RESOURCE USE BY ADULTS OF FOUR SPECIES OF ANURANS ALONG THE RÍO SALADO, PUEBLA, MEXICO

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Abstract.—How individuals, and ultimately species, use resources determines much about their ecology. We examined diet and microhabitat use in four anuran species along the Río Salado, Puebla, Mexico. *Dryophytes* (*Hyla*) *arenicolor* and *Incilius occidentalis* had specialized diets, eating primarily ants and termites, respectively. Both *Exerodonta xera* and *Lithobates spectabilis* had generalist diets, with *E. xera* consuming primarily coleopterans and ants, and *L. spectabilis* consuming a wide variety of insects, as well as conspecifics and *I. occidentalis*. Diet breadths were greater in the wet season in *E. xera* and *L. spectabilis*, but not *D. arenicolor* and *I. occidentalis*. Overlap between wet and dry season diets was high in *I. occidentalis* (0.99) and *D. arenicolor* (0.90), but intermediate in *L. spectabilis* (0.51) and *E. xera* (0.63). Diet overlap was greatest between *E. xera* and *L. spectabilis*, but was also substantial between *E. xera* and *I. occidentalis* and between *L. spectabilis* and *I. occidentalis*. *Dryophytes arenicolor* had the lowest diet overlaps, with highest overlap with *E. xera* and very low overlap with *L. spectabilis* and *I. occidentalis*. Each species used a small proportion of microhabitats observed, and diverged with respect to aquatic habitats: *D. arenicolor* used springs, *E. xera* used rocks and both springs and pools, *L. spectabilis* was rarely seen in aquatic habitats, and *I. occidentalis* was found in pools and the main river channel. We found no correlation between diet and microhabitat overlaps. Our study has shown that resource use of four anurans on the Río Salado shows variable overlap in diet and microhabitat use, but also that the overlap tends to be greater than expected.

Key Words.—diet; *Exerodonta xera*; *Dryophytes* (*Hyla*) *arenicolor*; *Incilius occidentalis*; *Lithobates spectabilis*; microhabitat use

Resumen.—La forma en que los individuos, y en última instancia las especies, usan los recursos, determina mucho sobre su ecología. Estudiamos la dieta y el uso de microhábitats en cuatro especies de anuros a lo largo del Río Salado, Puebla, México. *Dryophytes* (*Hyla*) *arenicolor* e *Incilius occidentalis* tuvieron dietas especializadas, consumiendo principalmente hormigas y termitas, respectivamente. *Exerodonta xera* y *Lithobates spectabilis* tuvieron dietas generalistas, con *E. xera* consumiendo principalmente coleópteros y hormigas, y *L. spectabilis* consumió una variedad amplia de insectos, así como individuos de su propia especie y de *I. occidentalis*. Las amplitudes de dieta fueron más grandes en la estación húmeda en *E. xera* y *L. spectabilis*, pero no en *D. arenicolor* e *I. occidentalis*. La sobreposición entre la dieta de la estación húmeda y la seca fue alta en *I. occidentalis* (0.99) e *D. arenicolor* (0.90), pero intermedia en *L. spectabilis* (0.51) y *E. xera* (0.63). La sobreposición de la dieta fue más grande entre *E. xera* y *L. spectabilis*, pero también fue sustancial entre *E. xera* e *I. occidentalis* y entre *L. spectabilis* e *I. occidentalis*. *Dryophytes arenicolor* tuvo las sobreposiciones de dieta más bajas, con la mayor sobreposición con *E. xera* y con una sobreposición muy baja con *L. spectabilis* e *I. occidentalis*. Cada especie utiliza una proporción pequeña de los microhábitats observados, y divergentes con respecto a los hábitats acuáticos: *D. arenicolor* utilizó arroyos, *E. xera* utiliza rocas y arroyos y posas, *L. spectabilis* raramente fue vista en hábitats acuáticos, y a *I. occidentalis* se le encontró en posas y canales del río principal. No encontramos sobreposición entre las sobreposiciones de dieta y uso de microhábitats. Nuestro estudio ha demostrado que el uso de recursos por cuatro anuros del Río Salado muestra sobreposiciones variables en la dieta y la utilización de microhábitats, pero también que la sobreposición tiende a ser más grande de lo esperado.

Introduction

How individuals, and ultimately species, use resources, such as food and microhabitats, determines much about their ecology. In particular, how individuals use resources can determine the extent of their interactions with other individuals of the same or different species (Chase and Leibold 2003; Mittelbach 2012). In addition, the use of resources by individuals can be important in determining how they may respond to habitat or environmental changes, whether natural or anthropogenic (Salido et al. 2012; Beckmann et al. 2015; Trice et al. 2015). It is therefore critical to understand how individuals and species use resources. Of particular interest in this context is how multiple sympatric species use important ecological resources (Tilman 1982; Chase and Leibold 2003). Such knowledge allows for an initial understanding of how these resources are partitioned, or not, among species.

