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ORIGINAL PAPER

Function predicts the allometry of contest-related traits, but not sexual or male dimorphism in the amazonian tusked harvestman

Alexandre V. Palaoro[1,2] · Solimary García-Hernández[2] · Bruno A. Buzatto[3,4] · Glauco Machado[5]

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Abstract
Animal contests involve threatening displays and physical coercion, which are respectively performed by threat devices used in mutual evaluation of size or strength, and weapons used for grasping, stabbing, striking, or dislodging a rival. According to the functional allometry hypothesis, directional selection consistently favors hyper-allometry in threat devices, whereas the allometry of weapons depends on the way they are used in contests. Here, we tested this hypothesis using the Amazonian tusked harvestman *Phareicranaus manauara* (Arachnida: Opiliones), a male-dimorphic species, as a study system. Behavioral observations allowed us to recognize four contest-related traits and three control traits, not used in contests. Two weapons used to grasp or prod the opponents from afar and one threat device were hyper-allometric, whereas one tactile signaling device (used to tap the opponent) and all control traits were either iso- or hypo-allometric. These findings support the hypothesis that function predicts the allometry of contest-related traits. However, function does not explain allometric differences in homologous traits between males and females (whose traits also were used as controls). We suggest that if a trait used in contests by males is used by both sexes in another context, natural selection and cross-sexual genetic correlations may constrain its developmental trajectory, preventing the evolution of sexual dimorphism in allometric slopes. Therefore, using female traits as controls for homologous contest-related male traits may not be appropriate. Finally, we show that function does not explain differences between male morphs in the allometric slopes of male-dimorphic traits. Thus, an important next step in allometric studies is to understand what factors affect the slopes of male-dimorphic traits.

Keywords Alternative reproductive tactics · Intrasexual dimorphism · Male-male contests · Threat device · Weapon

Extended author information available on the last page of the article

Introduction

Animal contests typically begin with threatening displays, which are ritualized signals used to indicate that attack or aggression may follow. These threatening displays usually convey information about individuals' size, strength, or fighting ability, which can then be used by opponents to decide to give up before escalating (Eberhard et al. 2018). If the contest is not resolved in this first phase, it may escalate to a second phase involving physical coercion between rivals (Hardy and Briffa 2013). The morphological traits involved in these two phases may be the same (e.g., claws in fiddler crabs and crayfish), but in many species they differ. In these cases, whereas threatening displays are performed by *threat devices* used in mutual evaluation of size or strength, *weapons* are used to perform numerous functions related to physical coercion, such as grasping, stabbing, striking, dislodging, or lifting a rival from the substrate (Eberhard et al. 2018). In the fish *Nannacara anomala* (Cichlidae), for instance, males use their fins to threaten rivals in the beginning of the contest, and then use their mouths to bite the rival when the contest escalates to physical coercion (Jakobsson et al. 1979). In a similar way, males of the flower beetle *Dicronocephalus wallichii bourgoini* (Scarabaeidae) use their elongated first pair of legs to threaten rivals in the beginning of the contest, and then use their horns to flip away the rival when the contest escalates to physical coercion (Kojima and Lin 2017).

Considering that the function of threat devices and weapons is markedly different, these two types of traits are likely under different selective pressures. Based on this assumption, Eberhard et al. (2018) proposed the hypothesis that directional selection on threat devices used mainly or exclusively to communicate male body size should lead to hyper-allometry, which means that larger males would have disproportionately larger threat devices than smaller males. According to the authors, this pattern occurs because larger males tend to engage in fights more often and threat devices are used to avoid risky and unwinnable fights with larger and potentially stronger rivals. Weapons, in turn, do not necessarily need to be big; instead, they need to be functional in making rivals withdraw from a contest (Palaoro et al. 2020). Because not all possible functions of weapons are expected to select for hyper-allometry, there are cases of weapons showing isometry (i.e., the trait has the same proportional size in large and small males) and even hypo-allometry (i.e., the trait is disproportionately smaller in larger than in smaller males) (examples in Bonduriansky 2007a). Although comparative (Eberhard et al. 2018) and single-species studies (Bertram et al. 2021) provide support for the so-called functional allometry hypothesis, it is important to stress that it is centered exclusively on adaptive mechanisms that shape the allometric slopes of sexually-selected traits, and possible cross-trait or cross-sex genetic correlations that can constrain the evolution of these allometric slopes have not been considered (see discussion in Cheverud 1984 and Badyaev 2002). Thus, studies including a large set of traits expressed both in males and females of the same species may shed light on possible limitations of the functional allometry hypothesis.

Developing disproportionally large traits — threat devices or weapons — may be costly and not all males can afford it (e.g., Cotton et al. 2004; Bonduriansky 2007b). At least among arthropods, the expression of exaggerated traits is usually condition dependent, as only males that have access to abundant food resources during development are able to pay the costs of growing these traits (reviewed in Emlen and Nijhout 2000). For instance, well-fed larvae of *Onthophagus* dung beetles develop into large, long-horned adults, whereas

poorly fed larvae develop into small, short-horned or even hornless males (Emlen 1994). As a result of these two developmental trajectories, there is a bimodal distribution of horn length among males of the same species (Eberhard 1982), leading to a pattern known as *intrasexual dimorphism* or simply *male dimorphism* (Gadgil 1972). In many insect species with male dimorphism, large males with exaggerated threat devices or weapons (hereafter 'majors') exhibit a dominant mating tactic based on guarding females or defending resources (examples in Brockmann 2008 and Buzatto et al. 2014a). In turn, small males with poorly developed threat devices or weapons (hereafter 'minors') usually exhibit an alternative mating tactic based on sneaking copulations, acting as satellites, or even mimicking females to invade harems or territories guarded by majors (Brockmann 2008; Buzatto et al. 2014a). Thus, given that the body size achieved during immature stages triggers adult morph expression, it affects the mating tactic that will maximize fitness (Eberhard 1982; Gross 1996).

The mechanisms underlying differences between male morphs in the allometric slopes of contest-related traits have been poorly explored in the literature, and no clear pattern exists among terrestrial arthropods. In the case of some male-dimorphic earwig species, for instance, the allometric slope of the forceps is steeper in majors than in minors (e.g., Tomkins and Simmons 1996; Forslund 2003). However, other species of insects and arachnids show either no difference in the allometric slopes between morphs, or minors have a steeper slope than majors (e.g., Buzatto et al. 2011; McCullough et al. 2015; Songvorawit et al. 2017; Goczał et al. 2019; Chen et al. 2020). The functional allometry hypothesis does not make any specific prediction on differences between majors and minors in the allometric slopes of contest-related traits. However, it is possible that the way males of each morph use these traits during contests could explain possible differences in their allometric slopes. Given that minors rely on a wide variety of reproductive tactics that rarely involve contests, the allometric slopes of contest-related traits (particularly threat devices) should be steeper in majors than minors.

Our main goal in this study was to test the functional allometry hypothesis, according to which directional selection consistently favors hyper-allometry in threat devices, whereas the allometry of weapons depends on their function, i.e., the way they are used in contests (Eberhard et al. 2018). The study species was the Amazonian tusked harvestman *Phareicranaus manauara* (Arachnida: Opiliones: Cranaidae), in which males fight each other for the possession of natural cavities used by females as oviposition sites (see 'Study species' below and also the video in Supplementary Material S1). As many other harvestmen (reviewed in Buzatto and Machado 2014), *P. manauara* males show great intraspecific variation in multiple contest-related traits, and this variation is associated with the existence of male dimorphism in some of these traits (see 'Results' below). Thus, the species offers the opportunity to explore the allometry of contest-related traits in a male-dimorphic species. To do that, we first provide a behavioral description of contests, focusing on how several traits are used by males in each phase of these contests. Based on this description, we identified the function of each trait, including "control" traits, i.e., traits that are not directly used in the contest (e.g., Willemart et al. 2009; Solano-Brenes et al. 2018; Graham et al. 2020; Bertram et al. 2021). Then, we measured all contest-related and control traits in both males and females. Given that females do not fight but have almost all traits found in males, the allometric slopes of these traits in females should also be regarded as controls (e.g., Eberhard et al. 2018; Solano-Brenes et al. 2018; Bertram et al. 2021). Second, we compared the slopes

of all traits with those predicted by the functional allometry hypothesis. Finally, we searched for male dimorphism in all contest-related and control traits and calculated the allometric slopes of all male-dimorphic traits to compare majors and minors.

Materials and methods

Study Species

Phareicranaus manauara is a large harvestman, with total body length ranging from 10 to 12 mm (Pinto-da-Rocha 1994). Individuals are strictly active at night, when they are found mostly on fallen logs, tree trunks, and on vegetation up to 2 m high. The reproductive season in Central Amazonia occurs during the rainy period, which lasts from November to June. Large males (majors) defend natural cavities on fallen logs and tree trunks that are visited by ovigerous females. After copulation, females lay eggs inside the natural cavities and care for the eggs and early hatched nymphs (Colmenares and Tourinho 2014; also see video in Supplementary Material S1). The entire period of maternal care may last more than 1.5 months, during which females do not leave their clutches to forage. Males play no role in offspring protection and do not feed the females while they are caring for the offspring.

Whereas some major males in small cavities guard only one female, other males in large cavities can guard as many as nine. Males fight for the possession of these cavities, and the contests may last from a few seconds to almost half an hour. Small males (minors) are usually found in the periphery of the cavities defended by majors. These minor males are constantly invading the cavities and sneaking copulations with the females, which can either accept or reject their mating attempts. As occurs with other harvestman species (e.g., Buzatto et al. 2011), *P. manauara* females do not lay all their eggs immediately after copulation with the territory owner (major). Instead, they retain some unfertilized eggs in their reproductive tract, and these eggs are the target of the sneak copulations performed by the minors.

