Utah State University

DigitalCommons@USU

Antipredator Mechanisms of Post-Metamorphic Anurans: A Global Database and Classification System

Rodrigo B. Ferreira
Utah State University

Ricardo Lourenço-de-Moraes
Universidade Estadual de Maringá

Cássio Zocca
Universidade Vila Velha

Charles Duca
Universidade Vila Velha

Karen H. Beard
Utah State University

Edmund D. Brodie Jr.
Utah State University

Follow this and additional works at: https://digitalcommons.usu.edu/eco_pubs

Part of the Ecology and Evolutionary Biology Commons

Recommended Citation

Ferreira, R.B., Lourenço-de-Moraes, R., Zocca, C. et al. Behav Ecol Sociobiol (2019) 73: 69. https://doi.org/10.1007/s00265-019-2680-1

UtahState University
MERRILL-CAZIER LIBRARY

1 **Antipredator mechanisms of post-metamorphic anurans: a global database and**

2 **classification system**

3

4 **Rodrigo B. Ferreira[1,2*], Ricardo Lourenço-de-Moraes[3], Cássio Zocca[1], Charles Duca[1], Karen H.**

5 **Beard[2], Edmund D. Brodie Jr.[4]**

6

7 [1] Programa de Pós-Graduação em Ecologia de Ecossistemas, Universidade Vila Velha, Vila Velha, ES,

8 Brazil

9 [2] Department of Wildland Resources and the Ecology Center, Utah State University, Logan, UT, United

10 States of America

11 [3] Programa de Pós-Graduação em Ecologia de Ambientes Aquáticos Continentais, Universidade Estadual

12 de Maringá, Maringá, PR, Brazil

13 [4] Department of Biology and the Ecology Center, Utah State University, Logan, UT, United States of

14 America

15

16 *Corresponding author: Rodrigo B. Ferreira, Laboratório de Ecologia da Herpetofauna Neotropical,

17 Programa de Pós-Graduação em Ecologia de Ecossistemas, Universidade Vila Velha, Av. José Dantas.

18 CEP: 29102-920 Vila Velha, ES, Brazil (E-mail: rodrigoecologia@yahoo.com.br; +55 27 99865-5395)

19

20 **Abstract**

21 A crucial step in any ethological study is to distinguish and classify the observed behavior into categories.

22 The literature on anuran antipredator mechanisms is largely scattered and descriptive due to the

23 opportunistic nature of the observations and the lack of a simple, widely accepted classification scheme.

24 We propose an explanatory classification system of antipredator mechanisms for post-metamorphic

25 anurans (i.e., juveniles and adults) based on a thorough review of the literature and observations made

26 during fieldwork and in the laboratory since 1970. In addition, we provide a freely available global

27 database on antipredator mechanisms of post-metamorphic anurans. The classification system is

28 composed of 12 antipredator mechanisms and 28 variations distributed into three stages of defense (avoid

29 detection, prevent attack, and counterattack). The database comprises 650 species and 39 families

30 providing a unique opportunity to investigate ecological and evolutionary questions regarding

31 antipredator mechanisms of anuran. We provide a general overview of geographic, taxonomic and

32 phylogenetic patterns found in the database. Both our studies and that of our colleagues added 70 species

33 to the database. The number of publications on antipredator mechanisms increased substantially after the

34 year 2000. We hope to spark a renewed interest in antipredator mechanisms of post-metamorphic anurans

35 to understand further the evolution of predator-prey interactions.

36

37 **Significance statement**

38 Predation is a phenomenon of great ecological and evolutionary significance. Hence, the study of

39 antipredator mechanisms may provide some of the most fascinating answers to questions regarding

40 species "struggle for existence". Based on extensive fieldwork, laboratory observations and a thorough

41 literature survey, we propose a classification system of antipredator mechanisms for anurans, and provide

42 a database of antipredator mechanisms elicited by frogs. We describe each mechanism, discuss the

43 variations, and provide images for most antipredator mechanisms.

44

45 **Running head:** Antipredator mechanisms of anurans.

46

47 **Keywords** Amphibians, Anura, defense, defensive behavior, ethology, predator-prey.

48

Introduction

55

56

57 A crucial step in any ethological study is to distinguish and classify observed behavior into separate

58 categories (Janik 1999). Pattern recognition is the most common approach of classification by human

59 observers because it is reproducible and communicable. Because of this, researchers often use images and

60 a detailed description of the behavior to describe animal behavior (Barrett and Seeley 2015).

61   Researchers have largely overlooked or superficially treated antipredator mechanisms in post-

62 metamorphic anurans. The literature on anuran defensive behavior is largely descriptive due to the

63 opportunistic nature of observations in the field and the lack of a classification scheme (Wells 2007). As

64 result, there are scattered studies on the topic throughout the literature, often published as short notes and

65 focused on single species. To date, there have been two reviews of anuran antipredator mechanisms (see

66 Dodd 1976; Toledo et al. 2011). Dodd (1976) listed 22 types of defensive behavior and provided a

67 bibliography list on the topic. Toledo et al. (2011) listed 30 types of defensive behavior and provided a

68 brief description of each one. Despite the advances of these studies, they lack: i) a comprehensive and

69 detailed scheme to classify antipredator mechanisms, ii) a compiled global-scale dataset, and iii) a general

70 overview of geographic, phylogenetic and taxonomic patterns. A unified classification system and a

71 global database of anuran antipredator mechanisms will facilitate and enhance studies focused on

72 predator-prey interactions of anurans.

73   Studies of predator-prey interactions continue to be one of the most fascinating and important

74 aspects of ecological research (Mukherjee and Heithaus 2013). Many studies have shown interactions

75 between anurans and their predators, such as arthropods, including insects, spiders, and centipedes, and

76 nearly all vertebrate groups from fish to mammals to birds (Toledo 1995; Zug et al. 2001). Thus, selective

77 pressure driving the evolution of antipredator mechanisms in anurans is likely strong.

78   Predation is a phenomenon of great ecological and evolutionary significance. Hence, the study of

79 antipredator mechanisms may provide answers to questions regarding species "struggle for existence"

80 (Zug et al. 2001). Based on extensive fieldwork, laboratory observations, and a thorough literature survey,

81 our goal is to: i) provide a freely-available global database with most records on antipredator mechanisms

82 elicited by anurans, and ii) propose an explanatory classification system of antipredator mechanisms in

83 post-metamorphic anurans. We describe each mechanism, discuss the variations, and provide images for

84   most antipredator mechanisms. In addition, we provide a general overview of geographic, taxonomic and

85   evolutionary patterns found in the database.

86

87   **Material and Methods**

88

89   **Data compilation**

90

91   We compiled a global database of antipredator mechanisms for post-metamorphic anurans based on a

92   literature survey, our own fieldwork, and consultation with colleagues. We conducted an extensive

93   literature survey of antipredator mechanisms for post-metamorphic anurans in the following databases:

94   Brill online books and journal, Google Scholar, Scientific Electronic Library Online (SciELO), Scopus,

95   Taylor and Francis Library Online, and Web of Science. In all cases, we used the following keywords:

96   antipredator mechanism, antipredator behavior, defensive behavior, and defensive strategy combined with

97   either frog or anuran. We searched the major herpetological journals often used to publish on this topic

98   (Amphibia-Reptilia, Journal of Herpetology, Herpetologica, Herpetological Review, and Herpetology

99   Notes) and consulted original cross-references before adding them to the database.

100   We also used observations on antipredator mechanism from our fieldwork since 1970 at many

101   locations in most zoogeographic regions (i.e., Australian, Afrotropical, Neotropical, Neartic, Palaeartic,

102   and Oriental). We used focal animal sampling (Altmann 1974) and simulated predator attack by using

103   finger-only stimuli and multiple stimuli (see Lourenço-de-Moraes et al. 2016). We tested anurans under

104   both field and laboratory conditions. In addition, we have emailed colleagues requesting observations on

105   antipredator mechanisms of anurans. The records of species without precise taxonomic identification at

106   the species-level (i.e., aff., cf., and gr.) were removed from the database. Taxonomic classification

107   follows Frost (2018).

108

109   **Classification criteria**

110

111   We adopted the term antipredator mechanism to include behavioral, morphological and physiological

112   adaptations aiming to reduce predation success during predator-prey interactions. Some behaviors should

4

113   not be considered antipredator mechanisms (Brodie Jr. et al. 1991), such as occupying microhabitat

114   refugee (e.g., burrow, crevice and dense vegetation), use of different foraging habitat (spatial avoidance),

115   or adjusting activity periods (temporal avoidance). These specific defense behaviors enhance the

116   survivorship of prey by reducing the probability that they will occupy the foraging microhabitat of

117   potential predators.

118   Because the assignment of antipredator mechanism is inherently a subjective process, we took

119   several steps to standardize the process:

120   1) All mechanisms were placed in one of three stages of defense (avoid detection, prevent attack, or

121   counterattack);

122   2) The mechanism should have the potential to be measured as reducing predation success in a situation

123   of predator-prey interaction (i.e., behaviors that only reduce injury (e.g., eye protection in Toledo et al.

124   2011) were not considered antipredator mechanisms);

125   3) Antipredator variations are specific adaptations within the mechanism;

126   4) All mechanisms and variations had to be observed in a minimum of three individuals consistently for

127   each genus; and

128   5) Individuals tested had to be observed by two observers to reduce misinterpretation of anuran

129   antipredator display.

130   We found that many mechanisms listed in the literature had similar purposes and therefore

131   should have been considered the same mechanism. Our goal was to assess each described antipredator

132   mechanism carefully to determine whether the trait is a variation of a broader category of mechanism, the

133   same mechanism that is known by another name, or a unique mechanism. The naming used in our

134   classification system is based on the purpose of the antipredator mechanism. When there was more than

135   one name assigned to a behavior, the most descriptive name was adopted.

136

137   **Reconstruction of ancestral states**

138

139   In order to provide a general overview on the evolution of the 12 proposed antipredator mechanisms, we

140   reconstructed these characters in a phylogenetic tree. Further analyses and/or exhaustive discussion will

141   be presented in a forthcoming manuscript.

142   First, we recreated the phylogenetic tree based on data published by Jetz and Pyron (2018). We

143   trimmed the tips to represent the 39 families for which we have data on antipredator mechanism. For this,

144   we created a matrix of the 12 antipredator mechanisms coding presence (1) or absence (0) at the family

145   level. We reconstructed the evolution of these antipredator mechanisms via parsimony using the "Trace

146   Character History" function in the program Mesquite version 3.0 (Maddison and Maddison 2015).

147

148   **Data availability**

149   Freely available database is on Online Resource 1. The references from the database are on Online

150   Resource 2.

151

152   **Results**

153

154   We compiled a global database comprising 2953 records on antipredator mechanisms of 650 post-

155   metamorphic anuran species within 180 genera and 39 families. Hylidae had the highest number of

156   species (N= 151; 23%) in the database. Out of 650 species, 147 (23%) were recorded from more than one

157   data source (i.e., literature, colleagues or fieldwork). From exclusively one data source, literature

158   provided data for 433 species (67%), colleagues for 40 (6%) species, and our fieldwork for 30 (5%)

159   species.