In amphibians, previous studies of resource use among sympatric species suggest a range of resource overlap in such resource axes as diet, habitat or microhabitat use, and temporal patterns of activity, either diel or seasonal (Toft 1985). Some studies show high overlap along one resource axis but low overlap along another resource axis (Díaz and Valencia 1985; Duré et al. 2009). However, others find a high degree of resource overlap (Hofer et al. 2004; Menin et al. 2005; Arroyo et al. 2008). Still others have found low overlap along multiple resource axes (Van Sluys and Rocha 1998; Cajade et al. 2010).

We examined diet and microhabitat use in an assemblage of four species of anurans (*Incilius occidentalis* (Pine Toad), *Lithobates spectabilis* (Showy Leopard Frog), *Dryophytes* [*Hyla*] *arenicolor* (Canyon Treefrog), and *Exerodonta xera* (Puebla Treefrog)) along the Río Salado in Puebla, Mexico. *Incilius occidentalis* is a species whose distribution is broad in Mexico (Oliver-López et al. 2009), as is that of *L. spectabilis* and *D. arenicolor* (Frost et al. 2006). However, *E. xera* is endemic to the semiarid region of Mexico (Canseco-Márquez et al. 2003). Very little is known about the diets of these four species. Indeed, we are not aware of any published reports of diet for *E. xera* or *L. spectabilis*, and the only reports for *I. occidentalis* and *D. arenicolor* are from reports based on small sample sizes (*I. occidentalis*: Mendelson et al. 2016; *D. arenicolor*: Winter et al. 2007; Bañuelos Alamillo and Carbajal-Márquez 2014). None of these observations come from the Río Salado region. We were also able to assess seasonal variation in the diet of these four species of anurans. Because many previous studies on resource use in anurans have found some degree of partitioning, and the four species in this assemblage are from three families, we expected there would be low resource overlap along at least one of the two resource axes we examined.

Materials and Methods

The Río Salado runs through El Valle de Zapotitlán Salinas in southeastern Puebla, Mexico. El Valle de Zapotitlán is part of the Valle de Tehuacan-Cuicatlán in central Mexico that is considered to be an ecologically important region due to high levels of both biodiversity and endemism (Dávila-Aranda et al. 1993). The Río Salado basin in the Zapotitlán Salinas Valley has an approximate area of 40,710 ha, and is formed by the Zapotitlán Salinas and San Juan Raya subbasins. The Río Salado is formed from several tributaries including Rio Zapotitlán, las Ventas, Salinas la Barranca, and Salinas San Pedro, whose waters have high amounts of carbonates (Woolrich-Piña 2010). Along the river the vegetation is thorny scrub, including cacti (*Neobouxbamia tetetzo*, *Cephalocereus* spp.), mesquite trees (*Prosopis laevigata*), "pata de elefante" trees (*Beucarnea gracilis*), and other plants (*Myrtillocactus geometrizans*, *Echinocactus viznaga*, and *Holocantha stewartii*), among others (Dávila-Aranda et al. 1993). Seven anuran species occur in the Zapotitlán Salinas Valley: *Craugastor agusti* (Barking Frog), *Eleutherodactylus nitidus* (Peter's Shiny Peeping Frog), *Spea multiplicata* (New Mexico Spadefoot), *I. occidentalis*, *L. spectabilis*, *E. xera*, and *D. arenicolor*; with the last four species being the only species found along the Río Salado (Woolrich-Piña et al. 2005).

We surveyed 12 randomized transects, with three in each tributary. The starting point of each transect was arbitrarily chosen. Transects were 2 km long × 6 m wide along the basin and separated by at least 5 km. Along each transect we searched all microhabitats, such as under rocks, in algae on the surface of the river, in riparian vegetation, etc. During monthly visits (4 d per visit) to the study area from February 2008 to January 2009, we captured individuals of each species by hand from habitats along these transects from 1900 to 0100 (24 h total per visit). We used stomach flushing (Legler and Sullivan 1979; LeClerc and Courtois 1993) to obtain stomach contents for each individual. We used an infant cannula model RT329 connected to a 5 ml syringe filled with 10% saline solution. The cannula was introduced through the mouth into the stomach and the entire contents of the syringe was injected until the frog regurgitated. Stomach contents were collected in plastic containers with lids and preserved in 70% ethanol.

