Tail movements by late-term fetal pitvipers resemble caudal luring: prenatal development of an ambush predatory behaviour

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With the advent of powerful imaging instruments, the prenatal behaviour of vertebrates has been discovered to be far more complex than previously believed, especially concerning humans, other mammals and birds. Surprisingly, the fetal behaviour of squamate reptiles (lizards, snakes and amphisbaenians), a group of over 11,000 extant species, are largely understudied. Using ultrasonography, 18 late-term pregnant copperhead snakes (\textit{Agkistrodon contortrix}) from a single population were inspected for fecundity (number of fetuses). Unexpectedly, during the ultrasound procedure that involved 97 fetuses, we observed sinusoidal tail movements in 11 individuals from eight different copperhead mothers. These movements were indistinguishable from caudal luring, a mimetic ambush predatory strategy which is exhibited by newborn copperheads and other snakes. Caudal luring is initiated shortly after birth and is employed to attract susceptible vertebrate prey. Using the same ultrasound equipment and methods, we tested for this behaviour in two species of rattlesnakes (genus \textit{Crotalus}) not known to caudal lure and none of the late-term fetuses showed any type of tail movements. Prenatal movements in humans and other vertebrates are known to be important for musculoskeletal and sensorimotor development. The fetal behaviours we describe for copperheads, and possibly other snakes, may be similarly important and influence early survival and subsequent fitness.
1. Introduction

Various imaging technologies clearly have opened the field of studying prenatal development and activities of vertebrates [1–6], and at present a remarkable range of behaviours is delineated for numerous taxa. Among the species that give live-birth (viviparity), prenatal behaviour is best studied in humans [1–3,7]. Behaviours documented at key developmental stages include kicking, scratching, yawning, facial expressions, and thumb-sucking to hiccupping, other vocalizations and possibly crying [1–3,7]. Prenatal vocalizations, thermoregulation and social behaviour of reptiles are recently documented [8–15]. Pre-hatch vocalizations (‘chirping’), given by many bird species [16–18] and all species of crocodilians [9,19–21], are among the most prominent examples in egg-laying (oviparous) taxa. Even some turtles are now known to vocalize prior to hatching [8–10,12]. Surprisingly, fetal behaviours are largely understudied in squamate reptiles (lizards, snakes and amphibiaenians), a group of over 11 000 extant oviparous and viviparous species [9,13,14].

Although each of the prenatal behaviours and activities previously mentioned is context-dependent (e.g. specific movements associated with musculoskeletal, motoneuron and sensorimotor development) and has different functional outcomes, they lend key insights to our overall knowledge of how developing embryos prepare for postnatal life and survival [22]. Whereas understanding normal fetal behaviour and movements in humans provides invaluable clinical perspectives for making specific diagnoses [22–24], studies of fetal behaviour in other vertebrates is important for understanding the evolutionary context for behavioural development.

Here, using ultrasonographic imaging, we show for the first time to our knowledge, that tail movements by late-term fetuses of the copperhead snake (Agkistrodon contortrix), a widespread viviparous pitviper from North America [25], strongly resemble caudal luring—a mimetic (ambush) predatory behaviour [26–28].

Caudal luring is a category of luring mimicry (commonly termed aggressive mimicry) often employed by newborn and juvenile snakes [26,27,29], and is most prevalent in vipers (26,29–37) but is present in several other snake lineages [38,39]. Our findings in this paper are significant for at least two main reasons. First, this is one of the few examples of prenatal behaviour in a viviparous squamate reptile (lizards and snakes). Second, sinusoidal tail movements (motor patterns) during prenatal growth have implications for the early postnatal development of caudal luring, a predatory behaviour which clearly influences survival and fitness.

