

# Die Hard: How Paraguayan snakes avoid predation and live to tell the tale

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Snakes are potential prey for many carnivorous animals, including birds, mammals, spiders, lizards and other snakes (Costa et al. 2014), with vertebrates being the main snake predators (Greene 1988). In order to avoid predation reptiles have evolved a number of different strategies, but many of these are poorly documented and incompletely understood (Green 1988; Martins 1996). Several anti-predator strategies have been described in snakes (Greene 1988), and the deployment of such behaviours is associated with increased stress levels during predation events (Gallup 1977) and may be influenced by environmental conditions (Passek & Gillingham 1997; Durso & Mullin 2013). Martins (1996) lists 32 defensive tactics from snakes in Manaus, Amazonian Brazil, with locomotor escape, mimicry, aposematic coloration, hiding the head, body thrashing, S-coiling, striking, cloacal discharge and biting being the most commonly employed strategies. However, the species inventory of such behaviours is far from complete, and is especially poorly documented in South American species.

Here we document 5 instances of defensive behaviours by 4 species of Paraguayan snakes in 3 genera that were recorded from 2014 to 2018 in the Atlantic Forest, Chaco and Pantanal eco-regions.

## *Erythrolamprus sagittifer* (Jan, 1863) (Dipsadidae: Xenodontinae)

*Erythrolamprus sagittifer* is a medium-sized snake, distributed in north-western Argentina, southern Bolivia, Brazil and western Paraguay (Dixon & Thomas 1982; Ceí 1993; Cacciali et al. 2016). In Paraguay the species is confined to the Dry Chaco ecoregion (Cacciali et al. 2016; Dinerstein et al. 1995). We observed two different defensive behaviours in this species.

An individual of *E. sagittifer* was observed and captured by AC at Pirizal, Boquerón department in the Pilcomayo River basin during July 2014 (23°1'54.78"S, 61°5'32.15"W, 180 m elevation). The habitat in this area is open, xerophytic, Chaco forest with an understory of bromeliads. As the individual was manipulated for a photograph it relaxed its body, and when deposited on the ground its movements became slow and unnatural, with supination of the head and body contortion and twisting (Figure 1a-b). Following this the snake remained motionless, with a lack of muscular resistance, and did not respond to physical stimulation in apparent thanatosis. After a few minutes of no disturbance it again moved normally.

A second observation of defensive behaviour in this species occurred on 13 August 2016 at 13:10 in Defensores del Chaco National Park, Alto Paraguay department (20°12'24.27"S, 59°45'31.47"W, 131 m high) and was observed by HC. A specimen of *Erythrolamprus sagittifer* was encountered crossing the road and capture was attempted. Upon approach the snake attempted to flee, elevating the anterior third of the body. Additionally, when cornered, the snake compressed the neck dorsoventrally (Figure 1c-d).

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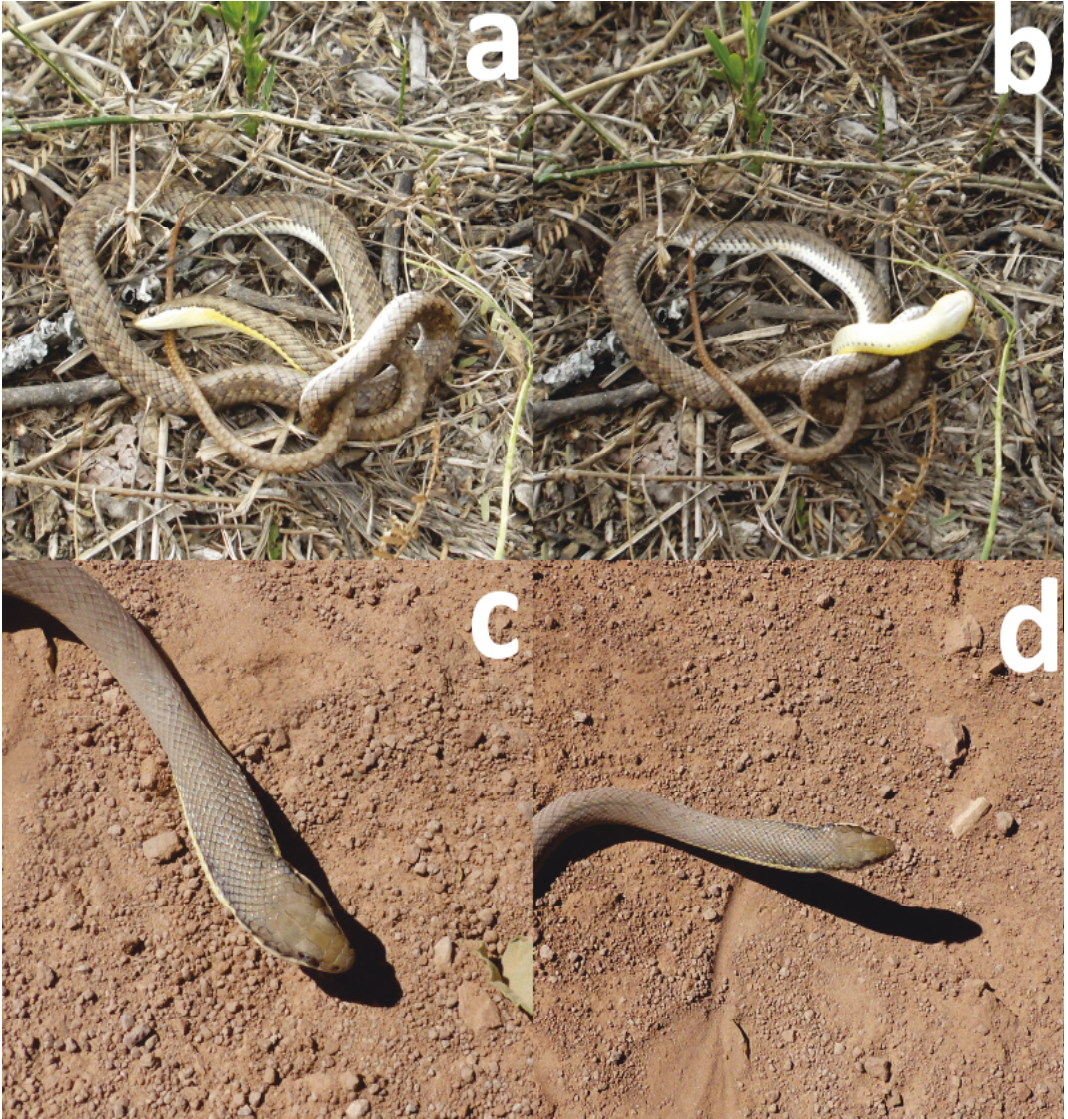
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**Figure 1.** Defensive behaviour in *Erythrolamprus sagittifer*, a-b) death-feigning or thanatosis, b-c) dorsoventral neck compression.

