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ORIGINAL RESEARCH

Sexual dimorphism in bite force performance and cheliceral muscle morphology in a wandering spider (Araneae, Ctenidae)

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Abstract

Bite force is a key performance trait in many animal taxa, directly influencing ecological and behavioral interactions such as predation, defense, and mating. In spiders, this trait could be modulated by both morphological and environmental factors, yet few studies have measured it directly. Here, we provide the first *in vivo* measurements of bite force in the wandering spider *Phoneutria depilata* and test the effects of sex, body size, diet, and predator-induced stress on bite force. We also investigate the volume and mechanical advantage of cheliceral muscles using μCT scans of male and female specimens. Our results show that females exhibit significantly higher bite forces than males, even after correcting for body size. This difference is primarily associated with sexual size dimorphism but is likely also influenced by the greater volume of specific adductor muscles (Anterior medial and Anterior medial outer). In contrast, neither dietary composition nor predator exposure had a significant impact on bite performance. These findings suggest that while environmental conditions may influence other traits, bite force in *P. depilata* is mainly determined by intrinsic morphological features. This study highlights the role of sexual dimorphism in shaping biomechanical traits and provides a basis for future research on functional performance in arachnids.

Introduction

Bite force is a crucial biomechanical trait in many animal species, playing a fundamental role in feeding, defense, and reproductive success. Across vertebrates and invertebrates, it has been linked to ecological specialization (Christiansen & Wroe, 2007), prey capture efficiency (García et al., 2022), and mating interactions (Adeola & Lailvaux, 2023). Among mammals, reptiles, birds, and arthropods, stronger bite forces have been associated with greater feeding versatility, allowing species to exploit a broader range of food items. It can play a significant role in intraspecific competition, where individuals with stronger bites have a competitive advantage in territorial and mating disputes (Adeola & Lailvaux, 2023; Christiansen & Wroe, 2007; Herrel et al., 2005; Law & Mehta, 2019; Taverne et al., 2020; Wroe et al., 2005).

Among invertebrates, spiders represent a particularly compelling model for studying bite force due to their ecological diversity and functional reliance on their chelicerae. In spiders, biting plays a central role in key ecological and behavioral processes such as prey capture, defense, and sexual interactions (Black et al., 2025; Schendel et al., 2019). These animals exhibit a wide range of predatory strategies, from reliance on venom and silk to more direct mechanical force via cheliceral bites (Foelix, 2011; González-Gómez et al., 2024; Sentenská et al., 2020; Valenzuela-Rojas et al., 2019; Zhang et al., 2024).

This ecological diversity appears to be mirrored in bite force capacity: free hunters have been suggested to possess higher estimated bite forces compared to web-builders, reflecting the importance of prey capture strategy in the evolution of force production (Black et al., 2025).

In many spider species, males and females differ markedly in morphology and behavior, including in venom composition, body size, and performance traits (González-Gómez et al., 2024; Haskell et al., 2001; Kuntner & Coddington, 2020; Sierra et al., 2023; Valenzuela-Rojas et al., 2019; Zobel-Thropp et al., 2017). In most cases, females are substantially larger than males, a difference commonly attributed to fecundity selection, where larger females gain higher reproductive output (Grossi & Canals, 2015; Huber, 2021). However, in some species, males possess longer or more developed chelicerae than females, a trait often linked to mating or prey capture strategies (Aisenberg et al., 2010; Costa-Schmidt & De Araújo, 2008; Walker & Rypstra, 2011). These pronounced size differences may have functional implications for traits such as bite force, where larger body and cheliceral dimensions could lead to a stronger bite force.

At the muscular level, bite force is determined by the physiology and architecture of the musculoskeletal system. Features such as muscle volume, moment arms, and pennation angles—particularly of the adductor muscles—directly influence force production (Holmes & Taylor, 2021; Penrose et al., 2020). In arthropods like ants, beetles, and scorpions, muscle architecture significantly affects both the magnitude and dynamics of bite force, in some cases revealing trade-offs between force and speed (Black et al., 2025; Goyens et al., 2014; Püffel et al., 2021; Simone et al., 2025; Simone & van der Meijden, 2018; Wood, 2020; Wood & Parkinson, 2019). However, in some ants and spiders, latch mechanisms exist that can enable power amplifiers that store elastic energy which then is released instantaneously (Aonuma et al., 2023; Divi et al., 2020; Kallal et al., 2021; Larabee et al., 2017).

Given the substantial sexual dimorphism, diverse hunting strategies, and ecological differences observed in males and females of *Phoneutria depilata*, this species represents a valuable model for exploring how morphology, performance, and environment interact to shape biomechanical traits such as bite force (González-Gómez et al., 2024; Sierra et al., 2023; Sierra Ramírez et al., 2021; Valenzuela-Rojas et al., 2019, 2020). Additionally, spiders offer an opportunity to investigate how external factors such as diet and stress influence phenotypic variation in performance-related traits.

