Intrapopulation Diet Variation in Four Frogs (Leptodactylidae) of the Brazilian Savannah

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Age and sex-based as well as individual-level diet variation are known to occur in many natural populations, and may have important ecological and evolutionary implications. In the case of individual-level diet variation, most examples come from species-poor, temperate communities, and it is currently believed that it results from population niche expansion following interspecific competitive release. We investigated and measured the intrapopulation diet variation in four species of frogs, *Leptodactylus* (=*Adenomera*) sp., *Eleutherodactylus* cf. *juipoca*, *L. fuscus*, and *Proceratophrys* sp., that are part of species-rich frog communities of the Brazilian Cerrado. Specifically, we investigated age and sex-related, as well as individual-level, diet variation. We measured individual-level diet variation with the *IS* index of individual specialization, which is a measure of the degree of overlap between individual niches and the population niches. We found no ontogenetic shifts or sex-related differences in the types of prey consumed. However, we found evidence of individual-level diet variation in the four studied species (*IS* ~ 0.2–0.5). There was a negative correlation between *IS* and the population niche width ($r = -0.980$; $P < 0.0001$), indicating that interindividual diet variation is more pronounced in more generalized populations. This pattern suggests that individual niche widths remain constrained even when population niche breadth is wide, consistent with the presence of functional trade-offs. We found no evidence that these trade-offs arise from morphology, since there was no diet–morphology correlation. We hypothesize that trade-offs have a behavioral or physiological basis, which needs further investigation. This is the first documented case of individual-level diet variation in a diverse tropical community, indicating that this phenomenon is not restricted to competitive release-driven niche expansion in temperate, depauperate communities.

A variação entre classes etárias, entre os sexos ou mesmo entre os indivíduos de uma população é um fenômeno comum na natureza, tendo implicações ecológicas e evolutivas importantes. A maioria dos exemplos de variação interindividual conhecidos ocorre em comunidades temperadas pouco diversas, e acredita-se que esse tipo de variação resulta da expansão do nicho populacional gerada por liberação competitiva. Nós medimos o grau de variação intra-populacional na dieta de quatro espécies de rãs, *Leptodactylus* (=*Adenomera*) sp., *Eleutherodactylus* cf. *juipoca*, *L. fuscus*, e *Proceratophrys* sp., pertencentes a comunidades de anuros de alta diversidade do Cerrado brasileiro. Nós medimos o grau de variação interindividual com o índice *IS* de especialização individual, que mede o grau de sobreposição entre os nichos individuais e o nicho populacional. Não houve mudança ontogenética nem diferença entre os sexos quanto ao tipo de recurso consumido. Houve, no entanto, variação interindividual na dieta das quatro espécies estudadas (*IS* ~ 0.2–0.5). Houve correlação negativa entre *IS* e a amplitude do nicho populacional ($r = -0.980$; $P < 0.0001$), indicando que o grau de especialização individual é maior nas populações mais generalistas. Isso indica que os nichos individuais permanecem estreitos mesmo que o nicho populacional seja amplo, o que sugere a presença de *trade-offs*. De modo geral, não houve correlação entre a dieta e a morfologia dos indivíduos, indicando que os *trade-offs* não têm base morfológica. Nós hipotetizamos que os *trade-offs* têm base comportamental e/ou fisiológica, o que precisa ser investigado. Esse é o primeiro relato de variação interindividual em comunidades tropicais de alta diversidade, indicando que esse fenômeno não necessariamente resulta da expansão do nicho populacional resultante de liberação ecológica, em regiões temperadas pouco diversas.

VARIATION in resource use between age classes and sexes has been widely documented in the literature (Schoener, 1968, 1986). Age-based niche variation may be a result of changes related to size or development (Lima, 1998; Lima and Magnusson, 1998), whereas sex-based variation in resource use may result from differences in morphology (Shine et al., 2002) or differences in behavior or energetic requirements related to reproduction (Belovsky, 1978; Martins et al., 2006). However, there is also a type of variation in resource use that cannot be attributed to sex or age and has been termed ''individual specialization'' (Bolnick et al., 2003). For example, individuals of the Cocos Finch, *Pinaroloxias inornata*, consistently use only a subset of the resources used by the population as a whole (Werner and Sherry, 1987). This phenomenon may have several ecological and evolutionary implications (Bolnick et al., 2003), such as the relief of intraspecific competition (Smith, 1990; Swanson et al., 2003) or the generation of frequency-dependent interactions that may drive populations to divergence (Dieckmann and Doebeli, 1999; Bolnick and Doebeli, 2003; Svanbäck and Bolnick, 2005).

