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Review

Long-term sperm storage in female snakes: derived innovation or overlooked ancestral trait?

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Abstract

Across animal taxa, sperm storage by females has long been recognized as a key reproductive strategy influencing mating systems, reproductive success, and sexual selection. Storage extending beyond a single reproductive cycle, termed long-term sperm storage (LTSS), is well documented in colubroid (late-diverged) snakes, where genetically validated cases include viable litters produced ≤6 years after last contact with a reproductive male. In contrast, the occurrence of LTSS in non-colubroid (all snakes basal to Acrochordidae) snake lineages remains poorly resolved. Here, we systematically review 125 years of literature (1900–2025) to evaluate evidence for LTSS in early-diverged snake lineages. In evaluating ~705 species representing 15 families, including well-known groups, such as boas (Boidae) and pythons (Pythonidae), we find limited and equivocal evidence for LTSS and none with definitive support. This phylogenetic pattern might reflect either true evolutionary rarity or persistent sampling and methodological limitations, particularly the historical inability to distinguish LTSS from facultative parthenogenesis. We outline targeted research priorities to resolve this uncertainty and highlight the importance of comparative reproductive studies across snake clades with divergent evolutionary histories and reproductive strategies.

Keywords Serpentes, reproductive strategy, sperm-storage tubules, facultative parthenogenesis, comparative reproduction, phylogenetic distribution

Introduction

The ability of female animals to store viable sperm for extended periods is a remarkable reproductive strategy, with major implications for mating systems, reproductive timing, and sexual selection (Devine 1984, Schuett 1992, Duvall *et al.* 1993, Zamudio and Sinervo 2000, Orr and Zuk 2012, Smith 2012). Female long-term sperm storage (LTSS), defined here as storage extending beyond a single reproductive season and resulting in viable offspring, occurs across diverse vertebrate and invertebrate taxa (Saint-Girons 1975, Racey 1979, Sever and Hamlett 2002, Bernal *et al.* 2015, Paynter *et al.* 2017, Degueldre and Aron 2023, Shankar *et al.* 2023). Interest in this phenomenon dates to the 19th and early 20th centuries (Agassiz 1857, Coker 1920, Blanchard 1943, Ludwig and Rahn 1943) and has intensified with advances in molecular parentage analysis (Booth and Schuett 2011, 2016, Levine *et al.* 2021, 2024, Shankar *et al.* 2023).

Among vertebrates, snakes have long occupied a central position in discussions of sperm storage owing to numerous reports of females having exceptionally prolonged storage durations (Saint-Girons 1975, Devine 1984, Birkhead and Møller 1993, Sever and Hamlett 2002, Braz and Almeida-Santos 2022). These observations render snakes a model system for understanding the ecological and evolutionary significance of LTSS (Schuett 1992, Sever and Ryan 1999, Siegel *et al.* 2011, Smith 2012). Here, we show that despite longstanding interest in the mechanisms underlying LTSS, the evolutionary distribution of this reproductive trait within Serpentes remains unresolved. Well-supported and sometimes genetically validated cases are concentrated in colubroid (late-diverged) snake lineages,

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including Viperidae, Elapidae, and Colubridae (Halpert *et al.* 1982, Fukada 1986, Almeida-Santos and Salomão 1997, Strugariu 2007, Booth and Schuett 2011, Friesen *et al.* 2014, Rojas *et al.* 2015, Bassi *et al.* 2020, Levine *et al.* 2021, 2024, Jurkfitz *et al.* 2023; but see Höggren and Tegelström 1996). In contrast, reports from the basal-most snake lineages, namely scolecophidians, and the early-diverging alethinophidians are rare and equivocal despite an abundance of studies of their mating systems and reproductive biology (Slip and Shine 1988, Shine 1992, Bertona and Chiaraviglio 2003, Pizzato and Marques 2007, Rivas *et al.* 2007, Tourmente *et al.* 2006, Booth *et al.* 2011a, b, 2014, Skelton *et al.* 2021). This disparity raises a key evolutionary question: does LTSS represent a derived reproductive trait in colubroid clades, or is its apparent absence in early-diverged lineages (i.e. non-colubroids) an artefact of uneven sampling, historical misclassification, and/or methodological limitations?

