

See discussions, stats, and author profiles for this publication at: <https://www.researchgate.net/publication/358503088>

First report of male–male combat in free–ranging Amazonian Common Lanceheads (*Bothrops atrox*)

Article in *Canadian Journal of Zoology* · February 2022

DOI: 10.1139/cjz-2021-0192

CITATIONS

0

READS

116

6 authors, including:



Wirven Lima da Fonseca

Universidade Federal do Acre

12 PUBLICATIONS 39 CITATIONS

[SEE PROFILE](#)



Henrique B. Braz

Instituto Butantan

43 PUBLICATIONS 341 CITATIONS

[SEE PROFILE](#)



Paulo Sérgio Bernarde

Universidade Federal do Acre, Campus Floresta

146 PUBLICATIONS 1,980 CITATIONS

[SEE PROFILE](#)

Some of the authors of this publication are also working on these related projects:



The evolution of viviparity in South American water snakes (*Helicops*) [View project](#)



História natural de Anfíbios Anuros e Répteis Squamata no Nordeste do Brasil [View project](#)

First report of male–male combat in free-ranging Amazonian Common Lanceheads (*Bothrops atrox*)

Wirven Lima da Fonseca, Radraque Rodrigues Correa, Andesson de Souza Oliveira, Henrique Bartolomeu Braz, Selma Maria de Almeida-Santos, and Paulo Sérgio Bernarde

Abstract: In many snakes, males engage in agonistic interactions (male–male combat) apparently to establish dominant–subordinate relationships to gain priority access to reproductive females. In the Neotropical genus *Bothrops* Wagler, 1824 (~45 species), male–male combat has been recorded only in three species of the monophyletic *Bothrops atrox* group. However, most male combats recorded in this clade occurred in captivity, an environment that facilitates the emergence of agonistic interactions. Here, we provide the first record of male–male combat in free-ranging Amazonian Common Lanceheads (*Bothrops atrox* (Linnaeus, 1758)) and discuss the implications of this observation for the species mating system. During field-work, we found one immature female and five active adult males, two of them fighting. These observations suggest that reproductive male *B. atrox* actively search and compete for widely dispersed and scarce receptive females.

Key words: mating system, ritual combat, reproductive, behaviour, *Bothrops atrox*, Common Lancehead.

Résumé : Chez de nombreux serpents, les mâles ont des interactions agonistes (combats entre mâles) pour établir, semblerait-il, des relations dominant–subordonné déterminant la priorité d'accès aux femelles reproductrices. Au sein du genre néotropical *Bothrops* Wagler, 1824 (~ 45 espèces), des combats entre mâles n'ont été observés que chez trois espèces du groupe monophylétique *Bothrops atrox*. La plupart des combats de mâles ont toutefois été observés en captivité, un milieu qui favorise l'émergence d'interactions agonistes. Nous présentons la première observation enregistrée d'un combat entre fers de lance (*Bothrops atrox* (Linnaeus, 1758)) amazoniens mâles en liberté et une discussion de sa signification en ce qui concerne le type d'accouplement de l'espèce. Durant les travaux de terrain, nous avons relevé une femelle immature et cinq mâles adultes actifs, dont deux s'adonnant à un combat. Ces observations donnent à penser que les mâles reproducteurs cherchent activement et se disputent de rares femelles réceptives dispersées sur un grand territoire. [Traduit par la Rédaction]

Mots-clés : type d'accouplement, combat rituel, comportement de reproduction, *Bothrops atrox*, fer de lance commun.

Introduction

In many snakes, males travel long distances during the mating season, apparently searching for females to mate (Duvall et al. 1992). During this search, males can encounter conspecific males and engage in male–male combat, which is a ritualized behaviour that involves body interaction sequences to establish dominant–subordinate relationships to gain priority access to reproductive females (Carpenter 1984; Madsen et al. 1993; Schuett 1997). The occurrence of male combat is also expected to influence the evolution of sexual size dimorphism (Shine 1978, 1994) because larger males usually win combat bouts (Madsen et al. 1993; Schuett 1997; Fearn et al. 2005).

