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3	Generalist, selective or "mixed" foragers? Feeding strategy of two tropical toads
4	across suburban habitats
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33 Abstract

34

35 Suitable habitats for anurans can be found in the ever-growing tropical urban environments but anurans'

- 36 adaptations to urban conditions, including their trophic ecology remain largely unknown. We studied the
- 37 food habits of two generalist, widespread West African Sclerophrys adult toads: African common (S.
- 38 regularis) and Hallowell's toad (S. maculata). The first was studied in Lomé (Togo), Cotonou (Benin) and
- 39 Ikeja (Nigeria), and the second in Port Harcourt and Ikeja (both Nigeria); the latter city represents the only
- 40 studied sympatric occurrence. Mean dietary overlap between population pairs was relatively high, and diet
- 41 composition of the two species when sympatric did not differ significantly. Food niche width was
- 42 significantly positively correlated with local rainfall in both species, and diet composition changed
- 43 significantly between the dry and wet seasons. Diversity metrics revealed that females had a more diversified
- diet, with higher evenness and lower dominance index values than males. The diet of both species was not
- 45 correlated to prey type availability, in both the wet and dry season. Both toad species targeted specific food
- 46 items rather than opportunistically consume prey as observed in most anurans which may be a response to
- 47 high anuran diversity typically found in the tropics or an adjustment to urban habitats.
- 48

49 Introduction

50

Research on the trophic ecology of adult anuran amphibians has greatly contributed to our understanding of 51 the role these organisms play in ecological communities (e.g., Toft 1985, Vignoli & Luiselli 2012). 52 53 Investigations on the role of anurans in tropical and subtropical natural amphibian communities have been 54 undertaken in South America (Toft 1980, 1981, Parmelee 1999, Piatti & Souza 2011, Talione Sabagh et al. 55 2012, Moreno-Barbosa & Hoyos-Hoyos 2014, Huckembeck et al. 2018, e.g., Brandão et al. 2020) and West Africa (Barbault 1974, Eniang et al. 2003, Hirschfeld & Rödel 2011, Onadeko 2011, Akani et al. 2011, 56 57 Enabulele & Aisien 2012, Tohé et al. 2015, Ofori et al. 2021). Whilst studies on urban anurans have typically 58 addressed species richness, population density and habitat availability (e.g., Rubbo & Kiesecker 2005, 59 Smallbone et al. 2011, Westgate et al. 2015, Konowalik et al. 2020), the impact of urban habitat modification on anurans' feeding ecology has been less studied (Kovács et al. 1995, López et al. 2015). In particular, 60 61 studies of the trophic ecology of amphibians in the tropics are rare (Santana et al. 2019, Ofori et al. 2021). 62 Urbanisation leads to changes in micro-climate, water balance, water quality, hydrology of wetlands and 63 adjacent habitats, and to pollution increase and stress. Urban habitats are often characterized by a reduced 64 amphibian diversity compared to the pre-urbanized habitat (Rubbo & Kiesecker 2005). Amphibian species 65 composition is often altered in urban habitats and new communities can emerge as the result of the inclusion of invasive species. Iglesias-Carrasco et al. (2017) have summarized the most severe effects of urbanisation 66 67 on amphibians as: 1) sensitivity to toxic substances because of their highly permeable skin, 2) artificial 68 limitations of dispersal opportunities, 3) reduced breeding opportunities due to the disappearance of

69 wetlands, and 4) increased numbers of stressors such as noise, light and increased temperatures, which might 70 disrupt acoustic signalling and change immune responses. In addition, native species can be exposed to competition with invasive amphibians (e.g., Gersava et al. 2020) and predation by introduced exotic species 71 72 such as crayfish or mosquitofish (Goodsell & Kats 1999, Riley et al. 2005). Urban anurans show higher 73 toxicant loads and greater physiological stress than non-urban anurans and other urban vertebrates (Murray 74 et al. 2019). Some species can thrive, others can take advantage without thriving and yet others may avoid 75 living in urban areas (i.e., urban exploiters, adapters and avoiders, respectively; Isaksson 2015). Because of 76 their specific dietary requirements and sensitive life stages, most amphibians are regarded as urban avoiders 77 (Isaksson 2015). However, anuran species may also respond in very different ways to urbanisation, ranging 78 from thriving and invading (Gersava et al. 2020) to disappearance of urban-sensitive species (Westgate et al. 79 2015). Examining different types of habitat alterations in eastern Argentina, similar habitat alterations were 80 shown to cause greater diet similarities independent of site location than different habitat alterations (López 81 et al. 2015). This indicates that urbanisation does not create the same effects on populations and species but 82 it is the specific types of anthropogenic habitat changes that result in specific changes in tropic niches.

83

Body condition is assumed to generally be reduced in altered landscapes as a consequence of anthropogenic 84 habitat changes (Brodeur et al. 2011). However, some anurans have been documented to be of larger body 85 86 size in urban settings than individuals of the same species in natural habitats, as in the case of the green frog 87 (Pelophylax perezi) studied in Spain (Iglesias-Carrasco et al. 2017). Prey availability and diet have been 88 hypothesized as one of several variables that can influence larger body size in birds (Shochat 2004) and in 89 amphibians (Iglesias-Carrasco et al. 2017). The latter authors observed increased densities of some exotic 90 invertebrate species in urban habitats and argued that an amphibious diet (including live insects, crustaceans 91 and worms) was advantageous for adapting to urban habitats because amphibians could more easily harvest recently created exotic communities of invertebrates compared to other vertebrate groups. Habitat alterations 92 93 create changes in available prey for anurans in complex ways with different changes impacting different prey 94 taxa (e.g., Basset et al. 2008, López et al. 2015). Urban areas tend to have lower invertebrate prey availability 95 (Coleman & Barclay 2013) although there is a large variability depending on habitat composition 96 (Jaganmohan et al. 2013). Some species can adjust their diet composition to resource availability whilst 97 others cannot, whereby the first group may have an adaptive advantage in changing environments in general and in urban landscapes in particular (López et al. 2015). For example, increases in ant populations because 98 99 of damming did not lead to increased consumption in tree frogs (López et al. 2015). Based on dietary 100 analysis of 57 individuals of the rufous frog Leptodactylus fuscus (family Leptodactylidae) in Brazil, Santana et al. (2019) demonstrated that urban frogs focussed on eating Coleoptera while rural frogs had a more 101 diverse diet. To complicate matters, feeding plasticity may not be linked to the relatedness between species 102 103 as it may significantly differ between closely related species (López et al. 2015). Thus, sensitivities to consequences of habitat changes following urbanisation are species-specific but remain unknown for most 104 105 amphibians, especially in the tropics.

