

# Independent effects of heart–head distance and caudal blood pooling on blood pressure regulation in aquatic and terrestrial snakes

Roger S. Seymour<sup>1,\*</sup> and Joachim O. Arndt<sup>2</sup>

<sup>1</sup>*Environmental Biology, University of Adelaide, Adelaide, SA 5005, Australia* and <sup>2</sup>*Department of Experimental Anaesthesiology, Heinrich-Heine-Universität, Universitätsstrasse 1, 40225 Düsseldorf, Germany*

\*Author for correspondence (e-mail: roger.seymour@adelaide.edu.au)

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## Summary

Changes in orientation in a gravitational field markedly alter the patterns of blood pressure and flow in animals, especially tall or long ones such as giraffes or snakes. Vertical orientation tends to reduce blood flow and pressure in the head for two major reasons. First, the increased vertical blood column above the heart creates a gravitational hydrostatic pressure against which the heart must work. Second, expansion of dependent vessels in the lower extremities causes blood pooling and reduces return of venous blood to the heart, thereby lowering flow and pressure. For most animals, it is difficult to separate these two effects, but snakes offer the possibility of bending the animal in the region of the heart and manipulating the two ends of the body independently. We studied

baroregulatory responses in terrestrial pythons (*Liasis fuscus*) and aquatic file snakes (*Acrochordus arafuræ*) by tilting only the front or rear parts and then the whole animal. Changes in head blood pressure during partial tilts added up to the change during full tilt. The vertical distance to the head had twice as much influence on head blood pressure than did blood pooling in the pythons and four times as much in file snakes. This accounts for the cephalad location of the heart in terrestrial species compared with aquatic ones.

Key words: blood pressure regulation, gravity, orthostasis, snake, tilting, *Liasis fuscus*, *Acrochordus arafuræ*.

## Introduction

When a terrestrial animal assumes an upright posture, gravity tends to pull blood away from the head toward the lower parts of the body and superimposes a hydrostatic pressure gradient on the circulatory system. Because this gradient is related to the absolute vertical height of the blood columns, the effect becomes more pronounced in larger or longer animals. To maintain perfusion pressure in the head, the system raises central arterial blood pressure by a combination of changes in heart rate, stroke volume and peripheral resistance, the so-called baroregulatory reflexes (Gauer and Thron, 1965). The ability of the heart to increase cardiac output is influenced by the arterial pressure that it must produce and the amount of blood available to it (the ‘venous return’). In upright posture, the arterial hydrostatic pressure gradient increases, and the venous return initially decreases, because blood collects in distended vessels below the heart. Stability of cephalic blood pressure, and hence blood flow, therefore partly depends on the vertical height of the head above the heart and blood pooling below it.

Animals subject to orthostatic problems have evolved morphological and physiological adaptations that help maintain circulation to the head in the upright posture (Lillywhite, 1995). These include a characteristically high arterial blood pressure, a heart closer to the head, powerful

vasomotor responses and stiffer vessels and surrounding tissues in lower parts of the body. The best examples come from studies of the giraffe (Hargens et al., 1987) and snakes (Lillywhite, 1996; Young et al., 1997). Snakes, in particular, are instructive because they have evolved in aquatic, terrestrial and arboreal habitats in which gravity has vastly different influences on the cardiovascular system. Aquatic snakes are in an essentially gravity-free environment because the hydrostatic pressure gradient of the medium approximately equals that in the vascular system; terrestrial snakes are subject to gravity, especially in arboreal species that climb vertically. Resting systemic arterial blood pressures in horizontal snakes is lowest in aquatic species and increases progressively in semi-aquatic, terrestrial and arboreal species (Seymour and Lillywhite, 1976). Arterial blood pressure increases in relation to head–heart distance in terrestrial species, and the heart moves relatively closer to the head from aquatic through terrestrial and arboreal species (Seymour, 1987). Terrestrial and arboreal species show more effective baroreflexes in response to tilting (Lillywhite and Donald, 1994; Lillywhite and Pough, 1983; Lillywhite and Seymour, 1978; Seymour and Lillywhite, 1976; Young et al., 1997), and they have more effective mechanisms to prevent blood pooling and oedema in the dependent end, including less compliant vessels or tissues, narrower bodies

and behavioural responses that facilitate venous return (Lillywhite, 1985a,b, 1987b, 1993a). Aquatic snakes and some non-climbing vipers have such poor baroregulation that blood pressure in the head becomes negative, and circulation ceases in head-up tilting in air (Seymour and Lillywhite, 1976; Lillywhite, 1993b; Young et al., 1997; R. S. Seymour and J. O. Arndt, unpublished). The result of this research is a picture of evolutionary loss of pressure-regulating mechanisms as snakes invaded the gravity-free aquatic habitat, and enhancement of these mechanisms as they began to climb in trees.