As many other species of the genus *Phareicranaus* (Pinto-da-Rocha and Kury 2003), there is marked sexual dimorphism in the presence of a structure we call *tusk*, which consists of a ventral pair of long and blunt apophyses on the posterior part of the males' body. Tusks are completely absent in females (Fig. 1 A). Among males, the length of the tusks shows tremendous variation, with some majors bearing tusks almost as long as their body length (Fig. 1B) and minors bearing only a small tubercle (Fig. 1 C). Tusks seem to be used only in male-male contests because both field and laboratory observations indicate this trait plays no role during male-female sexual interactions and also in other activities such as grooming, foraging, and locomotion (see video in Supplementary Material S1).

Collection of individuals

We collected males and females of *P. manauara* at Adolpho Ducke Forest Reserve (02°53′S, 59°59′W), an area of 100 km^2 located close to the city of Manaus, state of Amazonas, northern Brazil. The vegetation in the reserve is a pristine *terra firme* rainforest, where the climate is warm and wet, with mean annual temperature of 26 °C and mean annual rainfall

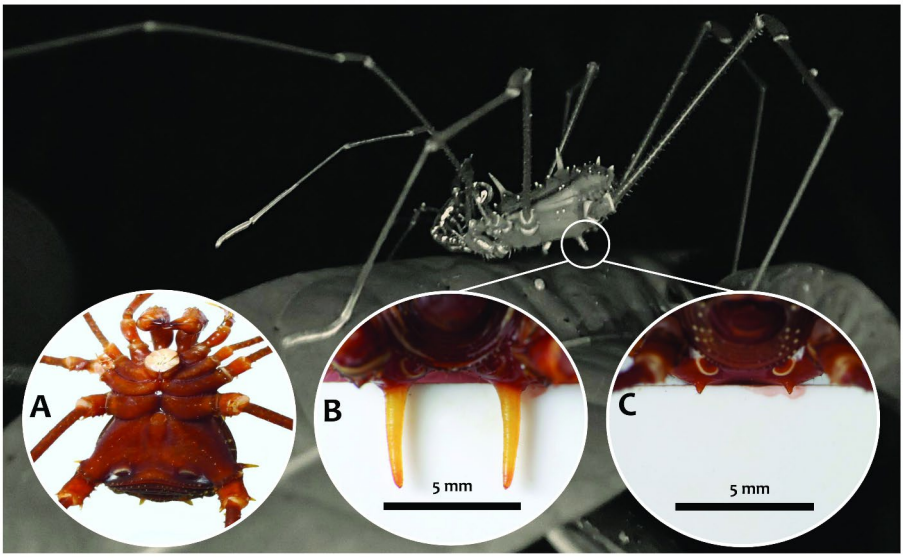

Fig. 1 Sexual and intrasexual dimorphism in the Amazonian tusked harvestman *Phareicranaus manauara*. (A) Ventral view of a female. (B–C) Posterior view of the venter of a (B) major male showing enlarged tusks and a (C) minor male showing poorly developed tusks

of nearly 2,400 mm. Rainfall is concentrated between November and June, with the peak of precipitation between March and April (Marques Filho et al. 1981). We visited the reserve in November 2016 and December 2017 (i.e., the beginning of the rainy period), totaling 10 days of fieldwork. In both trips combined, we collected a total of 136 individuals (72 males and 64 females), which were found active at night (between 18:00 and 00:00 h).

Behavioral observations

In our second field trip, we observed two male-male contests (one complete and another partial) under natural conditions. One contest occurred on a tree trunk and the other on a fallen log with a large natural cavity, inside which there was a harem with nine egg-tending females. In both cases, we followed the individuals, gathering information on the fighting behavior and, whenever possible, recording the contest using a digital camera (Olympus TG-4). In this second field trip, we also collected 30 adult males and 10 adult females that we brought alive to our laboratory at Universidade de São Paulo, São Paulo, Brazil. After we photographed all individuals (see below), males and females were individually maintained inside a plastic container (500 ml) with a wet layer of *Sphagnum* moss to provide moisture. We fed the individuals once per week with pieces of dead crickets (*Acheta* sp.).

After a period of three weeks of acclimation in the laboratory, we prepared 10 terraria (base: 25 × 50 cm; height: 20 cm) containing a wet layer of *Sphagnum* moss to provide moisture and a piece of bark (ca. 20 × 40 cm) to provide a diurnal shelter and a suitable substrate for male-male contests. In each terrarium, we randomly placed one female and one major male (hereafter ‘resident’), which is the morph that exhibits the territorial mating tactic (see

'Study Species' above). After two weeks, we randomly selected 10 males (either major or minor; hereafter 'intruder') and placed each of them inside a terrarium containing a resident pair. We then filmed any agonistic interaction between the intruder and the resident with a video camera (Sony Handycam HDR-CX405 or Canon T6i). If males did not engage in a contest for the 30 minutes after the first contact between them, we replaced the intruder with another randomly selected male to maximize our chances of observing contests. We kept the terraria in a room under a 12:12 h light:dark cycle and with minimal temperature variation (24.5–26.5°C). The observations were always performed during the first six hours of the dark phase, under dim red illumination to avoid disturbing the individuals. We used the behavioral data to describe male-male contests and to identify how males use different traits in each phase of the contests. Due to the qualitative nature of our observations, we did not perform statistical tests on the behavioral observations.

Male morph discrimination and static allometries

We gathered morphological data from three sources. First, we measured 96 individuals collected in the field and immediately preserved in 70% ethanol. Second, we measured the 40 individuals used in the behavioral observations. Third, we measured 89 individuals from the Entomological Collection of the Instituto Nacional de Pesquisas da Amazônia (INPA; Catalogue codes: INPA-OP 2452; 2458–2460, 2471–2475, 2480–90, 2859, and 2957), Manaus, Amazonas, Brazil. The total sample size was 125 adult males and 100 adult females. We photographed all individuals in dorsal and lateral view using a digital camera (CANON T6i). Then, we used the software *ImageJ* (Schneider et al. 2012) to measure the following traits (see Fig. S1A in Supplementary Material S2): (1) dorsal scute (i.e., carapace) length; (2) interocular distance; (3) femur length of all four right legs (hereafter 'legs I to IV') and right pedipalp; (4) length of the apophysis on the coxa of the right leg IV (hereafter 'coxa IV apophysis'); and (5) tusk length. We measured both the right and left tusks and used the measure of the longest one because tusks can be damaged at the tips, and we wanted to ensure we were analyzing the original full size of the structure.

We investigated male dimorphism in all traits we measured. To do so, we first inspected the distributions for bimodality using nonparametric kernel density curves. Second, we parameterized the distributions as mixtures of two skew-normal distributions or as a single skew-normal distribution with the package *mixsmsn* (Prates et al. 2013) for R version 3.6.1 (R Core Team 2019). We compared the fit of one distribution to the fit of a mixture of two distributions via their bias-corrected Akaike information criterion (AIC_c). Models describing one skew-normal distribution have three parameters (mean, variance, and skewness), whereas models describing two skew-normal distributions have seven parameters (two means, two variances, two skewness parameters, and the proportion of males in each distribution) (Prates et al. 2013). This approach to detect polymorphisms is well established and has been used before with insects (Rowland and Qualls 2005; Rowland and Emlen 2009; Kelly and Adams 2010) and harvestmen (Buzatto et al. 2014b; Painting et al. 2015; Solano-Brenes et al. 2018). Some of these studies used normal or gamma distributions instead of the skew normal distributions we used, but the advantage of the latter is that it can accommodate skew in any direction for males of either morph. Finally, if the best fit was a mixture of two distributions, we assigned individuals to either major or minor

morphs based on the probability of these males to belong to either morph. Some males, however, did not belong to either morph (based on an 80% probability threshold calculated by the mixture model). We classified these males (3.6% for tusk length and 7.1% for femur I length) as ambiguous and did not use them in further allometric analyses (following Pike et al. 2017). If the best fit was found in a model with one distribution, we considered the trait monomorphic.

After assigning males to their morphs, we calculated the static allometry of each trait (regressed on dorsal scute length as a proxy for body size) for majors and minors using standardized major axis regressions fit with the R package *lmodel2* (Legendre 2018). We compared the slopes between morphs using likelihood ratio tests implemented in the *sma*() function of the R package *smatr* (Warton et al. 2012). Because we are using female traits as controls, we also tested for bimodality in their dorsal scute length, pedipalp length, length of legs I to IV, and length of coxa IV apophysis. We also calculated the allometric slopes of these female traits using the same procedure described above and compared the slopes between males (or male morphs separately, if the trait was male-dimorphic) and females, also as described above.

Ethical note

The behavioral observations were conducted in accordance with ASAB/ABS Guidelines for ethical treatment of animals (ASAB/ABS 2012). The collection and maintenance of individuals in captivity were conducted with the appropriate permits from the Brazilian Government (SISBIO/ICMBio, permit 60,971).

Results

Description of male-male contests

Taking together field and laboratory observations, we recorded 13 male-male contests. From these observations, we identified three phases of the contests. Phases 1 and 2 were recorded in major-major ($n=7$), major-minor ($n=2$), and minor-minor ($n=1$) contests. Phase 3, however, was recorded only in major-major contests ($n=3$). The mean (± SD) duration of each phase was: phase 1 = 6.0 ± 3.9 min ($n=6$), phase 2 = 4.9 ± 4.7 min ($n=7$), and phase 3 = 8.2 ± 1.6 min ($n=3$). The mean duration of complete contests was 18.4 ± 8.3 min.

