



Dead Snake! A Strategy for Survival: Thanatosis in Some Panamanian Snakes with a Review of Death-feigning in American Snakes

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Abstract.—Thanatosis (pretending to be dead), sometimes called letisimulation, is widely used as an anti-predator strategy by snakes. Herein we report six cases of death-feigning in six species of Panamanian snakes (Pacific Banded Coffee Snake, *Ninia maculata*; Dark-headed Red Falseboa, *Pseudoboa newwiedii*; Double-banded False Coralsnake, *Erythrolamprus bizona*; Colombian Long-tailed Snake, *Enuliophis sclateri*; Rufous-headed Snake, *Amastridium veliferum*; and Forest Flamesnake, *Oxyrhopus petolaris*). We also present a literature review of thanatosis in American snakes and discuss the terminology associated with this behavior.

Thanatosis (pretending to be dead), sometimes called letisimulation, is a widely used defensive behavior during which an animal feigns death to avoid predation (Gehlbach 1970; Greene 1988; Humphreys and Ruxton 2018), typically as a last resort after other anti-predator behaviors have failed (Rogers and Simpson 2014; Bauder et al. 2015). Interactions between predators and prey often can be broken down into a sequence of stages, beginning with the two individuals being in proximity, leading through detection, identification, reduc-

ing separation, contact, subjugation, and finally consumption (Endler 1991; Caro 2005; Humphreys and Ruxton 2018).

In snakes, thanatosis has been documented in taxa ranging from ancient lineages such as pythonids to advanced colubroids (Gehlbach 1970; Greene 1988; Roze 1996; dos Santos and da Silva Muniz 2012; Pineda 2013; Almeida et al. 2016; Muscat and Entiauspe-Neto 2016; Gonzales and de Oliveira 2020; Thomas et al. 2020). Herein we present the first reports of thanatosis in snakes from Panama (Figs. 1–3):



Fig. 1. Thanatosis in Panamanian snakes: Pacific Banded Coffee Snake (*Ninia maculata*) (left) and Dark-headed Red Falseboa (*Pseudoboa newwiedii*) (right). Photographs by Abel Batista (left) and Melquiades Castillo (right).



Fig. 2. Thanatosis in Panamanian snakes: Double-banded False Coralsnake (*Erythrolamprus bizona*) (left) and Colombian Long-tailed Snake (*Enuliophis sclateri*) (right). Photographs by Eduardo Zambrano (left) and Rogemif Fuentes (right).



Fig. 3. Thanatosis in Panamanian snakes: Rufous-headed Snake (*Amastridium veliferum*) (left) and Forest Flamesnake (*Oxyrhopus petolarius*) (right). Photographs by Edmundo Belton (left) and Eduardo Zambrano (right).

the first reports for the Dark-headed Red Falseboa, *Pseudoboa newwiedii* (Duméril, Bibron, and Duméril 1854); Double-banded False Coralsnake, *Erythrolamprus bizona* (Jan 1863); Forest Flamesnake, *Oxyrhopus petolarius* (Linnaeus 1758); Rufous-headed Snake, *Amastridium veliferum* Cope 1861; and the second reports for the Colombian Long-tailed Snake, *Enuliophis sclateri* (Boulenger 1894), and the Pacific Banded

Coffee Snake, *Ninia maculata* (Peters 1861). We also review the literature on thanatosis in the Americas and discuss some of the relevant terminology.

Methods

Three of the six cases presented (*Pseudoboa newwiedii*, *Erythrolamprus bizona*, *Oxyrhopus petolarius*) emanated from

rescue operations in human settlements (Las Palmeras and La Soledad, Veraguas Province, and Tocúmen, Panama City) that consisted of answering calls from the community, rescuing, photographing, and then releasing the snakes. The other three (*Ninia maculata*, *Enuliophis sclateri*, *Amastridium veliferum*) were observed fortuitously in semi-wooded areas near Coclesito and Fort Sherman, Colón Province, captured, photographed, and released.

We conducted a thorough literature review to compile all reports of thanatosis in American snakes. We accessed papers published in *Herpetological Review*, *Herpetology Notes*, *Herpetological Bulletin*, *Mesoamerican Herpetology*, *Reptiles & Amphibians*, and *Herpetologica*. We also conducted “Google Scholar” searches in English, Spanish, and Portuguese to find papers published until August 2021, using the following keywords: “thanatosis,” “snakes,” “letisimulation,” “feign,” “defensive behavior,” and “death-feigning.”