***Dipsas turgidus* (Cope, 1868) (Dipsadidae: Dipsadinae)**

*Dipsas turgidus* is a small, snail-eating snake distributed in northern Argentina, Bolivia, southern Brazil, Uruguay and throughout much of Paraguay (Giraud & Scrocchi 2002; Carreira *et al.* 2005; Cacciali *et al.* 2016). It was until recently classified in the genus *Sibynomorphus* Fitzinger, 1843, this being designated as a junior subjective synonym of *Dipsas*

Laurenti, 1768 by Arteaga *et al.* (2018). In Paraguay the species is commonly referred to as Ñanduriré and there is a common belief that it is venomous because of its superficial resemblance to certain *Bothrops* species (Cacciali 2009).

Defensive behaviour was observed in an individual of this species by HC on 23 April 2016 at the Estación Biológica Tres Gigantes, Alto Paraguay department in the Paraguayan Pantanal (20° 4'40.03"S, 58° 9'35.75"W, 81 high). A snake captured the previous

night was kept in a nylon bag overnight for processing. On removal from the bag the following morning the individual began to rapidly twist and rotate the body, after a few seconds remaining motionless with the ventral side upwards and apparently dead (Figure 2a-b). The snake was photographed and, when left unmolested for a few minutes, again began to move, later being released in the same place it was found. This behaviour was apparently an example of thanatosis.

***Dipsas ventrimaculatus* (Boulenger, 1885)  
(Dipsadidae: Dipsadinae)**

*Dipsas ventrimaculatus* is another small “snail-eating” snake with a somewhat restricted distribution in Argentina, Brazil and eastern Paraguay (Giraud & Scrocchi 2002; Carreira et al. 2005; Cacciali et al. 2016). This species was also formerly placed in the genus *Sibynomorphus*. In Paraguay it is broadly associated with the former extent of the Atlantic Forest eco-region but is commonly found in urban gardens within this region (Cacciali 2006; 2009).

On 10 January 2019 an individual was found by PS inside a house in Encarnación, Itapúa department, southern Paraguay (27°19'48.41"S, 55°51'46.89"W, 137 high) with its entire head bound with a mass of cobwebs and fluff. Upon attempting to remove the handicap, the snake employed a series of defensive behaviours that have not been previously documented in this otherwise common snake. Initially on attempting to prise the cobwebs away from the head of the snake it performed brusque, flicking movements away from the annoyance, hiding the head under the body as it did so. This was repeated on five occasions, each time the snake rapidly flicked the body to change the direction of the head away from the perceived danger. On the sixth occasion it completely coiled the body with the head hidden in the middle. Besides protecting the head, these sudden, violent movements and coiling also recalled certain pre-strike behaviours exhibited by some viperid snakes, especially those of the genus *Bothrops* (Araújo & Martins 2006).

At this point the snake was handled in order to prise the body apart and manually remove the remaining cobwebs from the head. Upon doing so the snake changed its posture with lateral flattening occurring, giving the appearance of extreme thinness. It also became completely limp and motionless, which may have been an example of thanatosis (Humphreys & Ruxton 2018). After removal of the cobwebs it was placed on the ground and remained there motionless

for several minutes, again giving the impression of having died from the stress of the ordeal (Gallup 1977). However when left unmolested the snake soon began to move normally again.