Dietary composition and stress can alter physiological responses and behavior in various animals. In *Drosophila ananassae*, diet modulates stress tolerance, metabolic activity, and reproductive output (Sisodia et al., 2015). In scorpions, shifts in venom composition have been observed in response to repeated exposure to predators, but not to dietary changes (Gangur et al., 2017). In spiders, a forced diet shift did not lead to a plastic change in venom toxin expression (Sierra et al., 2023). Nevertheless, when animals are compelled to feed on rarely consumed prey, they may experience energetic limitations and a consequent decline in body condition. For example, Black widow spiders that consumed fence skinks, an abundant prey item in their urban habitats, showed low energetic gain, suggesting that despite its availability, this prey is not preferred due to its poor nutritional value (Wilder & Simpson, 2022). A reduced energetic intake can, in turn, compromise muscle performance and neuromuscular efficiency, ultimately limiting an individual's ability to perform demanding tasks. Animals in poor physical condition, whether due to stress or a suboptimal diet, may therefore exhibit reduced functional performance, such as weaker or slower biting, which could directly affect their ecological success. Similarly, to the effects of diet, in pufferfish, exposure to simulated predation stress significantly reduces bite force performance compared with individuals that did not experience such stress (Cull et al., 2015).

Despite increasing interest in the ecological and morphological determinants of bite force in spiders, to date, no studies have reported direct empirical measurements of this trait. Most studies to date have relied on anatomical proxies or modeling approaches (Black et al., 2025), leaving a gap in our understanding of real performance measurements. Here, we provide the first direct *in vivo* measurements of bite force in the spider *Phoneutria depilata* and examine how body size, sex, diet, and stress influence this performance trait. Particularly for intersexual comparisons, to infer determinants of differences in bite force performance with cheliceral morphology, we examined the internal cheliceral musculature using micro-computed tomography (μCT) and quantified the volumes of the principal extrinsic adductors acting at the paturon–carapace articulation. In addition, we note that the basal cheliceral articulation may not involve a discrete condyle and can include hydraulic contributions to motion; therefore, any basal "pivot" used below is an operational assumption for geometric consistency (Wood & Shultz, 2025). The overarching aim of this work is testing three main hypotheses: (1) bite force is positively correlated with body size due to increased muscle volume; (2) individuals fed with a vertebrate-based diet display stronger bite forces than those fed with smaller invertebrates. (3) Exposure to predator cues affects bite force, possibly due to stress-induced physiological alterations.

Materials and methods

Collection and maintenance of individuals

Adult individuals of *Phoneutria depilata* were collected in Oporapa, Huila, Colombia (N 2.0078, W 76.0067) and Ibagué, Tolima, Colombia (N 4.3133, W 75.0561). The collections were conducted through nocturnal sampling, using active search and manual collection methods. The collected spiders were transported to the Biology Laboratory at the University of Ibagué (Ibagué, Colombia) for housing and experimental setup. Each spider was housed individually in a plastic container with moistened cotton, under natural photoperiod conditions, 70% relative humidity, and a constant temperature of 25 ± 1°C, following the recommendations of Pekár (2004). For dietary and stress stimulus experiments, individuals were sorted by sex. All experiments were conducted under controlled temperature conditions (25 ± 1°C). After placement in the plastic containers, the spiders underwent a four-day acclimatization period before being randomly assigned to the experimental treatments.

Experimental treatments

Diet

Treatment 1 (T1): spiders ($n = 18$ ♀♀, 18 ♂♂) were subjected to a vertebrate-only diet consisting of *Hemidactylus frenatus*.
Treatment 2 (T2): spiders ($n = 18$ ♀♀, 18 ♂♂) were subjected to an invertebrate-only diet consisting of *Tenebrio molitor* larvae.
Treatment 3 (T3): spiders ($n = 17$ ♀♀, 19 ♂♂) were subjected to a mixed diet of *T. molitor* and *H. frenatus*.

Spiders in each treatment group were fed twice per week for 7 weeks. For individuals in the *T. molitor* diet group, the number of larvae provided was adjusted to match the approximate mass of an *H. frenatus* (~1.6 g). During the experiment, *T. molitor* was fed with oatmeal, while *H. frenatus* was fed *T. molitor*.

Stress stimuli terrariums

To assess the effect of stress, after the acclimatization period, spiders ($n = 31$ ♀♀, 22 ♂♂) were provided with *T. molitor* and water *ad libitum* for 1 week. Following this period, they were randomly assigned to one of two treatments: stress treatment (T4) or control treatment (T5). For both treatments, we designed an experimental arena using a plastic box (29 × 55 × 32 cm). The arena was divided into two compartments by an acrylic partition with multiple perforations (1 cm in diameter) to allow unrestricted airflow between the sections. To ensure continuous air circulation inside the arena, a fan was placed outside the setup, extracting air without directly touching the arena.