160   The number of publications on antipredator mechanisms increased substantially after the year

161   2000 (Fig. 1). The records from the Neotropical region represent 462 (71%) species, followed by 56 (9%)

162   species from Australian region, 46 (7%) species from Neartic region, 42 (6%) species from Oriental

163   region, 30 (5%) species from Afrotropical region, and 17 (2%) species from Palaeartic region. Three

164   (0.5%) species (*Bombina maxima*, *Hypopachus variolosus* and *Lithobates catesbeianus)* were recorded

165   from more than one zoogeographic region. The database has records from 52 countries, of which Brazil

166   has the most records (N= 368 species; 57%), followed by Australia (N= 51 species; 8%) and the United

167   States (N= 41 species; 6%).

168

169   **Classification system of antipredator mechanisms**

170

171 From our database and literature review, we present a classification system of antipredator mechanisms of

172 post-metamorphic anurans (Table 1). This classification system is composed of 12 antipredator

173 mechanisms and their respective variations placed in three phases of defense (avoid detection, prevent

174 attack, and counterattack).

175

176 **Defense phase: Avoid detection**

177

178 This phase of predator-prey interaction consist of the prey avoiding detection by a predator. This phase

179 occurs when the predator and prey share the same microhabitat and the prey is within the perceptual field

180 of the predator (see Brodie Jr. et al. 1991). This phase of avoid detection includes the following

181 antipredator mechanisms: camouflage, immobility, and interrupt calling (described below).

182

183   **1. Camouflage**

184 Camouflage includes several prey adaptations (e.g., behavior, coloration, and structures) that avoid

185 detection by the predator by becoming difficult to see (i.e., crypsis) or by disguise (i.e., mimesis). Other

186 terms have been commonly used, such as cryptic coloration (e.g., Cott 1940; Merilaita et al. 1999;

187 Merilaita 2003), obliterative coloration (Thayer 1909), concealing coloration (Cott 1940), or crypsis (e.g.,

188 Edmunds 1974). Camouflage is symplesiomorphic in Anura (Fig. 2a).

189

190   1a. Background matching is the prey's visual resemblance to its current or most commonly used

191 substrate (i.e., homochromy or imitation of reflected light). It is also called cryptic resemblance (Cott

192 1940) and crypsis (sensu Endler 1978). Some hylids have dorsal color patterns resembling lichen-covered

193 tree bark that resemble moss or lichens (Fig. 3a). Most leaf-litter anurans have brown as the dominant

194 dorsal colors to resemble leaf litter (Fig. 3b). Many anurans that escape from predators by diving into

195 water bodies have dark coloration and mottled patterns to resemble algae-covered, sandy or muddy

196 substrates (Wells 2007). Some anurans choose a microhabitat to increase similarity to a background, or

197 choose a background with greater scene complexity where predator's searching is difficult (i.e., substrate

198 selection) (Webster et al. 2011; Caro 2014). Some anurans (e.g., *Centrolenella* and *Vitreorana*) have

199 pronounced reflectance in the infrared wavelengths and partially transparent venter (i.e., transparency) to

7

200 remain cryptic in the foliage (Fig. 3c) (Schwalm et al. 1977; Emerson et al. 1990). Some anurans can also

201 match the background by actively changing their skin patterns and colors using special chromatophore

202 cells (i.e., color polyphenism). The color change may occur instantaneously, or may take a few minutes or

203 even weeks to happen. It has been observed in anurans as changes in reflectance, resulting in lightening or

204 darkening of the skin (King et al. 1994). In fact, most hylids are darker at night than during the day. For

205 example, the hylid *Boana albopunctata* has been observed changing color from yellowish at night to light

206 beige at daylight (RBF et al. pers. obs.).

207 Some species enhance background matching by eliminating shadow through the modification of

208 the skin to disrupt the outline of the animal (Zug et al. 2001). It is the continuity of surface, bounded by a

209 specific contour or outline, which chiefly enables the recognition of objects, thus preventing a match with

210 a predator's search image (Merilaita and Lind 2005). Among the morphological modifications related to

211 this mechanism are supraciliary processes, scalloped fringes along the outer margins of the limbs,

212 appendages, and a variety of warts and tubercles. For example, eliminating shadow is used by some

213 hylids that have flange to help hide the shadow and a pale fringe breaks up and averages out any shadow

214 that remains. Behaviorally an anuran presses itself against the substrate to flatten the body. Eliminating

215 shadow is probably more effective to avoid predation for diurnal-active anurans or those resting during

216 daylight. There is a substantial amount of evidence that risk of detection correlates with the degree of

217 resemblance between prey and background (e.g., Turner 1961; Sandoval 1994; Nystrand and Granström

218 1997; Merilaita et al. 2001; Merilaita and Lind 2005).

219 Some species developed the ability to resemble an uninteresting object (i.e., homomorphy or

220 imitation of morphology) or natural movement (i.e., homokinemy or imitation of movement). This

221 adaptation is called masquerade or mimesis and plays important roles in visual recognition. Masquerade

222 is considered deceptive because the prey resembles something else, which is of no special interest to the

223 predator. For example, anurans use coloration, spines, appendages, and a variety of warts and tubercles to

224 resemble stones, bird dropping, or fallen leaves (e.g., *Odontophrynus americanus*, Fig. 3d). Also, anurans

225 imitate natural movement, such as *Phasmahyla exilis* that sway slightly when walking on a branch

226 resembling the wind movement (RBF pers. obs.).

227 Background matching was displayed by 585 (90%) species within 171 (95%) genera and 39

228 (100%) families from all zoogeographic regions. *Boana* and *Leptodactylus* (N= 28 species each; 15%)

229   were the most frequently represented genera. Hylidae (N= 143 species; 24%) and Bufonidae (N= 91

230   species; 51%) were the most frequently represented families displaying background matching.

231

232   1b. Disruptive coloration is the use of contrasting markings to break up the appearance of body

233   form (Fig. 4a, b). The idea behind disruptive coloration is to make the detection of edges and boundaries

234   more difficult. Many anurans use disruptive coloration by having light dorsal stripes, irregular blotches or

235   spots, and dark eye lines or ocular marks (Wells 2007).

236   Disruptive coloration was displayed by 32 (5%) species within 14 (8%) genera and eight (21%)

237   families from three zoogeographic regions (Afrotropical, Neartic and Neotropical). *Allobates*, *Ameerega*,

238   *Dendropsophus*, *Boana* and *Kassina* (N= 4 species each; 12.5%) were the most frequently represented

239   genera displaying disruptive coloration. Dendrobatidae (N= 9 species; 28%) and Hylidae (N= 8 species;

240   25%) were the most frequently represented families displaying disruptive coloration.

241

242   **2. Immobility**

243   The behavior of remaining immobile during a predator's approach is a widespread antipredator

244   mechanism in anurans to avoid detection by a visually oriented predator. Anurans can detect the presence

245   of a predator through visual, acoustic or substrate vibration signals. Once the threat is detected, anurans

246   become immobile and may have heightened alertness and prepare to jump away (Fig. 5a), flatten

247   themselves against the ground to use the cryptic dorsal coloration (Fig. 5b), or remain still. Many species

248   that show morphological crypsis often move slowly or rest quietly for considerable portions of foraging

249   time (Caro 2014). This adaptation is possibly a precursor to other displays. Most predators attack only

250   moving prey and immobile prey do not fit that search image (Brodie Jr. 1977; Toledo et al. 1995). But if

251   the anuran is detected, immobility might reduce the likelihood of further predator attack or reduce the

252   intensity of attack (Nishiumi and Mori 2015, 2016). Additionally, immobility may cause less harm to the

253   anuran than would struggle within the predator's grip (Sazima 1974). Toledo et al. (2011) observed that a

254   predatory snake did not prey upon two immobile hylid species. Also a domestic cat did not detect an

255   immobile anuran (RLM pers. obs.).

256   Immobility was displayed by 159 (24%) species within 73 (41%) genera and 22 (56%) families of

257   anurans from all zoogeographic regions. *Rhinella*, *Boana* (N= 10 species each; 6%) and *Dendropsophus*

258   (N= 9 species; 6%) were the most frequently represented genera displaying immobility. Hylidae (N= 52

259   species; 33%) and Bufonidae (N= 24 species; 15%) were the most frequently represented families

260   displaying immobility. Immobility is symplesiomorphic in Anura (Fig. 2b).

261

262   **3. Interrupt calling**

263   The interruption of vocalization at predator approach aims to avoid giving predators a cue to anuran

264   location. Also, anurans in chorus can stop calling after emission of a distress or alarm call by a

265   conspecific (e.g., *Gastrotheca megacephala*, see Lourenço-de-Moraes et al. 2016).

266   The interruption of calling was displayed by 10 (2%) species within 10 (6%) genera and five

267   (13%) families of anurans from two zoogeographic regions (Nearctic and Neotropical). All genera were

268   represented by only one species. Hylidae (N= 5 species; 50%) was the most frequently represented family

269   displaying interruption of calling. Interruption of calling is homoplastic, having evolved independently in

270   Odontophrynidae, Hemiphractidae, Leptodactylidae and Hylidae (Fig. 2c).

271

272   **Defense phase: Preventing attack**

273   The antipredator mechanisms of this phase are responsible for warning predators to keep away and avoid

274   direct contact. In this phase, the anuran is within capture distance of the predator. This phase includes the

275   antipredator mechanisms: aposematism, charge, posture, escape, and warning sound (described below).

276

277   **4. Aposematism**

278   The display of bright coloration (often bright red, blue, orange, yellow), hypertrophied glands, and eye-

279   shaped spots on the dorsum, axila, underside of the body, thighs or post-femoral region serve as deceptive

280   signals to disorientate and confuse an attacking predator and/or warn predators of the presence of toxins

281   or unpalatability. Aposematism varies in the color (type and intensity), shape (spot, blotch, ring), and

282   body region. To be conspicuous, aposematism requires that the color patterns of prey species contrast

283   with the prevailing background coloration (Siddiqi et al. 2004). Aposematic signals are beneficial for both

284   the predator and prey, both of which avoid potential harm. It works for visually oriented predators, in

285   which birds are assumed to be the main selective agent favoring evolution of aposematic patterns (Wells

286   2007). Aposematism may also be for intraspecific communication. Aposematism is plesiomorphic in

287   Anura with many apomorphies across families (Fig. 2d).

288

289   4a. Exposed aposematism occur in species that have aposematic color over the entire body (e.g.,

290   *Atelopus*, *Brachycephalus* and *Mantella* species) (Fig. 6a). Exposed aposematism was displayed by 37

291   (6%) species within 14 (8%) genera and eight (21%) families of anurans from four zoogeographic regions

292   (Afrotropical, Australian, Neotropical and Oriental). *Brachycephalus* (N= 13 species; 35%), *Oophaga*

293   and *Ranitomeya* (N= 4 species each; 11%) were the most frequently represented genera displaying

294   exposed aposematism. Dendrobatidae (N= 16 species; 43%) and Brachycephalidae (N= 13 species; 35%)

295   were the most frequently represented families displaying exposed aposematism.