We analyzed the stomach contents of 238 individuals among the four species. We identified stomach contents to the lowest taxonomic level possible. To examine seasonal differences in diet, we assigned individuals to either wet season (June-October) or dry season

TABLE 1. The diet of *Exerodonta xera* from the Valle de Zapotítlan Salinas, Mexico. Number = Number of prey items found in stomach contents. Volume = Total volume of prey type in stomach contents (ml). Abbreviations are WSNI = wet season number of items, DSNI = dry season number of items, n.i. = not identifiable, IV = Importance Value. Values in parentheses are proportion of total number or volume.

Taxa	Number of Stomachs	Number of Items	Volume	IV	WSNI (stomachs)	DSNI (stomachs)
Coleoptera n.i.	2 (0.40)	7 (0.467)	0.38 (0.299)	0.456	5 (1)	2 (1)
Homoptera n.i.	1 (0.20)	1 (0.067)	0.12 (0.094)	1.166	1 (1)	0 (0)
Hymenoptera: Formicidae	1 (0.20)	6 (0.400)	0.53 (0.417)	0.361	6 (1)	0 (0)
Unidentified	1 (0.20)	1 (0.067)	0.24 (0.189)	1.017	1 (1)	0 (0)
Empty Stomachs	19				8	11
Total (not including empty)	5	15	1.27		13 (4)	2 (1)
Niche breadth		2.6	3.2		2.7	1.0

(November-May) based on the month they were captured. We recorded the microhabitat used for each individual we observed, which allowed us to establish the following microhabitat categories: bare soil, springs feeding the Río Salado, rocks, pools along the Río Salado, river (i.e., main river channel), anthropogenic substrate (e.g., wall, stairs, bridge), plants, sand, and grass.

We calculated an importance value (IV) for each prey taxon (i) using the sum of the proportions of total prey items (p_{Ni}), total prey volume (p_{Vi}), and total number of stomachs (p_{Si}) represented by prey item i (Powell et al., 1990):

$$IV_i = p_{Ni} + p_{Vi} + p_{Si}$$

The IV provides an index of the relative importance of each prey ítem that combines multiple aspects of the prey (prey number, prey volume, number of stomachs found in) into a single, integrated index. We used Pianka's (1975) overlap index

$$O_{jk} = \frac{\Sigma p_{ij} p_{ik}}{\sqrt{\Sigma p_{ij}^2 \Sigma p_{ik}^2}}$$

to examine diet and microhabitat overlap among the species, where pij is proportion of all resources used by species j that are resource item i and p_{ik} is proportion of all resource items used by species k that are resource item i. This index ranges from 0 (no overlap) to 1 (complete overlap). Values of niche overlap > 0.6 are considered biologically significant (Wallace 1981). For analyses of diet overlap, we pooled some prey taxa (often at the order level) to allow for the possibility that different levels of identification among anuran species might affect diet overlap values. For example, in the diets of each anuran species we found some prey items that we could not identify beyond order and others we could identify to family or genus. The relative numbers of such prey items in the diets of the different anurans

could affect the overlaps that were calculated. We therefore pooled by order for our analyses of overlaps. In addition, pooling at the order level helps to reduce the potential effects of different numbers of individuals examined in each anuran species. We calculated Levin's B for niche breadth:

$$\frac{1}{\Sigma p_i^2}$$

(p_i = proportion of all resources used that are type i), for prey volume, prey numbers, and microhabitat use. Higher values of this index indicate greater diversity of resources used.

We further analyzed niche overlaps in both diet and habitat use by using EcoSim Professional (Entsminger 2014) to compare the mean observed niche overlap of the assemblage to mean simulated niche overlaps (see Gotelli and Graves 1996). Simulated niche overlaps were generated using RA3 (Entsminger 2014). We also ran similar simulations for each pairwise combination of species.

RESULTS

Exerodonta xera.—Most (19 of 24; 79%) of the stomachs of *E. xera* we examined were empty. *Exerodonta xera* consumed 15 prey ítems from four taxa (Table 1). Of the prey items observed, unidentified Coleopterans and *Solenopsis* ants were the most common numerically; whereas, *Solenopsis* was the prey taxon with the largest volume consumed (Table 1). Based on the importance value, homopterans were the most important prey items in the diet (Table 1). Niche breadth based on prey numbers was 2.6, and based on prey volume was 3.2. Diet breadth in the wet season was nearly three times the diet breadth during the dry season (Table 1). Overlap in diet between the wet and dry seasons was 0.63. We found *E. xera* most frequently on rock microhabitats, and less frequently in spring and pool microhabitats (Table 2). We did not observe *E. xera* on any other microhabitat.

TABLE 2. Proportional microhabitat use of four species of anurans studied in the Valle de Zapotítlan Salinas, Mexico. Abbreviations are AnthroSub = anthropogenic substrate, NMU = number of microhabitats used.