According to theory, we would not expect to find individual specialization in natural populations (Roughgarden, 1972, 1974; Taper and Case, 1985) unless there are constraints on individuals' niche widths (Bolnick et al., 2003). Constraints generally arise from functional trade-offs, in which consumers efficiently exploiting one type of resource are inefficient using another type of resource (Robinson et al., 1996). Trade-offs are generally associated with the functional morphology of consumers (Price, 1987; Smith, 1990; Robinson et al., 1996), but may also have a behavioral or physiological basis (Bolnick et al., 2003). For example, in the Bluegill Sunfish, *Lepomis macrochirus*, individuals with deeper bodies are more efficient in feeding on benthic prey, whereas more streamlined individuals perform better on zooplankton (Ehlinger, 1990). Such trade-offs prevent individuals from using the full range of available resources, so that in phenotypically variable populations individuals may use different subsets, resulting in individual specialization. In this case, we would expect populations with broader niches to show higher degrees of individual specialization, which has been observed in *Anolis* lizards (Lister, 1976; Roughgarden, 1979). It would be informative to know how general this pattern is in natural populations.

The evolution of individual specialization has been interpreted as a consequence of the population niche expansion following interspecific competitive release. Examples supporting this idea are common in temperate lacustrine fish, such as sticklebacks (Schluter, 1995; Robinson, 2000; Bolnick, 2004) and sunfish (Robinson et al., 1993, 1996). In these fishes, when two species occur in the same lake, one of them occupies the littoral microhabitat and feeds on benthic prey, whereas the other is limnetic and feeds on zooplankton (Robinson et al., 1993). If one of the species is absent, however, the present species exploits both benthic and limnetic niches, indicating competitive release-driven niche expansion. This niche expansion is often achieved by increased between-individual variation, rather than increased niche width of all individuals (Ebenman and Nilsson, 1982; Robinson et al., 1993). Therefore, it is currently believed that the occurrence of individual specialization is a consequence of population niche expansion following the invasion of ''empty'' niches (Smith and Skúlason, 1996), generally in species-poor, temperate communities (Ebenman and Nilsson, 1982; Robinson et al., 1993, 1996; Schluter, 1995; Robinson, 2000). The few tropical taxa known to exhibit diet variation are also in species-poor communities (Roughgarden, 1974; Werner and Sherry, 1987).

To evaluate whether individual specialization really is stronger in low-diversity environments, one must be able to compare the degree of diet variation across systems. This comparison requires that, instead of simply testing for the presence of individual specialization, ecologists should actually try to measure it in a standardized manner (Bolnick et al., 2003). Bolnick et al. (2002) proposed indices to quantify individual-level diet variation and stirred researchers to use them when investigating individual specialization. In the present study, we investigated the intrapopulation diet variation in four species of Neotropical frogs inhabiting species-rich (around 20 frog species; Giaretta et al., unpubl. data) communities of the highly seasonal Brazilian Cerrado (Oliveira and Marquis, 2002). The character-release hypothesis suggests that the studied species should show negligible degrees of individual specialization. Specifically, we (1) tested for the presence of ontogenetic diet shifts; (2) tested for the presence and measured the degree of sex-related and individual-level diet variation; (3) tested the hypothesis that higher degrees of individual specialization are associated with broader niches; (4) tested if morphology is the underlying mechanism of individual specialization; and finally (5) tested the effect of season on the frogs' diets.

TABLE 1. SCHOENER'S (1968) PROPORTIONAL SIMILARITY INDEX (*PS*) BETWEEN THE DIETS OF MALES AND FEMALES OF FOUR SPECIES OF BRAZILIAN FROGS (*Leptodactylus* [=*Adenomera*] SP., *Eleutherodactylus* CF. *juipoca*, *L. fuscus*, AND *Proceratophrys* SP.). Comparisons were made in the wet and dry seasons. *P*-values were obtained in Monte Carlo bootstraps (1,000 simulations). *n*: number of frog specimens.

Species	Wet season			Dry season		
	PS	P	n	PS	P	n
Leptodactylus sp.	0.8251	0.823	86	0.4437	0.482	14
E. cf. *juipoca*	0.7402	0.779	54	—	—	—
L. fuscus	0.7157	0.826	62	0.4886	0.818	20
Proceratophrys sp.	0.6293	0.958	42	—	—	—

MATERIALS AND METHODS

Study system.—We analyzed the stomach contents and morphology of four species of frogs from a tropical savannah formation in southeastern Brazil (Cerrado; Oliveira and Marquis, 2002). A wet/warm season (henceforth ''wet season'') from September to March and a dry/mild season (henceforth ''dry season'') from April to August characterize the local climate. The mean annual precipitation is 1550 mm (range 750–2000), and in the drier months can be zero (Rosa et al., 1991). The monthly mean temperature ranges from 19 to 30 C, and winter frosts are frequent (Giaretta and Menin, 2004).