T4: Spiders ($n = 16$ ♀♀, 11 ♂♂) were exposed to a live vertebrate predator (a white *Rattus norvegicus*) once per day (5-min exposure per session), 4 days a week, for 4 weeks. The procedure involved:

(1) Randomizing the order in which spiders were exposed to the predator.
(2) Placing the spider in one section of the arena for a 4-min acclimatization period.
(3) Introducing the rat into the opposite section for an additional 4 min.

In all cases, spiders exhibited a defensive reaction upon the introduction of the rat into the terrarium.

T5: Spiders ($n = 15$ ♀♀, 11 ♂♂) underwent the same procedure as the stress treatment; however, instead of introducing a rat, a white paper—matching the rat's size and color—was placed in the opposite compartment. This control stimulus never elicited a defensive reaction from the spiders.

Body measurements

Each spider was photographed next to a millimeter-scale reference, and measurements were obtained using ImageJ software (Schneider et al., 2012). To determine overall spider size, prosoma width, prosoma length, chelicerae length, and chelicerae width were measured, combined, and projected on an isometric vector to calculate an isometric body size index (IsoSize) (Coelho et al., 2017; Kaliontzopoulou et al., 2010).

Bite force measurements

The *in vivo* bite force of *P. depilata* was measured for each treatment group. To assess the bite force, a force measurement device (model ENTFMSV1, manufactured by Entomopixel, for more information, see Appendix S2) was used. The device uses two load cells mounted in parallel with opposing bite plates. Prior to data collection, we calibrated the system with a set of known weights spanning the working range. This design allows the instantaneous comparison of the force on each plate. Vibrations caused by the experimenter or other unilateral forces can thus be discounted. Only forces where both plates measure an equal (within 10% of each other) and opposite forces are kept as valid bite forces, and we calculate the mean of both plate forces measured. During force measurements, spiders were placed inside a plastic funnel and gently guided forward until their chelicerae were exposed. To prevent injury, the spiders were immobilized with a cotton ball while remaining inside the funnel. Once the chelicerae were exposed, they were positioned against the force gauge plates to induce biting. To ensure accurate measurements and prevent false grips, the spiders were gently stimulated with a brush stroke between the chelicerae, which typically elicited a stronger biting response as they attempted to free themselves or bite at the brush. For all specimens, bite force was measured once per day for 5 consecutive days after the completion of the experimental treatments. For statistical analyses, only the maximum bite force recorded for each individual was used.

CT scanning and segmentation

Two specimens of *P. depilata* (one female and one male), preserved in 70% ethanol, were immersed in a 5% phosphomolybdic acid (PMA) solution for contrast enhancement and to improve the visualization of internal structures. To facilitate fluid penetration, small incisions were made in the prosoma, abdomen, and legs using an entomological pin. Subsequently, the prosoma of each spider was scanned using a Perkin Elmer Quantum FX µCT scanner at *Plateforme Imagerie du Vivant, Université Paris Cité*, with a voxel size of 20 µm.

Muscle segmentation and volume measurements for each specimen were performed using Avizo 8.0 (FEI Visualization Sciences Group, Hillsboro, OR, USA). Muscle volumes were obtained using the "Material Statistics" function in Avizo and corrected for body size using isometric scaling by extracting residuals from a linear model against the specimen IsoSize vector. Micro-CT scans revealed an area of increased keratinization at the antero-lateral basal area of the paturon, corresponding to the joints. Two landmarks were placed there to define the cheliceral axis of rotation and to extract 3D coordinates. For the purpose of estimating lever arms, we modeled the cheliceral base with an operational pivot at the sclerotized paturon–carapace interface. This point serves as a geometric reference only and should not be interpreted as a discrete condyle, consistent with the view that basal motion may be partly hydraulic (Wood & Shultz, 2025).

This axis of rotation allows each chelicera to rotate in a single plane, as verified in reference videos of a *Phoneutria* individual opening and closing its chelicerae. Additionally, two landmarks were placed at the lateral and medial joints of the fang to determine its axis of rotation. A final set of 3D coordinates was collected at the insertion points of the cheliceral muscles at the cheliceral base. These coordinates were used to calculate the mechanical advantage of each muscle.

The muscle in-lever was determined as the minimum normal distance between the 3D coordinates of each muscle's insertion point and the cheliceral rotation axis, using the *point-to-line distance* function (Rik, 2025) in MATLAB R2015a (The MathWorks Inc., Natick, MA, USA). The out-lever, identical for all muscles, was defined as the minimum normal distance between the chelicera and fang axes of rotation, calculated using MATLAB's *line-to-line distance* function (Douillet, 2025). The ratio of the in-lever to the out-lever was then used to determine the force mechanical advantage.

