ODT models can be associated with distinct network architectures, which allows hypotheses about resource partitioning among individuals to be tested (Araújo *et al.* 2009, 2010; Pires *et al.* 2011; Tinker *et al.* 2012). For example, we would expect a nested structure if there are both specialist and generalist individuals in a population, but the diet of the most selective ones are predicted subsets of the generalists' diets (shared preferences model, Svanbäck & Bolnick 2005; Pires *et al.* 2011; Cantor *et al.* 2013). Alternatively, a modular structure would be formed if subgroups of individuals consume different subsets of resources because they have different top-ranked resources (distinct preference model), or they share a preferred resource but differ in alternative resources (competitive refuge model, Araújo *et al.* 2008; Pires *et al.* 2011).

Frogs (Amphibian, Anura) can be good models to study IS because most species are considered generalist predators (Solé & Rödder 2010; Brito *et al.* 2012). Regardless of its importance, IS has only been studied in a few anuran species (Araújo *et al.* 2007, 2009; Da Rosa *et al.* 2011), corresponding to less than 1% of the group's diversity (Frost 2017). *Hypsiboas leptolineatus* (Braun & Braun 1977), *Pseudis cardosoi* Kwet 2000 and *Scinax granulatus* (Peters 1871) are three anuran species that occur in the subtropical Atlantic Forest of southern Brazil (Kwet *et al.* 2010). Previous studies about the diets of these three species revealed they are generalist predators, but none of these works took into account possible diet variation among individuals (Miranda *et al.* 2006; Solé & Pelz 2007; Barbosa *et al.* 2014).

Here, we investigated the diets of *H. leptolineatus*, *P. cardosoi* and *S. granulatus* populations. We hypothesized that all species will show generalized diets as previously reported. However, as a consequence of being generalist predators, we predicted that individuals of all species would show heterogeneity in resource use. Based on this, we hypothesized that individual-resource networks will show emergent patterns according to how individuals partition the available resources. Specifically, for each species, we described its diet and tested for the presence and measured the degree of IS. Furthermore, we tested for correlations between the morphological variation in individuals and IS. In addition, we depicted as networks the interactions between individuals and resources and tested for the presence of nestedness and modularity in the individual-resource networks.

MATERIALS AND METHODS

Study site

This study was conducted in a permanent pond (28° 8′ 32″ S; 49° 38′ 8″ W) located in an area of subtropical Atlantic Forest in São Joaquim National Park (SJNP), Santa Catarina State, southern Brazil. The pond is about 475 m^2, has a maximum depth of 1.5 m, is located at 1300 m a.s.l. and is surrounded by grasses, shrubs and *Araucaria* trees. The region has a humid subtropical oceanic climate without a dry season and a temperate summer (Cfb), and the mean annual temperature is 13.5°C (Alvares *et al.* 2014). The local climate has a cold and a warm season. In the cold season (April to August), the minimum temperatures stay below 10°C and negative temperatures are frequent, whereas in the warm season (September to March), the minimum temperatures stay above 14°C (Pandolfo *et al.* 2002).

Data collection

Fieldwork was conducted during the warm season from September 2014 to March 2015. We surveyed the pond monthly, on three consecutive nights, looking for individuals of *H. leptolineatus*, *P. cardosoi* and *S. granulatus*. The surveys always began one hour after dusk. We standardized the survey effort by four person-hours per night, corresponding to a total effort of 84 person-hours. We looked for individuals on the water surface, and above and underneath vegetation, rocks and logs that were inside and/or outside the pond, within a 10-m buffer from the pond margin.

Captured individuals were sexed and had four measurements taken with a digital calliper (nearest 0.01 mm), always by the same person (V.C.R.): snout–vent length (SVL), mouth width (MW), head length (HL) and lower jaw length (JL). We collected diet data of each individual by using a stomach-flushing technique, which allowed us to recover stomach contents without killing the frogs (Solé *et al.* 2005). Stomach flushes were conducted within three hours after individual capture, and the stomach content was preserved in 70% ethanol. Before release back in the pond, individuals had their right leg marked with a subcutaneous Visible Implant Alpha tag (VIA, Northwest Marine Technologies, Inc.) to identify

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recaptures, which provided multiple observations per individual over time.

The stomach content was analysed under a stereomicroscope; individual prey items were counted and identified to the lowest taxonomic level possible. For example, items consumed were identified to order or family level, and in some cases to the genus level. For posterior analysis, we grouped taxa in broader categories (mostly order and family) to avoid overestimated values of individual specialization (Araújo *et al.* 2011). Fragmented material in advanced decomposition, which could not be identified at least to the order level, was excluded and not categorized.