A remaining question, however, concerns the relative influences of the vertical blood column in arteries above the heart, and blood pooling in the dependent vasculature, on blood pressure regulation in snakes from different habitats. Specifically, is blood pressure in the head of a snake more influenced by the head–heart distance or by blood pooling and decreased venous return during head-up tilting? The shape of snakes offers a unique way of answering this question by permitting tilting of the anterior and posterior segments independently. By bending the snake at the heart, the head can be raised, or the tail lowered, to separate the two influences. This study compares the results from pythons (*Liasis fuscus* Peters; Boidae) and file snakes (*Acrochordus arafurae* McDowell; Acrochordidae). Although commonly called the ‘water python’, *L. fuscus* is essentially terrestrial, frequenting floodplains and feeding on rodents and birds, while *A. arafurae* is totally aquatic in fresh and brackish estuaries, where it feeds on fish (Shine, 1993).

### Materials and methods

The snakes were captured in the Northern Territory of Australia, air freighted to Adelaide and kept in individual aquaria and terraria. Pythons were fed white mice, and file snakes were fed goldfish once or twice a week. All of the measurements were performed in January and February 1993.

The animals were anaesthetised by cooling their body temperature below 5°C in a bed of chipped ice, preventing direct contact between the head and the ice. They were weighed and measurements made of body length and heart position, as determined by palpation. Small (2 cm) incisions were made in the ventrolateral body wall, between the midline and the ends of the ribs. Appropriately sized PVC catheters were fixed in a major artery and vein. The aorta was occlusively catheterised just anterior to the vent. Collateral circulation was sufficient to maintain perfusion of the tail, which retained mobility and sensation after the operation. A non-occlusive catheter was placed in the inferior vena cava, by passing it through the wall toward the heart and fixing it in place with a purse-string ligature and cyanoacrylate tissue adhesive. Both catheters passed out of the body through a puncture away from the incision, and enough loose tubing was left inside the body to accommodate shifts in the viscera. The sites of the catheter tip and the location of the heart were

marked on the skin with a permanent marking pen. The catheters were flushed with 0.85% saline (heparinised 250 units ml<sup>-1</sup>) and sealed.

Catheterised snakes were transferred to the tilting apparatus for recovery overnight. They were restrained in clear acrylic tubes of appropriate size to allow free ventilation but to prevent coiling and reversing direction. Each tube had a full-length slit for passage of the catheters, and it was divided by a ~10 cm gap at the location of the snake’s heart so that the animal could be flexed at this point to raise or lower the head or tail while maintaining the rest of the body horizontal (Fig. 1). To prevent escape through the gap, the entire snake was placed inside a loose hosiery sleeve, inside the acrylic tube and attached to its distal ends. We found that the snake’s ventilation was affected if the sleeve contacted its head, so this was prevented with a short length of rigid tube inside the sleeve around the head.

The restraining tube was attached to a bar that pivoted vertically in the middle of a large board equipped with an indicator of tilt angle. Half of the tube could be clamped horizontally while the other half was tilted. Like the two hands of a clock, therefore, the two halves of the snake could be oriented independently around the pivot point at the heart. We chose tilt angles of 30°, 45° and 70°. Because the effect of tilting relates to the sine of the tilt angle, these angles represented an added hydrostatic pressure equivalent to 50%, 71% and 94%, respectively, of that present at the bottom of a vertical column of blood equal in height to the length to the tilted segment. Thus, a 70° tilt had practically the same effect as a 90° tilt but did not bend the animal at a stressful angle.

The protocol consisted of tilting the snake to the desired angle within ~5 s, maintaining the tilt for 2 min and then returning to horizontal for at least 2 min. In some cases, the pressure transducer was attached to the tube being tilted, so

