

Males armed with big weapons win fights at limited cost in ant-mimicking jumping spiders

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Abstract

A core assumption of sexual selection theory is that sexually selected weapons, specialized morphological structures used directly in male contests, can improve an individual's reproductive success but only if the bearer can overcome associated costs, the negative effects on the bearer's fitness components. However, recent studies have shown that producing and wielding exaggerated weapons may not necessarily be costly. Rather, some traits can be selected for supporting, or compensating for, the expense of producing and wielding such exaggerated weapons. In the ant-mimicking jumping spider *Myrmarachne gisti*, exaggerated chelicerae are borne only by adult males and not females, showing sexual dimorphism and steep positive allometry with body size. Here, we determine the potential benefits of bearing exaggerated chelicerae during male contests and explore the potential for costs in terms of prey-capture efficiency and compensation between chelicera size and neighboring trait size. While males with longer chelicerae won most of their male-male contests, we found no significant differences in prey-capture efficiency between males and females regardless of whether prey was winged or flightless. Males' elongated chelicerae thus do not impede their efficiency at capturing prey. Furthermore, we found that the sizes of all neighboring traits are positively correlated with chelicera size, suggesting that these traits may be under correlational selection. Taken together, our findings suggest that *M. gisti* males armed with the exaggerated chelicerae that function as weapons win more fights at limited cost for performance in prey capture and compensate for neighboring structures.

Key words: allometry, ant-mimic, costs, elongated chelicerae, threat devices, trait compensations.

Sexual selection has led to the evolution of exaggerated traits (Darwin 1871; Andersson 1994). These exaggerated traits can act as weapons that aid in direct male–male combat with rivals over access to potential mates or as ornaments that make males attractive to potential mates, increasing their relative reproductive success (Andersson 1994). Although sexual selection theory assumes that developing and wielding such elaborate traits may also come with costs (i.e., negative effects on a component of the trait bearer's fitness) and constraints (Andersson 1994; Kotiaho 2001; Rico-Guevara and Hurme 2019), empirical evidence for the costs and constraints of most exaggerated traits remains limited, and others have argued that an exaggerated trait is unnecessarily costly (Hurd 1995; Maynard Smith and Harper 2003; Számadó 2011; Holman 2012; Prum 2017; Rosenthal 2017; Ryan 2018).

Sexually selection exaggerated traits often exhibit steep positive allometric (hereafter referred to as hyperallometry) relationships with larger individuals bearing disproportionately larger traits than smaller individuals, the basis for the positive or hyperallometry hypothesis (Kodric-Brown et al. 2006; Bonduriansky 2007; Eberhard et al. 2018; O'Brien et

al. 2018). According to the functional allometry hypothesis (Eberhard et al. 2018; Rico-Guevara and Hurme 2019), hyperallometry is usually favored for those traits that function as a threat device used in threatening displays to convey information about the male's size, strength, or fighting ability, which can be used by rival males to decide to withdraw before engaging in physical contact (Eberhard et al. 2018; O'Brien et al. 2018). Weapon is a specialized morphological structure used as a tool for grasping, stabbing, striking, pushing, or lifting rival males in direct physical combat (McCullough et al. 2016; Eberhard et al. 2018). The allometry of a weapon varies with how it is used in contests, that is, the fighting style (Eberhard et al. 2018; O'Brien et al. 2018; Rodríguez and Eberhard 2019; Palaoro and Peixoto 2022). Hyperallometry has been documented for sexually selected threat devices and weapons that are used for lifting or pushing rivals in taxa across the animal kingdom (Kodric-Brown et al. 2006; Emlen 2008; Eberhard et al. 2018; O'Brien et al. 2018; Rico-Guevara and Hurme 2019). However, for weapons to be functional in making rival males withdraw from a fight they may not have to be big (Palaoro et al. 2020), there are cases

of weapons, such as those that involve pinching, or grappling with rivals, exhibiting isometry (i.e., the trait size increases proportionately with body size) or even negative allometry, also known as hypoallometry (i.e., larger individuals show disproportionately smaller traits) (Bonduriansky and Day 2003; Bonduriansky 2007; Voje 2016; Eberhard et al. 2018; O'Brien et al. 2018; Palaoro et al. 2022). It is expected that hyperallometry in sexually selected traits is likely to be driven by size-dependent costs and benefits of those traits as well as their function (Kotiaho 2001; Fromhage and Kokko 2014; Eberhard et al. 2018).

Both threat devices and weapons can help resolve male-male contests (Emlen 2008; McCullough et al. 2016; Rico-Guevara and Hurme 2019). Larger males are more likely to engage in fights and threat devices are usually used by rival males to avoid risky and unwinnable fights (Eberhard et al. 2018; Palaoro et al. 2022). Animals then use these devices or weapons to win over rivals over direct access to potential mates (Painting and Holwell 2014; O'Brien et al. 2017) or indirectly over resources critical for their mates (Kelly 2006; Dennenmoser and Christy 2013). A larger weapon that also functions as a threat device in the beginning of fights may suggest a greater possibility of winning a contest, and this has been shown in various animal taxa (Andersson 1994; Hardy and Briffa 2013; Palaoro and Peixoto 2022), even though males with larger weapons may not always win contests (Eberhard et al. 2018). For example, in *Cyclommatus* stag beetles, males with larger mandibles win battles over rivals (Goyens et al. 2015). Thus, the increased relative weapon size is expected to yield increased mating success in general if these weapons are under directional sexual selection.