Phase 1 is characterized by intense leg tapping between males (see video in Supplementary Material S3). In this phase, males approach each other walking slowly, and when they are close to one another (ca. 10 cm), they orient their bodies until they are in a face-to-face position. In this position, both males use their legs I and II to touch and tap the legs, pedipalps, and occasionally the dorsum of the opponent. The parts of the front legs that contact the opponent are always the tarsus and the tip of the metatarsus. If one of the males does not retreat, the opponent intensifies the leg tapping, especially the tapping performed with legs I (Fig. 2 A). Meanwhile, legs II may be kept either extended backwards or laterally. In the latter case, legs II tap the tip of legs II of the opponent, which are also extended laterally (Fig. 2 A). During phase 1, legs III and IV are only used to support the body on the substrate,

and pedipalps are flexed on the dorsum most of the time (Fig. 2 A). Three contests ended in phase 1 (2 major-major and 1 major-minor).

Phase 2 is characterized by pedipalp attacks (see video in Supplementary Material S3). While males vigorously continue leg tapping (both with legs I and II), they extend their pedipalps frontwards and use them to strike and occasionally grasp the front legs or pedipalps of the opponent (Fig. 2B). When a male grasps a front leg of the opponent, he may use his chelicerae to bite it. At this point, the bitten male may stop fighting and flee, while the winner male chases him for a short distance (Fig. 2 C). As in phase 1, legs III and IV are only used to support the body on the substrate. Ten contests escalated to phase 2 and seven of them finished in this phase (5 major-major, 1 major-minor, and 1 minor-minor). Although the level of male aggressiveness in phase 2 is higher than in phase 1, we did not record any physical injury, even when one male bit an opponent's leg with his chelicerae.

Two contests in the laboratory and one contest in the field escalated to phase 3. This phase is characterized by a flip movement that places the males in a belly-to-belly position (see video in Supplementary Material S3). First, one or both males use their long pedipalps to grasp the opponent at the basal segments of legs I, II, or III. After the opponents mutually grasp each other, they raise the anterior part of their bodies and one of them flips the posterior end of his body forward. By doing so, the males keep the pedipalps interlocked and assume the belly-to-belly position, both facing the same direction (Fig. 2D-E). In this position, the tusks of one male may touch his opponent's venter (Fig. 2D–E). There is no consistent attempt to stab the opponent's venter using the tusks, but on one occasion we observed a male clearly inserting one of his tusks in one of the tracheal spiracles of the opponent (Fig. 2E). Males may stay in the belly-to-belly position for a long period (ca. 9.5 min) and during this time they constantly move their bodies laterally, sometimes rubbing their tusks onto each other. Moreover, males use the tip of their legs I to rub the tusks and the venter of the opponent (Fig. 2 F–G).

Over the course of phase 3, both males end up facing the substrate and supporting their bodies predominantly using legs II and III because legs I are touching the opponent and legs IV are raised in the air and performing conspicuous back and forth movements (Fig. 3 A–B, also see video in Supplementary Material S3). During these movements, the males' legs IV frequently touch each other (Fig. 2 F), and they seem to be attempting to hook one or both legs IV of the opponent using the large curved apophyses ("hooks") they have on the apex of their femur IV (Fig. 2 C and 3) and also on the mid portion of tibia IV. Although we observed this hooking only once, it was clear that it gave the necessary anchorage so that one of the males could force one or both of his tusks against the opponent's venter. Using individuals preserved in 70% ethanol, we simulated this hooking and confirmed that it allows the male with longer tusks to force the tip of this structure against the opponent's venter (Fig. 3). We stress, however, that even when we forced the tip of the tusk of a preserved male against the venter and tracheal spiracles of other preserved males, we were unable to cause any damage to the tegument. The lack of scars on the venter and tracheal spiracles of all males we analyzed reinforces the notion that tusks cannot cause injuries during the contests.

The contest ends when males release the pedipalp grasp and one of them flees. In none of the three phases males used the coxa IV apophysis to pinch their opponents, as reported for several gonyleptid harvestmen (e.g., Willemart et al. 2009; Stanley 2012). Thus, this trait, as well as the interocular distance, seem to have no role in male-male contests.

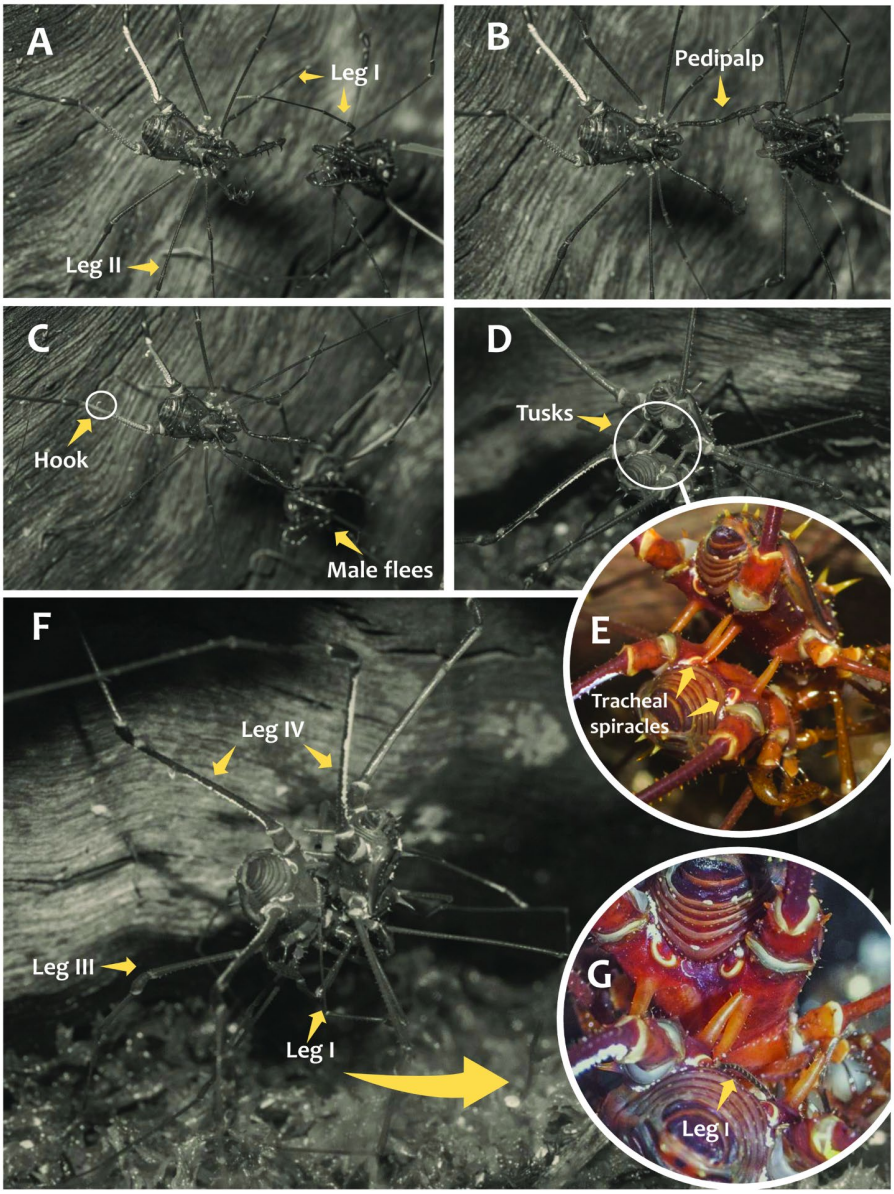

Fig. 2 Fighting behavior of the Amazonian tusked harvestman *Phareicranaus manauara.* (A) At the beginning of the contest (phase 1), males face each other and use their legs I and II to touch and tap the opponent. (B) As the contest escalates (phase 2), males use their pedipalps to strike the body or to grasp an appendage of the opponent. (C) At this point, one of the males may give up fighting and flee. The circle shows one of the large curved apophyses ("hooks") males have on the apex of their femur IV. These hooks are used in the next phase of the contest. (D) As the contest intensifies (phase 3), males grasp each other using their pedipalps, raise the anterior part of their bodies, and one of them flips the posterior end of his body forward. By doing so, males assume a (E) belly-to-belly position, touching the venter of each other with their own tusks. In this position, a male may insert one of his tusks in one of the tracheal spiracles of the opponent (arrow). (F) During the belly-to-belly position, males may tap the tip of their legs IV (arrow) and (G) rub the tip of their legs I on the tusks and venter of the opponent. See also the video in Supplementary Material S3