Statistical analysis

After testing for normality and homoscedasticity assumptions, a Multivariate Analysis of Variance (MANOVA) was performed to compare male and female body size, using chelicerae length, chelicerae width, prosoma length, and prosoma width as explanatory variables. Subsequently, independent ANOVAs were conducted to determine which specific variables contributed to the observed differences. To account for overall body size, an isometric projection was conducted to generate a composite size variable, incorporating prosoma width, prosoma length, chelicerae width, and chelicerae length (both chelicerae). Bite force was analyzed using a multiple regression, with spider IsoSize, sex, and treatment groups (diet and stress) as explanatory variables. Both bite force and size were $\log_{10}$-transformed. To account for differences in body size, we corrected bite force using residuals from a linear regression of $\log_{10}$-transformed bite force against $\log_{10}$-transformed IsoSize. This allowed us to isolate size-independent variation in bite force.

Results

Body size comparison

The MANOVA revealed a significant effect of sex on body size variables (Pillai's Trace = 0.549, $F_{4,79} = 24.06$, $P < 0.001$), indicating that males and females exhibit significant differences in prosoma length, prosoma width, chelicerae length, and chelicerae width. Since the MANOVA was significant, we conducted univariate ANOVAs to determine which specific variables contributed to the overall effect. These results confirm that sexual dimorphism in *P. depilata* is present, with females exhibiting larger prosoma and chelicerae dimensions than males (Table 1).

Table 1 Univariate ANOVA results for body size variables

Variable	Male $\overline{X} \pm$ SD	Female $\overline{X} \pm$ SD	F	df	P-value
Prosoma length	12.74 ± 1.61	13.94 ± 1.76	10.52	1.82	0.0017
Prosoma width	10.78 ± 1.17	11.66 ± 1.13	12.18	1.82	0.0008
Chelicerae length	5.30 ± 0.70	6.22 ± 0.73	33.72	1.82	<0.0001
Chelicerae width	2.49 ± 0.27	3.21 ± 0.38	96.79	1.82	<0.0001

Morphometric variables are expressed in mm. $\overline{X} \pm$ SD stay respectively for mean and standard deviation.

Bite force

The linear model revealed a significant difference in bite force between sexes ($F_{1,78} = 62.5$, $P < 0.0001$), with females (mean ± SD: 0.94 ± 0.23 N) exhibiting a stronger bite force than males (0.60 ± 0.14 N). This difference remained significant even after correcting bite force for body size (Fig. 1). The spiders' body size has a significant effect on bite force ($F_{1,78} = 15$, $P = 0.0002$), with females being larger than males. In contrast, neither diet nor stress treatments significantly affected bite force (Diet: $F_{1,78} = 0.05$, $P = 0.95$; Stress: $F_{1,78} = 1.6$, $P = 0.21$).

CT scanning and segmentation

For each sex, we segmented 11 muscles: 9 associated with paturon movement and 2 with fang movement, following the color code and nomenclature proposed by Wood and Parkinson (2019). Additionally, one apodeme associated with fang movement was identified and segmented (Fig. 2). The absolute and isosize-corrected volumes of each muscle are summarized in Table 2.

In relation to bite force, we identified six adductor muscles (responsible for closing the chelicerae). In both sexes, adductors accounted for a larger proportion of the total cheliceral muscle volume (Table 3) and no pronounced differences in overall muscle volume were observed between sexes.

However, isosize-corrected volumes revealed that the female had slightly larger *Anterior Medial* and *Anterior Medial Outer* muscles, while the male exhibited a larger *Posterior Medial* muscle (Fig. 3).

The mechanical advantage (MA) for individual muscles ranged between 0.19 and 0.44. Although minor differences were observed between sexes, the mechanical advantage was overall comparable. For instance, the Posterior Medial muscle showed the highest MA in both sexes (0.41 in females and 0.44 in males), while the Lateral Anterior muscle exhibited the lowest (0.19 in females and 0.21 in males) (Table 4).

