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Snake modulates constriction in response to prey's heartbeat

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Many species of snakes use constriction—the act of applying pressure via loops of their trunk—to subdue and kill their prey. Constriction is costly and snakes must therefore constrict their prey just long enough to ensure death. However, it remains unknown how snakes determine when their prey is dead. Here, we demonstrate that boas (*Boa constrictor*) have the remarkable ability to detect a heartbeat in their prey and, based on this signal, modify the pressure and duration of constriction accordingly. We monitored pressure generated by snakes as they struck and constricted warm cadaveric rats instrumented with a simulated heart. Snakes responded to the beating heart by constricting longer and with greater total pressure than when constricting rats with no heartbeat. When the heart was stopped midway through the constriction, snakes abandoned constriction shortly after the heartbeat ceased. Furthermore, snakes naive to live prey also responded to the simulated heart, suggesting that this behaviour is at least partly innate. These results are an example of how snakes integrate physiological cues from their prey to modulate a complex and ancient behavioural pattern.

Keywords: snake; constriction; behaviour

1. INTRODUCTION

Snakes are widely known for their ability to subdue and swallow enormous prey whole. As limbless, elongate predators, snakes have evolved efficient methods to restrain and kill their prey, including constriction. Relative to advanced snakes (Caenophidia [1]), most basal alethinophidians (as per Scanlon & Lee [1]) show less variation in constriction behaviour, and employ similar coil application behaviour regardless of prey type [2]. The shared kinematics among early snake lineages led researchers to propose constriction as a key innovation in their impressive radiation [3].

Boas (*Boa constrictor*) are non-venomous members of the early alethinophidian group Booidea [1] that use constriction to subdue a wide range of prey animals, including lizards, birds and mammals. Constriction in boas is initiated during the strike. The momentum of the strike is maintained after contact and as the snakes' head continues over the top of the prey, the snake's body twists and two or more loops are applied to the prey. This results in the snake's ventral and lateral sides in contact with the prey's thorax forming a ventral–lateral coil [4].

Constriction is an energetically costly and potentially dangerous activity. The act of striking and constricting prey exposes snakes to retaliatory attacks from the prey and other predators [5]. In boas, constriction demands a nearly sevenfold increase in aerobic metabolism above basal levels [6] and the duration of a constriction event can be extensive (9–16 min [4,6]). Thus, it would be greatly advantageous for constricting snakes to accurately and precisely determine when prey are incapacitated and no longer capable of retaliation or escape.

Here, we test whether snakes modulate the pressure and duration of constriction based on the presence or absence of a heartbeat in their prey. We developed a method of isolating a rat's heartbeat as a potential cue, by implanting a simulated heart in a dead rat that replicated the size, rate and stroke volume of an actual rodent heart. We tested how constriction effort (defined as duration (time from strike to when pressure dropped below 3% of the maximum) and total pressure (integral of pressure versus time) of constriction) varied as snakes constricted rats with (i) a simulated heartbeat throughout constriction, (ii) a simulated heartbeat for the first half of constriction and then shut off, and (iii) no heartbeat.

2. MATERIAL AND METHODS

We used 16 wild-caught boas (*Boa constrictor*) and F1 offspring from Belize, CA that varied in size from 98 to 149 cm snout-to-vent length (table 1). Snakes were maintained on a diet of dead chicks and rats and housed in a facility maintained at 28 ± 2°C. Snakes were a minimum of 14 days post-fed prior to testing. Pre-killed frozen rats (20 ± 1% of snake mass) were warmed and maintained at 38°C using a thermostatic heating blanket. Using cadaveric rats eliminated the possibility of muscular struggling and/or ventilation as confounding stimuli. Constriction pressure was measured by implanting two water-filled bulbs (cuffs on 3 or 4 mm I.D. endotracheal tubes) into the rat's thoracic and abdominal cavities hydraulically connected to pressure transducers (Gould-Statham P.T.J. 4771) via polyethylene tubing. To create our simulated heart, a water-filled bulb was conjoined with the thoracic (pressure sensing) bulb and implanted together into the rat's thoracic cavity adjacent to the rat's actual heart—placement was confirmed via ultrasonography in early trials (see electronic supplementary material, figure S1). The simulated heart bulb was hydraulically connected to a piston pump (Rodent Ventilator-Harvard Model 68 set to 195 cycles min^{-1} and a volume of 2.5 ml, resulting in a displacement volume of 0.85 ml that approximated actual rat stroke volume 1.3–2.0 ml [7]) via polyethylene tubing. Transducers were connected to a Biopac A/D recording system (recording frequency—200 Hz). A two-point calibration (0, 100 mmHg) was performed using a U-tube mercury manometer and transducers were tested for drift prior to all tests.