Producing and bearing an exaggerated weapon may also incur viability costs (Számádó 2011; reviewed in Podos 2022). Commonly studied costs include those imposed by attracting attention from enemies—such as rivals, predators, or parasites—or trade-offs between fighting efficiency and performance of other tasks such as locomotion and feeding (Allen and Levinton 2007; Emlen 2008; Doake et al. 2010; Cummings et al. 2018; Rico-Guevara and Hurme 2019; Podos 2022). For example, male horned dung beetles *Sulcophanaeus velutinus* with longer horns win access to females in physical competition but also suffer from reduced mobility in underground tunnels (Cummings et al. 2018). When the sexually selected weapon is a direct modification of the feeding apparatus, it may aid in male-male contests but the trade-off with feeding performance (Pollard 1994; Rico-Guevara 2017). However, bearing an exaggerated weapon may not necessarily come with a trade-off with performing other tasks. For example, rhinoceros beetle horns have no effect on flight performance (McCullough et al. 2012). Similarly, the exaggerated horns of male flower beetles *Dicronocephalus wallichii* play an important role in male-male competition (Kojima and Lin 2017), but do not impede maximum sprint speed (Kojima and Lin 2018). Nevertheless, such a weapon may be so exaggerated that it gets in the way of performing other tasks vital to the bearer's survival.

Sexually selected weapons may also be evolutionarily shaped by resource allocation trade-offs, which occur when one trait cannot increase without a decrease in another (or vice versa) caused by limited resources (Zara and Harshman 2001; Garland 2014), or constraints, the proximate limits on an animal's capacity to develop, express, or evolve certain traits (Brackefield and Roskam 2006; Podos 2022). Developing weapons such as horns and enlarged mandibles

may thus come at the expense of reduced size in neighboring traits due to such resource allocation trade-offs (Tomkins et al. 2005). For example, in *Onthophagus* dung beetles, relative horn size is negatively correlated with the relative size of eyes, wings, and antennae (Emlen 2001). However, other studies have shown that producing or bearing an exaggerated weapon may not necessarily require a high cost or even come at a relatively small cost. For example, rhinoceros beetle horns do not stunt the growth of nearby body structures (McCullough and Emlen 2013). Nevertheless, resource allocation trade-offs appear to be not very common in most animals (Emlen 2001).

Alternatively, the developmental integration of compensatory traits can offset the costs from bearing weapons (Tomkins et al. 2005). If compensation (i.e., correlated growth) occurs, weapon size is expected to be positively correlated with traits that physically support the growth of the weapons and offset costs. Such correlational selection of compensatory traits has been reported in several studies (e.g., Van Noordwijk and De Jong 1986; Kodric-Brown et al. 2006; McCullough and Emlen 2013; Painting and Holwell 2013; Schwab and Moczek 2014; Kojima and Lin 2018; Li et al. 2019; Palaoro et al. 2022). In general, the vast majority of these studies have found evidence for compensation rather than resource allocation trade-offs.

Resource allocation trade-offs and compensations between weapons and neighboring traits are tied to physiological mechanisms in which the weapon captures the resources of neighboring traits to develop (Tomkins et al. 2005; Okada and Miyatake 2009; Emlen et al. 2012). Pathways such as juvenile hormone and insulin/insulin-like growth factor are known to be responsible for the regulation of allometry and developmental integration of other traits in insects (Emlen et al. 2012; Okada et al. 2012). For example, in male rhinoceros beetle *Trypoxylus dichotomus*, the forked horn on their heads was more sensitive to insulin/insulin-like growth factor than other non-sexually selected body parts (wings, genitalia), which explains the trade-offs between weapons and neighboring traits (Emlen et al. 2012). However, in the horned flour beetle *Gnatocerus cornutus*, enhanced juvenile hormone analog, methoprene, resulted in large mandibles in males and also an increase in compensatory traits such as the head and prothorax (Okada et al. 2012).

Jumping spiders (Salticidae) constitute the largest spider family with more than 6,470 species (World Spider Catalog 2023). The Tribe Myrmarachnini (subfamily Salticinae: Clade Asticoidea) including the genera, *Myrmaplata*, *Myrmarachne*, and *Toxews*, comprises a majority of ant-like species (Maddison 2015; Prószyński 2016; World Spider Catalog 2023) and represents a promising lineage for studying sexual selection, trait allometry, costs, trade-offs and compensation of bearing exaggerated weapons. In myrmarachnines, adult males usually have elongated chelicerae but females and juveniles do not, showing extreme sexual dimorphism (Wanless 1978; Cushing 1997). As exaggerated male chelicerae are observed to be used in threatening displays and also in direct physical contact during male contests (Jackson 1982, 1986), it has been assumed that myrmarachnine males may use their exaggerated chelicerae as weapons during male contests, and males with longer chelicerae may have a higher chance of winning a contest (Jackson 1982, 1986). However, this notion has not been tested empirically. Furthermore, little is known about the potential costs, resource allocation trade-offs and

compensation for males to produce and carry elongated chelicerae.