Resolving this question has become increasingly complex with the recognition of facultative parthenogenesis (FP) in snakes. FP, now documented across multiple snake families (Dubach *et al.* 1997, Schuett *et al.* 1997, Reynolds *et al.* 2012, Miller *et al.* 2019, Booth and Schuett 2011, 2016, Booth *et al.* 2011a, b, 2012, 2014, 2024, Shibata *et al.* 2017, Allen *et al.* 2018, Card *et al.* 2021), can result in the production of offspring following extended periods of isolation from males and thus can superficially mirror the temporal patterns both expected and observed under LTSS. To deal with potential conflation, Booth and Schuett (2011) reviewed the early literature on LTSS in snakes and concluded that support is often weak. For instance, in several cases, such as the putative LTSS in the Javan file snake, *Acrochordus javanicus* (see Magnusson 1979), the data more strongly support FP over LTSS. As a result, historical reports of LTSS that lack genetic confirmation must be interpreted with caution. Any evolutionary synthesis of LTSS, therefore, requires explicit consideration of the evidentiary standards used to distinguish sperm storage from alternative reproductive modes, such as FP (Booth and Schuett 2011, 2016, Levine *et al.* 2021, 2024). We propose that lines of evidence should include the duration of isolation from reproductive males, genomic confirmation of the presence of paternal alleles in the offspring produced following prolonged isolation from a reproductive male, the presence of both male and female offspring in litters or clutches, oviductal characteristics, and/or sperm viability (Table 1; Fig. 1). Individual criteria vary in inferential strength, with the strongest support for LTSS being obtained when multiple, independent lines of evidence converge to exclude recent mating and parthenogenesis.

Here, we synthesize evidence for LTSS in female snakes within an explicitly phylogenetic and evidentiary framework to evaluate whether LTSS represents a derived character in colubroid snake clades or an overlooked ancestral reproductive trait in the early-diverging lineages. Initially, we place LTSS in a broader context of vertebrate reproduction and summarize the current understanding of anatomical and mechanistic bases of sperm storage in snakes. We then evaluate reported cases of LTSS across snake lineages, explicitly assessing evidentiary strength and the exclusion of FP. Finally, we examine the phylogenetic distribution of confirmed and putative LTSS and identify targeted research priorities necessary to resolve the origin and evolutionary history of this reproductive strategy.

Female sperm storage in vertebrates: scope and evolutionary significance

Sperm storage is widespread in female vertebrates and has evolved repeatedly across major lineages (Birkhead and Møller

Table 1 Conceptual framework outlining the principal lines of evidence required to diagnose LTSS robustly in snakes.

Claim of LTSS	Explanation
Verified absence of mating?	Long-term isolation from reproductively competent males
Stored sperm anatomically detected	Detection of viable spermatozoa in female oviduct despite long-term absence from a reproductively competent male
Temporal separation beyond sperm longevity without storage	The interval between mating and fertilization must exceed the known maximum lifespan of free sperm in reptiles without storage structures
Genetic paternity confirms earlier mating and rules out FP	Genomic/genetic parentage analysis, with the identification of paternal alleles. Use of software such as PARTHENOGENESIS (Levine and Booth 2025), COLONY (Jones and Wang 2010), CERVUS (Marshall *et al.* 1998), or PAPA (Duchesne *et al.* 2002).
Detection of oviductal morphology or biochemistry indicative of LTSS capacity	May include, but is not limited to: (i) Uterine twisting; (ii) uterine crypts; (iii) sperm-storage tubules, glandular polysaccharide-rich secretions, etc.
Repeatability across reproductive events	Evidence that sperm can be used across multiple ovulatory cycles or in multiple females of the same species. Repeatability indicates a species-level trait
Are both male and female offspring present in litters suspected of LTSS?	Faculative parthenogenesis will result in the production of only male (derived lineages) or female (early-diverging lineages) offspring owing to the sex chromosome system

Individual criteria vary in inferential strength; strongest support for LTSS is obtained when multiple, independent lines of evidence, particularly behavioural isolation, anatomical confirmation, offspring sex, and genetic parentage analyses, converge to exclude recent mating, parthenogenesis, and other alternative explanations.