Microhabitat	Dryophytes arenicolor	Exerodonta xera	Lithobates spectabilis	Incilius occidentalis
Bare Soil	0.21	0	0	0.02
Spring	0.69	0.29	0	0
Rocks	0.05	0.58	0.83	0.41
Pools	0.05	0.13	0.06	0.21
River	0	0	0.02	0.30
AnthroSub	0	0	0.02	0.04
Plants	0	0	0.03	0
Sand	0	0	0.04	0
Grass	0	0	0	0.02
NMU	4	3	6	6
Breadth	1.9	2.3	1.4	3.3

Dryophytes arenicolor.—Ten of the 39 (25.6%) stomachs of *D. arenicolor* we examined were empty. Formicid ants were the most abundant prey item in the stomachs, followed by hemipterans (Gerridae and Cicadellidae; Table 3). Based on importance values, ants were the most important prey in the diet (Table 3). Diet breadth based on number of prey items was 5.4, and based on volume of prey was 5.7. Diet breadth was similar in both the wet and dry seasons (Table 3). Overlap in diets between the wet and dry season (based on number of prey items) was 0.90. *Dryophytes*

arenicolor used four microhabitats; springs were the most frequently used microhabitat, followed by bare soil, rocks, and pools (Table 2). We did not observe *Dryophytes arenicolor* in river, anthropogenic substrate, plant, sand, or grass microhabitats.

Incilius occidentalis.—Twenty-four of the 47 (51.1%) *I. occidentalis* we examined had empty stomachs. The stomach contents were dominated by termites, but a few ants and unidentified coleopterans were also present (Table 4). Based on importance value, termites and ants were the two most important prey items. Diet breadth was quite narrow when considering only numbers of prey items (1.2), but was broader when considering volume of prey (4.5). Diet breadths for both wet and dry season were very similar to each other (Table 4). Diet overlap between the dry and wet season was very high (0.99). We most often found *I. occidentalis* using rock microhabitats, but they also used pool and river microhabitats (Table 2). We rarely saw *I. occidentalis* using anthropogenic substrates, bare soil, or grass microhabitats. We never saw *I. occidentalis* using spring, plant, or sand microhabitats.

Lithobates spectabilis.—Thirty-two of the 128 (25%) *L. spectabilis* we examined had empty stomachs. The diet of Lithobates spectabilis consisted primarily of gerrids, unidentified larvae, termites, and coleopterans; with smaller proportions of dipterans, homopterans, and hymenopterans (Table 5). We also found the remains of

TABLE 3. The diet of *Dryophytes arenicolor* from the Valle de Zapotítlan Salinas, Mexico. Number = Number of prey items found in stomach contents. Volume = Total volume of prey type in stomach contents (ml). Abbreviations are WSNI = west season number of items, DSNI = dry season number of items, n.i. = not identifiable, IV = Importance Value. Values in parentheses for Number of Stomachs, Number of Items, and Volume are proportion of total number or volume.

Taxa	Number of Stomachs	Number of Items	Volume	IV	WSNI (stomachs)	DSNI (stomachs)
Arachnida: Scorpionida	1 (0.034)	1 (0.008)	0.18 (0.039)	0.081	0 (0)	1 (1)
Coleoptera n.i.	2 (0.069)	8 (0.068)	0.34 (0.074)	0.211	5 (1)	3 (1)
Coleoptera: Carabidae	1 (0.034)	1 (0.008)	0.26 (0.056)	0.098	0 (0)	1 (1)
Diptera n.i.	1 (0.034)	2 (0.017)	0.28 (0.061)	0.112	0 (0)	2 (1)
Hemiptera n.i.	1 (0.034)	4 (0.034)	0.15 (0.032)	0.100	4 (1)	0 (0)
Hemiptera: Cicadellidae	2 (0.069)	17 (0.145)	0.17 (0.037)	0.251	12 (1)	5 (1)
Hemiptera: Gerridae	3 (0.103)	16 (0.137)	0.27 (0.058)	0.298	11 (1)	5 (2)
Homoptera n.i.	3 (0.103)	11 (0.094)	0.08 (0.017)	0.214	0 (0)	11 (3)
Hymenoptera: Formicidae	8 (0.276)	35 (0.299)	1.62 (0.351)	0.926	22 (4)	13 (4)
Isoptera: Termitidae	1 (0.034)	1 (0.008)	0.07 (0.015)	0.057	0 (0)	1 (1)
Lepidoptera n.i.	1 (0.034)	1 (0.008)	0.31 (0.067)	0.109	0 (0)	1 (1)
Lepidoptera (larva)	1 (0.034)	1 (0.008)	0.29 (0.063)	0.105	1 (1)	0 (0)
Neuroptera: Hemerobioidea:Mantispidae	1 (0.034)	1 (0.008)	0.16 (0.035)	0.077	1 (1)	0 (0)
Unidentified	3 (0.103)	18 (0.154)	0.43 (0.093)	0.35	10 (1)	8 (2)
Empty Stomachs	10				2	8
Total (not including empty)	29	117	4.61		66 (11)	51 (18)
Niche breadth		5.4	5.7		4.4	4.8

TABLE 4. The diet of *Incilius occidentalis* from the Valle de Zapotitlán Salinas. Number = Number of prey items found in stomach contents. Volume = Total volume of prey type in stomach contents (ml). Abbreviations are WSNI = wet season number of items, DSNI = dry season number of items, n.i. = not identifiable, IV = Importance Value. Values in parentheses are proportion of total number or volume.