2. Material and methods

In 2015 and 2018, a total of 18 different pregnant female copperheads (A. contortrix) were collected for ultrasonography (table 1). Seven females were collected from 7 July to 16 August in 2015, and 11 females were collected on 14 and 16 August 2018. The collection site was a 485 ha parcel of basalt trap rock ridge ecosystem situated 4.75 km northwest of Meriden, Connecticut [40]. In 2015, females were brought to the laboratory and provided with private enclosures, which consisted of plastic cages (61 cm L × 40 cm W × 12 cm H) supplied with paper as a floor covering and substrate heating by heat tape (8 cm wide) situated beneath and across the front end of the cage (35°C). Artificial lighting (eight 40 W fluorescent tubes) positioned 3 m above the cage was timer-controlled to simulate natural (Connecticut time) photoperiod. Water was available in glass bowls ad libitum. Because copperheads rarely eat in the latter stages of pregnancy (C.F. Smith 2009, personal observation), food (thawed mice) was not offered until after parturition. After birthing, all females (n = 7) brought to the laboratory were safely returned to their exact capture sites (e.g. GPS coordinates and field notes). In 2018, females were tested in the field (14 and 16 August) and released after ultrasonography testing.

To visually access the fetuses, we scanned the pregnant subjects using a SIUI-CTS-8800 + portable ultrasound (Shantou Institute of Ultrasonic Instruments Co., Ltd., Guangdong, China) equipped with a 17L50 K-G Linear 5–12 MHz probe set at a frequency of 7.5 MHz, 60 dB in gain, and resolution depth of 3.2 cm. In 2015, parturition dates were recorded for females (n = 7) housed in the laboratory. Duration of scanning during the ultrasound procedure for each female was approximately 10 min; each subject was tested once. Because females captured in 2018 were released at their capture sites following the ultrasound procedure, parturition dates for these females are not known. However, all females tested in 2018 were deemed to be late-term based on the ultrasound results and time of year.

We also tested for tail movements of late-term fetuses in two other North American pitvipers, Crotalus atrox (n = 1) and Crotalus scutulatus (n = 1) from Hidalgo County, NM (Chiricahua Desert Museum, July
using the same portable ultrasound equipment and procedure settings. Caudal luring has not been documented in the neonates or juveniles of either of these rattlesnake species [31,41]. We tested these rattlesnakes to determine whether the ultrasound procedure itself might be responsible for inducing tail motor patterns resembling caudal luring.

3. Results

On 16 August 2015, the seven pregnant copperheads held in the laboratory were subjected to ultrasound testing. In total, 34 fetuses were observed via ultrasound analysis. Ultrasound observations occurred from 2–23 days prior to births (mean: 12.71 ± 2.82 s.e.). Six fetuses were recorded to produce sinusoidal tail movements, i.e. caudal luring-like motor patterns (figure 1 and table 1; see the electronic supplementary material, videos S1 and S2). The duration of tail movements was 39–85 s (\( n = 6; \bar{x} = 65 \pm 6.54 \) s.e.). Parturition occurred in the laboratory from 18 August to 8 September (min–max: 3–7 neonates per litter; mean litter size: \( \bar{x} = 4.86, n = 7 \) females).

On 14 and 16 August 2018, 11 females were collected at the same location as in 2015. A total of 63 fetuses were observed via ultrasound as measured in the field the day they were captured. Five fetuses were recorded to produce caudal luring-like tail motor patterns (figure 1 and table 1; see the electronic supplementary material, videos S1 and S2). The duration of tail movements was 39–73 s (\( n = 5; \bar{x} = 52 \pm 7.26 \) s.e.). The females in this group were released at their exact capture sites following the ultrasound procedure; consequently, parturition dates for them are not know; however, based on ultrasonography, the projected litter size was min-max: 2–7 fetuses (\( \bar{x} = 5.72, n = 11 \) females).

