

CONTORTIONIST TREE FROG: NEW RECORDS AND AN UPDATED LIST OF ANTIPREDATOR MECHANISMS IN *BOANA* (ANURA: HYLIDAE) AND *PRISTIMANTIS* (ANURA: STRABOMANTIDAE)

PERERECA CONTORCIONISTA: NOVOS REGISTROS E ATUALIZAÇÃO DA LISTA DE MECANISMOS ANTIPREDATÓRIOS EM *BOANA* (ANURA: HYLIDAE) E *PRISTIMANTIS* (ANURA: STRABOMANTIDAE)

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Resumo. – Mecanismos antipredatórios são formas eficientes de lidar com as tentativas de predação e existem vários tipos na natureza. Anuros possuem um repertório diversificado de mecanismos defensivos por também desempenharem um papel crucial na cadeia trófica. No entanto, devido à vasta diversidade de anuros, pouco se sabe sobre o repertório de mecanismos antipredatórios de cada espécie. Aqui, apresentamos uma lista atualizada de mecanismos registrados para dois gêneros de anuros, *Pristimantis* e *Boana*, incluindo nove novos comportamentos antipredatórios para *Pristimantis* aff. *guianensis* e *Boana pardalis*. Um destes comportamentos é o entrelaçamento de membros (“limbs interweave”), um mecanismo raro relatado para apenas 14 espécies de anuros. Nossas descobertas destacam a importância da pesquisa empírica e da observação direta da história natural. Mesmo para espécies bem conhecidas, o conhecimento da história natural pode ser limitado.

Palavra chave. – *Boana pardalis*, comportamento defensivo, membros entrelaçados, pernas entrelaçadas, *Pristimantis guianensis*

Abstract. – Antipredator mechanisms are efficient ways to avoid attempted predations, and various forms exist in nature. Anurans play a crucial role in the trophic chain and show a diverse repertoire of mechanisms. However, due to the vast diversity of anurans, little is known about the antipredator mechanism repertoire of each species. Here, we present an updated list of mechanisms reported for two genera of anurans, *Pristimantis* and *Boana*, including nine new antipredator behaviors for *Pristimantis* aff. *guianensis* and *Boana pardalis*. One of those behaviors is the limbs interweave, a rare mechanism reported for only 14 anuran species. Our findings highlight the importance of empirical research and direct natural history observation. Even for well-known species, knowledge on natural history can be limited.

Key words. – *Boana pardalis*, defensive behavior, limbs interweave, legs interweaving, *Pristimantis guianensis*

Predators pressure induce diverse traits in prey (e.g., Riessen, 1992; Üveges et al., 2019), leading to varied mechanisms including behavioral, morphological, and physiological adjustments (Brodie et al., 1991; Caro, 2014). Commonly known as antipredator behaviors, these strategies are employed by prey to reduce predation success (Brodie et al., 1991; Caro, 2014). Anurans, as crucial components of the trophic web, serve as both prey and predator for numerous species (Toledo et al.,

2007; Ceron et al., 2018; Souza et al., 2023). Therefore, they exhibit various antipredator mechanisms, such as remaining motionless, fleeing, and displaying colors for defense (Toledo et al., 2011; Ferreira et al., 2019).

The Neotropical region is renowned for its richness in anuran diversity with many yet to be discovered (Moura & Jetz, 2021). Among this remarkable diversity, the genera *Pristimantis* and

Boana are prominent both in number of species and geographic range. *Pristimantis*, recognized as the most diverse genus among anurans, encompasses over 600 described species and *Boana*, with 99 known species, shares a similar Neotropical distribution (Padial et al., 2014; Frost, 2024).

Despite their vast diversity, only eight species of *Pristimantis* and 32 species of *Boana* have at least one antipredator mechanism reported (Ferreira et al., 2019). Here we describe six new antipredator mechanisms for *Pristimantis* aff. *guianensis*, a lineage distributed in Madeira River interfluvium (Fouquet et al., 2022; Mônico et al., 2022; Mônico, 2023), and three for *Boana pardalis*, a species inhabiting open and forested areas in the Atlantic Forest of southeastern Brazil (Caramaschi & Napoli, 2004). In addition, we updated the previous list of antipredator mechanisms provided by Ferreira et al. (2019) for both genera and the list of events of the rare limb interweave behavior.

To update the list of antipredator mechanisms we reviewed the literature published between January 2019 and December 2023 following van den Burg (2020). We consulted 12 natural history journals: Caribbean Herpetology, Cuadernos de Herpetología, Copeia, Herpetologia Brasileira, Herpetological Review, Herpetology Notes, Herpetozoa, Phyllomedusa, Reptiles & Amphibians, Revista Latinoamericana de Herpetología, Sauria, and The Herpetological Bulletin. Besides that, we also conducted a bibliographic search using published and peer-reviewed articles in Google Scholar (scholar.google.com.br), Scientific Electronic Library Online — Scielo (www.scielo.br), Web of Science (www.webofknowledge.com), and Research Gate (www.researchgate.com). The survey was conducted using the combination of the following words: “*Boana*”, “*Pristimantis*” “defensive behavior”, “defensive behaviour”, “antipredator mechanism”, “amphibian”, “predation”, and “prey”.

