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## Research

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### Author for correspondence:

Rory P. Wilson

e-mail: [R.P.Wilson@swansea.ac.uk](mailto:R.P.Wilson@swansea.ac.uk)

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## Evolutionary biology

# Mitigating the squash effect: sloths breathe easily upside down

Rebecca N. Cliffe<sup>1,3</sup>, Judy A. Avey-Arroyo<sup>3</sup>, Francisco J. Arroyo<sup>3</sup>, Mark D. Holton<sup>2</sup> and Rory P. Wilson<sup>1</sup>

<sup>1</sup>Swansea Lab for Animal Movement, Biosciences, College of Science, and <sup>2</sup>College of Engineering, Swansea University, Singleton Park, Swansea SA2 8PP, Wales, UK

<sup>3</sup>The Sloth Sanctuary of Costa Rica, PO Box 569-7300, Limon, Costa Rica, Central America

Sloths are mammals renowned for spending a large proportion of time hanging inverted. In this position, the weight of the abdominal contents is expected to act on the lungs and increase the energetic costs of inspiration. Here, we show that three-fingered sloths *Bradypus variegatus* possess unique fibrinous adhesions that anchor the abdominal organs, particularly the liver and glandular stomach, to the lower ribs. The key locations of these adhesions, close to the diaphragm, prevent the weight of the abdominal contents from acting on the lungs when the sloth is inverted. Using ventilation rate and body orientation data collected from captive and wild sloths, we use an energetics-based model to estimate that these small adhesions could reduce the energy expenditure of a sloth at any time it is fully inverted by almost 13%. Given body angle preferences for individual sloths in our study over time, this equates to mean energy saving of 0.8–1.5% across individuals (with individual values ranging between 0.01 and 8.6%) per day. Given the sloth's reduced metabolic rate compared with other mammals and extremely low energy diet, these seemingly innocuous adhesions are likely to be important in the animal's energy budget and survival.

## 1. Introduction

Mammalian lungs, with their large surface area, are essential in providing oxygen for the high metabolic rates associated with homoeothermy [1] and are associated with multiple adaptations to make them particularly efficient [2]. The lungs normally lie essentially dorsal to the other internal organs, which allows them to be ventilated easily. They bring about inspiration actively by contracting the thoracic diaphragm, external intercostal muscles and several groups of accessory muscles [3]. The situation seems therefore complicated in sloths, mammals renowned for hanging inverted [4]. In theory, this position should lead to the weight of the internal organs in the abdominal cavity causing increased pressure on the lungs and therefore making the process of inspiration energetically more costly. We considered that selection pressure would have led to mechanisms to mitigate this problem and examined this by undertaking a detailed anatomical examination of the thoracic and abdominal cavities in the three-fingered sloth *Bradypus variegatus*, examining ventilation rates in three-fingered sloths in captivity and deploying accelerometers on both captive and wild three-fingered sloths to determine how much time they adopted different body orientations.

## 2. Material and methods

Two adult three-fingered sloths were examined by dissection to identify any anatomical adaptations that might help breathing, paying particular attention to differences between their anatomy and that of other mammals. Both of these

animals had previously died of natural causes. Lungs were removed and their total capacities determined by inflating them underwater and noting volumetric changes. Ventilation rates were determined in captive sloths by observing the abdomens of each of three individual three-fingered sloths at intervals of 4 h for a total of 172 continuous days while, concomitantly, ambient temperature was noted. Tri-axial accelerometer loggers [5] were deployed on six individual three-fingered sloths in captivity, each for three days (18 days total) and one wild sloth for seven days. The loggers were attached via harnesses, positioning the devices firmly on the upper back. In this position, negative values represent a body orientation with the head pointing downwards and positive values signify the head pointing upwards. The loggers were set to record at rates between 5 and 40 Hz. The acceleration data were smoothed over 2 s to determine gravity-based acceleration from which body orientation could be derived [6]. Detailed methods can be found in the electronic supplementary material.