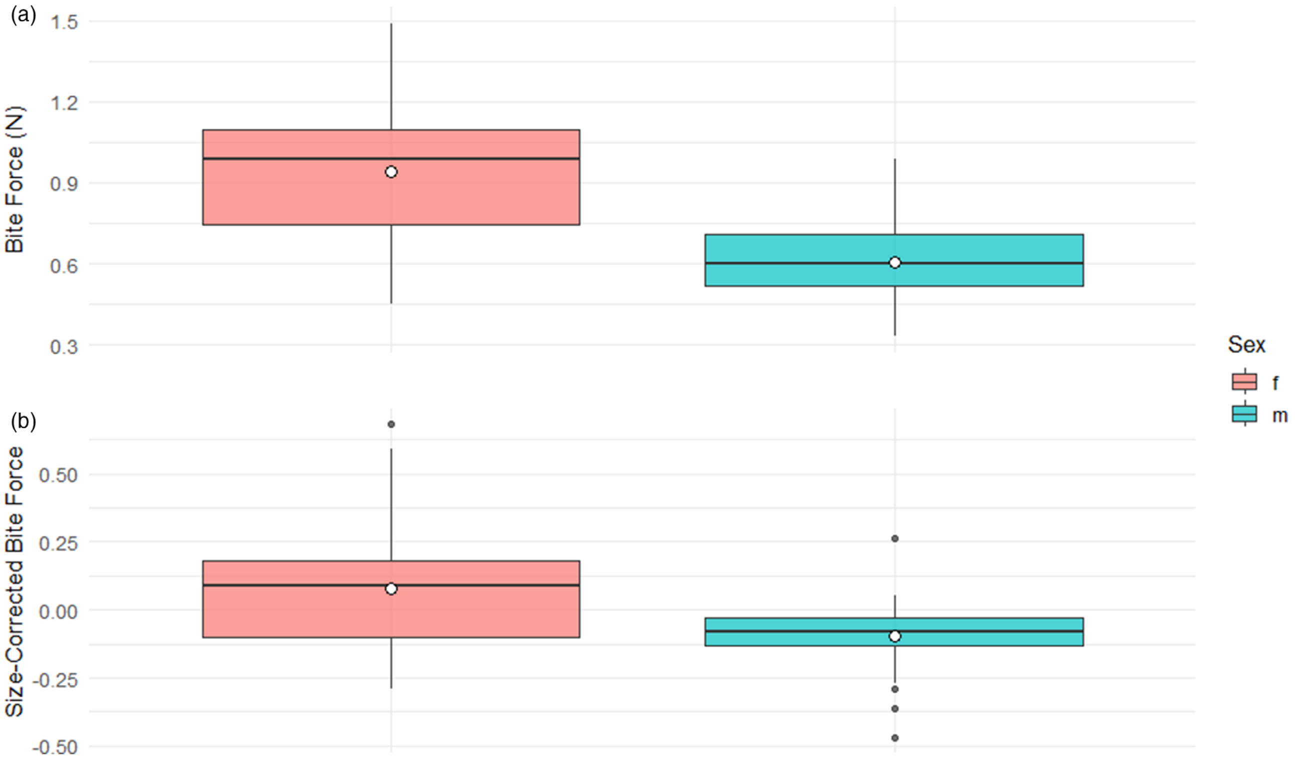

Figure 1 Comparison of the bite force between female and male *Phoneutria depilata*. (a) Raw bite force values between sexes. (b) Bite force after correction by size. White dots within the boxplots represent the mean bite force for each sex.

Discussion

In this study, we measured bite force and conducted CT scans of the prosoma in both male and female *Phoneutria depilata* to test three primary hypotheses: that sex-related differences in bite force can be attributed to (1) overall body size, muscle size, and mechanical advantage. Additionally, through controlled experiments, we tested whether two environmental factors —diet and predator-induced stress— could act as modulators of bite force performance (Hypotheses 2 and 3, respectively).

Our results indicate that bite force differences between sexes are primarily explained by size dimorphism, with some remarkable differences found in the size-corrected adductor muscle volumes across the two sexes. Furthermore, neither dietary changes nor predator-induced stress produced a measurable effect on bite force, suggesting that these environmental factors are unlikely to act as strong modulators of performance in *Phoneutria depilata*.

Sexual size dimorphism as a determinant of biting performance dimorphism in *Phoneutria depilata*

The larger prosoma and chelicerae dimensions observed in females confirm significant sexual size dimorphism (SSD), a common pattern across spider taxa where females are typically larger than males (Foellmer & Moya-Laraño, 2007; Grossi & Canals, 2015; Huber, 2021; Kuntner & Coddington, 2020). Since body size strongly influences biomechanical performance through increased muscle mass and muscle physiological cross-sectional area (PCSA), larger individuals generally exert greater force (Antón, 1999; van der Meijden et al., 2010). Similar patterns have been documented in other arthropods like ants and stag beetles, where bite force increases with size due to corresponding changes in muscle volume and leverage (Püffel et al., 2021, 2023).

In *P. depilata*, females exhibited significantly higher bite force than males, and this difference persisted even after correcting for body size, suggesting that traits other than overall size may contribute to the observed performance dimorphism. Relative muscle volumes were generally similar between sexes, and mechanical advantage (MA) values across all adductor muscles showed minimal variation. These findings suggest that the primary mechanical architecture supporting bite force is conserved in both sexes. This is consistent with results from other arthropods such as *Periplaneta americana*, in which bite performance is predominantly influenced by muscle activation and overall mass, rather than fine-scale anatomical differences in lever geometry (Weihmann et al., 2015). However, it is important to note that the study on *P. americana* did not compare males and females, and thus the observed patterns in that species cannot be directly extrapolated to sexual dimorphism. In contrast, in stag beetles, sexually dimorphic closing performance is