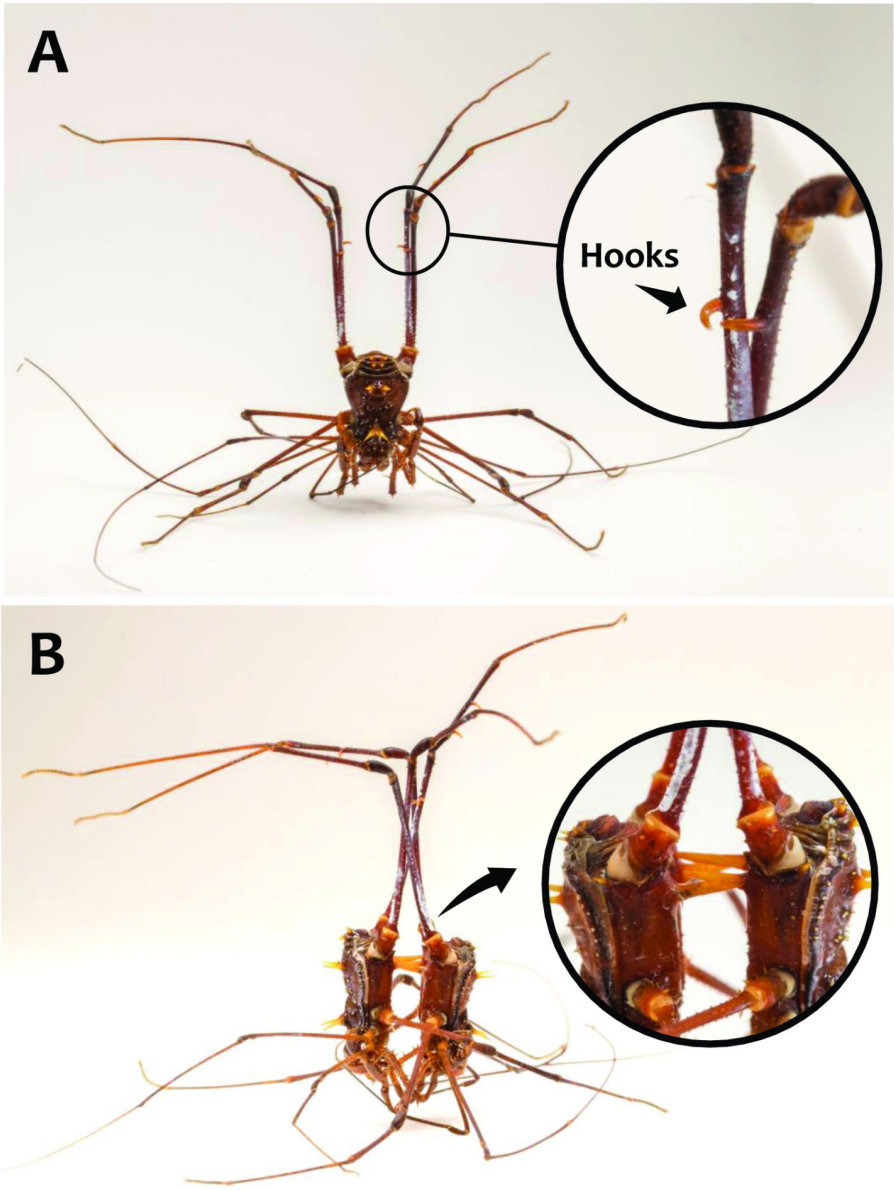

Fig. 3 Frontal (A) and lateral (B) view of a simulated hooking performed by the large curved apophyses ("hooks") that males of the Amazonian tusked harvestman *Phareicranaus manauara* have on the apex of their femur IV. This simulated posture was based on footage of the contests and is illustrated here with two major males preserved in 70% ethanol. The hooking occurs during the belly-to-belly position (phase 3 of the contest), when both males end up facing the substrate and supporting their bodies predominantly using legs II and III. While in the belly-to-belly position, males move their legs IV, which frequently touch each other. We suppose that one male is trying to hook one or both legs IV of the opponent using his hooks. Hooking may provide the necessary anchorage so that one of the males can force one or both of his tusks against the opponent's venter. See also the video in Supporting Supplementary Material S3

Based on our behavioral observations, we classified the traits according to their function during male-male contests (for an elaboration on this classification, see 'Allometry in male traits' below). Pedipalps were classified as weapons, legs I as tactile devices, and legs II as threat devices. Legs III, coxa IV apophysis, and interocular distance were not directly involved in any phase of the contest, and thus were classified as control traits. Tusks were tentatively classified as weapons and the precise function of legs IV could not be determined.

Male dimorphism and static allometry

Dorsal scute length was intrasexually dimorphic in males, but not in females (Table 1; Fig. 4 A-B). In males, two other traits were also intrasexually dimorphic: leg I length and tusk length (Table 1; Fig. 4 C-F). The remaining male traits, namely interocular distance, pedipalp length, length of legs II, III, and IV, and length of coxa IV apophysis were intrasexually monomorphic (Table 1; Figs. 5 and 6), as were all female traits (Table 1; Figs. 7 and 8). The mean (± SD) length of all male and female traits is presented in Table 2.

Pedipalp length had the steepest allometric slope in both males and females (Table 2), with no statistical difference between them (Table 3). The only isometric trait was the tusk

Table 1 Summary of the analyses to detect intrasexual dimorphism in male and female traits in the Amazonian tusked harvestman *Phareicranaus manauara*. For each trait, ΔAIC_c is the absolute difference between the AIC_c of models with 1 and 2 distributions. The AIC_c value of the best fitted model (i.e., the one with lower AIC_c) is highlighted in bold

Trait	AIC_c 1 distribution	AIC_c 2 distributions	ΔAIC_c	Intrasexual dimorphism
Male				
Dorsal scute length	−254.71	**−267.39**	12.68	Yes
Interocular distance	**−500.07**	−492.98	7.09	No
Pedipalp length	**79.79**	84.47	4.68	No
Femur I length	−319.37	**−325.86**	6.49	Yes
Femur II length	**−164.07**	−161.77	2.30	No
Femur III length	−219.16	**−222.18**	3.03	Marginal*
Femur IV length	**−166.21**	−164.69	1.51	No
Coxa IV apophysis length	**−597.57**	−590.25	7.32	No
Tusk length	−132.62	**−183.26**	50.65	Yes
Female				
Dorsal scute length	**−369.24**	−360.65	8.59	No
Interocular distance	**−617.87**	−611.29	6.58	No
Pedipalp length	**−17.52**	−7.72	9.80	No
Femur I length	**−424.84**	−415.99	8.85	No
Femur II length	−248.53	**−251.07**	2.53	Marginal*
Femur III length	**−323.59**	−316.20	7.39	No
Femur IV length	**−269.80**	−263.04	6.76	No
Coxa IV apophysis length	**−599.53**	−592.80	6.73	No

* Given that the ΔAIC_c value is close to the threshold (i.e., 2.0) and a visual inspection of the histogram does not indicate a clear bimodality (Fig. 8 C), we considered the length of femur III in males as monomorphic in the results presented in Table 3. A similarly low value of ΔAIC_c and no clear indication of bimodality in the histogram were found for the length of femur II in females (Fig. 6 C). Following the same rationale, this trait was considered monomorphic in the results presented in Table 3

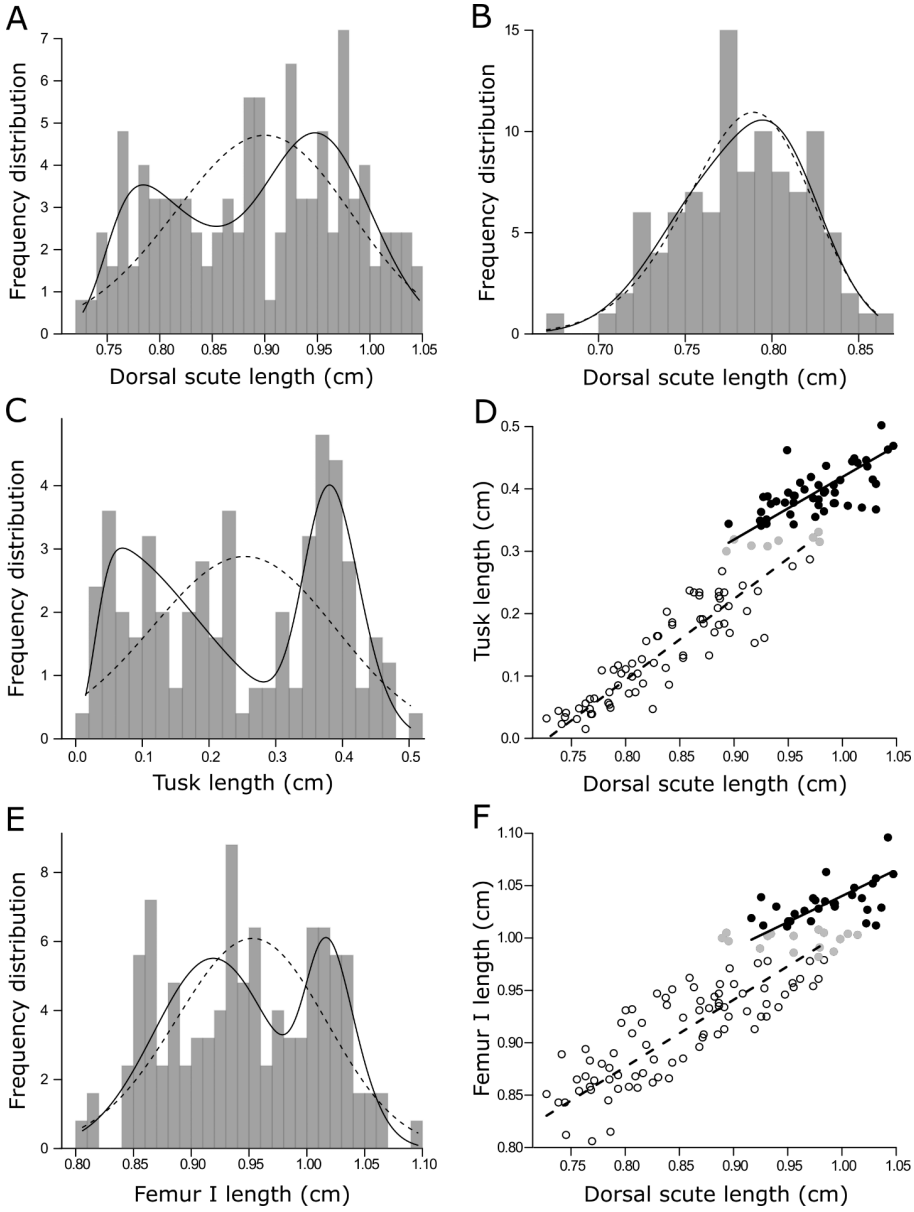

Fig. 4 Distribution of dorsal scute length (i.e., body size) of (A) males and (B) females of the Amazonian tusked harvestman *Phareicranaus manauara.* The histograms are overlaid by the fits of one or a mixture of two skew-normal distributions. The best fit (solid curves) for males is a bimodal distribution, whereas the best fit for females is a unimodal distribution (see Table 1). Two other male traits are also intrasexually dimorphic, namely (C) tusk length and (E) femur I length. Graphics (D) and (F) show the allometric relationships (fitted through standard major axis regression) between each of these two traits and dorsal scute length for each male morph (solid line = majors, dashed line = minors). Filled black circles indicate males with an estimated probability (from the finite mixture models) of being majors of at least 80%, whereas empty circles indicate males with a probability of being minors of at least 80%. Filled gray circles indicate males with probabilities lower than 80% of belonging to either morph. Due to ambiguity about which morph they belong to, no allometric relationships are fitted to these males