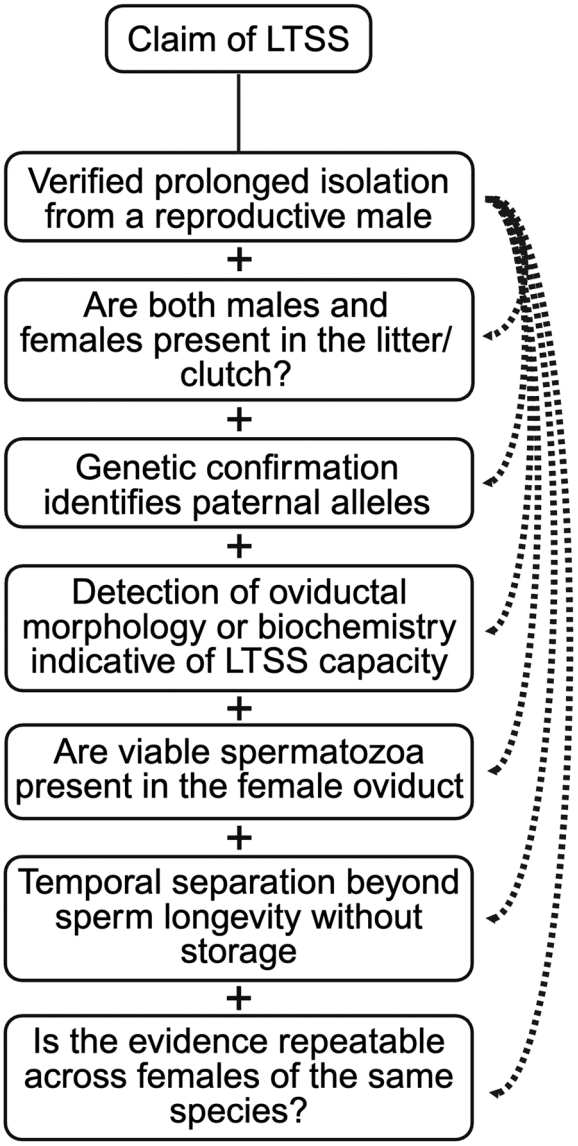

Figure 1 Decision framework for evaluating evidence of LTSS. This decision tree outlines a stepwise approach for assessing claims of LTSS following mating. Evidence accumulates from top to bottom, with increasing strength provided by multiple, independent lines of support. The most robust support for LTSS is achieved when these findings are repeatable across multiple females within the same species. Dashed lines indicate that criteria need not be met in a strictly sequential manner and that multiple forms of evidence can jointly support a claim of LTSS.

1993, Holt and Fazeli 2016, Braz and Almeida-Santos 2022, Brady *et al.* 2022, Ernst *et al.* 2025). In fishes, amphibians, reptiles, birds, and mammals, females may retain sperm within specialized reproductive tract structures, allowing fertilization to occur long after mating (Fox 1956, Fox and Dessauer 1962, Aldridge 1992, Almeida-Santos and Salomão 1997, Siegel and Sever 2006, Bernal *et al.* 2015, Silva *et al.* 2020, Braz and Almeida-Santos 2022). The duration of storage varies from days to weeks in many taxa, but in some lineages, including reptiles, storage can persist for months or longer, exceeding single reproductive seasons (Booth and Schuett 2011, Levine *et al.* 2021, 2024). From an evolutionary perspective, sperm storage can confer several advantages. It may buffer females against temporal or spatial variation in mate availability, facilitate synchronization of reproduction with favourable environmental conditions, and enable post-copulatory sexual selection through cryptic female choice (Birkhead and Møller 1993). These benefits are particularly relevant in taxa with seasonal reproduction, low encounter rates between sexes, or high costs associated with mating (Schuett 1992).

Reptiles exhibit some of the most extreme examples of sperm storage among vertebrates (Pearse and Avise 2001, Booth and Schuett 2011, Levine *et al.* 2021), where females may store sperm across hibernation or aestivation periods, enabling fertilization in subsequent breeding seasons (Ewing 1943, Schuett, 1982, Schuett and Gillingham 1986, Pearse and Avise 2001). Snakes, however, appear exceptional in both the duration and apparent prevalence of long-term storage, making them a focal group for understanding the evolutionary limits and consequences of this reproductive strategy (Booth and Schuett 2011, Levine *et al.* 2021, 2024).

Phylogeny of snakes and an overview of early-diverged lineages

The Squamata (lizards, snakes, and amphisbaenids) are a highly diverse clade of vertebrates, with 12038 extant species (Shine 1992, Greene 1997, Lillywhite 2014, Uetz *et al.* 2024). Of >4030 species of extant snakes, most belong to recent-diverged (colubroid) clades (Uetz *et al.* 2024). For this review of LTSS, all taxa below the node for Caenophidia are considered members of early-diverged lineages (Fig. 2). Of the ~4030 extant species of snakes, families belonging to the Scolecophidia and basal Alethinophidia comprise some 705 species (17.5%) (Table 2). Of these, 477 species of threadsnakes (67.7%) are members of the families Anomalepididae, Gerrhopilidae, Leptotyphlopidae, Typhlopidae, and Xenotyphlopidae. Detailed background information and reviews of early-diverged ('primitive') snakes are provided in the literature (e.g. Greene 1997, Reynolds and Henderson 2018).

