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Mating aggregation in the blind snake *Amerotyphlops brongersmianus*, with comments on the evolution of mating tactics in Scolecophidia

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Snakes exhibit two primary tactics during the breeding season: male-male combat and non-agonistic aggregations around reproductive females. However, the mating tactics of many species, particularly within the earliest-diverging snake lineages, remain poorly known. This knowledge gap hinders our understanding of the evolution of snake mating systems. Here, we document a multi-male/multi-female aggregation involving five males and two females of the South American striped blind snake, *Amerotyphlops brongersmianus* (Typhlopidae: Scolecophidia). Both females subsequently laid fertile eggs, thus confirming recent mating activity. We then critically reviewed literature reports of aggregation in scolecophidians to explore the evolution of mating tactics. We found various instances of mating aggregations in scolecophidians, indicating that this tactic is widespread within the group. We propose that mating aggregation is ancestral in Scolecophidia and evolved early in the evolutionary history of snakes. We encourage researchers to be vigilant and report observations of mating aggregations in snakes, especially in poorly known fossorial lineages. These records will help complement and validate current knowledge of reproductive behaviour and allow for testing the hypotheses proposed here.

Keywords: reproductive behaviour, courtship, fossorial snake, sexual aggregation, mating system

INTRODUCTION

Sexually reproducing animals exhibit a remarkable diversity in how they acquire mates. For example, in some species, males defend territories or resources to attract mates, while in others, they adopt sneaky tactics or mimicry to access females (Andersson, 1994; Gross, 1996). Mating tactics profoundly influence ecological interactions and evolutionary trajectories. Male competition for mates can drive the evolution of morphological traits, such as increased body size or weaponry (e.g. horns), to enhance reproductive success (Shine, 1989; Emlen, 2008). Similarly, female mate choice influences the evolution of secondary sexual traits (e.g. vibrant colouration) and courtship behaviours (Petersen, 2018). Therefore, documenting and understanding mating tactics provides valuable insights into how individual behaviours shape species ecology and evolution.

Among snakes, two primary mating tactics have been documented during the breeding season. In some species, males engage in physical combat to gain access to females (Shine, 1978a; 1994; Senter, 2022). In others, this agonistic interaction is never displayed; males tolerate proximity to one another and form small to large aggregations around receptive females (Crews & Garstka, 1982; Shine, 1986; Bertona & Chiaraviglio, 2003). Despite the importance of mating tactics, they

have been documented in only a limited number of snake species (Senter, 2022), largely due to the difficulty of observing mating behaviour in free-ranging snakes. This limited information hampers our understanding of the evolution of snake mating systems.

Scolecophidia is the earliest phylogenetic divergence of extant snakes and therefore a group of particular interest for understanding the ecological context of early snake evolution (Miralles et al., 2018; Braz & Almeida-Santos, 2022; Gower et al., 2022). Traditionally, extant snakes have been divided into Scolecophidia, which includes blind snakes and thread snakes, and Alethinophidia, which includes most other living snakes, such as boas, pythons, vipers, elapids and colubrids. Scolecophidia sensu lato (Miralles et al., 2018) comprises approximately 480 species allocated into five families: Anomalepididae, Gerrhopilidae, Leptotyphlopidae, Typhlopidae and Xenotyphlopidae (Uetz et al., 2026). Leptotyphlopidae is the sister group of Typhlopoidea, which includes Gerrhopilidae, Typhlopidae and Xenotyphlopidae (Hedges et al., 2014; Miralles et al., 2018). Anomalepididae has traditionally been included within Scolecophidia, but recent phylogenetic analyses placed it as the sister lineage to all other snakes, i.e. Alethinophidia (Miralles et al., 2018).