107 Anurans of the family Bufonidae (true toads) include 52 genera that are distributed worldwide and inhabit a variety of habitats, from deserts to tropical rainforests (e.g., Amphibian Survival Alliance 2021). The trophic 108 109 ecology of species within the Bufonidae has been widely studied throughout the world (e.g., Evans & Lampo 1996, Sabagh & Carvalho-e-Silva 2008, Duré et al. 2009, Maia-Carneiro et al. 2013, Flynn et al. 2021), 110 primarily suggesting that this group is made up of active foragers that search for and eat small, slow-moving 111 but highly aggregated prey, such as ants and termites (Toft, 1980, 1981; Simon and Toft, 1991). However, the 112 113 feeding strategy of Bufonidae remains controversially discussed (Sabagh & Carvalho-e-Silva 2008) with some authors classifying them as ant-specialists (Toft 1980, Isacch & Barg 2002) and others classify them as 114 generalists (Smith & Bragg 1949, Evans & Lampo 1996). Nonetheless, recent studies have argued that these 115 116 anurans have a mixed foraging strategy, only in part fitting that of typical active foragers (Crnobrnja-117 Isailović et al. 2012). For example, the common toad (Bufo bufo) is neither a feeding generalist nor a 118 myrmecophagous specialist (i.e., specialized on ants and termites), as some bufonids are proclaimed to be (Crnobrnja-Isailović et al. 2012). The very limited number of studies of Bufonidae in urban areas indicates 119 120 that the trophic ecology of toads in anthropogenic settings may change in response to differences in prey availability and to the type and intensity of habitat changes caused by urbanisation. For example, European 121 122 green toads (Bufotes viridis) preferentially consume insects attracted to artificial street lighting in urban environments (Covaciu-Marcov et al. 2010). Green toads can also benefit from fallen fruits from trees 123 124 typically planted in urban and suburban localities, becoming an important food source just after metamorphosis and also during the period of intensive growth preceding the first hibernation (Kaczmarski et 125 126 al. 2019). The Cururu toad Rhinella diptycha in Brazil is also reported to eat fruits in urban settings 127 (Severgnini et al. 2020). Fragmented wetlands and changes in habitat structure around wetlands and ponds 128 can also affect the diet composition and even body condition of resident anuran species (Mikoláš 2016). In the tropics and subtropics, several anuran species are capable of adapting to urban or peri-urban habitats. In a 129 study in Accra, the capital of Ghana, Ofori et al. (2021) compared the diets of the African common toad 130 131 Amietophrynus regularis (now Sclerophrys regularis, Poynton et al., 2016) in urban and agricultural habitats. 132 Being an opportunistic generalist predator with a broad dietary niche there were no demonstrable dietary differences between habitats. 133

134

In the present paper, we studied the trophic ecology of two adult stage Bufonidae species, the African 135 common toad (S. regularis) and the Hallowell's toad (S. maculata) in urban environments. These species are 136 ecologically and morphologically similar. We studied the food habits of the African common toad in Lomé 137 (Togo), Cotonou (Benin) and Ikeja (Lagos, Nigeria), and the Hallowell's toad in Port Harcourt and Ikeja 138 139 (both in Nigeria). Both species occurred sympatrically in Ikeja. The African common toad is a very abundant species widely distributed along the Atlantic coast, from Senegal to Cameroon, Ethiopia and Kenya in the 140 141 East, and along the Nile valley from South Sudan to Egypt, and along a coastal strip between Cameroon and 142 Angola (Rödel, 2000). Preferred habitats are moist and dry savannahs, montane grassland, forest margins

and agricultural habitats, often in association with rivers (IUCN SSC Amphibian Specialist Group 2016a).

- The Hallowell's toad is sympatric with the African common toad but restricted to an area ranging from
 Senegal to Cameroon (IUCN SSC Amphibian Specialist Group 2016b). Hallowell's toad is also very
- common, inhabiting a broad range of habitats including humid savannas, drier savannas along rivers, forest
- edges, degraded forest and agricultural land (IUCN SSC Amphibian Specialist Group 2016b). Both toad
- species are generalists that can also be found in anthropologically altered and fragmented habitats (Ernst et
- al. 2006). Due to its ecological elasticity, the African common toad in Qatar can even survive in irrigation
- 150 pipes and water transportation vehicles (Abdulkarim & Yamaguchi 2021).
- 151
- We investigated trophic niche breadth and explored (1) whether taxonomic diet composition of the two toads varied within and between urban localities, (2) if local conditions (using rainfall as a proxy) and prey type availability in the field affected diet similarity between the two toad species and (3) whether there were differences in diet in comparison with similar species in non-urban locations. We also analysed whether adult toad diets were affected by season (wet versus dry) and varied by sex. We hypothesised that because both these toad species are highly adaptable, their diets would vary remarkably among study areas and toad diets would be more similar between nearby sites than more distant ones.
- 159
- 160 Materials and methods
- 161

162 Study areas

163

We carried out the present study in four cities of three different West African countries: Lomé, the capital of 164 Togo, Cotonou, the economic centre of Benin, Ikeja, the capital of Lagos State in southwestern Nigeria, and 165 166 Port Harcourt, the capital of Rivers State in southeastern Nigeria. All four cities are situated near the Gulf of 167 Guinea coast. To minimize the effects of local habitat on diet composition, we selected sites with similar 168 characteristics, i.e., areas in the periphery of each city, with cement buildings surrounded by grassy patches and small ornamental house gardens. Locations varied from Port Harcourt, situated inside the rainforest zone 169 of southern Nigeria, Ikeja at the border between the moist forest and the West African savannah zone, and 170 171 Cotonou and Lomé within the Dahomey Gap savannahs. Thus, although locally similar, the four study sites 172 were found in different vegetation zones.

