

Stereotyped Defensive Behaviours in Frogs of the Genus *Odontophrynus* (Amphibia: Anura: Odontophrynidae)

CLAUDIO BORTEIRO^{1,2*}, SERGIO D. ROSSET³, FRANCISCO KOLENC¹,
DIEGO A. BARRASSO⁴, JULIÁN N. LESCANO⁵, AND DIEGO BALDO⁶

¹*Sección Herpetología, Museo Nacional de Historia Natural, 25 de mayo 582, Montevideo, URUGUAY*

²*Departamento de Patología, Facultad de Veterinaria, Universidad de la República, Lasplaces 1550, Montevideo, URUGUAY*

³*Sección Herpetología, División Zoología Vertebrados, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, Av. 60 y 122, La Plata, Buenos Aires, ARGENTINA*

⁴*IDEAUS (Instituto de Diversidad y Evolución Austral-CONICET) and Facultad de Ciencias Naturales y de la Salud, Universidad Nacional de la Patagonia “San Juan Bosco” (UNPSJB), Puerto Madryn, Chubut, ARGENTINA*

⁵*Instituto de Diversidad y Ecología Animal (CONICET—Universidad Nacional de Córdoba) and Centro de Zoología Aplicada (Universidad Nacional de Córdoba), Rondeau 798, Córdoba, ARGENTINA*

⁶*Laboratorio de Genética Evolutiva, Instituto de Biología Subtropical (CONICET-UNaM), Facultad de Ciencias Exactas Químicas y Naturales, Universidad Nacional de Misiones, Félix de Azara 1552, Posadas, Misiones, ARGENTINA*

Abstract: Observations on stereotyped defensive behaviours are presented for 7 frog species of the Neotropical genus *Odontophrynus* from Argentina and Uruguay. Seven stereotyped postures were observed, among which the most common observed were puffing up the body, contracting, and crouching down. Newly reported behaviours include tongue protrusion, eye protection, and some combinations of postures. We provide an account of defensive behaviours already described in *Odontophrynus* and discuss the correspondence between the terminology used by previous authors and recently proposed classifications. In addition, we highlight defensive mechanisms associated with the body raising posture in Neotropical anurans, which may include intimidating predators, body shape disruption, warning signaling, and exposure of skin macroglands.

Key words: Amphibians; Defenses; Neotropical anurans; Predation

INTRODUCTION

* Corresponding author. Tel: +598–26224078;
E-mail address: borteiro@gmail.com

Amphibians present several mechanisms to avoid predation, including chemical defences

and a wide variety of anti-predator behaviours. Most commonly, frogs evade predators by remaining motionless to go unnoticed, or eventually escape by leaping or swimming (Duellman and Trueb, 1994). However, frogs can exhibit many types of defensive behaviours such as vocalizations, discharge of offensive substances, biting, and death feigning (Williams et al., 2000; Toledo et al., 2011). Defensive behaviours may be of help to prevent the attack of visually oriented predators, or even to avoid subjugation and severe damage during predation attempts (Toledo et al., 2011). Several defensive postures have been described for Neotropical anurans, but their occurrence in burrowing frogs of the genus *Odontophrynus* remains scarcely studied (Toledo et al., 2010; Toledo et al., 2011). The genus *Odontophrynus* belongs to the family Odontophrynidae, along with the monotypic genus *Macrogenioglottus* and the species-rich genus *Proceratophrys* (Lynch, 1971; Pyron and Wiens, 2011). *Odontophrynus* currently contains 12 species that are widely distributed across different South American biomes, from the Monte and Pampas in central Argentina, to the Cerrado, Caatinga, and the Atlantic Forest in eastern Brazil (Cei, 1987; Caramaschi and Napoli, 2012; Rocha et al., 2017). Previous works on the defensive strategies exhibited by *Odontophrynus* include observations on *Odontophrynus americanus*, *Odontophrynus carvalhoi*, *Odontophrynus cultripes* and *Odontophrynus maisuma*, for which different stereotyped behaviours are reported, such as body inflation, deimatic behaviour, thanatosis, and shrinking (e.g., Bezerra et al., 2010; Moreira and Smaniotto, 2015; Borges-Nojosa et al., 2016). In addition, these frogs were reported to possess a significant number of skin macroglands, which contain defensive secretions (Cei et al., 1967; Mailho-Fontana et al., 2017). In the present work, we describe the display of defensive postures in 7 species of *Odontophrynus* from Argentina and Uruguay.