Taxa	Number of Stomachs	Number of Items	Volume	IV	WSNI (stomachs)	DSNI (stomachs)
Coleoptera n.i.	3 (0.130)	13 (0.011)	1.12 (0.176)	0.317	5 (1)	8 (2)
Hymenoptera: Formicidae	10 (0.435)	92 (0.077)	1.99 (0.312)	0.824	89 (9)	3 (1)
Isoptera: Termitidae	6 (0.261)	1071 (0.895)	1.45 (0.227)	1.383	987 (5)	84 (1)
Orthoptera: Gryllidae	2 (0.087)	9 (0.008)	1.08 (0.169)	0.336	9 (2)	0 (0)
Unidentified	2 (0.087)	11 (0.009)	0.74 (0.116)	0.212	11 (2)	0 (0)
Empty Stomachs	24				18	6
Total (not including empty)	23	1196	6.38		1101 (19)	95 (4)
Niche breadth		1.2	4.5		1.2	1.3

I. occidentalis and *L. spectabilis* in the stomachs of *L. spectabilis* (Table 5). No single prey item had a much higher importance value than any other prey items, although the prey items with the highest importance values were unidentified larvae, gerrids, and anuran prey. Diet breadth based on the number of prey items was 7.92. and based on prey volume was 12.71. Diet breadth was greater in the wet season than the dry season (Table 5). The dietary overlap between the wet and dry season was 0.51. Rock microhabitats accounted for 83% of our observations of *L. spectabilis* microhabitat use (Table 2). We occasionally saw *L. spectabilis* using pool, sand, plant, river, and anthropogenic substrate microhabitats, but we never saw them using bare soil, spring, or grass microhabitats.

Niche overlap.—Diet overlap was greatest between *D. arenicolor* and *E. xera*, and by volume, but not number, between *I. occidentalis* and both *D. arenicolor* and *E. xera* (Table 6). Lowest overlap was in prey number between *I. occidentalis* and both *D. arenicolor* and *E. xera* (Table 6). Other overlaps were intermediate. Overlap in microhabitat use varied greatly among species pairs (Table 6). Overlap was greatest between *E. xera* and *L. spectabilis*, but overlap was also substantial (> 70%) between *E. xera* and *I. occidentalis* and between *L. spectabilis* and *I. occidentalis*. *Dryophytes arenicolor* had the lowest overlaps, with the highest overlap with *E. xera* (49%) and very low overlap (< 10%) with *L. spectabilis* and *I. occidentalis*. There was no significant correlation between diet overlap and microhabitat overlap (prey volume: n = 6, r = 0.21, P = 0.692; prey number: n = 6, r = 0.09, P = 0.864).

Overall, mean observed diet overlap based on prey volume (prey identified to order) was greater than the mean of simulated overlaps (observed mean = 0.53, simulated mean = 0.26; standardized effect size = 3.32, P = 0.005). This was also true for diet overlap based on prey number (observed mean = 0.35, simulated mean =

0.19, standardized effect size = 2.00, P = 0.045). Mean observed microhabitat use overlap in this assemblage was greater than the mean simulated overlap (observed mean = 0.51, simulated mean = 0.24, standardized effect size = 2.51, P = 0.024).

DISCUSSION

Resource use and overlap.—Of the four species studied in the Río Salado anuran assemblage, *D. arenicolor* and *I. occidentalis* have the most specialized diets, eating primarily ants and termites, respectively. In comparison, *E. xera* and *L. spectabilis* are dietary generalists. The diet of *E. xera* consists largely of coleopterans and ants; whereas, the diet of *L. spectabilis* consists not only of a variety of insects, but also of other anurans, including *I. occidentalis* and conspecifics. Our observations on the diets of these four species of anurans fall within the range of diets found in these and other Mexican and Central American hylid, bufonid, and ranid species. For example, the contents of one stomach of *I. occidentalis* from Mexico consisted primarily of ants, but also included beetles and flies (Mendelson et al. 2016), and in six *D. arenicolor* from Chihuahua and Sonora, Mexico, 50% of the prey items were termites, although by volume the contents consisted primarily beetles and orthopterans (Winter et al. 2007). Previous studies of hylids found that some species eat mostly beetles (Lieberman 1986) or termites (Greding and Hellebuych 1980). Ants, termites, and beetles often dominate the diets of Mexican and Central American bufonids (Greding and Hellebuych 1980; Toft 1980; Lieberman 1986; Cabrera Peña et al. 1997; Smith et al. 2011). Mexican and Central American ranids consume a variety of insects, with some species also consuming vertebrates, including frogs (Greding and Hellebuych 1980; Ramirez et al. 1998).