Mechanisms of sperm storage in female snakes

Building on early findings of LTSS in the common garter snake (*Thamnophis sirtalis*) and the prairie rattlesnake (*Crotalus viridis*) (Blanchard and Blanchard 1941, Blanchard 1943, Ludwig and Rahn 1943), specialized sperm-storage tubules were identified and described (Fox 1956, Fox and Dessauer 1962). These tubules, which are typically located in the anterior oviduct, are formed by invaginations of the luminal epithelium and are ubiquitous in the anterior infundibulum (Braz and Almeida-Santos 2022). However, some species of snakes also store sperm in the posterior oviduct. For example, in many viperids the posterior oviduct becomes convoluted and contracted in newly mated females, a feature termed 'uterine muscular coiling' (cc, Siegel and Sever 2006, Silva *et al.* 2020, Braz and Almeida-Santos 2022). To date, oviductal morphology and putative sperm storage regions have been described

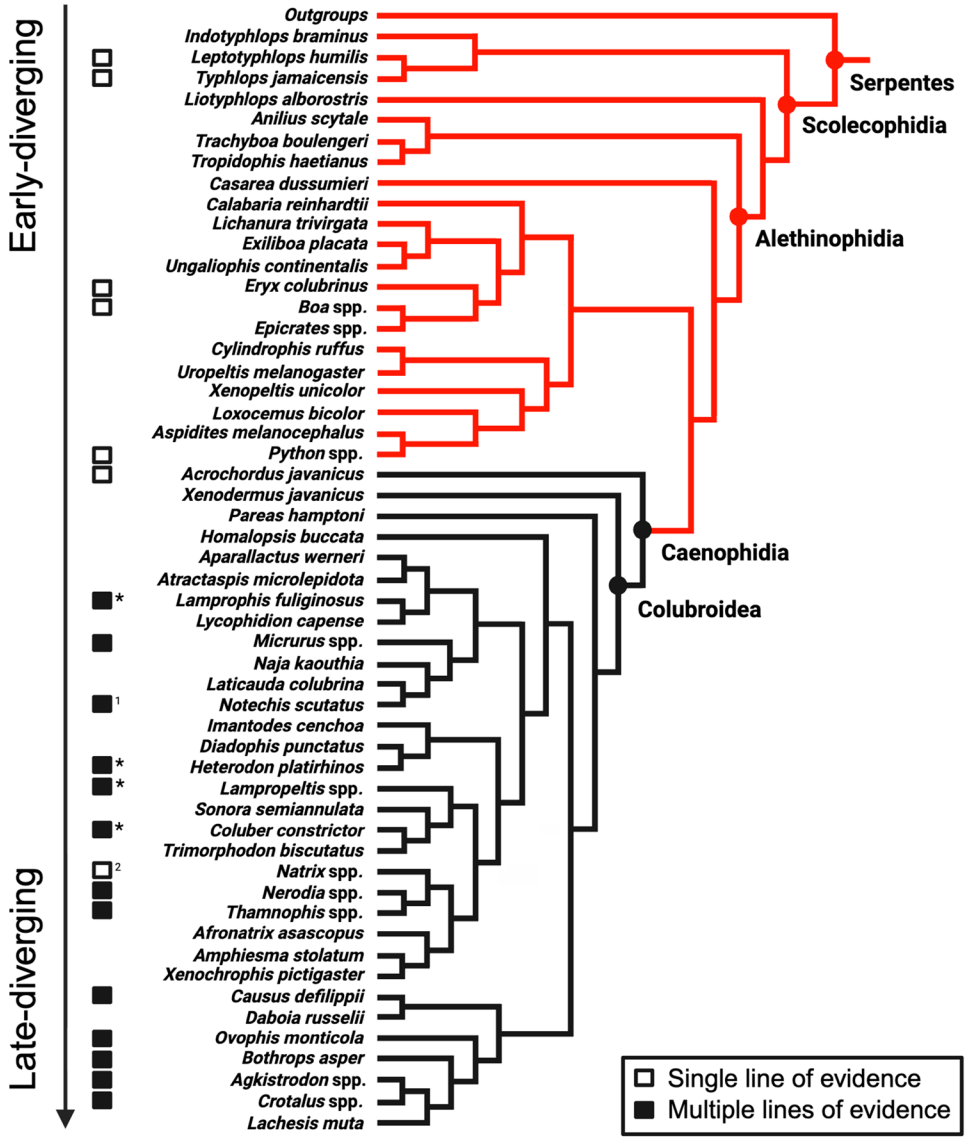

Figure 2 Phylogeny of snakes (Serpentes) constructed from molecular characters. Modified from Pyron *et al.* (2013). Modified from Gauthier *et al.* (2012) and Longrich *et al.* (2012). Nodes identify Serpentes, Scolecophidia, Alethinophidia, Caenophidia, and Colubroidea. Early-diverged taxa are highlighted in red. *Personal observation/personal communication. [1]Schwaner 1989. [2]Kopstein *et al.* (1938).

