

Behavioural defences of anurans: an overview

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Among vertebrates, defensive behaviours have been reviewed for fishes, salamanders, reptiles, birds, and mammals, but not yet for anuran amphibians. Although several defensive strategies have been reported for anurans, with a few exceptions these reports are limited in scope and scattered in the literature. This fact may be due to the lack of a comprehensive review on the defensive strategies of anurans, which could offer a basis for further studies and insights on the basic mechanisms that underlie these strategies, and thus lead to theoretical assumptions of their efficacy and evolution. Here we review the present knowledge on defensive behavioural tactics employed by anurans, add new data on already reported behaviours, describe new behaviours, and speculate about their origins. A total of 30 defensive behaviours (some with a few sub-categories) are here recognised. The terminology already adopted is here organised and some neologies are proposed. Some of the behaviours here treated seem to have an independent origin, whereas others could have evolved from pre-existent physiological and behavioural features. The role of predators in the evolution of defensive behaviours is still scarcely touched upon and this overview adds data to explore this and other evolutionary unsolved questions.

KEY WORDS: animal behaviour, anuran amphibians, defensive strategies, predation.

INTRODUCTION

The commonest defensive strategy of mobile animals is to remain motionless or to flee from potential predators. However, there is a wide array of defensive strategies that are alternatively used to cope with the risk posed by a predator. Anurans, in particular, display a wide range of behaviours between remaining motionless and fleeing extremes (e.g. DODD 1976; WILLIAMS et al. 2000; TOLEDO et al. 2005, 2010). Even when

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remaining motionless or whilst fleeing, anurans may employ different synergistic tactics to enhance their survival chances (e.g. MARCHISIN & ANDERSON 1978), especially in an environment in which almost every carnivorous organism may prey on a frog (reviews in TOLEDO 2005; TOLEDO et al. 2007a).

Different defensive strategies act in different phases of predation: localisation, identification, approach, subjugation, ingestion, and digestion. Thus, primary (those that do not depend on the presence of a predator) and secondary (those that are elicited by the presence of a predator) defensive strategies may have evolved to hamper or stop a predation attempt in one or more of these phases (EDMUNDS 1974). For example, a cryptic anuran may avoid detection and a venomous anuran may avoid ingestion. As a consequence, the evolution of defensive strategies is directly related to the senses predators employ to locate and handle their prey (e.g. GREENBAUM 2004). In some cases, predators may evolve strategies that overcome anuran defences, thus generating predator-prey arms races (e.g. BRODIE & BRODIE 1999).

Gathering data on defensive strategies of anurans in the field is not a difficult task; nevertheless, few extensive studies have been published (e.g. WILLIAMS et al. 2000). Most studies rely on scattered data, available as short notes (e.g. SAZIMA 1978; TOLEDO et al. 2005). The lack of comprehensive papers focusing on defensive strategies of anurans may be due to the lack of overviews which would organise current knowledge, lead to further discussion, and provide a starting point for more broad studies (see also TOLEDO & HADDAD 2009a).

Taxa-restricted reviews on animal defensive behaviours have been published on invertebrates, mostly insects (e.g. EVANS & SCHMIDT 1990; EISNER 2005), although such reviews are also available for fishes (RANDALL 2005; ZACCONE et al. 2009), reptiles (GREEN 1988), birds, and mammals (CARO 2005). For amphibians, knowledge on defensive behaviours of salamanders and newts (order Caudata) is reviewed in the extensive work of BRODIE JR and colleagues (e.g. BRODIE 1977, 1983, 1990; BRODIE et al. 1984; WILLIAMS et al. 2000). However, no such review is available for post-metamorphic anuran amphibians (order Anura). Recently, two of us published a review on the use of colouration and morphological traits in defensive strategies (TOLEDO & HADDAD 2009a), but behaviour was not the focus of the study.

Our aim with the present overview is not to draw from all the reports available on anuran defensive behaviours, but to provide a comprehensive view of the variety of defensive strategies in this vertebrate group. Thus, we collected what we regard as representative information on anuran behaviours for an overview that would encompass most, if not all, the defensive repertoires of post-metamorphic anurans. Besides reviewing the literature, we add new data based on naturalistic observations and experiments in the field and laboratory, and propose here some neologies that complement the terminology already in use.

MATERIALS AND METHODS

Major herpetological journals (e.g. *Amphibia-Reptilia*, *Copeia*, *Herpetologica*, *Herpetological Bulletin*, *Herpetological Journal*, *Herpetological Review*, and *Journal of Herpetology*) were searched for reports on anuran defensive behaviours (both natural and experimental conditions were considered for this review).

New data were obtained during several field trips from 1969 to 2009 in Brazil, mainly in the biomes of the Cerrado and the Atlantic rainforest. Besides this, a few data were collected in Panama (2005) and South Africa (2007). Staged encounters in the field were made by approaching an individual frog and recording its reaction to close approach, handling, grasping suddenly, hitting it gently with sticks (on the head and dorsum), lightly pinching the head, arms, and legs with

a blunt forceps, or by presenting the frog to a non-venomous snake (generally an adult Dipsadidae, *Liophis miliaris*). Although none of these procedures injure the frogs, they are regarded as effective in simulating predators' attacks, and thus to produce defensive responses in anurans (BRODIE 1977; BRODIE et al. 1998; WILLIAMS et al. 2000; TOLEDO et al. 2005; TOLEDO & HADDAD 2009b).

Experiments with captive anurans were generally avoided (although a few data were obtained from less than 1 week captive frogs), since the more a frog remains captive, the more it may change its physiological traits (NAVAS & GOMES 2001) and, thus, it may present both quantitative and qualitative changes in its defensive behaviours (BOICE & WILLIAMS 1971; pers. obs.).

In the results section, we present behaviours that involve staying motionless before those that involve movement. The presence/absence of defensive behaviours are presented in tables, with some of them highlighting specific characteristics, such as display of other behaviours, habitat use, diet, and colours. All scientific names of amphibians follow FROST (2010). Defensive strategies reviewed elsewhere (TOLEDO & HADDAD 2009a, 2009b; TOLEDO et al. 2010) are not described in detail in the present study.

RESULTS

Defensive behaviours in anurans are here organised into 30 categories (Table 1), described below. The most commonly observed defensive behaviour was fleeing,

Table 1.
Defensive strategies presented by post-metamorphic anurans and their putative main function against predators.

#	Behaviour	Variation	Possible main function against predators
1	Immobility or remaining motionless		Avoid visualisation
2	Crouching down		Avoid subjugation
3	Thanatosis or death feigning		Avoid subjugation
4	Contracting		Avoid injuries during subjugation and ingestion
5	Chin-tucking		Avoid subjugation
6	Phragmosis		Avoid subjugation
7	Puffing up the body		Avoid subjugation
8	Body-raising	Legs vertically stretched	Avoid subjugation
		Legs laterally stretched	Avoid subjugation
9	Body-tilting		Avoid subjugation
10	Stiff-legged behaviour		Avoid visualisation
11	Head-up sharp bend		Avoid subjugation
12	Eye-protection		Avoid injuries during subjugation and ingestion
13	Unken reflex		Avoid subjugation

(Continued)

Table 1.
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#	Behaviour	Variation	Possible main function against predators
14	Legs-interweaving		Avoid identification
15	Flipping onto the back		Avoid subjugation
16	Hiding		Avoid visualisation
17	Digging		Avoid visualisation
18	Active escape or fleeing		Avoid subjugation
19	Cloacal discharge	Liquid	Avoid subjugation
		Solid (defecation)	Avoid subjugation
20	Charging		Avoid subjugation
21	Head hitting		Avoid subjugation
22	Biting		Avoid subjugation
23	Mouth-gaping		Avoid subjugation
24	Tongue protrusion		Avoid subjugation
25	Fighting		Avoid ingestion
26	Spine aggression	Spine-puncturing	Avoid ingestion
		Spine-scratching	Avoid ingestion
		Spine-hurting	Avoid ingestion
27	Phalanx aggression		Avoid ingestion
28	Regurgitating		Avoid ingestion
29	Defensive vocalisation	Distress calls	Avoid ingestion
		Warning calls	Avoid subjugation
		Alarm calls	Avoid subjugation or ingestion
30	Production of secretions	Odoriferous	Avoid ingestion
		Adhesive	Avoid ingestion
		Noxious	Avoid ingestion/digestion
		Slippery	Avoid subjugation

followed by remaining motionless, which together represented about 50% of the records (Fig. 1).