173

174 **Toad diets**

175

176 Diet data were obtained from individuals found as (i) roadkills and (ii) from stomach flushing of live

177 individuals in night surveys. All animals were opportunistically collected over a period of 394 days across all

study areas: 133 during the wet season (April - September 2010-2020), and 261 in the dry season (October

and March 2010-2020). It took longer to collect an adequate sample size during the dry season because toads

180 of both species spend less active above-ground than in the wet season (unpublished observations),

181 influencing also the number of roadkills and live individuals available for examination.

182 Live animals were flushed within one hour from the capture, without any anaesthetising and using the

available potable water. The stomach flushing procedure followed Solé et al. (2005). Each toad was held

safely by fixing the forelimbs with one hand, and the water-filled tube attached syringe was held in the other.

185 We used a metal spatula to open the toad's mouth and then introduced the syringe tube through the

oesophagus into the stomach; the pyloric end of the stomach can normally be felt. The entire content of the syringe was then flushed into the stomach and any content forced out collected in the vessel. The same procedure was repeated until all the stomach contents were forced out. When no more stomach content appeared after flushing, the animal was released to the wild. No animals were killed or damaged during the stomach flushing procedure, and all individuals appeared in good conditions when released. Food contents were fixed in 70% alcohol and then examined under a dissecting microscope. Stomach contents of recently killed toads that were opportunistically collected in the various study areas, were also preserved in alcohol

193 before dissecting in the laboratory.

194

195 Dietary analyses of stomach contents did not include plant remains as they can be assumed to be secondarily ingested by toads in some cases while foraging on live insects (e.g., Korschgen & Moyle 1955, Mahan & 196 197 Johnson 2007). Stomach contents of sampled toads were analysed using standard procedures (Solé & Rödder 2010). The taxonomical composition of the diet was determined by identifying, under a dissecting 198 199 microscope, the various parts of insects and other invertebrates to the highest taxonomic level possible. We 200 identified the various items to the level of superfamily (e.g., Vespoidea), class (e.g., Gastropoda), subclass 201 (e.g., Oligochaeta), infraorder (e.g., termites, i.e., Isoptera) or order (e.g., Order: Coleoptera, Lepidoptera). 202 Coleoptera and Lepidoptera were identified as larvae or adults.

203

204 We evaluated the abundance of arthropods that were actively moving on ground or flying close to the ground 205 level, assuming that these were the only invertebrate categories being readily available to toads. We used 206 entomological sweep-net sampling (Hirai & Matsui 2000) and sticky traps (Beard et al. 2003, 2021) to 207 determine arthropod abundance in Port Harcourt and Cotonou. Netting was carried out in four ten-minutes 208 zigzag transects within each city (two in the dry and two in the wet seasons). These were conducted in 209 microhabitats in the same nights in which toads were observed either alive during random observation 210 sessions, or after roadkills were collected. Sticky traps were randomly set in the same places where multiple 211 toad individuals were observed, under the assumption that toads concentrate in sites with higher potential prey density. Sticky traps were vertically positioned at ground level, thus minimizing the risk of also 212 213 capturing toads by chance. In fact, only one toad was unintentionally trapped. In each study area, a total of 200 sticky traps per night were placed randomly at 18h00 and removed the next day at 06h00. Trapping was 214 carried out for three consecutive nights during each season, in each of the four study areas. Each sticky trap 215 216 was removed after the sampling night and replaced with another in the next trapping day. Data from sweep-

net transects and sticky trapping were combined for the analysis. We identified the taxonomical status of 217 trapped individuals to the same taxonomic level as for the diet analysis. 218

219

220 Statistical analyses

221

222 Food niche overlap between toad populations was assessed using the Pianka's (1986) symmetric equation,

with values ranging from 0 (no overlap) to 1 (total overlap): 223

224
$$O_{xy} = \frac{\sum_{i=1}^{n} p_{xi} p_{yi}}{(\sum_{i=1}^{n} p_{xi^2} \sum_{i=1}^{n} p_{yi^2})^{1/2}}$$

where p_{xi} is the proportional utilization of prey *i* by population x and p_{yi} the proportional utilization of prey *i* 225 226 by population *y*.

227

228 We also tested the effects of geography and local weather conditions on the inter-population food niche 229 overlap. The geographic pattern was estimated by linear distance between pairs of study sites (in km). 230 Weather conditions were approximated by the mean annual rainfall as a proxy of the site-specific conditions 231 using data on annual rainfall at each site from the Istituto Geografico de Agostini (2020). The difference in 232 mean annual rainfall (in mm) between pairs of study sites was calculated as follows: 233

 $\Delta_{\text{rainfall}} = \text{rainfall of the wetter place} - \text{rainfall of the drier place}$

234

Since $(\log)\Delta_{\text{rainfall}}$ and (\log) distance between pairs of sites were not significantly correlated (r = 0.579, P = 235

0.229), these two variables were entered independently in the analyses. The effect of air temperature was not 236

237 analysed because air temperatures were nearly identical among study areas throughout the year with a

nocturnal mean of 28°C and a diurnal mean of 33°C (Istituto Geografico de Agostini 2020). 238

239

We evaluated whether our sample sizes captured the "true" prev category richness and diversity within each 240 241 study site by (i) rarefaction analysis for species discoveries at each site with 95% confidence intervals of the estimates approximated by 9999 bootstraps simulations; and by (ii) calculating the Chao-1 index from 242 243 abundance data (Chao 1984). This latter index represents the theoretical number of prey categories that can 244 be expected on the basis of the sampling regime. In addition, the following univariate prey category diversity 245 metrics were calculated for each site: (i) species richness (total number of species recorded in the diet of 246 toads at each site); (ii) dominance, D; (iii) Simpson index, S with S = 1 - D; (iv) Shannon entropy index, H' (Shannon & Weaver 1963); and (v) evenness, e, calculated by Buzan and Gibson's formula (Magurran 247 1988). For each diversity metric, we also generated upper and lower 95% confidence intervals by bootstrap 248 analysis with 9999 random samples, each with the same total number of individuals as in each original 249 250 sample (Harper 1999). Food niche breadth of the various toad populations was evaluated by Simpson's

251 (1949) diversity index, S.