Our first record was made during a field expedition to Rio Manicoré (6°35'42.38" S, 61°22'06.27" W; datum WGS84; 48 m a.s.l.), state of Amazonas, Brazil, on June 10, 2022. One individual of *Pristimantis* aff. *guianensis* (snout-vent length = 18.99 mm; body mass = 0.5 g) was captured in the igapó forest during the day, when we were inspecting pitfall traps; the individual jumped in front of us. We carried it to the field lab, where it was kept in a plastic bag with one leaf and water. On June 13, 2022, at 14:01 h, we started to handle the individual to take pictures. During preparation and handling, the animal twisted its legs and remained motionless, displaying (1) limbs interweave behavior (Fig. 1A). After a few seconds (about 60 s), when we touched it, the individual returned to normal posture and rapidly bent down its body to lower than usual, displaying

the (2) crouching down behavior (Fig. 1B). The limbs remained next to the body and the eyes open, remaining motionless for a few minutes (1-2 min) until we touched the individual again. It remained immobile (3) in normal posture for 2 min (Fig. 1C). To take some pictures of the ventral view of the individual, we turned it upside down; however, it turned to a normal position. In a second attempt, it remained for a few minutes (1-2 min), displaying the (4) death-feigning behavior (Fig. 1D). During the handling process, the individual (5) jumped away several times. Additionally, we formally described the camouflage of background matching (6) as a defensive mechanism exhibited by *Pristimantis* aff. *guianensis*, a species with cryptic coloration. The species' coloration closely resembles the trunk and leaves of its habitat, providing effective camouflage against predator detection (Toledo & Haddad, 2009a; Ferreira et al., 2019). The specimen was deposited at the Amphibians and Reptiles Collection from the Instituto Nacional de Pesquisas da Amazônia (INPA-H), under voucher number INPA-Ho44572.

The second record was made occasionally on August 19, 2023, at 12:38 h, in a rural area of Alto Rio Doce, Minas Gerais, Brazil (21°02'07.00" S, 43°29'06.00" W; datum WGS84; 773 m a.s.l.). M.A.P.C. Dias was harvesting collard when an individual of *Boana pardalis* jumped away from a collard leaf and down on the floor with legs twisting over each other, displaying (1) limbs interweave behavior and remaining motionless (Fig. 1E-F). During the defensive behavior, the individual exhibited a contrasting yellow color, acting as (2) hidden aposematism (Fig. 1E-F). After a few minutes (1-2 min), when he approached the frog to take more pictures, it turned to normal posture and (3) jumped away. The frog was neither captured nor measured.

Limbs interweave (or legs interweaving) is a rare defensive behavior, with only six records for anuran species in the scientific literature by 2019 (Ferreira et al., 2019), as follows: for *Acris blanchardi*, *Dryophytes cinereus* and *Hylomantis aspera*, from the Hylidae family; for *Hylambates keithae*, from the Hyperoliidae family; for *Leptodactylus macrosternum*, from the Leptodactylidae family; and for *Rana temporaria*, from the Ranidae family. After Ferreira et al. (2019), the behavior was recorded six more times, as follows: for *Frostius pernambucensis*, from the Bufonidae family (Ramos et al., 2021); for *Boana semilineata* (Campos et al., 2023), *Boana geographica* (Campos & Silva-Soares, 2023), *Bokermannohyla oxente* (Souza et al., 2020a), and *Ololygon tripui* (Vieira et al., 2022) from the Hylidae family; and for *Haddadus binotatus* (Rojas-Padilla et al., 2019), from the Craugastoridae family. Therefore, our records coupled with the literature show the compilation of 14 anuran species exhibiting the defensive behavior of limbs interweave. Besides that, this study is the first