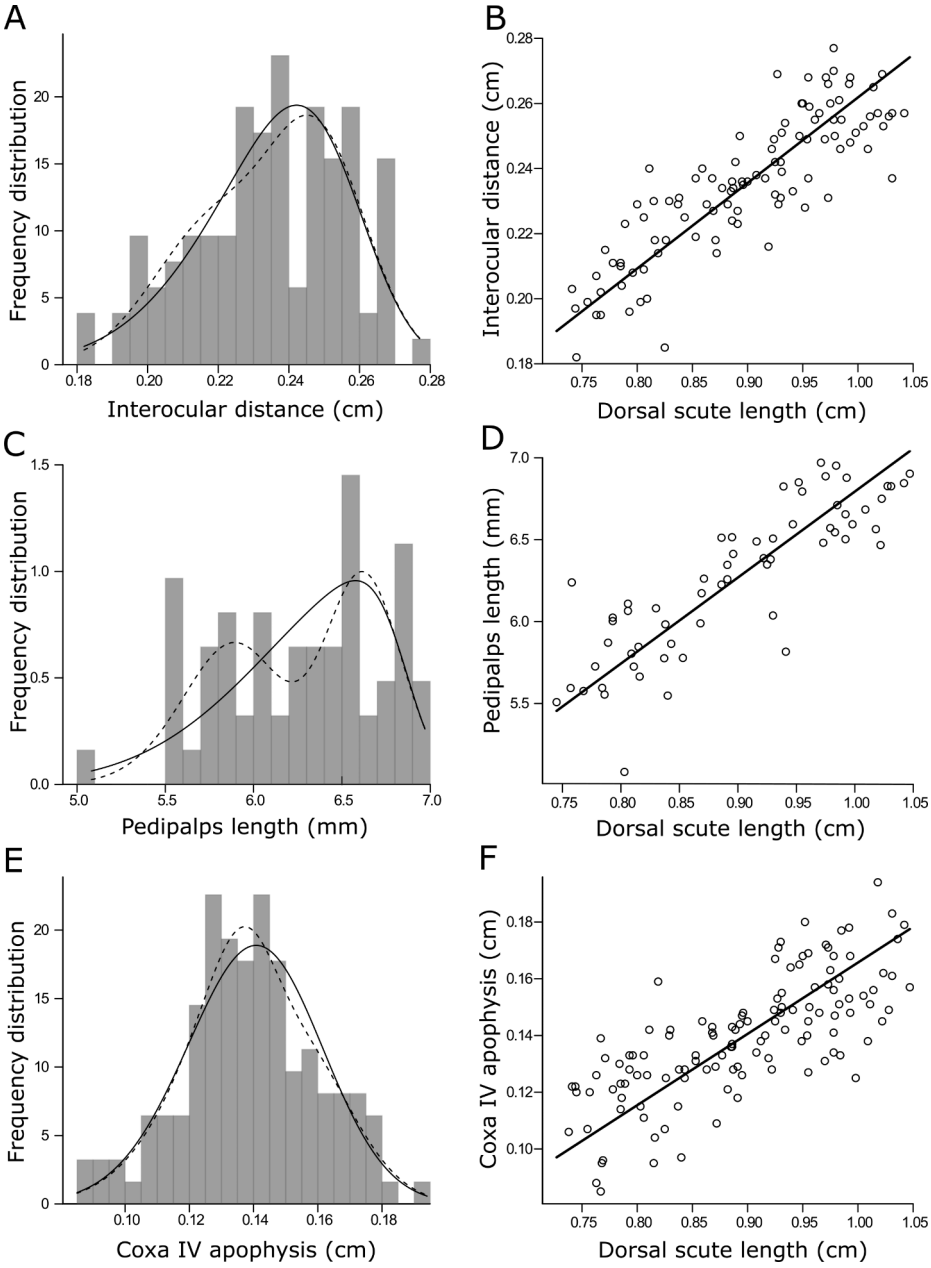

Fig. 5 Monomorphic traits in males of the Amazonian tusked harvestman *Phareicranaus manauara.* The histograms depict the (A) interocular distance and the length of the (C) pedipalps and (E) coxa IV apophysis. The histograms are overlaid by the fits of one (solid curves) or a mixture of two (dashed curves) skew-normal distributions. Graphics (B), (D), and (F) show the allometric relationships (fitted through standard major axis regression) between each of the three traits and dorsal scute length for all males

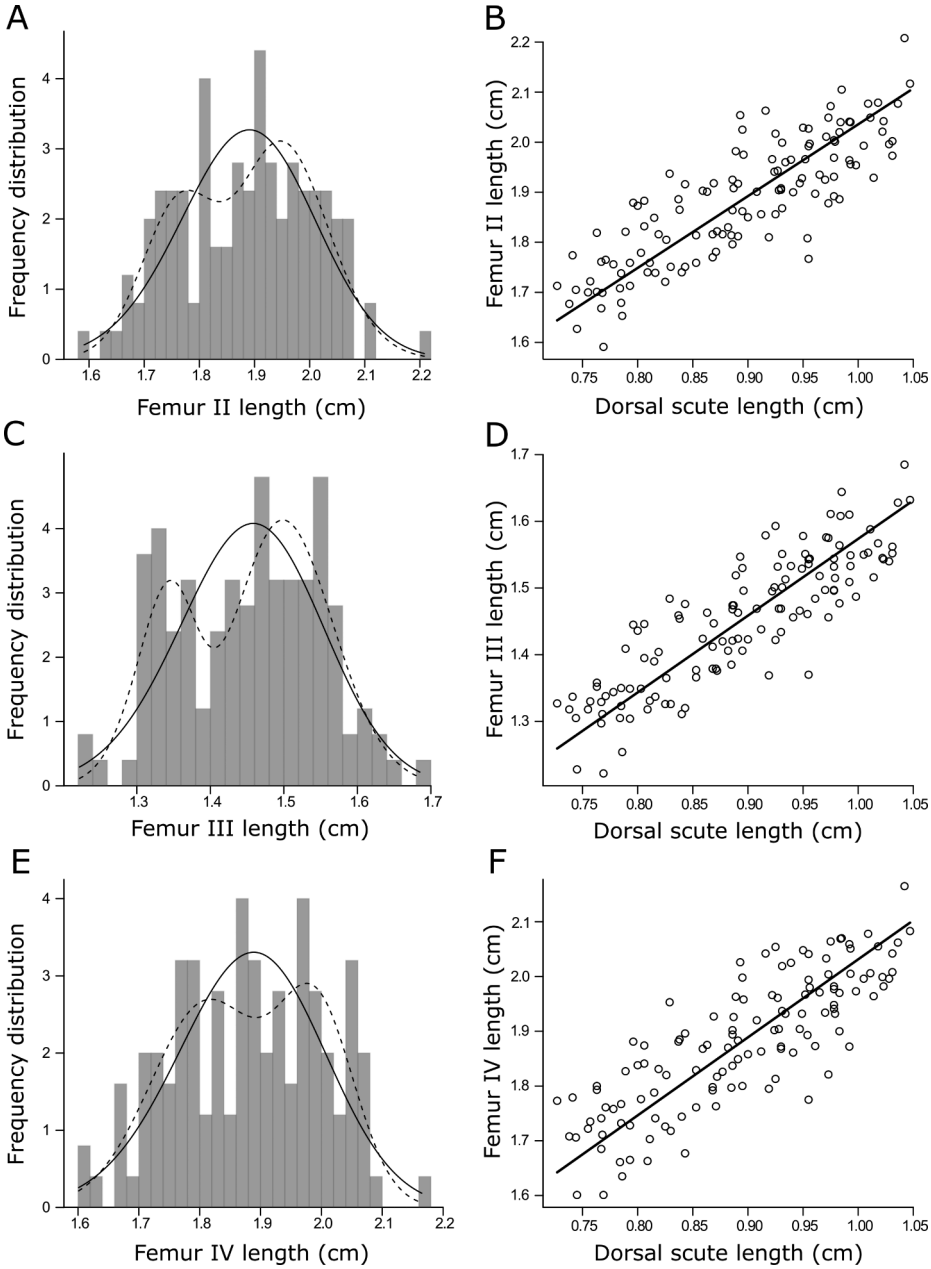

Fig. 6 Monomorphic traits in males of the Amazonian tusked harvestman *Phareicranaus manauara.* The histograms depict the length of (A) legs II, (C) legs III, and (E) legs IV. The histograms are overlaid by the fits of one (solid curves) or a mixture of two (dashed curves) skew-normal distributions. Graphics (B), (D), and (F) show the allometric relationships (fitted through standard major axis regression) between each of the three traits and dorsal scute length for all males