Data analyses

The use of longitudinal data, which consists of multiple observations of individual resource use over time, is considered ideal for IS studies (Araújo *et al.* 2011). Accordingly, we considered the diet of individuals as the sum of consumed items from each capture event. We used this approach because all individuals were captured from the same pond, and were capable to select prey from the same pool of available resources. We opted to analyse only individuals that consumed at least four items to avoid overestimating the IS indices (Araújo *et al.* 2011).

Before testing for the presence of IS, we tested for diet differences between sexes. For this, we used Schoener's (1968) proportional similarity index (*PS*):

$$\mathrm{PS}_{ij} = 1 - 0.5\sum_{k}\left|p_{ik} - p_{jk}\right|, \tag{1}$$

where p_{ik} and p_{jk} correspond to proportions of item category k in the diets of i (females) and j (males), respectively. PS_{ij} corresponds to the overlap between the female and male diets, varying from 0 (no overlap) to 1 (total overlap). To calculate the significance of PS_{ij}, we used a nonparametric Monte Carlo procedure based on Bolnick *et al.* (2002) to generate replicate null diet matrices drawn from the population distribution, from which the *P*-value could be computed. We used 10 000 replicates in the Monte Carlo bootstrap simulation to obtain the *P*-value of PS_{ij}. Given that only one female of *H. leptolineatus* was captured and that only one of the 10 females of *S. granulatus* captured had consumed at least four items, we tested for diet differences between sexes for only *P. cardosoi*. We grouped individuals when no differences in diet were found, and used only males of *H. leptolineatus* and *S. granulatus* for further analysis. We did not test for ontogenetic diet shifts because we found only adult individuals.

In order to test for the presence and measure the degree of IS, we used the individual-level diet variation index (E) (Araújo *et al.* 2008). The E index is based on network theory and quantifies the average density of connections among individuals, which corresponds to the average dissimilarity among individuals (degree of interindividual variation). In theory, the values of E range from 0, when individuals have identical diets, to 1, when each individual has a completely different diet without sharing any component among individuals. Due to stochastic sampling, individuals that have the same diet may be captured by chance with different stomach content, and the lower the number of consumed items, the greater the likelihood the individuals will have different stomach content. Therefore, the minimum value of E in practice is greater than zero. We used a null model approach to test the significance of the E values and used a bootstrap procedure with 10 000 iterations. In each iteration, each individual was reassigned the same number of items that it consumed, drawn randomly from the population diet distribution via multinomial sampling (Araújo *et al.* 2008). Calculating E for each iteration, the null hypothesis can be rejected if the E value observed is >95% of the null values. For example, low number of items consumed per individual tends to inflate the E index; null values of E are often elevated because most individuals are captured once. To control for inflated values and stochastic sampling, we rescaled E (E_{adj}) by the mean null values of E (E_{null}), in which $E_{\mathrm{adj}} = (E - E_{\mathrm{null}})/(1 - E_{\mathrm{null}})$. As with the E index, E_{adj} also ranges from 0 to 1, where 0 corresponds to the amount of diet variation expected under the null hypothesis of no individual specialization. We then used E_{adj} to quantify the degree of IS in each population.

If IS was present, we tested for its correlation with individual morphological variation. For this, we used an approach proposed by Araújo *et al.* (2007). First, we conducted a principal component analysis (PCA) on the four log-transformed morphological measurements (SVL, MW, HL and JL). The PC1 scores can be interpreted as size, while the PC2-PC4 scores can be interpreted as body shape. We then calculated a matrix of pairwise Euclidean morphological distances among all individuals based on each of the PCA component scores. Next, we calculated the PS index, where p_{ik} and p_{jk} correspond to proportions of item category k in the diets of i and j individuals, respectively, to generate a matrix of pairwise diet overlap among individuals. We tested the correlation between the diet overlap matrix and morphological distance matrices with a simple Mantel test (10 000 simulations). If functional morphology effects individual diet, we would expect a negative correlation between matrices of diet overlap and morphological distances, indicating that morphologically similar individuals (small Euclidean distances) also show similar diets (high diet overlap), and vice versa.