in ≥41 snake species representing several lineages (Braz and Almeida-Santos 2022), including early-diverged taxa such as scolecophidians (Fox and Dessauer 1962, Khouri *et al.* 2020, 2022) and the Amazon tree boa, *Corallus hortulana* (Silva *et al.* 2025). Despite an abundance of anatomical information, the precise role of sperm-storage tubules and related tissues in facilitating LTSS remains largely anecdotal, and thus their functional significance is based mostly on circumstantial evidence.

Materials and methods

We conducted a systematic literature review following PRISMA guidelines for ecology and evolution (O'Dea *et al.* 2021) using Web of Science (all databases) for publications from 1900 to 2025. Search terms included combinations of 'long-term sperm storage', 'sperm storage', 'seminal receptacle', and 'delayed reproduction' with 'reptiles', 'snakes', and 'primitive snakes'. Additional sources were identified via Google Scholar, JSTOR, PubMed, ResearchGate, the Reptile Database, archival materials, and reference list screening. Non-English articles were translated where necessary.

In cases where LTSS was suspected, evaluation was based upon characteristics outlined in Table 1 and Fig. 1. Specifically, these address behavioural isolation, anatomical confirmation, sperm viability, offspring sex, and genetic parentage analyses. Circumstantial evidence comes from a single line of evidence, whereas the strongest support for LTSS occurs when multiple lines of evidence converge. For example, both long-term isolation from a reproductive male in concert with genomic confirmation of paternal alleles would be viewed as conclusive evidence (e.g. Booth and

Schuett 2011, Levine *et al.* 2021). We consider sex an important line of evidence because parthenogenetic reproduction (an alternative to LTSS) produces litters or clutches that are exclusively female or exclusively male, depending on the sex-chromosome system (Gamble *et al.* 2017).

Table 2 Fifteen families of extant early-diverged snakes (for corresponding phylogeny, see Fig. 2).

Family	Number of species
Anomalepididae	23
Gerrhopilidae	29
Leptotyphlopidae	144
Typhlopidae	280
Xenotyphlopidae	1
Aniliidae	1
Anomochilidae	3
Cylindrophiidae	15
Uropeltidae	64
Boidae	64
Tropidophiidae	34
Bolyeriidae	2
Pythonidae	42
Xenopeltidae	2
Loxocemidae	1
Total	705

Results

Table 3 shows a list of searched and relevant literature located for this project. Our efforts yielded 54 publications that were identified as relevant for the present review. Evidence for LTSS in colubroid snakes is widespread, spanning multiple families (e.g. Blanchard and Blanchard 1941, Fukada 1986, Schuett 1992, Almeida-Santos and Salomão 1997, Strugariu 2007, Booth and Schuett 2011, Friesen *et al.* 2014, Rojas *et al.* 2015, Bassi *et al.* 2020, Levine *et al.* 2021, 2024, Jurkfitz *et al.* 2023).

In sharp contrast, despite extensive searching, no definitive cases of LTSS (defined as the production of viable offspring in the absence of mating for at least one reproductive season and confirmed though two or more lines of evidence as laid out in Table 1 and Fig. 1) were identified in any early-diverged (non-colubroid) snake species. We found only circumstantial evidence for LTSS in an African rock python, *Python sebae* (Visser 1985), and a Kenyan sand boa, *Eryx colubrinus loveridgei* (Ross and Marzec 1990), relating to time of isolation from a reproductively competent male. Additional evidence included the presence of sperm-storage tubules in several scolecophidian species (threadsnakes) and in the New World boid *Corallus hortulana* (Silva *et al.* 2025); however, these

Table 3 Literature search (1900–2025) of sperm storage in female snakes with the primary goal of recovering information on early-diverged taxa (see Table 2; Fig. 2).