The duration of luring was not significantly different in 2015 and 2018 (\( t \)-test: \( t \)-value = 1.354, \( p = 0.209 \), not significant at \( a = 0.05 \); two-tailed, \( n = 11 \)). Furthermore, in 2018, when using ultrasonography to project litter size, mean litter size for females was not significantly different in 2015 and 2018 (\( t \)-test: \( t \)-value = 1.216, \( p = 0.242 \), not significant at \( a = 0.05 \); two-tailed, \( n = 18 \)).

| date         | female ID | no. fetuses | no. lured | duration of luring (s) | parturition date | date of ultrasound | days before parturition |
|--------------|-----------|-------------|-----------|------------------------|------------------|---------------------|-------------------------|
| 7 July 2015  | 61 688    | 4           | —         | —                      | 21 Aug 2015      | 16 Aug 2015         | 5                       |
| 7 July 2015  | 61 716    | 3           | 1         | 56                     | 18 Aug 2015      | 16 Aug 2015         | 2                       |
| 9 July 2015  | 61 671    | 6           | 2         | 39, 66                 | 29 Aug 2015      | 16 Aug 2015         | 13                      |
| 9 July 2015  | 61 675    | 5           | —         | —                      | 27 Aug 2015      | 16 Aug 2015         | 11                      |
| 13 Aug 2015  | 61 602    | 7           | —         | —                      | 4 Sep 2015       | 16 Aug 2015         | 19                      |
| 16 Aug 2015  | DR1       | 6           | 2         | 72, 70                 | 1 Sep 2015       | 16 Aug 2015         | 16                      |
| 16 Aug 2015  | DR2       | 1           | 1         | 85                     | 8 Sep 2015       | 16 Aug 2015         | 23                      |
| 14 Aug 2018  | 15 181    | 7           | —         | —                      | unknown          | 14 Aug 2018         | unknown                 |
| 14 Aug 2018  | 15 266    | 7           | —         | —                      | unknown          | 14 Aug 2018         | unknown                 |
| 14 Aug 2018  | 15 256    | 7           | —         | —                      | unknown          | 14 Aug 2018         | unknown                 |
| 14 Aug 2018  | 15 215    | 6           | 1         | 65                     | unknown          | 14 Aug 2018         | unknown                 |
| 14 Aug 2018  | 15 258    | 2           | —         | —                      | unknown          | 14 Aug 2018         | unknown                 |
| 14 Aug 2018  | 15 197    | 5           | —         | —                      | unknown          | 14 Aug 2018         | unknown                 |
| 14 Aug 2018  | 15 218    | 6           | 2         | 43, 38                 | unknown          | 14 Aug 2018         | unknown                 |
| 16 Aug 2018  | 15 236    | 5           | 1         | 73                     | unknown          | 16 Aug 2018         | unknown                 |
| 16 Aug 2018  | 15 165    | 6           | —         | —                      | unknown          | 16 Aug 2018         | unknown                 |
| 16 Aug 2018  | 15 245    | 6           | 1         | 39                     | unknown          | 16 Aug 2018         | unknown                 |

Table 1. Ultrasound results and general data on the pregnant copperheads used in the present study. (—, no observations of luring.)
Testing procedures of the two rattlesnake species were identical to those of the copperheads. After 10 min of scanning no tail movements of any type were observed in the 13 late-term fetuses of *C. atrox* (*n* = 1) and 11 late-term fetuses of *C. scutulatus* (*n* = 1). No other fetal behaviours were observed.

4. Discussion

The tail movements of late-term copperhead fetuses we describe here are compellingly indistinguishable in form and appearance to actual caudal luring, a complex ambush predatory behaviour involving mimetic resemblance to wriggling worms (sensory exploitation) in newborn, juvenile and adult copperheads (electronic supplementary material, videos S1 and S2; C.F. Smith, G.W. Schuett 2015, personal observation). Caudal luring occurs in other viperid taxa [32–37] and in several other snake lineages [31,39,41]. Because snakes are extremely sensitive to air- and substrate-borne vibrations [42–44], it is possible that handling and use of ultrasonography incited the tail movements we have described; few studies have investigated motivation or stimulus control in caudal luring [26,31,45]. Accordingly, we also tested two closely related snake species (rattlesnakes) that do not caudal lure to determine whether identical measurement procedures would produce similar results. None of the late-term fetuses in the two rattlesnake species we tested exhibited tail movements. However, owing to the small sample of control subjects, a more thorough analysis will be needed in the future to adequately address whether tail movements occur during ultrasound testing in late-term fetuses of non-luring species, such as the two we used. Nonetheless, it was not the intent of this study to conduct a rigorous statistical comparison between copperheads and other pitviper species; rather we describe for the first time, to our knowledge, an *in utero* behaviour by a squamate reptile. Furthermore, we suggest that the tail movements by late-term fetal copperheads are potentially an essential developmental precursor to actual caudal luring, wherein the musculature and neuromotor systems are being prepared for an important postnatal activity. These tail movements may occur randomly and spontaneously, perhaps a form of fetal ‘motor babbling’ [46].