Specimens from four species, namely, *Leptodactylus* (=*Adenomera*) sp. ($n = 104$ individuals), *Eleutherodactylus* cf. *juipoca* ($n = 115$), *L. fuscus* ($n = 86$), and *Proceratophrys* sp., ($n = 55$), were collected in the municipality of Uberlândia (18°55′S, 48°17′W; 850 m), in the state of Minas Gerais, southeastern Brazil. The collection sites were located at the Clube de Caça e Pesca Itororó de Uberlândia, CCP (*Leptodactylus* sp., *L. fuscus*, and *Proceratophrys* sp.), and at the Estação Ecológica do Panga, EEP (*E.* cf. *juipoca*), two of the few remnants of original savannah vegetation still present in the municipality (Goodland and Ferri, 1979), characterized by shrubby grassland areas surrounding wet areas such as *veredas* (marshes with buriti-palms, *Mauritia flexuosa*) or temporal and permanent ponds (França et al., 2004; Giaretta and Menin, 2004; Kokubum and Giaretta, 2005). Frogs were collected weekly in the wet season and once every two weeks in the dry season, for a period of two years; specimens of *Leptodactylus* sp. were collected from October 1999 to March 2001; *E.* cf. *juipoca* from September 2000 to October 2001; *L. fuscus* from October 1999 to December 2000; and *Proceratophrys* sp. from November 1999 to August 2001. Frogs were immediately killed upon collection, preserved in 5% formalin, and later transferred to 70% ethanol. Voucher specimens were deposited at the collection of the Museu de Biodiversidade do Cerrado of the Universidade Federal de Uberlândia (AAG-UFU).

Data collection.—Frogs were dissected to obtain stomach contents. Prior to dissection, five measurements were taken from each specimen with a digital caliper (nearest 0.01 mm) always by the same person (M. S. Araújo): snout–vent length (SVL), mouth width (MW), lower jaw length (LJ), head length (HL), and eye–nostril distance (EN). We did not measure the mass of individuals, because preservative absorption was likely to bias our results. Diets were quantified by the analysis of stomach contents of the preserved specimens. Prey items were counted and identified to the lowest taxonomic level possible (family level in most cases). Upon dissection, individuals were sexed by examination of gonads. In a few cases we failed to determine the sex of individuals, which explains the differences in sample sizes between Tables 1 and 2.

Data analyses.—We found 97 prey taxa, spanning many families and orders, mostly insects and arachnids. Within orders, we grouped several families into functional groups, based on microhabitat (e.g., aquatic, soil, vegetation) and morphotypes (e.g., alates or workers of Isoptera), and ended up with 46 prey categories (Appendix 1). Within each frog species, most categories had very little abundance in the diets, so we used a rule of thumb (Krebs, 1989) in order to eliminate those poorly represented categories, retaining the most representative ones. This rule consists of calculating the reciprocal of the number k of prey categories consumed ($1/k$), and using it as a cutoff value for the inclusion of prey categories in further analyses. A category j is included if its proportion in the population diet $q_j \geq 1/k$. The cut-off value was 0.03 in all frog species, so that only categories representing less than 3% of diet items in each species were eliminated.

In order to investigate ontogenetic diet shifts, we took an approach that relates body size (a

TABLE 2. *IS* MEASURE OF INDIVIDUAL SPECIALIZATION IN THE DIET OF FOUR SPECIES OF BRAZILIAN FROGS (*Leptodactylus* [=*Adenomera*] SP., *Eleutherodactylus* CF. *juipoca*, *L. fuscus*, AND *Proceratophrys* SP.). Individual specialization was measured in the wet and dry seasons. *P*-values were obtained in Monte Carlo bootstraps (1,000 simulations). *n*: number of frog specimens.

Species	Wet season			Dry season		
	IS	P	n	IS	P	n
Leptodactylus sp.	0.3407	<0.001	86	0.4875	<0.001	14
E. cf. *juipoca*	0.2621	0.016	54	0.3054	0.011	53
L. fuscus	0.2507	<0.01	63	0.2065	<0.001	20
Proceratophrys sp.	0.1521	<0.001	42	0.3401	0.10	8

proxy for age) to interindividual diet overlap. Within each species, we first did a Principal Components Analysis (PCA) on the five log-transformed morphological measurements. We then took the PC1 scores (interpreted as size) and calculated the Euclidean distances between all pairs of individuals, which generated a matrix of individual pairwise size distances. Next, we calculated a measure of pairwise diet overlap among individuals based on Schoener's (1968) proportional similarity index (*PS*),

$$PS_{ij} = 1 - 0.5 \sum_k |p_{ik} - p_{jk}|,$$

in which p_{ik} and p_{jk} are the proportions of prey category k in individual i's and j's diet, respectively. PS_{ij} is the proportional similarity between the diets of individuals i and j, varying from 0 (no overlap) to 1 (total overlap). If there are diet shifts associated with body size, which would indicate ontogenetic diet shifts, we would expect that more similar sized individuals have more similar diets. If this is true, we would expect the matrix of body size differences to be negatively correlated with the matrix of pairwise diet overlap, since the higher the size distance the lower the diet overlap. We tested for the correlation between matrices with a simple Mantel test with 1,000 simulations.