A possible viability cost of bearing exaggerated chelicerae may manifest as impaired prey-capture efficiency. For example, the exaggerated chelicerae of the male spider *Myrmaplata plataleoides* lack chelicera fang ducts and have thus lost venom usage, which impedes prey immobilization and prey-capture efficiency (Pollard 1994; Nelson and Jackson 2006). Furthermore, there may be compensation between male elongated chelicerae and neighboring structures (Tomkins et al. 2005). Although a few studies have revealed trade-offs between weapons and neighboring structures in some beetles (Nijhout and Emlen 1998; Emlen 2001; Moczek and Nijhout 2004; Simmons and Emlen 2006), more studies provide support for compensation (see references above). In addition, resource allocation trade-offs seem to be especially unlikely to occur in spiders because spiders do not develop closed developmental systems (i.e., holometabolous) (Foelix 2011). We thus focused on compensation between elongated chelicerae and neighboring structures.

In the present study, we aimed to quantify chelicera allometry and determine the benefits as well as the potential costs and compensation of male elongated chelicerae in an ant-mimicking salticid spider, *Myrmarachne gisti* (Fox, 1937; Figure 1). In *M. lupata* (Jackson 1982), males often spread their chelicerae when they face each other. When approaching, both spread their chelicerae maximally. In many contests, one male, usually the smaller one, gives up (i.e., retreats) without engaging in physical contact. In other interactions, two males usually escalate by embracing (standing face to face and pressing their widely spread chelicerae together). Sometimes, a male places its fangs around both chelicerae of the other with erected legs I (i.e., biting) or attempts to step forward (i.e., pushing) while embracing. These behavioral observations suggest that male elongated chelicerae may be mainly used as a threat device at the beginning of contests and also function as a weapon when the contest escalates to the physical contact. Based on this suggestion and the hyperallometry hypothesis (Kodric-Brown et al. 2006; Eberhard et al. 2018; O'Brien et al. 2018), we expected a hyperallometry of the male chelicerae in *M. gisti* and that males with longer chelicerae win fights against males with shorter chelicerae. We also predicted that females have higher prey-capture efficiency than males. As the diet of *Myrmarachne* species contains winged prey (Jackson 1986, 1994; Greene et al. 1987) and the elongated chelicerae of male *M. gisti* may impede their locomotor activities (e.g., Fuchikawa and Okada 2013), we expected that males have a higher success at catching flightless insect prey than at catching winged insect prey. In contrast, we predicted that females have a similar success at both winged and wingless insect prey. Finally, we test whether male chelicera length is positively correlated with neighboring trait size, reflecting a compensation in resource allocation.

Materials and Methods

Spider maintenance

We collected 156 (females: $N = 68$; males: $N = 88$) *M. gisti* (Figure 1) from Wuhan City, Hubei Province, China (30.57°N, 114.33°E, 10 m a.s.l) and 22 (females: $N = 12$; males: $N = 10$) *M. gisti* from Hainan Province, China (18.698°N, 109.74°E, 508 m a.s.l). We kept them individually in cylindrical plastic

cages (height \times diameter: 8 \times 6 cm) under controlled environmental conditions (25 \pm 1 °C, 80–85% relative humidity, and 12:12 h light:dark photoperiod, lights turning on at 0800 h) following standard protocols described in other salticid studies (Lim et al. 2007; Zhou et al. 2021). The cages were wrapped with a sheet of opaque paper to prevent visual interactions among spiders. We fed spiders with 5–8 fruit flies *Drosophila melanogaster* twice a week and provided water *ad libitum*. Spiders collected as juveniles were reared and monitored until they reached sexual maturity.

Sexual dimorphism and allometry

To quantify sexual dimorphism and allometry, we measured carapace width as a proxy of body size (Jakob et al. 1996; Foelix 2011) and chelicera length (ChL) as the size of the sexually selected trait (Figure 1). We measured all body parameters to the nearest 0.01 mm as described above using preserved dead specimens following the behavioral experiments (see below).

We calculated coefficients of variation (CV%) for carapace width, chelicera length, and body length for both sexes. We \log_{10} transformed our data and calculated allometric slopes of the scaling relationship between chelicera length and carapace width (body size) using ordinary least squares (OLS) regression (Al-Wathiqui and Rodríguez 2011; Kilmer and Rodríguez 2017) in the R package *lmodel2* to investigate the static allometry of chelicera length against carapace width for both sexes. We first tested for a deviation from isometry (i.e., slope $\beta = 1$) for each sex independently by fitting an OLS regression to the scaling relationships. We then tested for a common slope between sexes by comparing these OLS regressions using sex as an interaction term in an ANCOVA (Painting and Holwell 2013).

Male–male contests

We performed male–male contest trials to test whether larger chelicerae would be advantageous to bearers during contests using a Petri dish (diameter \times height: 9 \times 2.5 cm) as the contest arena. The side of the arena was covered with white paper to preclude visual distractions due to their own reflections given that salticids have excellent vision (Nelson and Jackson 2007; Tedore and Johnson 2012). The top of the arena was covered with a piece of transparent glass to prevent the spiders from escaping during the experiments while enabling video recording from above using a Sony HDR-PJ600E camera.