296

297   4b. Hidden aposematism occur in species that have aposematic color at the axila, underside of

298   the body, tongue, thighs or post-femoral region. These species usually exhibit the hidden aposematic or

299   deceptive coloration through escape or postures such as rear elevation, unken reflex, and death feigning.

300   For example, a leptodactylid (*Edalorhina perezi*) and a miobatrachid (*Uperoleia lithomoda*) may show a

301   pair of eyespots by lifting their hindparts (Fig. 6b, c). These species have large poison glands below the

302   eyespots. Phyllomedusids (e.g., *Phyllomedusa rohdei* and *P. burmeisteri*) show bright coloration on the

303   thighs when walking on tree branches (Fig. 6d). The hyperoliid *Acanthixalus spinosus* shows bright

304   yellow tongue when displaying death feigning (Perret 1961).

305   Hidden aposematism was displayed by 244 (38%) species within 92 (51%) genera and 25 (64%)

306   families of anurans from all zoogeographic regions. *Melanophryniscus* (N= 20 species; 8%), *Boana* (N=

307   17 species; 7%) and *Phyllomedusa* (N= 11 species; 5%) were the most frequently represented genera

308   displaying hidden aposematism. Hylidae (N= 56 species; 23%), Bufonidae (N= 35 species; 14%) and

309   Leptodactylidae (N= 26 species; 11%) were the most frequently represented families displaying hidden

310   aposematism.

311

312   **5. Charge**

313   This mechanism is characterized by the anuran moving, mostly by jumping, toward the predator. The

314   anuran's apparent threat may intimidate the predator (see Nishiumi and Mori 2015). Charge may precede

11

315 biting or head butting the predator. Some leptodactylids (e.g., *Leptodactylus labyrinthicus* and *L. latrans*)

316 charge the predator, but if the predator faces off, the anuran may jump away. Only large-body species (>

317 7 cm) have been seen charging the predator (Toledo et al. 2011). Charging is often associated with biting

318 and a defensive scream (i.e., warning sound).

319   Charge was displayed by eight (1%) species within six (3%) genera and five (13%) families of

320 anurans from the Neotropical region. *Boana* and *Ceratophrys* (N= 2 species each; 25%) were the most

321 frequently represented genera displaying charge. Hylidae (N= 3 species; 38%) and Ceratophryidae (N= 2

322 species; 25%) were the most frequently represented families displaying charge. Charge is homoplastic,

323 emerging independently in Calyptocephalidae, Ceratophryidae, Odontophrynidae, Hemiphractidae and

324 Hylidae (Fig. 2e).

325

326 **6. Posture**

327   A variety of postures is intended to intimidate predators by changing the anuran's body shape.

328 Posture is symplesiomorphic in Anura (Fig. 2f).

329

330   6a. Body elevation is the extension of anterior or all limbs, lifting the anuran's body off the

331 ground. Body elevation is a deceptive mechanism because it increases the anuran's apparent size and

332 threat (Williams et al. 2000). It may be displayed by extension of front limbs (partial elevation, Fig. 7a) or

333 all limbs (full elevation, Fig. 7b). It is often displayed in synergy with vocalizing and/or biting. Some

334 species may do "push-ups" moving the body up and down (RBF et al. pers. obs.).

335 Body elevation was displayed by 54 (8%) species within 36 (20%) genera and 21 (54%) families of

336 anurans from all zoogeographic regions. *Leptodactylus* and *Uperoleia* (N= 4 species each; 7%) were the

337 most frequently represented genera displaying body elevation. Bufonidae (N= 9 species; 17%),

338 Microhylidae (N= 8 species; 15%) and Leptodactylidae (N= 7 species; 13%) were the most frequently

339 represented families displaying body elevation.

340

341   6b. Body inflation is characterized by the anuran inflating itself (Fig. 8a, b). Several terms have

342 been used to designate this behavior, such as lung inflation, inflation of the body, and puffing-up the body

343 (see Wells 2007; Toledo et al. 2011; Ferrante et al. 2014). All these behaviors are synonymous and

344   consist of filling the lungs with air. This deceptive posture makes gripping prey more difficult, it may fool

345   the predator into deciding that the prey is too large to handle and ingest, or both (Caro 2014). Because the

346   anuran displaying body inflation becomes larger, it is very likely that this behavior intimidates the

347   predator.

348   This behavior may be displayed in many substrates such as on vegetation, on the ground, and

349   floating in the water (Toledo et al. 2011). In one reported observation, body inflation was successful at

350   preventing predation of a *Rhinella marina* floating on the water (Blair 1947). This author reported that a

351   *Kinosternum* sp. (freshwater turtle) gave up predation attempts on *Rhinella marina* when its lungs were

352   inflated. Some species inside cavities (e.g., burrows, bromeliads, crevices) may also inflate the body to

353   avoid being extracted (Toledo et al. 2011; Ferreira et al. 2015).

354   Body inflation was displayed by 216 (33%) species within 95 (53%) genera and 30 (77%)

355   families of anurans from all zoogeographic regions. *Rhinella* (N= 16 species; 7%) and *Leptodactylus* (N=

356   12 species; 6%) were the most frequently represented genera displaying body inflation. Hylidae (N= 43

357   species; 20%), Bufonidae (N= 30 species; 14%) and Leptodactylidae (N= 23 species; 11%) were the most

358   frequently represented families displaying body inflation.

359

360   6c. Contraction is the contraction of the four limbs, arching of the body and is usually associated

361   with the head ventrally flexed. The anuran may have either the dorsum (Fig. 9a) or the venter (Fig. 9b)

362   pointing to the substrate. The eyes can remain either opened or closed. This behavior may be displayed

363   during the approach of a potential predator, or immediately after the potential predator touches the anuran

364   or even after the subjugation phase (Sazima 1974; Toledo et al. 2011). Contracting displays likely aim to

365   facilitate the release of skin secretions, cause prey to be difficult to swallow, or create the resemblance of

366   a dead organism. While contracting, most species remain motionless, protecting vital areas of the body

367   and, consequently, avoid more serious wounds (Sazima 1974).

368   During contracting, most species release some sort of repellant skin secretion (i.e., adhesive,

369   odoriferous and noxious). Toledo et al. (2011) mentioned that 20 out of 25 species (80%) were toxic

370   during their tests on anurans displaying contracting. Some species while contracting have been partially

371   swallowed by snakes but were regurgitated after some time (Sazima 1974; Brodie Jr. and Tumbarello

372   1978; Toledo et al. 2011). Choi et al. (1999) experimentally demonstrated that the "crouch" of the ranid

373 (*Rana rugosa*) decreased the likelihood of being preyed upon by a snake, possibly due to the release of

374 skin secretion. Some species displaying contracting may show aposematic coloration on the hidden

375 regions or on the tongue (Toledo et al. 2011). Some anurans on contracting also pull the chin toward the

376 pectoral region (called chin-tucking, Toledo et al. 2011).

377 Contraction was displayed by 149 (23%) species within 63 (35%) genera and 20 (51%) families

378 of anurans from five zoogeographic regions (Afrotropical, Australian, Neartic, Neotropical and Oriental).

379 *Boana* (N= 17 species; 11%) and *Bufonidae* (N= 10 species; 7%) were the most frequently represented

380 genera displaying contraction. Hylidae (N= 48 species; 32%) and Bufonidae (N= 25 species; 17%) were

381 the most frequently represented families displaying contraction.

382

383 6d. Gland exposure is the behavior of directing the glands toward the predator. It is a common

384 display in species of Bufonidae and Odontophrynidae (Fig. 10a). Some bromeliad-dwelling anurans for

385 instance, *Aparasphenodon brunoi* (Fig. 10b) and *Corythomantis greening*, display the co-ossified head

386 covered by noxious glands while blocking the bromeliad cup after disturbance by a predator inside a

387 bromeliad (Jared et al. 2005; Mailho-Fontana et al. 2014). Some authors have referred to gland exposure

388 as body tilting (Toledo et al. 2011) or phragmosis (Jared et al. 2005).

389 Gland exposure was displayed by 55 (8%) species within 25 (14%) genera and 11 (28%) families

390 of anurans from five zoogeographic regions (Afrotropical, Australian, Neartic, Neotropical and

391 Palaeartic). *Rhinella* (N= 11 species; 20%) and *Anaxyrus* (N= 5 species; 9%) were the most frequently

392 represented genera displaying gland exposure. Bufonidae (N= 20 species; 36%), Hylidae and

393 Odontophrynidae (N= 7 species each; 13%) were the most frequently represented families displaying

394 gland exposure.

395

396 6e. Limb interweave is the erratic movement of fore or hind limbs (Fig. 11a, b). It seems this

397 antipredator mechanism aims to show aposematic coloration, facilitate the spread of skin secretion or

398 feign injury. Also, the anuran may twist onto its back, throwing its limb across the body.

399 *Leptodactylus chaquensis* secreted a greenish, adhesive and odoriferous skin substance while

400 displaying limb interweaving (Lourenço-de-Moraes et al. 2014a). The African anuran *Phlyctimantis*

401 *keithae* displays a peculiar kind of limb interweaving by twisting onto its back, throwing its limbs across

14

402   its body and showing the dark purple with bright orange patches on the thighs (Channing and Howell

403   2003).

404   Limb interweave was displayed by six (1%) species within six (3%) genera and five (13%)

405   families of anurans from four zoogeographic regions (Afrotropical, Neartic, Neotropical and Palaeartic).

406   All genera were represented by only one species. Hylidae (N= 2 species; 33%) was the most frequently

407   represented family displaying limbs interweave.

408

409   6f. Mouth gape is the opening of anuran's mouth toward the predator (Fig. 12a, b). It may be

410   displayed once or continuously by a prey. This behavior may be interpreted as a warning signal to the

411   would-be predator and an attempt to intimate and avoid predation.

412   Mouth gaping may be displayed while the anuran has elevated its body and it is often associated

413   with defensive vocalization and biting (Toledo et al. 2011; Lourenço-de-Moraes et al. 2016; Figueiredo et

414   al. 2017). However, other species displaying mouth gaping did not emit defensive vocalization nor bite,

415   for example *Cycloramphus acangatan* and *Adelophryne glandulata* (Lourenço-de-Moraes et al. 2012,

416   2014b). Some species have contrasting colors of the mouth lining, tongue and/or lower jaws in

417   comparison to their body, which may be an aposematic display and influence predation avoidance

418   (Duellman and Trueb 1994; Wells 2007). Miniature species (e.g., *Brachycephalus* spp, *Adelophryne* spp,

419   *Pseudopalodicola* spp.) may use this mechanism to confuse predatory invertebrates, such as arachnids

420   (e.g., Lourenço-de-Moraes and Pertel 2011).