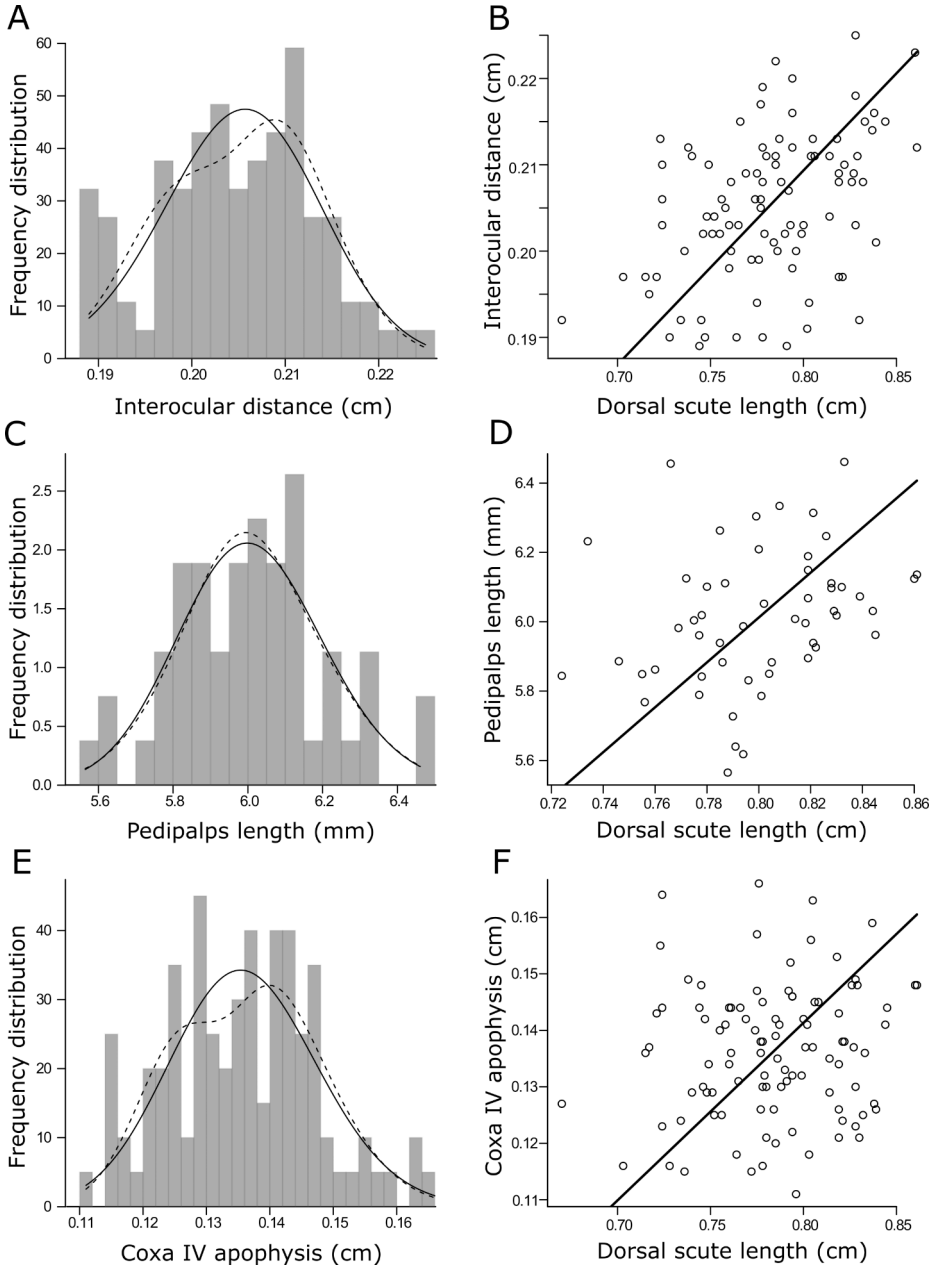

Fig. 7 Distribution of female traits of the Amazonian tusked harvestman *Phareicranaus manauara*. The histograms depict the (A) interocular distance and length of the (C) pedipalps and (E) coxa IV apophysis. The histograms are overlaid by the fits of one (solid curves) or a mixture of two (dashed curves) skew-normal distributions. For the three traits the best fit is a unimodal distribution (see Table 1). Graphics (B), (D), and (F) show the allometric relationships (fitted through standard major axis regression) between each of the three traits and dorsal scute length for all females

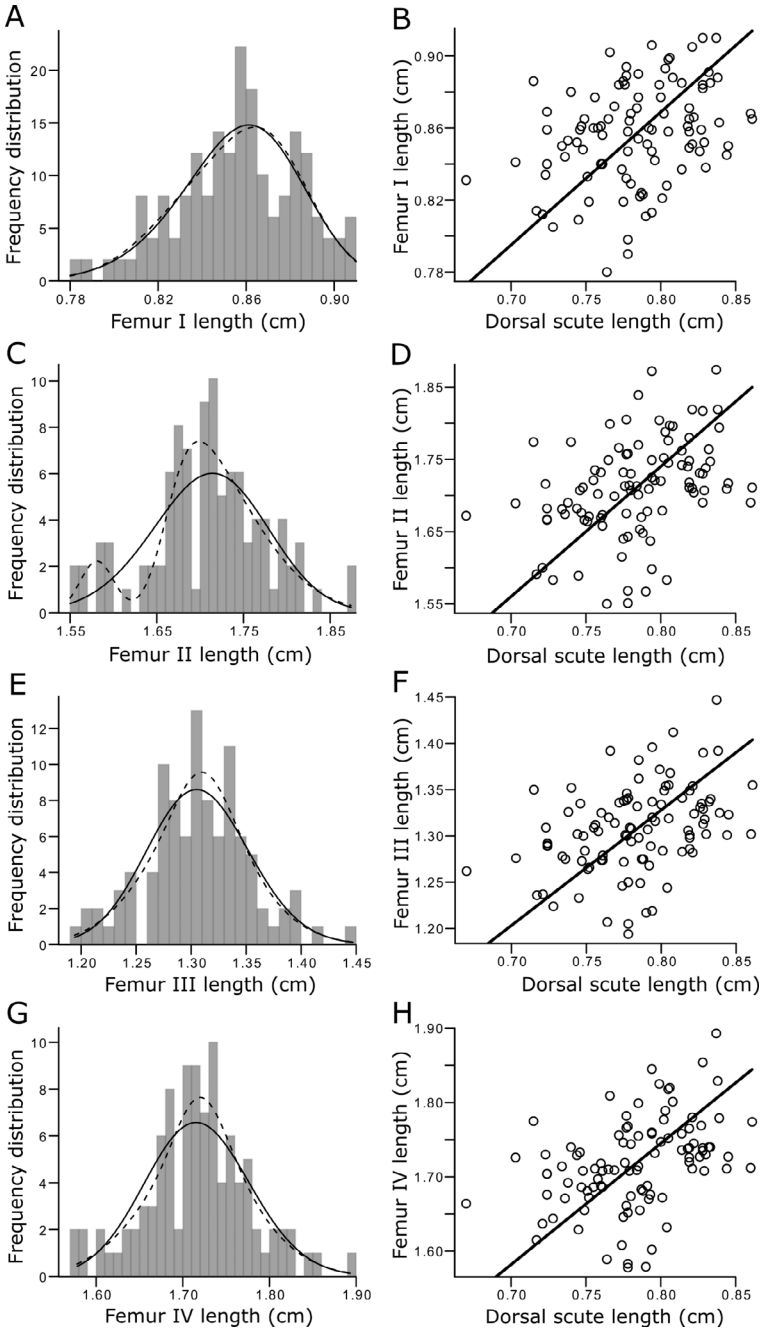

Fig. 8 Distribution of female traits of the Amazonian tusked harvestman *Phareicranaus manauara*. The histograms depict the length of (A) legs I, (C) legs II, (E) legs III, and (G) legs IV. The histograms are overlaid by the fits of one (solid curves) or a mixture of two (dashed curves) skew-normal distributions. For the four traits the best fit is a unimodal distribution (see Table 1). Graphics (B), (D), (F), and (H) show the allometric relationships (fitted through standard major axis regression) between each of the three traits and dorsal scute length for all females

Table 2 Summary of the analyses on the static allometry of contest-related traits (males) and control traits (males and females) of the Amazonian tusked harvestman *Phareicranaus manauara*. Whenever a trait is male dimorphic, we present the intercept and the slope of the allometric relationship separately for each morph. For all traits we present the mean (± SD) of females and males (separated in morphs when applicable). Sample sizes for each sex and morph are presented in Table 3. Hyper-allometric traits, i.e., those with slope higher than 1 and 95% confidence interval (95% CI) not overlapping 1, are highlighted in bold