Network analyses ware used to describe patterns of resource use by individuals. First, we built an individual-resource matrix (R) for each population, with individuals in rows and resource categories in columns. Each element r_{ij} of R was filled with the number of consumed items of resource j by individual i. From R, we depicted bipartite networks, which consisted of two sets of nodes (individuals and resource categories) and lines linking each individual to each of their consumed resource (Pires *et al.* 2011). Then, we described resource-sharing patterns between individuals testing for nestedness and modularity in the individual-resource networks. Nestedness is a network propriety that indicates the presence of highly connected nodes and other less connected nodes that interact in most cases with only the highly connected subset of nodes (Guimarães *et al.* 2006). Here, nestedness would indicate how much of the diet of the most specialist individuals represents a subset of the diet of the more generalist ones (Araújo *et al.* 2010;

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Pires *et al.* 2011). To estimate the degree of nestedness, we used both the NODF index, which uses absence and presence data of interactions, and WNODF index, which takes into account the quantitative information of interactions (Almeida-Neto *et al.* 2008; Almeida-Neto & Ulrich 2011). Both nestedness indices vary from zero (nestedness absent) to 100 (perfect nestedness). Modularity would indicate the presence of subsets of individuals (modules) that share the same resources but share few or none with other modules or individuals (Guimerà & Amaral 2005; Araújo *et al.* 2008). We used the weighted modularity index (C_{WS}) based on Saramaki's clustering coefficient to estimate the degree of modularity, which has values between −1 (indicating overdispersed individual diets) and +1 (maximum modularity) (Araújo *et al.* 2008).

Because some level of diet variation is expected, even if individuals are randomly sampling a shared distribution of resources, we tested the values of NODF, WNODF and C_{ws} against a null distribution of these indices using a bootstrapping procedure (10 000 iterations) as we did for E (Araújo *et al.* 2008). Values of each index were calculated for each iteration, and the null hypothesis could be rejected if the observed values of NODF and WNODF were >95% of the null values. For C_{WS}, the null hypothesis could be rejected if $C_{WS} > 0$ and higher than 97.5% of the null C_{WS} values, or if $C_{WS} < 0$ and lower than 97.5% of the null C_{WS} values (Araújo *et al.* 2008).

All analyses were performed with the software R version 3.2.4 (R Development Core Team 2016) using the packages ade4 (Dray & Dufour 2007), bipartite (Dormann *et al.* 2008) and RInSp (Zaccarelli *et al.* 2013). Individual-resource networks were built in Pajek (<http://vlado.fmf.uni-lj.si/pub/networks/pajek>).

DATA DEPOSITION

Data are available from the figshare repository: <https://doi.org/10.6084/m9.figshare.5379814.v1> (Carvalho-Rocha *et al.* 2017).

RESULTS

Population diet

We captured 27 individuals of *Hypsiboas leptolineatus* (1 female; 26 males), 83 of *Pseudis cardosoi* (43; 40) and 53 of *Scinax granulatus* (10; 43). The anurans consumed 47 item categories, including insects, annelids, crustaceans, arachnids, gastropods and even Gramineae seeds and other anurans (Table 1; see Supplementary material Appendix S1 for detailed diet data). The number of consumed item categories by *H. leptolineatus*, *P. cardosoi* and *S. granulatus* was 31, 41 and 24, respectively, and the average (range) number of consumed items per individual was 8.8 (1–28), 14.1 (0–49) and 2.5 (0–16), respectively. Twenty males of *H. leptolineatus*, 34 females and 31 males *of P. cardosoi* and 1 female and 14 males of *S. granulatus* consumed at least four items and were included in further analyses. The average number (±SD) of captures per individual of *H. leptolineatus*, *P. cardosoi* and *S. granulatus* was 3.5 (±1.36), 2.3 (±1.70) and 1.53 (±0.92), respectively (See Supplementary material Appendix S2 for detailed capture data). Females and males of *P. cardosoi* presented high diet overlap (PS = 0.73, $P = 0.11$, $n = 65$).

Interindividual variation

The average individual-resource network density of connections revealed significant IS in *H. leptolineatus* ($E_{adj} = 0.29$, $P < 0.001$), *P. cardosoi* ($E_{adj} = 0.41$, $P < 0.001$) and *S. granulatus* ($E_{adj} = 0.45$, $P < 0.001$). We found no significant correlations between morphological variation and diet overlap of individuals for all of the analysed species (Mantel, all *P*-values > 0.18), which indicates that the individual-level diet variation observed is not caused by the morphological characters here examined.

The networks of *H. leptolineatus* and *S. granulatus* exhibited a degree of nestedness higher than expected by chance, but only the *H. leptolineatus* network exhibited significant weighted nestedness (Fig. 1; Table 2). In contrast, none of the networks exhibited a significant modular pattern (Table 2).