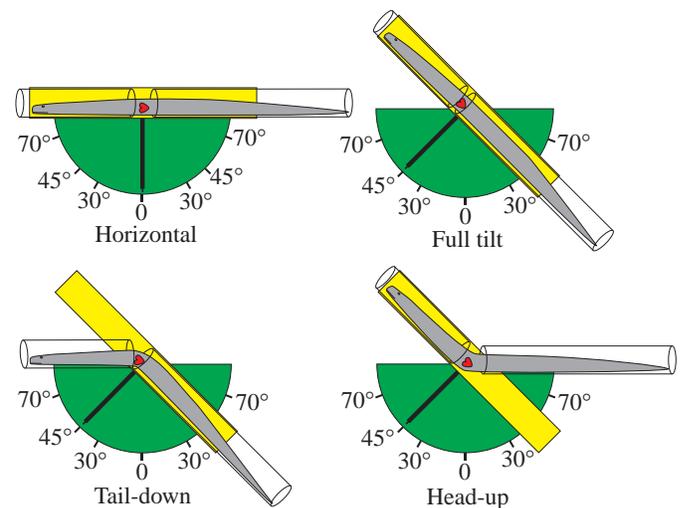


Fig. 1. Apparatus to tilt snakes about the heart, either partially or fully. The animal is restrained in two acrylic tubes and a hosiery sleeve (not shown).

measured blood pressure at the site of the catheter required conversion to pressure at heart level by calculation from the tilt angle and the linear distance between the transducer and the heart. Density of blood was assumed to be  $1.05 \text{ kg l}^{-1}$ . In other cases, when the catheter was long enough, the transducer was placed at heart level. Tilting often slightly shifted the location of the snake, so differences in elevation were noted and used to correct pressure to heart level.

Blood pressure was measured with Gould-Statham P23 transducers [Grass-Telefactor (Astro-Med Inc.), West Warwick, RI, USA] connected to Grass Model 7PIE low-level DC preamplifiers and Model 7DAF driver amplifiers within a Model 79D oscillograph (Grass-Telefactor). The signal was also recorded rectilinearly on a flat bed recorder, from which the reported data were taken. The transducers were calibrated with a water manometer before every experiment, and data were converted to the traditional units of mmHg for ease of understanding ( $1 \text{ mmHg} = 13.6 \text{ mmH}_2\text{O} = 133 \text{ Pa}$ ). Mean arterial blood pressure was taken as diastolic blood pressure plus one-third of the difference between systolic and diastolic blood pressure.

All measurements were made on healthy, conscious animals at body temperatures between  $22^\circ\text{C}$  and  $27^\circ\text{C}$ . After the tilting experiments, the animals were euthanized with an overdose of the anaesthetic Hypnomidate (Janssen GmbH, Neuss, Germany) and inspected to confirm the location of catheters and the heart.

## Results

Complete tilting sequences were obtained from five pythons and six file snakes (Table 1). Data were obtained from snakes in basically three body positions: straight 'full tilt', bent 'head-up' or bent 'tail-down'. Tilt angles were  $0^\circ$ ,  $30^\circ$ ,  $45^\circ$  or  $70^\circ$ . Head-down and tail-up positions are not reported because they did not address the central question. Blood pressures were means, measured at three sites: central aortic pressure at the heart (CAP), head artery pressure (HAP), central venous pressure at opening to the right atrium (CVP).

Pythons showed high systemic arterial pressures and crisp regulation during straight, head-up tilts (Fig. 2). Immediately upon tilting, there was a large drop in CVP, but CAP remained almost normal because of a rapid increase in heart rate. CVP generally remained positive and increased during the tilting period as heart rate decreased. This is interpreted as an

Table 1. *Morphometry of pythons (Liasis fuscus) and file snakes (Acrochordus arafurae) used in this study*

	Pythons ( $N=5$ )	File snakes ( $N=6$ )
Body mass (g)	$1707 \pm 459$	$800 \pm 226$
Body length (cm)	$157.6 \pm 30.8$	$120.2 \pm 6.3$
Heart-head length (cm)	$37.2 \pm 7.4$	$44.4 \pm 2.4$
Heart-head (% body)	$24 \pm 1$	$37 \pm 1$

Means  $\pm$  95% confidence intervals are listed.