Figure 1. *(a,b)* A schematic illustrating the tail motor patterns of a single fetal copperhead. See the electronic supplementary material, videos S1 and S2. Drawing by C. F. Smith.
Although the duration of tail movements in the copperhead fetuses was relatively brief when compared to caudal luring in juveniles and older snakes ([29,32]; C.F. Smith 2014, personal observation), this was not unexpected. Fetal movements in vertebrates, in general, are shorter lived than the same (or similar) ones exhibited postnataally [46].

Despite the fact that our two-dimensional ultrasonographic equipment adequately and clearly documented the tail movements of late-term fetal copperheads, ultrasound and other imaging technologies have undergone significant improvement over the past few decades. Imaging accuracy, for example, is enhanced with three- and four-dimensional ultrasonography and HDlive rendering lightning systems, coupled with enhanced software and computational analysis [25,26]. We envision the next steps in the study of fetal tail movements in snakes to employ these newer technological advancements and improved methods of analysis [4,47].

From extensive work on vertebrates, especially avian reptiles (e.g. chicks), different types of fetal activity appear to be important in the ontogeny of development [46,48]. In the developing fetus, establishment of the musculoskeletal system (e.g. cartilage, joints and bone) is accomplished by mechanical load generated by muscle contractions [49,50]. Similarly, though less understood, the development of muscles follows similar steps. Results from studies of chick embryos indicate novel molecular signalling mechanisms (TAP, JAG2, NOTCH) that act downstream of muscle contraction: YAP activates JAG2 expression in muscle fibres, which subsequently influence fetal muscle progenitors by way of NOTCH [51]. Correspondingly, fetuses undergo motor neuron differentiation and sensorimotor development [46].

5. Conclusion

From a functional viewpoint, the abundance and diversity of fetal movements and sounds in humans and other vertebrates appear to be obligate activities for successfully transitioning to postnatal environments [47]. This also may be the case for tail movements in fetal snakes that caudal lure shortly after birth. In copperheads, and in other snakes that exhibit caudal luring, this behaviour is exhibited shortly after their first ecdysis (natal shedding), typically which occurs from 6 to 10 days after birth [52]. Although individuals of this species are born with a small bolus of yolk that supplies nourishment and energy [52], luring for and feeding on appropriately sized prey (e.g. frogs and lizards) occurs within days after their natal ecdysis. Repeated success in securing prey in early life stages typically results in rapid growth in many snake taxa, which probably promotes survival and fitness [53–55]. The present study was limited to a single viviparous species that exhibits caudal luring, yet we anticipate the same type of tail movements we documented in late-term fetal copperheads will be present in egg-laying (oviparous) taxa that exhibit caudal luring, particularly in pitvipers (e.g. Calloselasma rhodostoma), true vipers (e.g. Pseudocerastes urarachnoides), and certain species of pythons (e.g. Morelia viridis). It is our perspective that highly focused academic-zoo research collaborations could greatly accelerate important advancements in the study of fetal behaviour of squamate reptiles [28,56–59].
References

1. Kunjak A, Azumendi G, Veček N, Kupišić S, Solak M, Varga D, Chervenak F. 2003 Fetal hand movements and facial expression in normal pregnancy studied by four-dimensional sonography. J. Perinat. Med. 31, 496–508. (doi:10.1515/JPM.2003.076)