OBSERVATIONS

The behavioural observations were made between 2003 and 2018, during fieldwork at the time of the collection of specimens, or later in the laboratory (Table 1). Frogs were captured in monitoring surveys or as part of other studies, mainly at breeding sites during explosive reproduction events. Recorded behaviours in the field correspond to spontaneous defensive displays of frogs when being captured by hand, and in the laboratory when gently manipulated to take photographs. Terminology of behaviours follows Toledo et al. (2011).

We observed seven different stereotyped postures in *Odontophrynus*: ‘body raising’, ‘contracting’, ‘crouching down’, ‘eye-protection’, ‘puffing up the body’ (lung inflation), ‘production of secretions’, and ‘tongue protrusion’ (Table 2). In some cases, these defensive displays were presented in combination; however, when this occurred, they were always accompanied by temporal immobility.

The ‘crouching down’ posture (Fig. 1) was recorded for *Odontophrynus lavillai* in the field, *Odontophrynus barrioi* in the laboratory and *O. americanus* in both situations. During these observations, the specimens remained immobile for several minutes, with the posterior part of the back slightly elevated, and the head flattened towards the ground with the eyes usually open (closed in *O. barrioi*). The hands were in contact with the substrate, or slightly elevated reaching eye level (‘eye-protection’). Combined crouching down and ‘puffing up the body’ was observed in *O. americanus* and *O. lavillai*.

The ‘contracting’ posture (Figs. 2 and 3) was observed in the laboratory for *Odontophrynus occidentalis*, and in the field for *Odontophrynus achalensis*, *O. americanus* and *O. lavillai*. The specimens remained immobile while contracting the body and limbs, with the dorsum usually noticeably arched. This posture was maintained for several minutes, even also when specimens were turned on their backs (*O. americanus*, *O. lav-*

TABLE 1. Studied specimens of *Odontophrynus* from Argentina (AR) and Uruguay (UY). Acronyms: MNHN, Museo Nacional de Historia Natural de Montevideo, Uruguay; LGE, Laboratorio de Genética Evolutiva, Instituto de Biología Subtropical (CONICET—Universidad Nacional de Misiones), Posadas, Misiones, Argentina; FML, Fundación Miguel Lillo, Tucumán, Argentina; CZA, Centro de Zoología Aplicada, Córdoba, Argentina. Abbreviations: Dpto., Departamento; Pcia., Provincia; NV, no voucher available.