Each contest trial was preceded by a 5-min acclimation phase to remove ownership effects (Elias et al. 2008), whereby two individual males were placed simultaneously into the arena separated by a removable opaque barrier dividing the arena equally. We began the contest trial by removing the barrier and ended the trial after three bouts of contests or until 15 min had passed, whichever occurred first. The start of a contest was defined as the moment both males stopped in their movements, faced each other with their anterior median eyes, and started displaying (e.g., waving legs, bent abdomen, and spread chelicerae; see display details in Jackson 1982). Retreat of a spider, characterized by the spider looking away, turning around/sideways, traveling two body lengths away from the opponent, and discontinuing their display, was considered a loss and the end of a bout. We thus defined the male that retreated as the loser and the other male as the winner. We returned the males to their individual cages after the contest

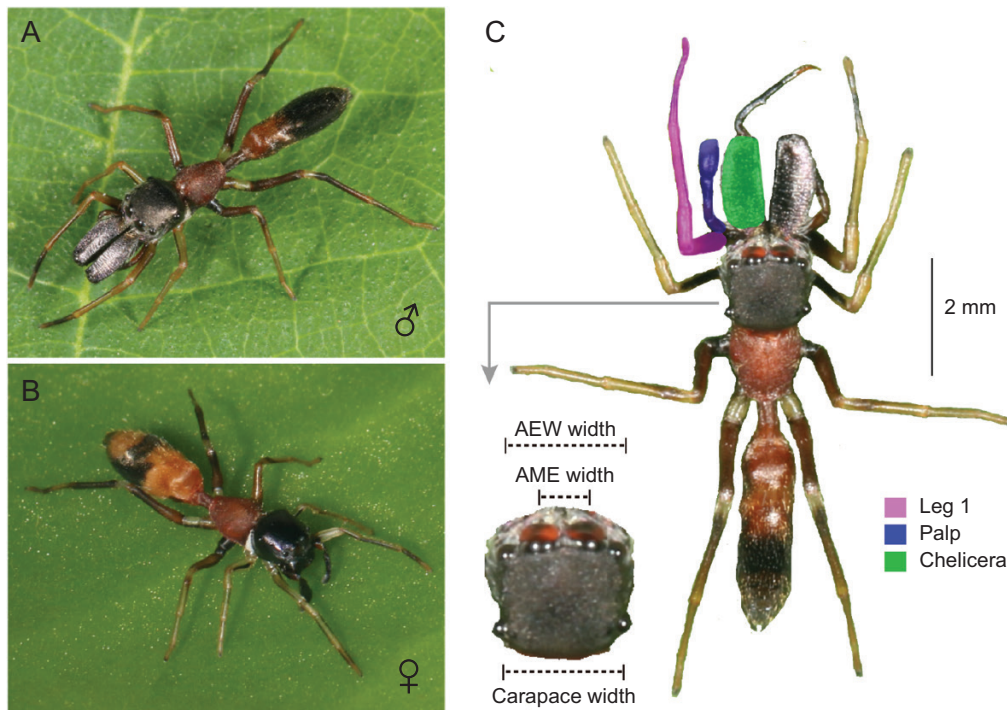


Figure 1 The ant-mimic jumping spider *Myrmarachne gisti*. (A) Adult male; (B) adult female; and (C) basic body form showing the measurements taken in this study for both males and females. AME width, anterior median eye width; AEW, anterior eye row width.

trial. We wiped the whole arena with 75% ethanol before carrying out contest trials with new individuals to eliminate chemical cues left by previous spiders (Kwek et al. 2021). We carried out a total of 25 contest trials in the spider laboratory between 0900 and 1700 h. Spiders were paired at random and no spider was used more than once. After the trials, we used a microscope (Leica M205C, German) to measure carapace width and chelicera length to the nearest 0.01 mm.

We carried out generalized linear models using *glm* function in the *lme4* package (Bates et al. 2019), with a binomial error structure and logit link function to test the effects of chelicera length and carapace width on the outcome of male-male contests. We performed the models with contest outcome for the focal male (winner = 1, loser = 0) as a binomial response variable, and included difference in chelicera length and difference in carapace width between two males as well as their interaction as predictors. We first performed the likelihood ratio test (LRT) to compare the full model (contest outcome ~ difference in chelicera length * difference in carapace width) with a null model (contest outcome ~ 1) to ensure that the full model was significant. We then ran subsequent tests for differences between the models by backward stepwise elimination of non-significant predictors using LRT tests to obtain the best-fit model with the lowest Akaike's information criterion (AIC).

Prey-capture efficiency

We carried out prey-capture trials in a Petri dish (diameter × height: 9 × 2.5 cm) to compare prey-capture efficiency between males and females using winged and flightless prey to examine whether the elongated chelicerae of male *M. gisti* impeded prey-capture efficiency with a set-up similar to that for the male-male contests. Before the trials started, all test spiders were starved for 5 days to ensure they would be motivated to catch prey.

Prey-capture trials were preceded by a 5-min acclimation phase with a spider and a prey item separated in the Petri dish. We lifted the barrier to begin the prey-capture phase and replaced the barrier to end the trial when the spider captured the prey at its first attack or 10 min elapsed, whichever came first. A trial started when the spider's anterior-median eyes oriented towards the prey (Forster 1979, 1982). Two types of prey were used: winged (wild-type) and flightless *D. melanogaster* fruit flies (mutant). Both winged and flightless fruit flies were laboratory-cultured. A total of 51 trials were performed with winged prey (females: $N = 26$; males: $N = 25$) and 45 trials with flightless prey (females: $N = 22$; males: $N = 23$). All spiders and prey were used only once.

All prey-capture trials were video-recorded from above the Petri dish using a digital HD video camera (Sony HDR-PJ600E, Japan) starting from the acclimation phase to the end of the trial. Videos were played back to record the following parameters: 1) time (s) taken from orienting towards the prey to catching it at the first attack; and 2) whether the spider caught the prey or not at the first attack. All spiders were preserved separately in 80% ethanol after the completion of male-male contest and prey-capture efficiency trials.