We tested for sex-related differences in diet also using the *PS* index, in which p_{ik} and p_{jk} represent the proportion of prey category k in males' and females' diets, respectively. In order to detect possible seasonal changes in the degree of sex-related diet variation, we analyzed samples from the wet and dry seasons separately. In the dry season, small sample sizes prevented us from analyzing *E.* cf. *juipoca* ($n = 2$ males) and *Proceratophrys* sp. ($n = 3$ females; $n = 5$ males).

When measuring individual-level diet variation, we also kept samples separated by season. We did this because the degree of individual-level diet variation may be affected by variations in resource abundance (Svanbäck and Persson,

2004; Svanbäck and Bolnick, 2005), and we know that the abundance of terrestrial arthropods varies seasonally in the Cerrado (Pinheiro et al., 2002; G. Machado, unpubl. data). We used the proposed adaptation of *PS* to measure individual-level diet variation (PS_i), which measures the overlap between an individual i's diet and the population diet (Bolnick et al., 2002). In the case of PS_i, p_{ik} represents the proportion of category k in individual i's diet, and p_{jk} is replaced by q_k, the proportion of category k in the population diet. For an individual i that specializes on a single prey category k, its PS_i will take on the value of the proportion of prey k in the population, whereas for individuals that consume prey in direct proportion to the population as a whole, PS_i will equal 1. The PS_i values of all individuals in the population can be calculated and summarized as a population-wide measure of individual specialization, which is the average of PS_i values, *IS* (Bolnick et al., 2002). *IS* varies from near 0 (maximum individual specialization) to 1 (no individual specialization). An interesting feature of PS_i is that it generates measures of individual specialization for each individual in the population, which allowed us to compare the degree of individual specialization between wet and dry seasons by performing a Mann–Whitney *U*-test on PS_i values.

In order to test the hypothesis that the degree of individual specialization increases with the population niche width, we did a Pearson's correlation test between the calculated *IS* measures and Roughgarden's (1979) index of total niche width (*TNW*), which uses the Shannon–Weaver diversity index as a measure of the population variance in resource use. If the degree of individual specialization increases with the expansion of the population niche, we would expect a negative correlation between *IS* and *TNW* (recall that lower *IS* values indicate higher individual specialization).

In order to test the hypothesis that individual-level diet variation is based on morphological trade-offs, we correlated the previously calculated

matrix of pairwise diet overlaps with a matrix of Euclidean morphological distances based on all but PC1 scores (interpreted as body shape). If there is an effect of functional morphology on diet, we would expect that morphologically similar individuals (small distances) also show similar diets (high diet overlap), and vice versa. If this is true, we would expect a negative correlation between the matrices of morphological distance and diet overlap. We tested the correlation between matrices with a simple Mantel test with 1,000 simulations. Finally, we did a MANOVA on the arcsine square-root transformed proportions of prey categories in individual diets, with prey categories as the dependent variables and season as the independent variable to test for seasonal variation in the frogs' diets.

The calculation of all indices was performed in IndSpec1, a program to calculate indices of individual specialization (Bolnick et al., 2002). We also used IndSpec1 to calculate the significance of the PS measures between sexes and the IS measures of individual specialization. IndSpec1 uses a nonparametric Monte Carlo procedure to generate replicate null diet matrices drawn from the population distribution (Bolnick et al., 2002), from which P-values can be computed. The null model relies on the assumption that each prey item in the diet corresponds to an independent feeding event, which we acknowledge is probably untrue in the case of termites and ants. We used 1,000 replicates in Monte Carlo bootstrap simulations to obtain P-values for these indices. The PCA, the Mann–Whitney U-test, the Pearson's correlation analysis, and the MANOVA were performed in SYSTAT11; the Mantel tests were carried out using the software PopTools 2.6.9 (G. M. Hood, PopTools version 2.6.9, 2005. Available at: http://www.cse.csiro.au/poptools).

RESULTS

The correlation between body size and diet overlap was not significant in any of the analyzed species (Mantel; all P-values > 0.104), indicating that there are no ontogenetic shifts in the prey categories consumed. None of the PS measures between sexes differed significantly from the Monte Carlo null expectations (all P-values > 0.482; Table 1), indicating the absence of sex-related differences in diet in the analyzed species. However, there was evidence of significant individual specialization in the four analyzed species, except in *Proceratophrys* sp. in the dry season (Table 2). Individual specialization was significantly weaker (higher IS) in the dry
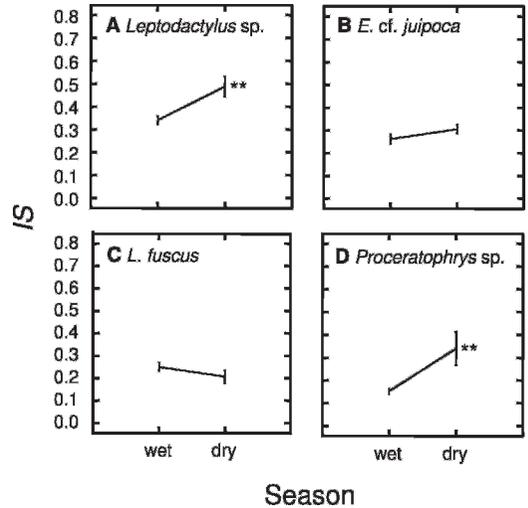
Fig. 1. Comparison between the degree of individual specialization (IS; mean ± Standard Error) in the wet and dry seasons in four species of Brazilian frogs. Lower IS values indicate stronger individual specialization. (A) *Leptodactylus* (=*Adenomera*) sp.; (B) *Eleutherodactylus* cf. *juipoca*; (C) *Leptodactylus fuscus*; and (D) *Proceratophrys* sp. Sample sizes are the same as in Table 2. **P < 0.01 (Mann–Whitney U-test).