Diet overlap was greatest between *E. xera* and *L. spectabilis*, but was also substantial (> 70%) between

TABLE 5. The diet of *Lithobates spectabilis* from the Valle de Zapotítlan Salinas. Number = Number of prey items found in stomach contents. Volume = Total volume of prey type in stomach contents (ml). Abbreviations are WSNI = wet season number of items, DSNI = dry season number of items, n.i. = not identifiable, IV = Importance Value. Values in parentheses are proportion of total number or volume.

Taxa	Number of Stomachs	Number of Items	Volume	IV	WSNI (stomachs)	DSNI (stomachs)
Arachnida: Aranae (aquatic)	1 (0.010)	2 (0.003)	0.09 (0.004)	0.017	2 (1)	0 (0)
Arachnida: Aranae (terrestrial)	2 (0.020)	15 (0.025)	0.47 (0.021)	0.066	0 (0)	15 (2)
Arachnida: Scorpionida	2 (0.020)	2 (0.003)	0.23 (0.010)	0.033	1 (1)	1 (1)
Arthropoda: Crustacea: Isopoda	1 (0.010)	1 (0.002)	0.05 (0.002)	0.014	1 (1)	0 (0)
Amphibia: Anura: Bufonidae: *Incilius occidentalis*	2 (0.020)	9 (0.015)	4.27 (0.195)	0.23	9 (2)	0 (0)
Amphibia. Anura: Ranidae: *Lithobates spectabilis*	2 (0.020)	2 (0.003)	3.41 (0.155)	0.178	2 (2)	0 (0)
Coleoptera n.i.	2 (0.020)	58 (0.098)	0.79 (0.036)	0.154	32 (1)	26 (1)
Coleoptera: Byrrhidae	1 (0.010)	1 (0.002)	0.06 (0.003)	0.015	1 (1)	0 (0)
Coleoptera: Carabidae	1 (0.010)	3 (0.005)	0.11 (0.005)	0.02	3 (1)	0 (0)
Coleoptera: Curculionidae	3 (0.029)	9 (0.015)	0.30 (0.014)	0.058	9 (3)	0 (0)
Coleoptera: Chrysomelidae	1 (0.010)	1 (0.002)	0.02 (0.001)	0.013	1 (1)	0 (0)
Coleoptera: Elateroidea	1 (0.010)	1 (0.002)	0.05 (0.002)	0.014	1 (1)	0 (0)
Coleoptera: Gyrinidae	1 (0.010)	3 (0.005)	0.15 (0.007)	0.022	3 (1)	0 (0)
Coleoptera: Ostomidae	1 (0.010)	1 (0.002)	0.04 (0.002)	0.014	1 (1)	0 (0)
Coleoptera: Passalidae	1 (0.010)	2 (0.003)	0.1 (0.004)	0.017	2 (1)	0 (0)
Coleoptera: Scarabaeidae	3 (0.029)	8 (0.014)	0.34 (0.016)	0.059	5 (2)	3 (1)
Coleoptera: Staphylinidae	1 (0.010)	1 (0.002)	0.09 (0.004)	0.016	1 (1)	0 (0)
Diptera n.i.	2 (0.020)	4 (0.007)	0.26 (0.012)	0.039	4 (2)	0 (0)
Diptera: Bibionidae	1 (0.010)	1 (0.002)	0.1 (0.004)	0.016	1 (1)	0 (0)
Diptera: Brachycera	1 (0.010)	1 (0.002)	0.13 (0.006)	0.018	1 (1)	0 (0)
Diptera: Culicidae	4 (0.039)	23 (0.039)	0.65 (0.030)	0.108	18 (3)	5 (1)
Diptera: Muscidae	3 (0.029)	17 (0.029)	0.41 (0.019)	0.077	17 (3)	0 (0)
Diptera (larva)	1 (0.010)	1 (0.002)	0.11 (0.005)	0.017	1 (1)	0 (0)
Hemiptera n.i.	2 (0.020)	6 (0.010)	0.21 (0.010)	0.04	6 (2)	0 (0)
Hemiptera: Cryptocerata: Naucoridae	1 (0.010)	3 (0.005)	0.16 (0.007)	0.022	3 (1)	0 (0)
Hemiptera: Cydnidae	1 (0.010)	2 (0.003)	0.12 (0.005)	0.018	2 (1)	0 (0)
Hemiptera: Gerridae	1 (0.010)	137 (0.231)	0.87 (0.040)	0.281	137 (1)	0 (0)
Hemiptera: Hydrometridae	1 (0.010)	1 (0.002)	0.09 (0.004)	0.016	1 (1)	0 (0)
Hemiptera: Nepidae	1 (0.010)	1 (0.002)	0.17 (0.008)	0.02	0 (0)	1 (1)
Hemiptera: Pentatomidae	1 (0.010)	1 (0.002)	0.2 (0.009)	0.021	0 (0)	1 (1)
Hemiptera (larva)	2 (0.020)	4 (0.007)	0.23 (0.010)	0.037	4 (2)	0 (0)
Homoptera n.i.	2 (0.020)	3 (0.005)	0.16 (0.007)	0.032	3 (2)	0 (0)
Homoptera: Cycadidae	1 (0.010)	3 (0.005)	0.19 (0.009)	0.024	3 (1)	0 (0)
Hymenoptera n.i.	1 (0.010)	1 (0.002)	0.13 (0.006)	0.018	1 (1)	0 (0)
Hymenoptera: Apidae: Ceratina	1 (0.010)	1 (0.002)	0.1 (0.004)	0.016	0 (0)	1 (1)
Hymenoptera: Formicidae	7 (0.069)	27 (0.046)	1.21 (0.055)	0.17	27 (7)	0 (0)
Hymenoptera: Vespidae	1 (0.010)	2 (0.003)	0.37 (0.017)	0.03	2 (1)	0 (0)
Isoptera: Termitidae	3 (0.029)	84 (0.142)	0.97 (0.044)	0.215	84 (3)	0 (0)
Lepidoptera n.i.	1 (0.010)	1 (0.002)	0.71 (0.032)	0.044	1 (1)	0 (0)
Lepidoptera (larva)	1 (0.010)	1 (0.002)	0.55 (0.025)	0.037	1 (1)	0 (0)
Odonata n.i.	1 (0.010)	1 (0.002)	0.36 (0.016)	0.028	1 (1)	0 (0)
Odonata (larva)	2 (0.020)	3 (0.005)	0.29 (0.013)	0.038	3 (2)	0 (0)