Male combat has been recorded in various viperid lineages (Senter et al. 2014). In the Neotropical genus *Bothrops* Wagler, 1824, male–male combat has been recorded only in 3 out of 45 species currently recognized: Common Lancehead (*Bothrops atrox* (Linnaeus, 1758)), Brazilian Lancehead (*Bothrops moojeni* Hoge, 1966), and Whitetail Lancehead (*Bothrops leucurus* Wagler, 1824) (Leloup

1975; Almeida-Santos and Salomão 2002; Almeida-Santos et al. 2017). These three species belong to the monophyletic *Bothrops atrox* group (Wüster et al. 1996), suggesting that male combat has evolved only in this clade. Except for one observation in *B. moojeni* (Almeida-Santos et al. 2017), all male combats recorded for this clade occurred in captivity (Leloup 1975; Almeida-Santos and Salomão 2002). Because captive conditions may facilitate the emergence of male combat and formation of hierarchies (Barker et al. 1979; Carpenter 1984; Almeida-Santos et al. 1999), confirming whether male combat occurs in nature is important for understanding the evolution of mating systems and sexual dimorphism in *Bothrops*.

Here, we provide the first record of male–male combat in free-ranging *B. atrox*, a large (up to 1720 mm total length), mostly nocturnal, and generalist pitviper found throughout the Amazon Rainforest, in northern South America (Oliveira and Martins 2001; Nogueira et al. 2019). In this species, mating occurs from mid-wet to early-dry season (January to May), as evidenced by numerous records in nature (Martins and Oliveira 1998; Almeida-Santos and Salomão 2002; Sanaïotti et al. 2005; Silva et al. 2019). Curiously, male combat

Received 13 October 2021. Accepted 6 January 2022.

W.L. da Fonseca. Laboratório de Herpetologia, Campus Floresta, Universidade Federal do Acre, Cruzeiro do Sul, Acre, 69980-000, Brazil; Programa de Pós-Graduação Bionorte, Universidade Federal do Acre, Campus Universitário, BR 364, Rio Branco, Acre, 69920-900, Brazil.

R.R. Correa, A. de Souza Oliveira, and P.S. Bernarde. Laboratório de Herpetologia, Campus Floresta, Universidade Federal do Acre, Cruzeiro do Sul, Acre, 69980-000, Brazil.

H.B. Braz and S.M. de Almeida-Santos. Laboratório de Ecologia e Evolução, Instituto Butantan, Avenida Vital Brasil, 1500, Butantan, São Paulo, 05503-900, Brazil.

Corresponding author: Paulo Sérgio Bernarde (email: SnakeBernarde@hotmail.com).

© 2022 The Author(s). Permission for reuse (free in most cases) can be obtained from copyright.com.

in nature has never been reported, even though the species is abundant and several field studies have been historically conducted within its range (e.g., Sexton 1956; Cunha and Nascimento 1993; Martins and Oliveira 1998; Oliveira and Martins 2001; Turci et al. 2009; Fraga et al. 2013). We discuss the implications of this observation for the mating system of the species.

Materials and methods

The observations reported here were made between 21 and 23 January 2019 while conducting fieldwork at the Lower Moa River Forest (07°37'24"S, 72°47'23.1"W, 188 m above sea level), in Cruzeiro do Sul, state of Acre, western Brazilian Amazon. This area presents a hot and humid tropical climate; annual temperature averages 24 °C and the wettest months occur from November to April (Ribeiro 1977). We conducted time-limited visual search (TLVS; Campbell and Christman 1982), which consisted of slowly walking along trails while searching for snakes visually exposed in the environment (for additional details on the sampling method used here see Fonseca et al. 2021). We conducted 816 TLVS person-hours for 1 year in an area of approximately 256 ha. Snake total length was estimated visually. Males ≥ 537 mm snout-vent length (SVL) and females ≥ 665 mm SVL were considered adults (Silva et al. 2019). Male-male combat was recorded using a digital camera and described after examining the videos in the laboratory. Behavioural nomenclature follows Carpenter et al. (1976) and Schuett and Gillingham (1989). Specimens were identified in situ by one of us (P.S.B.) based on the morphological characteristics and diagnosis provided in the snake identification book guide for the Alto Juruá region (Bernarde et al. 2017). A video of part of the combat is available in the Audiovisual Collection of the Museu de Zoologia da Universidade Estadual de Campinas "Adão José Cardoso" (<https://www2.ib.unicamp.br/fnjv/collection.php?zuec-vid=601>). Individual *B. atrox* collected in a previous study (Turci et al. 2009) at this same site are deposited in the herpetological collection of the Universidade Federal do Acre Campus Floresta (vouchers UFACF 1097, UFACF 1098, UFACF 1099, and UFACF 1175) in Cruzeiro do Sul, Acre, Brazil.