| Species | Locality | Date | Deposit number | Sex |
|----------------------------|--|---------------------------|--|----------------|
| <i>O. achalensis</i> | La Trinidad, Pcia. de Córdoba, AR (31°41'S, 64°51'W) | Oct. 18, 2014, 10:00 PM | NV (Fig. 2G) | Male |
| <i>O. americanus</i> | Villa Arcadia, Pcia. de Buenos Aires, AR (38°07'S, 61°46'W) | Oct. 26, 2015, 08:00 PM † | NV (Figs. 1B and 2C) | Males |
| | Gobernador Virasoro, Pcia. de Corrientes, AR (28°02'S, 56°00'W) | Sep. 28, 2004 | LGE 19826 (Fig. 4A) | Male |
| | Delta del Tigre, Dpto. de San José, UY (34°46'S, 56°21'W) | Oct. 5, 2009, 11:00 PM | NV (Fig. 3E) | Male |
| | Delta del Tigre, Dpto. de San José, UY (34°46'S, 56°21'W) | Sep. 8, 2013, 11:00 PM | NV | — |
| | Jauregutiberry, Dpto. de Canelones, UY (34°77'S, 55°41'W) | Jun. 16, 2012, 01:00 AM | MNHN 9747 (Fig. 2D) | Male |
| | Ruta 10, outskirts of La Paloma, close to Laguna de Rocha, Dpto. de Rocha, UY (34°38'S, 54°13'W) | Feb. 21, 2018 | MNHN 9748 | Male |
| <i>O. barrioi</i> | Parque del Plata, Dpto. de Canelones, UY (34°45'S, 55°42'W) | Feb. 24, 2009, 08:56 PM † | NV (Fig. 1A and 1C) | Males |
| | Puesto de José Flores, Km 52 Ruta Provincial 47, near Mina Capillitas, Pcia. de Catamarca, AR (ca. 27°20'S, 66°22'W) | Oct. 26, 2003, 03:45 PM † | FML 16060 (Fig. 2H) | Male |
| | Descanso Cuesta La Aguadita, Sierras de Famatina, Pcia. de La Rioja, AR (28°43'S, 67°36'W) | Jan. 29, 2018, 05:28 PM † | LGE 20594 (Fig. 1E), LGE 20595 (Fig. 1F) | Male Female |
| <i>O. cordobae</i> | Tanti, Pcia. de Córdoba, AR (31°21'S, 64°36'W) | Mar. 29, 2007, 06:00 PM | CZA 045 (Fig. 3A) | Male |
| | Mallín, Pcia. de Córdoba, AR (31°18'S, 64°34'W) | Nov. 5, 2015, 09:00 PM | NV | Male |
| <i>O. lavillai</i> | El Sauzal, Pcia. de Chaco, AR (24°34'S, 61°32'W) | Mar. 10, 2009, 11:00 PM | LGE 14179 (Fig. 1D), LGE 8599 (Fig. 2C) | Males |
| <i>O. occidentalis</i> | El Nihuil, Pcia. de Mendoza, AR (35°01'S, 68°40'W) | Oct. 31, 2004 | LGE 15200 (Fig. 3D) | Male |
| | El Volcán, Pcia. de San Luis, AR (33°15'S, 66°11'W) | Dec. 14, 2014 | LGE 9221, LGE 9292 (Fig. 3F) | Males |
| | Rincón del Atuel, Pcia. de Mendoza, AR (34°48'S, 68°27'W) | Oct. 30, 2004 | LGE 15199 (Fig. 2A) | Male |
| <i>O. aff. americanus*</i> | Gobernador Roca, Pcia. de Misiones, AR (27°19'S, 55°27'W) | Nov. 6, 2013 | LGE 7438 (Fig. 3B) | Male |

* diploid; † laboratory observation

TABLE 2. Defensive displays in the genus *Odontophrynus*. BR body raising; CD crouching down; CO contracting; DI digging; EP eye protection; PB puffing up the body; PS production of secretions; TP tongue protrusion; SL stiff-legged; CL cloacal discharge.

| Groups/Species | Behaviour | | | | | | | | | |
|---------------------------|----------------|------------------|----------------|--------------------|----------------|----------------|--------------------|------------------|------------------|----------------|
| | BR | CD | CL | CO | DI | EP | PB | PS | SL | TP |
| americanus | | | | | | | | | | |
| <i>O. americanus</i> | X ⁰ | X ^{0,1} | X ¹ | X ^{0,2} | X ³ | X ⁰ | X ^{0,1} | X ^{0,4} | X ^{3,5} | X ⁰ |
| <i>O. cordobae</i> | | | | | | | X ⁰ | X ⁰ | | |
| <i>O. lavillai</i> | | X ⁰ | | X ⁰ | | X ⁰ | X ⁰ | | | X ⁰ |
| <i>O. maisuma</i> | | | | | | | X ⁶ | | | |
| <i>O. aff. americanus</i> | | | | | | | X ⁰ | | | |
| occidentalis | | | | | | | | | | |
| <i>O. achalensis</i> | | | | X ⁰ | | | | X ⁰ | | |
| <i>O. barrioi</i> | | X ⁰ | | | | | | X ⁰ | | |
| <i>O. occidentalis</i> | | | | X ⁰ | | | X ⁰ | X ⁰ | | |
| cultripes | | | | | | | | | | |
| <i>O. carvalhoi</i> | | | | X ^{2,7,8} | X ⁹ | | X ^{7,8,9} | | | |
| <i>O. cultripes</i> | X ⁷ | | | X ⁷ | | | X ⁷ | | | |