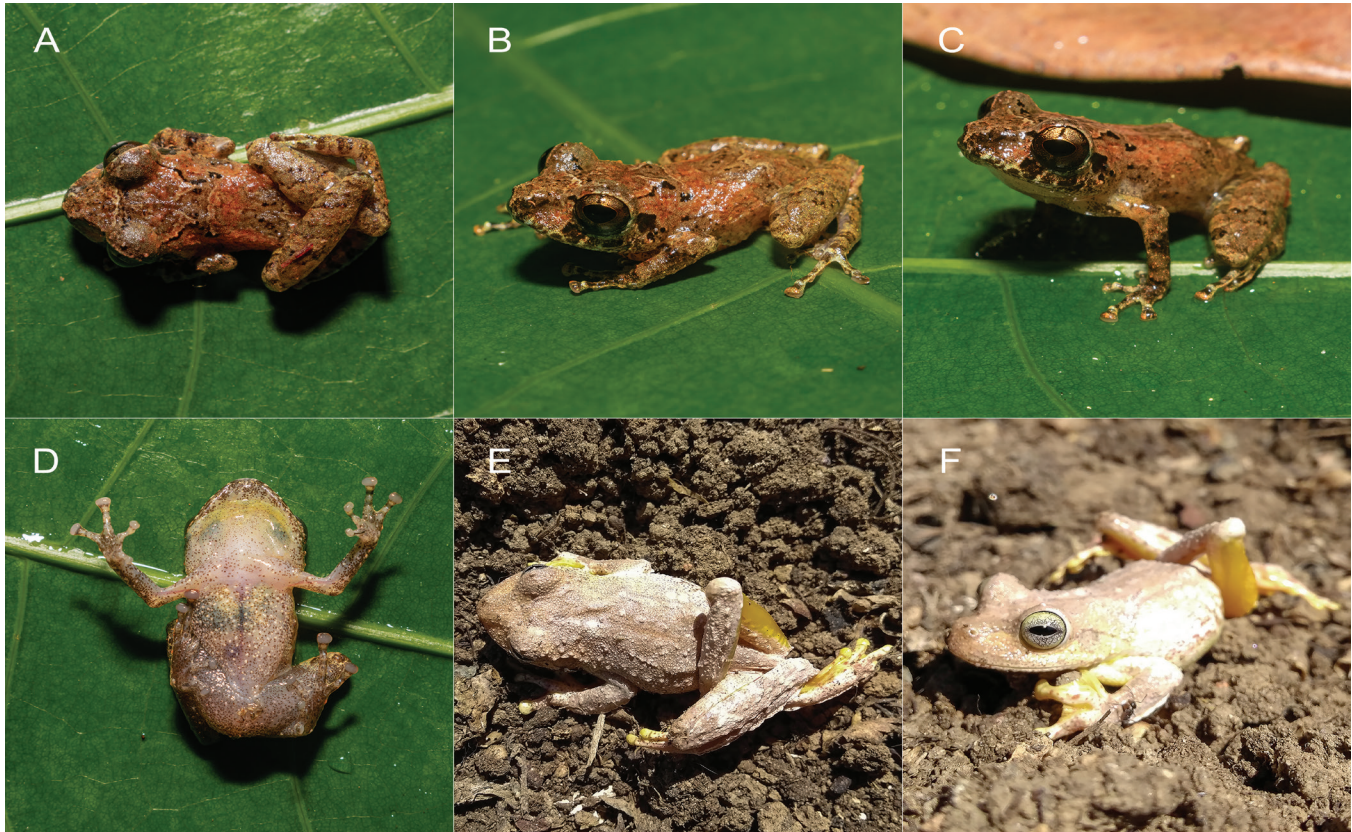


Figura 1. Comportamentos antipredatórios registrados para *Pristimantis* aff. *guianensis* (A-D) e *Boana pardalis* (E-F). A, E e F: entrelaçamento de membros; B: agachamento; C: imobilidade; D: tanatose. Fotos: Lucas R. Mendonça (*Pristimantis* aff. *guianensis*) e Marcelo A. P. C. Dias (*Boana pardalis*).

Figure 1. Antipredator behaviors reported for *Pristimantis* aff. *guianensis* (A-D) and *Boana pardalis* (E-F). A, E, and F: limbs interweave; B: crouching down; C: immobility; D: death feigning. Photos: Lucas R. Mendonça (*Pristimantis* aff. *guianensis*) and Marcelo A. P. C. Dias (*Boana pardalis*).

record of limbs interweave for the family Strabomantidae, for the genus *Pristimantis*, and for the *Boana faber* group, and also the third record for the genus *Boana* (Table 1).

Limbs interweave behavior may be associated with the exhibition of aposematic coloration and facilitation of the spread of skin secretion (Toledo et al., 2011; Ferreira et al., 2019). In *Pristimantis* aff. *guianensis* this behavior does not seem to be associated with aposematic coloration, similar to what was observed in *Bokermannohyla oxente* and *Oloolygon tripui* (Souza et al., 2020a; Vieira et al., 2022). However, for *B. pardalis*, limbs interweave is associated to hidden aposematism, as observed in *Frostius pernambucensis* (Ramos et al., 2021). When *B. pardalis* rotates its legs, the bright yellow color present on the ventral surface of its legs becomes visible, acting as a warning signal to the predators regarding the presence of toxins and the lack of palatability (Ferreira et al. 2019). While the association of limb interweave with skin secretion is not observed in both species,

it remains a possibility for *B. pardalis*, considering recorded skin secretion instances in the species and other members of the genus (Table 1).

Immobility and jumping are common defensive behaviors in anurans, observed across all species in nature (Toledo et al., 2011). Remaining immobile enhances the chances of avoiding visual detection by potential predators, especially when combined with cryptic coloration (Toledo et al., 2010; Ferreira et al., 2019). During immobility, individuals often prepare to jump away from predators, either by flattening against the ground or performing crouching down behavior, as seen in *Pristimantis* aff. *guianensis* (Fig. 1C; Toledo et al., 2010; Ferreira et al., 2019). Jumping away facilitates hiding and can be coupled with other defensive behaviors, as observed in *B. pardalis*, which exhibits limb interweave following a jump (Toledo et al., 2010; Ferreira et al., 2019).

Tabela 1. Lista atualizada de mecanismos antipredatórios de *Boana* e *Pristimantis*. 1. Camuflagem correspondente ao fundo; 2. Camuflagem disruptiva; 3. Imobilidade; 4. Canto interrompido; 5. Aposematismo escondido; 6. Investida; 7. Inflação corporal; 8. Contração; 9. Entrelaçamento de membros; 10. Abertura da boca; 11. Alongamento de membros; 12. Tanatose; 13. Reflexo unken; 14. Escalada; 15. Esconder-se; 16. Saltar para longe; 17. Nadar; 18. Som de aviso; 19. Descarga cloacal; 20. Secreção odorífera; 21. Secreção adesiva; 22. Secreção escorregadia; 23. Secreção venenosa; 24. Mordida; 25. Cabeçada; 26. Chute; 27. Perfurar; 28. Chamada de socorro; 29. Polifenismo; 30. Proteção ocular; 31. Agachamento.

Table 1. An updated list of antipredator mechanisms of *Boana* and *Pristimantis*. 1. Matching background camouflage; 2. Disruptive background camouflage; 3. Immobility; 4. interrupted calling; 5. Hidden aposematism; 6. Charging; 7. Body inflation; 8. Contraction; 9. Interweaving limbs; 10. Mouth gape; 11. Stretching limbs; 12. Death feigning; 13. Unken reflex; 14. Climbing; 15. Hiding; 16. Jump away; 17. Swim; 18. Warning sound; 19. Cloacal discharge; 20. Adhesive secretion; 21. Odoriferous secretion; 22. Slippery secretion; 23. Poisonous secretion; 24. Bite; 25. Headbutt; 26. Kick; 27. Puncture; 28. Distress call; 29. Polyphenism; 30. Eye protection; 31. Crouching down.

