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George Middendorf, *Howard University*



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## Is There an Antipredator Blood-Squirting Defense in the Bull Horned Lizard, *Phrynosoma taurus*?

**WADE C. SHERBROOKE**

Southwestern Research Station, American Museum of Natural History  
P.O. Box 16553, Portal, Arizona 85632, USA  
e-mail: wcs@amnh.org

**ELIZABETH BELTRAN-SANCHEZ**

Instituto de Investigaciones Científicas Area de Ciencias Naturales  
Universidad Autónoma de Guerrero, Avenida Lázaro Cárdenas S/N  
Ciudad Universitaria, Interior del Jardín Botánico, C. P. 39000  
Chilpancingo, Guerrero, México  
e-mail: elybeltran@hotmail.com

**FERNANDO MENDOZA-QUIJANO**

Instituto Tecnológico Agropecuario de Hidalgo, Laboratorio de Biología  
Apdo. Postal 94, Huejutla de Reyes, 43000, Hidalgo, México  
e-mail: mendozaq2000@yahoo.com.mx

**BERTRAND BAUR**

Mühlestrasse 23, CH-3053 Münchenbuchsee, Switzerland  
e-mail: bertrandebaur@bluewin.ch

and

**GEORGE A. MIDDENDORF III**

Department of Biology, Howard University  
415 College Street, NW, Washington, D.C. 20059, USA  
e-mail: gmiddendorf@howard.edu

Understanding of the phenomenon of the squirting of blood from orbital sinuses of horned lizards has been slow in unfolding since its early historic (Spanish Empire 1651 and 1767; Manaster 1997) and scientific reports (Middendorf and Sherbrooke 1992; Wallace 1871). Only infrequently do conditions during capture by humans result in blood squirting. In contrast, this defensive behavior is elicited with much greater frequency by exposure of the lizards to native canid predators such as Coyotes, *Canis latrans* (Sherbrooke and Mason, unpubl. data) and Kit Foxes, *Vulpes macrotis*; (Sherbrooke and Middendorf, *in press*), or a Dog (*Canis familiaris*) model (*P. cornutum*: 70–100%, *P. hernandesi*: 50%, and *P. solare*: 60% of trials; Middendorf and Sherbrooke 1992; Sherbrooke and Middendorf 2001). Indeed, this defensive behavior may be elicited by only a subset of would-be predators. For example, *P. cornutum* did not squirt blood in response to a variety of non-canid predators including Greater Roadrunner (*Geococcyx californianus*), Southern Grasshopper Mouse (*Onychomys torridus*), Long-nosed Leopard Lizard (*Gambelia wislizenii*), Western Diamondback Rattlesnake (*Crotalus atrox*), or whipsnakes (*Masticophis* spp.) (Sherbrooke 1990, 1991, 2003, unpubl. data). Anecdotal field observations of human encounters with a specific species of horned lizards can be useful for determining the presence of the behavior if the results are positive, but negative reports leave doubt as to the ability of the species to squirt blood under more appropriate conditions. Nevertheless, negative records under controlled conditions are useful for comparing the relative frequency of occurrence of blood squirting among species.

Recently, field encounters with humans and several species of *Phrynosoma* were combined with controlled encounters with dogs and literature records to identify which of the 13 currently

recognized species of horned lizards exhibit antipredator blood-squirting behavior (Sherbrooke and Middendorf 2001). These studies concluded that a clade of three species—*Phrynosoma mcallii*, *P. modestum*, and *P. platyrhinos*—does not use antipredator blood squirting. Individuals of those three species ( $N = 10\text{--}15$  for each) failed to squirt blood in controlled trials with a dog as a model canid and had a remarkably low frequency of blood-squirting events in encounters with humans (0.07%, compared to ~5% for *P. solare* and *P. cornutum*; Sherbrooke and Middendorf 2001). The blood-squirting proclivity of several other species in the genus remains in doubt pending tests with appropriate predators or predator models such as dogs. Therefore, Sherbrooke and Middendorf (2001) reported that the propensity to squirt blood in *P. douglasii* and *P. braconnieri* was unknown although expected because of the phylogenetic affinities of the two species with others in the genus that also appear not to squirt blood. Based on reports of human encounters in the literature, these researchers accepted that *P. asio*, *P. coronatum*, *P. orbiculare*, and *P. taurus* squirt blood when approached by predators for which the defense has evolved (i.e., canids). For these species the frequency of these responses in human encounters is unknown, but any positive response to humans apparently indicates the capacity of the species to utilize this defense during encounters with appropriate predators.