season in *Leptodactylus* sp. (Mann–Whitney $U = 900$; $P = 0.003$; Fig. 1A) and *Proceratophrys* sp. ($U = 287$; $P = 0.002$; Fig. 1D). *Eleutherodactylus* cf. *juipoca* showed the same trend, but the difference was only marginally significant ($U = 1743$; $P = 0.052$; Fig. 1B), whereas *L. fuscus* showed an opposite trend, but not significant ($U = 525$; $P = 0.263$; Fig. 1C). There was a significant negative correlation between IS and TNW (Pearson's $r = -0.980$; $P < 0.0001$; $n = 8$), indicating that the wider the population niche, the higher the degree of individual specialization. We did not observe any significant correlations between body shape and diet overlap (Mantel; all P-values > 0.194), indicating that the observed individual-level diet variation has no morphological basis. There was no effect of season on the diets of *Leptodactylus* sp. (MANOVA; Wilk's $\Lambda = 0.895$; $P = 0.319$), *L. fuscus* (Wilk's $\Lambda = 0.889$; $P = 0.791$), and *Proceratophrys* sp. (Wilk's $\Lambda = 0.706$; $P = 0.697$), but a marginally significant effect in *E.* cf. *juipoca* (Wilk's $\Lambda = 0.818$; $P = 0.062$).

DISCUSSION

We found no age or sex-related diet differences in any of the four studied species. However, we found evidence of significant individual specialization in all species. Additionally, the degree of individual specialization seems to

vary among species and seasons. The morphological traits we investigated were not good predictors of individuals' diets, suggesting that among-individual diet variation may not have a morphological basis. In the following paragraphs we discuss (i) the observed patterns of intrapopulation diet variation in the studied frogs; (ii) the possible mechanisms underlying the observed diet variation; and (iii) the temporal consistency of individual-level diet variation.

Patterns of intrapopulation diet variation.—Ontogenetic shifts in prey type, which have been reported for several Amazonian frogs and may have important implications in terms of resource partitioning at both the population and community level (Lima and Moreira, 1993; Lima, 1998; Lima and Magnusson, 1998; Biavati et al., 2004) were not observed in our study. Apparently, the differences in body size as well as possible differences in behavior between juveniles and adults are not important in determining the types of food consumed in the studied species. Likewise, sex seems not to be an important factor in food consumption in the studied frogs, which was also observed in other frog species (Lima and Moreira, 1993; Biavati et al., 2004) and perhaps is a general trend in frogs. In spite of the overall lack of age and sex-related diet differences, we did find evidence of individual-level variation in all species. In the only exception, *Proceratophrys* sp. in the dry season, we probably lacked statistical power due to the very small sample size ($n = 8$; Table 2). Our results, therefore, suggest that frog populations, although exploiting a variety of food taxa (many arthropod orders and families), may be actually composed of individuals with different preferences or prey capture abilities.

The degree of individual specialization was not the same among species (Table 2), being the highest in *Proceratophrys* sp. in the wet season (~0.15; recall that values closer to zero indicate stronger individual specialization) and the lowest in *Leptodactylus* sp. in the dry season (~0.49; Table 2). A likely explanation for these differences might be the relationship we found between the degree of individual specialization and the population niche width. We found that the broader the population niche, the higher the interindividual diet variation. This is in accordance with the patterns previously reported for *Anolis* lizards (Lister, 1976; Roughgarden, 1979) and experimentally confirmed in three-spine sticklebacks (Svanbäck and Bolnick, 2007), suggesting that this may be a general pattern in natural populations. This pattern is expected in the presence of trade-offs, in which individuals are not able to master and consume all resource

types used by the population as a whole. In such cases, individual niches remain constrained when the population niche expands, and individual specialization arises as a consequence. Note that this correlation between *TNW* and *IS* is not corrected for phylogenetic non-independence among datapoints. We find this acceptable since individual specialization likely shows substantial variation even among populations and over time as ecological conditions change, so we do not expect a strong phylogenetic signal (Price, 1997). Moreover, in our case the use of comparative methods would suffer seriously from the poor taxon sampling and the lack of branch length estimates (Ackerly, 2000).