Results and Discussion

The six cases of thanatosis in Panamanian snakes are described in Table 1 and descriptions and abbreviations for associated behaviors are in Table 2. All snakes presented tonic immobil-

ity (TI) and all but *A. veliferum* and *N. maculata* engaged in contortions (C). The most behaviors (C, TI, S, CH) were exhibited by *E. bizona*, which was the only snake that cocked its head. Both *P. newwiedii* and *N. maculata* exhibited stiffness (ST), and *A. veliferum* was the only one that gaped (MG) and protruded its tongue (TP).

Our literature search generated reports of thanatosis for one American leptotyphlopoid, one typhlopoid, seven colubrids, 29 dipsadids, six elapids, nine natricids, and three viperids (Table 3). Many of the observations were made in captivity or in controlled situations, so evidence of this behavior in the wild is quite scarce (dos Santos and da Silva Muniz 2012). Stress caused by handling snakes is likely a determining factor for this process to occur (Muscat and Entiauspe-neto 2016). Of our observations, all but one of the snakes exhibited thanatosis during and after being manipulated; only in the case of *Amastridium veliferum*, which was found while feigning death, do we think that a failed predatory event or successful thanatosis occurred.

Thirty-four of the 67 reports were from North America, 19 from South America, 10 from Central America, and two from the West Indies. That over half of the reports come

Table 1. Observations of thanatosis in five species of Panamanian snakes. Abbreviations as in Table 2.

Species	Location	Date
Pacific Banded Coffee Snake (<i>Ninia maculata</i>)	Chiriquí Grande (8°56'56.60"N, 82°08'27.46"E; 19 m asl)	8 November 2007
Found during a tour, this snake was captured and relocated for photographs. During the photographic session, it began to contort (C) and invert (S) its body, partially exposing its venter while remaining immobile (TI) and stiff (ST) for 5 min before righting itself.		
Dark-headed Red Falseboa (<i>Pseudoboa newwiedii</i>)	Tocumen, Panamá (9°04'03.01"N, 79°23'59.98"E; 17 m asl)	29 March 2019
This snake inverted its body (C) before becoming immobile (TI) and rigid (ST). After a few minutes of being placed in a container without any response, it was trying to escape. Before being released about an hour later, it repeated the same behavior.		
Double-banded False Coralsnake (<i>Erythrolamprus bizona</i>)	Las Palmeras, Santiago de Veraguas (8°06'29.20"N, 80°57'20.49"E; 106 m asl)	10 March 2020
Three minutes after being placed on a white background for photographs, this snake engaged in atypically abrupt movements (CH, C) before inverting its body and becoming motionless (S, TI), remaining in that position for almost 2 min until gently stimulated and resuming a normal posture.		
Colombian Long-tailed Snake (<i>Enuliophis sclateri</i>)	Sherman, Colón (9°20'42.39"N, 79°58'40.67"E; 74 m asl)	12 April 2021
Placed on bare ground for a photographic session, this snake inverted its body (C) and remained motionless (S, TI) for about 2 min before slowly moving its head and investigating its surrounding; appearing to realize that it was safe, it slowly righted its body and moved away.		
Rufous-headed Snake (<i>Amastridium veliferum</i>)	Coclesito, Colón (8°48'54.14"N, 80°33'19.82"E; 61 m asl)	11 July 2021
Found immobile (TI) on a roadside with its tongue protruding (TP) and its mouth agape (MG), this snake was photographed and removed with a herpetological hook, to which it did not react; when placed back on the ground, it quickly righted itself and escaped.		
Forest Flamesnake (<i>Oxyrophus pletoralius</i>)	La Soledad, Veraguas (8°07'56.78"N, 80°58'45.98"E; 110 m asl)	21 July 2021
When placed in a grassy area for photographs, this snake tried to escape; when caught and replaced in the same area, it inverted its body pretending to be dead (C, S), and remained motionless (TI) for about a minute and a half before righting itself and trying to escape again.		

Table 2. Behaviors associated with thanatosis in the literature.