Recently one of us (BB) noted that the only literature report of blood squirting in *P. taurus* (Ruthling 1919) was apparently based on a misidentification of the species. Ruthling's (1919) reports of blood squirting for two species of horned lizards, *P. orbiculare* and *P. taurus*, in México were not based on personal observations, but on experiences reportedly made by Carlos Cuesta Terrón, a Mexican herpetologist (see Cuesta Terrón 1932). In recounting Cuesta Terrón's observations, Ruthling (1919) stated that both species were "abundant in the Valley of Mexico." Current information indicates that *P. taurus* does not occur in the Valley of México, where only *P. orbiculare* occurs (Baur and Montanucci 1998; Gonzáles et al. 1996; Sherbrooke 2003; Zamudio and Parra-Olea 2000), bringing into doubt the identification of a species known primarily from Oaxaca, Puebla, and Guerrero (an additional report places *P. taurus* in southeastern Morelos; Castro Franco 1987). The uncertainty, in 1919, of Ruthling's report stems also from the dubious taxonomic designation and identification of some Mexican species of horned lizards. Cuesta Terrón (1932) failed to mention *P. taurus* in his "Los Camaleones Mexicanos," and Martín del Campo (1934), who included *P. taurus* in his additions, did not mention blood squirting for the species. Therefore, we conclude that Ruthling's report of blood squirting by *P. taurus* is erroneous and should be rejected. This casts doubt on the ability of this species to squirt blood defensively in response to a predator. Here we attempt to resolve this question by presenting data from (1) numerous human field encounters with *P. taurus*, and (2) trials with a dog model of a native canid predator.

Between 1996 and 2003 one of us (EBS) made repeated observations of individuals of *Phrynosoma asio* and *P. taurus* at Cerro Tepelayo, Zumpango del Río, Municipio de Eduardo Neri, Guerrero, México (17°83'09"N, 99°31'31"W; 1280 m). Between 28 March and 16 September there were 35 human field encounters with individual *P. taurus*; of these 7 lizards were males, 21 females, and 7 juveniles. None of the Bull Horned Lizards squirted blood when captured by hand. Because juvenile *P. cornutum* and *P.*

*hernandesi* squirt blood in response to a dog (Sherbrooke and Middendorf 2001), we expect age is not a critical determinant. Thus, if *P. taurus* has a similar blood-squirting reaction rate to humans as that recorded for Texas horned lizards (*P. cornutum*; 5.9%, Lambert and Ferguson 1985) and Regal Horned Lizards (*P. solare*; 4.6 %, Parker 1971), we might predict that 1–2 (~5%) of the 35 *P. taurus* encountered would have squirted blood. However, not all horned lizard species have the same frequency of this defensive behavior when tested with canids (Sherbrooke and Middendorf 2001).