2. Kunjak A, Stanjevic M, Azumendi G, Cameron JM. 2005 The potential of four-dimensional (4D) ultrasonography in the assessment of fetal awareness. J. Perinat. Med. 33, 46–53. (doi:10.1515/JPM.2005.008)

3. Hata T, Dai S-Y, Marumo G. 2010 Ultrasound for evaluation of fetal neurobehavioural development: from 2-D to 4-D ultrasound. Infant Child Dev. 19, 99–118. (doi:10.1002/icd.659)

4. Grigore M, Guftanu D, Socolov D, Grigore A, Nemet G, Mircu R. 2018 The role of 4D US in evaluation of fetal movements and facial expressions and their relationship with fetal neurobehaviour. Med. Ultrason. 20, 88–94. (doi:10.11152/amu-1350)

5. Hayat TT, Rutherford MA. 2018 Neuroimaging perspectives on fetal motor behavior. Neurosci. Biobehav. Rev. 92, 390–401. (doi:10.1016/j.neubiorev.2018.06.001)

6. Karasik AB, Senkulu SS, Kupkova B. 2021 Analysis of the relationship between fetal magnetic resonance imaging indications and findings with ultrasonographic examination. Eur. Res. J. 7, 265–269.

7. Kúšilevský BS, Low JA. 1998 Human fetal behaviour: 100 years of study. Dev. Rev. 18, 1–29. (doi:10.1006/drev.1998.0452)

8. Doody JS, Stewart B, Camacho C, Christian K. 2012 Good vibrations? Sibling embryos expedit hatch in a turtle. Anim. Behav. 83, 645–651. (doi:10.1016/j.anbehav.2011.12.006)

9. Doody JS, Dinets V, Burghardt GM. 2021 The secret social lives of reptiles. Baltimore, MD: Johns Hopkins University Press.

10. McGlashan JK, Spencer R-J, Old JM. 2012 Embryonic communication in the nest: metabolic responses of reptilian embryos to developmental rates of siblings. Proc. R. Soc. B 279, 1709–1715. (doi:10.1098/rspb.2011.2074)

11. Du W-G, Shine R. 2015 The behavioural and physiological strategies of bird and reptile embryos in response to unpredictable variation in nest temperature. Biol. Rev. 90, 19–30. (doi:10.1111/brw.12089)

12. Ferrana CR, Vogt RC, Sousa-Lima RS, Tardio BMR, Dinz Bernardez VC. 2014 Sound communication and social behavior in an Amazonian river turtle (Podocnemis expansa). Herpetologica 70, 149–156. (doi:10.1655/HERPETOLOGICA-D-13-00050R2)

13. Aubert F, Blanvillain G, Bignon F, Kok PJ. 2016 Heartbeat, embryo communication, and hatching synchrony in snake eggs. Sci. Rep. 6, 23519. (doi:10.1038/srep23519)

14. Aubert F, Bignon F, Kok PJ, Blanvillain G. 2016 Only child syndrome in snakes: eggs incubated alone produce asocial individuals. Sci. Rep. 6, 35752. (doi:10.1038/srep35752)

15. Shine R, Du W-G. 2018 How frequent and important is behavioral thermoregulation by embryonic reptiles? J. Exp. Zool. Ecol. Integr. Physiol. 329, 215–221. (doi:10.1002/jez2.1533)

16. Rumpf M, Tischentke B. 2010 Perinatal acoustic communication in birds: why do birds vocalize in the egg? Open Ornitol. 3, 141–149. (doi:10.2174/18745312001010141)

17. Colombelli-Negrel D, Kleindorfer S. 2017 Prenatal environment affects embryonic response to song. Biol. Lett. 13, 20170302. (doi:10.1098/rsbl.2017.0302)

18. Colombelli-Negrel D, Hauber ME, Robertson J, Solloway FJ, Hof H, Griggio M, Kleindorfer S. 2012 Embryonic learning of vocal passwords in superb fairy-wrens reveals intruder cuckoo nestlings. Curr. Biol. 22, 2155–2160. (doi:10.1016/j.cub.2012.09.025)