(1) *Immobility or remaining motionless*

Remaining motionless in the same posture the frog held before the approach of a threat (which, besides the observers, could occasionally be a predator or a larger animal passing nearby) is widespread. Individuals of all species observed in the field remained motionless as a first line of defence during the approach of a potential predator. In

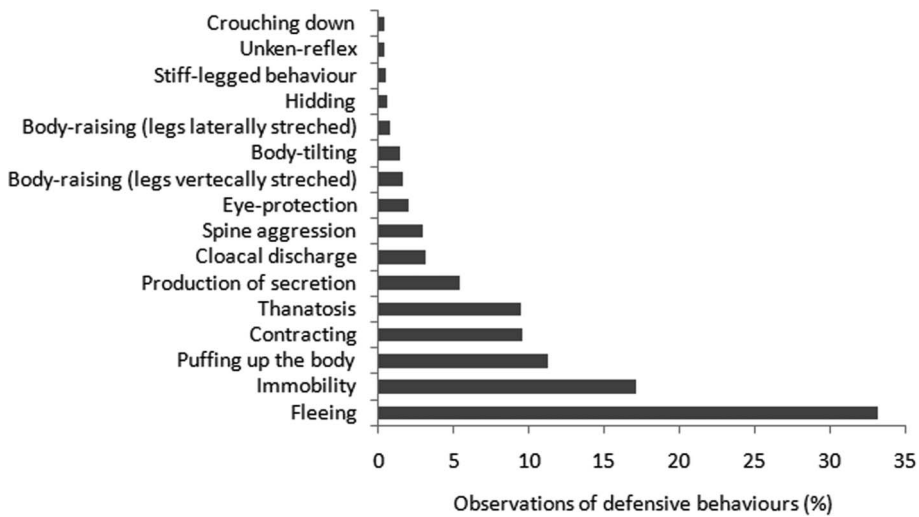


Fig. 1. — Percentage of field records of selected anuran defensive behaviours.

experimental conditions this strategy was successful in two cases: one adult male of *Bokermannohyla circumdata* and one adult male of *Dendropsophus elianeae* (Hylidae) remained motionless when offered to a dipsadid snake (*Liophis miliaris*). As a result, they apparently went unnoticed by the snake, and were not preyed upon.

Possible synergistic behaviours. Immobility is the basis of most of the behaviours discussed below, including fleeing, which may precede or follow a motionless period. Additionally, colouration, morphology, and granular glands may enhance immobility.

(2) *Crouching down*

The frog holds itself in a lower than the habitual sitting posture, ranging from a slightly lowered position to a full crouch in which the chin touches the substrate. The eyes may remain closed and the forearms may be extended forward or flexed toward the body. This behaviour was observed in some species and is found in the literature (see Appendix 1, available online, and Fig. 2A).

Possible synergistic behaviours. Chin-tucking (see below) is almost always present, and puffing up the body and skin secretions may co-occur with this behaviour (Fig. 2A).

(3) *Thanatosis or death feigning*

This behaviour (Fig. 2B) was recently reviewed by TOLEDO et al. (2010) and the misuse of this terminology is commented upon.

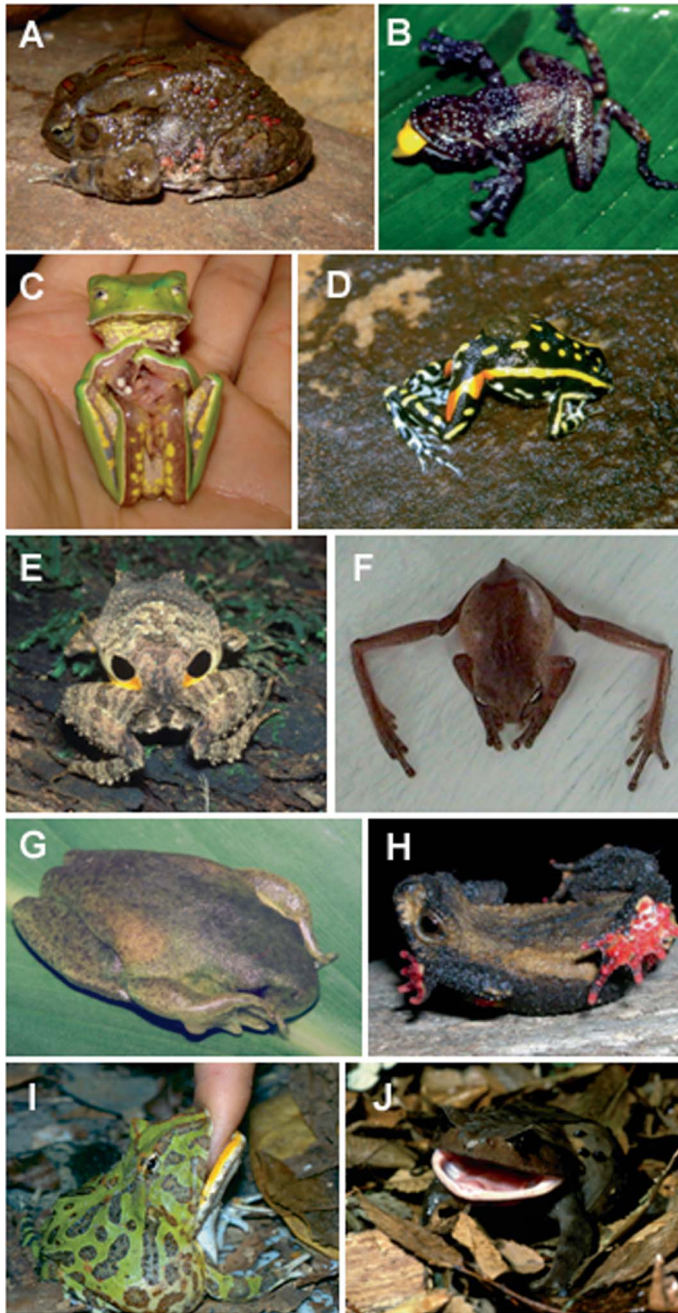


Fig. 2. — A sample of anuran defensive behaviours. (A) Crouching down by *Amietophrynus garmani* (Bufonidae); note white secretions expelled by the parotoid glands; (B) thanatosis and tongue protrusion in *Acanthixalus spinosus* (Hyperoliidae); (C) contracting in *Phyllomedusa bahiana* (Hyllidae); (D) body-raising with legs vertically stretched (partial) in *Ameerega flavopicta* (Aromobatidae) and (E) the same with eyespot-like glands in *Edalorhina perezii* (Leiuperidae); (F) body-raising with legs laterally stretched (full) in *Aplastodiscus cochranae* (Hyllidae) in dorsal view; (G) eye-protection in *Aplastodiscus perviridis* (Hyllidae); (H) full unken reflex in *Melanophryniscus* sp. (Bufonidae); (I) biting by *Ceratophrys joazeirensis* (Ceratophryidae); and (J) mouth-gaping by *Megophrys* sp. (Megophryidae).

(4) Contracting

This behaviour (Fig. 2C) was recently reviewed and placed apart from thanatosis (see TOLEDO et al. 2010).

(5) Chin-tucking

This behaviour is recorded for several species (Appendix 1, available online) and is characterised by the chin pulled toward the pectoral region, flexing the head towards the belly. Eyes may be closed in some cases. Although probably widespread, reports on this behaviour are scarce, probably because it precedes other, more conspicuous behaviours in most cases.

Possible synergistic behaviours. Chin tucking may precede or be part of crouching, contracting, phragmosis, and puffing the body up.

(6) Phragmosis

During this defensive behaviour the frog uses its head to obstruct the access to its body. Thus, there must be a tunnel-like structure to shelter the frog's body. Species known to use phragmosis use rock crevices, burrows, tree holes, or bromeliads as shelter (BARBOUR 1914; STUART 1935; LUTZ & LUTZ 1939; FIRSCHEIN 1951; DUELLMAN & KLAAS 1964; JARED et al. 2005). Besides the species cited by these authors, we also observed this behaviour for *Rhinella granulosa* (Bufonidae), *Aparasphenodon bokermanni* (Hylidae), and suggest the inclusion of the hylid *Anotheca spinosa* in this defensive category (see "Evolution of defensive behaviours" below).

Possible synergistic behaviours. Chin-tucking is almost always present and puffing up the body may be present in some cases. Presence of bony spines associated with noxious glands in the head may be related to phragmosis as well (see JARED et al. 2005).

(7) Puffing up the body

This behaviour consists of filling the lungs with air, and thus enlarging the frog's size. It may be displayed whilst on the ground or in vegetation, floating in the water, or while seized by a predator. During the deflation of the lungs, some bufonids may emit a noise produced by the expiration. In snakes a similar noise is considered a defensive strategy (MARTINS 1996). For anurans there is no evidence that it would function as a defensive behaviour.

Possible synergistic behaviours. Puffing up the body may be accompanied by crouching, chin-tucking, thanatosis, phragmosis, body-raising, body-tilting, mouth-gaping, and eye protection (for the four latter behaviours, see below).