| Species | Antipredator mechanism | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | References | |
|--|------------------------|---|---|---|---|---|---|---|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|------------|---|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 | 24 | 25 | 26 | 27 | 28 | 29 | 30 | 31 | | |
| <i>Boana albomarginata*</i> (Spix 1824) | 1 | | 3 | | 5 | | 7 | | 8 | | 12 | | | | 16 | | 19 | | 21 | | 22 | | | 26 | | | | 28 | | | | | Toledo & Haddad, 2009b; Figueiredo-de-Andrade et al., 2010; Toledo et al., 2010; Toledo et al., 2011; Baracho et al., 2013; Haddad et al., 2013; Just & Zocche, 2017; Ferreira et al., 2019 |
| <i>Boana albopunctata</i> (Spix 1824) | 1 | | 3 | | 5 | | 7 | | 8 | | 12 | | | | | 16 | | 19 | | | | | | | | | | | | 30 | | | Sazima, 1972; Toledo & Haddad, 2009b; Toledo et al., 2010; Haddad et al., 2013; Costa et al., 2014; Toledo et al., 2011; Ferreira et al., 2019 |
| <i>Boana beckeri</i> (Caramaschi and Cruz 2004) | 2 | | | | 5 | | | 8 | | | | | | | | | | | | | | | | | | | | | | | | | Toledo et al., 2010 |
| <i>Boana bischoffi</i> (Boulenger 1887) | 1 | | | | 5 | | 8 | | 10 | | 12 | | | | | | 19 | | 21 | | | | | | | | | | 28 | | | | Toledo & Haddad, 2009b; Toledo et al., 2010; Toledo et al., 2011; Haddad et al., 2013; Foerster et al., 2017 |
| <i>Boana boans</i> (Linnaeus 1758) | 1 | | | | 5 | | 6 | | 7 | | 10 | | 11 | | 16 | | | 24 | | | | | | | 27 | | | 28 | | | | | Bogert, 1960; Hödl & Gollmann, 1986; Lima et al., 2005; Rocha & López-Baucells, 2014 |



Tabela 1 (cont.). Lista atualizada de mecanismos antipredatórios de *Boana* e *Pristimantis*. 1. Camuflagem correspondente ao fundo; 2. Camuflagem disruptiva; 3. Imobilidade; 4. Canto interrompido; 5. Aposematismo escondido; 6. Ingestão; 7. Infiliação corporal; 8. Contração; 9. Entrelaçamento de membros; 10. Abertura da boca; 11. Alongamento de membros; 12. Tanatose; 13. Reflexo unken; 14. Escalada; 15. Esconder-se; 16. Saltar para longe; 17. Nadar; 18. Som de aviso; 19. Descarga cloacal; 20. Secreção odorífera; 21. Secreção adesiva; 22. Secreção escorregadia; 23. Secreção venenosa; 24. Mordida; 25. Cabeçada; 26. Chute; 27. Perfurar; 28. Chamada de socorro; 29. Polifenismo; 30. Proteção ocular; 31. Agachamento.

Table 1 (cont.). An updated list of antipredator mechanisms of *Boana* and *Pristimantis*. 1. Matching background camouflage; 2. Disruptive camouflage; 3. Immobility; 4. Interrupted calling; 5. Hidden aposematism; 6. Charging; 7. Body inflation; 8. Contraction; 9. Interweaving limbs; 10. Mouth gape; 11. Stretching limbs; 12. Death feigning; 13. Unken reflex; 14. Climbing; 15. Hiding; 16. Jump away; 17. Swim; 18. Warning sound; 19. Cloacal discharge; 20. Adhesive secretion; 21. Odoriferous secretion; 22. Slippery secretion; 23. Poisonous secretion; 24. Bite; 25. Headbutt; 26. Kick; 27. Puncture; 28. Distress call; 29. Polyphenism; 30. Eye protection; 31. Crouching down.

| Species | Antipredator mechanism | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | References | | |
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| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 | 24 | 25 | 26 | 27 | 28 | 29 | 30 | 31 | | | |
| <i>Boana caingua</i> (Carrizo 1991) | 1 | | | | 5 | | | 8 | | | | | | | | | | | | | | | | | | | | | 28 | | | | | Toledo & Haddad, 2009b; Toledo et al., 2010; Haddad et al., 2013 |
| <i>Boana caipora</i> (Antunes, Faivovich & Haddad 2008) | 1 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | Antunes et al., 2008; Toledo & Haddad, 2009b; Haddad et al., 2013 |
| <i>Boana calcarata</i> (Troschel 1848) | 1 | | | | 5 | | | 8 | | | | | | | | | | | | | | | | | | | | | | | | | | Angulo & Funk, 2006; Pedroso-Santos et al., 2020a; Pedroso-Santos et al., 2022 |
| <i>Boana cinerascens</i> (Spix 1824) | 1 | | | | | 6 | | | | | | | | | | 16 | | | | | | | | | | | | | | | | | | Ferreira et al., 2019 |
| <i>Boana courtisae</i> Fouquet, Marinho, Réjaud, Carvalho, Caminer, Jansen, Rainha, Rodrigues, Werneck, Lima, Hrbek, Giaretta, Venegas, Chávez & Ron 2021 | 1 | | | | | | | | | | 12 | | | | | | | | | | | | | | | | | | | | | | | Pedroso-Santos et al., 2022 |
| <i>Boana crepitans</i> (Wied-Neuwied 1824) | 1 | | 3 | | 5 | | 7 | | | | 12 | | | 16 | | | | | | 22 | | | | 26 | | 28 | | | | | | | Toledo & Haddad, 2009b; Haddad et al., 2013; Ferreira et al., 2019 | |
| <i>Boana curupi</i> (García, Faivovich & Haddad 2007) | 1 | | | | 5 | | | | | | | | | | | | | | 21 | | | | | | | | | | | | | | | Haddad et al., 2013 |



Tabela 1 (cont.). Lista atualizada de mecanismos antipredatórios de *Boana* e *Pristimantis*. 1. Camuflagem correspondente ao fundo; 2. Camuflagem disruptiva; 3. Imobilidade; 4. Canto interrompido; 5. Aposematismo escondido; 6. Investida; 7. Inflação corporal; 8. Contração; 9. Entrelaçamento de membros; 10. Abertura da boca; 11. Alongamento de membros; 12. Tanatose; 13. Reflexo unken; 14. Escalada; 15. Esconder-se; 16. Saltar para longe; 17. Nadar; 18. Som de aviso; 19. Descarga cloacal; 20. Secreção adesiva; 21. Secreção odorífera; 22. Secreção escorregadia; 23. Secreção venenosa; 24. Mordida; 25. Cabeçada; 26. Chute; 27. Perfurar; 28. Chamada de socorro; 29. Polifenismo; 30. Proteção ocular; 31. Agachamento.