Trait (function)	Intercept (95% CI)	Slope (95% CI)	Trait size ± SD (mm)*
Contest-related			
Male pedipalp length (weapon)	1.542 (0.865, 2.134)	**5.252 (4.593, 6.005)**	6.264 ± 0.459
Male femur I length (tactile device)	Major: 0.542 (0.348, 0.681) Minor: 0.367 (0.292, 0.432)	Major: 0.499 (0.358, 0.695) Minor: 0.638 (0.561, 0.726)	Major: 10.338 ± 0.189 Minor: 9.090 ± 0.441
Male femur II length (threat device)	0.601 (0.468, 0.721)	**1.435 (1.300, 1.583)**	18.84 ± 1.230
Male femur IV length (not determined)	0.606 (0.470, 0.729)	**1.425 (1.288, 1.577)**	18.81 ± 1.221
Male tusk length (weapon)	Major: −0.585 (−0.831, −0.388) Minor: −0.945 (−1.072, −0.832)	Major: 1.004 (0.802, 1.256) **Minor: 1.299 (1.162, 1.451)**	Major: 3.956 ± 0.375 Minor: 1.351 ± 0.749
Control			
Male interocular distance	−0.001 (−0.026, 0.022)	0.263 (0.238, 0.291)	2.235 ± 0.022
Female interocular distance	0.029 (−0.007, 0.060)	0.225 (0.186, 0.272)	0.205 ± 0.008
Male coxa IV apophysis length	-0.086 (−0.115, −0.060)	0.252 (0.223, 0.284)	1.395 ± 0.213
Female coxa IV apophysis length	−0.110 (−0.164, −0.066)	0.314 (0.258, 0.383)	0.136 ± 0.012
Female femur I length	0.278 (0.158, 0.378)	0.738 (0.611, 0.892)	8.570 ± 0.278
Female femur II length	0.300 (0.0134, 0.539)	**1.800 (1.495, 2.166)**	17.100 ± 0.674
Male femur III length	0.422 (0.323, 0.512)	**1.152 (1.051, 1.262)**	14.520 ± 0.987
Female femur III length	0.331 (0.134, 0.495)	**1.246 (1.037, 1.498)**	13.074 ± 0.467
Female femur IV length	0.440 (0.184, 0.654)	**1.631 (1.359, 1.958)**	17.181 ± 0.611
Female pedipalp length	0.781 (−0.798, 1.993)	**6.530 (5.015, 8.502)**	6.007 ± 0.197
Body size			
Female dorsal scute length	NA	NA	7.835 ± 0.375
Male dorsal scute length	NA	NA	Major: 9.723 ± 0.360 Minor: 7.956 ±± 0.340

* For sexual and intrasexual differences in the size of each trait, see Table S1 in Supplementary Material S2

Table 3 Comparison of the allometric slopes of different traits between females and males (separated in morphs when applicable) of the Amazonian tusked harvestman *Phareicranaus manauara*. Number in parentheses indicate sample sizes for each sex and morph. Contest-related traits are underlined. Significant differences are highlighted in bold

Trait	Comparison	Statistics	*P*-value
Interocular distance	Male (104) x Female (93)	LR = 2.046; df = 1	0.153
Pedipalp length	Male (62) x Female (53)	LR = 1.896; df = 1	0.169
Femur I length	Major (29) x Minor (81)	LR = 1.936; df = 1	0.164
	Major (29) x Female (99)	LR = 4.078; df = 1	**0.044**
	Minor (81) x Female (99)	LR = 1.456; df = 1	0.228
Femur II length	Male (125) x Female (99)	LR = 4.498; df = 1	**0.034**
Femur III length	Male (125) x Female (100)	LR = 0.572; df = 1	0.450
Femur IV length	Male (125) x Female (100)	LR = 1.614; df = 1	0.204
Coxa IV apophysis length	Male (124) x Female (100)	LR = 3.582; df = 1	0.058
Tusk length	Major (48) x Minor (69)	LR = 4.109; df = 1	**0.043**

length of majors; in minors this trait had a hyper-allometric slope significantly steeper than majors (Tables 2 and 3). Femur length of leg I was hypo-allometric in both majors and minors, and also in females (Table 2), with no difference in the slopes between male morphs; females, however, had a significantly steeper slope than majors (Table 3). The length of all other legs (II-IV) was slightly hyper-allometric in both males and females (Table 2), and the only significant difference between sexes was found in legs II, with females showing a steeper slope (Table 3). Finally, interocular distance and length of coxa IV apophysis were hypo-allometric in both males and females (Table 2), with no difference between sexes (Table 3).

Discussion

Here, we tested the functional allometry hypothesis, which proposes that directional selection consistently favors hyper-allometry in threat devices, whereas the allometry of weapons depends on their function, i.e., the way they are used in contests (Eberhard et al. 2018). To understand and describe the function of several morphological traits (including controls not used in the contests), we first conducted behavioral observations of male-male contests in the Amazonian tusked harvestman *Phareicranaus manauara*. Knowing the function of these traits allowed us to contrast the results of our morphometric analyses with predictions of the functional allometry hypothesis. Except for legs IV, whose function we could not precisely infer, function correctly predicted the allometry of almost all male traits investigated here. However, contrary to what we expected, the allometric slopes of most of the homologous female traits measured here showed no sexual difference. Finally, the allometric slopes of some contest-related traits showed differences between male morphs that cannot be easily explained by the way these traits are used during the contests. The best example are tusks, which showed higher slopes in minors than in majors, even though these structures are used only in major-major contests. In what follows, we explore how information on function can help with understanding the allometry of a trait and the limits for this exercise. We also discuss how the allometry of female traits may not offer appropriate comparisons for the allometry of homologous male traits.

Allometry in male traits

Behavioral observations show that some traits investigated here are unequivocally used as weapons to grasp opponents from afar (pedipalps) or as threat devices in the beginning of the contests (legs II). Both functions should select for hyper-allometry because length is a key component of their efficiency (Eberhard et al. 2018). Males with long pedipalps, for instance, may have advantage in pulling and grasping rivals with short pedipalps. For threat devices, males with longer legs II may be better at communicating their size and win more contests before they escalate to physical coercion (i.e., phases 2 and 3). Legs II are also used as a threat device in other harvestman species, such as the cranaid *Phareicranaus* aff. *spinulatus* (García-Hernández and Machado 2018) and the gonyleptid *Serracutisoma proximum* (Buzatto et al. 2011). A key difference between *P. manauara* and the well-studied *S. proximum* is that minors of the former species engage in contests with other minors and even with majors, whereas minors of the latter never do so (Buzatto et al. 2011). Thus, minors of *P. manauara* may benefit from having long legs II, whereas minors of *S. proximum* may not. This behavioral difference could explain why legs II in *P. manauara* have a unimodal distribution whereas in *S. proximum* they have a bimodal distribution (Buzatto et al. 2011).

Tusks are a unique contest-related trait in harvestmen present only in some species of the family Cranaidae (Pinto-da-Rocha and Kury 2003). These structures are used exclusively in the final phase of the contests, thus are unlikely to function as threat devices, which tend to be used in the initial phases when males are evaluating whether to escalate the contest or not (e.g., Jakobsson et al. 1979; Eberhard and Briceño 1985; Wilkinson and Dodson 1997; Kojima and Lin 2017). Although the precise function of the tusks is not clear, we suggest that they are weapons that are forced against the venter of the opponent. Although tusks are unable to puncture the opponent's tegument, the pressure applied by the tusks on the opponent may provide reliable information on strength. More importantly, a large male with long tusks may be able to press the rival's venter, while his own venter is not pressed by the short tusks of a smaller rival. Thus, if our functional hypothesis is correct, tusks should be hyper-allometry, which was the case of minors but not majors (see discussion in 'Cautionary messages' below). As a final remark, we stress that the presence of many sensilla covering the tusks (Fig. S1B in Supplementary Material S2) deserves further investigation. Considering that they are mechanoreceptors (R.H. Willemart pers. comm.), males may use them to acquire tactile information on the relative size of their own tusks when they touch the opponent's tusk. This hypothesis may explain why males seem to rub their tusks while they are in the belly-to-belly position.

Legs I do not seem to function as a weapon or threat device. Because harvestman eyes only perceive changes in light intensity (Schultz and Pinto-da-Rocha 2007), legs I may provide tactile information on the position and posture of the opponent in the beginning of the contests. Moreover, once males are in front of each other, legs I are used to tap the opponent (phases 1–2), as previously reported for the gladiator harvestman *Neosadocus bufo* (mentioned as *N. maximus* in Willemart et al. 2009). These tapings may stimulate mechanoreceptors that cover the opponent's body and legs, and the tapping rate may provide tactile information on body condition of the touching male, as already reported for male-female courtship interactions in some insects (e.g., Kotiaho 2002). In phase 3, legs I are used to touch the tusks and venter of the opponent. We suggest these touches allow males to acquire further tactile information on the length of the opponent's tusks. Therefore, legs I probably

function as devices that transmit (phases 1–2) and receive (phase 3) tactile stimuli throughout the entire contest. Current theory on tactile devices focuses exclusively on male-female courtship interactions and predicts that these traits are under stabilizing selection, leading to hypo-allometry (Eberhard et al. 2018). In accordance with this prediction, males' legs I were indeed hypo-allometric. We found no mention of tactile devices in male-male contests of other arthropods, either because it is rare or there is a bias in the sensory modalities to which researchers pay attention (see Coleman 2009). The second pair of antennae in lobsters and crayfish, which are used to touch rivals during contests (e.g., Moore 2007; Bergman et al. 2005; Vickery et al. 2012), may function as a tactile device, but we are unaware of studies on the allometry of these appendages. Future studies should consider male traits that function as tactile devices in contests to test whether the general pattern of hypo-allometry described for male-female courtship interactions (Eberhard 2009; Eberhard et al. 2018) also holds for male-male agonistic interactions.