All variables were tested for normality and homoscedasticity prior to applying parametric tests, and, if required, log transformed to achieve normality. When normalization was impossible, we applied nonparametric tests. Correlations between (1) linear distance between pairs of sites and food niche overlap, and between (2) Δ_{rainfall} and food niche overlap were tested using the non-parametric Spearman's rank correlation coefficient, r_s.

258

259 One-way Analysis of Similarities (ANOSIM) was used to test for significant inter-population differences 260 among diet compositions, based on Bray-Curtis distance measure and 10,000 permutations (Clarke 1993). In 261 this analysis, the distances were converted to ranks (Clarke 1993). ANOSIM analysis was performed in the R 262 statistical environment, using the Vegan package version 2.5-7 (Oksanen et al. 2020). A VARIMAX rotated Principal Component Analysis, PCA, was applied to arrange the various toad populations within the 263 multivariate space in regard to their taxonomic diet composition. The VARIMAX rotation is an adjustment 264 of the PCA that maximizes the variance shared among items in order to better depict the relationship 265 266 amongst them (Kaiser 1958). This PCA was carried out using Statistica v. 8.0 (Statsoft). Frequency differences in the occurrence of prey type categories in the diets of sympatric or allopatric toad species were 267 assessed by contingency table χ^2 tests. Frequency differences in the occurrence of prey type categories in the 268 269 diets of males versus females in the two study species, and between dry and wet seasons (all sites being 270 pooled in order to increase sample sizes) were assessed by contingency table χ^2 tests. Correlations between prey resource availability and consumption by toads were assessed by Spearman's rank correlation 271 272 coefficient. Ivlev's electivity index and the forage ratio, two commonly used measures of food selection, 273 were not used because they are significantly biased when the sizes of the prey samples from the gut of the 274 predator and the habitat are unequal (Strauss, 1979) as it was in our case of study. All other analyses were conducted using PAST 4, version 4.04, statistical package (Hammer 2020), with alpha being set at 5% and 275 276 all tests being two tailed.

- 277
- 278 **Results**
- 279
- 280 **Diets**

281

We examined the food contents of 146 toads, including 46 *S. maculata* from Port Harcourt, 33 *S. regularis* from Cotonou, 13 *S. maculata* and 13 *S. regularis* from Ikeja (all inhabiting the same microhabitat and thus being strictly sympatric) and 41 *S. regularis* from Lomé. The taxonomical composition of the diet of these toad populations is given in Table 1. Rarefaction analysis confirmed that diet composition was satisfactorily assessed in all study areas (Online Supplemental Figure S1).

- Across all four cities, Formicoidea and Oligochaeta were by far the main food items (both categories eaten by 26.7% of the individuals), followed by Coleoptera adults (15.8%) and Coleoptera larvae (14.4%). All
- other prey categories were relatively rare. The diet composition of sympatric *S. maculata* and *S. regularis* in
- Ikeja did not differ significantly (contingency table $\chi^2 = 3.48$, df = 9, *p* = 0.979) and consisted mainly of
- Formicoidea (Figure 1). Food niche breadth was slightly higher in *S. maculata* (B = 1.497) than in *S.*
- *regularis* (B = 1.208), and the niche overlap was very high (O = 0.976). The taxonomic composition of the
- diet did not differ significantly among study areas in both *S. regularis* (contingency table $\chi^2 = 10.9$, df = 11,
- 295 p = 0.451) and *S. maculata* ($\chi^2 = 22.1$, df = 15, p = 0.104). Because of this similar diet composition between 296 the species, we pooled the data from the two species at Ikeja for further analyses.
- 297

298 There was a considerable variation in diet composition across populations: in terms of food niche breadth, Port Harcourt showed by far the greatest width (B = 8.96), followed by Cotonou (B = 3.57), Ikeja (B = 2.59) 299 and Lomé (B = 1.09). Log values for food niche width and local rainfall were significantly positively 300 correlated (r = 0.997, n = 4, p < 0.001). The mean dietary overlap between population pairs was relatively 301 302 high (O = 0.721) but with a wide variation from 0.448 to 0.901. Maximum overlap was observed between 303 Port Harcourt and Cotonou (O = 0.901) and the least between Lomé and Ikeja (O = 0.448). The smallest dietary overlap observed for the latter cities corresponded with the greatest distances of the qualitatively 304 305 assessed degree of urbanisation. The linear distances between pairs of sites were not correlated with food niche overlap ($r_s = -0.03$, p = 0.954) and the same was observed for the $\Delta_{rainfall}$ ($r_s = -0.657$, p = 0.136). 306 307

Diversity profiles (Figure 2) showed that the Port Harcourt population's diet differed substantially from the
Ikeja population. Dietary diversity metrics also revealed significant differences among sites (Table 2).
Dominance was considerably higher in Ikeja than elsewhere, whereas the other three metrics were lower in
Ikeja than in the other three sites. The toad population in Port Harcourt had the lowest dominance and the
highest values for evenness, Simpson and Shannon indices (Table 2). Chao-1 index revealed that the Lomé
population had a much wider potential dietary spectrum than all the other populations (Table 2).