Upon capturing the snake again, it then inverted the body in a stiff, twisted posture, showing the underside, but with the head in an upright and apparently alert position. This immobility position was retained when it was placed on a hard surface (Fig. 2c) and maintained until a loud noise caused it to seek to flee. When it was once again handled the snake repeated the behaviour, again retaining it until PS clapped (in an experimental repetition of the loud noise that had previously caused a behavioural change). The snake was then liberated.

***Leptodeira annulata* (Linnaeus, 1758) (Dipsadidae: Dipsadinae)**

One of the multiple defensive behaviours documented in this snake involves attempting to mimic a venomous *Bothrops* (Viperidae). This behaviour has been previously described in detail (Martins & Oliveira 1998; Guimarães & Sawaya 2011; Mesquita et al. 2013). The behaviour involves triangulation of the head which, coupled with the pattern, gives a viperine appearance. This behaviour was observed by PS in a Paraguayan individual in the Dry Chaco at Fortín Toledo, Boquerón department (22°21'32.73"S, 60°20'19.11"W, 154 high) on 13 October 2017. We take the opportunity to illustrate this behaviour photographically here (Figure 2d).

Defensive behaviours are clearly widespread amongst snakes, yet the taxonomic inventory and the conditions which lead to their employment remain incompletely known. Thanatosis (or tonic immobility), as reported here in the genera *Erythrolamprus* and *Dipsas* (formerly *Sibynomorphus*) is apparently used to reduce the motivation of predators that only consume live prey and to escape from predators which store prey following a kill (Ratner & Thompson 1960; Rovee et al. 1976). In snakes, thanatosis typically involves immobility, body contorting and mouth gaping, and usually occurs when the snake is under great stress (Gehlbach 1970; Gallup 1977; Misslin 2003).

Dorso-ventral neck compression (often referred to as “hooding”) is another tactic observed here that has been reported in several snake species and is typically used when attempting to flee from a threat (Martins 1996; Marques et al. 2013). At its extreme intensity it may involve the raising of the forebody, gaping and even striking. It is hypothesised that adopting a hooding posture causes the snake to appear larger in order to





**Figure 2.** Defensive behaviour, a-b) death-feigning or thanatosis in *Dipsas turgida*, c) death-feigning or thanatosis in *D. ventrimaculatus*, d) triangulation of the head by *Leptodeira annulata*.

deter a predation attempt (Jara & Pincheira-Donoso 2015). Araújo & Martins (2006) link hooding behaviour in *Bothrops* to possible predation pressure from birds of prey, adding that it may help decrease the visibility of snakes in open situations when viewed from the air. Hooding has been reported in several South American genera that also occur in Paraguay including *Bothrops*, *Dipsas*, *Erythrolamprus*, *Xenodon* and *Hydrodynastes* (Greene 1975; Cadle & Myers 2003; Araújo & Martins 2006; Kahn 2011; Menezes *et al.* 2015). The authors

have also observed this behaviour in *Xenodon merremi* and *Hydrodynastes gigas* in the Paraguayan Chaco (PS pers. obs.).

The defensive behaviours described here are similar to those documented in other species of snakes, but we are not aware of previous reports of them in *Erythrolamprus sagittifer*, *Dipsas turgida* and *D. ventrimaculatus*. Cadle & Myers (2003) provided a review of the defensive behaviours employed by the Dispadini but did not mention such behaviours in either of the species cited

here. Cacciali (2009) later stated that the only defences of *Dipsas turgidus* and *D. ventrimaculatus* are to remain immobile or to rely on the resemblance of colouration to members of the genus *Bothrops*. Our observations suggest however that the defensive behaviours of these species are more complex than previously understood.

Members of the genus *Erythrolamprus* commonly omit strong, foul cloacal odours when handled (observed in *E. poecilogyrus*, *E. miliaris* and *E. almadensis* in Paraguay by HC and PS), but despite handling many dozens of individuals, this is the first member of the genus that the authors have recorded that has displayed thanatosis. However, thanatosis has been previously documented in other members of the genus (Muscat et al. 2016). Thanatosis may be used as a terminal defense or “last resort” by prey that have been detected or seized by a predator (Thompson et al. 1981; Miyatake et al. 2004; Gregory 2008) and may vary with sex, body size/age, or environmental factors (Gregory & Gregory 2006; Gerald 2008; Durso & Mullin 2014).

For *Leptodeira annulata*, diverse defensive behaviours have been reported in the subspecies *L. a. ashmeadii* (Hallowell, 1845) in Venezuela, *L. annulata rhombifera* (Günther, 1872) in Panama (often considered a distinct species) (Cadle & Myers 2003) and *L. a. annulata* in the Brazilian Caatinga (Mendoza 1999; Guimarães & Sawaya 2011), and we now add *L. a. pulchriceps* Duellman, 1958 from Paraguay to this list. We encourage the publication of observations such as these to better understand the taxonomic inventory of such behaviours and to obtain further data on situations in which they are employed.

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