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Extended Mate Accompaniment and a Novel Context for Female Body-Bridging in Pygmy Rattlesnakes, *Sistrurus miliarius* (Linnaeus 1766)

Zander E. Perelman[1] and Jenna N. Palmisano[2]

[1]Program in Ecology, Evolution, and Conservation Biology, University of Illinois Urbana-Champaign, Champaign, Illinois 61820, USA (zanderp2@illinois.edu; ORCID: 0009-0005-8133-9624)
[2]Department of Biology, University of Central Florida, Orlando, Florida 32816, USA (ORCID: 0000-0001-9779-7826)

Snake reproductive strategies vary across lineages and are relatively well studied (review in Shine 2003). Among snakes, the mating systems of temperate pitvipers have previously been modeled (Duvall et al. 1992; Schuett 1992; Aldridge and Duvall 2002), but information on the mating systems and associated reproductive behaviors of free-ranging populations is limited. Pitvipers typically employ either a female-defense polygyny (FDP) mating system, wherein males accompany and guard spatially predictable females through male-male fighting, or prolonged mate-searching polygyny (PMSP), wherein males search extensively for spatially unpredictable females and male-male interactions are infrequent (Duvall et al. 1992; Aldridge and Duvall 2002).

While multi-day male accompaniment of reproductive females is a key component of FDP pitviper mating-system models, it has been documented in only a few free-ranging species of rattlesnakes (Duvall and Schuett 1997; Shepard et al. 2003; Mauger and Wilson 2005; Jellen et al. 2007; Reinert et al. 2008; Clark et al. 2014; Perelman et al. 2022). Furthermore, comprehensive accounts of antagonistic interactions among free-ranging pitvipers during the reproductive season are lacking for most North American species (Perelman et al. 2022). We herein describe an instance of extended female accompaniment by a male Pygmy Rattlesnake (*Sistrurus miliarius*) and a novel observation of body-bridging displayed by the accompanied female in response to an interloping male.

Figure 1. A male-female pair of Pygmy Rattlesnakes (*Sistrurus miliarius*) observed on 13 October 2023. The male (Pyg116; right) had accompanied the female (Pyg115; left) for at least ten days (first observed on 3 October 2023). Photograph by Jenna N. Palmisano.

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At 1345 h on 13 October 2023 at a site in northeastern Florida, we visually located and captured a male-female associated pair of Pygmy Rattlesnakes (Pyg115–female, Pyg116–male; Fig. 1) in order to assess their health. At 1400 h, while Pyg115 was being processed, we found another adult male Pygmy Rattlesnake (Pyg117) approximately 20 m away from the associated pair's initial location. Pyg117 was tongue-flicking rapidly and moving continuously with his head close to the ground, behaviors typical of male mate-searching in *Sistrurus* (Perelman et al. 2023). This male was followed and manually filmed using a handheld camcorder (Sony HDR-CX330).

Pyg115 was processed and released at the capture site at 1410 h and began to move slowly toward a patch of dense vegetation. Meanwhile, Pyg117 continued chemosensory searching and at 1420 h approached within 1 m of Pyg115, who oriented toward him. Pyg117 continued tongue-flicking and slowly approached within about 15 cm of Pyg115, at which point she began body-bridging (Carpenter and Gillingham 1975) in response to the interloping male's approach (Fig. 2). In an apparent response to Pyg115's body-bridging, Pyg117 ceased all movement. After one minute of body-bridging from Pyg115, Pyg117 turned around, resumed tongue-flicking, moved in the opposite direction before making a wide loop approximately 4 m from the defensive female, and continued to move in the direction he was traveling prior to the interaction. Pyg116 was being processed approximately 5 m away during the interaction between Pyg115 and Pyg117. The full male-female interaction between Pyg115 and Pyg117 was captured on video (available at: https://www.youtube.com/watch?v=oXj4W-qba8Y).

Pygmy Rattlesnakes are commonly found in male-female pairs during the reproductive season (Farrell et al. 1995; Lind et al. 2018). The associated pair described herein was first encountered on 3 October 2023, indicating a minimum of 10 days that the male (Pyg116) had been accompanying the female (Pyg115) prior to the time of capture. The 10-day or longer period of pairing observed here provides the first report of extended mate-accompaniment for Pygmy Rattlesnakes, a species which displays all characteristics of FDP pitviper mating systems. Although these mating systems often feature instances of male-male antagonism (Duvall et al. 1992), the antagonistic interaction we describe herein was between the female of the associated pair (Pyg115) and an interloping male (Pyg117), who appeared to have been actively mate-searching in the area. Female behaviors typically observed during male-female pitviper reproductive interactions include tail-whipping, tail-waving, head-raising, and head-lifting (Gillingham et al. 1983; Schuett and Gillingham 1988; Schuett and Duvall 1996; Maag et al. 2023), and these behaviors are not known to be associated with female non-receptivity.

Body-bridging is a well-documented defensive behavior in North American pitvipers (Cowles 1938; Bogert 1941; Carpenter and Gillingham 1975) and has previously been observed in Pygmy Rattlesnakes (Greene et al. 2002). Previous research suggested that body-bridging is used exclusively in situations during which pitvipers are responding to the potential predation threat of ophiophagous snakes (Weldon and Burghardt 1979; Hoss and Clark 2014), and never in response to other crotalids (Bogert 1941). Given that Pyg117 was displaying mate-searching behaviors, Pyg115 was larger than Pyg117, frogs and lizards are the main prey items for Pygmy Rattlesnakes (Roth et al. 1999), and cannibalism has not been reported in Pygmy Rattlesnakes (Ernst and Ernst 2011); this interaction almost certainly did not represent the female's response to a potential ophiophagous event.

Similar to head-lifting and head-raising observed in Copperheads (*Agkistrodon contortrix*) (Schuett and Duvall 1996), Western Diamond-backed Rattlesnakes (*Crotalus atrox*) (Gillingham et al. 1983), and Mohave Rattlesnakes

Figure 2. An interaction between two Pygmy Rattlesnakes (*Sistrurus miliarius*): Pyg115 (female; left) body-bridging in response to the approach of Pyg117 (an interloping male; right). Photograph by Zander E. Perelman.

(*Crotalus scutulatus*) (Maag et al. 2023), the body-bridging exhibited by Pyg115 could indicate female mate choice. Prior to the interaction, Pyg115 had been accompanied by Pyg116 for at least 10 days, suggesting that she might have wanted to avoid courtship attempts from additional males such as Pyg117. Body-bridging effectively minimized Pyg115's interaction time with the interloping male, as Pyg117 retreated after only one minute and subsequently avoided her as he continued searching.

Despite their reproductive importance, documenting female mate-choice behaviors in pitvipers, both in captivity (Schuett and Gillingham 1988; Schuett and Duvall 1996) and in nature (Maag et al. 2023), is exceptionally rare. The male-female Pygmy Rattlesnake interaction described herein not only represents a novel context for body-bridging — a behavior previously thought to be used strictly as a defensive response to ophiophagous snakes — but provides a new insight into female mate-choice behaviors in free-ranging pitvipers, an area of study deserving of increased attention.

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