### 3. Results

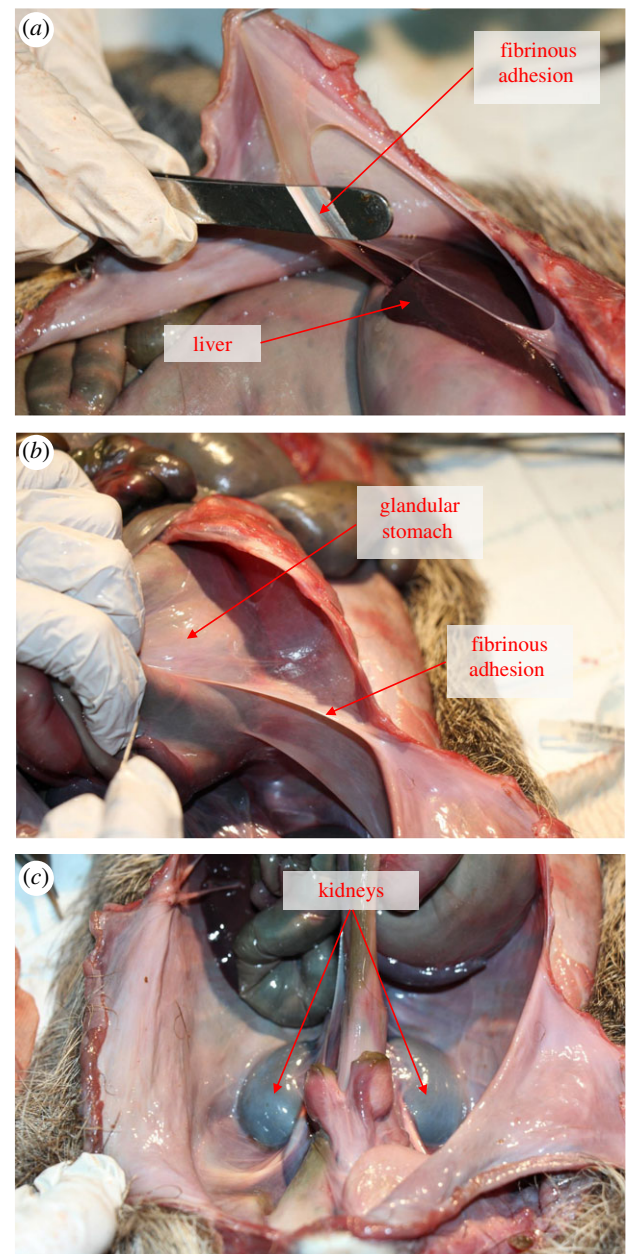
During dissection, we identified multiple unusual fibrinous adhesions within and between the organs in the abdominal cavity. In particular, there were prominent adhesions connecting both the liver and the glandular stomach to the lower ribs (figure 1*a,b*). Further such adhesions were found dividing the thoracic cavity. The kidneys were located in the posterior abdomen and were bound by connective tissue against the pelvic girdle with no mobility (figure 1*c*). Total lung capacities for the two individual three-fingered sloths were 125 and 121 ml kg<sup>-1</sup>, and the abdominal organs, including contents (but excluding urine and faeces), weighed 0.595 and 1.05 kg equating to 29 and 35% of total body weight.

Sloth ventilation rates ranged between 6 and 108 breaths per minute with a mean of 27 but with substantial variance (s.d. 18.6,  $N = 3096$ ). Some of this variation was explained by ambient temperature (figure 2*a*), with there being a significant relationship between ambient temperature and ventilation rate in all three individuals ( $p < 0.02$ ). The combined best-fit regression equation was ventilation rate =  $2.58 \times \text{temperature} - 41.4$ .