Results

During the 3 days, we observed five adult males and one immature female. The sex of individuals was determined by tail length and body stoutness, as males have relatively longer tails and are less stout than females (Silva et al. 2017). On 21 January 2019, at 18:45 h, we found an immature female (ca. 360 mm total length) coiled on a log 40 cm from the ground in a hunting posture. At 19:20 h, we observed an adult male *B. atrox* (ca. 800 mm total length) moving over the vegetation on a wetland trail. No individuals were seen the next day.

On 23 January 2019, we observed two adult males (ca. 1000 mm total length; one at 19:25 h and the other at 20:10 h) moving on the ground. About 300 m away from these individuals, we later (21:25 h) found two other adult males moving on the ground, approximately 50 cm apart. At 21:28 h, the larger individual (ca. 1300 mm total length; hereinafter alpha) moved towards the smaller one (ca. 1200 mm total length; hereinafter beta).

As alpha approached beta, both snakes lifted their heads off the ground and ascended to a vertical posture (Fig. 1A). At that time, each male tried to lift his head higher than the rival, and the vertical posture was held with up to 40%–50% of the anterior body (Fig. 1B). Once in this position, the snakes began to sway from side to side (Fig. 1C). During the vertical posture, one male attempted to entwine its head and neck around its opponent's body by hooking either to the left or to the right. After topping, both males fell to the ground and separated briefly, but they soon established contact and resumed the combat. Examination of this behavioural sequence indicates that alpha exhibited higher and more vertical posture, and therefore, we considered him to