Period	Basal snakes mentioned	Authority
1850–1924	No	Agassiz (1857), Coker (1920)
1925–1949	No	Woodward (1933), Trapido (1940), Blanchard and Blanchard (1941), Blanchard (1943), Ludwig and Rahn (1943)
1950–1999	Yes[1]	Fox (1956[a], 1965[a]), Fox and Dessauer (1962[a]), Hoffman and Wimsatt (1972), Saint-Girons (1975), Schuett (1982, 1992), Halpert *et al.*(1982), Devine (1984), Visser (1985[a]), Fukada (1986), Schuett and Gillingham (1986), Slip and Shine (1988[a]), Ross and Marzec (1990[a]), Aldridge (1992), Aldridge and Semlitsch (1992), Birkhead and Møller (1993), Luiselli (1993), Almeida-Santos and Salomão (1997), Dubach *et al.*(1997), Schuett *et al.*(1997)
2000–present	Yes[2]	Almeida-Santos and Salomão (2002), Höggren and Tegelström (1996), Bertona and Chiaraviglio (2003[b]), Tourmente *et al.* (2006[b]), Pizzato and Marques (2007[b]), Rivas *et al.* (2007[b]), Strugariu (2007), Uller and Olsson (2008), Booth and Schuett (2011), Booth *et al.* (2011a, b, 2014[b]), Kinney *et al.* (2013[b]), Friesen *et al.* (2014), Orr and Brennan (2015), Orr and Zuk (2012), Smith (2012), Friesen *et al.* (2014), Rojas *et al.* (2015), Holt and Fazeli (2016), Bassi *et al.* (2020), Khouri *et al.* (2020[b], 2022[b]), Skelton *et al.* (2021[b]), Levine *et al.* (2021, 2024), Braz and Almeida-Santos (2022[b]), Jurkfitz *et al.* (2023), Shankar *et al.* (2023), Almeida-Santos and Ramalho (2025[b]), Silva *et al.* (2025[b])

[a]Papers by Fox (1956, 1965) and Fox and Dessauer (1962) discuss sperm-storage tubules in threadsnakes (scolecophidians). Visser (1985) presents evidence of LTSS in the genus *Python*. Slip and Shine (1988) discuss the mating system of diamond pythons, *Morelia spilota*. Ross and Marzec (1990) present evidence of LTSS in the boid genus *Eryx*. [b]
Bertona and Chiaraviglio (2003) discuss reproduction in the boid genus *Boa*. Tourmente *et al.* (2006) investigated spermatozoa and the mating system of the boid genus *Boa*. Pizzato and Marques (2007) review boid and pythonid reproduction. Rivas *et al.* (2007) discuss the mating system of the boid *Eunectes murinus*. Booth *et al.* (2011a, b, 2014) discuss FP in boids and pythonids. Kinney *et al.* (2013) discuss FP in the boid *Epicrates cenchria*. Papers by Khouri *et al.* (2020, 2022) mention sperm-storage tubules in female threadsnakes (scolecophidians). Skelton *et al.* (2021) discuss multiple paternity in the pythonid *Python bivittatus*. Braz and Almeida-Santos (2022) discuss scolecophidians and boids. Almeida-Santos and Ramalho (2025) discuss mating aggregations in the boid genus *Boa*. Silva *et al.* (2025) discuss sperm-storage tubules in the boid *Corallus hortulana*; in this case, however, no sperm was observed in the tubules.

observations lacked corroborating evidence for LTSS. Several unpublished observations suggest LTSS in several species of boids and pythonids (W. Booth, personal communication and unpublished data); however, in these cases important confirmatory analyses, such as parent–offspring genotyping, were not conducted, leaving open alternative explanations, such as FP (e.g. Booth and Schuett 2011, 2016).

Discussion

Evidence from colubroid snake lineages

There is robust evidence that LTSS is concentrated in colubroid snakes, including numerous species of viperids, elapids, and colubrids. In these taxa, females have produced viable offspring following isolation from males for periods ranging from 1 to 6 years (Schuett 1982, 1992, Schuett and Gillingham 1986, Strugariu 2007, Booth and Schuett 2011, Levine *et al.* 2021, 2024). Indeed, the longest supported case of LTSS reported in a vertebrate species is from a western diamondback rattlesnake (*Crotalus atrox*) held in isolation from males that produced several litters of viable offspring over a period of 71 months (Levine *et al.* 2021). Some cases have been strengthened through genetic analyses, confirming biparental inheritance and conclusively demonstrating sperm storage over FP (Booth and Schuett 2011, Levine *et al.* 2021, 2024). Once considered out of reach of many researchers owing to financial or methodological constraints, genomic analysis is now commonplace, with the falling price of genomic sequencing and the availability of bioinformatic software capable of conclusively disentangling LTSS from FP (Levine and Booth 2025). Accordingly, it is likely that we will see an increase in studies reporting LTSS supported by molecular data in snakes and other reptiles. These well-supported cases provide compelling evidence that LTSS is a functional and evolutionarily significant trait in colubroid snake lineages.