Overall, captive sloths and the wild sloth had broadly similar patterns of hanging angle, spending relatively little of their time (an overall mean of 26%) with body angles less than 0° from the horizontal (with the head tending to point downwards) (figure 2*b*). The exception to the trend was one (captive) individual that spent 97.7% of its 3 day monitoring period hanging at angles below 0° (figure 2*b*). For comparison, the equivalent value for the wild sloth was only 10.4% of the 7 day monitoring time (see electronic supplementary material).

### 4. Discussion

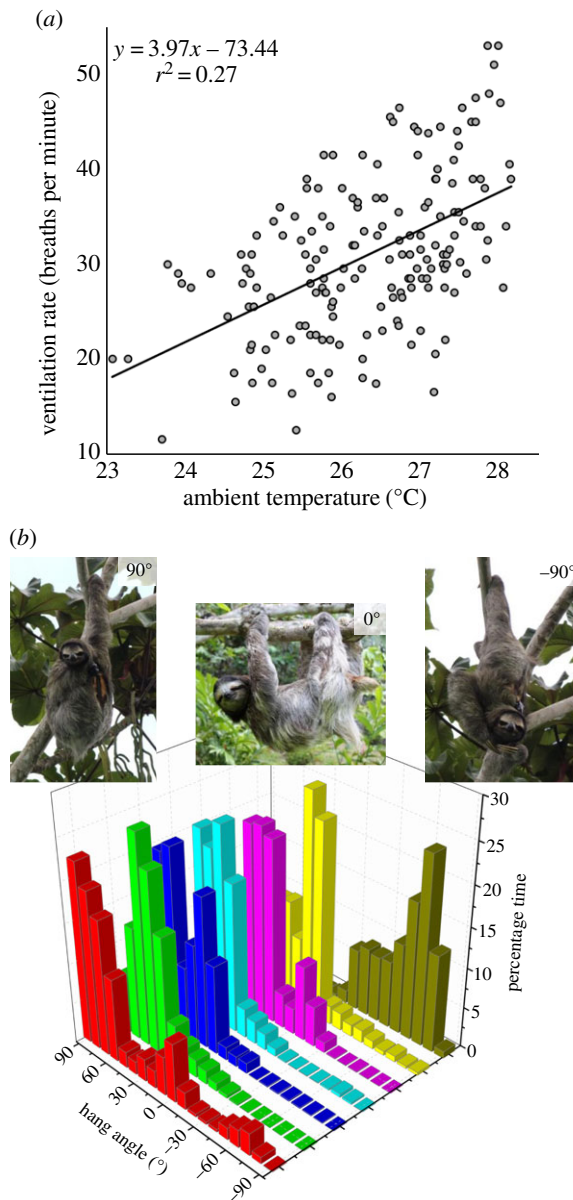
Our observations of fibrinous adhesions within the abdominal cavity accord with a previous report by Quandt & Nesbit [7] who examined two-fingered sloths (*Choleopus didactylus*), without ascribing a function to these tissues; it is likely that these adhesions are a general feature of sloth anatomy. The precise position of these adhesions, linking the organs closest to the diaphragm to the ribs, means that they can bear the weight of all abdominal organs preventing their forces acting on, and compressing, the lungs and thereby easing inspiration when the animals are inverted. Consistent with this notion, Hoffman



**Figure 1.** Fibrinous adhesions anchoring (*a*) the liver and (*b*) glandular stomach to the lower ribs in the three-fingered sloth, *B. variegatus*. (*c*) The kidneys are bound by connective tissue against the pelvic girdle with no mobility. This prevents their weight from acting on the lungs when the sloth is hanging inverted.

*et al.* [8] noted no change in diaphragm shape according to body orientation in (two-fingered) sloths compared with a radical change observed in dogs between the prone and supine positions. In addition, the unusual configuration of the kidneys being bound against the pelvic girdle means that they too are exempt from contributing to the abdominal weight.