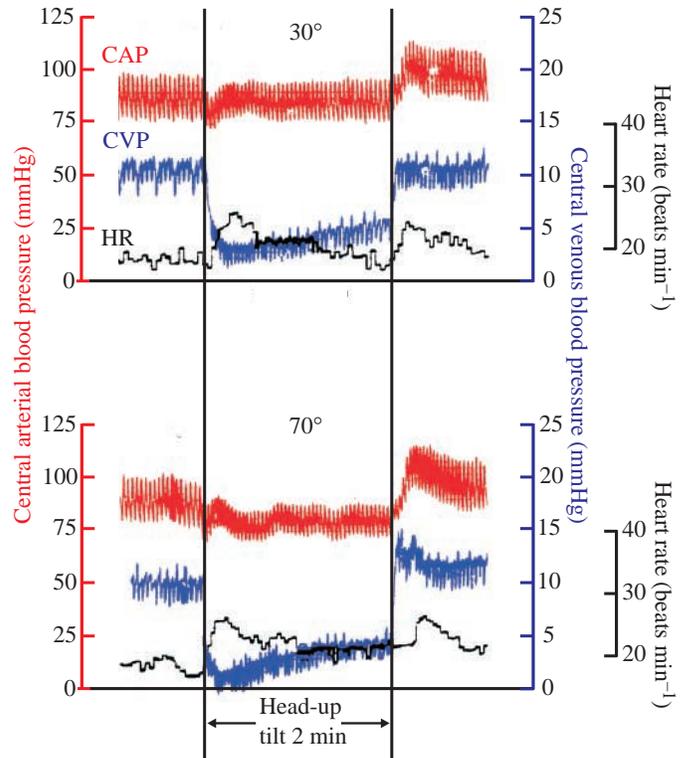


Fig. 2. An example of the patterns of blood pressure and heart rate of a python (*Liasis fuscus*) associated with head-up, straight tilts to either  $30^\circ$  or  $70^\circ$ . Blood pressures at heart level in the central aorta (CAP) and central post caval vein (CVP) and heart rate (HR;  $\text{beats min}^{-1}$ ) are shown.

immediate caudad flow of venous blood that reduced cardiac filling. Increased heart rate compensated for this while the posterior circulation filled with blood and reflexogenic venous constriction gradually raised CVP and allowed the heart rate to decrease.

Straight head-up tilts in file snakes resulted in a different pattern of regulation (Fig. 3). Tilting immediately resulted in a fall in CVP, tachycardia and an initial rise in CAP. Then CAP began to fall back to normal, and the rises in CVP were small. In some cases, CVP became negative but recovered to positive values after  $\sim 1$  min at  $30^\circ$  and  $45^\circ$  tilts. When CVP became positive, CAP stabilised at levels not greatly below normal. However, at  $70^\circ$ , CVP remained negative and CAP continued to fall. A loss in pulse pressure in CVP trace indicates that the blood in the posterior veins had lost connection with the heart. Pulse pressure almost disappeared in the CAP trace at 2 min, but CAP remained positive.

The temporal patterns of blood pressure reflexes were consistent within each species, but there were large differences between species. Blood pressure stabilised after 2 min of full and partial tilting in both species, and the separate effects of heart-head distance and blood pooling can be observed in the mean values from all snakes. CAP in pythons was much higher than in file snakes in the horizontal orientation (Fig. 4). In pythons, CAP tended to rise during head-up tilts and fall during

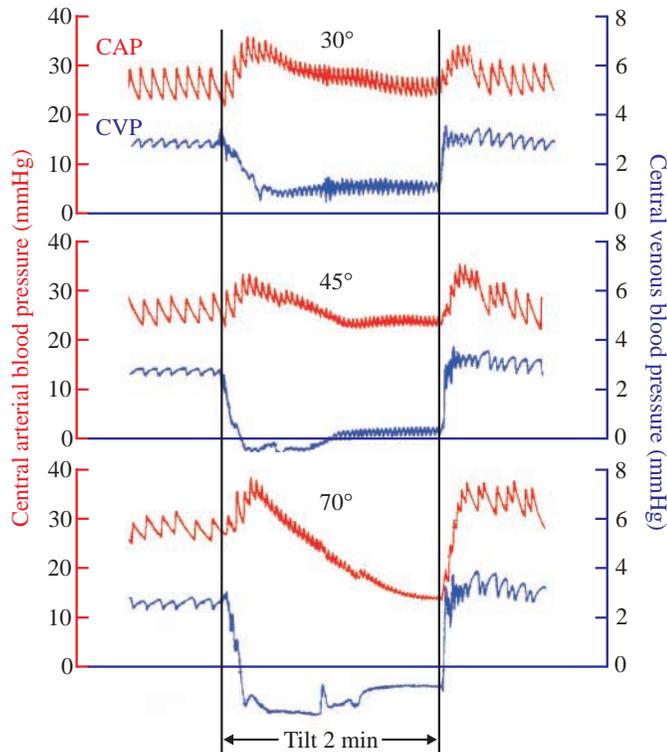


Fig. 3. An example of the patterns of blood pressure of file snakes (*Acrochordus arafurae*) associated with head-up, straight tilts to 30°, 45° or 70°. Blood pressures at heart level in the central aorta (CAP) and central post-caval vein (CVP) are shown. CVP was measured below the heart but adjusted to heart level, causing apparent negative values.

tail-down tilts but did not change during full tilts (Fig. 4; Table 2). In file snakes, CAP increased significantly during head-up tilts but did not change consistently under other conditions.