Ten *P. taurus* (9 females, 1 male; mean mass = 15.3 g, range = 8.0–30.5 g; mean SVL = 65.1 mm, range = 53–84 mm) were collected between 18 May and 16 June 2003, and were held in captivity in indoor terraria under natural lighting and fed ants and other insects. Tests for dog-elicited bloodsquirting were conducted on 16 June (N = 9; air temperature 22°C) and 17 June (N = 1; air temperature 26°C) in late afternoon. The dog, a Cocker Spaniel-mix, was held on a leash during the 3-min trials while one of us (WCS) handled the Bull Horned Lizards. During trials, the dog vigorously pawed and barked at the lizards, and in most trials (60%) the dog briefly took the lizard into its mouth, from which it was quickly removed. All lizards repeatedly ran from the dog, but were immediately returned to the study arena. None of the lizards closed their eyelids or engorged them with blood, a precursor to blood squirting (Middendorf and Sherbrooke 1992; Sherbrooke and Middendorf 2001; Sherbrooke and Middendorf, *in press*), or squirted blood. Immediately following the trials with *P. taurus*, we conducted a single trial with a large (SVL = 110 mm) male *P. asio* (a species known to squirt blood; Alvarez del Toro 1960; Hodges 2004) to confirm the appropriateness of the experimental conditions for eliciting blood squirting. This trial was terminated after 50 s when the horned lizard squirted blood from one orbital sinus onto the dog's muzzle (for comparable times with *P. cornutum*, see Middendorf and Sherbrooke 1992). Both of this lizard's eyelids were engorged with blood prior to squirting.

The negative results with *P. taurus* are similar to those for three other species of horned lizards, *P. mcallii*, *P. modestum*, and *P. platyrhinos* (Sherbrooke and Middendorf 2001). Combined with our negative encounters for blood squirting with humans (N = 35) and those of Hodges (N = 20; Hodges 2004), these data suggest that *P. taurus* either does not squirt or is not easily induced into a blood-squirting defensive behavior. In this sense, *P. taurus* resembles the *P. mcallii-modestum-platyrhinos* clade of “nonsquirting” species of *Phrynosoma* (Sherbrooke and Middendorf 2001). If blood-squirting is not a defensive strategy of *P. taurus*, based on the cladogram presented by Sherbrooke and Middendorf (2001), there may be more than one lineage of *Phrynosoma* that lacks or nearly lacks blood-squirting as a defense response. If *P. taurus* is a nonsquirting species, in contradiction to Ruthling's (1919) report, this calls for reinterpretation (Sherbrooke and Middendorf 2001) of this characteristic in the sister taxon to *P. taurus*, *P. braconnieri* (Hodges and Zamudio, unpubl. data).

No published data on blood squirting exist for *P. braconnieri*, but it was suggested that the species might exhibit a blood-squirting defense because of its putative close relationship with *P. taurus* and *P. asio* (Sherbrooke and Middendorf 2001). Recently collected data on blood squirting in *P. braconnieri* suggest that this species

may not respond, or displays a reduced frequency of defensive blood squirting (Sherbrooke and Mendoza, *in press*). Thus, there may be two or three clades—*P. douglasii* (Sherbrooke and Middendorf 2001; Zamudio, unpubl. data), *P. mcallii-modestum-platyrhinos* (Sherbrooke and Middendorf 2001), and *P. braconnieri-taurus* (this paper; Sherbrooke and Mendoza, *in press*)—of species in which the frequency of blood squirting is absent or significantly reduced. Although these groupings are interesting, because the phylogenetic relationships among *Phrynosoma* species are not completely resolved (Hodges and Zamudio, unpubl. data; Reeder and Montanucci 2001; Zamudio et al. 1997), the determination of the number of times blood squirting has been acquired or lost during the evolution of the genus remains in question.

As was noted with the *P. mcallii-modestum-platyrhinos* clade and *P. douglasii* (Sherbrooke and Middendorf 2001), *P. braconnieri* and *P. taurus* are relatively small bodied. The species best known for blood squirting (*P. asio*, *P. cornutum*, *P. coronatum*, *P. hernandesi*, *P. orbiculare*, and *P. solare*) are the six largest species in the genus (Baur and Montanucci 1998; Sherbrooke 2003). The large robust species *P. asio* seems to have the highest frequency (12%) of blood squirting toward humans (Hodges 2004). This suggests that the size and armament of larger *Phrynosoma* species narrows the range of potential predators to include canids and possibly others, where blood squirting is an effective defense.