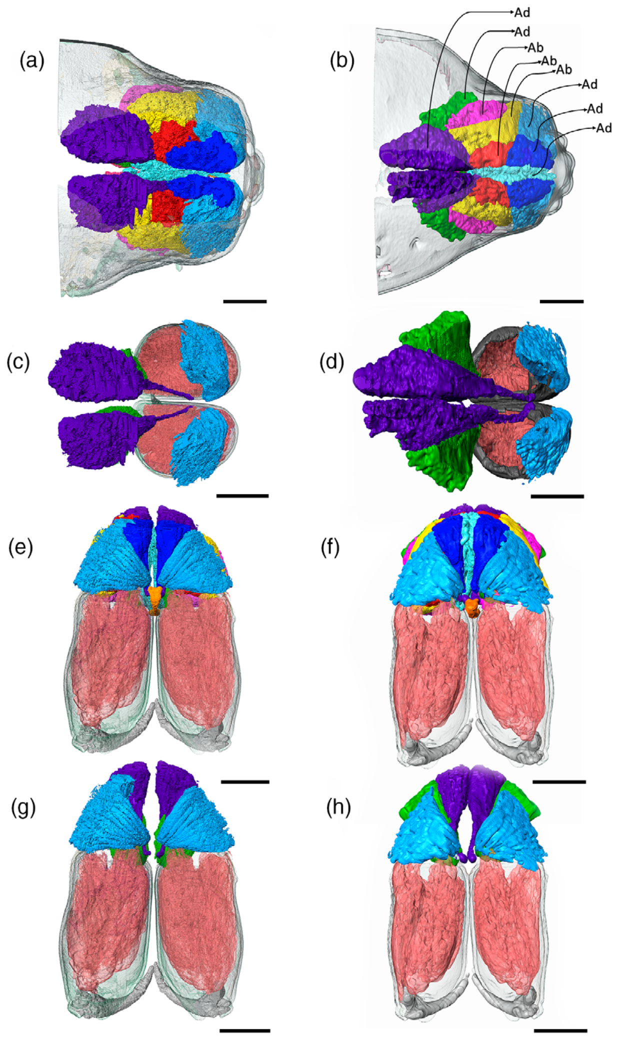

Figure 2 Representative µCT scan images showing the segmented cheliceral and fang muscles in *Phoneutria depilata*. Muscle color codes correspond to those listed in Table 2. (a) Dorsal view of all segmented muscles in the female specimen. (b) Dorsal view of all segmented muscles in the male specimen. (c) Dorsal view of the female showing the Anterior Medial (purple), Anterior Medial Outer (light blue), and Posterior Medial (green) muscles. (d) Dorsal view of the male showing the Anterior Medial (purple), Anterior Medial Outer (light blue), and Posterior Medial (green) muscles. (e) Frontal view of all segmented muscles in the female specimen. (f) Frontal view of all segmented muscles in the male specimen. (g) Frontal view of the female showing the Anterior Medial (purple), Anterior Medial Outer (light blue), and Posterior Medial (green) muscles. (h) Frontal view of the male showing the Anterior Medial (purple), Anterior Medial Outer (light blue), and Posterior Medial (green) muscles. Scale bars = 2 mm in all panels. Arrows indicate muscle function: labels "Ad" denote adductors and labels "Ab" denote abductors.

observed, where the elongated out-levers in males are compensated by longer in-levers (Goyens et al., 2014).

It is particularly interesting to report that despite the broad similarity in muscle architecture, isosize-corrected data revealed that females possess notably larger *Anterior medial* and *Anterior medial outer* muscles in volume compared to males. These two muscles have been identified in other spider species as key contributors to cheliceral closure force (Kallal et al., 2021; Wood, 2020). The *Posterior medial* muscle, which contributes more to stabilization or modulation than to direct force generation, appeared slightly more developed in males. While these anatomical observations are based on one individual per sex, the observation suggests a potential mechanism underlying female-biased bite performance. We therefore hypothesize that the greater force observed in females may be driven not only by their larger overall body size but also by the enhanced development of these specific adductor muscles. These differences could reflect sex-specific ecological demands, such as the need for females to subdue larger prey or defend nests, although this remains to be tested. It is known that in *Phoneutria depilata*, males and females have a similar diet despite differences in body size (Sierra Ramírez et al., 2021; Valenzuela-Rojas et al., 2020).

A foraging niche separation between males and females may exist, potentially related to differences in the ontogeny or size of the prey consumed. Such differences are difficult to detect through metabarcoding analyses. However, field observations report that female spiders often capture prey ranging from 0.63 to 3.27 times their own body size (Valenzuela-Rojas et al., 2020). It is possible, however, that males may need to optimize other aspects of cheliceral functionality that are in contrast with the optimizing closing force. For instance, males might be under pressure to increase the angle of lateral extension of chelicerae to increase the success rates during male–male contests. Cheliceral display is an agonistic behavior that is frequently observed in preliminary phases of male–male aggressive behavior in salticids, desids (Jackson, 1982; Tedore & Johnsen, 2012; Walker & Holwell, 2018; Yu et al., 2024). In species using largely cheliceral display as male–male agonistic behavior, the paturon tends to be elongated and therefore not apt for exerting large forces.