Thus far, no male-male combat has been reported for Scolecophidia (Shine, 1994; Senter, 2022). In

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contrast, mating aggregations have been unambiguously recorded in members of two of the five scolecophidian families: Leptotyphlopidae and Typhlopidae. In leptotyphlopids (the most basal scolecophidian family), mating aggregations have been recorded in *Myriopholis algeriensis* (Bouazza et al., 2018). In typhlopids, mating aggregations have been recorded in the genus *Anilius* (Shine & Webb, 1990; Ehmann & Bamford, 1993; Scanlon & Davidson, 1999), a derived genus within the subfamily Asiatyphlopinae (Sidharthan & Karanth, 2021). Many other conspecific aggregations have been reported in scolecophidians, involving as few as three to as many as 64 individuals (McCoy, 1960; Hibbard, 1964; Thomas, 1965; Hoser, 1980; Dyer, 1990; Amr et al., 1997). However, the causes of these aggregations remain uncertain, as snakes may aggregate for various reasons other than mating, such as hibernation, predator avoidance or thermoregulation (Noble & Clausen, 1936; Gregory, 2004; Aubret & Shine, 2009). Clarifying the ecological context of these aggregations will help differentiate between mating-related interactions and other behaviours, thus shedding light on the evolution of mating tactics in Scolecophidia.

Our aims here are twofold. First, we provide evidence of mating aggregation in the South American striped blind snake, *Amerotyphlops brongersmianus*, a member of the most basal typhlopoid subfamily (Typhlopinae). Second, we critically review aggregation records in Scolecophidia to identify further instances of mating aggregation. By doing this, we seek to shed light and formulate hypotheses on the evolution of mating tactics within Scolecophidia sensu lato.

MATERIALS & METHODS

Original observations

Our original observations were made during faunal surveys conducted by Instituto Butantan staff (including one of us, SMAS) in the surroundings of the 'Engenharia Sérgio Motta' Hydroelectric Power Plant, in the Paraná River, mid-western Brazil (-22.48817, -52.94687; 302 m above sea level). This area is an ecotone between the Atlantic Forest and Cerrado biomes, with a tropical savanna climate (Aw in Köppen's classification; Peel et al., 2007).

Amerotyphlops brongersmianus were captured during expeditions conducted in September, November and December 1998, February 1999, August 2000 and April 2001. Snakes were searched for during surveys and transported to Instituto Butantan for further analysis. In the laboratory, snakes were measured (snout-vent length, SVL) using a flexible measuring tape (± 1 mm) and dissected via midventral incisions to assess their reproductive status. We considered females sexually mature if they had vitellogenic follicles, oviductal eggs or folded oviducts (Shine, 1978b). We considered males sexually mature if they had enlarged testes and convoluted ductus deferentia (Slip & Shine, 1988).

Two females found aggregated with males (see Results) were housed individually in plastic containers

at room temperature. Clutches laid in the laboratory were incubated separately in containers containing moist vermiculite at room temperature. Hatchlings were measured (± 1 mm) and weighed (± 0.1 g). Values are presented as mean $\pm$ standard deviation.

Literature data

To gain insights into the evolution of mating tactics in scolecophidians, and snakes more broadly, we compiled literature and citizen science records of aggregation in Scolecophidia. We defined citizen science records as observations made outside formal scientific publications, including records from public natural-history platforms or unpublished observations provided by contributors, when they included enough contextual information to evaluate the aggregation. We defined aggregation as two or more individual snakes, either conspecifics or not, found together in a specific microhabitat at a higher density than that in the surrounding area (Gregory et al., 1987; Graves & Duvall, 1995). We critically evaluated these records to identify potential mating aggregations.