(8) Body-raising

Two types ("legs vertically stretched" and "legs laterally stretched") of body-raising are considered here:

- (a) *Body-raising with legs vertically stretched.* This behaviour is described mostly for toxic species (Appendix 2, available online). This body-raising type may

be displayed in two forms: (i) partial, in which the frog stretches the legs vertically and keeps its snout close to, or touching, the ground (Fig. 2D–E); or (ii) full, in which the frog stretches the legs and arms, thus lifting its belly and snout off the ground. In both postures the eyes may be closed and aposematic colours and eyespot-like glands (which were hidden in the normal posture) may be displayed (Fig. 2E).

- (b) *Body-raising with legs laterally stretched*. In this type of body-raising, the frog stretches the hind limbs, keeping its snout close to, or touching, the ground, similarly to the partial body-raising; however, it also stretches the legs laterally in such a way that in its extreme the legs are stretched in front of the snout (Appendix 2, available online, and Fig. 2F).

Possible synergistic behaviours. Body-raising of both types is closely related to puffing up the body (almost always present) and body-tilting (almost always present), and is common in species with noxious or odoriferous skin secretion. Eye-protection (most common among species that display body-raising of the first type) and mouth-gaping may co-occur with body-raising (most commonly among species that display body-raising with legs laterally stretched).

(9) *Body-tilting*

Upon close proximity to a potential predator, during which time tactile contact may be the strongest stimulus for the display of a defensive behaviour, a body-raising frog may direct its dorsum towards the predator (Appendix 2, available online).

Possible synergistic behaviours. Body-tilting always involves body-raising (both types) and is strongly marked by the presence of puffing up the body, a display of glands and aposematic colouration, and skin secretions (noxious, odoriferous, or slippery).

(10) *Stiff-legged behaviour*

This peculiar behaviour, as described by SAZIMA (1978), is a motionless behaviour preceded by short leaps. After leaping once or a few times in an erratic way, the frog ends with its body flattened and limbs stretched backwards. This defensive behaviour is known for a few Neotropical species that dwell on the forest floor and have cryptic colouration of fallen brown or green leaves (SAZIMA 1978; SCHLÜTER & SALAS 1991; ROCHA et al. 1998; GARCIA 1999; TOLEDO & ZINA 2004; BERTOLUCI et al. 2007; MENIN & RODRIGUES 2007; GIARETTA & MARTINS 2009). Besides the species listed by these authors, we also observed this behaviour in *Euparkerella cochranæ* (Brachycephalidae), *Paratelmatobius poecilogaster* (Leptodactylidae), *Dendrophryniscus berthaltutzae* (Bufonidae), and *Proceratophrys melanopogon* (Cycloramphidae). KOLENC et al. 2009 misinterpreted the stiff-legged behaviour displayed by *Pleurodema bibroni*, cited in their paper as death feigning (see their fig. 7B).

Possible synergistic behaviours. Stiff-legged behaviour is related to cryptic (leaf-like) dorsal colouration. No other defensive behaviour has been reported to co-occur with this behaviour.

(11) Head-up sharp bend

This behaviour was recently described for the megophryid *Leptobrachium smithi*, during which the frog arches its back, elevating the head about 90° from the ground. During this behaviour the contrasting coloured eyes are kept open, the forearms are outstretched, and the frog remains motionless (see CHUAYNKERN et al. 2007 and a picture therein).

(12) Eye-protection

While remaining motionless in chin-tucking or other defensive postures, some frog species may cover the head, eyes, and/or the tympanum with the forearms. Some species may slightly arch the body upwards while displaying eye protection behaviour (some individuals close the eyes while in the arched posture). This behaviour was described for a variety of species (see HABERL & WILKINSON 1997; MCCALLUM 1999; VRCIBRADIC & VAN SLUYS 2000; WILLIAMS et al. 2000; ANDREONE 2002; MCCALLUM et al. 2003; DAS et al. 2004; MEANS 2004; ANGULO & FUNK 2006; WILKINSON 2006) and we also observed it in the hylids *Aplastodiscus albosignatus*, *A. cochranæ*, *A. leucopygius*, *A. perviridis* (Fig. 2G), *Bokermannohyla izecksohni*, and *Hypsiboas albopunctatus*.

Possible synergistic behaviours. Puffing up the body and body-raising may come with eye-protection. Additionally, some species produce odoriferous secretions.

(13) Unken reflex

This behaviour is known for species of the genera *Bombina* (Bombinatoridae), *Melanophryniscus* (Bufonidae), *Pseudophryne* (Myobatrachidae), and *Smilisca* (Hylidae) (FIRSCHEIN 1951; BAJGER 1980; CEI 1980; HABERL & WILKINSON 1997; WILLIAMS et al. 2000; BRUSQUETTI et al. 2007). Besides the species cited above we observed the unken reflex in *Melanophryniscus cambaraensis*, *M. moreirae*, *M. fulvoguttatus*, *M. pachyrhynchus*, and *M. cf. tumifrons*. The unken reflex involves withdrawing and lifting the four legs off the substratum and arching the body, showing contrasting aposematic colours on the belly, throat, and ventral surfaces of the feet and hands (except for *Smilisca fodiens*, which do not present conspicuous colourations, see FIRSCHEIN 1951). While displaying the unken reflex, the frog may close its eyes and produce noxious secretions.

This behaviour shows individual presence/absence variation (LÖHNER 1919) and variation in the extent to which it is displayed (BAJGER 1980). Young *Bombina* sp., which have no contrasting abdominal colours, do not display the unken reflex (LÖHNER 1919). In adult *Bombina* spp. and *Melanophryniscus* spp., the behaviour may vary from a partial unken reflex to a full one (sensu BAJGER 1980). In the full unken reflex the bright ventral colour is clearly visible (Fig. 2H) and the eyes are closed. In the partial unken reflex the limbs are off the ground, the bright ventral colour is sometimes visible, and the eyes are open. The species that were recorded displaying the full unken reflex also displayed the partial one, although the opposite was not recorded (BAJGER 1980; present study).

Possible synergistic behaviours. Unken reflex may be accompanied by noxious secretions, puffing up the body (BAJGER 1980), and ventral aposematic colours as a rule (except for *Smilisca fodiens*).

(14) *Legs-interweaving*

This unusual behaviour has been described only for the hyperoliid *Phlyctimantis keithae*. When disturbed the frog twists onto its back, throwing its limbs across the body and displaying aposematic or disruptive colours on its legs and belly. This behaviour breaks the outline of the frog (CHANNING & HOWELL 2003).

Possible synergistic behaviours. Legs-interweaving is accompanied by disruptive or aposematic colour patterns and possibly by the presence of noxious secretions.

(15) *Flipping onto the back*

Some frogs when frightened may jump and end with the belly facing upwards (*Scinax hiemalis* and *Melanophryniscus cambaraensis*: present study), or they may just flip onto the back (*Pseudophryne bibronii* and *P. semimarmorata*: WILLIAMS et al. 2000), generally displaying aposematic (warning) colours.

Possible synergistic behaviours. Immobility followed by thanatosis and eventual fleeing.

(16) *Hiding*

This behaviour involves movements behind or under an object, such as a leaf fallen on the ground, dead or live vegetation, or into burrows or crevices.

(17) *Digging*

Some individuals of a few species (*Leptodactylus mystaceus*, *Eupemphix natereri*, *Odontophrynus americanus*, *Proceratophrys cururu*, *P. moratoi* (present study), *Gastrophryne carolinensis*, and *Scaphiopus holbrookii* (MARCHISIN & ANDERSON 1978)) when disturbed or cornered bury themselves in the ground by digging with their hindlimbs. All these species are fossorial (burrowing) for at least a period of the year.

(18) *Active escape or fleeing*

This widespread behaviour may be used by all anuran species. Indeed, all individuals of the species observed in the field tried to escape. This escape can be either quick and erratic, or slower but directed and vigorous. Besides fleeing in any direction, the frog may also move backward, climb, walk, jump into the water, enter into a burrow, or parachute (e.g. ROBERTS 1994; WELLS 2007).

There is a particular case of fleeing, called “balling behaviour”, described for bufonid species of the genus *Oreophrynella*: *O. nigra*, *O. quelchii*, and *O. vasquezii*. The frogs adopt a crouched posture with chin-tucking, and fold their arms and legs under the body; further, when they are on a sloping terrain, they would move downhill as would a rolling stone (MCDIARMID & GORZULA 1989). A similar behaviour was observed for the salamander *Hydromantes platycephalus* (Plethodontidae) and was referred to as “rolling escape” (GARCÍA-PARÍS & DEBAN 1995).

Possible synergistic behaviours. Fleeing may be accompanied with liquid cloacal discharge, defensive calls, and flash colours. Balling behaviour may be accompanied by aposematic colourations, and erratic jumps can be followed by stiff-legged behaviour.

(19) Cloacal discharge

When a frog is seized by, or fleeing, from a predator it generally discharges wastes from the cloaca. The discharged material may be liquid or solid. Liquid cloacal discharge (extrusion of bladder contents) is the commonest behaviour, occurring in many species (Appendix 2, available online). Solid discharge or defecation (faeces expelled with force from the intestine) was reported for the bufonid *Anaxyrus terrestris* only, when seized by a snake (MARCHISIN & ANDERSON 1978).