Evidence from early-diverged snake lineages

In contrast to colubroid snakes, reports of LTSS in early-diverged lineages are sparse and equivocal. Only a single report of a female African rock python (*P. sebae*) laying 10 fertile eggs in a clutch of 33, 4 years after last contact with a male, provides evidence suggestive of LTSS (Visser 1985). However, the author failed to report the sex of the offspring; thus, these results cannot be differentiated from FP (Booth and Schuett 2011, 2016). Anecdotal evidence of a female Kenyan sand boa (*E. c. loveridgei*) that produced viable offspring 1 year after last contact with a male except for her male offspring from the prior season (Ross and Marzec 1990) is suggestive of LTSS; yet, sexual reproduction with what might appear to be an immature male offspring cannot be ruled out in the absence of genetic analysis. Other anecdotal observations and reports exist from private hobbyists of boas or pythons producing offspring in the prolonged absence of males (W. Booth, personal communication), but the lack of detailed records of mating history and genetic verification of offspring parentage, in concert with the subsequent recognition that FP is common in related taxa, raises the possibility and concern that these observations have been misinterpreted (Booth and Schuett 2011, 2016).

The paucity of definitive evidence of LTSS in early-diverged snake lineages does not necessarily indicate its absence. Rather, it might reflect the limited number of long-term reproductive studies conducted in these lineages, in addition to the challenges associated with maintaining large colonies of snakes in captivity. Consequently, the evidentiary standard supporting LTSS in early-diverged snakes remains substantially weaker than that for colubroid clades. Nonetheless, numerous species of boas and pythons (and thousands of individuals) are routinely kept in the collections of private hobbyists and are bred for heritable colour or pattern morphs. Instances are routinely reported of offspring produced after prolonged periods of isolation from males and correspond to FP owing to offspring colour or pattern; however, reports supporting LTSS are infrequent or absent. Although reports of mating aggregations and multiple paternity in early-diverged snakes might suggest a role for sperm storage (Slip and Shine 1988, Bertona and Chiaraviglio 2003, Schuett *et al.* 2019, Skelton *et al.* 2021, Almeida-Santos and Ramalho 2025), the limited duration of aggregations (4–6 weeks; Slip and Shine 1988) does not support LTSS as defined in this review.

With few exceptions, the absence of definitive evidence for female LTSS in the extant early-diverged snakes investigated (Table 3) is striking, especially given that many of these taxa are commonly kept in zoological gardens, laboratories, and private herpetoculture. Furthermore, the application of DNA-based genetic analysis has demonstrated that several cases initially suspected of being LTSS in primitive snakes were, instead, instances of FP (Booth *et al.* 2011a, 2014, Kinney *et al.* 2013, Shibata *et al.* 2017, Seixas *et al.* 2019). Even so, it remains surprising that formal anatomical studies of sperm storage in early-diverged snakes are limited to only a few species of scolecophidians (Fox and Dessauer 1962, Fox 1965, Fox 1997, Khouri *et al.* 2020, 2022, Braz and Almeida-Santos 2022) and a single species of boid (Silva *et al.* 2025). In sharp contrast, numerous species of late-diverging (caenophidian) snakes exhibit unambiguous evidence of LTSS, confirmed using a variety of histological, behavioural, and molecular approaches (Saint-Girons 1975, Devine 1984, Birkhead and Møller 1993, *Levine et al.* 2021, 2024, Braz and Almeida-Santos 2022). Research on oviductal sperm storage in colubroid snakes spans more than eight decades (Trapido 1940, Fox 1956, Fox and Dessauer 1962, Fox 1965, Hoffman and Wimsatt 1972, Braz and Almeida-Santos 2022), highlighting a sharp contrast between the well-documented reproductive biology of colubroids and the paucity of comparable data in early-diverged snakes.