19. Vergne AL, Mathieu N. 2008 Crocodile egg sounds signal hatching time. Curr. Biol. 18, R513–R514. (doi:10.1016/j.cub.2008.04.011)

20. Vergne AL, Pritz MB, Mathieu N. 2009 Acoustic communication in crocodilians: from behaviour to brain. Biol. Rev. 84, 391–411. (doi:10.1111/j.1469-1841.2009.00795.x)

21. Chabert T, Colin A, Aubin T, Shacks V, Bourquin SL, Eley RM, Acosta JG, Mathieu N. 2015 Size does matter: crocodile mothers react more to the voice of smaller offspring. Sci. Rep. 5, 15547. (doi:10.1038/srep15547)

22. Visser GHA, Mulder EJH. 2009 Fetal movement patterns and fetal behavioural states. In Ultrasound in obstetrics and gynecology (eds JW Wladimiroff, S Eik-Nes), pp. 271–284. Philadelphia, PA: Elsevier.

23. Tonni G, Martins WP, Guimarães Filho H, Araujo Jr E. 2015 Role of 3-D ultrasound in clinical obstetric practice: evolution over 20 years. Ultrasound Med. Biol. 41, 1180–1211. (doi:10.1016/j.ultrasmedbio.2014.12.009)

24. Tonni G, Castigliego AP, Grussila L, Lituania M, Meagher S, Costa FD, Araujo E. 2016 Three-dimensional ultrasonography by means of HDlive rendering in the first trimester of pregnancy: a pictorial review. J. Turk.- Ger. Anat. J. 17, 110–119. (doi:10.5152/jtga.2016.15201)

25. Gloyd HK, Conant R. 1990 Feeding and other feeding responses: a program of the deceptive use of caudal lures by arboreal green pit vipers. Aquar. Int. J. Ichthyol. 11, 117–124.

26. Schuett GW, Dorr SW, Whited WD, Freamyll GA, Putman BL. 2016 Activity cycles and foraging behaviors of free-ranging sidewinder rattlesnakes (Crotalus cerastes): the ontogeny of hunting in a precocial vertebrate. Zoology 119, 196–206. (doi:10.1016/j.zool.2016.02.005)

27. Glaudas X, Alexander GI. 2017 A lure at both ends: aggressive visual mimicry signals and prey-specific luring behaviour in an ambush-foraging snake. Behav. Ecol. Sociobiol. 71, 2. (doi:10.1007/s00265-016-2244-6)

28. Nelson XJ, Garnett DT, Evans CS. 2010 Receiver psychology and the design of the deceptive caudal luring signal of the death adder. Anim. Behav. 79, 555–561. (doi:10.1016/j.anbehav.2009.12.011)

29. Crowe-Riddell JM et al. 2011 From matte banded to glossy black: structures underlying colour change in the caudal lures of southern death adders (Acanthophis antarcticus, Reptilia: Elapidae). Biol. J. Linnean Soc. 132, 666–675. (doi:10.1093/biolinnean/blb218)

30. Smith CF, Schuett GW, Earley RL, Schwenk K. 2009 The spatial and reproductive ecology of the copperhead (Agkistrodon contortrix) at the northeastern extreme of its range. Herpetological Monographs 23, 45–73. (doi:10.1655/08-026.1)

31. Rabinisky AM. 2008 Caudal luring as a precursor in the evolution of the rattlesnake: a test using an ancestral rattlesnake, Sistrurus miliarius barbouri. In The biology of rattlesnakes (eds WK
42. Proskie U. 1969 Vibration-sensitive mechanoreceptors in snake skin. Exp. Neurol. 23, 187–194. (doi:10.1016/0014-4886(69)90055-7)

43. Hill PSM. 2009 How do animals use substrate-borne vibrations as an information source? Naturwissenschaften 96, 1355–1371. (doi:10.1007/s00114-009-0588-8)