Possible synergistic behaviours. Cloacal discharge occurs during fleeing or fighting a predator. Besides this, it may co-occur with puffing up the body.

(20) Charging

Cornered anurans may charge at the predator as an intimidating technique. This behaviour was observed for the leptodactylids *Leptodactylus labyrinthicus*, *L. latrans*, the ceratophryids *Ceratophrys aurita* and *C. joazeirensis*, and the bufonid *Rhinella rubescens* (present study). All these are large species, generally larger than 7 cm SVL.

Possible synergistic behaviours. While charging the frog may emit warning calls, display mouth-gaping and/or aposematic colouration, puff up the body, and display body-raising. If the frog gets close to the predator, charging may end in biting or head hitting.

(21) Head hitting

Some leptodactylids (*Leptodactylus bolivianus*, *L. chaquensis*, *L. latrans*, and *L. podicipinus*) are known to hit predators with the head. In all these instances the frogs were females guarding foam nests or tadpoles (VAIRA 1997; PRADO et al. 2000; present study). Head hitting was also displayed by one bufonid (*R. rubescens*), but it was not related to parental care (present study).

Possible synergistic behaviours. Charging generally precedes head hitting.

(22) Biting

This defensive tactic is reported for 16 frog species, and we add here seven species to this list: *Ceratophrys aurita*, *C. joazeirensis*, *Cycloramphus acangatan*, *C. eleuthero-dactylus*, *C. lutzorum*, *Cycloramphus* sp., and *Hemiphractus johnsoni* (Appendix 3, available online, and Fig. 21).

Possible synergistic behaviours. Puffing up the body and body-raising are related to biting. Besides this, biting may be preceded or followed by mouth-gaping.

(23) *Mouth-gaping*

Mouth-gaping is reported at least for three frog species, *Eupsophus emiliopugini* (FORMAS & POBLETE 1996), *Hemiphractus fasciatus* (MYERS 1966), and *Gastrotheca helenae* (DUELLMANN & TRUEB 1994). While handling or approaching some frogs in the field we also observed mouth-gaping for 15 other species (Appendix 3, available online, Fig. 2J).

Some individuals of *Hemiphractus fasciatus* and *Haddadus binotatus* may arch (slightly or vigorously, respectively) the body backwards during mouth-gaping displays (MYERS 1966; present study).

Possible synergistic behaviours. All species that display mouth-gaping also emit defensive vocalisations (except for *C. acangatan* and *Brachycephalus* spp., which were not tested for distress calls, and *P. boiei*, for which we tested four individuals), but these two behaviours cannot be linked as a sequence of events. A mouth-gaping display may precede charging, and may be preceded or followed by biting.

(24) *Tongue protrusion*

PERRET (1961) described this behaviour for the hyperoliid *Acanthixalus spinosus*: the frog half-closes its eyes, keeps its limbs motionless and close to the body, and protrudes its orange/yellow tongue (Fig. 2B).

Possible synergistic behaviours. This behaviour may be displayed while in relaxed thanatosis.

(25) *Fighting*

During subjugation by a potential predator, a frog may fight. The most commonly observed movements while fighting were holding (frogs that have adhesive disks hold onto nearby objects and try to pull themselves out of the predator's hands or mouth) and kicking (when the frog is grasped by the head it pushes the predator's face or hands with its hind legs and kicks).

Possible synergistic behaviours. Spine aggression, puffing up the body, production of secretions (odoriferous, noxious, or adhesive), defensive vocalisations (distress or alarm calls), cloacal discharge, regurgitating, and biting.

(26) *Spine aggression*

Use of spines of the prepollex, prehallux, chest, and/or head as a defence is recorded for several frog species (Appendix 1, available online). However, not all species that present spines use them in defence. This is, for example, the case of species of the *Hypsiboas pulchellus* group (Hylidae), of which we tested several individuals of *Hypsiboas beckeri*, *H. bischoffi*, *H. caingua*, *H. guentheri*, *H. leptolineatus*, *H. polytaenius*, *H. prasinus*, and *H. pulchellus*, and species of the genus *Crossodactylus* (Hylodidae) as well. Species that do not use their spines defensively are smaller than those that use their spines (ANOVA $F = 65.87$; $P < 0.001$; $n = 48$ individuals; $df = 8$: Fig. 3). We divided spine aggression into three types. (i) Spine-puncturing is the piercing of spines of the frog's prepollex against any reachable body part of a predator (e.g. skin, tympanum, eyes, and oral mucosa). (ii) Spine-scratching is the use of spines on the frog's prepollex, prehallux or claws in the terminal phalanges (as of *Xenopus* spp.) to scratch any

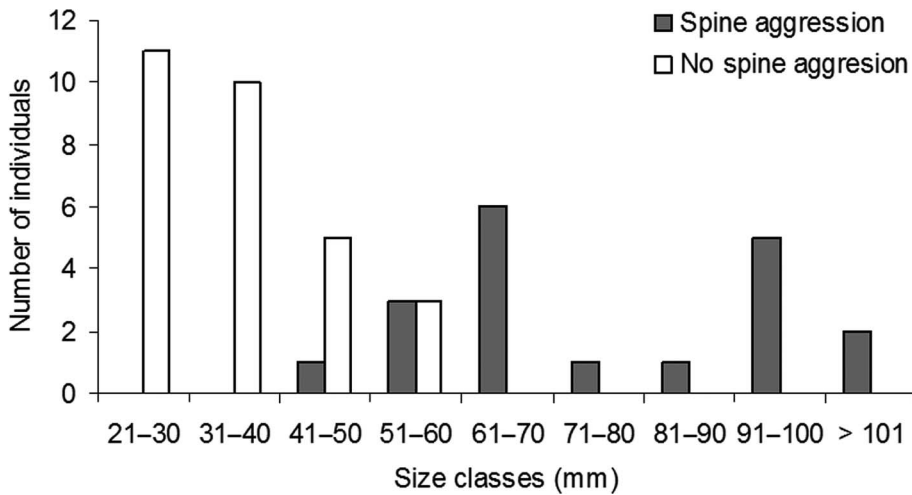


Fig. 3. — Size classes (mm) of frog individuals that use spine aggression (puncturing) as a defensive behaviour (grey bars) and those that do not use them (white bars), although spines on prepollex are present in all of them.

reachable body part of a predator (e.g. skin, eyes, and oral mucosa). In *Corythomantis greeningi* (Hylidae) a set of skull spicules is used to scratch and to introduce noxious secretions into the predator's body, a behaviour associated with phragmosis (see JARED et al. 2005). (iii) Spine-traumatising is the use of spines against a predator without penetrating the skin (or other body parts) as occurs in spine-puncturing.

Possible synergistic behaviours. Spine aggression may co-occur with defensive vocalisations, puffing up the body, fighting, cloacal discharge, and production of secretions (odoriferous, noxious, and slippery).

(27) *Phalanx aggression*

Some African arthroleptids (*Astylosternus* spp. and *Trichobatrachus robustus*) have openings in the distal skin of the fingers (BOULENGER 1902). These openings allow the protrusion of distal phalanges of the fingers, which are used to deeply scratch a possible predator (W. BÖHME pers. com.).

(28) *Regurgitating*

Two individuals of *Spea intermontana* (Scaphiropodidae) regurgitated stomach contents or bubbles while handled (WAYE & SHEWCHUK 1995).

Possible synergistic behaviours. Odour production.

(29) *Defensive vocalisation*

Defensive high-pitched screams are almost universal among vocal vertebrates and may be a basal character among anurans. Based on the context of emission,

three terminologies for defensive vocalisations have been proposed: (i) distress calls (the commonest when the frog is seized or while fleeing from a predator), (ii) warning calls (an intimidating scream directed towards a predator), and (iii) alarm calls (a kind of “help” scream that may attract other animals to the predation scene). Further definitions, discussion, and a recent literature review are in TOLEDO & HADDAD (2009b).

Possible synergistic behaviours. Defensive vocalisations may be coupled with fleeing, charging, body-raising, puffing up the body, mouth-gaping, fighting, spine aggression, and production of secretion. While screaming, *Litoria australis* jumps vertically and lands in the spot on the ground where it was previously resting (BEHLER & BEHLER 2005).