314

The value of ANOSIM on the taxonomic composition of the diet in the four cities was significant (mean rank within groups = 5333; mean rank between groups = 7123; p < 0.001). The first two axes of the PCA explained 96.5% of the variance (PC1: 84.5%, PC2: 12%). Ikeja, Lomé and Port Harcourt were positioned about equidistantly in the multivariate space and Cotonou was intermediate to the latter two populations (Figure 3).

320

321 Intersexual differences

- 322
- To determine sexual differences in diets (Online Supplemental Table S1) we examined 52 *S. maculata* (31
- females and 21 males) and 79 *S. regularis* (44 females and 35 males). The taxonomic units of the diet

- composition did not differ significantly between sexes in *S. maculata* (contingency table $\chi^2 = 11.4$, df = 11, *p* = 0.409) and in *S. regularis* ($\chi^2 = 14.84$, df = 14, *p* = 0.389). Diversity metrics in both species revealed that females had a more varied diet, with higher evenness and lower dominance index values than males (Table 3). The Chao-1 index predicted 15 (95% CI = 12-18) prey type categories for females and only 9.5 (95% CI = 11-13.75) for males, indicating that *S. maculata* females had a remarkably higher dietary taxonomic
- richness than males. The same trend was also present in *S. regularis*, but less pronounced and with more
- overlapping 95% CI intervals between the sexes (13.75, 8.38-19.13, versus 11.75, 5.75-17.75; Table 3).
- 332

In interspecific comparisons, *S. maculata* showed greater extremeness in trophic variability as indicated by
the Chao-1 index with (i) *S. maculata* females having a potential trophic diversity greater than that of *S. regularis* females, and (ii) *S. maculata* males having less trophic diversity than those of *S. regularis* (Table
3).

337

338 Interseasonal differences

339

340 Online Supplemental Table S2 summarises the dietary data by season and study area. Contingency table analysis showed that diet compositions differed significantly between seasons ($\chi^2 = 40.39$, df = 15, p < 341 342 0.001), with Oligochaeta, Gastropoda and Coleoptera adults being eaten significantly more often by wet season whereas Formicoidea by dry season (at least p < 0.0001 in all pairwise comparisons at sequential χ^2 343 tests). The frequencies of consumption of all the other prey categories did not differ significantly between 344 seasons (at least p > 0.05 in all pairwise comparisons at sequential γ^2 tests). Table 4 presents the values of 345 346 diversity metrics for the interseason variations. The values of the diversity metrics of the pooled populations 347 were similar between seasons (Table 4) except for Chao-1, which predicted a much wider breadth of food type categories for the wet season than for the dry season (95% confidence intervals: 15.5-26.75 versus 11.5-348 349 17.5).

350

351 **Prey availability**

352

Online Supplemental Table S3 summarises prey availability by season and by study area (Cotonou and Port Harcourt). The overall number of recorded individuals of all taxa was higher in the wet season (1729 versus 1610 in Cotonou and 3613 versus 3323 in Port Harcourt), and the frequencies of occurrence of the various prey types were higher by wet season at the two study areas (contingency table $\chi^2 = 1998$, df = 57, *p* < 0.0001). The richness of available prey types was 20 taxa in the wet season and 15 taxa in the dry season.

358

In Port Harcourt, where we only recorded *S. maculata*, toads did not feed on the available prey type, both in the wet season ($r_s = 0.06$, p = 0.811) and the dry season ($r_s = 0.21$, p = 0.369). Equally in Cotonou, where we only recorded *S. regularis*, diet and food availability were not significantly correlated with each other for

the wet season ($r_s = -0.09$, p = 0.703) and the dry season ($r_s = 0.37$, p = 0.097). When we compared the 362 observed frequencies of consumption of prey items by toads in relation to those expected on the basis of the 363 364 availability of each food category in the field, we observed for both species and either seasons the following 365 patterns (that were significant at P < 0.05 at χ^2 tests with df = 1): (i) toads tended to avoid eating on 366 Collembola, Thysanoptera, Hemiptera and Homoptera despite being very abundant in the field; (ii) toads 367 feed upon Gastropoda much more than their availability; and (iii) toads feed upon Formicoidea relative to 368 their availability in the field. For all other prey type categories, no significant patterns emerged from our analyses. 369

370

371 Discussion

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In this study we documented the diet differences of two relatively common toad species living in urban 373 environments in several cities in West Africa. Our two study species have wide geographical distributions 374 and are known to be habitat generalists. Both toads thrive in a variety of ecological conditions (IUCN SSC 375 376 Amphibian Specialist Group 2016b, 2016a), and similarly to Ofori et al.'s (2021) study in Ghana we confirm 377 that the two toad species occupy and thrive in urban habitats in other countries in West Africa. Significantly, 378 we showed that the dietary composition of urban toads varied between populations; both species being able 379 to exploit strictly terrestrial prey (e.g., Oligochaeta, Coleoptera larvae, Formicoidea) as well as flying prey 380 (e.g., Vespoidea, Diptera). In all toad populations, the most frequently eaten foods were always terrestrial taxa (Formicoidea, Coleoptera adults and larvae, and Oligochaeta). Moreover, in two of the studied 381 382 populations where we measured prey availability and diets, toads were actively targeting potential prey 383 rather than opportunistically hunting them, since there was no correlation between prey availability and diets. 384 This suggests that the studied toads are selective predators where foraging for terrestrial prey is the primary feeding strategy whereas consumption of flying organisms is only secondary. These findings contrast with 385 386 other studies that suggest that in a number of studied anuran species (e.g., Cogălniceanu et al. 1998, Hirai & Matsui 1999, Heise-Pavlov & Longway 2011) opportunistic predation is the norm. This conclusion was also 387 388 reached by Ofori et al. (2021) for S. regularis in urban and agricultural habitats in Ghana.