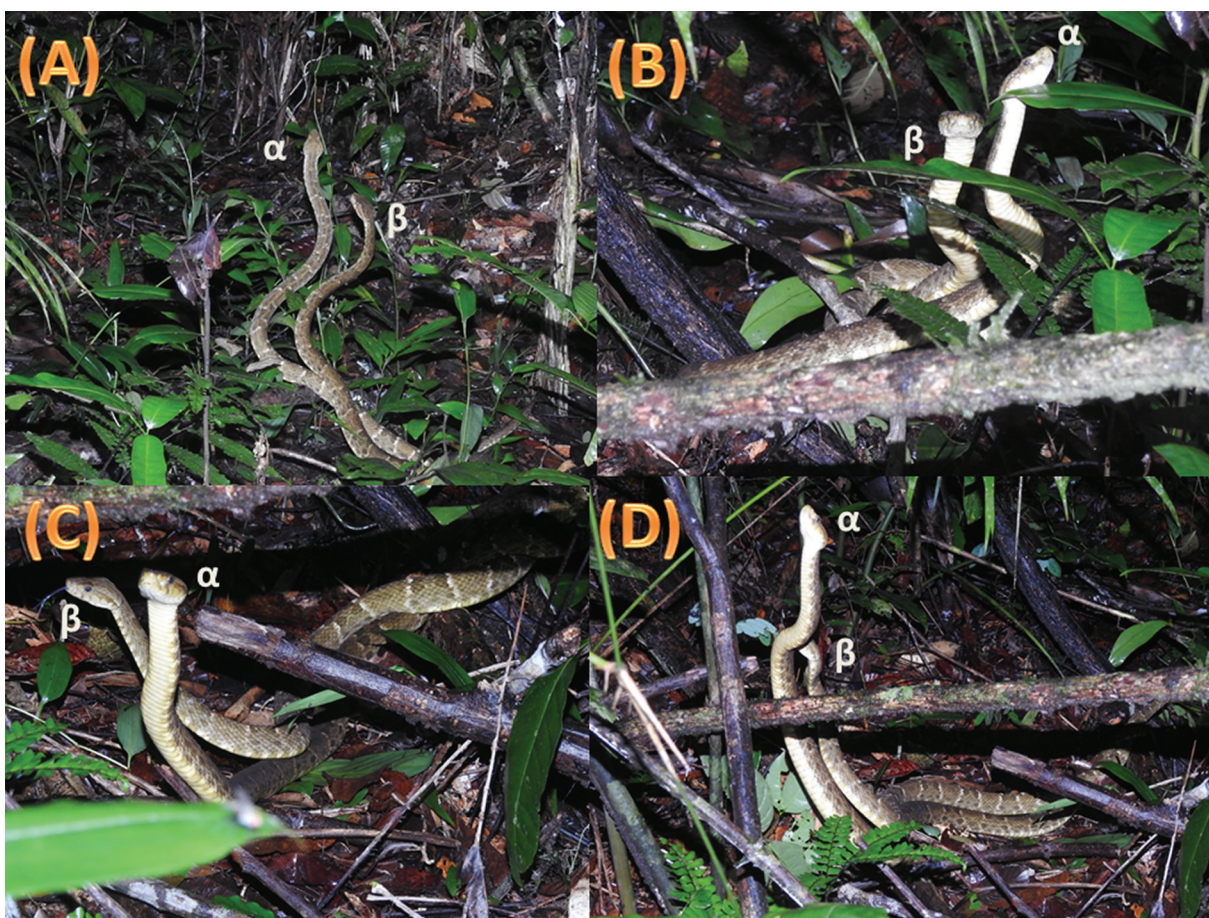
be the dominant and beta to be the subordinate (Fig. 1D). The combat bout lasted about 5 min, and it ended with beta moving away. Alpha remained in the combat site until we left. We thoroughly searched the surroundings of the combat site but found no female.

Discussion

Our observations confirm that free-ranging male *B. atrox* engage in combat while actively searching for females during mating season. The ritual combat behaviour of *B. atrox* (i.e., intense tongue-flicking, solicitation display, ascent, vertical display with swaying of the anterior trunk, bending over backwards, and topping) is similar to that reported for other *Bothrops* (Leloup 1975; Almeida-Santos et al. 2017). Our observation of male-male combat coincides with the mating season (November–May) described for the species (Silva et al. 2019). In this period, the vast majority of adult males exhibit peak of spermatogenesis and hypertrophy of the sexual segment of the kidneys and are therefore reproductive (Silva et al. 2019). In contrast, most female *B. atrox* probably reproduce non-annually, as we interpreted from the nearly 50:50 ratio of reproductive versus non-reproductive females during the mating season provided by Silva et al. (2019). Non-annual female reproduction suggests that the operational sex ratio (OSR) during mating season is male-biased. The finding of only adult males moving around during the sampled days and the virtual absence of females near the combat site corroborates a male-biased OSR and indicates that reproductive males search for widely dispersed and scarce receptive females. This pattern is consistent with the prolonged mate searching polygyny system (Duvall et al. 1992). However, in many snakes (including viperids), both sexes have been found to mate with multiple partners during a mating season, probably because male-biased OSR reduces mating opportunities for many males and creates opportunities for reproductive females to mate multiple times (Duvall and Schuett 1997; Lind et al. 2016). Consequently, males sire offspring with multiple females, whose offspring may be sired by multiple males (Duvall and Schuett 1997; Lind et al. 2016). This polygynandrous mating system is argued to better describe snake mating systems (Rivas and Burghardt 2005). However, it remains unclear whether female *Bothrops* also copulate with multiple males, although their ability to store sperm for prolonged periods (Almeida-Santos and Salomão 2002; Silva et al. 2020a, 2020b) creates opportunities for sperm mixing and competition and thus multiple paternity.