DISCUSSION

We demonstrated the presence of IS in the study population of the three species, showing that generalist species are composed of specialist individuals. Individual-level diet variation in anuran species is still poorly understood, but available data indicate that IS is present in some studied species (Araújo *et al.* 2007, 2009; Benard & Maher 2011; Da Rosa *et al.* 2011; Schriever & Williams 2013).

Bolnick *et al.* (2003) suggest that functional trade-offs (e.g. morphological ones) preclude individuals from using all available resources, which results in IS. *Pseudis cardosoi* females and males differ in size, where females, on average, are larger than males (Kwet 2000). However, we found no significant diet differences between the sexes, indicating that size and possible behavioural differences do not determine the category of consumed items. Similar diets between females and males seem to be commonplace, which is probably due to similar metabolic requirements, as observed in other species (Maneyro *et al.* 2004; Wachlevski *et al.* 2008; Sugai *et al.* 2012).

The lack of correlation between diet and morphology of individuals of the studied species indicates that

Table 1. Diet composition of *Hypsiboas leptolineatus* (*n* = 27), *Pseudis cardosoi* (*n* = 83) and *Scinax granulatus* (*n* = 53), in São Joaquim National Park, represented as the number of items consumed and their proportions (in parentheses) for each species

		Species	
Prey categories	*H. leptolineatus*	*P. cardosoi*	*S. granulatus*
Annelida			
Hirudinoidea	–	9 (0.01)	–
Crustacea			
Isopoda	10 (0.04)	–	–
Gammaridea	–	6 (0.01)	1 (0.01)
Arachnida			
Acari	3 (0.01)	7 (0.01)	7 (0.05)
Amblypygi	–	–	1 (0.01)
Araneae	17 (0.07)	16 (0.01)	13 (0.10)
Opiliones	–	1 (0.00)	–
Collembola	13 (0.05)	36 (0.03)	–
Insecta			
NI	10 (0.04)	70 (0.06)	8 (0.06)
Blattaria	–	8 (0.01)	6 (0.05)
Coleoptera			
NI	5 (0.02)	29 (0.02)	7 (0.05)
AQ	1 (0.00)	183 (0.16)	–
Larvae NI	1 (0.00)	4 (0.00)	–
Larvae AQ	–	14 (0.01)	–
Larvae TE	–	–	1 (0.01)
TE	10 (0.04)	23 (0.02)	3 (0.02)
Diptera			
Brachycera			
Adult	11 (0.05)	71 (0.06)	4 (0.03)
Larvae	1 (0.00)	–	–
Pulp	1 (0.00)	–	–
Nematocera			
Adult	22 (0.09)	109 (0.09)	6 (0.05)
Larvae	–	2 (0.00)	–
Pulp	9 (0.04)	83 (0.07)	1 (0.01)
Ephemeroptera	–	38 (0.03)	–
Hemiptera			
Auchenorrhyncha	18 (0.08)	22 (0.02)	4 (0.03)
Heteroptera			
NI	9 (0.04)	17 (0.01)	4 (0.03)
AQ	1 (0.00)	33 (0.03)	–
TE	9 (0.04)	7 (0.01)	–
Sternorrhyncha	2 (0.01)	10 (0.01)	1 (0.01)
Hymenoptera			
NI	–	6 (0.01)	1 (0.01)
Apidae	–	14 (0.01)	–
Formicidae	7 (0.03)	51 (0.04)	2 (0.02)
Other	5 (0.02)	35 (0.03)	2 (0.02)
Isoptera	13 (0.05)	52 (0.04)	–
Lepidoptera			
Adult	6 (0.03)	6 (0.01)	1 (0.01)
Larvae	3 (0.01)	1 (0.00)	2 (0.02)
Mantodea	1 (0.00)	1 (0.00)	–
Odonata			
Adult	–	23 (0.02)	–
Nymph	–	23 (0.02)	–
Orthoptera	4 (0.02)	5 (0.00)	2 (0.02)
Plecoptera	1 (0.00)	1 (0.00)	–
Psocoptera	1 (0.00)	–	–
Trichoptera			
Adult	8 (0.03)	30 (0.03)	1 (0.01)

Table 1. *Continued*

	Species		
Prey categories	*H. leptolineatus*	*P. cardosoi*	*S. granulatus*
Larvae	–	3 (0.00)	–
Gastropoda	1 (0.00)	8 (0.01)	2 (0.02)
Anura			
Adult	–	2 (0.00)	–
Imago	–	11 (0.01)	–
Plantae			
Gramineae seed	34 (0.14)	96 (0.08)	52 (0.39)
Total Items	237	1166	132

AQ, aquatic; NI, nonidentified; TE, terrestrial.

