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Biomechanics

Gripping during climbing of arboreal snakes may be safe but not economical

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On the steep surfaces that are common in arboreal environments, many types of animals without claws or adhesive structures must use muscular force to generate sufficient normal force to prevent slipping and climb successfully. Unlike many limbed arboreal animals that have discrete gripping regions on the feet, the elongate bodies of snakes allow for considerable modulation of both the size and orientation of the gripping region. We quantified the gripping forces of snakes climbing a vertical cylinder to determine the extent to which their force production favoured economy or safety. Our sample included four boid species and one colubrid. Nearly all of the gripping forces that we observed for each snake exceeded our estimate of the minimum required, and snakes commonly produced more than three times the normal force required to support their body weight. This suggests that a large safety factor to avoid slipping and falling is more important than locomotor economy.

1. Introduction

The steep cylindrical surfaces in arboreal habitats pose many functional challenges to animal locomotion. For example, climbing requires continually lifting the entire body weight, which is energetically costly compared with horizontal locomotion [1]. Climbing animals also must prevent downward slipping, which often involves: (i) using claws (generalized lizards and mammals), (ii) adhering to surfaces (geckoes, anole lizards and tree frogs) or (iii) using muscles to generate a normal force sufficient for gripping via friction (primates and snakes) [2]. Although diverse arboreal animals use frictional grips, the normal forces used to support the entire body weight during vertical climbing are unknown. Nearly the entire elongate body of snakes can be used to grip. Hence, snakes seem well suited for gripping a wide variety of branch diameters assuming they can generate sufficient force.

Phylogenetically diverse species of snakes are arboreal [3,4], and they often climb steep cylindrical surfaces using a type of concertina locomotion, which involves periodic static gripping [5]. Similarly, concertina locomotion in tunnels involves applying normal force to surfaces to avoid slipping, and large changes in momentum arise from stopping periodically, both of which contribute to an energetic cost several times higher than that of both lateral undulation and limbed locomotion [6]. Some snakes that can perform arboreal concertina locomotion nonetheless may perform a locomotor mode (lateral undulation) without static gripping when they are on horizontal cylinders or on cylinders with pegs, and this may reflect better energetic economy [5,7]. Some gait changes of limbed animals provide additional precedents for expecting an important role of energetic economy in determining modes of locomotion [8].

Climbing arboreal snakes likely encounter trade-offs between economy and the safety afforded by a strong grip. Hence, we quantified the gripping forces of climbing snakes to determine how frequently they gripped the substrate with safety factors [9,10] that indicated forces exceeded the minimum required to prevent slipping. Unlike passive adhering mechanisms, which could require little metabolic cost to prevent slipping, frictional gripping requires substantial

Table 1. Morphological and biomechanical variables of individual snakes. L is total length, μ_s is the coefficient of static friction for the snake on the grip tape and n is sample size.

| species | mass (g) | L (cm) | μ_s | F_{req} (N) | observed normal force, F_{obs} | | | | | |
					n	mean (N)	s.d. (N)	max (N)	$>F_{req}$ (%)	$>3F_{req}$ (%)
B. constrictor	187	75	1.02	2.09	1477	11.02	5.71	30.2	96	76
B. constrictor	257	87	0.94	3.10	1031	17.05	7.35	46.2	100	89
B. constrictor	237	90	0.99	2.73	1035	12.80	5.83	34.6	99	75
M. nauta	64	80	1.35	0.54	490	1.53	1.67	9.3	81	30
M. nauta	47	75	1.49	0.36	734	0.78	0.65	3.2	76	24
M. spilota	191	110	1.04	2.10	1028	6.52	4.42	29.1	93	38
M. spilota	80	89	1.04	0.88	1452	1.66	0.89	7.9	82	15
M. viridis	155	90	1.04	1.63	717	5.93	4.23	28.6	97	43
B. irregularis	229	146	0.70	3.73	537	10.37	4.88	28.9	96	39
B. irregularis	258	152	0.74	3.97	1455	11.67	5.58	32.7	98	41

muscular effort and thus might exhibit smaller safety factors. In addition, some snakes have the ability to carefully modulate the pressure and duration of constriction in response to the heartbeat of the prey [11]. Therefore, to reduce the likely high overall cost of climbing, we expected that snakes might grip economically.