There are at least nine published records of mating in free-ranging *B. atrox* (Martins and Oliveira 1998; Sanaïotti et al. 2005; Silva et al. 2019). In contrast, our observation is the first report of male-male combat in nature. Why is male combat in free-ranging *B. atrox* so rarely observed in comparison with mating? We offer two possible hypotheses. The first is that the duration of combat bouts may be much briefer than that of mating, which would decrease their chance of being observed (Shine et al. 1981). While the combat bout reported here lasted about 5 min, courtship or mating in nature has been reported to last at least 12 h in *B. atrox* (Sanaïotti et al. 2005) and at least 3 h in two congeners (Zacariotti et al. 2011; Marques et al. 2013). The second hypothesis is that the mating system of *B. atrox* varies geographically, with male combat occurring in some areas but not in others. All observations of mating in free-ranging *B. atrox* have been made in the surroundings (<100 km) of Manaus city, Central Amazonia (Martins and Oliveira 1998; Sanaïotti et al. 2005; Silva et al. 2019), and male-male combat has never been observed in this area. Our observation occurred about 1500 km southwest of Manaus. Geographic variation in mating system has been recorded in at least another widely distributed snake. In the Australian Diamond Python (*Morelia spilota* (Lacépède, 1804)), males from some populations engage in physical combats during the breeding season, whereas males from other populations do not (Shine and Fitzgerald 1995).

Fig. 1. Male–male combat behaviour in free-ranging Amazonian Common Lanceheads (*Bothrops atrox*). (A) Vertical posture assumed by alpha (larger male) and beta (smaller male) during the interaction. (B) Alpha orients beta in a vertical display. (C) Alpha in the vertical position, and beta following alpha, although in a lower vertical position. (D) Alpha keeps his head higher and more upright than beta. Colour version online.



In snakes, larger males usually win combat bouts over smaller ones (Madsen et al. 1993; Schuett 1997; Fearn et al. 2005), which was also our interpretation of the interaction presented here. Accordingly, selection is expected to favour larger male body sizes in species exhibiting male–male combat (Shine 1978, 1994). In keeping with the hypothesis of geographic variation in mating system, we expect that sexual size dimorphism (SSD) also varies among populations, as observed in *M. spilota* (Shine and Fitzgerald 1995). Thus, SSD would be female-biased in Manaus and other areas where males do not engage in combat for mating opportunities but less female-biased, absent, or male-biased in populations from our study site. As expected, SSD in Manaus region is largely female-biased (SSD = 048; calculated from body size data from Oliveira 2003). Unfortunately, we currently lack data from our study site to adequately test this hypothesis. Two other studies have also found female-biased SSD in *B. atrox*, but these studies combined data from specimens collected throughout the range of the species, which precludes testing for interpopulation differences (Silva et al. 2017; Silva et al. 2019). Interestingly, in *B. leucurus* (another member of the *atrox* group exhibiting male combat; Almeida-Santos and Salomão 2002), SSD varies geographically, with southern populations (Espírito Santo state) lacking SSD and northern populations (Bahia state) exhibiting female-biased SSD (Barros et al. 2014). Future studies could assess how widespread male–male combat is in *B. atrox* and test for geographic variation in SSD and mating system in the species.

Funding statement

We thank the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior – Brasil (CAPES) – Finance Code 001 and Conselho Nacional de Desenvolvimento Científico e Tecnológico – CNPq (through the Institutional Scientific Initiation Scholarship Program PIBIC/UFAC) for providing financial support to R.R.C. and A.S.O., and research productivity grant to S.M.A.-S. (310357/2018–7) and P.S.B. (311509/2020–7).

Acknowledgements

We thank the Instituto Chico Mendes de Conservação da Biodiversidade (ICMBio) for providing collection permits (SISBIO/12.178).