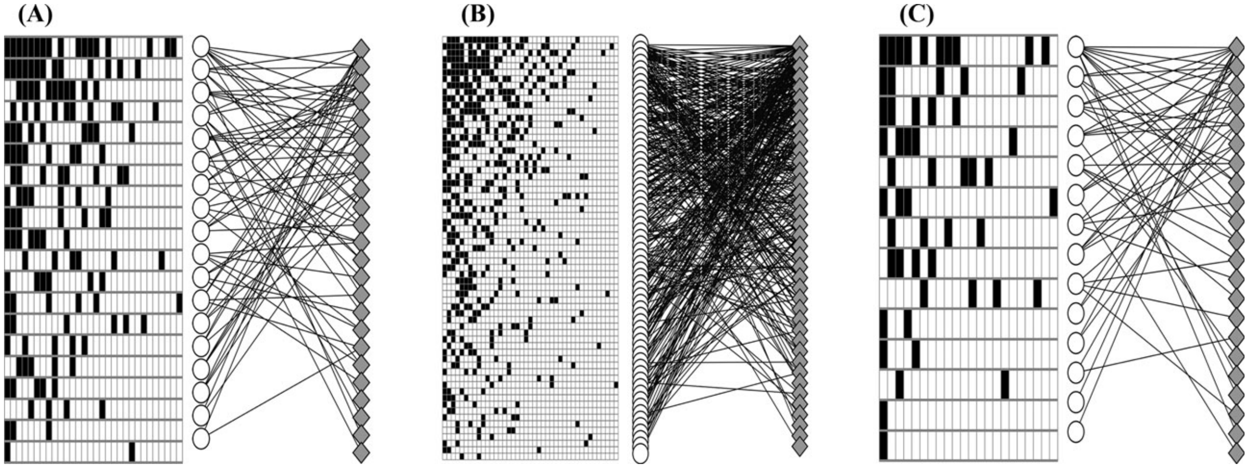

Fig. 1. Graphical representation of qualitative individual-resource matrices and networks of *Hypsiboas leptolineatus* (a), *Pseudis cardosoi* (b) and *Scinax granulatus* (c), at São Joaquim National Park. In the matrices, black cells indicate a given resource (column) consumed by an individual (row). In the networks, white circles represent individuals, diamonds represent resources and lines represent the consumption of a given resource by an individual.

Table 2. Nestedness (NODF and WNODF) and modularity (C_{WS}) indices in individual-resource networks of *Hypsiboas leptolineatus* (n = 20), *Pseudis cardosoi* (n = 65) and *Scinax granulatus* (n = 14) at São Joaquim National Park

	Nestedness						Modularity		
Species	NODF_{obs}	$\text{NODF}_{\text{null}}$	P	$\text{WNODF}_{\text{obs}}$	$\text{WNODF}_{\text{null}}$	P	$C_{WS\text{obs}}$	$C_{WS\text{null}}$	P
H. leptolineatus	39.65	32.71	0.01	16.33	11.92	<0.001	0.15	0.17	0.79
P. cardosoi	35.18	45.12	0.99	14.94	22.81	0.99	0.11	0.13	0.84
S. granulatus	29.74	22.97	0.02	6.99	11.03	0.99	0.09	0.12	0.73

All P-values are based on 10 000-bp iterations.

possible functional trade-offs associated with measured cranial traits are not responsible for limiting the diet of the individuals. Similar results were found for eight anuran species from the Brazilian Cerrado, indicating that this may be a general trend in frogs (Araújo *et al.* 2007, 2009). These authors noted that it is possible that cognitive and/or physiological trade-offs correspond to the mechanism of diet variation in frogs. For example, if the learning capacity of individuals is limited and different prey demand unique hunting strategies, learning trade-offs may reduce the number of different prey consumed per individual (Werner *et al.* 1981; Kato *et al.* 2000). Aquatic species like *P. cardosoi* might need to use different strategies to hunt prey under water, on the water surface or near vegetation. However, the same

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can be applied to terrestrial species like *H. leptolineatus* and *S. granulatus*, and a limitation on learning hunting techniques is a plausible mechanism of diet variation in these species. Furthermore, obtained energy for a given prey can differ between individuals if they have different digestive efficiencies (Burrows & Hughes 1991; Afik & Karasov 1995). This variable energy intake may cause individuals to have different rank preferences, leading to diet variation. Cognitive and/or physiological variation between individuals are plausible mechanisms of IS, and future studies are needed to test this variation.