Table 1 (cont.). An updated list of antipredator mechanisms of *Boana* and *Pristimantis*. 1. Matching background camouflage; 2. Disruptive camouflage; 3. Immobility; 4. Interrupted calling; 5. Hidden aposematism; 6. Charging; 7. Body inflation; 8. Contraction; 9. Interweaving limbs; 10. Mouth gape; 11. Stretching limbs; 12. Death feigning; 13. Unken reflex; 14. Climbing; 15. Hiding; 16. Jump away; 17. Swim; 18. Warning sound; 19. Cloacal discharge; 20. Adhesive secretion; 21. Odoriferous secretion; 22. Slippery secretion; 23. Poisonous secretion; 24. Bite; 25. Headbutt; 26. Kick; 27. Puncture; 28. Distress call; 29. Polyphenism; 30. Eye protection; 31. Crouching down.

| Species | Antipredator mechanism | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | References | | |
|--|------------------------|---|---|---|---|---|---|---|---|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|------------|--|--|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 | 24 | 25 | 26 | 27 | 28 | 29 | 30 | 31 | | | |
| <i>Boana dentei</i> (Bokermann 1967) | | | | | | | | | | | | | | | | | | | | | | | | | | | | 28 | 29 | 30 | | | Figueiredo et al., 2020; Pedroso-Santos et al., 2020b | |
| <i>Boana diabolica</i> (Fouquet, Martinez, Zeidler, Courtois, Gaucher, Blanc, Lima, Souza, Rodrigues & Kok 2016) | | | | | 5 | | | 8 | | | | | | | | | | | | | | | | | | | | | | | | | | Pedroso-Santos et al., 2022 |
| <i>Boana exastis</i> (Caramaschi & Rodrigues 2003) | 1 | | | | | | | | | | | | | | | | | | | | | | | | | | 27 | 28 | | | | | | Loebmann et al., 2008; Toledo & Haddad, 2009b; Haddad et al., 2013 |
| <i>Boana faber</i> (Wied-Neuwied 1821) | 1 | | 3 | | 5 | | 7 | 8 | | 10 | | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | | 21 | 22 | | 26 | 27 | 28 | | | | | | Toledo & Haddad, 2009b; Toledo et al., 2010; Toledo et al., 2011; Forti & Bertoluci, 2012; Haddad et al., 2013; Manoel & Almeida, 2017; Ferreira et al., 2019; Dias-Silva et al., 2021 | |
| <i>Boana fasciata</i> ** (Günther 1858) | 1 | | 3 | | 5 | | | 8 | | | | | | | | | | | | | | | | | | | | | | | | | | Angulo & Funk, 2006 |
| <i>Boana cf. fasciata</i> | | | | | | | | | | | | | | | | | | | | | | | | | | | | 28 | | | | | | Forti & Costa-Campos, 2020 |



Tabela 1 (cont.). Lista atualizada de mecanismos antipredatórios de *Boana* e *Pristimantis*. 1. Camuflagem correspondente ao fundo; 2. Camuflagem disruptiva; 3. Imobilidade; 4. Canto interrompido; 5. Aposematismo escondido; 6. Investida; 7. Inflação corporal; 8. Contração; 9. Entrelaçamento de membros; 10. Abertura da boca; 11. Alongamento de membros; 12. Tanatose; 13. Reflexo unken; 14. Escalada; 15. Esconder-se; 16. Saltar para longe; 17. Nadar; 18. Som de aviso; 19. Descarga cloacal; 20. Secreção odorífera; 21. Secreção adesiva; 22. Secreção escorregadia; 23. Secreção venenosa; 24. Mordida; 25. Cabeçada; 26. Chute; 27. Perfurar; 28. Chamada de socorro; 29. Polifenismo; 30. Proteção ocular; 31. Agachamento.

Table 1 (cont.). An updated list of antipredator mechanisms of *Boana* and *Pristimantis*. 1. Matching background camouflage; 2. Disruptive camouflage; 3. Immobility; 4. Interrupted calling; 5. Hidden aposematism; 6. Charging; 7. Body inflation; 8. Contraction; 9. Interweaving limbs; 10. Mouth gape; 11. Stretching limbs; 12. Death feigning; 13. Unken reflex; 14. Climbing; 15. Hiding; 16. Jump away; 17. Swim; 18. Warning sound; 19. Cloacal discharge; 20. Adhesive secretion; 21. Odoriferous secretion; 22. Slippery secretion; 23. Poisonous secretion; 24. Bite; 25. Headbutt; 26. Kick; 27. Puncture; 28. Distress call; 29. Polyphenism; 30. Eye protection; 31. Crouching down.