References

- Almeida-Santos, S.M., and Salomão, M.G. 2002. Reproduction in neotropical pit-vipers, with emphasis on species of the genus *Bothrops*. In *Biology of the vipers*. Edited by G.W. Schuett, M. Höggren, M.E. Douglas, and H.W. Greene. Eagle Mountain Publishing, LC, Eagle Mountain, Utah. pp. 445–462.
- Almeida-Santos, S.M., Peneti, E.A., Salomão, M.G., Peneti, E.A., Sena, P.S., and Guimarães, E.S. 1999. Predatory combat and tail wrestling in hierarchical contests of the Neotropical rattlesnake *Crotalus durissus terrificus* (Serpentes: Viperidae). *Amphib.-Reptilia*, 20: 88–96. doi:10.1163/156853899X00105.
- Almeida-Santos, S.M., Barros, V.A., Rojas, C.A., Sueiro, L.R., and Nomura, R.H.C. 2017. Reproductive biology of the Brazilian lancehead, *Bothrops moojeni*.

- (Serpentes, Viperidae), from the state of São Paulo, southeastern Brazil. *S. Am. J. Herpetol.* **12**(2): 174–181. doi:[10.2994/sajh-d-16-00047.1](https://doi.org/10.2994/sajh-d-16-00047.1).
- Barker, D.G., Murphy, J.B., and Smith, K.W. 1979. Social behavior in a captive group of Indian pythons, *Python molurus* (Serpentes, Boidae) with formation of a linear social hierarchy. *Copeia*, **1979**(3): 466–471. doi:[10.2307/1443224](https://doi.org/10.2307/1443224).
- Barros, V.A., Rojas, C.A., and Almeida-Santos, S.M. 2014. Is rainfall seasonality important for reproductive strategies in viviparous Neotropical pitvipers? A case study with *Bothrops leucurus* from the Brazilian Atlantic Forest. *Herpetol. J.* **24**(2): 69–77.
- Bernarde, P.S., Turci, L.C.B., and Machado, R.A. 2017. Serpentes do Alto Juruá, Acre — Amazônia Brasileira. EDUFAC, Rio Branco.
- Campbell, H.W., and Christman, S.P. 1982. Field techniques for herpetofaunal community analysis. In *Herpetological communities*. Edited by N.J. Scott, Jr. Wildlife Res. Rep. No. 13, U.S. Department of the Interior, Fish and Wildlife Service, Washington, D.C. pp. 193–200.
- Carpenter, C.C. 1984. Dominance in snakes. In *Vertebrate ecology and systematics: a tribute to Henry S. Fitch*. Edited by R.A. Seigel, L.E. Hunt, J.L. Knight, L. Malaret, and N.L. Zuschlag. University of Kansas Publications, Lawrence. pp. 195–202.
- Carpenter, C.C., Gillingham, J.C., and Murphy, J.B. 1976. The combat ritual of the rock rattlesnake (*Crotalus lepidus*). *Copeia*, **1976**(4): 764–780. doi:[10.2307/1443461](https://doi.org/10.2307/1443461).
- Cunha, O.R., and Nascimento, F.P. 1993. Ofídios da Amazônia. As cobras da região leste do Pará. *Bol. Mus. Para. Emilio Goeldi. Ser. Zool.* **9**(1): 1–191.
- Duvall, D., and Schuett, G.W. 1997. Straight-line movement and competitive mate searching in prairie rattlesnakes, *Crotalus viridis viridis*. *Anim. Behav.* **54**(2): 329–334. doi:[10.1006/anbe.1996.0418](https://doi.org/10.1006/anbe.1996.0418). PMID:9268464.
- Duvall, D., Arnold, S.J., and Schuett, G.W. 1992. Pitviper mating systems: ecological potential, sexual selection, and microevolution. In *The biology of pitvipers*. 1st ed. Edited by J.A. Campbell and E.D. Brodie. Selva Publishing, Arlington, Tex. pp. 321–336.
- Fearn, S., Schwarzkopf, L., and Shine, R. 2005. Giant snakes in tropical forests: a field study of the Australian scrub python, *Morelia kinghorni*. *Wildl. Res.* **32**(2): 193–201. doi:[10.1071/WR04084](https://doi.org/10.1071/WR04084).