TABLE 5—CONTINUED.

Taxa	Number of Stomachs	Number of Items	Volume	IV	WSNI (stomachs)	DSNI (stomachs)
Orthoptera n.i.	2 (0.020)	4 (0.007)	0.44 (0.020)	0.047	4 (2)	0 (0)
Orthoptera: Blattidae	2 (0.020)	2 (0.003)	0.51 (0.023)	0.046	1 (1)	1 (1)
Orthoptera: Phasmatidae	1 (0.010)	1 (0.002)	0.29 (0.013)	0.025	1 (1)	0 (0)
Unidentified Larvae	16 (0.157)	110 (0.186)	0.49 (0.022)	0.365	87 (5)	23 (11)
Unidentified	12 (0.118)	28 (0.047)	0.88 (0.040)	0.205	17 (7)	11 (5)
Empty Stomachs	26				6	20
Total (not including empty stomachs)	102	592	21.93		505 (76)	88 (26)
Niche breadth		7.92	12.71		7.02	4.88
Niche breadth (pooled)					5.9	4.4

E. xera and *I. occidentalis* and between *L. spectabilis* and *I. occidentalis*. In general, *D. arenicolor* had the lowest overlaps, with the highest overlap with *E. xera* (49%) and very low overlap (< 10%) with *L. spectabilis* and *I. occidentalis*. Our data suggest that the diets of these four species are not substantially partitioned on an assemblage basis, but that some specific pairs of species show very little overlap. Indeed, the mean observed diet overlap was greater than the mean simulated overlap, suggesting diets are on average more similar than would be expected by chance. The wide range in overlaps may indicate resources are not limited or that diets are determined by other factors, such as microhabitat use, gape size, or time of activity Unfortunately, we did not estimate the availability of prey in the environment. Such data on the abundance of prey would permit further interpretation of our observations with regard to the extent and mechanism of partitioning of prey items (or lack thereof). Regardless, our observations suggest that further investigations into how these species use their resources and potentially interact over resources would be of interest.

In terms of microhabitat use, each species uses a relatively small subset of the microhabitats available. *Dryophytes arenicolor* primarily uses spring microhabitats, *E. xera* and *L. spectabilis* used rock microhabitats, and *I. occidentalis* uses rock, pool, and river microhabitats. Our observations of *E. xera* using rock microhabitats is consistent with observations of *E. xera* being found under rocks during the day in Zapotitlán Salinas, Mexico (Canseco-Márquez et al. 2003). Quantifying the total availability of each microhabitat in the environment would allow for a better understanding of the potential for microhabitat use partitioning in this assemblage.