421   Mouth gape was displayed by 60 (9%) species within 31 (17%) genera and 16 (41%) families of

422   anurans from five zoogeographic regions (Afrotropical, Australian, Neartic, Neotropical and Oriental).

423   *Boana* (N= 8 species; 13%) and *Leptodactylus* (N= 5 species; 8%) were the most frequently represented

424   genera displaying mouth gape. Hylidae (N= 17 species; 28%), Hemiphractidae (N= 7 species; 12%) and

425   Leptodactylidae (N= 6 species; 10%) were the most frequently represented families displaying mouth

426   gape.

427

428   6g. Rear elevation is the elevation of the posterior hind parts by leg extension. The degree of leg

429   extension varies from low intensity (partially stretched, Fig. 13a) to high intensity (totally stretched, Fig.

430   13b). Another variation involves the position of the posterior limbs. During rear elevation, anurans may

15

431   display aposematism by showing bright colorations, hypertrophied glands, eye-shaped spots on the axila,

432   groin, underside of the body, thighs or post-femoral region (Sazima and Caramaschi 1986; Toledo and

433   Jared 1995). For example, *Physalaemus* anurans have eyespot-like toxic glands on their lateral skin and

434   elevate the body to display it when alarmed (Lenzi-Mattos et al. 2005; Fig. 13a). Some species have

435   neither aposematic coloration nor odoriferous skin secretion.

436   Rear elevation was displayed by 71 (11%) species within 41 (23%) genera and 18 (46%) families

437   of anurans from all zoogeographic regions. *Ranoidea* (N= 9 species; 13%). *Uperoleia* (N= 8 species;

438   11%) and *Limnodynastes* (N= 4 species; 6%) were the most frequently represented genera displaying rear

439   elevation. Myobatrachidae (N= 13 species; 18%), Pelodryadidae and Microhylidae (N= 10 species; 14%)

440   were the most frequently represented families displaying rear elevation.

441

442   6h. Stretching limbs is the full extension of the fore or hind limbs (Fig. 14a, b). The limb

443   extension may be full or partial. It presumably aims to create a resemblance to a dead leaf or makes it

444   difficult to be swallowed. Anurans display this posture after being touched by the predator. Stretching

445   limbs posture is displayed by species of different clades, but this behavior is only known in leaf-litter

446   anurans (Mângia and Santana 2013). It seems effective in avoiding detection by avian predators that

447   forage on leaf litter (Sazima 1978).

448   Stretching limbs was displayed by 39 (6%) species within 26 (14%) genera and seven (18%)

449   families of anurans from four zoogeographic regions (Afrotropical, Neartic, Neotropical and Oriental).

450   *Proceratophrys* (N= 7 species; 18%), *Dendrophryniscus* and *Rhinella* (N= 3 species; 8%) were the most

451   frequently represented genera displaying stretching limbs. Microhylidae (N= 11 species; 28%),

452   Odontophrynidae (N= 9 species; 23%) and Bufonidae (N= 7 species; 18%) were the most frequently

453   represented families displaying stretching limbs.

454

455   6i. Death feigning is when the fore and hind limbs are loose, and usually the dorsum is on the

456   substrate (Fig. 15a, b). It is probably a mechanism to resemble a dead organism. Death feigning is also a

457   strategy used by some species to show bright coloration on the exposed venter or members, which serve

458   as an aposematic cue to predators (Brodie 1977). Death feigning is often displayed after the anuran has

459   jumped away from the observer or was handled by the observer (Toledo et al. 2011). In general,

460   individuals can remain immobile with the venter up for up to five minutes, and then actively flip to the

461   normal position (i.e., dorsum up) and jump away. Death feigning is often used in synergy with

462   odoriferous secretions that resemble a plant-like odor.

463   In cases of disturbance, some species may get flipped by the predator with the venter up to

464   further increase the resemblance of a dead organism (Duellman and Trueb 1994; Toledo et al. 2011).

465   *Acanthixalus spinosus*, *Odontophrynus americanus* and *O. lavillai* have been reported sticking the tongue

466   out of the mouth (i.e., tongue-protrusion) while displaying death feigning (Perret 1961; Borteiro et al.

467   2018). Some species may actively flip onto the back and remain immobile in death feigning (i.e.,

468   flipping-onto the back; Toledo et al. 2011).

469   Death feigning was displayed by 203 (31%) species within 79 (44%) genera and 25 (64%)

470   families of anurans from all zoogeographic regions. *Leptodactylus* (N= 14 species; 7%), followed by

471   *Dendropsophus* and *Boana* (N= 11 species each; 5%) were the most frequently represented genera

472   displaying death feigning. Hylidae (N= 53 species; 26%), Leptodactylidae (N= 37 species; 18%) and

473   Bufonidae (N= 27 species; 13%) were the most frequently represented families displaying death feigning.

474

475   6j. Unken reflex is characterized by the body convexly arched and palms lifted and twisted off

476   the substrate. This posture usually exhibits bright coloration on the ventral or palm regions. An anuran in

477   unken reflex may be difficult for a predator to swallow. The bright coloration and distinctive posture

478   displaying the ventral coloration are cues that are associated with noxiousness by predators (Duellman

479   and Trueb 1994).

480   Unken reflex seems more displayed by species that have concentrations of granular glands

481   widely distributed on the body and bright coloration on the ventral surfaces. Some species may show only

482   the venter portion of the limbs, called partial unken reflex (e.g., *Dendrophryniscus boulengeri*, Fig. 16a)

483   (*Proceratophrys avelinoi*, Lourenço-de-Moraes and Lourenço-de-Moraes 2012; *Zachaenus carvalhoi*,

484   Zocca et al. 2014). Species with aposematic venters may show the palms of all limbs (i.e., full unken

485   reflex; e.g., *Bombina variegata*, Fig. 16b). Also, some species do not present conspicuous coloration (e.g.,

486   *Smilisca fodiens*, Firschein 1951) (juveniles of *Bombina* spp., Löhner 1919). *Leptobrachium smithi* may

487   elevate the head about 90° from the ground (i.e., head-up sharp bend, Toledo et al. 2011), which functions

488   like the unken reflex.

489   Unken reflex was displayed by 41 (6%) species within 22 (12%) genera and 14 (36%) families

490   of anurans from all zoogeographic regions. *Melanophryniscus* (N= 14 species; 34%), *Bombina* (N= 4

491   species; 10%) and *Rana* (N= 3 species; 7%) were the most frequently represented genera displaying

492   unken reflex. Bufonidae (N= 15 species; 37%) and Hylidae (N= 5 species; 12%) were the most frequently

493   represented families displaying unken reflex.

494

495   **7. Escape**

496   Escape includes behaviors displayed upon detection and approach of the predator to avoid further

497   approach or direct contact. Escape depends on the locomotor capabilities of the species.

498   Escape is symplesiomorphic in Anura (Fig. 2g).

499

500   7a. Climb is mostly displayed by arboreal species that climb higher to escape from predators that

501   are coming from below.

502   Climb was displayed by 10 (2%) species within six (3%) genera and two (5%) families of

503   anurans from two zoogeographic regions (Neartic and Neotropical). *Dryophytes* (N= 3 species; 30%),

504   *Pseudacris* and *Trachycephalus* (N= 2 species each; 20%) were the most frequently represented genera

505   displaying climb. Hylidae (N= 9 species; 90%) and Bufonidae (N= 1 species; 10%) were the most

506   frequently represented families displaying climb.

507

508   7b. Glide consists of an anuran jumping from a vertical substrate and gliding until reaching

509   another substrate. In addition to escape from predation, gliding is also used for anurans to descend to

510   reproductive sites (McCay 2001). Gliding anurans (e.g., *Rhacophorus dennysi* and *R. nigropalmatus*)

511   (Fig. 17a) have some morphological features such as enlarged, extensively webbed hands and feet or skin

512   flaps on elbows and ankles (Emerson and Koehl 1990; McCay 2001).

513   Glide was displayed by three (0.5%) species within one (1%) genera and one (3%) family of

514   anurans from the Oriental zoogeographic region. *Rhacophorus* (Rhacophoridae; N= 3 species; 100%) was

515   the only genera displaying glide.

516

517   7c. Hide is to move out of sight of a predator. Anurans from sandy or leaf-litter environments

518   may dig down into the substrate to hide. Burrowing anurans look for refugia in crevices. Bromeligenous

519   anurans retreat down the bromeliad leaf and hide in the base of the axils (e.g., Ferreira et al. 2015).

520   Hide was displayed by 61 (9%) species within 38 (21%) genera and 17 (44%) families of

521   anurans from five zoogeographic regions (Afrotropical, Australian, Neartic, Neotropical and Oriental).

522   *Dendropsophus* (N= 5 species; 8%), *Anaxyrus* and *Ololygon* (N= 4 species each; 7%) were the most

523   frequently represented genera displaying hide. Hylidae (N= 21 species; 34%) was the most frequently

524   represented family displaying hide.

525

526   7d. Jump away is the saltatorial locomotion for escaping predators. This mechanism is especially

527   effective at increasing distance from predators that depend on chemosensory cues for trailing prey

528   (Duellman and Trueb 1994).

529   This escape behavior may involve any of several strategies depending on the species and its

530   environment. For example, some *Eleutherodactylidae* display a single, long leap and subsequent

531   immobility with the anuran relying on the camouflage to avoid subsequent discovery (i.e., evade). It

532   seems that there is a tendency for large species to display this behavior. Some small species (e.g.,

533   *Eleutherodactylus planirostris* and *Adelophryne glandulata*) display a series of quick, short, and

534   multidirecional hops and subsequent immobility (i.e., flee).

535   Jump away was displayed by 219 (34%) species within 88 (49%) genera and 25 (64%) families

536   of anurans from all zoogeographic regions. *Dendropsophus* (N= 15 species; 7%), *Boana* and

537   *Leptodactylus* (N= 10 species each; 5%) were the most frequently represented genera displaying jump

538   away. Hylidae (N= 72 species; 33%), Leptodactylidae (N= 23 species; 11%) and Bufonidae (N= 21

539   species; 10%) were the most frequently represented family-displaying jump away.

540

541   7e. Roll is the contraction of limbs and arching the body to roll down sloped terrain. It is also

542   called "balling" and "tumbling". It has been observed in few anuran species (e.g., *Oreophrynella nigra*,

543   *O. quelchii*, and *O. vasquezi*; Garcia-París and Deban 1995) (Fig. 17b).

544   Roll was displayed by three (0.5%) species within one (1%) genus and one (3%) family of

545   anurans from the Neotropical region. *Oreophrynella* (Bufonidae) was the only genus-displaying roll.

546

547   7f. Swim is displayed mostly by anurans adapted to bodies of water (i.e., river, streams or

548 ponds). Normally these anurans have webbed toes to aid in swimming and can remain under water for

549 minutes.