HAP of individual snakes were calculated from the vertical distance between the heart and the head, ignoring any pressure drop due to viscous resistance. Consequently, these were identical to CAP in horizontal or tail-down tilted snakes (Figs 4, 5). HAP always fell significantly in both pythons and file snakes during head-up and full tilts but decreased significantly in pythons only during tail-down tilts to 30° and 45° (Fig. 5; Table 2). Nevertheless, HAP remained relatively high in pythons at all angles but dropped to much lower values in file snakes. File snake HAP became negative in full tilt at 45° and 70° and reached zero in head-up tilts to 70°.

CVP was positive and increased slightly during head-up tilts, but it decreased to values insignificantly different from zero during tail-down or full tilts (Fig. 6). In pythons, CVP could become negative, but pulse pressures were always evident. In file snakes, however, CVP pulse pressures disappeared at full tilts to 45° and 70°.

Heart rates were significantly higher in pythons than in file snakes resting horizontally (Fig. 7). In pythons, heart rate did not change much, increasing significantly only at 70° tail-down

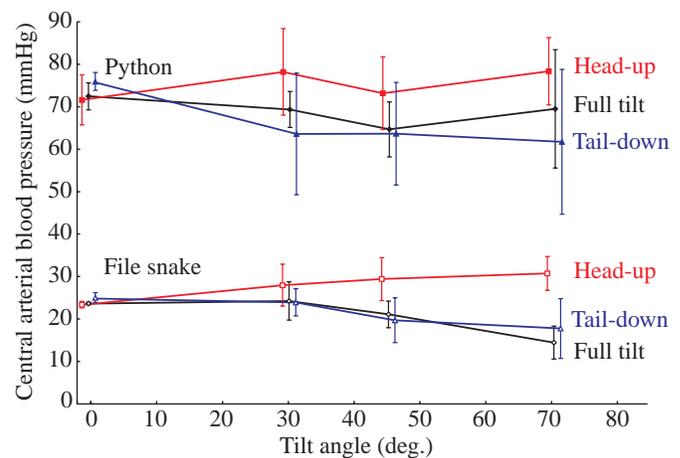


Fig. 4. Means ( $\pm$  95% confidence intervals) of central arterial blood pressures at the heart in five pythons (*Liasis fuscus*; filled symbols) and six file snakes (*Acrochordus arafurae*; open symbols) near the end of 2 min partial (head-up and tail-down) and full tilts. Some angles shifted slightly for clarity.

and full tilting; in file snakes, heart rate increased significantly at all angles of tail-down and full tilting (Fig. 7; Table 2). Within each species, there was no significant difference between full and tail-down tilts (Table 2). There was also no change in heart rate during head-up tilting in pythons, and a slight significant rise in file snakes at 45°.

Partial and full tilting in the same animals permitted partitioning of the effects of arterial blood column and blood pooling, shown for example in 45° tilting data. In horizontal pythons, mean CAP and HAP were 73 mmHg, and CVP was 5 mmHg (Fig. 8). With a head-up partial tilt, CAP and CVP were unchanged, but HAP decreased 27%, to 53 mmHg. With a tail-down partial tilt, CAP decreased to 64 mmHg, CVP went to approximately zero but the decrease in HAP was only 14%. In full tilt, however, CAP was 65 mmHg, CVP went to zero and HAP dropped 42%, to 42 mmHg. Thus, the decreases in HAP brought about by partial tilts (27+14%=41%) approximately added up to the decrease resulting from full tilt (42%) and showed that the vertical distance to the head was about twice as important as blood pooling. The sum of changes to HAP in partial tilts was also close to the change in full tilts to 30° and 70° in pythons.

The effects of tilting were more extreme in file snakes. Horizontal snakes had a mean CAP and HAP of 24 mmHg, and a CVP of 2 mmHg (Fig. 9). Upon head-up partial tilting to 45°, CAP increased to 29 mmHg, HAP dropped 79%, to 5 mmHg, and CVP rose to 3 mmHg. Tail-down partial tilting resulted in CAP and HAP decreasing only 17%, to 20 mmHg, while CVP became zero. Full tilting resulted in CAP remaining at 21 mmHg, and a calculated value of -3 mmHg for HAP. In this case, the vertical distance to the head was over four times more important than blood pooling in diminishing head blood pressure.

