



Research paper

## Reproductive modes of the South American water snakes: A study system for the evolution of viviparity in squamate reptiles

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## ARTICLE INFO

## Article history:

Received 31 January 2016

Received in revised form 11 April 2016

Accepted 12 April 2016

Available online 13 April 2016

Corresponding Editor: Alexander Kupfer.

## Keywords:

Hydrosini

Oviparity

Reproductive bimodality

Reproductive biology

Live-bearing

Egg-laying

## ABSTRACT

Viviparity has evolved at least 115 times in squamates and these multiple origins have raised a series of functional and evolutionary questions. Ideally, testing evolutionary hypotheses on squamate viviparity requires focusing on closely related taxa that exhibit both reproductive modes. South American water snakes of the tribe Hydrosini (genera *Hydrops*, *Pseudoeryx*, and *Helicops*) are a potential model system for studying the evolution of viviparity. However, available information about reproductive modes in this group is often confusing and contradictory. Herein, we identify the reproductive modes of the Hydrosini species by combining original data taken from both museum and live specimens with a critical review of the published literature. In addition, we mapped the reproductive modes on different phylogenetic hypotheses to identify origins of viviparity. The genus *Hydrops* is exclusively oviparous. Contrary to previous suggestions, we found *Pseudoeryx plicatilis* to be oviparous, and available evidence suggests that females of the species remain with eggs throughout incubation. Our results show that reproductive mode varies only in the genus *Helicops*. Two *Helicops* species are oviparous and eight species are viviparous. Interestingly, we also found that one species (*Helicops angulatus*) exhibits both reproductive modes. Intraspecific variation in reproductive mode is a rare phenomenon in squamates, and *H. angulatus* is the only snake species in which reproductive bimodality has been confirmed. *H. angulatus* is oviparous from northern to mid-eastern and north-eastern South America, and viviparous from north-western to mid-western South America. The allopatric distribution of oviparous and viviparous forms of *H. angulatus* does not support the hypothesis of facultative changes in the reproductive mode. Geographic variation in the embryonic stage at oviposition is likely to occur in *H. angulatus*. Ancestral state reconstructions suggest that oviparity is plesiomorphic in Hydrosini, as well as in the bimodal genus *Helicops*, and that viviparity has evolved independently at least three times in *Helicops*. We argue that the water snakes of the tribe Hydrosini (and more importantly, the genus *Helicops* and the bimodal *H. angulatus*) are an excellent model to test hypotheses on the evolution of squamate viviparity.

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### 1. Introduction

The term “reproductive mode” refers to the type of reproductive product deposited by the mothers (Blackburn, 1993). Accordingly, two modes of reproduction are recognized in amniotes. Oviparity is characterized by the deposition of shelled eggs that undergo or just complete their development outside the uterus, whereas viviparity

consists of the retention of fertilized eggs in the uterus throughout development and the subsequent parturition of fully developed young, which may or may not be surrounded by transparent shell membranes (Blackburn, 1993). Oviparity is the ancestral and most common reproductive mode in reptiles. All turtles, archosaurs, the tuatara, and a majority of squamates (lizards, snakes, and amphisbaenians) reproduce by laying eggs (Packard et al., 1977; Shine, 1985). Nevertheless, embryonic stage at oviposition varies substantially among reptile lineages. Whereas turtles, archosaurs, and the tuatara lay eggs at very early stages (Bellairs, 1991; Ewert, 1985; Ferguson, 1985; Moffat, 1985), most oviparous squamates lay eggs with embryos between the late organogenesis and early growth stages (Andrews and Mathies, 2000; Blackburn, 1995; Shine, 1983). Viviparity occurs in nearly 20% of the squamate

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species (Shine, 1985), but despite this low proportion, it has evolved independently at least 115 times (Blackburn, 2015a). These multiple origins of viviparity in various squamate lineages have raised a series of functional and evolutionary questions of broad interest, and consequently, researchers have put effort into understanding how and why viviparity evolved so often in squamate reptiles (see reviews in Andrews and Mathies, 2000; Blackburn, 2015a, 2000; Guillette, 1993; Shine, 2014, 1985; Stewart and Thompson, 2000; Thompson et al., 2002). Nevertheless, a major challenge in studying historical events is that they involve past processes that are not directly observed (Mayr, 2004). In the case of the evolution of viviparity, the difficulties arise because many features of current taxa may actually be specializations developed after viviparity has evolved (Blackburn, 2000; Guillette, 1993). A robust approach has been to focus on closely related taxa that exhibit both reproductive modes and show minor differences in other features (Blackburn, 2000; Guillette, 1993; Shine, 1985; Tinkle and Gibbons, 1977). In these cases, modifications observed in viviparous taxa are more likely to be related to the evolution of viviparity.

Many genera and some species of Squamata are reported to contain both oviparous and viviparous representatives, and consequently are ideal models of closely related taxa varying in reproductive modes (Shine, 1985; Tinkle and Gibbons, 1977). However, many of the cases of reproductive bimodality have been challenged and suggested to be the result of taxonomic misidentification or incorrect interpretation of reproductive modes (Blackburn, 1993; Shine, 1985; Tinkle and Gibbons, 1977). The genera and the few species in which reproductive bimodality is confirmed have been extensively used as model systems for studying the evolution of viviparity in a range of biological disciplines (e.g., Adams et al., 2007; Heulin et al., 2005; Stewart et al., 2010; Watson et al., 2014; Whittington et al., 2015). Comparative studies at such taxonomic levels have clarified the sequence of events during the evolution of viviparity, as well as the selective pressures that favour it, and its subsequent adaptations and specializations (Blackburn, 2000; Shine, 1985). Most of these studies have generally focused on a few lizard groups (e.g., scincids and phrynosomatids), but they have revealed considerable diversity of ways that viviparity has evolved (Blackburn, 2000; Stewart and Thompson, 2000; Thompson et al., 2002; Whittington et al., 2015). This likely reflects the multiple origins of viviparity and the several evolutionary pathways used to solve a physiological problem (Blackburn, 2006, 2000). Thus, studies involving a few species are not enough to explain the evolution of reproductive modes, and additional groups are useful to capture the range of ways viviparity can evolve in squamates (Blackburn, 2006, 2000).