Behavior (abbreviation)	Description
Mouth-gape (MG)	Mouth partially or totally open, exposing the glottis and sometimes the tongue.
Tonic immobility (TI)	Adoption of a motionless posture triggered by contact or very close proximity of — but not injury inflicted by — a predator or other threat. Assumption of this posture does not reduce the sensory ability of the predator to locate or identify the prey or reduce the vulnerability of the prey if the attack is pursued. This state of motor inhibition is maintained even after release by the predator. When in this state, the prey exhibits reduced responsiveness to external stimulation (although monitoring of the environment can occur). In the absence of mortality or injury, the prey can recover its original physiological state after emerging from TI (Humphreys and Ruxton 2018).
Tongue protrusion (TP)	Tongue partial or totally protruded, erect or hanging from one side of the mouth; usually with an open mouth, but occasionally with the mouth closed.
Stiffness (ST)	Body rigid in irregular positions, usually inverted but sometimes in a normal position and even with body extended; generally associated with tonic immobility (TI), although the latter can occur with flaccidity.
Eye-rotation (ER)	Partial or complete rotation of the eyes and exposing the sclera.
Tightly coiled tail (TCT)	Tail folded laterally or tightly curled; also exhibited while feeding and as an anti-predator behavior alone.
Salivation (Sal)	Emission of oral secretions that might be perceived chemically as well as visually by a predator.
Cocked head (CH)	Erratic side-to-side movements of the head, sometimes continuing until the body is inverted and immobile (TI).
Contortions (C)	Erratic movements of the body, generally turning on itself repeatedly, often accompanied by mouth gape (MG), defecation (D), and/or supination (S).
Defecation (D)	Generally used as a primary anti-predatory strategy but sometimes part of thanatosis; defecation releases substances with penetrating and unpleasant odors in order to be unappealing to a predator.
Cloacal extrusion (CE)	Partial projection of the cloaca, usually accompanied by defecation (D).
Mouth-bleeding (MB)	Bleeding or spraying blood from the mouth can be an anti-predator strategy in itself; thanatosis is sometimes accompanied by the production of small bloody bubbles forming a red foam in the open mouth (Golubovi et al. 2021).
Supination (S)	Body partially or totally inverted, exposing the venter.
Bradycardia (B)	Reduced heart rate, a condition measurable only in the laboratory, which is why it likely is more common than currently recognized (McDonald 1974).

Table 3. Reports of thanatosis in American snakes. Abbreviations as in Table 2.

Species	Locality	Source	Behavior
Leptotyphlopidae			
<i>Rena dulcis</i>	USA (Texas)	Gehlbach 1970	TI, ST
Typhlopidae			
<i>Cubatyplops binimiensis</i>	Bahamas	Richmond 1955	TI
Colubridae			
<i>Coluber constrictor flaviventris</i>	Canada, USA (Missouri)	Lynch 1978; D.D. Smith et al. 1983	S, TI
<i>Drymarchon couperi</i>	USA (Georgia)	Stevenson 2010; Bauder et al. 2015	MG, TI
<i>Drymarchon melanurus erebenus</i>	USA (Texas)	Johnson et al. 2017	MG, TI
<i>Drymobius margaritiferus</i>	Mexico	Farr and Lazcano 2011	TI
<i>Lampropeltis alterna</i>	USA (Texas)	Tyron and Guese 1984	TI, CH, MG

(continued)