389

390 Some studies of have suggested that Bufonidae species are relatively specialized ant-feeders (e.g., Isacch & 391 Barg 2002) especially in the tropics (Toft 1980, 1981), or else they concentrate on ants and beetles (Sulieman et al. 2016). Ants and beetles were indeed the main food types in S. regularis populations from Ghana (Ofori 392 et al. 2021) but ants and Oligochaeta were more important for S. maculata in deforested areas of Akwa Ibom 393 394 State in south-eastern Nigeria (Eniang et al. 2003). Beetles were prominent in the diet of another southern Nigerian population of S. maculata (Akani et al. 2011). However, as in Isacch and Barg (2002) we observed 395 that S. regularis and S. maculata fed upon a wide variety of prey types; ants were the dominant prey type in 396 one site (>80% of individuals containing them in their guts) and an important food source in the other three 397 398 sites. Given these findings, it is not possible to corroborate the hypothesis that Bufonids are ant specialists

(Toft, 1980, 1981), more in line with the observations by Crnobrnja-Isailović et al. (2012) for the European *Bufo bufo*. We conclude that in our study, toads were consuming ants relative to their availability, thus not
selected or preferred prey items. As indicated by Clarke (1974) the abundance of ants and beetles in
stomachs of studied toads simply reflects the abundance of these taxa in areas where the toads feed (Berry &
Bullock 1962, Klimstra & Myers 1965).

404

405 Differences in dietary metrics amongst the studied toads populations can be attributable to local ecological 406 characteristics. For instance, toad diets appeared to be affected by the degree of urbanisation. This is clearly shown by the fact that diet diversity in Ikeja and Lomé, the most and the least urbanised of our study sites 407 respectively, were lowest and highest in all sites. Conversely, the linear distance between the populations 408 409 was not correlated with the respective food niche overlap. The non-effect of the linear distance between sites on the food niche overlap between pairs of populations was counterintuitive. In fact, we would have 410 expected that nearby locations would also be characterized by a more similar availability of potential prev 411 412 than between more distant ones, with a consequent greater similarity in the diet of toad populations in nearby 413 locations. Moreover, the single population studied inside a tropical forest area (Port Harcourt) had a significantly wider diet breadth than all other toad populations. Thus, we suggest that the available diversity 414 of potential prey was much higher in Port Harcourt than in the other cities (forest versus savannah patterns in 415 416 species diversities), although we did not carry out prey type availability surveys in Port Harcourt to confirm 417 this.

418

419 In both males and females of the two study species, diet composition was relatively similar in all sites 420 though females had a wider niche breadth than males. This result is consistent with data on S. regularis from urban and agricultural habitats in Ghana (Ofori et al. 2021) and is likely due to intersexual differences in 421 body size, with females being significantly larger than males in both species (Rödel 2000). Although in 422 423 theory the larger body size may allow females to target specifically larger prey items than males, our data do not confirm this prediction since we found no statistical intersexual differences in frequency of occurrence of 424 large prey items (e.g., Oligochaeta) in toad stomachs. Therefore, it can be speculated that the wider niche 425 426 breadth of females depends on additional small-to-medium size taxonomic categories than in males. 427 Although in other anurans the larger sex has a more varied diet composition (e.g., Magalhães et al. 2016), this is not always the case. For example, in the European Bufo bufo, males consumed small prey items in 428 higher proportions than did females, but the opposite was true for medium-size prey, which suggests possible 429 430 dietary niche partitioning in prey size rather than in taxonomical dietary composition (Crnobrnja-Isailović et al. 2012). 431

432

The values of Chao-1 index indicated that food niche breadth was substantially higher in the wet season than
in the dry season. This result is in concordance with the observed patterns of higher numbers of trapped
arthropods and trapped prey categories during the prey availability screens (Table 7). Sympatric

- 437 (Dendi et al. 2019). It indicates that these patterns are linked to the seasonal fluctuating availability of
- 438 arthropods in tropical environments (Wolda 1978a, 1978b, 1980, e.g., Kishimoto-Yamada & Itioka 2015).
- 439 For example, in Tanzania, significant increases in insect density followed rains and were largely due to both
- an increase in the number of individuals per species and an increase in the number of species (Denlinger
- 441 1980). The abundance of tephritic flies was also positively correlated with precipitations in Benin
- 442 (Gnanvossou et al. 2017). Toft (1980) suggested that in dry season food is less abundant and in short supply,
- thus causing dietary changes in the feeding ecology of tropical anurans (including for instance enhancing
- 444 trophic niche partitioning among sympatric species).
- 445

436

446 **Conclusions**

447

In the tropics, species diversity is greater than in the subtropics and in temperate climates, and anurans have more specialized diets, resulting in the structuring anuran communities (Toft 1980). Therefore, the observed pattern of targeted prey consumption in *S. regularis* and *S. maculata* rather than the opportunistic prey consumption observed in most anurans, might be an adaptation to high anuran diversity in the tropics rather than an adaptation to urban habitats. Further comparisons between urban and un-disturbed habitats are required to elucidate this question.

454

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456

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459

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- 465
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- 467
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- 469
- 470 Ethical statement
- 471

- authorization to carry out this study was required. In addition, the research protocol did not damage any
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Table 1 Diet composition of toad individuals in four West African cities. Shown are the numbers of 703 toads containing a given prey item (No.) and the percentage of toad stomachs containing that given 704 prey item. The percentages are calculated on the basis of the total number of individuals examined 705 per species (46, 33, 26, 41 for the four study areas, respectively). Note that the total sum of the 706 numbers in each cityexceeds the total number of toads examined as single stomachs could contain 707 more than one prey item type. Data for the two Sclerophys species are pooled for Ikeja, as there 708 were no significant interspecific differences (see the main text); their species-specific diets are 709 given in Figure 2. 710