After a pilot study, we determined that boas constricted rats with a simulated heartbeat for an average of 20 min. Thus, we measured snake response to three treatments: a heartbeat throughout constriction, a heart beating for the first 10 min (half our pilot study average) and then shut off, and no heartbeat. To test the influence of experience on this behaviour, we tested both wild-caught (experienced, $n = 9$) and captive-born (naive, $n = 7$) snakes, the latter having never been exposed to live prey.

Data were analysed using mixed linear models in SAS 9.3 (SAS Institute Inc., Cary, NC, USA). Numbers of coil adjustments were treated as discrete variables in the GLIMMIX procedure in SAS where the response distribution was Poisson. We ran two MIXED procedures to analyse constriction effort: (i) duration and (ii) total pressure (integral of pressure versus time). For all procedures, heart treatment was a fixed effect and individual was a random effect to account for repeated measurements on individual snakes. We examined the influence of body mass, gender and origin (wild-caught versus captive-born) by testing these as fixed effects, and examined all possible interactions. After a significant effect was identified, we tested for differences within effects using the LSMEANS statement with a Tukey–Kramer adjustment for

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Table 1. Morphometric characters for the boas (*Boa constrictor*) used in this study. Origin, wild-caught (wild) or born in captivity (captive) from wild-caught parents.

snake	sex	snout-to-vent length (cm)	tail (cm)	mass (g)	origin
03–15	M	113.0	19.6	963.1	wild
03–8	M	118.4	20.2	1212.7	wild
03–24	M	108.8	19.4	852.0	wild
03–23	M	114.0	17.9	743.6	wild
02–12	F	127.5	14.1	1166.8	wild
02–14	F	112.0	11.0	1009.9	wild
02–17	F	132.8	14.5	1844.5	wild
17–3	M	131.0	22.1	1873.7	captive
02–26	F	126.0	15.1	1833.7	wild
37–10	F	113.8	13.0	1050.2	captive
38N4	M	130.0	21.0	1795.4	captive
2N5	F	133.8	16.9	2202.1	captive
02–28	F	149.0	14.0	2848.7	wild
37–12	F	106.2	12.3	778.9	captive
37–6	F	97.8	11.4	756.3	captive
38N1	M	137.0	22.3	1701.3	captive

multiple comparisons. We found no effect of gender or body mass on our dependent variables so these were removed from future models. We analysed a total of 70 measures (after removing two data points with Cook's distance values (D) exceeding $4/n$ [8] we achieved an $n = 68$) from 16 individuals and report means $\pm$ 1 s.e.m. as our measure of central tendency. Alpha was set at 0.05 for all tests.

3. RESULTS

Snakes responded to the beating of the simulated heart by periodically adjusting (i.e. tightening) their coils (figure 1*a*,*c*; see electronic supplementary material, video S1). Coil adjustments were abundant when snakes constricted rats with a simulated heartbeat (4.7 ± 0.9), but were virtually absent when snakes constricted rats without a heartbeat (0.9 ± 0.2; $F = 26.90$, d.f. $= 2$, $p < 0.0001$, $n = 68$; figure 1).

Boas constricted rats with a simulated heartbeat for nearly twice as long (22.3 ± 2.2 versus 12.2 ± 2.1 min; $F = 8.52$, d.f. $= 2$, $p = 0.0007$, $n = 68$) and more than twice the total pressure ($99\,670 \pm 11\,121$ versus $38\,874 \pm 10\,798$ s $\times$ mmHg) as when they constricted rats without the heart beating ($F = 9.59$, d.f. $= 2$, $p = 0.0003$, $n = 68$; figure 2). Peak pressures were higher when Boas constricted rats with a simulated heartbeat (189 ± 13 mmHg) as when they constricted rats without the heart beating (140 ± 14 mmHg). Snakes constricting rats where the heartbeat was discontinued after 10 min exhibited constriction times (17.5 ± 2.5 min) and pressures ($70\,378 \pm 12\,580$ s $\times$ mmHg) midway between our continuous and no heart treatments (figure 2).