Species	Locality	Source	Behavior
<i>Masticophis flagellum flagellum</i>	USA (Oklahoma, Missouri)	Tucker 1989; Pflanz and Powell 1990	TP, C
<i>Masticophis flagellum testaceus</i>	USA (Texas)	Gehlbach 1970; D.D. Smith 1975	MG, TP, ER, Sal, CH, TI
<i>Sonora episcopa</i>	USA (Texas)	Gehlbach 1970	ST, TI, CH
Dipsadidae			
<i>Amastridium veliferum</i>	Panamá	Present study	TP, MG, TI
<i>Carphophis vermis</i>	USA	Wright 1986	TI
<i>Conophis vittatus</i>	Mexico	Ahumada-Carrillo 2013	TI, MG, S, TP
<i>Crisantophis nevermanni</i>	Honduras	Marineros-Sánchez 2017	TI, MG, CH, S, CE, D, MB
<i>Cubophis cantherigerus</i>	Cuba	Rodríguez-Cabrera et al. 2014	S
<i>Diadophis punctatus</i>	USA (Texas)	Gehlbach 1970	TI, ER, TCT, CH
<i>Dipsas turgida</i>	Paraguay	Cabral et al. 2019	S, TI, C
<i>Dipsas ventrimaculata</i>	Paraguay	Cabral et al. 2019	TI, ST, S
<i>Enuliophis sclateri</i>	Nicaragua	Salazar-Saavedra et al. 2021	S, TI
	Panamá	Present study	C, S, TI
<i>Erythrolamprus bizona</i>	Panamá	Present study	CH, C, S, TI
<i>Erythrolamprus miliaris</i>	Brazil	Muscat et al. 2016	TI, C, S
<i>Erythrolamprus sagittifer</i>	Paraguay	Cabral et al. 2019	S, TI, CH, C
<i>Farancia abacura</i>	USA (Mississippi)	Doody et al. 1996	TI, S, D
<i>Heterodon nasicus</i>	USA	Edgren 1955	TI, C, TP, D, S, CE, MB
<i>Heterodon platyrhinos</i>	USA	Edgren 1955; Platt 1969; McDonald 1974	TI, C, TP, S, D, CE, MB, B
<i>Heterodon simus</i>	USA (Florida)	Myers and Arata 1961	TI, C, TP, S, D, CE
<i>Hydrodynastes gigas</i>	Brazil	Marques et al. 2013	MG
<i>Hydrodynastes melanogigas</i>	Brazil	Marques et al. 2013	MG, TI, TP
<i>Leptodeira ashmeadii</i>	Venezuela	Mendoza 2009	S, C
<i>Lystrophis sp (Xenodon sp)</i>	South America	Shaw and Campbell, 1974	—
<i>Ninia maculata</i>	Costa Rica	Savage 2002	TI, S, TP
	Panamá	Present study	S, TI, ST
<i>Oxyrophus petolarius</i>	Panamá	Present study	C, S, TI
<i>Phalotris multipunctatus</i>	Paraguay	Atkison et al. 2018	S
<i>Philodryas chamissonis</i>	Chile	Zañartu and Urra 2020	S, TI
<i>Philodryas patagoniensis</i>	Brazil	Tozetti et al. 2012	TI
<i>Pseudoboa neuwiedii</i>	Panamá	Present study	C, TI, ST
<i>Rhadinaea decorata</i>	Costa Rica	Donini and Ussa 2016	C, MG, D, S, TI
<i>Taeniophallus occipitalis</i>	Brazil	Fiorillo et al. 2019	S
Elapidae			
<i>Micrurus frontalis</i>	Brazil	Roze 1996	ST, S
<i>Micrurus hemprichii</i>	Brazil	Almeida et al. 2016	S
<i>Micrurus ortonii</i>	Brazil	Gonzales and de Oliveira 2020	S, ST, MG
<i>Micrurus paraensis</i>	Brazil	Almeida et al. 2016	S
<i>Micrurus remotus</i>	Brazil	Almeida et al. 2016	S
<i>Micrurus tener</i>	USA (Texas)	Gehlbach 1970; Pineda 2013	TI, ST

Species	Locality	Source	Behavior
Natricidae			
<i>Haldea striatula</i>	USA (Texas)	Thomas and Hendricks 1976	C, TP, MG, ST, S
<i>Nerodia erythrogaster</i>	USA (Texas)	Everitt and Phillips 2019	S
<i>Nerodia fasciata</i>	USA (Texas)	Everitt and Phillips 2019	S
<i>Regina septemvittata</i>	USA (Kentucky)	Oldham et al. 2015	TI, S
<i>Storeria dekayi limnetes</i>	USA (Michigan, Louisiana)	Hayes 1987; Liner 1977	TI, C, TP, MG, ST, S
<i>Storeria occipitomaculata</i>	USA (Alabama)	Jordan 1970	C, MG, TP, ST, S
<i>Thamnophis elegans</i>	Canada	Gregory and Gregory 2006	TI, S
<i>Thamnophis sauritus</i>	USA (Florida)	Engel 2015	ST
<i>Thamnophis sirtalis</i>	Canada	Gregory and Gregory 2006	S
Viperidae			
<i>Bothrops erythromelas</i>	Brazil	dos Santos and da Silva Muniz 2012	MG, S
<i>Bothrops jararacussu</i>	Brazil	Muscat and Entiauspe-Neto 2016	S
<i>Crotalus cerastes</i>	USA (Nevada)	Thomas et al. 2020	S, MG