The water snakes of the tribe Hydropsini are a potential model system for studying the evolution of viviparity. Hydropsini contains 21 species allocated to three genera (*Hydrops*, *Helicops*, and *Pseudoeryx*) widely distributed in South America (Uetz and Hošek, 2015; Zaher et al., 2009). The tribe contains both oviparous and viviparous species, and at least one genus (*Helicops*) is certainly reproductively bimodal. Well-supported instances of both oviparity [e.g., *Helicops angulatus* (Linnaeus, 1758); Ford and Ford, 2002; *Hydrops caesurus* (Scrocchi et al., 2005); Etchepare et al., 2012] and viviparity [e.g., *H. leopardinus* (Schlegel, 1837); Scartozzoni and Almeida-Santos, 2006] are available for some species. Indeed, early studies have suggested at least two origins of viviparity in the genus *Helicops* (Blackburn, 1985; Shine, 1985). However, there is considerable uncertainty about the reproductive mode of many Hydropsini. As occurs with many squamates (Blackburn, 1993), statements about the reproductive modes of Hydropsini are often presented with no empirical evidence and explicit criteria to support them (e.g., Albuquerque and Camargo, 2004; Chippaux, 1986; Whitworth and Beirne, 2011), and therefore confirmation is required. Moreover, published information is often confusing and

contradictory, and interpretations are fairly hampered by the recurrent use of the term “ovoviviparous” (e.g., Amaral, 1978; Chippaux, 1986; Cunha and Nascimento, 1993), an ambiguous and obsolete term that was largely used to refer to a wide variety of reproductive patterns, some mutually exclusive (see Blackburn, 1994, 1993). For example, the genus *Helicops* has been described as exclusively oviparous (e.g., Abuys, 1983), viviparous (Fitch, 1970) or “ovoviviparous” (e.g., Pérez-Santos and Moreno, 1991). *Helicops gomesi* (Amaral, 1921) and *H. hagmanni* (Roux, 1910) were first described as oviparous (Amaral, 1921; Cunha and Nascimento, 1981), but subsequently reported as “ovoviviparous” by the same authors (Amaral, 1978, 1927; Cunha and Nascimento, 1993). Intraspecific variation in reproductive mode is suggested in at least two species of Hydropsini, but confirmation is still required. *Pseudoeryx plicatilis* (Linnaeus, 1758) has been reported to lay eggs (Chippaux, 1986; Hoge, 1980) and give birth to young (Abuys, 1986). Moreover, Cunha and Nascimento (1981) reported a preserved female of *P. plicatilis* that contained 33 oviductal eggs, of which four had small developing embryos surrounded by thin membranes, and 29 were non-embryonated eggs surrounded by thick and leathery membranes. The authors interpreted this finding as evidence that such female could be simultaneously oviparous and viviparous. However, this assumption has never been confirmed. The other species suggested to be reproductively bimodal is *H. angulatus*, with some well-documented reports of egg-laying (e.g., Ford and Ford, 2002; Gorzula and Señaris, 1998; Rossman, 1973), but at least one record of viviparity (Rossman, 1984). A preserved female collected in Peru contained seven apparently fully developed young in the uterus without eggshell and residual yolk (Rossman, 1984). Nevertheless, there are no other records of viviparity for *H. angulatus*. In addition to all these issues, the reproductive mode of several Hydropsini species is unknown and, therefore, a clear overview on how reproductive mode varies within the tribe remains to be developed.

Our objectives here are twofold. Firstly, we aim to clarify how the reproductive modes vary within the Hydropsini. For that, we identify the reproductive modes of the Hydropsini species by combining original data collected from both museum and live specimens with a critical review of the published literature. Secondly, we mapped the reproductive modes on different phylogenetic hypotheses available for the group to identify origins of viviparity, and thereby to explore the potential for the group to act as a model system to test hypotheses on the evolution of squamate viviparity.

## 2. Material and methods

### 2.1. Original data

We collected original data from observations of both oviductal contents of museum specimens and the reproductive product at parition (i.e., young or eggs; Blackburn, 1993) in live specimens. Information about preserved specimens was collected from individuals housed in 24 scientific collections throughout Brazil (see Appendix A for a full list of museums). Whenever available, we also re-examined the specimens reported in two previous studies (Albuquerque and Camargo, 2004; Cunha and Nascimento, 1981). Specimens were identified using diagnostic characters provided in several taxonomic studies on the tribe members (Albuquerque and Lema, 2008; Amaral, 1921; Frota, 2005; Hofstadler-Deiques and Cechin, 1991; Kawashita-Ribeiro et al., 2013; Rossman, 2010, 1975, 1973, 1970). Efforts were made to gather information from different locations along the geographical distribution of each species.

A mid-ventral incision was made in 1424 adult females of 12 species to expose the reproductive tract. When a female was gravid/pregnant, we opened longitudinally one uterine incubation chamber and collected one egg. Then, we recorded whether a

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