Currently there are two methods for determining the blood-squirting response of horned lizards—human encounters and canid trials. Negative results in either case do not prove that a species is incapable of a positive response under other experimental or natural conditions. Even non-*Phrynosoma* iguanian lizards may occasionally exude blood from the orbital sinus, a condition that may have led to the evolution of blood squirting (Sherbrooke 2000). Consequently it is difficult to assign a “nonsquirting” status to a species of horned lizards. Indeed, Sherbrooke and Middendorf (2001) recorded infrequent human-encounter blood squirting within the *P. mcallii-modestum-platyrhinos* “nonsquirting” clade (0.07% of encounters), although the three species did not squirt when tested with dogs. Nevertheless, the dramatic differences in responses among *Phrynosoma* species, to both human and canid predators, suggests that the 13 species in the genus, and perhaps populations thereof, do not employ a blood-squirting defense to the same extent or under the same conditions. Our growing understanding of the circumstances that elicit blood squirting may lead to an appreciation of the selective pressures that fostered its development and diversification of use in species of *Phrynosoma*.

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## ***Dryadophis* Versus *Mastigodryas* (Ophidia: Colubridae): A Proposed Solution**

JAMES R. DIXON

and

BOB L. TIPTON

*Department of Wildlife and Fisheries Sciences, Texas A&M University  
College Station, Texas 77843, USA*

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The nomenclatural history of the Neotropical colubrid snake genera *Mastigodryas* and *Dryadophis* is convoluted. The oldest specific name in either of these genera is *Coluber boddaerti* Sentzen, 1796. Fitzinger (1843) assigned the generic name *Eudryas* to *C. boddaerti*. Brongersma (1937) pointed out that *Eudryas* Boisduval, 1836 predated Fitzinger’s name. Stuart (1939) proposed *Dryadophis* as a replacement name for all of the species in the group. Dunn (1944), in his report on the amphibians and reptiles of Colombia, suggested that *Mastigodryas danieli* Amaral, 1935a is a synonym of *Dryadophis boddaerti*. Dunn (1944) apparently thought *Dryadophis* was the older name and included *M. danieli* as *Dryadophis* in his discussion (p. 202) of the latter genus. Inadvertently, Dunn’s synonymy made *Mastigodryas* the oldest available name for the species recognized in the genus *Dryadophis*. Romer (1956) also suggested that the two genera were congeneric. Smith (1963), prompted by Romer’s suggestion, proposed the validation of *Dryadophis* as the accepted name and the suppression of *Mastigodryas* as a senior synonym to the International Code of Zoological Nomenclature (ICZN). Amaral (1964) commented to the ICZN that Smith’s request should not be granted because *Mastigodryas* is distinguished from *Dryadophis* by the absence of apical scale pits and a relatively shorter tail in the former. Amaral (1964) concluded that on taxonomic grounds both genera should be recognized. Peters and Orejas-Miranda (1970) placed *Dryadophis* as a synonym of *Mastigodryas* because Peters had examined the holotype of *M. danieli* and concluded that the two genera are not separable. However, Peters did not discuss the characters of *Mastigodryas* presented by Amaral, leaving the subject open for further comment. Smith and Larsen (1973) argued that it was premature to replace *Dryadophis* with *Mastigodryas*, based on Amaral’s (1964) comments. Apparently, the aforementioned discussions rekindled the ICZN members to vote on Smith’s (1963) proposal. ICZN Opinion 1035 was published in 1975, wherein the commission rejected suppressing the generic name *Mastigodryas*, based on Amaral’s (1964) comments.

Between 1935 and 1969 *Mastigodryas* is used as a valid generic name six times, whereas *Dryadophis* was reported in the literature 67 times during nearly the same time frame (1939–1969). The rare use of *Mastigodryas* is likely due to the absence of specimens in collections and/or its recognition as a valid genus.

Despite Peters and Orejas-Miranda’s (1970) synonymy of *Dryadophis* with *Mastigodryas*, *Dryadophis* continued to be used as a valid generic name by some herpetologists (Hidalgo 1981; Köhler 1999, 2003; McCoy et al. 1986; Smith and Larsen 1973; Wilson 1979; Wilson and Meyer 1982; Wilson et al. 1976), but others used *Mastigodryas* (Amaral 1976; Boos 2001; Cei 1993; Chippaux 1986; Cunha and Nascimento 1978; de Lema 1994;