**Nota**

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# Limbs interweaving for Neotropical anurans

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ABSTRACT

Anurans have developed a variety of antipredator behaviors, including aposematism, posturing, and leg interweaving, to enhance survival against predators. Leg interweaving, observed in species like *Dendropsophus branneri* and *D. oliverai*, involves crossing limbs and may serve as a displaced behavior rather than a true defense. Unlike species with bright aposematic colors, these frogs rely primarily on camouflage for protection. The variability and limited documentation of leg interweaving highlight the need for further experimental research to clarify its function and significance, contributing to a deeper understanding of the adaptive strategies employed by anurans under predation pressure.

Key Words: Legs interweaving; Anuran behavior; Displaced behavior; Defensive strategies.

Predation has been a crucial selective force driving the evolution of behavioral and life-history traits in amphibians (Wells, 2007). Anurans, in particular, exhibit a wide array of antipredator mechanisms that may act independently or synergistically to enhance survival (Marchisin & Anderson, 1978; Duellman & Trueb, 1994; Toledo *et al.* 2011). These mechanisms fall into 30 categories (Toledo *et al.* 2011) and are classified based on their roles in avoiding detection, preventing attacks, or countering predators. Prevention tactics include aposematism, charging, posturing, escape, and warning sounds (Ferreira *et al.* 2019). Legs interweaving is a postural defense mechanism that may serve to avoid identification, often accompanied by disruptive or aposematic coloration and potentially toxic secretions (Toledo *et al.* 2011). This behavior involves intertwining the limbs and may display bright colors, aid in skin secretion dispersion, or simulate injury, as observed in *Leptodactylus chaquensis* and *Hylomantis aspera* (Toledo *et al.* 2011; Ferreira *et al.* 2019). It was first documented in *Hylambates keithae*, a species endemic to Tanzania (Channing & Howell, 2003). Observations of leg interweaving in *Dendropsophus branneri* and *D. oliverai* suggest it may function as a defensive mechanism or a displaced behavior, warranting further investigation.

Behavioral observations were made alongside a temporary pond located within the campus of Universidade Federal de Pernambuco (UFPE) (8°2'47.84" S 34°57'9.70" O), in the city of Recife, state of Pernambuco, Brazil. The pond surface had an approximate area of 14 m² and was surrounded by herbaceous vegetation, mainly tall grass. On May 29, 2024, the authors visited the pond at night with the objective of collecting couples of *Dendropsophus branneri* for research, and defensive behaviors were recorded upon capture of adult specimens of *D. bran-*

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*neri* and *D. oliveirai*. To document the behavior, the specimens were captured by hand and restrained by one of their forelimbs. Other individuals of *D. branneri* were manually captured, always held by the left forelimb, to allow for free movement of hindlimbs. When the behavior of legs interweaving (the frog turns onto its back, throwing its limbs over its body and displaying aposematic or disturbing colors on its legs and belly), thanatosis (the individual adopts a posture that gives it the appearance of being dead, which can inhibit or deflect the attack of a potential predator), or kicking (the frog is grasped by the head it pushes the predator's face or hands with its hind legs and kicks) occurred, the duration of the behavior was recorded, and the number of kicks was counted. After the behavior ceased, the individuals were released at the original capture site. Handling procedures were conducted under authorization granted by the Sisbio/ICMBio license n°. 84573-1 and approved by the Animal Use Ethics Committee of the Federal University of Pernambuco (protocol n° 141/2022).

The observation of limb interweaving behavior occurred during handling of specimens. A gravid female of *D. branneri* was captured by hand and immediately interwove her hindlimbs (Fig. 1A). Upon collection, it immediately assumed this posture, which lasted approximately 1 minute and 13 seconds. The specimen crossed the right hindlimb over the left. Once she uncrossed her legs, she jumped back into the vegetation. Additional 13 specimens of *D. branneri* were manually captured using the same procedure. Seven exhibited thanatosis (limbs and curving their bodies and retracting their limbs) and maintained this posture for approximately 2 minutes and 35 seconds (minimum 2 minutes and maximum 3 minutes and 10 seconds). Once the posture ended, they jumped back into their natural habitat. The most frequently observed behavior among the *D. branneri* specimens was kicking, performed by eleven of the fourteen individuals. Of these, five were the same individuals that exhibited thanatosis. The kicks were predominantly delivered with the left hindlimb (ten out of eleven), with only one individual kicking with the right hindlimb. While collecting *D. branneri* we accidentally captured a female of *D. oliverai*, which displayed a similar behavior of legs interweaving (Fig. 1C), crossing her right leg over her left. After 1 minute and 15 seconds maintaining this posture, the female return to its resting position and was released into the vegetation.