Niche overlap for microhabitats was very low between *D. arenicolor* and both *L. spectabilis* and *I. occidentalis*. Microhabitat overlap was highest between *E. xera* and *L. spectabilis*, *E. xera* and *I. occidentalis*, and *L. spectabilis* and *I. occidentalis*. As with diet overlap, the extent of overlap in microhabitat use was highly variable among species pairs and overall was on average greater than expected by chance. The species that show the highest levels of overlap were those that used rocks, perhaps reflecting differences between some species in the use of terrestrial microhabitats. Indeed, if one looks more closely at how these species are using microhabitats, they appear to potentially diverge with respect to the aquatic habitats with which they are most associated: *D. arenicolor* uses mostly springs, *E. xera* primarily uses rocks, but uses both springs and pools, *L. spectabilis* is rarely seen in purely aquatic habitats, and *I. occidentalis* is found in pools and the river. Given the range in overlaps for both diet and microhabitat use in this anuran assemblage, one might wonder if there is a relationship between overlap in these two niche dimensions, with a negative correlation expected if partitioning is occurring on multiple niche dimensions (i.e., high overlap in diet is possible if low overlap in microhabitat use) exists. We found no such correlation,

TABLE 6. Values of Pianka's (1975) niche overlap index for the diets (based on both prey number and prey volume) and microhabitat use of four species of anurans studied in the Valle de Zapotítlan Salinas. + indicates observed overlap is significantly greater than simulated overlaps; S indicates overlap is not different from simulated overlap (α = 0.05). Species abbreviations are DA = *Dryophytes arenicolor*, EX = *Exerodonta xera*, and LS = *Lithobates spectabilis*.

Species	*Exerodonta xera*			*Lithobates spectabilis*			*Incilius occidentalis*		
	Prey Number	Prey Volume	Microhabitat	Prey Number	Prey Volume	Microhabitat	Prey Number	Prey Volume	Microhabitat
DA	0.58[+]	0.84[+]	0.49[S]	0.64[+]	0.33[S]	0.07[S]	0.08[S]	0.70[+]	0.04[S]
EX				0.39[S]	0.27[S]	0.89[+]	0.07[S]	0.78[+]	0.73[+]
LS							0.39[S]	0.31[S]	0.78[+]

positive or negative, in overlaps, suggesting no apparent trade-off in overlap between these niche axes.

Seasonal variation.—Diet niche breadths were greater in the wet season than the dry season in *E. xera* and *L. spectabilis*, but not *D. arenicolor* and *I. occidentalis*. The overlap between wet and dry season diets was very high ($\geq$ 90%) in *I. occidentalis* and *D. arenicolor*, but intermediate in *L. spectabilis* (51%) and *E. xera* (63%). This pattern is consistent with the observation that *I. occidentalis* consumes high numbers of termites and *D. arenicolor* consumes a high number of ants. Because the other two species eat a wider variety of prey items, they potentially change their prey consumption between the wet and dry season as prey availability shifts; whereas, the two specialist species consume the same plentiful diet items in both seasons. The ant fauna of the Valle de Tehuacán, which includes the Valle de Zapotitlán de las Salinas where the Río Salado is found, is relatively diverse, has a relatively high abundance (Rios-Casanova et al. 2004; Guzmán-Mendoza et al. 2010), and can vary with season, with some species more abundant in the wet season and others more abundant in the dry season (Guzmán-Mendoza et al. 2010). However, ants appear to be abundant in both seasons (Guzmán-Mendoza et al. 2010). In contrast, the greatest abundance of some beetles in the Zapotitlán de las Salinas was highest during the wet season (Quezada-García et al. 2014; Trujillo-Miranda et al. 2016). Thus, the differences in seasonal variation in diets in the four species we studied may be the result of variation in the availability of major prey items. However, more detailed studies including the abundance of available prey are needed to confirm this.

Conclusions.—Although there is variable diet and microhabitat use overlap among species in this anuran assemblage, when taking all the evidence together, our data suggest that the four species of anurans in the assemblage along the Río Salado do not partition resources; rather, they overlap in resource use more than would be expected by chance. These data are consistent with previous studies that found high levels of resource overlap in anuran assemblages. Schalk et al. (2015) found that anurans in the Chihuahuan Desert are morphologically more similar than expected, and they attribute this to the dry desert environment filtering species and this leads to greater similarity among species. Similarly, Hofer et al. (2004) found that frogs with similar ecologies occurred together more than would be expected by chance. Three hylid species in Argentina showed higher trophic niche overlap than expected by chance (Macale et al. 2008). Clearly, there is a great deal of variability among anuran assemblages in the extent of resource overlap. Such variability suggests that different anuran assemblages are governed by different factors (Toft 1985).

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