Apart from potential underlying mechanisms of IS, we can use models based on ODT to predict differences in rank preferences among individuals (Svanbäck & Bolnick 2005; Pires *et al.* 2011). Despite low values, nestedness found in the individual-resource networks of *H. leptolineatus* and *S. granulatus* indicates that their populations comprise both specialist and generalist individuals, where the diets of the former are a predictable subset of the diets of the latter (Araújo *et al.* 2010; Pires *et al.* 2011). Nestedness is predicted by the shared preferences model, in which individuals share similar rank preferences of resources, but differ in their willingness to include lower-ranked ones (Svanbäck & Bolnick 2005). Based on this model, individuals include novel resources in a predicted order, leading to a nested pattern (Svanbäck & Bolnick 2005; Araújo *et al.* 2010). Thus, the shared preference model could explain the nested pattern we found.

Recent studies suggest nestedness as a common pattern in trophic interactions at the individual level (Pires *et al.* 2011; Cantor *et al.* 2013), just as it is at the species level (Bascompte *et al.* 2003; Guimarães *et al.* 2006). However, this pattern was not ubiquitous in all of the analysed networks. Although the qualitative individual-resource network of *S. granulatus* showed significant nestedness, the pattern was not observed when considering quantitative data. This indicates that although specialist individuals use a predictable subset of resources used by generalists, they use similar proportion of resources (Almeida-Neto & Ulrich 2011). The networks of *P. cardosoi* also did not show a nested pattern, even though the population of this species comprises both generalist and specialist individuals (Fig. 1). In this case, the shared preference model does not explain how individuals of *P. cardosoi* share resources.

The distinct preferences and competitive refuge are alternative ODT models that we can use to try to explain the patterns found (Svanbäck & Bolnick 2005). In the distinct preferences model, individuals have different top-ranked resources, and in the competitive refuge model, individuals share the same top-ranked resources but differ in the alternative resources. However, when IS is present, both models predict a modular pattern; that is, groups (modules) of individuals share similar diets but differ from other groups of individuals (Araújo *et al.* 2008; Pires *et al.* 2011). In contrast, modularity was not found in any analysed networks. Thus, the shared resources pattern in *P. cardosoi* does not follow previous ODT models (Svanbäck & Bolnick 2005). Among individuals of *P. cardosoi*, we observed low diet overlap, indicating divergence in the top-ranked resources consumed, but they shared similar alternative resources. In addition, because network modules have more connections within than between modules (Tinker *et al.* 2012), the use of similar alternative resources increases the number of connections among all individuals, transforming the network into a large unique group, without the formation of distinct modules.

Recent studies suggest that nestedness (Araújo *et al.* 2010; Pires *et al.* 2011; Cantor *et al.* 2013) and modularity (Araújo *et al.* 2008; Moleón *et al.* 2012; Ballesteros *et al.* 2014) are frequent patterns in individual-resource networks. Here, we showed that the presence of IS does not necessarily imply a nested or modular network, but random patterns can also emerge in the interaction between individuals and the resources they consume. This result reinforces that network analyses are useful tools to reveal individual-level patterns of resource use, and future studies should explore how individual trait variation and ecological parameters, such as competition and resource availability, reflect on different network patterns.

CONCLUSIONS

We reported new IS cases in three subtropical frogs. Although the studied species have generalist diets, individuals use only a small subset of resources used by populations. Our findings increase the list of known frog species that exhibit IS, suggesting that this phenomenon may be recurrent in anurans. Cranial morphological variation was not a good predictor of IS in the frogs, suggesting cognitive and/or physiological trade-offs as possible underlying mechanisms of interindividual diet variation.

ODT models can be useful in providing mechanistic bases to explain variations in resource use but they do not encompass all the patterns observed here. Diet variation in *H. leptolineatus* and *S. granulatus* was consistent with the shared preferences model. In contrast, diet variation in *P. cardosoi* was not consistent with any ODT models. Although recent works suggest nestedness and modularity as frequent patterns reported in individual-resource networks, our results indicate that random patterns can also occur.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Appendix S1. Detailed diet data of *Hypsiboas leptolineatus*, *Pseudis cardosoi* and *Scinax granulatus*.

Appendix S2. Detailed capture data of *Hypsiboas leptolineatus*, *Pseudis cardosoi* and *Scinax granulatus*.

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