Table 2. Results of paired, two-tailed t-tests comparing head-up and tail-down partial tilts and full tilts in pythons and file snakes

Conditions	Head-up			Tail-down			Full tilt		
	CAP	HAP	HR	CAP	HAP	HR	CAP	HAP	HR
Python									
0 vs. 30°	0.695	0.001↓	0.374	0.005↓	0.005↓	0.374	0.499	0.001↓	0.256
0 vs. 45°	0.002↑	0.001↓	0.374	0.036↓	0.036↓	0.135	0.231	0.010↓	0.107
0 vs. 70°	0.000↑	0.009↓	0.374	0.074	0.074	0.016↑	0.409	0.024↓	0.026 ↑
File snake									
0 vs. 30°	0.085	0.001↓	0.475	0.911	0.911	0.032↑	0.849	<0.000↓	0.021↑
0 vs. 45°	0.020↑	0.000↓	0.042↑	0.075	0.075	0.007↑	0.323	<0.000↓	0.017↑
0 vs. 70°	0.010↑	<0.000↓	0.098	0.118	0.118	0.001↑	0.007↓	<0.000↓	<0.000↑

Conditions	30°			45°			70°		
	CAP	HAP	HR	CAP	HAP	HR	CAP	HAP	HR
Python									
Head-up vs. tail-down	0.020↓	0.966	0.089	0.014↓	0.007↑	0.142	0.075	0.209	0.004↑
Tail-down vs. full tilt	0.470	0.057	0.814	0.858	0.011↓	0.602	0.068	0.012↓	0.562
Head-up vs. full tilt	0.197	0.030↓	0.614	0.129	0.077	0.352	0.191	0.191	0.149
File snake									
Head-up vs. tail-down	0.046↓	0.000↑	0.487	0.021↓	0.003↑	0.092	0.016↓	0.003↑	0.015↑
Tail-down vs. full tilt	0.779	<0.000↓	0.711	0.390	<0.000↓	0.573	0.298	<0.000↓	0.128
Head-up vs. full tilt	0.098	0.098	0.034↑	0.003↓	0.006↓	0.076	<0.000↓	<0.000↓	0.016↑

Stabilized central arterial pressure (CAP) at heart level, head arterial pressure (HAP) and heart rate (HR) are represented at three tilt angles. Significant results ( $P < 0.05$ ) are indicated by an arrow that shows whether the second condition was higher (↑) or lower (↓) than the first. For example, during head-up tilting, head arterial blood pressure (HAP) was significantly lower at 30° than at 0°.

**Discussion**

Our results show that the vertical blood column above the heart is the most important factor determining blood pressure in the head in both species. Blood pooling can decrease arterial blood pressures measured at the heart (Fig. 4), but the effect of the vertical distance above the heart overshadows it (Fig. 5). This conclusion is strengthened by examination of heart

position in snakes from different habitats (Seymour, 1987; Seymour and Lillywhite, 1976). If blood pooling were more important than vertical height, one would expect to see a more caudally placed heart, which would minimise the volume and length of the body in which pooling could occur. On the other hand, if vertical height were more influential, one would expect the heart to be closer to the head to minimise the hydrostatic

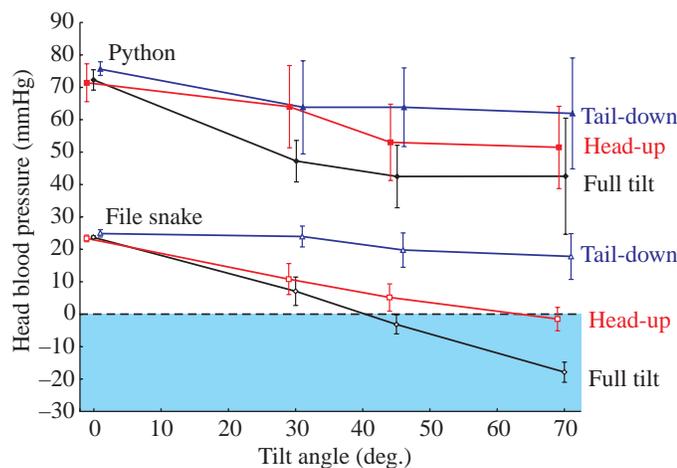


Fig. 5. Means ( $\pm$  95% confidence intervals) of calculated arterial blood pressures at head level in five pythons (*Liasis fuscus*; filled symbols) and six file snakes (*Acrochordus arafuræ*; open symbols) near the end of 2 min partial (head-up and tail-down) and full tilts. Negative values (blue area) are calculated.