Compared with captive-born snakes, wild-caught snakes constricted rats for longer (mean of 7.2 ± 2.6 min longer; $F = 9.17$, d.f. $= 1$, $p = 0.004$, $n = 68$) and with greater total pressure ($F = 5.69$, d.f. $= 1$, $p = 0.021$, $n = 68$). Captive-born snakes constricted rats with a simulated heart with greater total effort (duration and total pressure) relative to when they constricted rats without the heart beating (origin $\times$ heart interaction for duration: $F = 0.81$, d.f. $= 2$, $p = 0.450$, $n = 68$; for total pressure: $F = 0.96$, d.f. $= 2$, $p = 0.391$, $n = 68$).

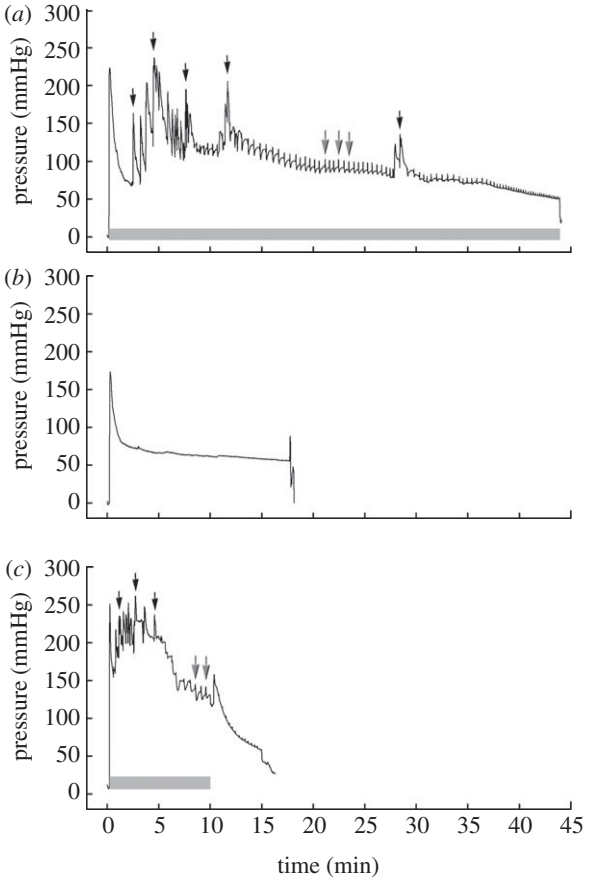

Figure 1. Constriction pressures generated by *Boa constrictor* in response to our three heart treatments: (*a*) continuously beating heart, (*b*) no heartbeat, and (*c*) a heart beating for 10 min and then shut off. Pressure (mmHg) was recorded as snakes compressed water-filled bulbs implanted within the thoracic cavity of dead rats. Grey rectangles oriented along the *x*-axes indicate when the simulated heart was beating within the rat; black arrows, coil adjustments; grey arrows, snake ventilation.

4. DISCUSSION

Our results are the first to demonstrate that snakes use the heartbeat in their prey as a cue to modulate constriction effort and to decide when to release their prey. In response to a simulated heartbeat, snakes frequently adjusted their coils and applied periodic bursts of pressure but did not show this response while constricting rats without a heartbeat. Even snakes naive to live prey responded to the simulated heartbeat. Naive snakes also constricted rats from all three treatments with less overall effort relative to experienced snakes. Thus, our findings suggest that the ability to respond to a heartbeat is innate, whereas the magnitude of the response is guided by experience. We suggest that the capacity to improve performance through learning enable snakes to become efficient predators of variable and unpredictable prey animals.