711

		t Harcourt (<i>S.</i> culata)		Cotonou (S. regularis) II		Ikeja (sympatric)		Lomé (S. regularis)		
	No.	%	No.	%	No.			%		
Oligochaeta	11	23.9	12	36.4	2	7.7	14	34.2		
Gastropoda	0	0	1	3.0	5	19.2	7	17.1		
Isopoda	0	0	0	0	1	3.8	0	0		
Araneidae	13	28.3	5	15.1	1	3.8	0	0		
Chilopoda	0	0	0	0	0	0	1	2.4		
Coleoptera adults	11	23.9	7	21.2	2	7.7	3	7.3		
Coleoptera larvae	14	30.4	7	21.2	0	0	0	0		
Lepidoptera adults	0	0	1	3.0	0	0	1	2.4		
Lepidoptera larvae	5	10.9	1	3.0	0	0	5	12.2		
Vespoidea	3	6.5	1	3.0	1	3.8	2	4.8		
Apoidea	2	4.3	0	0	1	3.8	0	0		
Formicoidea	7	15.2	6	18.2	21	80.8	5	12.2		
Dermaptera	0	0	2	6.1	0	0	0	0		
Blattodea	8	17.4	3	9.1	2	7.7	0	0		
Mantoidea	0	0	0	0	1	3.8	0	0		
Diptera	4	8.7	4	12.1	0	0	0	0		
Isoptera	0	0	0	0	0	0	1	2.4		

712

Table 2 Diversity indices for the diet composition for each city. 95% confidence intervals (CI) were calculated using 9,999 bootstrap simulations.

715 Data for the two *Sclerophys* species are pooled for Ikeja.

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	Port Harcourt (S. maculata)			Cotonou (S. regularis)			Ikeja (sympatric)			Lomé (S. regularis)		
	Estimate	Lower CI	Upper CI	Estimate	Lower CI	Upper CI	Estimate	Lower CI	Upper CI	Estimate	Lower CI	Upper Cl
Prey type richness	10	10	10	11	10	11	10	7	10	10	9	10
Dominance	0.1272	0.1183	0.1631	0.1395	0.1195	0.2012	0.3528	0.2316	0.5457	0.2032	0.1506	0.3097
Simpson	0.8728	0.8369	0.8817	0.8605	0.7988	0.8805	0.6472	0.4543	0.7684	0.7968	0.6903	0.8494
Shannon	2.157	1.988	2.207	2.135	1.907	2.238	1.553	1.029	1.84	1.87	1.593	2.067
Evenness	0.8645	0.7303	0.9086	0.7688	0.6303	0.8534	0.4726	0.3704	0.6465	0.6487	0.5147	0.7901
Chao-1	10	10	11	12.5	10.5	17	12.5	7.5	25	20	9.75	20

Table 3 Diversity indices of diet composition of males and females of two toad species. 95% confidence intervals (CI) were calculated using 9,999

	S. macu	S. maculata S.							S. regularis						
	females	Lower CI	Upper CI	males	Lower CI	Upper CI	females	Lower CI	Upper CI	males	Lower CI	Upper CI			
Prey type richness	12	12	12	9	9	9	13	12	14	11	9	12			
Dominance	0.117	0.089	0.144	0.145	0.114	0.175	0.144	0.103	0.186	0.163	0.107	0.220			
Simpson	0.883	0.856	0.911	0.855	0.825	0.886	0.856	0.814	0.897	0.837	0.780	0.893			
Shannon	2.279	2.150	2.408	2.015	1.894	2.137	2.197	2.006	2.388	2.050	1.830	2.270			
Evenness	0.814	0.716	0.912	0.834	0.738	0.930	0.692	0.579	0.805	0.707	0.588	0.825			
Chao-1	15	12	18	9.5	8	11	13.750	8.375	19.130	11.750	5.750	17.750			

bootstrap simulations. Data are pooled for each species across populations.

- **Table 4** Diversity indices for seasonal diet composition for each city. 95% confidence intervals (CI)
- were calculated using 9,999 bootstrap simulations. Data are pooled for each species across
- 723 populations.

	Wet season	Lower CI	Upper CI	Dry season	Lower CI	Upper CI
Prey type richness	15	14	16	13	13	13
Dominance	0.142	0.1067	0.1772	0.1479	0.1092	0.1867
Simpson	0.858	0.8229	0.8932	0.8521	0.8133	0.8908
Shannon	2.244	2.091	2.397	2.181	2.037	2.324
Evenness	0.6287	0.5412	0.7161	0.6808	0.5838	0.7778
Chao-1	21	15.25	26.75	14.5	11.5	17.5

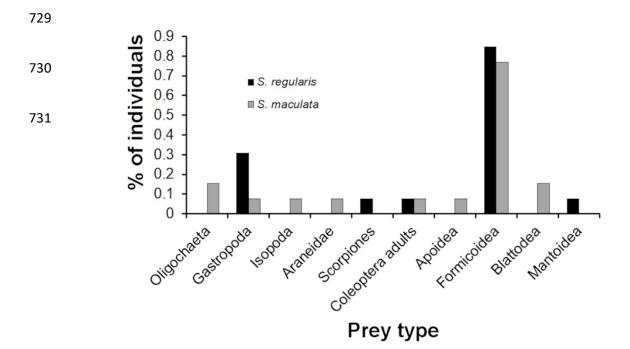
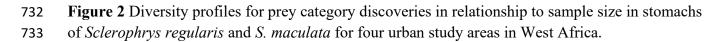


Figure 1 Diet composition of sympatric toads in Ikeja (Lagos). For each species, 13 individuals
were analysed.



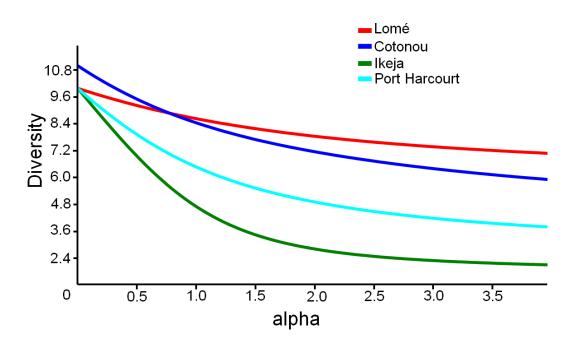
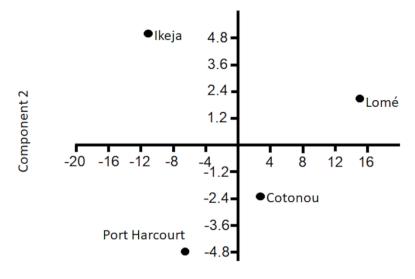


Figure 3 Principal Component Analysis, PCR, with VARIMAX rotation of diversity index values
for toad populations in four West African cities.