550   Swim was displayed by 22 (3%) species within 17 (9%) genera and 10 (26%) families of anurans

551 from five zoogeographic regions (Afrotropical, Australian, Neartic, Neotropical and Oriental). *Lithobates*

552 (N= 5 species; 23%) and *Anaxyrus* (N= 2 species; 9%) were the most frequently represented genera

553 displaying swim. Ranidae (N= 6 species; 27%) and Hylidae (N= 4 species; 18%) were the most

554 frequently represented family-displaying swim.

555

556 **8. Warning sound**

557 Warning sound is emitted by anurans to threaten predators before apprehension (Toledo et al. 2015) and

558 also after the touch of potential predator. It aims to warn sound-oriented predators (e.g., birds and

559 mammals) about any risk offered by would-be prey. Anurans can emit different types of warning sound

560 that may be related to the intensity of stress stimuli by predator (Lourenço-de-Moraes et al. 2016).

561 Warning sound can be emitted through the mouth or nostril. Warning sound has been observed in

562 *Gastrotheca megacephala* and *G. recava* (Lourenço-de-Moraes et al. 2016), *Rhinella crucifer* and *R.*

563 *diptycha* (RBF et al. pers. obs.).

564   Warning sound was displayed by 26 (4%) species within 16 (9%) genera and 14 (36%) families

565 from four zoogeographic regions (Afrotropical, Australian, Neartic and Neotropical). *Ranoidea* (N= 4

566 species; 15%), *Rhinella* and *Lithobates* (N= 3 species each; 12%) were the most frequently represented

567 genera displaying warning sound. Pelodryadidae (N= 4 species; 15%), Bufonidae and Ranidae (N= 3

568 species each; 12%) were the most frequently represented families displaying warning sound. Warning

569 sound is homoplastic in Anura (Fig. 2h).

570

571 **Defense phase: Counterattack**

572 This phase is characterized by antipredator mechanisms that are responses to apprehension by the

573 predator, and the prey tries to escape through physical contact or noise. This phase includes the

574 antipredator mechanism: cloacal discharge, secretion, aggression, and distress call (described below).

20

575

9. Cloacal discharge

577 This is the extrusion of liquid or solid content through the cloaca. Liquid is the most common cloacal

578 discharge. Most species (e.g., *Haddadus binotatus* and *Ischnocnema oea*) normally discharge cloacal

579 liquid after being approached or apprehended by a predator. Also, some species lift up the cloaca, point it

580 toward the collectors, and release liquid content (e.g., *Haddadus binotatus*). Solid discharge was reported

581 for *Anaxyrus terrestris* seized by a snake (Marchisin and Anderson 1978), and *Boana albopunctata*,

582 *Boana faber* and *Boana semilineata* (RBF et al. pers. obs.) after disturbance by collector's finger.

583 Cloacal discharge was displayed by 71 (11%) species within 33 (18%) genera and 15 (38%) families from

584 two zoogeographic regions (Neotropical and Oriental). *Rhinella, Boana* (N= 10 species each; 14%) and

585 *Leptodactylus* (N= 7 species; 10%) were the most frequently represented genera displaying cloacal

586 discharge. Hylidae (N= 28 species; 39%) and Bufonidae (N= 12 species; 17%) were the most frequently

587 represented families displaying cloacal discharge. Cloacal discharge arised independently in Anura with

588 extensive homoplasy (Fig. 2i).

589

10. Secretion

591 Most amphibians use secretory products of cutaneous glands (e.g., granular, mucous or poison glands) as

592 antipredator mechanisms (Brizzi and Corti 2007). The glands produce many different compounds, such as

593 amines, bioactive peptides, alkaloids, and their various combinations. The result is the synthesis of

594 adhesive, odoriferous, slippery and poisonous substances, with specific toxicities. Secretion is

595 symplesiomorphic in Anura (Fig. 2j).

596

597 10a. Adhesive is the production and release of skin secretion that has adhesive effect. It has been

598 reported as an effective mechanism to *Dyscophus antongili*, *Trachycephalus* spp. and *Hyophryne histrio*

599 by preventing predation because it may render the predator immobile and/or unable to feed (Evans and

600 Brodie 1994; Williams et al. 2000; Toledo et al. 2011). The adhesive secretion has been an effective

601 antipredator mechanism against small mammals and snakes. In an experiment, Evans and Brodie (1994)

602 showed that anurans able to produce adhesive secretions survived the trials with snakes.

603   Adhesive secretion was displayed by 23 (4%) species within 18 (10%) genera and seven (18%)

604   families from five zoogeographic regions (Afrotropical, Australian, Neartic, Neotropical and Oriental).

605   *Dendropsophus*, *Trachycephalus*, *Leptodactylus*, *Dyscophus* and *Notaden* (N= 2 species each; 9%) were

606   the most frequently represented genera displaying adhesive secretion. Microhylidae (N= 9 species; 39%)

607   and Hylidae (N= 8 species; 35%) were the most frequently represented families displaying adhesive

608   secretion.

609

610   10b. Odoriferous is characterized by the production and secretion of odor through the skin or

611   mouth. Some species produce floral, leaf-like, or ammonia odors possibly deceiving the predator that a

612   larger danger is present (Smith et al. 2004). Williams et al. (2000) speculated that if predators learn that

613   an unpalatable prey is associated with a certain odor, they may avoid prey with that odor in the future,

614   even if the odor itself is benign. It is recognized that some snakes assess the palatability of the prey prior

615   to attack (Shine 1993). In our observations, most odors were benign to observers, but some odors (e.g.,

616   released by *Itapotihyla langsdorffii* and *Leptodactylus labyrinthicus*) caused unpleasant effects, such as

617   nasal congestion and sneezing. Many anurans released odors in synergy with immobility and some

618   defensive postures (e.g., death feigning).

619   Odoriferous secretion was displayed by 102 (16%) species within 29 (16%) genera and 14 (36%)

620   families from five zoogeographic regions (Afrotropical, Australian, Neartic, Neotropical and Palaeartic).

621   *Bokermannohyla* (N= 17 species; 17%), *Aplastodiscus* (N= 13 species; 13%), *Dendropsophus* (N= 11

622   species; 11%), were the most frequently represented genera displaying odoriferous secretion. Hylidae (N=

623   63 species; 62%) and Pelodryadidae (N= 12 species; 12%) were the most frequently represented families

624   displaying odoriferous secretion.

625

626   10c. Slippery is the production and release of slippery secretions through skin glands. It has been

627   successful against tactile predators because they reduce the likelihood of being seized (Toledo et al.

628   2011). Slippery secretions generally are produced by aquatic or semi-aquatic anurans (e.g., *Leptodactylus*

629   and *Lithobates*) (Toledo et al. 2011).

630   Slippery secretion was displayed by 36 (6%) species within 15 (8%) genera and eight (21%)

631   families from three zoogeographic regions (Afrotropical, Australian and Neotropical). *Litoria* (N= 8

632 species; 22%), *Ranoidea* (N= 7 species; 19%) and *Boana* (N= 5 species; 14%) were the most frequently

633 represented genera displaying slippery secretion. Pelodryadidae (N= 15 species; 42%) and Hylidae (N=

634 13 species; 36%) were the most frequently represented families displaying slippery secretion.

635

636   10d. Poisonous is the liberation of toxic substances through the skin. The secretion can be either

637 passively or actively released (see Mailho-Fontana et al. 2014). Most species passively release secretions

638 after being apprehended by a predator. Some species (e.g., *Corythomantis greeningi* and *Aparasphenodon*

639 *brunoi*) have active release mechanisms through bony spines on the skull that pierce the skin in areas with

640 concentrations of skin glands (Jared et al. 2015). Poisonous skin secretion is the main antipredatory

641 strategy of anurans to avoid predation (Jared et al. 2015).

642   Skin secretion acts simultaneously with other antipredator mechanisms such as defensive

643 postures and aposematic color patterns. Toledo et al. (2011) reported that 80% of the species displaying

644 "contracting" also released skin secretions. Lourenço-de-Moraes et al. (2014a) reported *Leptodactylus*

645 *chaquensis* displaying death feigning in synergy with noxious secretions. Many species displaying "body

646 elevation" have aposematic colors warning the predator about its toxicity.

647   Poisonous secretion was displayed by 198 (30%) species within 74 (41%) genera and 25 (64%)

648 families from all zoogeographic regions. *Rhinella* (N= 19 species; 10%), *Brachycephalus* (N= 13 species;

649 7%), *Melanophryniscus* and *Leptodactylus* (N= 11 species each; 6%) were the most frequently

650 represented genera displaying poisonous secretion. Bufonidae (N= 63 species; 32%), Dendrobatidae (N=

651 23 species; 12%) and Phyllomedusidae (N= 18 species; 9%) were the most frequently represented

652 families displaying poisonous secretion.

653

654 **11. Aggression**

655 Aggression is the use of morphological or behavioral adaptations to interact directly with predators.

656 Aggression involves attempts to injure or hurt the predator to get released after being apprehended.

657 Agression is symplesiomorphic, but was not recorded in families such as Bombinatoridae and

658 Leiopelmatidae (Fig. 2k).

659

660   11a. Bite is biting the predator. It is displayed mostly by species of wide mouth and large body

661   (Fig. 18a). It is suggested that this behavior is related to diet (i.e., consumption of vertebrates) and

662   parental care (i.e., defense of progeny) (Lourenço-de-Moraes et al. 2016; Figueiredo et al. 2017).

663   Bite was displayed by 30 (5%) species within 16 (9%) genera and 12 (31%) families from four

664   zoogeographic regions (Afrotropical, Australian, Neotropical and Oriental). *Cycloramphus* (N= 5 species;

665   17%), *Ceratophrys* and *Leptodactylus* (N= 4 species each; 13%) were the most frequently represented

666   genera displaying bite. Hemiphractidae (N= 6 species; 20%), Ceratophryidae and Cycloramphidae (N= 5

667   species each; 17%) were the most frequently represented families displaying bite.

668

669   11b. Headbutt is the hitting of the head on the predator. It occurs mostly in species that exhibit

670   parental care such as some leptodactylids (Toledo et al. 2011). Some species walk or jump toward the

671   predator and if reached, the predator may either be bitten or butted by the anuran's head. Headbutt is a

672   common behavior in most bufonids where the parotoid glands are butted into an attacking predator.

673   Headbutt was displayed by 10 (2%) species within eight (4%) genera and six (15%) families

674   from three zoogeographic regions (Afrotropical, Neotropical and Oriental). *Leptodactylus* (N= 3 species;

675   30%) was the most frequently represented genera displaying headbutt. Hylidae and Leptodactylidae (N=

676   3 species each; 30%) were the most frequently represented families displaying headbutt.

677

678   11c. Kick is the act of using the limbs to kick or slap the predator. This behavior is very common

679   and generally displayed in the counterattack phase. The captured anuran pushes the predator's face or

680   hands, sometimes with vigorous kicks (e.g., *Myersiella microps*, Mônico et al. 2016).