The most recent report on antipredator mechanisms in anurans was made by Ferreira *et al.* (2019). Extensive research has highlighted interactions between anurans and their predators, encompassing arthropods, fishes, mammals and birds (Toledo 1995, Zug *et al.* 2001). Although many of these records are opportunistic in nature, they play a crucial role in ethological studies, as they provide fundamental insights into animal behavior and the complex interactions between species (Wells 2007), acting as a selective pressure driving the evolution of antipredator strategies in anurans. In this context, behavioral displacement often occurs during defensive actions, manifesting as deviations from typical behaviors or the engagement in seemingly unrelated

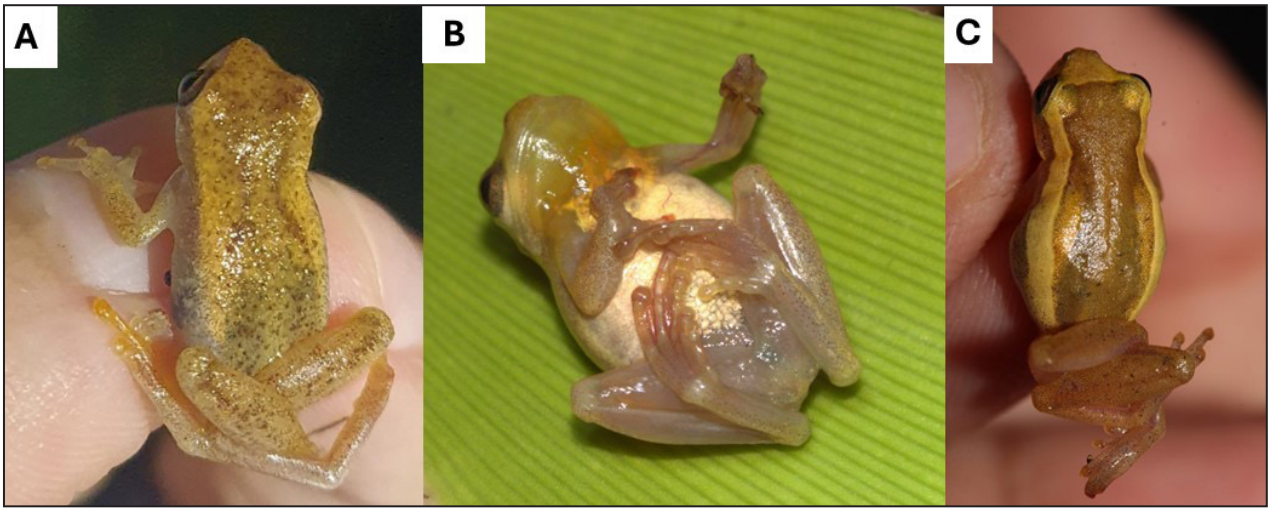


**Figure 1.** Defensive postures of some *Dendropsophus* specimens when handled by their forearm: (A) female *D. braneri* displaying legs interweaving; (B) male *D. branneri* displaying thanatosis; (C) female *D. oliveirai* displaying legs interweaving. All specimens recorded at the campus of Universidade Federal de Pernambuco, in Recife, northeastern Brazil.

activities. This phenomenon indicates that animals may adopt seemingly irrelevant behaviors as coping mechanisms in response to perceived threats or stressors (Lorenz 1966 , Moyer 1967). Understanding this interplay between defensive behavior and displacement can further elucidate the adaptive strategies employed by anurans and other animals under threat, highlighting the nuanced ways in which these species evolve their antipredator mechanisms.