⁰present study; ¹Toledo et al. (2011); ²Toledo et al. (2010); ³Rolim (2017); ⁴Laspiur et al. (2010) as *O. cf. americanus*; ⁵Maffei and Ubaid (2016); ⁶Moreira and Smaniotto (2015); ⁷Borges-Nojosa et al. (2016, contracting as ‘thanatosis’, and body raising as ‘deimatic behaviour’); ⁸Bezerra et al. (2010, contracting as ‘death feigning’); ⁹da Costa et al. (2017).

illai). The eyes remained open (*O. americanus*), partially closed (*O. occidentalis*), or closed (*O. lavillai*). Concurrent ‘tongue protrusion’ was observed in *O. lavillai* and *O. americanus*; in the latter Figs 2 and 3 were positioned behind the tongue and inside the mouth, whose opening allowed visualisation of a bluish colour of the oral mucosa. The specimen of *O. achalensis* also darkened its colouration and produced a great amount of markedly contrasting bluish skin secretions.

In addition to *O. lavillai* and *O. americanus*, puffing up the body was documented in *Odontophrynus cordobae*, *O. occidentalis*, and *O. aff. americanus* (Figs. 2A–E). The limbs were stretched to varying degrees, being extremely straight in a specimen of *O. americanus* handled in the laboratory. This specimen also markedly inflated the vocal sac but without producing any vocalisations and remained in this posture for several minutes

while releasing grey coloured skin secretions on the head.

The ‘production of secretions’ by skin macroglands was also evident on the head and dorsum of studied specimens of *O. achalensis*, *O. barrioi*, *O. cordobae* and *O. occidentalis*, and on the head of a specimen of *O. americanus* that also displayed puffing up the body. These individuals remained motionless while releasing whitish to bluish secretions (Figs. 2F–H). In addition, the combination of toxic skin secretions, puffing up the body, and ‘body raising’, by completely elevating the body from the substrate, was recorded in *O. americanus* (Fig. 4A).

DISCUSSION

Odontophrynus exhibits a rich repertoire of stereotyped postures, of which tongue protrusion, eye protection, and the combinations

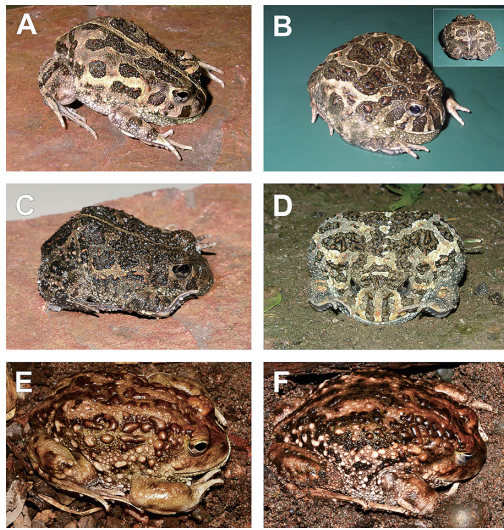


FIG. 1. Crouching down in *Odontophrynus*. A, *O. americanus*. B, *O. americanus*, also puffing up the body. Inset: same specimen viewed from the back. C, *O. americanus*, displaying concurrent eye-protection. D, same posture in *O. lavillai* simultaneously puffing up the body. E and F, *O. barrioi*, with moderate eye protection and eyes closed respectively.

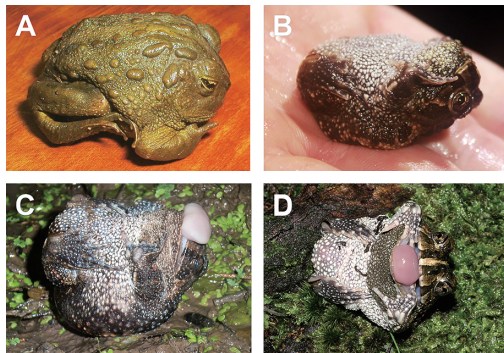


FIG. 2. Contracting in *Odontophrynus*. A, *O. occidentalis*. B, *O. americanus*. C and D, contracting and tongue protrusion in *O. lavillai* and *O. americanus*, respectively.