681   Kick was displayed by 54 (8%) species within 30 (17%) genera and 13 (33%) families from four

682   zoogeographic regions (Nearctic, Neotropical, Oriental and Palaearctic). *Ololygon* (N= 7 species; 13%),

683   *Boana* and *Dendropsophus* (N= 5 species each; 9%) were the most frequently represented genera

684   displaying kick. Hylidae (N= 26 species; 48%), Bufonidae (N= 6 species; 11%) and Leptodactylidae (N=

685   5 species; 9%) were the most frequently represented families displaying kick.

686

687   11d. Puncture is the presence and use of spines on prepollex or phalanx that may puncture,

688   scratch, or inject venom and, consequently, injure the predator (Fig. 18b). A peculiar structure is reported

689 for some genera of African arthroleptids such as *Astylosternus*, *Scotobleps* and *Trichobatrachus*, which

690 have erectile-bony claws that protrude through the skin on the ventral side (Blackburn et al. 2008). When

691 males or females are grabbed, these anurans kick their legs and rake claws against one's skin (Boulenger

692 1902). It is hypothesized that phalanx and prepollex have evolved primarily for reproduction purposes,

693 such as grasping the female during amplexus and intraspecific male-male interaction (Wells 2007).

694   Puncture was displayed by 17 (3%) species within eight (4%) genera and four (10%) families

695 from three zoogeographic regions (Afrotropical, Neotropical and Oriental). *Boana* (N= 5 species; 29%),

696 *Bokermannohyla* (N= 4 species; 24%) and *Leptodactylus* (N= 3 species; 18%) were the most frequently

697 represented genera displaying puncture. Hylidae (N= 11 species; 65%) and Leptodactylidae (N= 4

698 species; 24%) were the most frequently represented families displaying puncture.

699

700 **12. Distress call**

701 Distress call is the emission of a vocalization during subjugation by predator (Toledo et al. 2015). It is

702 intended to avoid predation by scaring the predator, and also to attract other potential predators (Brodie

703 and Formanowicz 1981; Toledo et al. 2015).

704   Distress calls may be emitted during expiration, when disinflation of the lungs may produce a

705 noise (Toledo et al. 2011). When handled by observer, distress calls were emitted by many species during

706 our observations.

707   Distress call was displayed by 99 (15%) species within 38 (21%) genera and 17 (44%) families

708 from five zoogeographic regions (Afrotropical, Australian, Neartic, Neotropical and Oriental). *Boana* (N=

709 17 species; 17%), *Leptodactylus* (N= 13 species; 13%) and *Ranoidea* (N= 7 species; 7%) were the most

710 frequently represented genera displaying distress call. Hylidae (N= 36 species; 36%), Leptodactylidae

711 (N= 15 species; 15%) and Pelodryadidae (N= 12 species; 12%) were the most frequently represented

712 families displaying distress call. It is homoplastic in Anura, arising independently (Fig. 2l).

713

714

715 **Characterization of post-metamorphic antipredator mechanisms**

716

717 Regarding the phases of antipredator mechanisms, 620 (95%) species exhibited "avoid detection", 585

718 (90%) species exhibited "prevent attack", and 404 (62%) species exhibited "counterattack". Individuals

719 of 466 (72%) species displayed "posture" and 305 (47%) species released "secretion". The mechanisms

720 "interrupt calling" (N= 10 species; 2%) and "charge" (N= 8 species; 1%) were the rarest displayed.

721 Regarding "postures", the variations "body inflation" (N= 216 species; 33%) and "death feigning" (N=

722 203 species; 31%) were the most displayed. The postures "limbs interweave" (N= 6 species; 1%) was the

723 rarest displayed. Regarding "secretion", "poisonous" substance was the most produced (N= 198 species;

724 30%), followed by "odoriferous" (N= 102 species; 16%), "slippery" (N= 36 species; 6%), and "adhesive"

725 (N= 23 species; 4%) substances.

726   Regarding species, *Boana faber*, *Odontophrynus americanus* and *Leptodactylus latrans*

727 displayed the highest mean number of antipredator mechanisms (N= 10; N= 10; N= 8, respectively) and

728 many antipredator variations (N= 16; N= 10; N= 13, respectively). Regarding genera, *Myersiella* (mean=

729 9) and *Haddadus* (mean= 8) had the highest mean number of antipredator mechanisms. Regarding

730 families, Calyptocephalellidae (mean= 6), Leiopelmatidae (mean= 5) and Dicroglossidae (mean= 5)

731 displayed the highest mean number of antipredator mechanisms.

732

733

734 **Discussion**

735

736 Our freely available global database provides a unique resource to facilitate the investigation of

737 ecological and evolutionary questions regarding antipredator mechanisms in anuran, especially if

738 combined with quantitative measurements of morphological and ecological traits. The remarkable work

739 done by some researchers in the previous decades (e.g., C. Jared, C. Haddad, L.F. Toledo and

740 collaborators) may explain the increase in the number of publications on antipredator mechanisms of

741 anurans through time. Toledo et al. (2011) compiled their observations of anti-predatory mechanisms, and

742 this probably influenced the substantial increase in the number of publications on this topic. Another

743 explanation for the increase in published anuran antipredator mechanisms may be related to the

744 emergence of journals specialized in natural history observations (e.g., Herpetology Notes and

745 Herpetological Review).

746   A potential problem with categorizing antipredator mechanisms is any two human observers will

747   weigh parameters differently in their pattern recognition and thus come up with different categories. By

748   using several observers, this potential problem may be reduced and a measure of observer agreement

749   obtained. Because our level of agreement was high, this argues that disagreement among observers is not

750   inherently a huge issue, and one can assume that our classification system is reproducible by others.

751   Nevertheless, we may have missed some small parameter differences that might be relevant to the

752   animals, for example, those caused by our limited sense of smell. Consequently, while this classification

753   system provides a useful starting point for further discussion, the various mechanisms should not be

754   viewed as clearly differentiated grades of evolution or the final word on the diversity of defensive

755   behavior in anurans.

756   It is noteworthy that the three species that displayed the highest number of mechanisms (i.e., *B.*

757   *faber*, *L. latrans*, and *O. americanus*) have wide geographic distribution. This may suggest that

758   antipredator mechanisms are favored by selection. The various antipredator mechanisms displayed by

759   these frogs appear to interact and total protection may be greater than the sum of each of the behaviors

760   alone. It has been hypothesized in other taxa that the display of simultaneous mechanisms may be more

761   effective in transmitting signals to predators (Williams et al. 2000). This hypothesis remains to be tested

762   in anurans. In salamanders, the interaction of toxic skin secretions, aposematic coloration and postures is

763   important in predator avoidance (Johnson and Brodie 1975). It seems that an individual can switch

764   between mechanisms depending on the threat. For instance, we observed *Gastrotheca megacephala* and

765   *G. recava* emplying escalating antipredator mechanisms according to the degree of stress imposed by the

766   potential predator (see Lourenço-de-Moraes et al. 2016). Predation involves several phases such as locate,

767   identify, approach, subjugate, ingest, and digest prey (Mailho-Fontana et al. 2014). Therefore, the more

768   types of antipredator mechanisms a species can display, the more likely this species is to escape

769   predators.

770   Species that have many antipredator mechanisms may choose to display them simultaneously.

771   For instance, most mechanisms displayed by two species of *Gastrotheca* were displayed simultaneously

772   (Lourenço-de-Moraes et al. 2016). *Gastrotheca recava* displayed warning call simultaneously with body

773   inflation and mouth gaping (Lourenço-de-Moraes et al. 2016). It is noteworthy that the release of skin

774 secretion and display of hidden aposematic colors is commonly associated with defensive postures such

775 as body raising, contracting, and leg interweaving (Brodie et al. 1998; Lourenço-de-Moraes et al. 2014a).

776 The reconstruction of the ancestral states of the antipredator mechanisms in the phylogenetic tree

777 showed that most mechanisms are plesiomorphic in Anura. It is likely that the plesiomorphic mechanisms

778 originated from the common ancestors of anurans and other amphibians (i.e., salamanders and caecilians).

779 For example, many salamanders display camouflage, immobility, posture, escape and secretion. Many

780 antipredator mechanisms arose independently across families suggesting extensive homoplasy in Anura.

781 However, some of the apparently homoplastic antipredator mechanisms may be a consequence of the lack

782 of observations on species displaying them. For example, distress call, warning sound and interrupting

783 call are rarely reported in the literature and may be more widespread in anurans.

784 The remarkable convergent evolution in aposematic color pattern across species suggests

785 mimicry is a common protective strategy in anurans. However, the lack of studies on the potential toxicity

786 (or other defense) of most apparent mimic species prevents further generalization about mimicry in

787 anurans. The few studied cases of Batesian mimicry in anurans show that mimics successfully deceive

788 predators (Darst et al. 2006). For instance, in a Batesian mimicry system the non-toxic *Allobates* species

789 successfully avoided predation by imitating the toxic *Epipedobates* species (Darst et al. 2006). In

790 Dendrobatids the aposematism is a complex trait, which integrates evolution in diet (to which the

791 defensive alkaloid is sequestered), physiology, morphology and behavior (see Santos and Cannatella

792 2011). Williams et al. (2000) showed that non-toxic *Crinia* species expose aposematic ventral coloration

793 to possibly mimic the toxic *Pseudophryne*. Müllerian mimicry in anurans has been documented in

794 congeners of *Ranitomeya*, *Mantella*, and *Phyllobates* (Toledo and Haddad 2009a). But it is not simple to

795 distinguish real, nondeceitful homotypy from a possible phylogenetic influence because some closely

796 related species may resemble one another due to a symplesiomorphic (i.e., sharing of an ancestral

797 character, secretion) and not because of coloration convergence (homoplasy, aposematism).

798 The classification of antipredator mechanisms depicted in the present study should not be

799 considered an immutable scheme but actually an evolving set of descriptions. We hope to spark renewed

800 interest in antipredator mechanisms of post-metamorphic anurans to understand further the extent to

801 which they are deployed by a given prey species must depend on the background on which it lives, the

802   relation of prey morphology and defenses, the visual capabilities and behavior of the predator, its relative

803   size compared to its predators, and even the defenses of sympatric prey species.

804

805

806   **Compliance with ethical standards**

807

818

819   **Ethical approval**

820   All applicable international, national, and/or institutional guidelines for the care and use of animals were

821   followed. All procedures performed in studies involving animals were in accordance with the ethical

822   standards of the institution or practice at which the studies were conducted (Institutional Animal Care and

823   Use Committee from Utah State University, permit 2002 and from Universidade Vila Velha, permit 355-

824   2015). Sampling permits were issued by Sistema de Autorização e Informação em Biodiversidade

825   (SISBIO, 28607-3; 50402; 30344; 44755; 63575).