2. Material and methods

(a) Subjects and protocol

We analysed data from 10 cycles of locomotion for each of 10 snakes from five species, including four boids and one colubrid (table 1). The snakes climbed an instrumented vertical cylinder (length = 240 cm, diameter = 4.1 cm) covered with a textured tape (Tourna Gauze Grip Tape, Unique Sports Products, Alpharetta, GA, USA). The snakes were videotaped at 30 images s^{-1} using two cameras that were synchronized to each other and to the system described below that was used to record normal gripping forces.

(b) Force measurement

The 1×1 cm capacitance-based pressure sensors (Tact Array, Pressure Profile Systems, Los Angeles, CA, USA) were arranged in four lengthwise strips 1 cm wide by 128 cm long positioned at 90° intervals around the circumference of the cylinder. We calculated total observed normal force (F_{obs}) for each snake by summing the normal forces on all active sensors. Active sensors were those where pressure exceeded a threshold of 0.138 N cm^{-2}, thereby exceeding the background noise in the system.

(c) Estimation of the required normal forces

Estimating the total normal force required to prevent slipping (F_{req}) requires knowing: (i) the coefficient of friction of the surface and (ii) any added force related to accelerating the body upward against gravity (F_{acc}). Using the same methods as previous studies [5], we determined the coefficient of static friction, μ_s (table 1), of each snake on a flat board covered with the same tape and the same wrapping angle as the instrumented cylinder. We determined the single maximum vertical acceleration across all snakes from the position of kinematic markers on each snake. This maximum acceleration (1.56 m s^{-2}) times the total

mass of each snake was added to the weight of each snake to estimate the total downward slipping force (F_{slip}) and subsequently F_{req} ($=F_{slip} \mu_s^{-1}$). Hence, our estimates of F_{req} were probably high and resulting safety factors ($F_{obs} F_{req}^{-1}$) were probably underestimated because: (i) the entire snake does not accelerate simultaneously (figure 1) and (ii) the upward accelerations are probably less for the other snakes compared with that of the snake with the single greatest acceleration. Furthermore, values of F_{obs} are probably conservative because the pressure system sampled four discrete locations rather than the entire circumference of the perch. The electronic supplementary material provides a more detailed description of these methods and an analysis of force correcting for the spaces between sensors (F_{est}).

3. Results

All snakes climbed using concertina locomotion, and the boid species commonly, were able to support their weight using less of their body compared with the colubrid, *Boiga irregularis* (figure 1). The values of F_{obs} varied widely between species (table 1). Much of the variation in F_{obs} between both individuals and species was due to increased force associated with increased body mass ($R^2 = 0.80$; $p = 0.001$; figure 2a). Despite variation between species, all snakes had a mean value of F_{obs} (table 1) greater than required to avoid slipping (paired $t_9 = 3.71$; $p = 0.002$). Safety factors ($F_{obs}F_{req}^{-1}$) commonly exceeded three (table 1) and even five, when snakes were both moving and stationary (electronic supplementary material, figures S2 and S3). Forces corrected to include the spaces between sensors (F_{est}) were on average 65% higher than F_{obs}, resulting in even greater safety factors (electronic supplementary material, figures S4 and S5). An ANOVA (individuals nested within four species) revealed that the mean values of safety factor per cycle differed significantly among species, with *Boa constrictor* having higher values than all of the other species ($F_{3,5} = 25.2$, $p = 0.002$). This is intriguing because boa constrictors are viewed as less specialized for an arboreal existence than the other species in this study [4].