All scolecophidian species studied thus far exhibit highly seasonal reproduction, with mating generally occurring between late winter and spring (Shine & Webb, 1990; Ataev et al., 1994; Werler & Dixon, 2000; Webb et al., 2000; 2001; Goldberg, 2003; Khouri et al., 2020; 2022; Braz & Almeida-Santos, 2022; Dyugmedzhiev et al., 2023). Because other reproductive traits are also phylogenetically conserved within this group (Braz & Almeida-Santos, 2022), we interpreted adult aggregations recorded in late winter or spring as potential mating aggregations. Records explicitly describing snakes as intertwined, tangled or forming a knotted mass were also considered indicative of mating aggregation when no alternative explanation, such as hibernation, oviposition, feeding or flooding, was evident. To summarise the phylogenetic distribution of mating aggregation in Scolecophidia, we mapped genera with unambiguous or potential records onto a simplified phylogenetic tree. This mapping was intended as an illustrative synthesis of current knowledge, not as a formal ancestral-state reconstruction. Relationships among genera followed Martins et al. (2019) for Leptotyphlopidae and Sidharthan & Karanth (2021) for Typhlopoidea.

RESULTS

Original observations

Thirty-one *A. brongersmianus* individuals were collected during the sampling period. Of these, 24 were found solitarily under logs and stones; these specimens included 11 adult females (four gravid, 184–285 mm SVL; seven non-reproductive, 180–260 mm SVL), 11 adult males (174–197 mm SVL), one juvenile female (154 mm SVL) and one juvenile male (124 mm SVL). Seven *A. brongersmianus* individuals were found aggregated on 30 November 1998, around 09:00 h, intertwined between the leaf sheath and the stem (~10 cm above the ground) of a decaying palm tree (Arecaceae). The aggregation consisted of five males (SVL = 150–213 mm) and two



Figure 1. A hatchling *Amerotyphlops brongersmianus* (Typhlopidae: Scolecophidia) from a clutch laid by a female found in a spring mating aggregation with five males and another female in the Porto Primavera Dam, right margin of the Paraná River, state of Mato Grosso do Sul, mid-western Brazil.

females (SVL = 205 and 240 mm). No overt aggression was observed among the males. Dissections revealed that all five males in the aggregation were sexually mature. Both females laid fertile eggs in the laboratory. The first female (205 mm SVL) laid seven fertile eggs on 12 December 1998. Four of these eggs hatched on 2–4 February 1999 after 52–54 days of incubation (Fig.

1), and the hatchlings measured 80–85 mm SVL (mean = 82.8 ± 2.2 mm) and weighed 1.1–1.3 g (mean = 1.2 ± 0.1 g). The second aggregated female (240 mm SVL) laid seven fertile eggs on 28 December 1998, but all failed to develop due to fungal contamination.

Current knowledge of mating aggregation in Scolecophidia

Our search identified 45 reports of aggregation across 19 scolecophidian species (Table S1 in supplementary materials). We identified unambiguous records of mating aggregation for four leptotyphlopoid species (*Leptotyphlops conjunctus*, *Myriopholis algeriensis*, *Myriopholis macrorhyncha* and *Rena dissecta*) and four typhlopoid species (*A. brongersmianus*, *Anilius nigrescens*, *Anilius wiedii* and *Typhlops rostellatus*; Table S1 in supplementary materials). We detected potential mating aggregations for four leptotyphlopoid species (*Epictia albipuncta*, *Epictia australis*, *Epictia munoai* and *Rena humilis*) and two typhlopids (*Xerotyphlops vermicularis* and *Antillotyphlops platycephalus*; Table S1 in supplementary materials). Other instances of aggregations were related to hibernation, feeding, oviposition, hatching and flooding (Table S1 in supplementary materials). Current evidence shows that mating aggregation is a widespread tactic in leptotyphlopids and typhlopids, as summarised on a simplified phylogenetic tree (Fig. 2). No information is available for the other three scolecophidian families (Anomalepididae, Gerrhopilidae and Xenotyphlopidae).