In addition to the records described herein, legs interweaving was documented in ten species of anurans, distributed in five families (Table 1). Interweaving posture varies among different species and can be roughly classified based on limb position: Type 1: interweaving arms and legs over the body ventrally (*Hylambates keithae* – Fig.2A); Type 2: knees in touch and interweaving ankles (*Adenomera hylaedactyla* – Fig. 2H); Type 3: interweaving legs on the back and sides (*Hylomantis aspera* – Fig. 2E); Type 4: interweaving legs and overlap them (*Leptodactylus macrosternum, Leptodactylus latrans* – Fig. 2G and F, respectively); Type 5: interweaving legs over the back (*Physalaemus crombiei* – Fig. 2F); Type 6: interweaving legs in the inguinal region (*Frostius*

**Table 1.** Anuran species for which the behavior of "limb interweaving" has been documented.

| Family | Species | Local | Reference |
|---|---|---|---|
| Bufonidae | *Frostius pernambucensis* | Alagoas (Brazil) | Ramos *et al.* (2021) |
| Craugastoridae | *Haddadus binotatus* | Bahia (Brazil) | Rojas-Padilla *et al.* (2019) |
| Hylidae | *Bokermannohyla oxente* | Bahia (Brazil) | Souza *et al.* (2020) |
| | *Dendropsophus branneri* | Perrnambuco (Brazil) | present |
| | *Dendropsophus oliverai* | Pernambuco (Brazil) | present |
| | *Hylomantis aspera* | Bahia (Brazil) | Gally *et al.* (2014) |
| | *Scinax tripui* | Minas Gerais (Brazil) | Vieira *et al.* (2022) |
| Hyperolidae | *Hylambates keithae* | Tanzania | Channing & Howell (2003) |
| Leptodactylidae | *Adenomera hylaedactyla* | Piauí (Brazil) | Eduardo *et al.* (2021) |
| | *Leptodactylus macrosternum* | São Paulo; Paraná; Pernambuco (Brazil) | Lourenço-de-Moraes *et al.* (2014); Santiago *et al.* (2021) |
| | *Leptodactylus latrans* | Espírito Santo (Brazil) | Mathielo *et al.* (2022) |
| | *Physalaemus crombiei* | Espírito Santo (Brazil) | Mathielo *et al.* (2022) |

*pernambucensis*, *Haddadus binotatus*, *Bokermannohyla oxente, Dendropsophus branneri, D. oliverai* and *Scinax tripui* – Fig. 2A and C, and Fig. 2B, C, D, respectively).

Given that in our study only one specimen out of 14 *Dendropsophus branneri* (ten males and four females) displayed legs interweaving behavior, we hypothesize that it may represent a case of displaced behavior, instead of a defensive mechanism. Displacement activities are behavioral patterns exhibited by an animal that are apparently irrelevant to its ongoing activity (Tinbergen 1952) and may be categorized as displaced when evaluated in terms of the expected norms compared to the actual behavior observed in other individuals. This behavior can occur, for example, in conflict situations (McFarland 1966). There are different hypotheses about the emergence of displacement activities. Some authors suggest that tension builds up during conflict and is released in some way through the performance of displacement activity (e.g., Tinbergen 1952). Others propose that conflicting tendencies inhibit each other, allowing a third and irrelevant tendency to manifest, thus giving rise to displacement activity (e.g., van Iersel & Bol 1958). In rhesus monkeys, displacement activities are anxiety signals (Maestripieri *et al.* 1992b). Other examples of atypical behavior in Anura include reproductive displacement in *Anaxyrus fowleri* and *Anaxyrus terrestris* during their release calls (Leary 2011), and in *Phyllomedusa bicolor*, where a male separates nearby pairs in amplexus (Venâncio & Melo-Sampaio 2010).

Some species exhibit defensive mechanisms to display their aposematic coloration, which is plesiomorphic in Anura and shows numerous apomorphies across families (Toledo & Haddad, 2009). This display involves bright colors (such as red, blue, orange, or yellow), hypertrophied glands,