(30) Production of secretions

Four broad secretion types may be released by frogs while seized or otherwise threatened. The secretion released by a given frog species may be of more than one type at the same time. For example, it is adhesive and noxious (e.g. *Trachycephalus venulosus*) or odoriferous and noxious (e.g. *Leptodactylus labyrinthicus*). (i) Odoriferous: varies from malodorous, pepper-like, to floral-like odours (see SMITH et al. 2004). (ii) Adhesive: viscous secretions typically produced, for example, by *Trachycephalus* spp. and *Hyophryne histrio*. In an experimental trial we fed the colubrid snake *Xenodon merremii* with an adult male of the hylid *Trachycephalus venulosus*. When seized, the frog released a copious amount of viscous secretion and simultaneously tried to escape. After 2 min the anuran freed itself and the snake had its mouth glued by the secretion. During 2 days the snake remained with its mouth partially glued, trying to remove the secretion by vigorously rubbing its snout and mouth against the substratum. (iii) Noxious: toxic secretions produced by several frog species (see Appendix 1, available online). In an experimental trial we fed the snake *Liophis miliaris* with an adult male of the hylid *Trachycephalus mesophaeus*. When seized, the frog remained motionless and was ingested. After ca 5 min the snake regurgitated its prey unharmed and alive. We attribute this outcome to production of secretions noxious to the snake’s digestive system (see also SAZIMA 1974 for *Phyllomedusa rohdei*). (iv) Slippery: lubricating secretions produced generally by aquatic or semi-aquatic species, such as pipids, ranids, and leptodactylids.

Possible synergistic behaviours. Production of secretion may co-occur with several other defensive behaviours: immobility, thanatosis, phragmosis, crouching, puffing up the body, body-raising, body-tilting, unken reflex, eye-protection, biting, mouth-gaping, tongue protrusion, fighting, spine aggression, regurgitation, and defensive vocalisations.

DISCUSSION

Function and effectiveness of selected behaviours

Thanatosis and eye-protection may work similarly. Both would probably be effective against predators that do not feed on carrion or prey found already dead, and against those which need movement cues to find and handle further their prey. Contracting would also work for those anurans that are able to produce noxious

secretions while in the mouth or other parts of the digestive tract of predators, as these secretions may elicit regurgitation of the frog by the predator (e.g. SAZIMA 1974; TOLEDO et al. 2010).

Some frog species are known to flip onto their back to display aposematic (warning) colourations. Similarly, frogs that rely on thanatosis may also display aposematic colourations on the belly, when they are turned with their belly up by the predator (present study).

It is suggested that the partial body-raising with vertically stretched legs occurs during the day only, because it may involve visual signalisation (MARTINS 1989). However, we have seen this behaviour during the night as well (for the leiuiperids *Eupemphix nattereri* and *Physalaemus marmoratus*). Additionally, we doubt that this signalisation will work only with daily visually orientated predators. Nocturnal, visual signaling has already been described for frogs (e.g. HARTMANN et al. 2005; TOLEDO et al. 2007b), and thus other potential predators (including frogs) may also be able to recognise visual signals during the night or in conditions of reduced luminosity, such as in retreat sites.

Body-raising with laterally stretched legs results in losing the characteristic frog shape, and makes it difficult to subdue and ingest the prey. However, information is still lacking about the effectiveness of this strategy.

Body-tilting may be effective, as the frog presents its dorsal macroglands to the predator (sensu TOLEDO & JARED 1995). In this case the first body parts that the predator would bite are the glands, which would squeeze noxious secretions into the predator's mouth. These secretions may cause paralysis, irritation, or simply be distasteful, hampering or precluding the predation. Alternatively or non-exclusively, when performing body-tilting a frog is showing its largest surface to the predator. This may act as an intimidating behaviour, as the frog is actually larger when compared to the size initially perceived by the predator, or it may discourage the predator by making the prey more difficult to seize or to swallow.

Cloacal discharge during active fleeing may be effective in three ways: (i) the cloacal contents may be distasteful to the predator (if the discharge hits the predator's mouth; most probably during seizing); (ii) it may startle an endothermic predator with the cold discharge; and/or (iii) it may make the frog lighter, and consequently the frog can flee more quickly.

Regurgitating is recorded only once, in a well-studied species, *Scaphiopus intermontanus* (e.g. MOREY & REZNICK 2000; HALL et al. 2002 and references therein). Thus, care should be taken to consider this behaviour as an actual defensive strategy. The recorded regurgitating behaviour could be a consequence of stomach squeezing while handling the frog.

Puffing up the body is suggested to enlarge the size of the frog upon seeing a predator (STEBBINS & COHEN 1995; WILLIAMS et al. 2000). It is also reported to be effective in causing flotation. An aquatic turtle (*Kinosternum* sp.) could not easily sink a *Rhinella marina* toad with its lungs inflated; after struggling for a while, the turtle gave up and the toad escaped with traces of poison on its paratoid glands, which may have played an important role during the predatory/defensive interaction (BLAIR 1947). Furthermore, synergistically with phragmosis, anurans may easily wedge themselves into crevices, bromeliad axils, or burrows (in trees and in the ground) by inflating the body (pers. obs.). This is another example in which the association between behaviours (in this case, phragmosis and puffing up the body) may amplify the effectiveness of several behaviours (see below). Another behaviour that acts synergistically with puffing up the body is the display of eye-like glands, some of which produce a distasteful and/or

noxious secretion (e.g. SAZIMA & CARAMASCHI 1986; TOLEDO & JARED 1995; LENZI-MATTOS et al. 2005).

Multiple behaviour benefits

A number of defensive strategies used together probably result in higher chances of the frog's escape from a predator. Moreover, when two or more defensive strategies are used concomitantly, it is likely that the net benefit is higher than the simple sum of effective, isolated behaviours. For example, the emission of warning calls by *Ceratophrys aurita* and *C. joazeirensis* is strengthened by the visual signal given by the contrasting colours of the bright yellow lips against the white mouth lining and the mottled green dorsal pattern, by puffing up the body, by charging, and by biting. This multiple signalisation may stop the action of those predators that are intimidated by the defensive scream, those that are intimidated by the gaping display, and those that are only intimidated when multiple signals are emitted (however, this suggestion needs experimental confirmation). Defensive vocalisations seem to be useless against some predators, such as snakes, probably the major anuran predators (TOLEDO et al. 2007a), which are unlikely to hear frogs' screams (TOLEDO & HADDAD 2009b). Thus, the use of multiple behaviours, such as mouth-gaping, is probably effective not only because of the advantageous sum of the isolated behaviours, but because the multiple strategy enhances the probability of broadcasting a signal that can be recognised as dangerous to the predator.

The commonest situation is that of a sequence of defensive behaviours that helps the prey to avoid or to escape predation. For example, the leaf frog *Phyllomedusa* (Hylidae) is camouflaged amidst green leaves while resting. If it is disturbed by a predator it flees (by walking) in an attempt to escape. While walking the frog becomes aposematic, displaying the contrasting colouration of the concealed parts of groin, thigh, and axilla. If handled by the predator, the leaf frog may display contracting (Fig. 2C). If swallowed in contracting posture, it may produce noxious secretions while in the predator's gut, and has a fair chance of surviving after being regurgitated (SAZIMA 1974).

Evolution of defensive behaviours

Immobility in anurans and salamanders has been demonstrated to be successful against several predator types, mainly birds and snakes (BRODIE 1977; MARCHISIN & ANDERSON 1978; present study). Besides the frog species reported here, two *Lithobates pipiens* individuals were offered to a snake and the one that remained crouched (and thus motionless) went undetected by the snake, which chased and preyed upon the moving one (MARCHISIN & ANDERSON 1978). Even when the amphibian is detected, remaining motionless rather than attempting to flee may reduce the intensity of the predator attack (BRODIE 1977). Thus, the risks of detection and lethal injuries may have been two selective pressures acting separately or in concert in the evolution of motionless defences and the synergistic behaviours displayed whilst fleeing. Examples are flash-colours (BRODIE & FORMANOWICZ 1981) and stiff-legged behaviour (SAZIMA 1978), which enhance the chances of misleading a predator after the prey is detected.

Some postures occur synergistically with poison glands (SAZIMA & CARAMASCHI 1986; TOLEDO & JARED 1995; LENZI-MATTOS et al. 2005). In some cases the glands

may have evolved after the behaviour has. This seems to be the case of phragmosis in *Corythomantis greeningi* (JARED et al. 2005). Phragmosis also occurs in closely related species (*Aparasphenodon* spp.), and thus it seems to be a phylogenetically restrained behaviour. However, species of *Aparasphenodon* have no spines and gland structures on the head such as those found in *C. greeningi* (see JARED et al. 2005; C. JARED pers. com.). *Anothea spinosa* is an arboreal hyliid that calls and reproduces in tree holes or bamboo internodes containing water (JUNGFER 1996). Its skull is ornamented with sharp and dorsally pointed spines in the margins of the frontoparietal, maxilla, nasal (including canthal ridge), and squamosal bones, and it is a sister group of *Tripriion* (FAIVOVICH et al. 2005). It is possible that *A. spinosa* displays phragmosis and has noxious glands similar to those of *C. greeningi*. In *Rhinella granulosa* the origin of macroglands (sensu TOLEDO & JARED 1995) on the head probably anteceded phragmotic behaviour, since all *Rhinella* species have such glands but only *R. granulosa* is known to display phragmosis. Indeed, in most other cases in which the glands are directed towards the predator, especially while body-tilting (but also in chin-tucking, crouching, and body-raising), the origin of such behaviours probably occurred after the origin of dorsal macroglands.