- Fonseca, W.L., Correa, R.R., de Souza Oliveira, A.S., de Oliveira, I.S., and Bernarde, P.S. 2021. Habitat use and activity of *Bothrops bilineatus smaragdinus* Hoge, 1966 in the western Brazilian Amazon (Serpentes: Viperidae). *Herpetol. Notes*, **14**: 567–580.
- Fraga, R., Magnusson, W.E., Abrahão, C.R., Sanaiotti, T., and Lima, A.P. 2013. Habitat selection by *Bothrops atrox* (Serpentes: Viperidae) in Central Amazonia, Brazil. *Copeia*, **2013**(4): 684–690. doi:[10.1643/CE-11-098](https://doi.org/10.1643/CE-11-098).
- Leloup, P. 1975. Observations sur la reproduction de *Bothrops moojeni* Hoge en captivité. *Acta Zool. Pathol. Ant.* **62**: 173–201.
- Lind, C.M., Flack, B., Rhoads, D.D., and Beaupre, S.J. 2016. The mating system and reproductive life history of female timber rattlesnakes in north-western Arkansas. *Copeia*, **104**(2): 518–528. doi:[10.1643/CE-15-254](https://doi.org/10.1643/CE-15-254).
- Madsen, T., Shine, R., Loman, J., and Håkansson, T. 1993. Determinants of mating success in male adders, *Vipera berus*. *Anim. Behav.* **45**(3): 491–499. doi:[10.1006/anbe.1993.1060](https://doi.org/10.1006/anbe.1993.1060).
- Marques, O.A.V., Kasperoviczus, K.N., and Almeida-Santos, S.M. 2013. Reproductive ecology of the threatened pitviper *Bothrops insularis* from Queimada Grande Island, southeast Brazil. *J. Herpetol.* **47**(3): 393–399. doi:[10.1670/11-267](https://doi.org/10.1670/11-267).
- Martins, M., and Oliveira, M.E. 1998. Natural history of snakes in forests of the Manaus region, Central Amazonia, Brazil. *Herpetol. Nat. Hist.* **6**(2): 78–150.
- Nogueira, C.C., Argôlo, A.J.S., Arzamendia, V., Azevedo, J.A., Barbo, F.E., Bérnills, R.S., et al. 2019. Atlas of Brazilian snakes: verified point-locality maps to mitigate the Wallacean shortfall in a megadiverse snake fauna. *S. Am. J. Herpetol.* **14**(sp1): 1–274. doi:[10.2994/SAJH-D-19-00120.1](https://doi.org/10.2994/SAJH-D-19-00120.1).
- Oliveira, M.E. 2003. História natural de jararacas brasileiras do grupo *Bothrops atrox* (Serpentes, Viperidae). Doctoral dissertation, Paulo State University, Rio Claro, Brazil.
- Oliveira, M.E., and Martins, M. 2001. When and where to find a pitviper: Activity patterns and habitat use of the lancehead, *Bothrops atrox*, in Central Amazonia, Brazil. *Herpetol. Nat. Hist.* **8**(2): 101–110.
- Ribeiro, A.G. 1977. O clima do Estado do Acre. *Boletim Geográfico*. **35**(255): 112–141.
- Rivas, J.A., and Burghardt, G.M. 2005. Snake mating systems, behavior, and evolution: The revisionary implications of recent findings. *J. Comp. Psychol.* **119**: 447–454. doi:[10.1037/0735-7036.119.4.447](https://doi.org/10.1037/0735-7036.119.4.447). PMID:16366778.
- Sanaiotti, T.M., Vale, J.D., Biavati, G.M., and Campos, Z. 2005. *Bothrops atrox* (common lancehead). Mating. *Herpetol. Rev.* **36**(3): 321–322.
- Schuett, G.W. 1997. Body size and agonistic experience affect dominance and mating success in male copperheads. *Anim. Behav.* **54**(1): 213–224. doi:[10.1006/anbe.1996.0417](https://doi.org/10.1006/anbe.1996.0417). PMID:9268451.