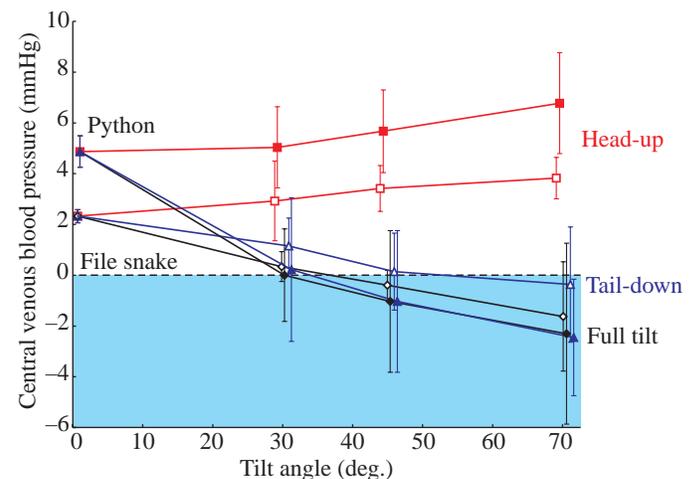


Fig. 6. Means ( $\pm$  95% confidence intervals) of central venous blood pressures at the heart in five pythons (*Liasis fuscus*; filled symbols) and six file snakes (*Acrochordus arafuræ*; open symbols) near the end of 2 min partial (head-up and tail-down) and full tilts. Negative values (blue area) are calculated.

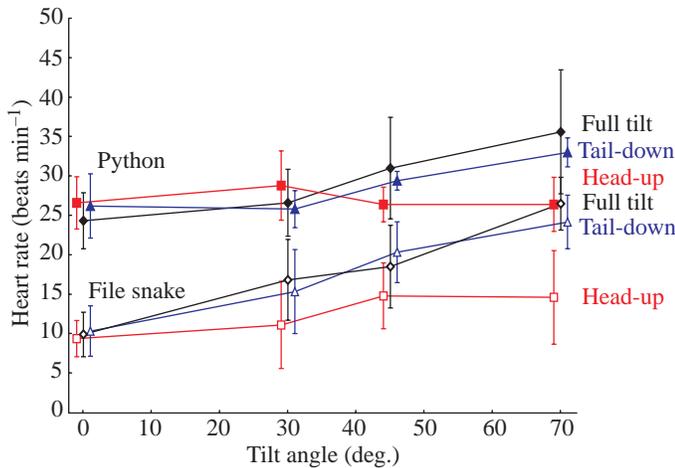


Fig. 7. Means ( $\pm$  95% confidence intervals) of heart rates at the heart in five pythons (*Liasis fuscus*; filled symbols) and six file snakes (*Acrochordus arafurae*; open symbols) near the end of 2 min partial (head-up and tail-down) and full tilts.

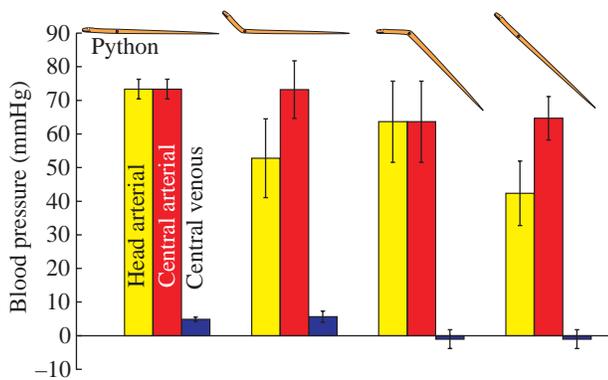


Fig. 8. Effect of full and partial tilting to 45° on blood pressures in the python (*Liasis fuscus*). Means  $\pm$  95% confidence intervals represent head arterial pressure (HAP), central arterial pressure at the heart (CAP) and central venous pressure at the heart (CVP).

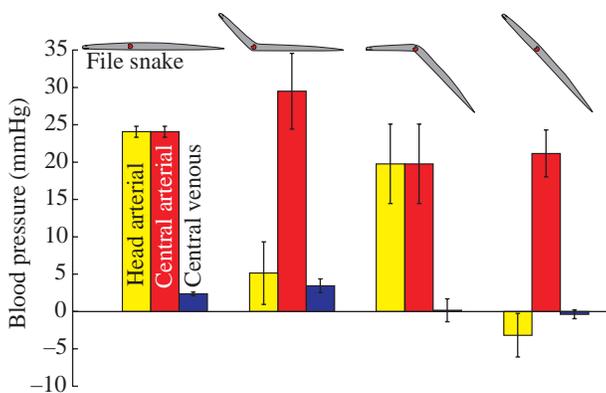


Fig. 9. Effect of full and partial tilting to 45° on blood pressures in the file snake (*Acrochordus arafurae*). Means  $\pm$  95% confidence intervals represent head arterial pressure (HAP), central arterial pressure at the heart (CAP) and central venous pressure at the heart (CVP).