Odoriferous secretions may act as a chemical warning, in which a specific odour is related to noxiousness and/or unpalatability (SMITH et al. 2004). Furthermore, it is possible that it functions as a chemical camouflage and/or mimicry as well. Some frog species produce odours that resemble smashed plants (SMITH et al. 2004; present study), which may mislead a predator, especially if the frog remains motionless and the predator cannot rely on visual or chemical cues to find its prey. In any case, chemical as well as acoustic defences (e.g. vocalisation) are signals especially useful to emit at night (SMITH et al. 2004) or in underground retreats.

There is a suggestion that the full body-raising posture with vertically stretched legs evolved before the partial body-raising (BRODIE et al. 1998). Furthermore, it is suggested that the origin of aposematic colourations (involving noxious glands) preceded the origin of partial body-raising (BRODIE et al. 1998). These authors suggest three steps: (i) full body-raising with vertically stretched legs; (ii) aposematic colourations; (iii) partial body-raising with vertically stretched legs.

Some authors (e.g. HARBEL & WILKINSON 1997; MCCALLUM 1999; ANDREONE 2002) compared eye-protection to the unken reflex. However, this seems inappropriate, as the unken reflex could be an aposematic signal in most of the cases, whereas eye-protection may function, for example, as a protection that allows a frog to be swallowed without much harm after regurgitation (e.g. SAZIMA 1974).

Biting is a defensive behaviour strongly related to diet and/or parental care. Frogs that eat large prey items have large heads and wide mouths (EMERSON 1985; POUGH et al. 1998), and frogs that eat other vertebrates have a specialised cranial architecture with rigid and fused lower jaws, large maxillary teeth, hyperostosis of the cranium, and are, in most cases, ambushing predators (LYNCH 1971; DUELLMAN & LIZANA 1994; FABREZI & EMERSON 2003; SCOTT & AQUINO 2005). Thus, a frog-eating habit is probably at the evolutionary origin of defensive biting (SCOTT & AQUINO 2005; present study). In the cases of *Hyalinobatrachium colymbiphylum* (which do not feed on large or vertebrate prey) and *Leptodactylus latrans*, and probably in the case of *Cycloramphus* spp., biting occurs mainly or exclusively during parental care (VAZ-FERREIRA & GEHRAU 1974, 1975; COOK et al. 2001; HARTMANN et al. 2003; DRAKE & RANVESTEL 2005).

Mouth-gaping, on the other hand, calls the attention of the predator to a visual display that may intimidate the predator and thus hamper the predatory sequence. Mouth-gaping is intensified by the contrasting colours of the mouth lining, tongue,

and/or the lower jaws in relation to body pattern (MYERS 1966; DUELLMANN & TRUEB 1994). Mouth-gaping also seems to be related to emission of defensive vocalisations. Some frog species that are reported to display mouth-gaping are also known to emit defensive vocalisations induced by predator approach or seizing. Furthermore, the emission of defensive vocalisation is almost exclusively done with the mouth open (TOLEDO & HADDAD 2009b). Thus, it is possible that mouth-gaping has originated from species that used to scream defensively, but lost this ability and maintained the behaviour of opening the mouth.

Constraints in the origin of anuran defensive behaviours

Spines on the hands and chest are generally used during aggressive interactions between male frogs (e.g. MARTINS et al. 1998; TOLEDO et al. 2007b) and their presence is widespread among anurans (see FABREZI 2001). However, not all species use them as a defensive strategy (present study). Thus, spines on the hands and chest apparently evolved initially for territorial/aggressive interactions, as most of the species that have spines use them during intraspecific fights. However, there may be a size constraint involved, as only large species use them as a defensive weapon. Spines of small species may not be effective in hurting predators, and thus use of spine aggression against predators seems to have evolved only among large species. The same relationship (only large-sized species present effective defences) may occur with charging, where only large individuals displayed the behaviour.

Besides the above-mentioned examples, there are other relationships between size and some defensive behaviours. For instance, small juveniles of *Bombina* spp. have no aposematic colouration and do not display the unken reflex (LÖHNER 1919); defensive vocalisation is rare in small species (TOLEDO & HADDAD 2009b); and larger frogs may benefit simply from their size, since size alone reduces the assemblage of predators that is able to handle large prey (review in TOLEDO et al. 2007a). Furthermore, it has been suggested that long-legged or very small species may lack defensive behaviours other than active fleeing (WILLIAMS et al. 2000; BEHLER & BEHLER 2005). Thus, there seems to be upper and lower limits that shape the quantity and quality of defensive behaviours for size classes at the individual ontogenetic level and at species level. In this context, it is important to note that recently-metamorphosed *Hypsiboas faber* can emit defensive calls (SAZIMA 1975).

Another factor that may have shaped the presence/absence of some particular defensive behaviours is the microhabitat. For example, the stiff-legged behaviour is reported only for species that dwell in the leaf litter and that have a dead-leaf dorsal colour pattern, independently of the taxonomic group (SAZIMA 1978; present study). Another example is that stream-dwelling species (such as the hylodids *Hylodes* spp. and *Megaelosia* spp.) use a camouflaging pattern and jumping into fast-running water as defensive strategies (HADDAD & GIARETTA 1999; SAZIMA 2006; pers. obs.).

There are several widespread behaviours that seem to have originated in the beginning of the diversification of the living anurans, such as defensive vocalisation, puffing up the body, immobility, and fleeing. On the other hand, there are some behaviours that seem to be exclusive to particular groups of species, therefore being homologies (most likely synapomorphies), such as the unken reflex among the genera *Melanophryniscus* and *Bombina* (L.F. TOLEDO & D. BALDO unpub.), the presence of eyespot-like glands synergistically with body rising and puffing behaviour in species of Leiuperidae, and balling behaviour in the genus *Oreophrynella*. There

are even some behaviours currently known for one species only, such as the legs-interweaving and defecation. There are still others that possibly are instances of convergence, such as the unken reflex (considering its presence among the genera *Melanophryniscus* and *Bombina*), phragmosis, and stiff-legged behaviour (this latter almost certainly is, as it occurs in apparently unrelated frog groups). The origin of defensive behaviours is difficult to assess, and frogs in different geographic regions were probably selected by different environmental conditions and predator pressures (although there are surely some “universal predators” such as snakes and birds). Studies that focus on geographic variation of defensive behaviours (e.g. WILLIAMS et al. 2000), reactions to the actual presence of predators (e.g. BRODIE et al. 1978), and testing the efficacy of defensive behaviours (e.g. BRODIE & TUMBARELLO 1978; BRODIE & FORMANOWICZ 1981; BRODIE & NUSSBAUM 1987) will ultimately help to elucidate at least some of the several questions about the evolution of defensive behaviours in anurans.

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<i>Cycloramphus eleutherodactylus</i>				X			Present study
<i>Eupsophus emilitopugini</i>	X						FORMAS & POBLETE 1996
<i>Macrogenioglottus alipioi</i>	X			X			Present study
<i>Odonotophrynus americanus</i>	X			X			Present study
<i>Proceratophrys boiei</i>	X						Present study
<i>Proceratophrys cururu</i>	X			X			Present study
Dendrobatidae							
<i>Oophaga pumilio</i>						X	HAGMAN 2006
Dicroglossidae							
<i>Hoplobatrachus tigerinus</i>	X						BRODIE JR & NUSSABAUM 1987
Hemiphractidae							
<i>Stefania woodleyi</i>	X						KOK et al. 2007
Hylidae							
<i>Acris crepitans</i>	X						MCCALLUM 1999
<i>Acris gryllus</i>	X			X			MARCHISIN & ANDREWS 1978
<i>Aplastodiscus arillidae</i>				X		X	Present study
<i>Bokermannohyla alvarengai</i>						X	Present study
<i>Bokermannohyla circumdata</i>	X			X		X	Present study
<i>Bokermannohyla hylax</i>	X			X		X	Present study
<i>Bokermannohyla luctuosa</i>						X	Present study
<i>Corythomantis greeningi</i>							JARED et al. 2005
<i>Hyla arenicolor</i>						X	POWELL & LIEB 2003

(Continued)