of postures presented herein have not previously been described (Table 2). Puffing up the body, contracting and crouching down have been the most commonly observed and probably generalised behaviours show by most

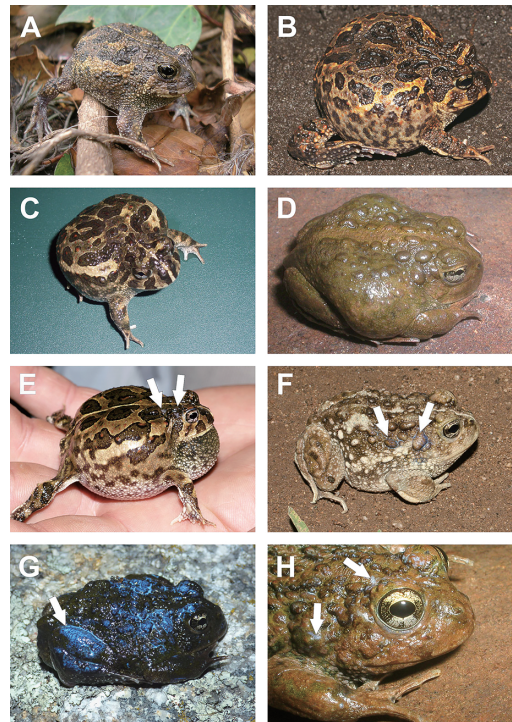


FIG. 3. Puffing up the body (A-E) and production of secretions (E-H, arrows) in *Odontophrynus*. A, *O. cordobae*. B, *O. aff. americanus*. C, *O. americanus*. D, *O. occidentalis*, puffing up plus crouching down. E, *O. americanus*. F, *O. occidentalis*. G, *O. achalensis*, notice the contracting posture and the profuse amount of bluish skin secretions. H, *O. barrioi*.

species in the genus. During crouching down, anurans usually close their eyes (Toledo et al., 2011), but in *Odontophrynus* they are commonly open. Puffing up the body and crouching down may be of help to avoid subjugation, and the forelimbs elevated may further protect the eyes (Toledo et al., 2011). Contracting diminish injuries during ingestion by snakes, enhancing survival after regurgitation due to the effect of skin toxins (Sazima, 1974). Toledo et al. (2010) distinguished between contracting and ‘death feigning’ (or ‘relaxed thanatosis’). Previous observations of death feigning or thanatosis in *O. carvalhoi* and *O. cultripes* (Bezerra et al., 2010; Borges-Nojosa

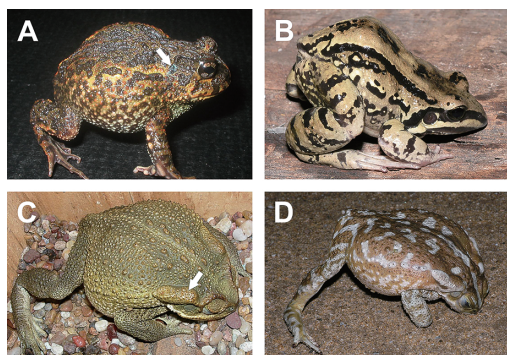


FIG. 4. Body raising. A, full posture in *Odontophrynus americanus* combined with puffing up the body, along with toxin secretion production (arrow). B, partial elevation of the body in *Leptodactylus mystacinus* from Colonia Delta, San José, UY (laboratory, Nov. 23, 2009). C, partial posture with exposure of parotoid glands (arrow) and the eyes closed, male of *Rhinella achavali* from Curticeras, Rivera, UY (MNHN 9513, laboratory, Oct. 10, 2005). D, same posture in adult *R. arenarum* from Laguna de Rocha, UY (Sept. 29, 2012).

et al., 2016) seem to match with contracting. However, contracting along with protrusion of the tongue in *O. americanus* and *O. lavillai* at first sight, gave frogs the appearance of being dead. Protrusion of the tongue as a defensive mechanism is not common in anurans (Kofron and Schmitt, 1992; Toledo et al., 2010), and resembling a dead individual would make the predator hesitate during a predation attempt. This provides frogs an opportunity to discharge a greater amount of defensive chemicals to favour regurgitation once swallowed, eventually leading to escape. The fingers of fore limbs positioned behind the tongue and inside the mouth observed in *O. americanus* were not reported during tongue protrusion in anurans.