44. Crowe-Riddell JM, Snelling EP, Watson AP, Suh AK, Partridge JC, Sanders KL. 2016 The evolution of scale sensilla in the transition from land to sea in elapid snakes. Open Biol. 6, 160054. (doi:10.1098/rsob.160054)

45. Fagard J, Esseily R, Jacquey L, O'Regan K, Somogyi E. 2018 Fetal origin of sensorimotor behavior. Front. Neuro robotics 12, 23. (doi:10.3389/fnbot.2018.00023)

46. Mantziaras G, Gaia Cecilia Luvoni GC. 2020 Advanced ultrasound techniques in small animal reproduction imaging. Reprod. Domestic Animals 55(Suppl. 2), 17–25. (doi:10.1111/nda.15587)

47. Shea CA, Rollie RA, Murphy P. 2015 The importance of foetal movement for co-ordinated cartilage and bone development in utero: clinical consequences and potential for therapy. Bone It Res. 4, 105–116. (doi:10.1302/2046-3758.4.2000387)

49. Nowlan NC, Sharpe J, Roddy KA, Prendergast PJ, Murphy PM. 2010 Mechanobiology of embryonic skeletal development: Insights from animal models. Embryo Today: Rev. 90, 203–213. (doi:10.1002/bdr.20184)

50. Rollie RA, Nowlan NC, Kenny EM, Cormican P, Morris DW, Prendergast PJ, Kelly S, Murphy P. 2014 Identification of mechanosensitive genes during skeletal development: alteration of genes associated with cytoskeletal rearrangement and cell signalling pathways. BMC Genom. 15, 48. (doi:10.1186/1471-2164-15-48)

51. de Lima E, Bonnin M-A, Birchmeier C, Durez D. 2016 Muscle contraction is required to maintain the pool of muscle progenitors via YAP and NOTCH during fetal myogenesis. Elife 5, e15593. (doi:10.7554/eLife.15593)

52. Fitch HS. 1960 Autecology of the copperhead. Univ. Kans. Mus. Nat. Hist. Misc. Publ. 13, 85–288.

53. Ford NR, Burghardt GM. 1992 Perceptual mechanism and the behavioral ecology of snakes. In Snakes: ecology and behavior (eds RA Seigel, JT Collins), pp. 117–164. New York, NY: McGraw-Hill.

54. Pike DA, Pizzato L, Pike BA, Shine R. 2008 Estimating survival rates of uncatchable animals: the myth of high juvenile mortality in reptiles. Ecology 89, 607–611. (doi:10.1890/06-2162.1)

55. Bawens D, Claus K. 2018 Do newborn adders suffer mass mortality or do they venture into a collective hide-and-seek game? Biol. J. Linn. Soc. 124, 99–112. (doi:10.1093/biolinnean/bby023)

56. Pough HF. 1993 Zoo-academic research collaborations: how close are we? Herpetologica 49, 500–508.

57. Lawson DP, Ogden J, Snyder RJ. 2008 Maximizing the contribution of science in zoos and aquariums: organizational models and perceptions. Zoo Biol. 27, 458–469. (doi:10.1002/zoom.20216)

58. Burghardt GM. 2013 Environmental enrichment and cognitive complexity in reptiles and amphibians: concepts, review, and implications for captive populations. Appl. Anim. Behav. Sci. 147, 286–298. (doi:10.1016/j.applanim.2013.04.013)

59. Mendelson III JR, Schuett GW, Lawson DP. 2019 Kingh's principle and why the modern zoo is important to academic research. In Scientific foundations of zoos and aquariums: their role in conservation and research (eds A Kaufman, M Bashaw, T Maple), pp. 586–617. Cambridge, UK: Cambridge University Press.

60. Smith CF, Schuett GW. 2022 Tail movements by late-term fetal pitvipers resemble caudal luring: prenatal development of an ambush predatory behaviour. Figshare. (https://doi.org/10.6084/m9.figshare.c.5978490)