<i>Scinax similis</i>				X				Present study
<i>Trahycephalus</i> <i>venulosus</i>	X	X			X			MANZANILLA et al. 1998; Present study NAPOLI 2001
<i>Xenohyla truncata</i>		X						
Hyperoliidae								
<i>Kassina cochranae</i>	X							CHANNING & HOWELL 2003
<i>Kassina kuvangensis</i>	X							CHANNING & HOWELL 2003
<i>Kassina lamottei</i>	X							CHANNING & HOWELL 2003
<i>Kassina maculata</i>	X							CHANNING & HOWELL 2003
<i>Phyllotmantis</i> <i>verrucosus</i>								
Leiopelmatidae								
<i>Leiopelma archeyi</i>	X							GREEN 1988
<i>Leiopelma hamiltoni</i>	X							GREEN 1988
<i>Leiopelma</i> <i>hochstetteri</i>	X							GREEN 1988
Leiuperidae								
<i>Eitpeuphix nattereri</i>	X	X						RODRIGUES & OLIVEIRA FILHO 2004
								KOLENC et al. 2009
<i>Pleurodema thaul</i>	X							
Leptodactylidae								
<i>Leptodactylus fuscus</i>				X				Present study
<i>Leptodactylus</i> <i>labyrinthicus</i>	X	X			X			TOLEDO et al. 2005; Present study
<i>Leptodactylus lairams</i>				X				Present study
<i>Leptodactylus</i> <i>mystaceus</i>				X				Present study
<i>Leptodactylus</i> <i>mystacinus</i>	X	X						CARVALHO JR 2005; Present study

(Continued)

Appendix 1.
(Continued)

Species	Chin-tucking	Crouching down	Puffing up the body	Hiding	Cloacal discharge	Spine-puncturing	Spine-scratching	Spine-traumatising	Secretion (odour)	Secretion (adhesive)	Secretion (noxious)	Secretion (slippery)	Source
Limnodynastidae													
<i>Heleioporus eyrei</i>	X	X											WILLIAMS et al. 2000
<i>Limnodynastes tasmaniensis</i>	X	X											WILLIAMS et al. 2000
<i>Neobatrachus pictus</i>	X	X	X										WILLIAMS et al. 2000
<i>Neobatrachus sudelli</i>	X	X	X										WILLIAMS et al. 2000
<i>Notaden melanoscaphus</i>	X	X	X										WILLIAMS et al. 2000
<i>Notaden nicholksi</i>	X	X	X										WILLIAMS et al. 2000
Mantellidae													
<i>Boophis albilabris</i>								X					ANDREONE 2002
<i>Mantella laevigata</i>									X				HEYING 2001
Microhylidae													
<i>Ctenophryne geayi</i>	X	X	X										MENIN & RODRIGUES 2007
<i>Elachistocleis enythrogaster</i>			X										KWET & SOLE 2002
<i>Elachistocleis ovalis</i>			X										KOKUBUM & MENIN 2002
<i>Gastrophryne carolinensis</i>		X		X									MARCHISIN & ANDREWS 1978
<i>Kaloula pulchra</i>			X										CHUANKEERN et al. 2008
<i>Phrynomantis microps</i>		X											RÖDEL & BRAUN 1999
<i>Plethodonohyla tuberata</i>		X	X	X							X		NINCHERI & ANDREONE 2002
Myobatrachidae													
<i>Crinia glauerti</i>	X	X	X										WILLIAMS et al. 2000

<i>Mixophyes fasciolatus</i>	X	X																	WILLIAMS et al. 2000
<i>Paracrinia haswelli</i>	X	X																	WILLIAMS et al. 2000
<i>Pseudophryne bibroni</i>	X	X	X																WILLIAMS et al. 2000
<i>Pseudophryne sentinamoraia</i>	X	X	X																WILLIAMS et al. 2000
<i>Uperoleia laevigata</i>			X																TORR 1991
Pipidae																			
<i>Pipa pipa</i>			X																Present study
<i>Xenopus laevis</i>																			Present study
Ranidae																			
<i>Lithobates capito</i>																			GRANT 2001; MEANS 2004
<i>Lithobates clamitans</i>	X	X	X																MARCHISIN & ANDREWS 1978
<i>Lithobates palustris</i>	X	X	X																MARCHISIN & ANDREWS 1978; GRANT 2001
<i>Lithobates pipiens</i>	X	X	X																MARCHISIN & ANDREWS 1978
<i>Lithobates septentrionalis</i>																			GRANT 2001
<i>Lithobates sylvaticus</i>	X	X																	MCCALLUM et al. 2003
<i>Rana muscosa</i>																			GRANT 2001
Scaphiopodidae																			
<i>Spea hammondi</i>																			WAYE & SHEWCHUK 1995
<i>Scaphiopus holbrookii</i>	X	X																	MARCHISIN & ANDREWS 1978
<i>Spea intermontana</i>																			WAYE & SHEWCHUK 1995
<i>Spea multiplicata</i>	X	X																	LIVO et al. 1997

Appendix 2.

Frog species that display body-raising (“legs vertically stretched” and “legs laterally stretched”) and “legs laterally stretched” types and body-tilting. Presence/absence of aposematic (warning) colouration in the posterior region (post-femoral and groin), eyespot-like glands, and noxious skin secretions. See text for further explanations. Families, genera, and species in alphabetical order.

Species	Body-raising type	Aposematic colouration	Noxious skin secretion	Intensity of body-raising	Body-tilting	Source
Bufo						
<i>Inclitus alvarius</i>	Legs vertical	No	Yes	Full	Yes	HANSON & VIAL 1956
<i>Rhinella ornata</i>	Legs vertical	No	Yes	Full	Yes	TOLEDO 2004b
Ceratophryidae						
<i>Atelognathus praebasaliticus</i>	Legs vertical	No	?	Full	?	CEI 1980
Cycloramphidae						
<i>Eupsophus emiltoppugini</i>	Legs vertical	?	?	?	?	FORMAS & POBLETE 1996
<i>Macrogenioglottus alipioi</i>	Both	Yes	?	Full	Yes	Present study
<i>Thoropa taophora</i>	Legs vertical	Yes	?	Full	?	I. MARTINS pers. comm.
Dendrobatidae						
<i>Ameerega flavopicta</i>	Legs vertical	Yes	Yes	Partial	No	TOLEDO et al. 2004
Dicroglossidae						
<i>Hoplobatrachus tigerinus</i>	Legs vertical	No	Yes	Partial	?	BRODIE JR & NUSSABAUM 1987
Hylidae						
<i>Aplastodiscus albosignatus</i>	Legs lateral	No	?	NA	Yes	Present study
<i>Aplastodiscus arildae</i>	Legs lateral	No	?	NA	Yes	Present study
<i>Aplastodiscus callipygius</i>	Legs lateral	No	?	NA	Yes	Present study
<i>Aplastodiscus coehranae</i>	Legs lateral	No	?	NA	Yes	Present study
<i>Aplastodiscus leucopygius</i>	Legs lateral	No	?	NA	Yes	Present study
<i>Aplastodiscus perviridis</i>	Legs lateral	No	?	NA	Yes	Present study
<i>Hyla versicolor</i>	Legs vertical	Yes	Yes	Partial	Yes	BRODIE JR & FORMANOWICZ 1981
<i>Hyloscirtus tapichalaca</i>	Legs lateral	?	?	NA	?	KIZIRIAN et al. 2003
<i>Hypsiboa semilineatus</i>	Legs lateral	?	?	NA	?	AZEVEDO-RAMOS 1995
<i>Litoria alboguttata</i>	Legs vertical	Yes	Yes	Full	Yes	WILLIAMS et al. 2000
<i>Litoria aturea</i>	Legs vertical	Yes	Yes	Partial	Yes	WILLIAMS et al. 2000