from North America was somewhat surprising given the latitudinal diversity gradient toward the tropics (e.g., B.T. Smith et al. 2012). We attribute this to a lack of sampling or perhaps under-reporting, as we are aware of thanatosis in snakes that had been witnessed by colleagues but was not reported.

The most frequently recorded adjunct behaviors were supination (S) and tonic immobility (TI), and the least frequently recorded behaviors were salivation (Sal), tightly coiled tail (TCT), and bradycardia (B), each reported only once. The highest number of behaviors (8) were recorded for the genus *Heterodon*, which was the only genus that displayed bradycardia (B) (in *H. platyrhinos*) and only one of two genera (with *Crisantophis*) that bled from the mouth (MB). Although supination might simulate a dead snake (Myers and Arata 1961), the fact that it is the most frequently recorded behavior associated with thanatosis could reflect that showing-the-venter might serve as a defense mechanism on its own. Revealing unexpected colors or patterns could confuse an aggressor, a condition known as deimatic behavior (Leonard and Stebbins 1999; Cyriac and Kodandaramaiah 2019; Gonzalez and de Oliveira 2020). Among our reports, this could apply to *N. maculata* and *E. bizona*. Similarly, a tightly coiled tail (TCT), although recorded only once in the context of thanatosis, has been documented as a defensive behavior (a form of self-mimicry that diverts the attention of a predator away from the snake's head) in species included in our review that are not known to associate it with thanatosis (Greene 1973, 1988; Roze 1996; Almeida et al. 2016)

Unlike authors (e.g., Rogers and Simpson 2014) who consider tonic immobility (TI) the most neutral concept to describe thanatosis, we consider TI a behavior that can be part of the thanatonic process. However, a snake may occasion-

ally present TI outside the context of thanatosis; for example, we have observed that *Mastigodryas alternatus* exhibits tonic immobility in the face of an imminent predator, but it is predisposed to escape at the first opportunity instead of exhibiting a reduced responsiveness to the putative threat. Similarly, behaviors such as defecation can be part of thanatosis, but snakes of many species defecate while biting or trying to escape.

Thanatosis is probably underreported across taxa (Humphreys and Ruxton 2018) and, given the wide variety of families that exhibit it, could be an ancestral trait. For example, thanatosis was reported recently in the genus *Hydrodynastes* (Marques et al. 2013), which is part of the same clade as the pseudoboinines (Grazziotin et al. 2012), a group that includes *O. petolaris* and *P. newwiedii* in this study. If true, additional species employing thanatosis should be in clades with species known to use this anti-predator behavior.

Two of the species in this study (*E. bizona* and *O. petolaris*) are known as false coral snakes that, by mimicking the aposematic patterns of sympatric venomous snakes, appear to reduce their risk of predation (Dunn 1954; Campbell and Lamar 1989; Buasso et al. 2006; Ray and Knight 2013; Batista and Miranda 2020). That might lead one to think that other defense mechanisms (such as thanatosis) would not be necessary. However, aposematic coloration might be part of a composition of anti-predator behaviors that, as a whole, is more effective than the sum of its parts, something suggested for coral snakes by Roze (1982). At least for visually guided predators, both coloration and behavior are effective (Gonzales and de Oliveira 2020), so presenting them together would appear to improve a snake's chances of survival. Snakes that exhibit thanatosis also employ other defense mechanisms

that include neck-twisting, non-locomotive body undulations, jumping (Davis Rabosky 2021), and tail flipping (N.G. Smith 1969). The strategy or strategies deployed and their duration may depend on factors such as the type of predator (Moore et al. 2020), size of the snake (Gerald 2008), or state of pregnancy (Gregory and Gregory 2006). Likewise, within the same species or population, behaviors can be employed to various degrees and with differing frequencies (Golubović et al. 2021).

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