Additionally, seasonality seems to be an important factor in the degree of individual specialization in *Leptodactylus* sp. and *Proceratophrys* sp. (Fig. 1). In both species, we observed a reduction in the degree of individual specialization in the dry season, when there is a great reduction in arthropod abundance in the Cerrado (Pinheiro et al., 2002; G. Machado, unpubl. data). Individual niche widths may vary over time as a function of resource abundances (Svanbäck and Persson, 2004; Svanbäck and Bolnick, 2007). Optimal diet theory (Pulliam, 1974) predicts that individuals will be more specialized on preferred resources when resources are abundant. As a result, individual niches would tend to shrink in the 'fat' season and expand in the 'lean' season (Schoener, 1986). If individuals have distinct preference ranks for resources (see Svanbäck and Bolnick, 2005), we might expect a higher degree of individual specialization in the 'fat' season—when individual niches are narrower—and less individual specialization in the 'lean' season—when individual niches are wider and tend to overlap more with the population niche. This expectation is in accordance with the pattern observed in the three species that showed significant or marginally significant seasonal differences in the degree of individual specialization, namely *Leptodactylus* sp., *Proceratophrys* sp., and *E.* cf. *juipoca* (Fig. 1). An alternative explanation relies on the fact that the population niche width increased in the wet season (not shown), when there is a higher diversity of resources available. If individual niche widths remain constant while the population niche expands, the degree of individual specialization will increase. This is in accordance with the idea of population niche expansion through increasing between-individual variation, but in a much faster time scale than the evolutionary diet diversification suggested by Lister (1976) and Roughgarden (1979). This quick intrapopulation diet diversification is more

in line with behaviorally based diet shifts (see below) in response to changes in resource abundance, which have been experimentally demonstrated in natural populations of sticklebacks (Svanbäck and Bolnick, 2007).

Mechanisms of individual-level diet variation.—An important task in the study of individual specialization is to identify its underlying mechanisms (Bolnick et al., 2003; Svanbäck and Persson, 2004), which in general is associated with the presence of functional trade-offs, either morphological, behavioral, or physiological (Bolnick et al., 2003). In the case of frogs, an association between morphology and diet is apparent when we compare ant-specialist against generalist species: the former have narrower mouths than the latter (Toft, 1980, 1981). In fact, the specialization in ants seems to result from a combination of morphological, behavioral (active searching vs. sit-and-wait tactic), and physiological (aerobic vs. anaerobic metabolism) characters, and it has been suggested that ant-specialization and generalization correspond to two different adaptive peaks in frogs (Toft, 1985). In the present study, all the studied species belong to a guild of generalist feeders (Toft, 1981, 1985), and we had no *a priori* reason to expect a correlation between individual morphology and diet. We tested it mainly for two reasons. First, the only way of ruling out morphology as the underlying mechanism of the observed individual-level diet variation was to test morphology against diet. Second, morphology–diet correlations can be a useful way to infer temporal consistency in resource use, which is especially important in the absence of repeated observations of single individuals (see below).

We found no evidence that individual-level diet variation has a morphological basis in the studied frogs, which calls for an alternative explanation. One possible explanation is the existence of learning trade-offs. If resources require learning to be used and individuals are neurologically limited in their learning abilities, learning trade-offs may happen (Werner et al., 1981; Lewis, 1986; Werner and Sherry, 1987; Bernays and Funk, 1999). For example, in the Bluegill Sunfish, *Lepomis macrochirus*, learning was found to increase foraging efficiency sharply on either benthic (midge larvae) or limnetic prey (*Daphnia*), and was an important factor in determining habitat choice by individuals (Werner et al., 1981). It is possible that in the studied frogs, which feed both on highly mobile, elusive prey (e.g., beetles, spiders, roaches) and slow-moving, patchily distributed, prey (e.g., ants, termites), there is some learning involved in prey

search, detection, capture, and handling. We acknowledge this is very speculative, but learning trade-offs could be tested experimentally in these frogs by measuring capture rates and handling times of consumers on different prey types (Werner et al., 1981; Ehlinger, 1990). Another possibility that cannot be dismissed is that frogs differ in their physiological abilities to digest prey, which might also generate trade-offs (Bolnick et al., 2003) resulting in individual specialization (West, 1986). The studied frogs feed on ants and termites, which are known to be highly toxic prey (Caldwell, 1996; Santos et al., 2003). These toxins in turn might impose a cost to be detoxified, which may result in trade-offs and generate individual-level diet preferences.