- Schuett, G.W., and Gillingham, J.C. 1989. Male–male agonistic behaviour of the copperhead, *Agkistrodon contortrix*. *Amphib.-Reptilia*, **10**(3): 243–266. doi:[10.1163/156853889X00412](https://doi.org/10.1163/156853889X00412).
- Senter, P., Harris, S.M., and Kent, D.L. 2014. Phylogeny of courtship and male–male combat behavior in snakes. *PLoS One*, **9**(9): e107528. doi:[10.1371/journal.pone.0107528](https://doi.org/10.1371/journal.pone.0107528). PMID:25250782.
- Sexton, O. 1956. The distribution of *Bothrops atrox* in relation to food supply. *Bol. Mus. Cien. Nat.* **2–3**: 47–54.
- Shine, R. 1978. Sexual size dimorphism and male combat in snakes. *Oecologia*, **33**(3): 269–277. doi:[10.1007/BF00348113](https://doi.org/10.1007/BF00348113). PMID:28309592.
- Shine, R. 1994. Sexual size dimorphism in snakes revisited. *Copeia*, **1994**(2): 326–346. doi:[10.2307/1446982](https://doi.org/10.2307/1446982).
- Shine, R., and Fitzgerald, M. 1995. Variation in mating systems and sexual size dimorphism between populations of the Australian python *Morelia spilota* (Serpentes: Pythonidae). *Oecologia*, **103**(4): 490–498. doi:[10.1007/BF00328688](https://doi.org/10.1007/BF00328688). PMID:28306998.
- Shine, R., Grigg, G.C., Shine, T.G., and Harlow, P. 1981. Mating and male combat in Australian blacksnakes, *Pseudechis porphyriacus*. *J. Herpetol.* **15**(1): 101–107. doi:[10.2307/1563652](https://doi.org/10.2307/1563652).
- Silva, F.M., Oliveira, L.S., Nascimento, L.R.S., Machado, F.A., and Prudente, A.L.C. 2017. Sexual dimorphism and ontogenetic changes of Amazonian pit vipers (*Bothrops atrox*). *Zool. Anz.* **271**: 15–24. doi:[10.1016/j.jcz.2017.11.001](https://doi.org/10.1016/j.jcz.2017.11.001).
- Silva, K.M.P., Silva, K.B., Sueiro, L.R., Oliveira, M.E.E.S., and Almeida-Santos, S.M. 2019. Reproductive biology of *Bothrops atrox* (Serpentes, Viperidae, Crotalinae) from the Brazilian Amazon. *Herpetologica*, **75**(3): 198–207. doi:[10.1655/D-18-00023](https://doi.org/10.1655/D-18-00023).
- Silva, K.M.P., Barros, V.A., Rojas, C.A., and Almeida-Santos, S.M. 2020a. Infundibular sperm storage and uterine muscular twisting in the Amazonian lancehead, *Bothrops atrox*. *Anat. Rec.* **303**(12): 3145–3154. doi:[10.1002/ar.24309](https://doi.org/10.1002/ar.24309).
- Silva, K.M.P., Braz, H.B., Kasperoviczus, K.N., Marques, O.A.V., and Almeida-Santos, S.M. 2020b. Reproduction in the pitviper *Bothrops jararacussu*: large females increase their reproductive output while small males increase their potential to mate. *Zoology*, **142**: 125816. doi:[10.1016/j.zool.2020.125816](https://doi.org/10.1016/j.zool.2020.125816).
- Turci, L.C.B., Albuquerque, S., Bernarde, P.S., and Miranda, D.B. 2009. Uso do habitat, atividade e comportamento de *Bothriopsis bilineatus* e de *Bothrops atrox* (Serpentes: Viperidae) na floresta do Rio Moa, Acre, Brasil. *Biota Neotrop.* **9**(3): 197–206. doi:[10.1590/S1676-06032009000300020](https://doi.org/10.1590/S1676-06032009000300020).
- Wüster, W., Thorpe, R.S., and Puerto, G. BBBSP. 1996. Systematics of the *Bothrops atrox* complex (Reptilia: Serpentes: Viperidae) in Brazil: A multivariate analysis. *Herpetologica*, **52**(2): 263–271.
- Zacariotti, R.L., Zimak, T.F., and Valle, R.R. 2011. *Bothrops moojeni* (Brazilian lancehead): Mating. *Herpetol. Bull.* **115**: 33–34.