The instantaneous values of F_{obs} also varied considerably within trials as each snake gripped and extended (figures 1, 2b), but F_{obs} rarely dropped below F_{req} (figure 2b). For example,
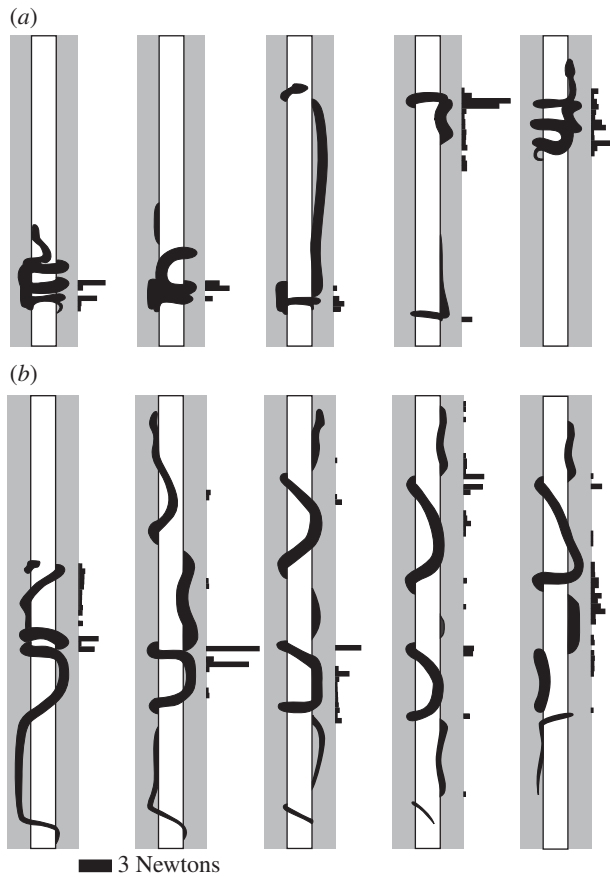
Figure 1. Longitudinal distribution of normal forces for one locomotor cycle for (*a*) *M. spilota* and (*b*) *B. irregularis*. Horizontal bars indicate the total normal forces from four sensors at each longitudinal location. The time intervals between successive images in (*a*) and (*b*) are 1.4 and 1.8 s, respectively.

the cumulative frequency distribution of F_{obs} for the 10 cycles of locomotion of one *Morelia spilota* (figure 2*c*) shows that this snake gripped with $F_{obs} > F_{req}$ in 93% of the samples. High percentages of excessive values of F_{obs} also occurred in all of the other snakes (table 1; electronic supplement material, figures S2 and S3). The three smallest snakes accounted for 72% of the samples in which $F_{obs} < F_{req}$ and had more samples in which F_{obs} was zero, suggesting that occasionally the gripping pressures at all sensors were within the noise threshold of the system.