gradient. In terms of percentage of total body length, the heart-head distance averages 17% in arboreal, 19% in terrestrial, 23% in semiaquatic and fossorial and 33% in aquatic and viperid species (Seymour, 1987). Thus, those species that are more likely to climb have diminished the heart-head distance while augmenting the heart-tail distance and potentially suffering greater blood pooling. However, this problem is compensated for by less compliant posterior vessels of terrestrial and arboreal snakes (Lillywhite, 1985b, 1987b, 1993a) and the anterior movement of the hydrostatic indifferent plane (J. O. Arndt and R. S. Seymour, unpublished).

Totally aquatic species are protected from the effects of gravity while in water. This is correlated with hearts closer to the centre of the body (Seymour, 1987) and inherently low arterial blood pressure (Seymour and Lillywhite, 1976), both of which reduce the energy cost of circulation. When the animals are removed from water and tilted, the consequences are obvious and dire. A long heart-head distance, coupled with a low central arterial pressure, causes head arterial pressure to decrease greatly, with calculated values even below zero. This is shown in file snakes in head-up partial tilts to 70° (Fig. 5). In this case, there is no blood pooling, yet blood flow to the head apparently ceases, because unprotected arteries and microvessels close under negative blood pressure. Blood flow in the carotid artery of snakes has been shown to cease when the central arterial blood pressure equals or falls below the equivalent of the hydrostatic blood column above the heart (Lillywhite, 1993; Lillywhite and Donald, 1994). On its own, blood pooling in file snakes has little influence on head arterial pressure, but when combined in a full tilt exacerbates the problem by causing head arterial pressure to become negative at lower tilt angles (Fig. 5). Pooling appears to increase during a full tilt, probably because dependent vasculature is further distended by increased hydrostatic pressures generated in longer vertical blood columns in arteries and valve-less veins (Lillywhite, 1987a).

It has been proposed that the anterior heart placement in terrestrial and arboreal snakes is not related to the heart-head distance but is related to the filling pressure of the systemic veins (Badeer, 1998). The principle of the siphon is thought to make blood flow to the head independent of the height of the vascular loop. This notion is derived from the idea that the heart does not work against gravity in the circulatory system but works only against viscous resistance (Hicks and Badeer, 1992), although the idea and its experimental evidence have been shown to be seriously flawed (Pedley et al., 1996; Seymour et al., 1993). Nevertheless, Badeer proposes that the hearts of arboreal snakes are closer to the head because they can fill better in this location when the animal is tilted head-up (Badeer, 1998). This appears to be false, because the heart would fill even better if it were further back in the body, where systemic venous pressures are higher. If filling pressure affected heart placement, then there would be no selective advantage of an anteriorly placed heart. On the other hand, if a given level of arterial blood pressure were necessary at the entrance to vascular beds in the head in order to perfuse them,

then an anterior heart would have to produce less pressure and consequently expend less energy.

The effects of blood pooling on the heart are mediated through a fall in CVP in the post-cava (Fig. 6). In horizontal snakes, CVP was slightly positive in file snakes and more so in pythons. Despite the long post-heart length in pythons (Table 1), they regulated CVP well and it dropped to about zero only during tail-down partial tilts (Fig. 6). Nevertheless, pulse pressures were always evident in pythons, which is evidence that they continued to fill the heart from posterior vessels. In file snakes, on the other hand, calculated CVP went slightly negative in acute tail-down and full tilts and pulse pressure oscillations disappeared (Figs 2, 6). This might indicate that circulation to the posterior part of the snake ceased, but it is apparent that venous return from the posterior parts in fact continued, even at CVP down to about  $-2$  mmHg and loss of venous pulse pressure, because central arterial pressure remained substantially positive (Fig. 4), and arterial pulse pressure oscillations were evident (Fig. 3).

It is interesting that heart rate changes were more pronounced during full tilts and tail-down tilts than head-up tilts (Fig. 7), despite considerable falls in arterial blood pressure in the neck and head (Figs 8, 9). This implies that the effective site of baroreception lies near the heart rather than further up the neck. It is also consistent with morphological and physiological evidence of baroreceptors in the truncus arteriosus and central arteries of snakes (Lillywhite and Donald, 1994).

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