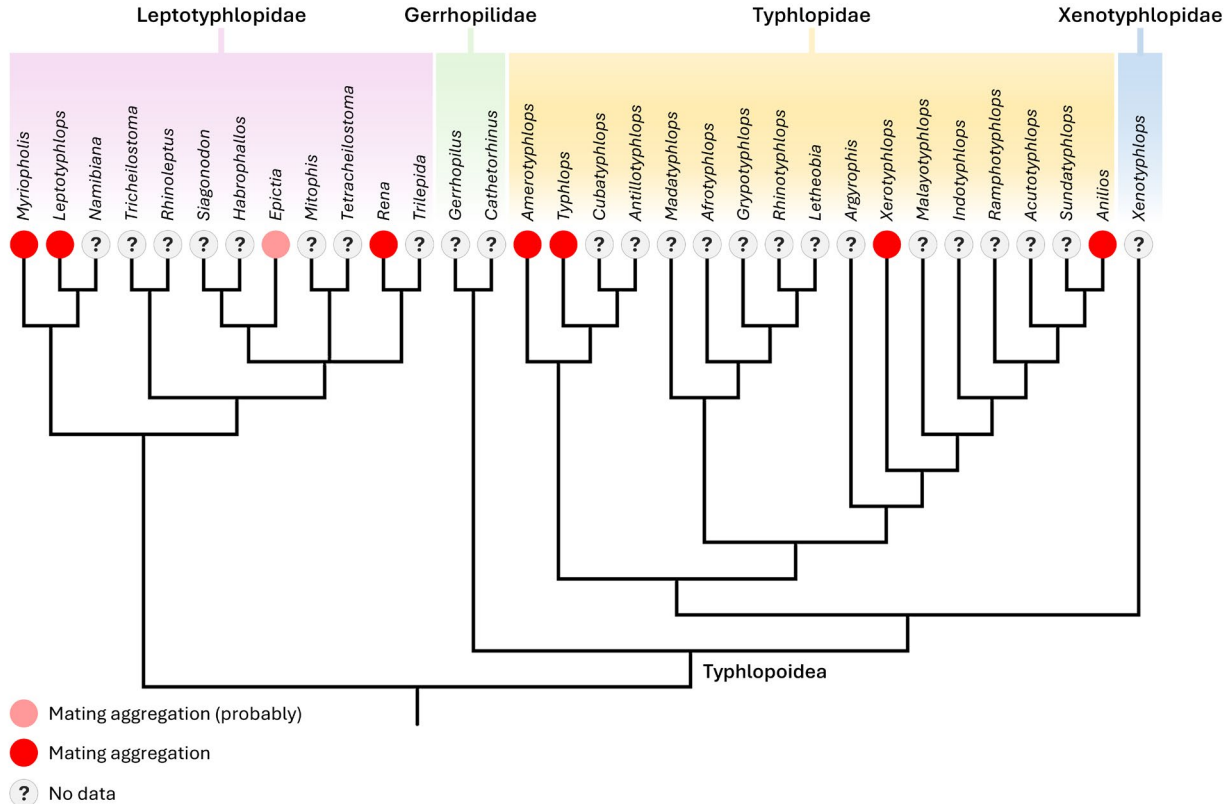


Figure 2. Phylogenetic distribution of mating aggregation in scolecophidian (sensu stricto; Miralles et al., 2018) genera. Relationships among genera follow Martins et al. (2019) for Leptotyphlopidae and Sidharthan & Karanth (2021) for Typhlopoidea.

DISCUSSION

The seven individuals of *A. brongersmianus* found intertwined were engaged in a mating aggregation. Several lines of evidence lead us to this conclusion. First, all males were sexually mature. Second, the timing of the aggregation (mid-spring) coincided with the period when ductus deferentia are nearly devoid of sperm produced in late winter, i.e. the timing of spermatogenesis (Khoury et al., 2020), indicating recent use. Third, the aggregation occurred synchronously with the timing of vitellogenesis and ovulation in this species (Ávila et al., 2006; Khoury et al., 2020). Finally, both females in the aggregation laid fertile eggs 12 and 28 days after the aggregation.