The predominance of adductor muscle volume observed in both sexes likely reflects a general functional demand for strong cheliceral closure. In latch-mediated spring actuation (LaMSA) systems, elastic elements are typically loaded relatively slowly and released nearly instantaneously by a latch/trigger, producing ultrafast motion. Thus, ultrafast movements do not depend on rapid contraction by large 'opening' muscles per se (Aonuma et al., 2023; Divi et al., 2020; Kallal et al., 2021; Larabee et al., 2017). This adductor-dominant pattern has been documented across vertebrates and arthropods, where forceful but slower movements are favored for tasks such as prey capture and subjugation (Law, 2020; Püffel et al., 2021; Simone & van der Meijden, 2018). Our findings in *P. depilata* align with this pattern, as both sexes exhibited a higher relative volume of adductor muscles compared to abductors, suggesting that bite performance in this species is optimized for strength rather than speed.

Our bite-force measurements reflect the combined output of the extrinsic adductor muscles operating across the paturon–carapace articulation. Accordingly, the data do not allow us to determine which specific extrinsic adductors contribute most to

Table 2 Muscle names, color codes (following Wood & Parkinson, 2019), and muscle volume measurements in *P. depilata*

No.	Color	Name	Function	Average male volume (mm^3)	Average female volume (mm^3)	Isosize-corrected male	Isosize-corrected female
i	Yellow	Lateral anterior	Abductor	3.03	3.32	0.27	0.19
ii	Magenta	Lateral posterior	Abductor	1.75	3.13	0.03	0.16
iii	Red	Anterior outer	Abductor	1.91	2.19	0.07	0.01
iv	Green	Posterior medial	Adductor	3.25	2.94	0.30	0.13
v	Purple	Anterior medial	Adductor	1.92	4.07	0.07	0.28
vi	Blue	Anterior median inner	Adductor	1.83	2.43	0.05	0.05
vii	Light blue	Anterior median outer	Adductor	1.60	3.51	−0.01	0.21
viii	Aqua	Inter-cheliceral-sclerite muscle	Adductor	0.92	1.35	−0.25	−0.20
ix	Light orange	Endosternite muscle	Adductor	0.36	0.28	−0.65	−0.89
x	Pink	Fang apodeme		0.25	0.25	−0.81	−0.94
xi	Light yellow	Fang Extensor	Abductor	1.79	2.13	0.04	−0.01
xii	Light purple	Fang Flexor	Adductor	12.16	22.09	0.87	1.01

Averages represent the mean volume of both the right and left muscles.

Table 3 Relative volume of adductor and abductor muscles in *P. depilata*

No.	Color	Name	Function	Volume % male	Volume % female
i	Yellow	Lateral anterior	Abductor	40.35	37.20
ii	Magenta	Lateral posterior	Abductor		
iii	Red	Anterior outer	Abductor		
iv	Green	Posterior medial	Adductor	59.65	62.80
v	Purple	Anterior medial	Adductor		
vi	Blue	Anterior medial inner	Adductor		
vii	Light blue	Anterior medial outer	Adductor		
viii	Aqua	Inter-cheliceral-sclerite muscle	Adductor		
ix	Light orange	Endosternite muscle	Adductor		