826

827   **Conflict of interest**

828   The authors declare that they have no conflict of interest.

829

830

831   **References**

832

833   Altmann J (1974) Observational study of behavior: sampling methods. Behav 49:227–267

834   Barrett AK, Seeley TD (2015) The declining use of animal and behaviour images in animal behavior

835   Journals. Anim Behav 103:171–177

836   Blackburn DC, Hanken J, Jenkins Jr (2008) Concealed weapons: erectile claws in African frogs. Biol Lett

837   4:355–357

838   Blair AP (1947) Defensive use of parotoid secretion by *Bufo marinus*. Copeia 1947:137

839   Borteiro C, Rosset SD, Kolenc F, Barrasso DA, Lescano, JN, Baldo D (2018) Stereotyped defensive

840   behaviours in frogs of the genus *Odontophrynus* (Amphibia: Anura: Odontophrynidae). Curr Herpetol

841   37:172–179

842   Boulenger GA (1902) Further notes on the African batrachians *Trichobatrachus* and *Gampsosteonyx*.

843   Proc Zool Soc Lond II:709–710

844   Brizzi R, Corti C (2007) Cutaneous antipredatory secretions and pheromones in anurans and urodeles.

845   Mar Freshw Behav Physiol 40:225–231

846   Brodie ED Jr (1977) Salamander antipredator postures. Copeia 1977:523–535

847   Brodie ED Jr, Formanowicz DR, Brodie ED III (1991) Predator avoidance and antipredator mechanisms:

848   distinct pathways to survival. Ethol Ecol Evol 3:73–77

849   Brodie ED Jr, Tumbarello MS (1978) The antipredator functions of *Dendrobates auratus* (Amphibia:

850   Anura: Dendrobatidae) skin secretion in regard to a snake predator (*Thamnophis*). J Herpetol 12:264–265

851   Brodie ED Jr, Williams CR, Tyler MJ (1998) Evolution of aposematic behavior and coloration in the

852   Australian frog genus *Uperoleia*. J Herpetol 32:136–139

853   Brodie ED III, Feldman CR, Hanifin CT, Motychak JE, Mulcahy DG, Williams BL, Brodie ED Jr (2005)

854   Parallel arms races between garter snakes and newts involving tetrodotoxin as the phenotypic interface of

855   coevolution. J Chem Ecol 31:343–356

856   Caro T (2014) Antipredator deception in terrestrial vertebrates. Curr Zool 60:16–25

857   Channing A, Howell K (2003) *Phlyctimantis keithae* (Wot-wot). Herpetol Rev 34:52–53

858   Choi I, Lee SH, Ricklefs RE (1999) Effectiveness and ecological implications of anuran defenses against

859   snake predators. Korean J Biol Sci 3:247–252

860   Cott HB (1940) Adaptive coloration in animals. Methuen, London

861   Darst CR, Cummings ME, Cannatella DC (2006) A mechanism for diversity in warning signals:

862   conspicuousness versus toxicity in poison frogs. P Natl Acad Sci USA 103:5852–5857

863   Dodd CK (1976) A bibliography of anuran defensive mechanisms. Smithson Herpetol Inf Serv 37:1–10

864   Duellman WE, Trueb L (1994) Biology of amphibians. The Johns Hopkins University Press, London

865   Edmunds M (1974) Defence in animals. Longman, Essex, Harrow

866   Emerson SB, Cooper TA, Ehleringer JR (1990) Convergence in reflectance spectra among treefrogs.

867   Funct Ecol 4:47–51

868   Emerson SB, Koehl MAR (1990) The interaction of behavioral and morphological change in the

869   evolution of a novel locomotor type: "flying" frogs. Evolution 44:1931–1946

870   Endler JA (1978) A predator's view of animal color patterns. Evol Biol 11:319–364

871   Evans CM, Brodie ED Jr (1994) Adhesive strength of amphibian skin secretions. J Herpetol 28:499–502

872   Ferrante L, Sacramento M, Angulo A (2014) Defensive behaviour in *Aplastodiscus leucopygius* (Cruz

873   and Peixoto 1985) (Anura: Hylidae). Herpetol Notes 7:135–138

874   Ferreira RB, Faivovich J, Beard KH, Pombal J (2015) The first bromeligenous species of *Dendropsophus*

875   (Anura: Hylidae) from Brazil's Atlantic Forest. PLoS ONE 10:e0142893

876   Figueiredo GT, Lourenço-de-Moraes R, Neto NGP, Anjos L (2017) *Ischnocnema henselii* (Defensive

877   behavior). Herpetol Rev 48:163

878   Firschein L (1951) Phragmosis and the "unken reflex" in a Mexican hylid frog, *Pternohyla fodiens*.

879   Copeia 1951:74

880   Frost DR (2019) Amphibian species of the world: and online reference. American Museum of Natural

881   History, http://research.amnh.org/herpetology/amphibia/index.html

882   Janik VM (1999) Pitfalls in the categorization of behaviour: a comparison of dolphin whistle

883   classification methods. Anim Behav 57:133–143

884   Jared C, Antoniazzi MM, Navas CA, Katchburian E, Freymuller DV, Tambourgi DV, Rodrigues MT

885   (2005) Head co-ossification, phragmosis and defence in the casque-headed tree frog *Corythomantis

886   greening*. J Zool 265:1–8

887   Jared C, Mailho-Fontana PL, Antoniazzi MM, Barbaro KC, Rodrigues MT, Brodie ED Jr (2015)

888   Venomous frogs use heads as weapons. Curr Biol 25:2166–2170

889   Jetz W, Pyron AR (2018) The interplay of past diversification and evolutionary isolation with present

890   imperilment across the amphibian tree of life. Ecol Evol 2:850–858

891   Johnson JA, Brodie ED Jr (1975) The selective advantage of the defensive posture of the newt *Taricha*

892   *granulosa*. Am Midl Nat 93:139–148

893   King G, Keohane RO, Verba S (1994) Designing social inquiry: scientific inference in qualitative

894   research. Princeton University Press, Princeton

895   Lenzi-Mattos R, Antoniazzi MM, Haddad CFB, Tambourgi DV, Rodrigues MT, Jared C (2005) The

896   inguinal macroglands of the frog *Physalaemus nattereri* (Leptodactylidae): structure, toxic secretion and

897   relationship with deimatic behaviour. J Zool 266:385–394

898   Löhner L (1919) Über einem eigentümlichen reflex der feuerunken. Archiv Gesamte Physiol 174:324–

899   351

900   Lourenço-de-Moraes R (2012) *Proceratophrys avelinoi*, *Cycloramphus acangatan*. Defensive behavior.

901   Herpetol Rev 43:324–325

902   Lourenço-de-Moraes R, Batista VG, Ferreira RB (2014a) Defensive behaviors of *Leptodactylus*

903   *chaquensis* (Anura: Leptodactylidae). Herpetol Notes 7:391–392

904   Lourenço-de-Moraes R, Ferreira RB, Fouquet A, Bastos RP (2014b) A new diminutive frog species of

905   *Adelophryne* (Amphibia: Anura: Eleutherodactylidae) from the Atlantic Forest, southeastern Brazil.

906   Zootaxa 3846:348–360

907   Lourenço-de-Moraes R, Ferreira RB, Mira-Mendes CV, Zocca CZ, Medeiros T, Ruas DS, Rebouças R,

908   Toledo LF, Brodie ED Jr, Solé M (2016) Escalated antipredator mechanisms of two neotropical marsupial

909   treefrogs. J Herpetol 26:237–244

910   Lourenço-de-Moraes R, Pertel W (2011) *Pseudopalodicola* cf. *mystacalis*. Predation. Herpetol

911   Rev 42:414

912   Lourenço-de-Moraes R, Solé M, Toledo LF (2012) A new species of *Adelophryne* Hoogmoed and

913   Lescure (1984) (Amphibia: Anura: Eleutherodactylidae) from the Atlantic rainforest of southern Bahia,

914   Brazil. Zootaxa 344:59–68

915   Maddison WP, Maddison DR (2015) Mesquite: a modular system for evolutionary analysis, Version 3.04.

916   Mesquite Project Team, http://mesquiteproject.org

917   Mailho-Fontana PL, Antoniazzi MM, Toledo LF, Verdade VK, Sciani JM, Barbaro KC, Pimenta DC,

918   Rodrigues MT, Jared C (2014) Passive and active defense in toads: the paratoid macroglands in *Rhinella*

919   *marina* and *Rhaebo guttatus*. J Exp Zool 321:65–77

920   Mângia S, Santana DJ (2013) Defensive behavior in *Rhinella granulosa* (Spix 1824) (Amphibia: Anura:

921   Bufonidae). Herpetol Notes 6:45–46

922   Marchisin A, Anderson JD (1978) Strategies employed by frogs and toads (Amphibia: Anura) to avoid

923   predation by snakes (Reptilia: Serpente). J Herpetol 12:151–155

924   McCay M (2001) Aerodynamic stability and maneuverability of the gliding frog *Polypedates dennysi*. J

925   Exp Biol 204:2817–2826

926   Merilaita S (2003) Visual background complexity facilitates the evolution of camouflage. Evolution

927   57:1248–1254

928   Merilaita S, Lind J (2005) Background-matching and disruptive coloration, and the evolution of cryptic

929   coloration. Proc R Soc Lond B 272:665–670

930   Merilaita S, Lyytinen A, Mappes J (2001) Selection for cryptic coloration in a visually heterogeneous

931   habitat. Proc R Soc Lond B 268:1925–1929

932   Merilaita S, Tuomi J, Jormalainen V (1999) Optimisation of cryptic coloration in heterogeneous habitats.

933   Biol J Linn Soc 67:151–161

934   Miyatake T, Katayama K, Takeda Y, Nakashima A, Sugita A, Mizumoto M (2004) Is death feigning

935   adaptive? Heritable variation in fitness difference of death-feigning behaviour. Proc R Soc Lond B

936   271:2293–2296

937   Mônico AT, Zocca CZ, Lourenço-de-Moraes R, Campos FS, Ferreira RB (2016) *Myersiella microps*

938   (Antipredator mechanisms). Herpetol Rev 47:644

939   Mukherjee S, Heithaus MR (2013) Dangerous prey and daring predators: a review. Biol Rev 88:550–563

940   Nishiumi N, Mori A (2015) Distance-dependent switching of anti-predator behavior of frogs from

941   immobility to fleeing. J Ethol 33:117–124

942   Nishiumi N, Mori A (2016) Immobile defence of a frog distracts attention of approaching predators to

943   other prey. Behaviour 153:1387–1401

944   Nystrand O, Granström A (1997) Post-dispersal predation on *Pinus sylvestris* seeds by *Fringilla* spp:

945   ground substrate affects selection for seed color. Oecologia 110:353–359

946   Perret JL (1961) La biologie d'*Acanthixalus spinosus* (Amphibia: Salientia). Rech Etud Camerounaises

947   1:90–101

948   Sandoval CP (1994) The effects of the relative geographic scales of gene flow and selection on morph

949   frequencies of *Timema cristinae*. Evolution 48:1866–1879

950   Santos JC, Cannatella DC (2011) Phenotypic integration emerges from aposematism and scale in poison

951   frogs. P Natl Acad Sci USA 108:6175–6180

952   Sazima I (1974) Experimental predation on the leaf-frog *Phyllomedusa rohdei* by the water snake *Liophis*

953   *miliaris*. J Herpetol 8:376–377

954   Sazima I (1978) Convergent defensive behavior of two leaf-litter frogs of southeastern Brazil. Biotropica

955   10:158

956   Sazima I, Caramaschi U (1986) Descrição de *Physalaemus deimaticus* sp. n., e observações sobre

957   comportamento deimatico em *P. nattereri* (Steindachner 1863) (Anura: Leptodactylidae). Rev Bras Biol