Temporal consistency.—Gut contents are a 'snapshot' of an individual's diet and may not necessarily reflect long-term preferences (Warburton et al., 1998). This sampling problem may make one believe that individuals are more specialized than they really are, leading to overestimation of the degree of individual specialization in the population (Bolnick et al., 2003). Therefore, in studies using gut-content data, it is desirable to have some measure of temporal consistency in food resource use by individuals (Bolnick et al., 2003). In a companion study concerning the studied frogs (Araújo et al., 2007), we measured the among-individual variance in carbon stable isotopes ($\delta^{13}C$), quantified from the frogs' muscle tissue, as well as their food resources' signatures. Muscle tissue is known to integrate several months of an individual's past food consumption (Tieszen et al., 1983; Dalerum and Angerbjörn, 2005) and is therefore a useful measure of long-term diet. If the individuals in a given population all have similar diets, they will also show similar isotopic signatures, so that the population isotopic variance will be close to zero (Fry et al., 1978). On the other hand, if individuals vary in their isotopic signatures, this can be taken as evidence of long-term interindividual diet variation. The studied frogs had isotopic variances ranging from 1.38 in *E.* cf. *juipoca* to 8.35 in *Proceratophrys* sp. (Araújo et al., 2007), indicating the existence of among-individual diet variation. Additionally, Araujo et al. (2007) developed a method to convert this variance into the *IS* index of individual specialization. By comparing the isotope-derived *IS* measures with those obtained from gut contents, these authors demonstrated that gut contents only slightly overestimated individual-level diet variation in *Leptodactylus* sp., *L. fuscus*, and *Proceratophrys* sp., while greatly overestimating the degree of individual specialization in *E.* cf.

juipoca. Bearing this caveat in mind, we feel confident to state that with the exception of *E.* cf. *juipoca*, whose isotope-derived *IS* measure was around 0.8, there is evidence of strong individual-level diet variation in the studied species.

We have documented the first cases of individual specialization in tropical, diverse communities of frogs. Our results are at odds with the general pattern of competitive release-driven niche expansion in depauperate communities, leading to increased intra-population variation described in the ecological literature (e.g., Roughgarden, 1974; Werner and Sherry, 1987; Smith and Skúlason, 1996). The observed pattern is particularly striking since the actual degree of individual specialization observed in these tropical frogs is comparable to many of the most ecologically variable populations described from temperate regions (e.g., *Nucella* snails; West, 1986, 1988; three-spine sticklebacks; Svanbäck and Bolnick, 2007) and depauperate tropical habitats (e.g., Cocos Finches; Werner and Sherry, 1987). While we have not statistically compared levels of diet variation in these tropical frogs to temperate taxa (there are too few comparable studies for a robust test), our results clearly indicate that individual specialization does occur in diverse communities. The description of this new pattern, by challenging an established view, may promote a better understanding of the necessary conditions for the evolution and maintenance of individual specialization as well as its implications for species coexistence.

MATERIAL EXAMINED

Leptodactylus sp. Brazil: Minas Gerais: Uberlândia, Clube de Caça e Pesca Itororó de Uberlândia, 850 m, AAG-UFU 3742–60.

E. cf. *juipoca*. Brazil: Minas Gerais: Uberlândia, Estação Ecológica do Panga, 850 m, AAG-UFU 4122–4.

Leptodactylus fuscus. Brazil: Minas Gerais: Uberlândia, Clube de Caça e Pesca Itororó de Uberlândia, 850 m, AAG-UFU 3931–4.

Proceratophrys sp. Brazil: Minas Gerais: Uberlândia, Clube de Caça e Pesca Itororó de Uberlândia, 850 m, AAG-UFU 3817–45.

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APPENDIX 1. DIET COMPOSITION OF *Leptodactylus* SP. ($n = 100$), *Eleutherodactylus* CF. *juipoca* ($n = 107$), *L. fuscus* ($n = 83$), AND *Proceratophrys* SP. ($n = 50$) IN THE BRAZILIAN CERRADO, REPRESENTED AS THE NUMBER OF PREY ITEMS CONSUMED AND THEIR PROPORTIONS (IN PARENTHESES) IN EACH SPECIES. *Categories included in the analyses (see text for details).