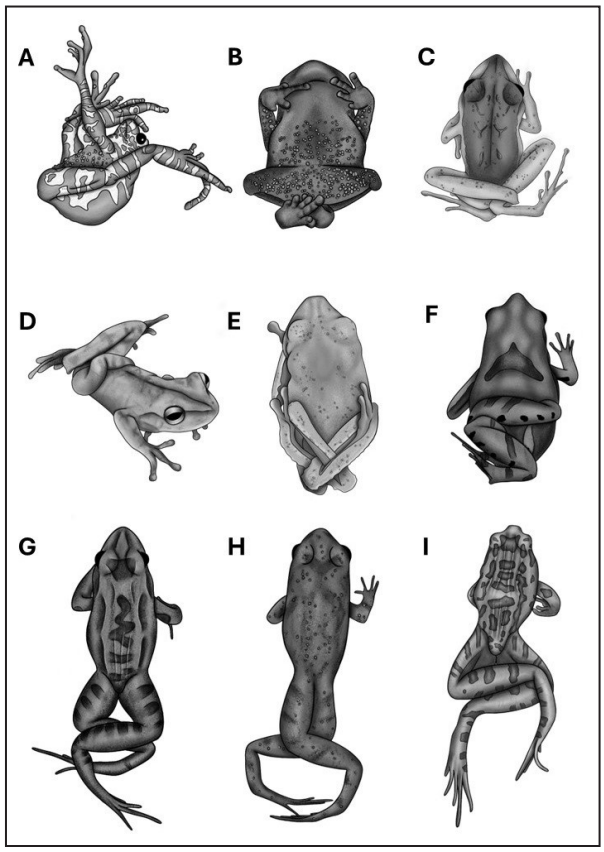


**Figure 2.** Anurans species showing legs interweaving when threatened by a potential predator: (A) *Hylambates keithae* (Channing & Howell 2003), (B) *Frostius pernambucensis* (Ramos *et al.* 2021), (C) *Haddadus binotatus* (Rojas-Padilla *et al.* 2019), (D) *Bokermannohyla oxente* (Souza *et al.* 2020), (E) *Hylomantis aspera* (Gally *et al.* 2014), (F and G) *Physalaemus crombiei* and *Leptodactylus latrans,* respectively (Mathielo *et al.* 2022), (H) *Adenomera hylaedactyla* (Eduardo *et al.* 2021) and I: *Leptodactylus macrosternum* (Lourenço-de-Moraes *et al.* 2014).

or eye-shaped spots located on the dorsum, axilla, underside of the body, thighs, or postfemoral region (Toledo & Haddad, 2009). These features act as deceptive signals to disorient and confuse attacking predators or to warn them of the presence of toxins or unpalatability (Siddiqi *et al.* 2004). Based on observations of defensive behaviors of *Adenomera hylaedactyla, Bokermannohyla oxente* and *Haddaus binotatus*, authors claim that legs interweaving is not related with aposematism because of the absence of bright coloration, hypertrophied glands, or eye-shaped spots on their bodies indicating the presence of toxins and unpalatability (Ferreira *et al.* 2019, Souza *et al.* 2020). We suggest that legs interweaving in *D. branneri* and *D. oliverai* are also not related with aposematism, due to the lack of warning colors. It is known that the skin of *Hyla* species (the former genus that included *H. branneri* and *H. oliverai*) produces a diverse array of bioactive peptides that act as a first line of defense against predators and pathogens. These peptides are stored in specialized glands and secreted onto the skin surface when the frog is threatened (Wu *et al.* 2011, Chai *et al.* 2021, Yin *et al.* 2023). For *Dendropsophus* species, there is a gap in knowledge regarding the composition of secretions produced and stored in their skin, and therefore it cannot be confirmed whether or not they possess any toxic substances that function as a defense against predators. It is well known that frogs in genus *Dendropsophus* employs camouflage with disruptive coloration as a defense mechanism to avoid detection. This involves the use of contrasting markings to make the detection of body edges and boundaries more challenging for predators. This coloration may manifest as light dorsal stripes (as seen in *D. oliverai*), irregular spots or patches, dark lines around the eyes, or ocular markings (as in *D. branneri*) (Wells 2007).

It is possible that legs interweaving is actually a type of displaced behavior and that, at least in *D. branneri*, individuals will generally count on alternative defensive strategies (kicking, feigning death) when threatened by a potential predator. Most records of legs interweaving to date were based on a small number of observations conducted in the field, and the resulting display is extremely variable (Fig. 2). Hence, the study of potential alternative defensive mechanisms in anurans would greatly benefit from experimental approaches, with an increased number of samples and well-defined experimental controls.

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