| Species | Antipredator mechanism | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | References | | |
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| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 | 24 | 25 | 26 | 27 | 28 | 29 | 30 | 31 | | | |
| <i>Boana geographica</i> (Spix 1824) | 1 | | 3 | | 5 | | 7 | | 8 | | 9 | | 10 | | 12 | | | | 19 | | 21 | | | | | | | 28 | | 29 | | 30 | 31 | Azevedo-Ramos, 1995; Lima et al., 2005; Angulo et al., 2007; Toledo et al., 2010; Pedroso-Santos et al., 2020a; Pedroso-Santos et al., 2022; Campos & Silva-Soares, 2023; Soares et al., 2023 |
| <i>Boana guentheri</i> (Boulenger 1886) | 1 | | | | | | | | | | 12 | | | | | | | | | | | | | | | | | | | | | | Toledo et al., 2010; Haddad et al., 2013 | |
| <i>Boana lanciformis</i> (Cope 1871) | 1 | | | | | | 7 | | | | 12 | | | | | 16 | | 19 | | | | | | | | | | 28 | | | | | Höld & Gollmann, 1986; Ferreira et al., 2019; Pedroso-Santos et al., 2020a | |
| <i>Boana latistriata</i> *** (Caramaschi & Cruz 2004) | 2 | | | | | | 8 | | | | | | | | | | | | | | | | | | | | | 28 | | | | | Toledo & Haddad, 2009b; Toledo et al., 2010; Haddad et al., 2013 | |
| <i>Boana leptolineatus</i> (Braun & Braun 1977) | 2 | | | | | | 8 | | | | | | | | | | | | | | | | | | | | | | | | | | Toledo et al., 2010; Haddad et al., 2013 | |
| <i>Boana leucocheila</i> (Caramaschi & Niemeyer 2003) | 1 | | | | | | | | | 10 | | | | | | | | | | | | | | | | | | 28 | | | | | Santana et al., 2013 | |



Tabela 1 (cont.). Lista atualizada de mecanismos antipredatórios de *Boana* e *Pristimantis*. 1. Camuflagem correspondente ao fundo; 2. Camuflagem disruptiva; 3. Imobilidade; 4. Canto interrompido; 5. Aposematismo escondido; 6. Investida; 7. Infilção corporal; 8. Contração; 9. Entrelaçamento de membros; 10. Abertura da boca; 11. Alongamento de membros; 12. Tanatose; 13. Reflexo unken; 14. Escalada; 15. Esconder-se; 16. Saltar para longe; 17. Nadar; 18. Som de aviso; 19. Descarga cloacal; 20. Secreção adesiva; 21. Secreção odorífera; 22. Secreção escorregadia; 23. Secreção escorregadia; 24. Mordida; 25. Cabeçada; 26. Chute; 27. Perfurar; 28. Chamada de socorro; 29. Polifenismo; 30. Proteção ocular; 31. Agachamento.

Table 1 (cont.). An updated list of antipredator mechanisms of *Boana* and *Pristimantis*. 1. Matching background camouflage; 2. Disruptive camouflage; 3. Immobility; 4. Interrupted calling; 5. Hidden aposematism; 6. Charging; 7. Body inflation; 8. Contraction; 9. Interweaving limbs; 10. Mouth gape; 11. Stretching limbs; 12. Death feigning; 13. Unken reflex; 14. Climbing; 15. Hiding; 16. Jump away; 17. Swim; 18. Warning sound; 19. Cloacal discharge; 20. Adhesive secretion; 21. Odoriferous secretion; 22. Slippery secretion; 23. Poisonous secretion; 24. Bite; 25. Headbutt; 26. Kick; 27. Puncture; 28. Distress call; 29. Polyphenism; 30. Eye protection; 31. Crouching down.

| Species | Antipredator mechanism | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | References | |
|---|------------------------|---|---|---|---|---|---|---|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|---|--|--|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 | 24 | 25 | 26 | 27 | 28 | 29 | 30 | 31 | | |
| <i>Boana lundii</i> (Burmeister 1856) | 1 | | | | | | 7 | | | | | | | | | | | | | | | | | | | | 28 | | | | | | Toledo & Haddad, 2009b; Haddad et al., 2013; Nascimento et al., 2020 |
| <i>Boana marginata</i> (Boulenger 1887) | 1 | | | | | | 8 | | | | | | | | | | | | | | | | | | | | | | | | | Toledo et al., 2010; Haddad et al., 2013 | |
| <i>Boana microderma</i> (Petry 1977) | 1 | | | | | | | | | | 12 | | | | 16 | | | | | | | | | | | | | | | | | Ferreira et al., 2019 | |
| <i>Boana multifasciata</i> (Günther 1859) | | | | | | | | | | | | | | | | | | | | | | | | | | 28 | | | | | | Forti & Costa-Campos, 2020 | |
| <i>Boana paradisalis</i> (Spix 1824) | 1 | | 3 | 4 | 5 | 7 | 8 | 9 | 10 | 10 | | | | | 16 | 19 | 21 | 21 | | 25 | 27 | 28 | | | | | | | | | This study: Toledo & Haddad, 2009b, Toledo et al., 2011; Heitor et al., 2012; Haddad et al., 2013; Koski et al., 2018; Ferreira et al., 2019 | | |
| <i>Boana polytaenia</i> (Cope, 1870) | | 2 | | | | | 8 | | | | | | | | | | | | | | | | | | | | | | | | | Toledo et al., 2010; Haddad et al., 2013 | |
| <i>Boana pombali</i> (Caramaschi, Pimenta & Feio 2004) | 1 | | 3 | 5 | 8 | | | | | | | | | | | | | | | | | | | | | | 30 | | | | Haddad et al., 2013; Ferreira et al., 2019; Souza et al., 2020b | | |
| <i>Boana prasina</i> (Burmeister 1856) | 1 | | | 5 | | | | | | | | | | | | 19 | | | | | | | | | | | | | | | Toledo et al., 2011; Haddad et al., 2013 | | |

Tabela 1 (cont.). Lista atualizada de mecanismos antipredatórios de *Boana* e *Pristimantis*. 1. Camuflagem correspondente ao fundo; 2. Camuflagem disruptiva; 3. Imobiltidade; 4. Canto interrompido; 5. Aposematismo escondido; 6. Investida; 7. Inflação corporal; 8. Contração; 9. Entrelaçamento de membros; 10. Abertura da boca; 11. Alongamento de membros; 12. Tanatose; 13. Reflexo unken; 14. Escalada; 15. Esconder-se; 16. Saltar para longe; 17. Nadar; 18. Som de aviso; 19. Descarga cloacal; 20. Secreção adesiva; 21. Secreção odorífera; 22. Secreção escorregadia; 23. Secreção venenosa; 24. Mordida; 25. Cabeçada; 26. Chute; 27. Perfurar; 28. Chamada de socorro; 29. Polifenismo; 30. Proteção ocular; 31. Agachamento.