We used a negative binomial generalized linear model to analyze the data on the time taken to capture prey at the first attack due to the overdispersion of the data. We then conducted a generalized model with binomial error structure and logit link to determine the differences in the success (success or failure) of prey capture at the first attack between females and males for both winged and flightless prey. For both models, we included the type of prey (winged and flightless) and sex (male and female) as well as their interaction as predictors. For the first model, we used the time taken to capture at the first attack as the response variable, and we used prey-capture success (success = 1, failure = 0) as a binomial response variable for the second model. As in male-male contests, for each

analysis, we performed an LRT to compare the full model with a null model to ensure the significance of the full model. We then carried out subsequent tests for differences between the models by backward stepwise elimination of non-significant predictors using LRT to obtain the best-fit model with the lowest AIC.

Relationships between chelicera length and neighboring trait size

To assess if there are trade-offs or compensations between chelicera length and neighboring trait size, we measured chelicera length (ChL) as the size of the sexually selected trait and four traits that neighbor the chelicerae including palp length (PL), leg I length (Leg I), anterior median eye (AME) width, and anterior eye row width (AEW) (Figure 1). We defined AME width as the distance between the centers of the two large anterior median eyes, and AEW width as the width of the anterior eye row. We measured all body parameters to the nearest 0.01 mm as described above using preserved dead specimens following the behavioral experiments.

We tested for the differences in possible trade-offs and/or compensation between males and females by testing whether the relationships between chelicera length and size of each morphological trait (leg I length, palp length, AME width, and AEW) depend on sex. We performed separate linear regression models (LMs) with leg I length, palp length, AME width, and AEW as the response variable, and included the chelicera length and sex as the interaction term as the predictor. If elongated chelicerae affect the developing neighboring trait size, we expected trade-offs as negative correlations or compensation as positive correlations between chelicera length and the sizes of other morphological traits. If there is a significant interaction effect, we expected a significant difference between males and females in the relationship between chelicera length and that neighboring trait size.

All data were analyzed using R v4.2.1 (R Core Team 2022).

Results

Chelicera size, sexual dimorphism, and allometry

Myrmarachne gisti showed a high degree of sexual dimorphism in chelicera length and carapace width, but not in body length (Table 1). Males had longer chelicerae and wider carapaces than females. In addition, males showed higher coefficients of variation (CVs) than females for all body size parameters except body length. The CVs of the measures of chelicera length were much higher than other measures of body size in males, but CVs of the measures of chelicera length were slightly higher than other measures of body size in females.

Chelicera length showed a hyperallometric relationship with carapace width (body size) for males (slope $b = 1.84$, 95% confidence interval (CI) = 1.45–2.23) but isometry for females (slope $b = 0.89$, 95% CI = 0.47–1.30) (Figure 2). The slope of the allometry in males was significantly steeper than that in females as sex was a significant interaction term in the ANCOVA ($F_{155,157} = 334.68$, $P < 0.0001$, Figure 2).

Male–male contests

Male–male interactions often started when they faced each other. Then, they spread their chelicerae during posturing. When approaching, both spread their chelicerae maximally. Next, one usually decamped and then they backed apart or

ensued embracing. Sometimes biting or pushing followed embracing. There were cases of contests in which smaller males with short chelicerae retreated without escalating to physical contact, and other cases in which larger males that matched in chelicera length often escalated to physical contact by embracing, biting, or pushing using their chelicerae.

The full model was significantly better than the null model in fitting the data on male contest outcomes (likelihood ratio test: $\chi^2 = 12.32$, $df = 3$, $P = 0.006$, AIC = 27.03). The difference in chelicera length between the two males alone was the best predictor of the outcomes of male contests (GLM: $\beta = 3.53$, $Z = 2.54$, $P = 0.011$; Table 2). Males with longer chelicerae were more likely to win a contest (Figure 3). The difference in carapace width between the two males alone and the interaction between difference in carapace width and difference in chelicera length had no significant effects on the outcomes of male contests (Table 2).

Prey-capture efficiency

The full model was not significantly better than the null model in fitting the data on the time taken to capture prey at the first attack (LRT: $\chi^2 = 4.03$, $df = 3$, $P = 0.258$). Sex ($\beta = -0.97$, $Z = -0.92$, $P = 0.055$) and prey type ($\beta = -0.61$, $Z = -1.21$, $P = 0.226$) alone had no significant effects on the time taken to capture prey at the first attack (Figure 4A). There was also no significant interaction between sex and prey type ($\beta = 1.23$, $Z = 1.787$, $P = 0.074$).

The prey-capture success at the first attack was slightly higher in females compared to in males for winged prey (male: 44%; female: 50%) but much higher in males compared to in females for flightless prey (male: 61%; female: 36%). The full model was also not significantly better than the null model in fitting the data on whether or not the spiders successfully captured prey at their first attack (LRT: $\chi^2 = -2.95$, $df = 3$, $P = 0.400$). Sex ($\beta = 1.00$, $Z = 1.63$, $P = 0.104$) and prey type ($\beta = 0.56$, $Z = 0.95$, $P = 0.334$) alone, as well as their interaction ($\beta = -1.243$, $Z = -1.49$, $P = 0.136$), had no significant effect on whether the spider successfully captured prey at its first attack (Figure 4B).