Both definitive and circumstantial cases of LTSS in snakes reveal a pronounced concentration within colubroid clades, and we suggest several evolutionary scenarios that could account for this pattern. LTSS might have evolved once within colubroid snakes (e.g. vipers) and subsequently diversified in the remaining colubroid lineages. Alternatively, it might represent an ancestral trait that has been lost or reduced in early-diverged taxa or a widespread trait that

remains undetected owing to sampling bias. At present, available data do not permit a confident or robust phylogenetic reconstruction of the evolution of LTSS in Serpentes. Distinguishing among alternative scenarios will require phylogenetically informed comparative studies that explicitly target early-diverged snake lineages and apply standardized criteria for diagnosing sperm storage. Several non-mutually exclusive factors might explain the apparent rarity of LTSS in early-diverged snake lineages. First, sampling bias is substantial, in that early-diverged taxa are underrepresented in long-term reproductive studies. Second, ecological and life-history traits, such as fossorial habits, low encounter rates, or seasonal activity, might reduce opportunities to observe delayed reproduction. Third, historical methodological limitations, particularly the absence of genetic tools, have hindered the ability to distinguish LTSS from FP. These considerations caution against interpreting the absence of documented LTSS in early-diverged snakes as evidence of genuine evolutionary absence; instead, they underscore the need for targeted empirical work designed explicitly to test for LTSS in these taxa.

Conclusion

The most compelling data supporting LTSS are provided by the production of offspring following prolonged absence of male contact, in concert with genetic/genomic data from the mother and offspring that refute FP and evidence of oviductal morphology such as sperm-storage tubules, uterine twisting, etc. (Table 1); future work should thus focus on robust and systematic screening of offspring potentially produced via LTSS in snakes of early-diverged lineages, in addition to investigating the oviductal morphology of adult virgin and mated females. Such work could be accomplished by: (i) establishing breeding colonies of captive-born and previously unmated females; (ii) collecting blood samples from all individuals in the breeding colony for future genetic parentage analysis; (iii) maintaining mated females in strict isolation from all males for an extended period of time (i.e. multiple years) in a manner conducive to stimulate reproduction (e.g. proper thermal, photoperiod, humidity, and feeding regimens); and (iv) conducting genetic parentage and FP analysis on all resulting offspring to parse LTSS from the competing hypothesis of FP (Booth and Schuett 2011, Levine *et al.* 2021, 2024, Levine and Booth 2025). Additional work should focus on surveying the anatomy of early-diverged snakes for traits associated with the capacity for LTSS. We concur with Braz and Almeida-Santos (2022) that greater attention should be directed towards identification and and characterization of sperm-storage sites and organs in early-diverged snakes, ideally by surveying the entire oviduct throughout a reproductive cycle to capture temporal variation in morphology and function. Such data are essential for reconstructing the evolutionary history of LTSS across Serpentes. This should be complemented by a robust histological analysis of all candidate sperm storage sites identified in early-diverged snakes to screen for the presence of stored sperm.

We propose that understanding the genomic basis of LTSS in snakes is a priority of future studies. Accordingly, this would entail screening genomes of early-diverged snakes for the presence of genes relevant to LTSS. Such work could be accomplished via transcriptomics of colubroid species that exhibit obligate sperm storage during their reproductive season, thus guaranteeing sperm storage in mated females during the study (e.g. the copperhead, *Agkistrodon contortrix*, a colubroid snake species with obligate over-winter sperm storage in some areas of its range; Schuett 1982, Schuett and Gillingham 1986, Smith *et al.* 2009). A framework for study would involve performing various -omics analyses of female reproductive tissues in captive virgin females (e.g. mated females at different time points post-mating), similar to research on domestic turkeys (Brady *et al.* 2022) and *Drosophila melanogaster* (Prokupek *et al.* 2009). Mapping of RNA-sequencing reads onto an annotated, high-quality genome and subsequent differential gene expression analysis, for instance, could potentially identify genes that are upregulated during sperm storage. Accordingly, genome sequences of early-diverged snakes could be screened to determine whether genes relevant to LTSS are present.

LTSS in females is well supported in several colubroid snake lineages, yet its evolutionary distribution across Serpentes remains unresolved. Our synthesis highlights a striking absence of verifiable LTSS in snakes of basal clades despite more than a century of study. This pattern might reflect true evolutionary disparity but is equally consistent with persistent sampling and methodological bias. Resolving this uncertainty will require targeted study of early-diverged taxa, rigorous exclusion of FP, and explicit phylogenetic comparative methods (Kerr *et al.* 2011, Bellini *et al.* 2017). Clarification of the evolutionary origin of LTSS will not only refine our understanding of snake reproductive evolution but will also inform broader questions about the evolution of female reproductive strategies across vertebrates.

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Author contributions

Gordon W. Schuett (Conceptualization, Data curation, Investigation, Validation, Writing–original draft, Writing–review and editing), Brenna A. Levine (Investigation, Visualization, Writing–original draft, Writing–review and editing), and Warren Booth (Conceptualization, Investigation, Writing–original draft, Writing–review and editing)

Conflicts of interest

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