Prey categories	Species			
	Leptodactylus sp.	*E.* cf. *juipoca*	*L. fuscus*	*Proceratophrys* sp.
Collembola	6 (0.01)	49 (0.11)*	0	0
Odonata (naiads)	0	0	0	1 (0.01)
Dermaptera	3 (0.00)	0	2 (0.00)	1 (0.01)
Orthoptera (NI)	2 (0.00)	7 (0.02)	12 (0.03)*	7 (0.04)
Orthoptera (soil)[a]	4 (0.01)	6 (0.01)	27 (0.06)*	4 (0.02)
Orthoptera (vegetation)[b]	2 (0.00)	4 (0.01)	14 (0.03)*	6 (0.03)*
Blattodea	44 (0.07)*	13 (0.03)*	22 (0.05)*	16 (0.09)
Mantodea	0	1 (0.00)	2 (0.00)	0
Isoptera (NI)	2 (0.00)	5 (0.01)	1 (0.00)	0
Isoptera (alates)	24 (0.04)*	5 (0.01)	13 (0.03)*	9 (0.05)
Isoptera (non-alates)	31 (0.05)*	0	53 (0.12)*	0
Psocoptera	0	21 (0.05)*	0	0
Thysanoptera	0	1 (0.00)	0	0
Hemiptera				
Auchenorrhinca[c]	34 (0.06)*	41 (0.09)*	22 (0.05)*	9 (0.05)
Sternorrhinca[d]	1 (0.00)	4 (0.01)	1 (0.00)	4 (0.02)
Heteroptera (NI)	14 (0.02)	1 (0.00)	7 (0.02)	1 (0.01)
Heteroptera (aquatic)[e]	0	0	1 (0.00)	0
Heteroptera (soil)[f]	2 (0.00)	1 (0.00)	3 (0.01)	2 (0.01)
Heteroptera (vegetation)[g]	9 (0.01)	6 (0.01)	3 (0.01)	10 (0.05)
Coleoptera (NI)	15 (0.02)	12 (0.03)*	14 (0.03)*	5 (0.03)
Coleoptera (soil)[h]	36 (0.06)*	23 (0.05)*	26 (0.06)*	4 (0.02)
Coleoptera (vegetation)[i]	12 (0.02)	8 (0.02)	36 (0.08)*	8 (0.04)
Lepidoptera	0	1 (0.00)	2 (0.00)	0
Trichoptera	0	1 (0.00)	0	0
Diptera (NI)	0	0	7 (0.02)	0
Diptera (Nematocera)	7 (0.01)	6 (0.01)	3 (0.01)	2 (0.01)
Diptera (other)[j]	7 (0.01)	7 (0.02)	6 (0.01)	2 (0.01)
Hymenoptera[k]	6 (0.01)	7 (0.02)	3 (0.01)	2 (0.01)
Formicidae	149 (0.25)*	101 (0.22)*	79 (0.18)*	13 (0.07)
Insect larvae (aquatic)[l]	11 (0.02)	3 (0.01)	3 (0.01)	1 (0.01)
Insect larvae (terrestrial)[m]	64 (0.11)*	8 (0.02)	17 (0.04)*	16 (0.09)
Chilopoda	1 (0.00)	12 (0.03)*	4 (0.01)	5 (0.03)
Diplopoda	10 (0.02)	0	0	5 (0.03)
Isopoda	4 (0.01)	0	1 (0.00)	11 (0.06)
Scorpiones	0	0	1 (0.00)	2 (0.01)
Pseudoscorpiones	4 (0.01)	0	0	0
Acari	6 (0.01)	1 (0.00)	9 (0.02)	0
Opiliones	4 (0.01)	6 (0.01)	1 (0.00)	6 (0.03)
Araneae (NI)	19 (0.03)*	20 (0.04)*	7 (0.02)	5 (0.03)
Araneae (soil)[n]	18 (0.03)*	20 (0.04)*	11 (0.02)	5 (0.03)
Araneae (vegetation)[o]	12 (0.02)	24 (0.05)*	8 (0.02)	2 (0.01)
Araneae (both)[p]	14 (0.02)	21 (0.05)*	5 (0.01)	3 (0.02)
Gastropoda	8 (0.01)	7 (0.02)	2 (0.00)	2 (0.01)
Oligochaeta	4 (0.01)	0	2 (0.00)	1 (0.01)
Anura	0	0	1 (0.00)	0
Seeds	12 (0.02)	0	13 (0.03)*	12 (0.07)
Total	601	453	444	182

NI: non-identified; a: Gryllacrididae, Gryllidae, Gryllotalpidae, Tridactylidae; b: Acrididae, Tettigoniidae; c: Cicadidae, Cercopidae, Membracidae, Cicadellidae; d: Aphididae, Coccidae, Psyllidae; e: Veliidae; f: Cydnidae, Gelastocoridae; g: Berytidae, Reduviidae, Ploiariidae, Coreidae, Lygaeidae, Pyrrhocoridae, Rhopalidae, Pentatomidae, Miridae, Tingidae; h: Scarabaeidae, Tenebrionidae, Carabidae, Staphylinidae, Limulodidae, Pselaphidae, Nitidulidae; i: Chrysomelidae; Cerambycidae; Coccinelidae; Elateridae; Cantharidae; Lampyridae; Bostrichidae; Scolytidae; Endomychidae; j: Brachycera, Cyclorrhapha; k: Chalcidoidea; l: Dytiscidae; m: Coleoptera, Lepidoptera, Elateridae, Diptera, Neuroptera; n: Actinopodidae, Theraphosidae, Ctenidae, Lycosidae, Oonopidae, Caponidae, Corinnidae; o: Thomisidae, Mimetidae, Salticidae, Oxyopidae, Philodromidae, Anyphaenidae, Dictynidae, Araneidae, Scytodidae; p: Linyphiidae, Theridiidae, Pholcidae, Pisauridae, Miturgidae.