<i>Litoria australis</i>	Legs vertical	No	No	Full	?	WILLIAMS et al. 2000
<i>Litoria caerulea</i>	Legs vertical	Yes	Yes	Partial	Yes	WILLIAMS et al. 2000
<i>Litoria cultripes</i>	Both	No	No	Partial	?	WILLIAMS et al. 2000
<i>Litoria novaehollandiae</i>	Legs vertical	No	No	Partial	?	WILLIAMS et al. 2000
<i>Xenohyla truncata</i>	Legs lateral	?	?	NA	?	NAPOLI 2001
Hyperoliidae						
<i>Phyllotimantis boulengeri</i>	Legs vertical	Yes	?	?	?	RÖDEL & ERNST 2001
<i>Phyllotimantis keithae</i>	Legs vertical	Yes	?	?	?	RÖDEL & ERNST 2001
Leuperidae						
<i>Edalorhina perezii*</i>	Legs vertical	No	Yes	Partial	Yes	Present study
<i>Eupemphix nattereri*</i>	Legs vertical	No	Yes	Partial	Yes	SAZIMA & CARAMASCHI 1986; LENZI-MATTOS et al. 2005
<i>Physalaemus deimaticus*</i>	Legs vertical	No	Yes	Partial	Yes	SAZIMA & CARAMASCHI 1986
<i>Physalaemus marmoratus</i>	Legs vertical	No	Yes	Partial	Yes	Present study
<i>Pleurodema bibroni*</i>	Legs vertical	Yes	Yes	Partial	Yes	KOLENC et al. 2009
<i>Pleurodema brachyops*</i>	Legs vertical	Yes	Yes	Partial	?	MARTINS 1989
<i>Pleurodema bifoninum*</i>	Legs vertical	No	Yes	Partial	?	CEI 1962; KOLENC et al. 2009
<i>Pleurodema kriegel*</i>	Legs vertical	No	Yes	Partial	?	CEI 1962; KOLENC et al. 2009
<i>Pleurodema thaul*</i>	Legs vertical	No	Yes	Partial	?	CEI & ESPINA 1957; KOLENC et al. 2009
Leptodactylidae						
<i>Leptodactylus labyrinthicus</i>	Legs vertical	Yes	Yes	Full	Yes	TOLEDO et al. 2005
<i>Leptodactylus laticeps</i>	Legs vertical	Yes	Yes	Full	Yes	CEI 1980; HEYER & SCOTT JR 2006
<i>Leptodactylus latrans</i>	Legs vertical	No	No	Partial	Yes	Present study
<i>Leptodactylus mystacinus</i>	Legs vertical	Yes	Yes	Full	Yes	CARVALHO JR 2005
Limnodynastidae						
<i>Heleioporus eyrei</i>	Legs vertical	No	Yes	Full	?	WILLIAMS et al. 2000
<i>Limnodynastes convexisculus</i>	Legs vertical	No	No	Partial	?	WILLIAMS et al. 2000
<i>Limnodynastes dumerilii</i>	Legs vertical	No	No	Partial	?	WILLIAMS et al. 2000
<i>Limnodynastes lignarius</i>	Legs vertical	No	No	Partial	?	WILLIAMS et al. 2000
<i>Limnodynastes tasmaniensis</i>	Legs vertical	No	No	Full	?	WILLIAMS et al. 2000

(Continued)

Appendix 2.
(Continued)

Species	Body-raising type	Aposematic colouration	Noxious skin secretion	Intensity of body-raising	Body-tilting	Source
<i>Limnodynastes terraereginae</i>	Legs vertical	Yes	No	Partial	?	WILLIAMS et al. 2000
<i>Platyplectrum spenceri</i>	Legs vertical	No	No	Partial	?	WILLIAMS et al. 2000
Microhylidae						
<i>Ctenophryne geayi</i>	Legs vertical	No	?	Partial	?	MENIN & ROGRIGUES 2007
<i>Elachistocleis erythrogaster</i>	Legs lateral	?	?	NA	?	KWET & SOLÉ 2002
<i>Elachistocleis ovalis</i>	Both	Yes	No	Partial	?	KOKUBUM & MENIN 2002
<i>Phrynomantis microps</i>	Legs lateral	?	?	NA	?	RÖDEL & BRAUN 1999
<i>Plethodontohyla tuberata</i>	Legs vertical	Yes	?	?	?	NINCHERI & ANDREONE 2002
Myobatrachidae						
<i>Pseudophryne bibronii</i>	Legs lateral	Yes	Yes	NA	?	WILLIAMS et al. 2000
<i>Pseudophryne seminarmorata</i>	Legs lateral	Yes	Yes	NA	?	WILLIAMS et al. 2000
<i>Uperoleia altissima</i>	Legs vertical	Yes	Yes	Partial	Yes	WILLIAMS et al. 2000
<i>Uperoleia aspera</i>	Legs vertical	Yes	Yes	Partial	?	BRODIE JR et al. 1998
<i>Uperoleia borealis</i>	Legs vertical	Yes	Yes	Partial	?	BRODIE JR et al. 1998
<i>Uperoleia laevigata</i>	Legs vertical	Yes	Yes	Partial	Yes	TORR 1991
<i>Uperoleia lithomoda</i>	Legs vertical	Yes	Yes	Partial	Yes	BRODIE JR et al. 1998
<i>Uperoleia litilejohni</i>	Legs vertical	Yes	Yes	Partial	Yes	WILLIAMS et al. 2000
<i>Uperoleia mjobergii</i>	Legs vertical	No	Yes	Full	?	BRODIE JR et al. 1998
<i>Uperoleia tapia</i>	Legs vertical	No	Yes	Full	?	BRODIE JR et al. 1998
Scaphiropodidae						
<i>Spea intermontana</i>	Legs vertical	No	?	Partial	Yes	WAYE & SHEWCHUK 1995
Strabomantidae						
<i>Pristimantis curtipes</i>	Legs vertical	No	No	NA	?	DUELLMAN & TRUEB 1994

*Species with eyespot-like glands. NA = not applicable.

Appendix 3.

Frog species that bite and mouth-gape defensively, presence/absence of parental care, batrachophagic habits and defensive vocalisation.

	Family/Species	Parental care	Frog eating	Defensive vocalisation	Source
Biting	Centrolenidae				
	<i>Hyalinobatrachium colymbiphyllum</i>	Yes	No	No	DRAKE & RANVESTEL 2005
	Ceratobatrachidae				
	<i>Ceratobatrachus guentheri</i>	?	?	?	NOBLE 1931
	Ceratophryidae				
	<i>Ceratophrys aurita</i>	No	Yes	Yes	Present study
	<i>Ceratophrys cranwelli</i>	No	Yes	?	FABREZI & EMERSON 2003
	<i>Ceratophrys joazeirensis</i>	No	Yes	Yes	Present study
	<i>Ceratophrys ornata</i>	No	Yes	Yes	DONOSO-BARROS 1972
	<i>Lepidobatrachus</i> sp.	?	Yes	Yes	FABREZI & EMERSON 2003
	Cycloramphidae				
	<i>Cycloramphus acangatan</i>	?	?	?	Present study
	<i>Cycloramphus boraceienseis</i>	Yes	Yes	?	HARTMANN et al. 2003; Present study
	<i>Cycloramphus dubius</i>	Yes	?	?	GIARETTA & CARDOSO 1995
	<i>Cycloramphus eleutherodactylus</i>	Yes	?	?	Present study
	<i>Cycloramphus lutzorum</i>	Yes	Yes	?	Present study
	<i>Cycloramphus</i> sp.	Yes	?	?	Present study
	Hemiphractidae				
	<i>Hemiphractus fasciatus</i>	Yes	Yes	Yes	MYERS 1966
	<i>Hemiphractus johnsoni</i>	Yes	Yes	?	M. BARBOSA pers. comm.
	Leptodactylidae				
	<i>Leptodactylus chaquensis</i>	Yes	Yes	?	Present study
	<i>Leptodactylus latrans</i>	Yes	Yes	Yes	VAZ-FERREIRA & GEHRAU 1974, 1975
	<i>Leptodactylus pentadactylus</i>	Yes	Yes	Yes	VILLA 1969
	Megophryidae				
	<i>Brachytarsophrys carinenses</i>	?	?	?	NOBLE 1931
	<i>Megophrys</i> sp.	?	Yes	Yes	Present study
Pyxicephalidae					
<i>Aubria subsigillata</i>	?	Yes	?	FABREZI & EMERSON 2003	
<i>Pyxicephalus adpersus</i>	Yes	Yes	Yes	COOK et al. 2001; FABREZI & EMERSON 2003	
<i>Pyxicephalus edulis</i>	Yes	Yes	?	LOVERIDGE 1945	
Mouth-gaping	Brachycephalidae				
	<i>Brachycephalus ephippium</i>	No	No	No	Present study
	<i>Brachycephalus hermogenesi</i>	No	No	No	Present study
	<i>Brachycephalus pitanga</i>	No	No	No	Present study

(Continued)

Appendix 3.

(Continued)

Family/Species	Parental care	Frog eating	Defensive vocalisation	Source
<i>Ischnocnema ramagii</i>	?	No	?	D. LOEBMANN pers. comm.
Ceratophryidae				
<i>Ceratophrys aurita</i>	No	Yes	Yes	Present study
<i>Ceratophrys joazeirensis</i>	No	Yes	Yes	Present study
Craugastoridae				
<i>Haddadus binotatus</i>	?	No	Yes	Present study
Cycloramphidae				
<i>Cycloramphus acangatan</i>	?	?	?	Present study
<i>Eupsophus emiliopugini</i>	?	?	Yes	FORMAS & POBLETE 1996
<i>Proceratophrys boiei</i>	No	Yes	?	R. SAWAYA pers. comm.
Hemiphractidae				
<i>Gastrotheca helenae</i>	Yes	?	Yes	DUPELLMANN & TRUEB 1994
<i>Hemiphractus johnsoni</i>	Yes	Yes	Yes	Present study
<i>Hemiphractus fasciatus</i>	Yes	Yes	Yes	MYERS 1966
<i>Hemiphractus scutatus</i>	Yes	Yes	Yes	P. BERNARDE pers. comm.
<i>Stefania woodleyi</i>	?	?	Yes	KOK et al. 2007
Hylidae				
<i>Bokermannohyla izecksohni</i>	No	No	Yes	I. MARTINS pers. comm.
Megophryidae				
<i>Megophrys</i> sp.	?	Yes	Yes	Present study