The stabilizing effect of the adhesions can be characterized in energetic terms by way of a simple model if we assume no adhesions to support the weight of the abdominal tissue. If the lungs are approximated by a cylinder of length  $L$  and radius  $r$  (with  $L$  equal to  $2r$ ) and changed by 12.5% during normal ventilation [9], this would equate to a volumetric change in the length alone of 0.96 cm for every breath taken (using our data on lung volumes). Here, in the worst case scenario, where the sloth is fully inverted, the work done, therefore, in a single breath (excluding elasticity effects of the lung [10,4] which would be additive) would



**Figure 2.** (a) Mean daily ventilation rate (breaths per minute) for one captive three-fingered sloth (*B. variegatus*) against mean daily ambient temperature (°C). Ventilation rate ( $N = 1032$ ) and ambient temperature ( $N = 1032$ ) taken at intervals of 4 h for a total of 172 continuous days. Points show means taken over 24 h. (b) Per cent of total time allocated to different degrees of body orientation in  $10^\circ$  bins for one wild (red bars) and six captive three-fingered sloths, *B. variegatus*. A body angle of  $-90^\circ$  corresponds to the animals hanging with their head pointing vertically downwards and  $90^\circ$  corresponds to the animals being fully upright.

be  $F \times \Delta L$ , where  $F$  is the force and  $\Delta L$  is equal to the change in length of the lung during ventilation.

Sloths store up to a third of their body weight in faeces and urine before voiding their contents [11], something they do

approximately weekly [12]. Thus, taking the mass of the abdominal contents to be 32% of body weight and assuming between 2 and 33% in assumed faecal and urine weight, we calculate this to equate to a necessary work done of between 0.13 and 0.24 joules per breath for a typical 4 kg three-fingered sloth [13], depending on whether the rectum and bladder are voided or not. At a ventilation rate of 27 breaths per minute, this is between 3.51 and 6.48 J min<sup>-1</sup>. Assuming a conversion ratio of physical to metabolic work done of 1 : 8.05, twice as efficient as humans [14], this translates to between 28.3 and 52.2 J min<sup>-1</sup>. The field metabolic rate of a three-fingered sloth is 588 kJ day<sup>-1</sup>, which converts to 408.3 J min<sup>-1</sup> [13], so we calculate that a fully inverted sloth would expend between 6.9 and 12.8% more energy than when upright were it not for the fibrinous adhesions. Given their extremely low metabolic rate, it may be that sloths would not have the metabolic power to move their abdominal contents as projected and thus find it impossible to breathe while hanging fully inverted were it not for the fibrinous adhesions. Over longer time periods, most sloths do not, however, appear to spend all their time fully inverted (figure 2b). Where sloths do not hang perfectly upside down, and assuming that sloths hanging at body angles of  $0^\circ$  or greater (head increasingly up—see figure 2b) experience no force from the abdominal contents, the abdominal contents would exert a force equivalent to  $M \times \sin \theta$ , where  $\theta$  is the angle of the horizontal inverted position ( $0^\circ$ ; see figure 2b) with a corresponding drop in energy savings per breath.

Our data on body angles of three-fingered sloths show that hanging at head-down body angles accounts for between 2 and 98% of their total time (mean of all animals = 20%) (figure 2b). The variance in this translates into individual energy invested in breathing values ranging between 0.01 and 8.6% (means of 0.8–1.5% depending on the weight of the digestive system) of their daily energy expenditure. Data from more, particularly wild, individuals would help put this into proper perspective. Nevertheless, given that the sloth is considered to have one of the lowest mass-specific metabolic rates of any mammal for its size [13,15,16], we suggest that the simple addition of the fibrinous adhesions may prove important in allowing them to hang fully inverted to access food from difficult sites while incurring no extra power, or overall energetic, costs stemming from the considerable weight of their internal organs. Advantages in not having adhesions and suspended abdominal organs, as is the norm in other mammals, may include greater body flexibility in that area, so the slow movement of sloths with perhaps limited abdominal flexibility may be a consequence and restriction to its unique lifestyle.

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