Component 1

739 Online Supplementary Materials

740 Table S1 Intersexual differences in diet composition of the two studied toad in four West African

cities. Data from all populations are pooled for each species. Percentage of stomachs containing that

742 given prey itemare relative to the total number of individuals per species.

	S. maculata females				<u>S. regularis</u> females			
	(<i>n</i> =31)	%	males $(n=21)$	%	(<i>n</i> =44)	%	males (<i>n</i> =35)	%
Oligochaeta	5	16.1	8	38.1	12	27.3	14	40
Gastropoda	1	3.2	0	0.0	3	6.8	5	14.3
Isopoda	1	3.2	0	0.0	0	0.0	0	0.0
Araneidae	7	22.6	7	33.3	4	9.1	1	2.9
Chilopoda	0	0.0	0	0.0	1	2.3	0	0.0
Coleoptera adults	7	22.6	5	23.8	8	18.2	6	17.1
Coleoptera larvae Lepidoptera	6	19.4	8	38.1	2	4.5	5	14.3
adults Lepidoptera	0	0.0	0	0.0	1	2.3	0	0.0
larvae	4	12.9	1	4.8	4	9.1	2	5.7
Vespoidea	3	9.7	1	4.8	3	6.8	0	0.0
Apoidea	1	3.2	2	9.5	0	0.0	0	0.0
Formicoidea	11	35.5	6	28.6	14	31.8	8	22.9
Dermaptera	0	0.0	0	0.0	2	4.5	0	0.0
Blattodea	4	12.9	6	28.6	1	2.3	2	5.7
Mantoidea	0	0.0	0	0.0	0	0.0	1	2.9
Diptera	4	12.9	0	0.0	2	4.5	2	5.7
Isoptera	0	0.0	0	0.0	0	0.0	1	2.9

743

- **Table S2** Interseasonal differences in diet composition of the two studied toad species in West
- 746 African cities. Numbers indicate the number of stomachs containing a given prey item.

	Port Har	court (S. maculata)	Cotono	u (<i>S. regularis</i>)	Ikeja (s	sympatric)	Lomé (S. regularis)	TOTAL	
	wet	dry	wet	dry	wet	dry	wet	dry	wet	dry
Oligochaeta	10	1	9	3	2	0	11	3	32	7
Gastropoda	0	0	0	1	5	0	7	0	12	1
Isopoda	0	0	0	0	1	0	0	0	1	0
Araneidae	6	7	3	2	0	1	0	0	9	10
Chilopoda	0	0	0	0	0	0	0	1	0	1
Coleoptera adults	8	3	4	3	2	0	2	1	16	7
Coleoptera larvae	6	8	3	4	0	0	0	0	9	12
Lepidoptera adults	0	0	0	1	0	0	1	0	1	1
Lepidoptera larvae	1	4	1	0	0	0	1	4	3	8
Vespoidea	1	2	1	0	0	1	2	0	4	3
Apoidea	1	1	2	0	0	1	0	0	3	2
Formicoidea	1	6	2	4	8	13	1	4	12	27
Blattodea	5	3	1	2	0	2	0	0	6	7
Mantoidea	0	0	0	0	1	0	0	0	1	0
Diptera	1	3	2	2	0	0	0	0	3	5
Isoptera	0	0	0	0	0	0	1	0	1	0

	Port Ha	rcourt			Cotono	u		
	Wet sea	son	Dry sea	son	Wet sea	Wet season		son
	No.	%	No.	%	No.	%	No.	%
Oligochaeta	19	0.5	0	0	16	0.9	3	0.2
Gastropoda	4	0.1	0	0	11	0.6	1	0.1
Collembola	631	17.5	731	22.0	491	28.4	517	32
Isopoda	8	0.2	91	2.7	2	0.1	0	0.0
Araneidae	116	3.2	119	3.6	2	0.1	0	0.0
Chilopoda	2	0.1	0	0.0	46	2.7	7	0.4
Orthoptera	213	5.9	71	2.1	0	0.0	2	0.1
Coleoptera adults	311	8.6	107	3.2	48	2.8	22	1.4
Coleoptera larvae	8	0.2	2	0.1	13	0.8	3	0.2
Lepidoptera adults	6	0.2	1	0.0	3	0.2	2	0.1
Lepidoptera larvae	21	0.6	6	0.2	7	0.4	1	0.1
Vespoidea	31	0.9	3	0.1	6	0.3	1	0.1
Apoidea	0	0.0	0	0.0	0	0.0	0	0.0
Formicoidea	198	5.5	841	25.3	166	9.6	312	19.4
Blattodea	3	0.1	24	0.7	9	0.5	8	0.5
Mantoidea	1	0.0	0	0.0	1	0.1	0	0.0
Diptera	1435	39.7	883	26.6	447	25.9	416	25.8
Isoptera	11	0.3	0	0.0	0	0.0	0	0.0
Thysanoptera	258	7.1	116	3.5	211	12.2	134	8.3
Hemiptera	138	3.8	147	4.4	133	7.7	122	7.6
Homoptera	202	5.6	181	5.4	118	6.8	63	3.9
TOTAL	3616	100	3323	100	1729	100	1610	100

Table S3 Prey availability by season and by study city.

Figure S1 Rarefaction curves with 95% confidence intervals generated after 9999 bootstraps for
prey category discoveries in relationship to sample size (b) in stomachs of *Sclerophrys regularis*and *S. maculata* for four urban study areas in West Africa.