Table 1 (cont.). An updated list of antipredator mechanisms of *Boana* and *Pristimantis*. 1. Matching background camouflage; 2. Disruptive camouflage; 3. Immobility; 4. Interrupted calling; 5. Hidden aposematism; 6. Charging; 7. Body inflation; 8. Contraction; 9. Interweaving limbs; 10. Mouth gape; 11. Stretching limbs; 12. Death feigning; 13. Unken reflex; 14. Climbing; 15. Hiding; 16. Jump away; 17. Swim; 18. Warning sound; 19. Cloacal discharge; 20. Adhesive secretion; 21. Odoriferous secretion; 22. Slippery secretion; 23. Poisonous secretion; 24. Bite; 25. Headbutt; 26. Kick; 27. Puncture; 28. Distress call; 29. Polyphenism; 30. Eye protection; 31. Crouching down.

| Species | Antipredator mechanism | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | References | | | |
|--|------------------------|---|---|---|---|---|---|---|---|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|------------|--|---|--|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 | 24 | 25 | 26 | 27 | 28 | 29 | 30 | 31 | | | | |
| <i>Boana pulchella</i> (Duméril & Bibron 1841) | 1 | | | | 5 | | | 8 | | | | | | | | | | | | | | | | | | | | | | | | | | | Toledo et al., 2010; Haddad et al., 2013 |
| <i>Boana punctata</i> (Schneider 1799) | 1 | | | | | | | | | | 12 | | | | 16 | | | | | | | | | | | | | | | | | | | | Haddad et al., 2013; Ferreira et al., 2019 |
| <i>Boana raniceps</i> (Cope 1862) | 1 | | 3 | | 5 | | 7 | | | 10 | | 12 | | | 15 | | 16 | | 19 | | 21 | | 22 | | | 26 | | 27 | | 28 | | | | Höld & Gollmann, 1986; Toledo & Haddad, 2009b; Toledo et al., 2011; Haddad et al., 2013; Guerra et al., 2018; Ferreira et al., 2019 | |
| <i>Boana semilineata</i> (Spix 1824) | 1 | | 3 | | | | 7 | | 8 | 9 | | | | | | 16 | | 19 | | 21 | | 22 | | | 26 | | | | | | | | | Azevedo-Ramos, 1995; Toledo et al., 2010; Haddad et al., 2013; Ferreira et al., 2019; Campos et al., 2023 | |
| <i>Boana wavrini</i> (Parker 1936) | 1 | | | | 5 | | | | | 10 | | | | | | | | | | | | | | | | | | 28 | | | | | | | Lima et al., 2005 |
| <i>Pristimantis altamazonicus</i> (Barbour & Dunn 1921) | 1 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | Ferreira et al., 2019 |
| <i>Pristimantis chiastonotus</i> (Lynch & Hoogmoed 1977) | 1 | | | | | | | | | | 12 | | | | | | | | | | | | | | | | | | | | | | | | Pedroso-Santos et al., 2022 |
| <i>Pristimantis conspicillatus</i> (Günther 1858) | 1 | | | | | | | 7 | | | | | | | 16 | | | | | | | | | | | | | | | | | | | | Ferreira et al., 2019 |



Tabela 1 (cont.). Lista atualizada de mecanismos antipredatórios de *Boana* e *Pristimantis*. 1. Camuflagem correspondente ao fundo; 2. Camuflagem disruptiva; 3. Imobilidade; 4. Canto interrompido; 5. Aposematismo escondido; 6. Investida; 7. Inflação corporal; 8. Contração; 9. Entrelaçamento de membros; 10. Abertura da boca; 11. Alongamento de membros; 12. Tanatose; 13. Reflexo unken; 14. Escalada; 15. Esconder-se; 16. Saltar para longe; 17. Nadar; 18. Som de aviso; 19. Descarga cloacal; 20. Secreção adesiva; 21. Secreção odorífera; 22. Secreção escorregadia; 23. Secreção venenosa; 24. Mordida; 25. Cabeçada; 26. Chute; 27. Perfurar; 28. Chamada de socorro; 29. Polifenismo; 30. Proteção ocular; 31. Agachamento.

Table 1 (cont.). An updated list of antipredator mechanisms of *Boana* and *Pristimantis*. 1. Matching background camouflage; 2. Disruptive camouflage; 3. Immobility; 4. Interrupted calling; 5. Hidden aposematism; 6. Charging; 7. Body inflation; 8. Contraction; 9. Interweaving limbs; 10. Mouth gape; 11. Stretching limbs; 12. Death feigning; 13. Unken reflex; 14. Climbing; 15. Hiding; 16. Jump away; 17. Swim; 18. Warning sound; 19. Cloacal discharge; 20. Adhesive secretion; 21. Odoriferous secretion; 22. Slippery secretion; 23. Poisonous secretion; 24. Bite; 25. Headbutt; 26. Kick; 27. Puncture; 28. Distress call; 29. Polyphenism; 30. Eye protection; 31. Crouching down.