The traits we used as controls were predicted to show iso- or hypo-allometry because natural selection would act to maintain the phenotype within a size range that enables optimal performance, hence better survival (Voje 2016). In fact, two control traits, namely interocular distance and coxa IV apophysis, followed this pattern and showed hypo-allometric slopes. Legs III, however, were slightly hyper-allometric, and we propose two possible explanations for this pattern. First, the slope value was 1.152, with the lower bound of the confidence interval almost overlapping 1 (1.051). Thus, the deviation from isometry is only marginal, and this slight hyper-allometry may not be biologically significant. Alternatively, even though legs III are not directly used in contests, they may be used as a weapon supportive trait (sensu Okada et al. 2012), i.e., a structure that helps males to use their enlarged weapons. In beetles, for instance, a larger head, prothorax, and forelegs may function as weapon supportive traits for males that use their horns and mandibles in contests (e.g., Tatsuta et al. 2004; Tomkins et al. 2005b; Okada and Miyatake 2009). In the case of *P. manauara*, longer legs III may help males in the pedipalp attacks observed in phase 2 and/or may confer stability in the complex belly-to-belly position observed in phase 3 (Fig. 3). Legs III may also be used as a compensatory trait (sensu Tomkins et al. 2005b) during non-antagonistic situations, such as to avoid dragging the tusks on the ground while males are walking (see video in Supplementary Material S1). If legs III act as a weapon supportive and/or a compensatory trait, they are expected to be under a similar (but perhaps weaker) selection regime as some contest-related traits, such as pedipalps and tusks. In this way, males exhibiting the suitable combination of multiple traits may have higher chances of winning contests, monopolizing oviposition sites, and thus copulating with a large number of females (Irschick et al. 2008).

Cautionary messages

Aside from tusks, all male traits measured here are also present in females and have functions outside of male-male contests. These additional functions may constrain the developmental trajectory and the action of sexual selection on a trait, so that no sexual dimorphism in allometric slopes is expected to evolve. For instance, pedipalps are raptorial feeding appendages in both sexes in many harvestman species (Acosta and Machado 2007). As occurs with other arachnids with raptorial pedipalps, such as whip spiders, individuals of

both sexes may benefit from hyper-allometric appendages that allow them to grasp food from afar (McLean et al. 2020). In fact, in *P. manauara* and several whip spiders (McLean et al. 2018), male and female pedipalps are hyper-allometric, suggesting that the raptorial function favors pedipalp elongation in both sexes. The absence of sexual dimorphism in allometric slopes of specialized feeding appendages that are also used in male-male contests is not unprecedented. In mantis shrimps, for instance, the allometric slopes of the raptorial appendages are similar between the sexes, even though males also use them to hit opponents from afar during contests (Claverie et al. 2011). In crabs, males use their claws as threat devices and weapons in contests, but both sexes tend to have similar allometric slopes when these claws are also used to feed on hard prey (e.g., Schenk and Wainwright 2001; Fujiwara and Kawai 2016). Thus, a first cautionary message from our study is that understanding the function of a trait across contexts is important to predict not only the allometry, but also the occurrence of sexual dimorphism in the allometric slope of this trait.

Sexual selection theory has mostly focused on the evolution of allometric slopes rather than intercepts (e.g., Bonduriansky 2007a; Eberhard et al. 2018), probably because: (i) the intercept has no biological interpretation in male-monomorphic species, and (ii) significant differences in slopes between morphs necessarily cause differences in intercepts that have no biological cause (Tomkins et al. 2005a). However, intercepts and absolute sizes of traits are easier to evolve away from the phenotypic optimum when compared to slopes (Bolstad et al. 2015). When we consider sexual dimorphism, males and females probably share the reaction norm that determines the allometric scaling (i.e., slope), but the intercept may be freer to evolve. Our results suggest that this is the case of *P. manauara*: when we detected sexual differences in the slopes, they were either subtle or in some cases reversed (i.e., females have higher slopes for legs I–II). However, for most traits, males and females differed in the intercept and absolute size. Based on this evidence, it is likely that the genetic architecture of these traits results in cross-sexual genetic correlations (Poissant et al. 2009; Buzatto et al. 2015; Pike et al. 2017) that constrain the evolution of diverging allometries between sexes. Such genetic correlations would explain why traits under different selective regimes in females and males exhibit similar allometric slopes, despite having different intercepts and absolute sizes. Thus, a second cautionary message that emerges from our findings is that homologous traits in females may not be ideal controls. The best alternative would be to focus on non-contest-related traits that are likely not under directional sexual selection in males (e.g., interocular distance and coxa IV apophysis in *P. manauara*) and compare their allometric slopes and intercepts with the sexually selected traits in the same sex (e.g., Eberhard et al. 2018; O'Brien et al. 2019; Solano-Brenes et al. 2018; Bertram et al. 2021). However, even in this case, phenotypic integration and cross-trait correlations may still constrain the independent evolution of allometric slopes (Cheverud 1984).

Contrary to legs I–II and pedipalps, tusks are the only trait studied here that can be regarded as a 'pure' contest-related trait, because they are absent in females, and males seem to use them only in a specific moment of the contest. Based on our observations, we suggest that tusks function as weapons and, as discussed above, males with longer tusks may have advantages in contests. According to the functional allometry hypothesis, tusks should be hyper-allometric. However, these unique structures are male-dimorphic, with a significant difference between morphs in the allometric slopes: minors have hyper-allometric tusks, while majors have isometric tusks. The fact that minors do not use their tusks in contests (because they may never escalate to phase 3) raises a question on the relationship between

function and allometry: why is the slope of this trait higher in minors than in majors? This question has been addressed from a theoretical perspective by Tomkins et al. (2005a), who proposed that correlated evolution in allometric parameters (i.e., intercept and slope) may lead to differences between male morphs. More specifically, selection against trait exaggeration in minors may be associated with a reduction in the intercept. Because intrasexual selection may favor trait exaggeration in majors, the reduction in the intercept must be followed by an increase in the slope. The resulting pattern is: minors with low intercept and high slope, and majors with high intercept and low slope (see Fig. 5 in Tomkins et al. 2005a), a pattern consistent with that obtained here for the tusks. Thus, the third cautionary message from our study is that function is not a good predictor of differences between male morphs in the allometric slopes of contest-related traits.

Legs I also showed marked male dimorphism, despite the fact that they are hypo-allometric. Most studies assume that male-dimorphic traits are linked to exaggeration and consequently steep (i.e., hyper-allometric) slopes (see discussion in Tomkins and Moczek 2009 and Tomkins et al. 2005a). Our data, however, provide evidence that even hypo-allometric traits can be under disruptive selection in males. Moreover, contrary to the tusks, we found no difference in the allometric slopes of legs I in majors and minors. The difference between morphs was found only in the absolute size, with majors bearing longer legs than minors (but not higher intercept). Longer legs I may favor majors to reach the posterior part of the opponent's venter, where the tusks are located (Fig. 2 F-G). However, directional selection on legs I may promote an increase only in the absolute size, because the tactile function of this appendage may constrain the increase in slope, maintaining the trait as hypo-allometric (Eberhard et al. 2018). Thus, our last cautionary message is that male dimorphism can be found even in hypo-allometric contest-related traits and that differences between morphs in the absolute size of a contest-related trait are not necessarily followed by differences in their allometric slopes and intercepts.

Conclusions

Overall, our results support the hypothesis that function predicts the allometry of contest-related male traits (Eberhard et al. 2018). Using behavioral observations of male-male contests, we identified weapons, threat devices, tactile devices, and control traits (i.e., traits not used in contests). As should be expected by their function in the contests, weapons and threat devices were hyper-allometric, whereas tactile devices and control traits were either iso- or hypo-allometric. However, function does not explain allometric differences between males and females in homologous traits. We argue that if a trait used in contests by males is used by both sexes in another context, such as foraging, natural selection and cross-sexual genetic correlations may constrain its developmental trajectory, preventing the evolution of sexual dimorphism in the allometry. A practical implication of this suggestion is that using female traits as controls for homologous contest-related male traits is not the best option. Finally, there is no current hypothesis providing predictions on how the allometry of contest-related traits should differ between male morphs. Our findings suggest that function does not explain differences in the allometric slopes of male-dimorphic traits, such as the tusks and legs I. Thus, an important next step in allometric studies is to understand what factors affect the intercept and slopes of male-dimorphic traits.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10682-022-10152-1.

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Declarations

Conflict of interest The authors declare no conflict of interest.

Consent to participate All authors consent to participate.

Data and code availability The analyses reported here can be reproduced using the data and scripts that are available on the Mendeley repository (doi: https://doi.org/10.17632/9nh9nj5y7w.1).

Authors' contributions GM conceptualized the study; SGH and GM collected data in the field; AVP and SGH conducted the behavioral observations in the laboratory; AVP, SGH, BAB, and GM analyzed the videos; SGH assisted in the measurement of the individuals and curated the data; AVP, SGH, BAB analyzed the data; AVP, SGH, BAB, and GM wrote and edited the manuscript; SGH and GM performed visualization; GM acquired funding.

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Authors and Affiliations

Alexandre V. Palaoro[1,2] · Solimary García-Hernández[2] · Bruno A. Buzatto[3,4] · Glauco Machado[5]

✉ Glauco Machado
glaucom@ib.usp.br

1 LUTA do Departamento de Ecologia e Biologia Evolutiva, Universidade Federal de São Paulo, São Paulo, Brazil

2 Programa de Pós-graduação em Ecologia, Instituto de Biociências, Universidade de São Paulo, São Paulo, Brazil

3 Centre for Evolutionary Biology, School of Biological Sciences (M092), The University of Western Australia, 35 Stirling Highway, 6009 Crawley, WA, Australia

4 Department of Biological Sciences, Faculty of Science and Engineering, Macquarie University, Sydney, Australia

5 LAGE do Departamento de Ecologia, Instituto de Biociências, Universidade de São Paulo, 05.508-090 São Paulo, SP, Brazil