Relationship between chelicera length and neighboring trait size

We found that chelicera length was significantly positively correlated with all neighboring trait size parameters in both males and females (Figure 5). There was a significant difference between males and females in the relationship of chelicera length with palp length (interaction ChL: sex[male]: $\beta = -1.77$, $t = -5.85$, $P < 0.0001$) and legs I (interaction ChL: sex[male]: $\beta = -2.30$, $t = -4.41$, $P < 0.0001$). However, there was no significant difference between males and females in the

Table 1 Mean (\pm SD) and coefficient of variation (CV%) of three traits for adult males (N = 79) and females (N = 80) of *Myrmarachne gisti*

Trait	Male		Female	
	Mean \pm SD	CV (%)	Mean \pm SD	CV (%)
Chelicera length	1.49 \pm 0.54	36.24	0.50 \pm 0.11	22.00
Carapace width	1.12 \pm 0.17	15.18	1.07 \pm 0.12	11.21
Body length	5.46 \pm 0.92	16.85	5.52 \pm 0.90	16.30

The unit of measurement is mm.

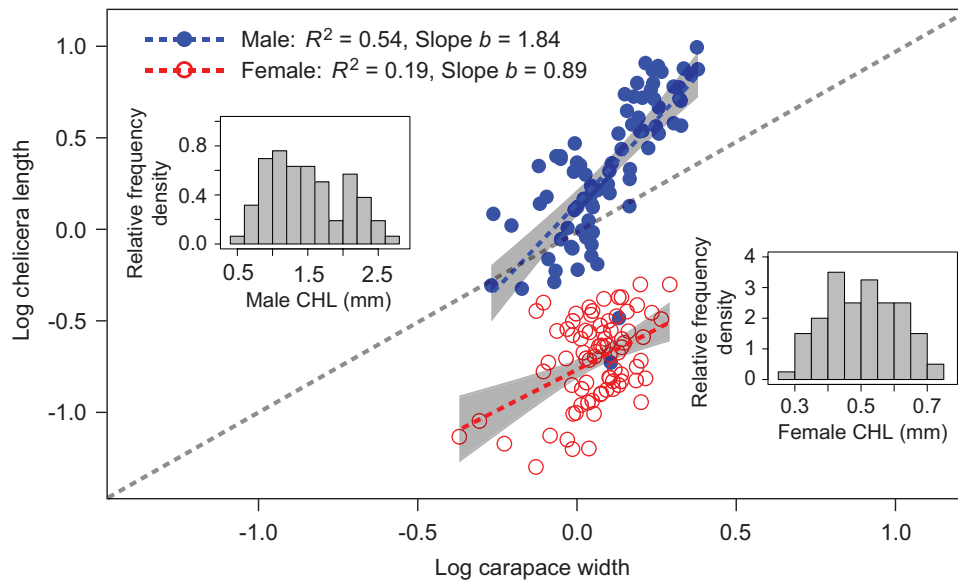


Figure 2 Frequency distribution of chelicera length (ChL) for adult *Myrmarachne gisti* males ($N = 79$) and females ($N = 80$) as well as the scaling relationship between log chelicera length and log carapace width for both males (blue filled circles) and females (red circles). A linear regression line is fitted for both males (blue dashed line) and females (red dashed line) and 95% confidence intervals around the regression line are shown in gray. The dotted line represents isometry (1:1 relationship on a log scale). The slope of the allometric relationship for males was significantly steeper than that for females ($F_{155,157} = 334.68, P < 0.0001$).

Table 2 Results of the generalized linear model (GLM) testing for the effects of difference in chelicera length (ChL) between males, difference in carapace width (CW) between males, and the interaction between the two main factors on the male contest outcomes

Predictor	β	SE	Z	P
Intercept	-0.53	0.78	-0.68	0.498
Difference in chelicera length (ChL)	3.52	1.39	2.54	0.011
Difference in carapace width (CW)	-1.70	1.90	-0.89	0.372
Difference in ChL: difference in CW	1.93	5.33	0.36	0.717

Number of trials: $N = 25$.

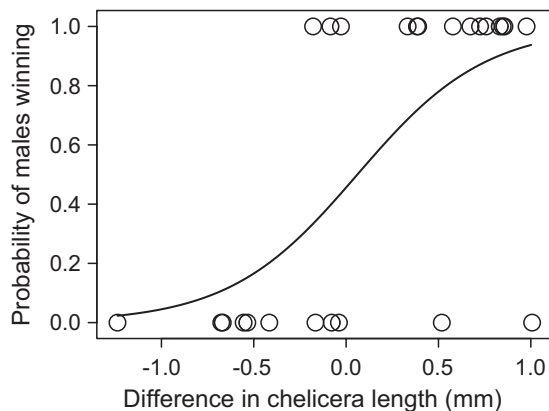


Figure 3 The relationship between difference in chelicera length between two males and the probability of the males winning a contest in *Myrmarachne gisti*. Number of trials: $N = 25$.

relationship of chelicera length with AME width (interaction ChL: sex[male]: $\beta = -0.13, t = -1.74, P = 0.085$) and AEW (interaction ChL: sex[male]: $\beta = -0.11, t = -0.82, P = 0.411$).