Recently, Borges-Nojosa et al. (2016) observed a defensive posture in *O. cultripes* consisting of elevation of the body posteriorly along with puffing up, resulting in exposure of the lumbar area. The authors considered this as the ‘deimatic behaviour’ of exhibition of

eyespot-like structures and/or flash colouration (not visible in resting position), commonly present in leptodactylid frogs. According to the classification of Toledo et al. (2011) adopted herein, the observation in *O. cultripes* more likely fit with ‘body raising’, as *Odontophrynus* lacks warning colouration in the lumbar region.

Body raising in anurans can be performed with the legs laterally, or vertically stretched as in *Odontophrynus* (Toledo et al., 2011). Independent of puffing up the body and body tilting, body raising postures with legs vertically stretched may be linked to different defensive mechanisms in Neotropical anurans: 1) ‘intimidation’ of the predator, stemming from the sudden full body raising from the ground, and enlarging anuran body size from the perspective of a predator (Fig. 4A); 2) ‘shape disruption’, that may confuse predators, achieved by partial elevation of the posterior part of the body while hiding the head, as is the case in *O. cultripes* (Borges-Nojosa et al., 2016) and large species of *Leptodactylus* (Leptodactylidae) in Fig. 4B (Borteiro and Kolenc, 2007; Toledo et al., 2011; de Castro et al., 2017); 3) ‘exposure of macroglands’ that produce noxious secretions, for instance bufonid parotoids of large species of *Rhinella* (Gallardo, 1958) in Figs. 4C–D. or 4) ‘warning’ predators by exposure of flash colouration and eyespot lumbar macroglands. The latter behaviours are seen in leptodactylid frogs (Borteiro and Kolenc, 2007; Toledo et al., 2011; de Castro et al., 2017), these warning postures also disrupt the normal appearance of resting frogs, and could be displayed by arching the dorsum and puffing up the body without body raising. This defensive mechanism is not present in species such as *L. mystacinus* as indicated by Toledo et al. (2011), which lack warning colouration (Fig. 4B).

The ‘stiff-legged’ posture recently reported in *O. americanus* (Maffei and Ubaid, 2016; Rolim, 2017) is commonly displayed by related genera *Proceratophrys* spp. and *Macrogenioglottus alipioi* (Sazima, 1978; de Mira-

Mendes et al., 2016). It has been suggested to provide disruptive background matching in the leaf litter, as predators could confuse frogs with dead leaves (Toledo et al., 2011; de Mira-Mendes et al., 2016). Kolenc et al. (2009) recorded this in *Pleurodema bibroni* (Leiu-peridae), which inhabit non-forested habitats, such as open coastal sandy soils and grasslands, and interpreted it as death feigning. The stiff-legged posture deserves further study, as hind limbs of dead frogs may become stiff for a time because of rigor mortis. Like tongue protrusion, stiff hind limbs resembling a dead frog may discourage the attack of a predator.

The wide geographic distribution of the genus *Odontophrynus* provides the opportunity to study the phylogenetic and ecological constraints involved in the expression of diverse behavioural defences. Future systematic observations and experimental work should aim to test the association of behaviours with factors such as differences in the number of skin macroglands among species groups (Savage and Ceï, 1965), composition of defensive secretions (Mailho-Fontana et al., 2017), ploidy level (Murphey et al., 1981; Rosset et al., 2006), and predator pressure.

ACKNOWLEDGMENT

CB and FK acknowledge Diego Arrieta (MNHN) and Agencia Nacional de Investigación e Innovación (ANII). DB thanks Agencia Nacional de Promoción Científica y Tecnológica (PICTs 0404/2013, 1343/2014, 1930/2014, 2035/2014, 0813/2015, 0820/2015, 2381/2015). LF Toledo kindly shared bibliography.

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Accepted: 27 June 2018