Our measures of constriction pressure exceed those recorded for smaller non-boid species [9], but are within the range of those for similar-sized species, including other boas [10]. The average time boas constricted rats without a heartbeat (12.2 ± 2.1 min) was similar to previous work with boas [4,6]. However,

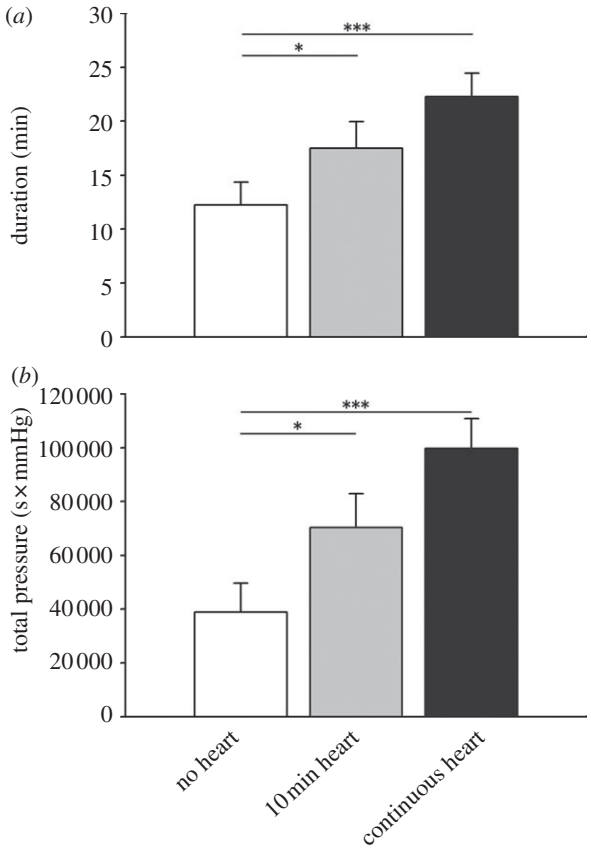

Figure 2. Constriction effort ((*a*) duration and (*b*) total pressure, means ± s.e.m.) in boas in response to our three heart treatments. Duration, the number of minutes a snake constricted a rat from the initial strike to when pressure dropped below 3% of the maximum. Total pressure = the integral of pressure (mmHg) versus time (s) recordings by employing the trapezoidal rule using S+. Asterisks indicate *p*-values ($*p < 0.05$, $***p < 0.001$).

the average time that boas constricted rats with a simulated heartbeat (22.3 ± 2.2 min) exceeded previous records and, to our knowledge, is longer than any previous observation of a snake constricting a mammalian prey item—live or dead.

These findings are interesting, but seem to conflict with what we know about the physiology of endothermic prey animals. Birds and mammals, with their high metabolic rates and concomitant demand for oxygen, are quite vulnerable to constriction. This enables snakes to dispatch them within minutes [11]. Why then might snakes have evolved such an acute ability to detect prey cardiovascular function? We speculate that the ability to detect a heartbeat in prey coevolved with constriction early in the snake radiation in order to precisely identify when physiological death had occurred in ectothermic prey [12] that exhibit low vascular pressures and a remarkable resistance to hypoxia [13]. For instance, iguanas (*Iguana iguana*) can remain submerged in water for up to 4.5 h [14] at least partially mediated by extreme bradycardia (slowing their heart rate to one beat every 5 min), and a variety of lizards, snakes and crocodilians can survive anoxia for up to 1.5 h [15]. Therefore, it may have been necessary for early snakes preying on large ectotherms to confirm prey death via cardiovascular failure rather than the cessation of muscular or ventilatory movement. Alternatively, this acute tactile sensitivity could have been associated with the evolution of limbless locomotion, well before constriction behaviour evolved. Efficient locomotion in terrestrial snakes depends on a complicated coordination of weight redistribution across multiple points along the ventral surface [16]. High tactile acuity associated with locomotion could have later benefited constriction once this behaviour evolved. Either way, the apparent ability to detect a heartbeat in at least two advanced snake species [9] suggests this ability is not restricted to basal alethinophidians. Modulating constriction effort in response to the prey's heartbeat may characterize many extant snakes, and could explain how constriction became a behavioural key innovation in the snake radiation beginning in the Late Cretaceous [2,12].

All experiments were approved by the Dickinson College IACUC (Institutional Animal Care Committee), protocol no.: FA08ASR05.

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