Discussion

Sexually selected contested-related weapons are expected to improve male fitness in various ways (Andersson 1994; Painting and Holwell 2014; O’Brien et al. 2018) and may also impose a number of different costs (Kotiaho 2001; Bonduriansky 2007; Goyens et al. 2015; Rico-Guevara and Hurme 2019). Focusing on just the benefit or just one type of cost may lead to the oversight of some important fitness consequences of sexual trait exaggeration (Kotiaho 2001). This study is among the few studies that simultaneously investigates both the benefit and a combination of several types of costs of a sexually selected weapon. After first having tested the prediction of the hyperallometry hypothesis by quantifying the allometry of chelicerae size in the ant-mimicking jumping spider *M. gisti*, we then determined the competitive advantage of the exaggerated chelicerae in male contests and measured two types of relevant costs associated with producing and bearing such an exaggerated trait. As in an earlier study of *M. luptala* (Jackson 1982), our behavioral observations of male-male contests in *M. gisti* suggest that the elongated chelicerae function as both a threat device and a weapon: it is first used as a threat device during the initial phase of the fights and as a weapon for embracing or pushing rivals when the fight escalates. As predicted, male chelicerae scale steeply positively with overall body size, showing hyperallometry. We also provide strong evidence for the competitive advantage of *M. gisti* males bearing longer chelicerae during contests with males with relatively shorter chelicerae. Despite being beneficial in male contests, there is no evidence for any of the costs in terms of foraging performance or allocation trade-off. The elongated chelicerae do not impair overall prey-capture efficiency at the functional level and also do not stunt the growth of neighboring structures at the physiological level. In fact, palps, legs I, and anterior eye row width (AEW) are positively correlated with chelicera length in males. Taken together, the exaggeration of male *M. gisti* chelicerae is likely driven by

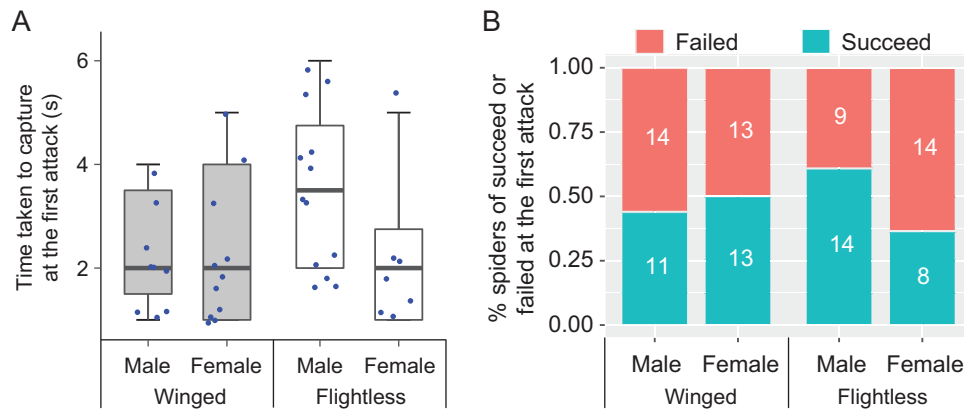


Figure 4 Prey-capture efficiency of male and female *Myrmarachne gisti* showing (A) the median time (s) taken to capture winged (male: $N = 25$; female: $N = 26$) and flightless prey (male: $N = 23$; female: $N = 22$) at the first attack; and (B) percentage (%) of males and females that succeeded or failed to capture winged prey and flightless prey at their first attack. The number inside the bar represents the number of spiders. Boxplots show the data as jittered dots, with the box indicating the interquartile range (IQR), the whiskers showing the range of values that are within 1.5*IQR and a horizontal line indicating the median.

sexual selection via male-male competition at a limited performance or physiological cost.

As expected and also demonstrated in other *Myrmarachne* species (Jackson 1982, 1986; 1994; Qu et al. 2017), *M. gisti* shows extreme sexual dimorphism in chelicera size with males bearing much longer chelicerae than females, which may be driven by sexual selection via male-male competition. Despite being sexually dimorphic, this sexual dimorphism in chelicera size alone does not provide sufficient evidence for sexual selection because other selective pressures, such as differences in foraging behavior, can also produce sexual dimorphism (i.e., ecological selection; reviewed in Rico-Guevara and Hurme 2019). Among spiders, the potential drivers of the extent of sexual dimorphism within a species are mainly natural versus sexual selection, and also sexual conflict and ecological factors (Kuntner and Cottington 2020). In this way, *M. gisti* males would be expected to have traits that reflect their more mobile and competitive reproductive role (Aisenberg et al. 2010). It is thus not surprising that males have longer chelicerae in contests and longer legs for increased mobility. Sexual selection might therefore have driven sexual dimorphism in chelicera length owing to their roles in male contests (this study) and/or female mate choice (Qu et al. 2017) in *Myrmarachne*.

Males also exhibited a much higher degree of variation in chelicera length compared to females. This is not surprising because evidence shows that sexually selected traits show greater phenotypic and genetic variation compared to non-sexually selected traits, given that they are heightened condition dependent (Pomiankowski and Møller 1995). If developing weapons through time and energy is costly (Kotiaho 2001), variation in the ability to acquire and allocate resources would lead to high variation in trait expression (Zahavi 1975; Cotton et al. 2004; Painting and Holwell 2014). This has been reported in the sexually selected traits of other species of spiders, such as in the New Zealand sheetweb spider *Cambridgea plagiata* (McCambridge et al. 2019), of insects, such as horns of the rhinoceros beetles (Johns et al. 2014; Bertram et al. 2021; reviewed in Emlen and Nijhout 2000) and of vertebrates such as tusks of narwhals (Graham et al. 2020).