4. Discussion

Although many species of snakes commonly climb steep cylindrical surfaces, our data are the first to quantify the associated gripping forces. All of the snakes that we observed climbed using concertina locomotion, often with F_{obs} much greater than F_{req}, despite a likely high energetic cost of climbing using concertina locomotion. Recent work with snakes climbing in channels inclined up to 60° found a similar surplus of friction-generating lateral forces [12]. For snakes with similar size, most of the gripping pressures that we observed were lower than those used while constricting prey [13], but the peak pressures we observed resembled those reported for constriction. Thus, the snakes in our study used neither an amount of force consistently near the minimum required nor consistently near their likely maximum as suggested by values reported for constriction.
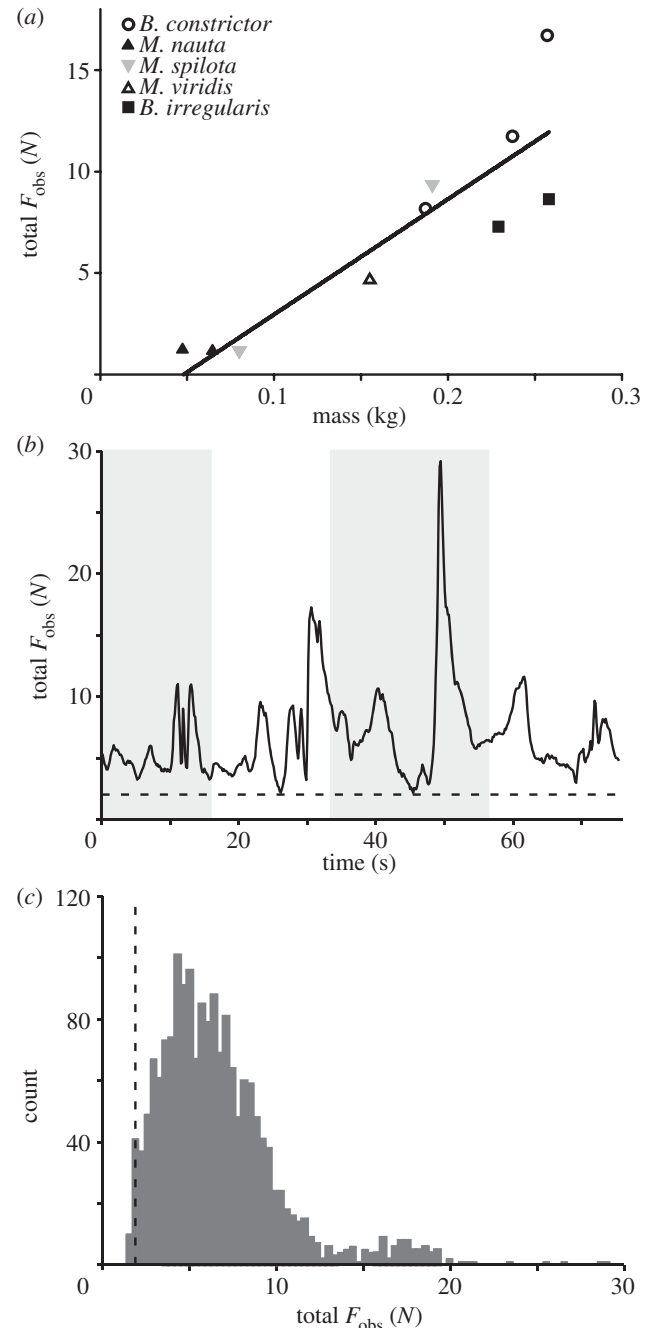
Figure 2. Total observed normal force, F_{obs}. (*a*) With increased body mass, F_{obs} increased significantly. (*b*) Values of F_{obs} versus time for one trial with four locomotor cycles (denoted alternately by grey and white) of *M. spilota* (191 g). One cycle is the time between successive initiations of static contact for a single point on the snake. (*c*) Frequency distribution of F_{obs} for 10 locomotor cycles of *M. spilota*. The dashed lines indicate F_{req}.

The ability to carefully modulate the pressure used to constrict prey [11] suggests that snakes can also modulate force production in other situations. Assuming this is so, then why do snakes apply so much surplus force during climbing, which seems likely to be demanding even without excess force production? One possibility is simply that there is little cost for doing so. Perhaps, climbing is so infrequent that it adds little to the overall energy budget of snakes despite the high transient demands. For example, to gain sufficient height to glide, some mammals engage in energetically costly climbing, but its cumulative cost is low due to the short duration of climbing bouts [14]. Similarly, arboreal snakes often move little each day or remain in the same location for several

consecutive days [15]. Even if the energetic cost of an activity exceeds the aerobic scope of an animal, this may be of little consequence because many squamate reptiles including snakes regularly have brief bursts of locomotion that greatly exceed what is aerobically sustainable [6].

Although excessive gripping force during climbing possibly has little overall cost, this behaviour may have a substantial benefit. Namely, if the consequences of failure are high, it may be beneficial for climbing snakes to use a large safety factor for gripping. No data are available for gripping to support the entire body weight in any other taxa, but humans often grip vertically oriented objects with safety factors of two to four [16,17]. Owing to large adhesive forces, safety factors greater than 10 occur for geckos and anoles, allowing some of these animals to support their entire body weight with just a single toe [18,19]. Similarly, the boid snakes in our study were able to support their weight with a single gripping loop. During climbing, this redundancy could prevent catastrophic failures when one

gripping region loses static contact by having greater than required gripping forces with another region or structure. However, unlike lizards adhering with toepads, the gripping of climbing snakes could be fundamentally different in that it requires substantial muscular force. Hence, despite diverse mechanisms for preventing slipping and a wide variety of body plans in arboreal animals, large safety factors to prevent falling may be the rule rather than the exception.

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