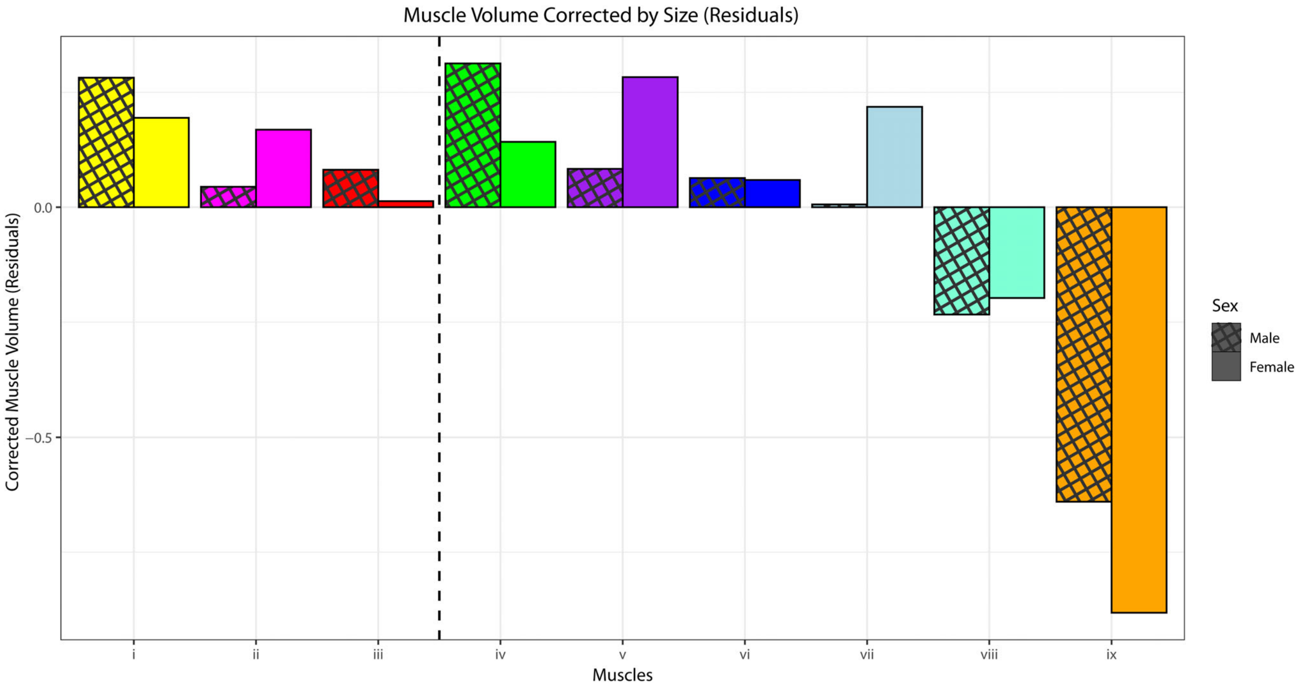

Figure 3 Isosize-corrected muscle volumes for individual adductor muscles, comparing male and female. Values represent the average volume of left and right muscles.

Table 4 In-lever, out-lever, and mechanical advantage (MA) values for each cheliceral adductor muscle in both sexes of *P. depilata*

Out-lever female (mm)	6.04			
Out-lever male (mm)	5.39			
Muscle	**In-lever female (mm)**	**In-lever male (mm)**	**MA female**	**MA male**
Posterior Medial	2.45	2.39	0.41	0.44
Lateral Posterior	2.60	2.31	0.43	0.43
Anterior Medial Inner	1.96	1.64	0.32	0.30
Anterior Medial Outer	2.04	1.59	0.34	0.30
Anterior Medial	1.83	1.51	0.30	0.28
Anterior Outer	1.54	1.44	0.26	0.27
Lateral Anterior	1.15	1.12	0.19	0.21

the measured forces, nor to estimate their relative contributions. We note that distal, fang-level muscles are not considered drivers of the compressive forces reported here, and our interpretation is restricted to the extrinsic adductors of the paturon.

Accordingly, our mechanical-advantage (MA) values at the paturon–carapace interface should be interpreted as comparative geometric indices rather than evidence for a discrete basal fulcrum: recent work suggests that basal cheliceral motion can lack a hard pivot and may involve hydraulic components, potentially allowing facultative lever configurations (Wood & Shultz, 2025).

Diet and stress are not modulators of biting performance in *Phoneutria depilata*

In contrast to body size and muscle volume, neither dietary nor stress treatments produced significant effects on bite force in *P. depilata*. This result could stem from two main factors. First, the duration of the experimental treatments—7 weeks for diet and 4 weeks for stress exposure—may have been insufficient to induce structural or physiological changes affecting bite force. Other studies have shown that phenotypic plasticity in traits such as muscle performance or venom composition often requires prolonged exposure or developmental modulation to manifest (Gangur et al., 2017; Sisodia et al., 2015). Thus, longer-term exposure may be required to reveal potential plasticity in bite performance in spiders. Second, it is possible that bite force represents a relatively canalized trait in this species, with low plasticity in response to short-term environmental change. While traits like venom composition can shift rapidly in response to ecological conditions, biomechanical traits rooted in musculoskeletal architecture may be less plastic.

Conclusions

Altogether, our results suggest that the greater bite force observed in female *P. depilata* is primarily driven by larger body size, but potentially augmented by increased volume in specific adductor muscles such as the *Anterior medial* and *Anterior medial outer*. Although the current sample size for muscle volume measurements precludes definitive conclusions, these anatomical differences present a compelling hypothesis that warrants further exploration. Future studies including larger sample sizes and ontogenetic data could help clarify the extent and origin of sex-based differences in bite performance, and whether they arise from ecological, behavioral, or developmental pressures.

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Author contributions

Conceptualization, J.C.G.-G., A.v.d.M., A.H., G.G., L.M.F.P.; Methodology, J.C.G-G., G.G., L.M.F.P., A.v.d.M., A.H. and Y.S.; Software, J.C.G.-G., A.v.d.M., A.H., and Y.S.; Formal analysis, J.C.G-G., A.v.d.M.; Data curation, A.v.d.M., J.C.G.-G.; Writing—original draft, J.C.G-G., A.v.d.M and Y.S.; Writing—review & editing, J.C.G.-G.; Supervision, A.v.d.M., G.G., L.M.F.P.; Project administration, L.M.F.P.; Funding acquisition, L.M.F.P. All authors have read and agreed to the published version of the manuscript.

Conflict of interest

All authors declare no competing interests.

Data availability statement

All data are available in Appendix S1.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Complete dataset including spider body and chelicerae measurements, bite forces, muscle volumes, and values used to calculate mechanical advantage.

Appendix S2. Technical datasheet of the ENTFMSV1 bite-force device (Entomopixel), including specifications, components, calibration procedure, and usage instructions.