958   13:91–101

959   Schwalm PA, Starrett PH, McDiarmid RW (1977) Infrared reflectance in leaf-sitting Neotropical frogs.

960   Science 196:1225–1227

961   Shine RG (1993) Sexual dimorphism in snakes. In: Seigel RA, Collins JT (eds) Ecology and Behavior.

962   McGraw-Hill, New York, pp 49–86

963   Siddiqi A, Cronin TW, Loew ER, Vorobyev M, Summers K (2004) Interspecific and intraspecific views

964   of color signals in the strawberry poison frog *Dendrobates pumilio*. J Exp Biol 207:2471–2485

965   Smith BPC, Williams CR, Tyler MJ, Williams BD (2004) A survey of frog odorous secretions, their

966   possible functions and phylogenetic significance. Appl Herpetol 2:47–82

967   Thayer GH (1909) Concealing-coloration in the animal kingdom. Macmillan, New York

968   Toledo LF (1995) Predation of juvenile and adult anurans by invertebrates: current knowledge and

969   perspectives. Herpetol Rev 36:395–400

970   Toledo LF, Becker CG, Haddad CFB, Zamudio KR (2014) Rarity as an indicator of endangerment in

971   Neotropical frogs. Biol Conserv 179:54–62

972   Toledo LF, Haddad CFB (2009) Colors and some morphological traits as defensive mechanisms in

973   anurans. Int J Zool 2009:910892

974   Toledo LF, Martins IA, Bruschi DP, Passos MA, Alexandre C, Haddad CFB (2015) The anuran calling

975   repertoire in the light of social context. Acta Ethol 18:87–99

976   Toledo LF, Sazima I, Haddad CFB (2010) Is it all death feigning? Case in anurans. J Nat Hist 44:1979–

977   1988

978   Toledo LF, Sazima I, Haddad CFB (2011) Behavioural defences of anurans: an overview. Ethol Ecol

979   Evol 23:1–25

980   Toledo RC, Jared C (1995) Cutaneous granular glands and amphibian venoms. Comp Biochem Physiol

981   111:1–29

982   Turner GC (1961) Bacilluria in pregnancy. Lancet 2:1062–1064.

983   Webster RJ, Callahan A, Godin J-GJ, Sherratt TN (2011) Camouflage behaviour and body orientation on

984   backgrounds containing directional patterning. In: Wells KD (ed) Animal camouflage: mechanisms and

985   function. Cambridge University Press, Cambridge, pp 101–117

986   Wells KD (2007) The ecology and behavior of amphibians. University of Chicago Press, Chicago

987   Williams CR, Brodie ED Jr, Tyler MJ, Walker SJ (2000) Antipredator mechanisms of Australian frogs. J

988   Herpetol 34:431–443

989   Zocca CZ, Ferreira FCL, Ferreira RB (2014) Observações sobre história natural de *Zachaenus carvalhoi*

990   Izecksohn 1983"1982" (Amphibia: Anura: Cycloramphidae). Bol Mus Biol Mello Leitão 34:63–74

991   Zug GR, Vitt LJ, Caldwell JP (2001) Herpetology: an introductory biology of amphibians and reptiles.

992   Academic Press, New York

Table 1 Classification of antipredator mechanisms of post-metamorphic anurans

Phases	Antipredator mechanisms	Variations
Avoid detection		
	1. Camouflage	a. Background matching b. Disruptive
	2. Immobility	-
	3. Interrupt calling	-
Prevent Attack		
	4. Aposematism	a. Exposed b. Hidden
	5. Charge	-
	6. Posture	a. Body elevation b. Body inflation c. Contraction d. Gland exposure e. Limbs interweave f. Mouth gape g. Rear elevation h. Stretching limbs i. Death feigning j. Unken reflex
	7. Escape	a. Climb b. Glide c. Hide d. Jump away e. Roll f. Swim
	8. Warning sound	-
Counterattack		
	9. Cloacal discharge	-
	10. Secretion	a. Adhesive b. Odoriferous c. Slippery d. Poisonous
	11. Aggression	a. Bite b. Headbutt c. Kick d. Puncture
	12. Distress call	-

995   **Figures captions**

996

997   **Fig. 1** Number of publications of antipredator mechanisms of anurans over the years

998

999   **Fig. 2** Reconstruction of ancestral state of the 12 antipredator mechanisms in Anura. Black branches=

1000   presence of the mechanism, and white branches= absence of the mechanism. a) Camouflage; b)

1001   Immobility; c) Interrupt calling; d) Aposematism; e) Charge; f) Posture; g) Escape; h) Warning sound; i)

1002   Cloacal discharge; j) Secretion; k) Aggression; l) Distress call; m) Tree of life (families); (*) outgroup.

1003

1004   **Fig. 3** Background matching: a) *Bokermannohyla alvarengai* (Hylidae) resemble lichen-covered rock

1005   with flange and a pale fringe that breaks up the shadow; b) *Dendrophryniscus brevipollicatus* (Bufonidae)

1006   has brownish dominant dorsal color to resemble leaf litter; c) *Hyalinobatrachium cappelei*

1007   (Centrolenidae) has partial transparent venter resembling green leaf; d) *Odontophrynus americanus*

1008   (Odontophrynidae) has a variety of warts and tubercles to resemble stones, bird dropping, or fallen leaves.

1009   Photos: F. Leal (a), T. Silva-Soares (b), R. Oliveira (c), and RL-d-M (d)

1010

1011   **Fig. 4** Disruptive coloration: a) *Boana cipoensis* (Hylidae); b) *Dendropsophus elegans* (Hylidae) have

1012   contrasting markings that break up the appearance of body form. Photos: F. Leal (a) and RL-d-M (b)

1013

1014   **Fig. 5** Immobility: a) *Haddadus binotatus* (Craugastoridae) alert and prepared to jump away; b) *Thoropa*

1015   *miliaris* (Cycloramphidae) flat against the ground to use the cryptic dorsal coloration. Photos: F.S.

1016   Campos (a) and T. Silva-Soares (b)

1017

1018   **Fig. 6** Aposematism: a) *Brachycephalus alipioi* (Brachycephalidae) has aposematic coloration over the

1019   entire body (exposed aposematism); b) *Uperoleia lithomoda* (Myobatrachidae) showing four red

1020   eyespots; c) *Edalorhina perezi* (Leptodactylidae) showing a pair of black eyespots; d) *Phyllomedusa*

1021   *burmeisteri* (Hylidae) showing the bright yellow color on the thighs (hidden aposematism). Photos: J.L.

1022   Gasparini (a), EDB (b, c), and A.T. Mônico (d)

1023

1024 **Fig. 7** Posture of body elevation: a) *Rhaebo gutattus* (Bufonidae) extending the front limbs (partial body

1025 elevation) and b) *Rana areolata* (Ranidae) extending the four limbs (full body elevation). Photos: T.

1026 Silva-Soares (a) and EDB (b)

1027

1028 **Fig. 8** Posture of body inflation: a) *Dermatonotus muelleri* (Microhylidae) and b) *Dyscophus antongilii*

1029 (Microhylidae) inflating the body. Photos: J.F.R. Tonini (a) and EDB (b)

1030

1031 **Fig. 9** Posture of contraction: *Itapotihyla langsdorffii* (Hylidae) contracting with: a) the dorsum and b)

1032 venter pointing to the substrate. Photo: RL-d-M (a) and CZ (b)

1033

1034 **Fig. 10** Posture of gland exposure: a) *Proceratophrys paviotii* (Odontophrynidae) directing the parotoid

1035 glands toward the predator and b) *Aparasphenodon brunoi* (Hylidae) exposing the ossified head with

1036 glands and obstructing the bromeliad. Photos: RBF (a) and T. Silva-Soares (b)

1037

1038 **Fig. 11** Posture of limbs interweave: a) *Leptodactylus chaquensis* (Leptodactylidae) and b) *Hylomantis*

1039 *aspera* (Phyllomedusidae) spreading skin secretion over the body. Photo: RL-d-M (a) and M. Gally (b)

1040

1041 **Fig. 12** Posture of mouth gape: a) *Lepidobatrachus laevis* (Ceratophryidae) and b) *Ceratophrys ornata*

1042 (Ceratophryidae) opening the mouth toward the predator. Photo: EDB (a, b)

1043

1044 **Fig. 13** Posture of rear elevation: *Physalaemus nattereri* (Leiuperidae): a) partial rear elevation and b) full

1045 rear elevation. Photo: EDB (a, b)

1046

1047 **Fig. 14** Posture of stretching limbs: a) *Stereocyclops incrassatus* (Microhylidae) and b) *Proceratophrys*

1048 *schirchi* (Odontophrynidae) stretching the limbs. Photos: J.F.R. Tonini (a) and A.T. Mônico (b)

1049

1050 **Fig. 15** Posture of death feigning: a) *Pristimantis vinhai* (Brachycephalidae) and b) *Ischnocnema*

1051 *erythromera* (Brachycephalidae) have the fore and hind limbs loose and laying the dorsum on the

1052 substrate. Photos: RL-d-M (a, b)

1053

1054 **Fig. 16** Posture of unken reflex: a) *Dendrophryniscus boulengeri* (Bufonidae) displaying the reddish

1055 palms of the front limbs (partial unken reflex) and b) *Bombina variegata* (Bombinatoridae) showing

1056 aposematic venter and palms of the four limbs (full unken reflex). Photos: RL-d-M (a) and EDB (b)

1057

1058 **Fig. 17** Escape: a) *Rhacophorus* sp. (Rhacophoridae) that jumps from a vertical substrate to glide until

1059 reaching another substrate (glide) and b) *Oreophrynella nigra* (Bufonidae) rolls down sloped terrain.

1060 Photos: P. Gambale (a) and C. Brooke (b)

1061

1062 **Fig. 18** Aggression: a) *Gastrotheca megacephala* (Hemiphractidae) biting the predator (bite) and b)

1063 *Leptodactylus pentadactylus* (Leptodactylidae) has spines (red arrow) used to puncture the predator

1064 (puncture). Photo: RBF (a) and EDB (b)