| Species | Antipredator mechanism | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | References | | | | | | | | | |
|---|------------------------|---|---|---|---|---|---|---|---|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|------------|--|--|--|--|--|--|--|--|-----------------------|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 | 24 | 25 | 26 | 27 | 28 | 29 | 30 | 31 | | | | | | | | | | |
| <i>Pristimantis diadematus</i> (Jiménez de la Espada 1875) | 1 | | | | 5 | | | | | | | | | | 16 | | | | | | | | | | | | | | | | | | | | | | | | Ferreira et al., 2019 | | |
| <i>Pristimantis fenestratus</i> (Steindachner 1864) | 1 | | | | | | | | | | 12 | | | | | | | | | | | | | | | | | | | | | | | | | | | | Lima et al., 2005; Ferreira et al., 2019 | | |
| <i>Pristimantis gutturalis</i> (Hoogmoed, Lynch & Lescure 1977) | 1 | | | | | | | | | | 12 | | | | | | | | | | | | | | | | | | | | | | | | | | | | Pedroso-Santos et al., 2022 | | |
| <i>Pristimantis inguinalis</i> (Parker 1940) | | | | | 5 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | Pedroso-Santos et al., 2022 | |
| <i>Pristimantis paulodutrai</i> (Bokermann 1975) | 1 | | | | | | | | | | 12 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | Haddad et al., 2013; Ferreira et al., 2019 | |
| <i>Pristimantis racemus</i> (Lynch 1980) | | | | | | | | | | | | | | | | | | | | | | | | | | | | 28 | | | | | | | | | | | | Pisso-Florez et al., 2023 | |
| <i>Pristimantis ramagii</i> (Boulenger 1888) | 1 | | | | | | | | | 10 | | 12 | | | | | | | | | | | | | | | | | | | | | | | | | | | | Haddad et al., 2013; Ferreira et al., 2019 | |
| <i>Pristimantis skydmainos</i> (Flores & Rodriguez 1997) | 1 | | | | | 7 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | Ferreira et al., 2019 |



Tabela 1 (cont.). Lista atualizada de mecanismos antipredatórios de *Boana* e *Pristimantis*. 1. Camuflagem correspondente ao fundo; 2. Camuflagem disruptiva; 3. Imobilidade; 4. Canto interrompido; 5. Aposematismo escondido; 6. Investida; 7. Infiliação corporal; 8. Contração; 9. Entrelaçamento de membros; 10. Abertura da boca; 11. Alongamento de membros; 12. Tanatose; 13. Reflexo unken; 14. Escalada; 15. Esconder-se; 16. Saltar para longe; 17. Nadar; 18. Som de aviso; 19. Descarga cloacal; 20. Secreção adesiva; 21. Secreção odorífera; 22. Secreção escorregadia; 23. Secreção venenosa; 24. Mordida; 25. Cabeçada; 26. Chute; 27. Perfurar; 28. Chamada de socorro; 29. Polifenismo; 30. Proteção ocular; 31. Agachamento.

Table 1 (cont.). An updated list of antipredator mechanisms of *Boana* and *Pristimantis*. 1. Matching background camouflage; 2. Disruptive camouflage; 3. Immobility; 4. Interrupted calling; 5. Hidden aposematism; 6. Charging; 7. Body inflation; 8. Contraction; 9. Interweaving limbs; 10. Mouth gape; 11. Stretching limbs; 12. Death feigning; 13. Unken reflex; 14. Climbing; 15. Hiding; 16. Jump away; 17. Swim; 18. Warning sound; 19. Cloacal discharge; 20. Adhesive secretion; 21. Odoriferous secretion; 22. Slippery secretion; 23. Poisonous secretion; 24. Bite; 25. Headbutt; 26. Kick; 27. Puncture; 28. Distress call; 29. Polyphenism; 30. Eye protection; 31. Crouching down.

| Species | Antipredator mechanism | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | References |
|---|------------------------|---|---|---|---|---|---|---|---|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|--|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 | 24 | 25 | 26 | 27 | 28 | 29 | 30 | 31 | |
| <i>Pristimantis vinhai</i> (Bokermann 1975) | 1 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | Haddad et al., 2013; Ferreira et al., 2019 |
| <i>Pristimantis aff. guianensis</i> | 1 | | 3 | | | | 9 | | | | 12 | | | | 16 | | | | | | | | | | | | | | | | 31 | This study |

* Ferreira et al. (2019) used *Boana albomarginatus*; ** Ferreira et al. (2019) used *Boana fasciatus*; *** Ferreira et al. (2019) used *Boana latistriatus*

The crouching down behavior, not covered in the recent antipredator mechanism review by Ferreira et al. (2019), is described by Toledo et al. (2011) as a defensive strategy to avoid subjugation by predators. This behavior may be associated with skin secretion and body puffing, but these synergies were absent during crouching down in *Pristimantis aff. guianensis*. A similar not synergistic behavior was recently observed by Pedrosa-Santos et al. (2020a) in *Boana geographica* and *B. calcarata*.

Death feigning behavior (thanatosis), commonly observed in anurans and triggered by handling, has potential interactions with aposematic color and odoriferous secretions (Toledo et al., 2010; 2011; Ferreira et al., 2019). However, the synergy of death feigning and odoriferous secretion was not observed in *Pristimantis aff. guianensis*. Instead, aposematism, achieved by contrasting the light ventral color with the dark background after death feigning, might be present (Gamberale-Stille, 2001; Toledo & Haddad, 2009a; Barnett et al., 2016). The species' light cream ventral view with tiny gray dots creates a strong contrast with the substrate, potentially serving as an aposematic signal against the predators. In this case, further studies are required to test this hypothesis.

Documenting defensive strategies provides valuable data on the autoecology of the species. This natural history information plays a crucial role in comparative investigations, enhancing our understanding of the evolutionary, behavioral, and trophic aspects of anuran biology. The elucidation of six novel defensive behaviors in an undocumented species (*Pristimantis aff. guianensis*) and three in a well-established species (*B. pardalis*) highlights the importance of fieldwork and direct natural history observation in species sampling. Our findings emphasize the importance of ongoing empirical research, even for well-known species like *B. pardalis*, where comprehensive knowledge of natural history remains limited.

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