Mating aggregations in snakes commonly involve multiple males courting and attempting to mate with a single female (Shine, 1986; Weatherhead et al., 1995; Shetty & Shine, 2002; Bertona & Chiaraviglio, 2003; Passos & Borges-Nojosa, 2015). However, our observation involved two females and five males. Multi-male/multi-female mating aggregations (five males and two females) have been documented in the typhlopod *A. nigrescens* (Ehmann & Bamford, 1993), a species also known to form multi-male/single-female mating aggregations (Shine & Webb, 1990; Scanlon & Davidson, 1999). Therefore, it is possible that *A. brongersmianus* also forms multi-male/single-female mating aggregations. In another scolecophidian, the leptotyphlopod *R. dissecta*, a presumed mating aggregation involved eight males and five females (McCoy, 1960). Collectively, these observations suggest that the aggregation patterns are variable within and among scolecophidian species, with both multi-male/multi-female and multi-male/single-female aggregations occurring.

One hypothesis for multi-male/multi-female mating aggregations in scolecophidians is that, in addition to chemical cues, both sexes may be attracted to certain environmental features. Scolecophidians are often found under logs and stones after rain floods underground galleries (McCoy, 1960; Clark & Clark, 1973; Emsley, 1977; Gasc & Rodrigues, 1980; Shine & Webb, 1990; Ehmann & Bamford, 1993; Mulder, 1995; Greene, 1997). Because the mating season coincides with the rainy season in many scolecophidians, limited availability of surface shelters could drive males and females to congregate at these sites. This idea may also explain the recurrent presence of subadult scolecophidians in springtime mating aggregations alongside adults (e.g. Thomas, 1965; Hoser, 1980; Scanlon & Davidson, 1999). Thus, environmental constraints, combined with reproductive behaviour, may drive aggregation formation.

The production of viable eggs by both *A. brongersmianus* females in the aggregation implies that they both mated. Available evidence suggests that female scolecophidians lack long-term sperm storage (Braz & Almeida-Santos, 2022). However, it remains unclear whether male and female scolecophidians copulate with multiple partners within an aggregation and whether both sexes participate in further mating aggregations during the breeding season. Nevertheless,

there is potential for various mating systems to evolve, i.e. polygyny (males mating with multiple females), polyandry (females mating with multiple males) or polygynandry (both sexes mating with multiple mates). In the colubrid *Hydrodynastes gigas*, at least one male and one female copulated with two different mates in a multi-male/multi-female mating aggregation (Couto et al., 2022). In the natricid *Nerodia sipedon*, both sexes may join multiple mating aggregations in a single breeding season (Barry et al., 1992). These cases show the potential of mating aggregations to cause polygynandry in scolecophidians.

The pattern of phylogenetic distribution of mating aggregation in scolecophidians suggests two evolutionary possibilities. The first is that mating aggregation has evolved multiple times independently in the group. Alternatively, mating aggregation is ancestral and evolved early in the evolutionary history of snakes. We find this hypothesis more plausible because scolecophidians exhibit many conserved morphological, behavioural and ecological traits. For example, scolecophidians are essentially fossorial and have tiny eyes, a limited gape size, a body covered in polished, round, equal-sized scales and feed on small invertebrate prey, mostly ants and termites (Greene, 1997; Miralles et al., 2018). Moreover, scolecophidians also share many reproductive traits, including highly seasonal gametogenesis concentrated in spring (Braz & Almeida-Santos, 2022). However, we note that scolecophidians are a speciose group (~475 species; Uetz et al., 2026), and mating tactics are unknown for many lineages (Fig. 2). Additional data are needed to assess the prevalence of mating aggregation in scolecophidians and thus test these evolutionary hypotheses. We encourage researchers to be vigilant and report observations of mating aggregations in snakes. These attitudes will help clarify the prevalence of this behaviour within this group and allow for testing of the hypotheses proposed here.

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Author contributions

Henrique Bartolomeu Braz compiled and analysed the literature data and wrote the first draft of the manuscript. Selma Maria Almeida-Santos contributed the original field observations and critically revised the manuscript. Both authors conceived the study, interpreted the results and approved the final version.

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