Male chelicerae showed a steeper positive allometric relationship in *M. gisti*, indicating that larger males have

disproportionately larger chelicerae than do smaller males. This is consistent with the functional allometry hypothesis (Eberhard et al. 2018) that direction selection often favors positive allometry in threat devices, such as elongated chelicerae in this study and long legs II in harvestman (Palaoro et al. 2022), or weapons used for lifting or pushing rival males during the physical combat, that is, depending on their fighting style. Large chelicerae may improve the fighting ability of *M. gisti* males by allowing them to inflict more costly contests (Foelix 2011; Segalerba and Toscano-Gadea 2016) or by providing a large gape that allows them to bite, embrace, and push rivals (Mills et al. 2016). As in another ant-mimicking salticid, *M. lupata* (Jackson 1982), in *M. gisti*, chelicerae were directly involved during male-male contests by widely spreading them during posturing (i.e., as threat devices), biting, embracing, and pushing with the rivals (i.e., as weapons). Whenever there were obvious disparities in body size during contests, the smaller male withdrew from the larger male, whereas larger males that also had larger chelicerae always had them spread during contests. Perhaps smaller males detected chelicera size visually from a distance and acquired further information on prowess tactually during embracing and pushing (Jackson 1982). As other sexually selected weapons in many other animals (Eberhard et al. 2018; Rico-Guevara and Hurme 2019; Palaoro et al. 2020), the exaggerated chelicerae that function as both threat devices and weapons for embracing and pushing during male contests are thus more likely to exhibit hyperallometry, which is driven by sexual selection via male-male competition in *M. gisti*.

This hyperallometry may explain the significant role of long chelicerae in winning a contest in our male contest trials. In many animals, a larger threat device is often correlated with an honest signal (e.g., size, strength, and fighting ability) (Eberhard et al. 2018) and a larger weapon involved in lifting and pushing usually correlates with better measures of performance (McCullough et al. 2014, 2015; reviewed Palaoro et al. 2022). Thus, the fact that larger *M. gisti* males had larger chelicerae which were always spread during contests may convey the information about the size and fighting ability, and also reflect the better measure of performance provided by larger chelicerae. Similar results were also reported in the jumping spider *Lyssomanes viridis*, where chelicera length influenced the outcomes of male contests (Tedore and

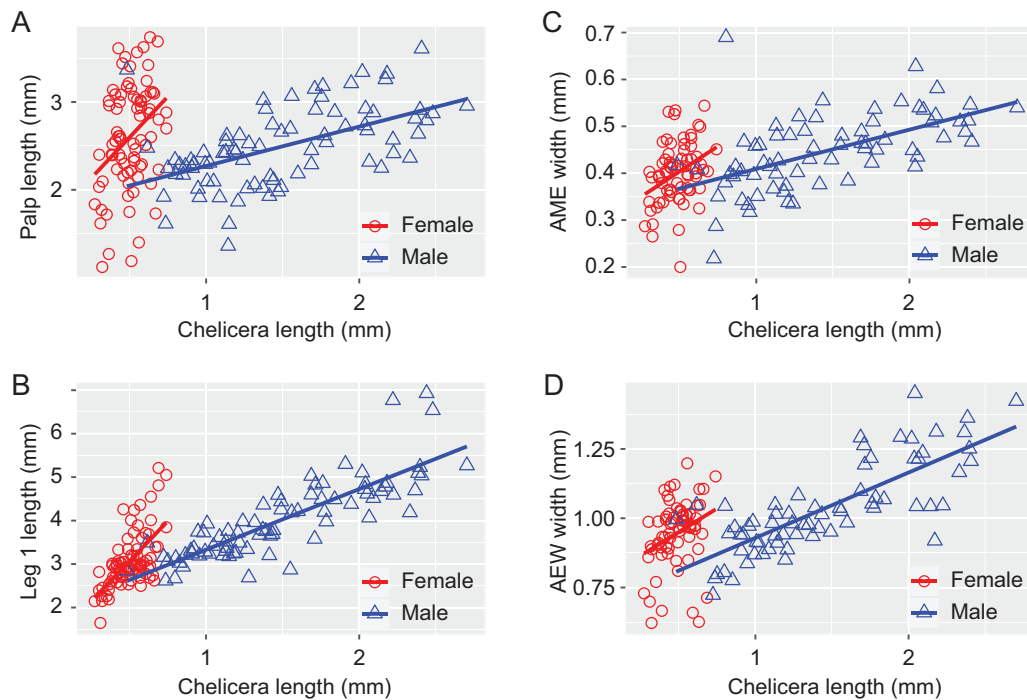


Figure 5 The relationship between chelicera length and (A) palp length; (B) leg I length; (C) anterior median eye (AME) width; and (D) anterior eye row width (AEW) in both males and females of *Myrmarachne gisti*. Linear regression lines are plotted for all significant relationships.

Johnsen 2012). The function (e.g., the fighting style and the way chelicerae are used during the contests) of chelicerae can thus be important for predicting contest outcomes as found in other animals (reviewed in Rico-Guevara and Hurme 2019; Palaoro et al. 2022).

Contrary to our prediction, the elongated chelicerae of *M. gisti* males had no significant impact on the efficiency of catching either winged or flightless prey, albeit males took longer to capture winged prey than flightless prey. Previous studies have shown that there was a trade-off in prey-capture efficiency in *Myrmarachne* species so far examined (Jackson 1986, 1994). Males were less efficient than females at capturing winged insects and large moths, but appeared to be as efficient as females at capturing flightless prey and winged insects that are slow to take flight such as small moths (Jackson 1986, 1994). This difference could be due to different *Myrmarachne* species or testing procedures between our study and previous studies. However, our results showed that for flightless prey, mean prey capture time at their first attack for males was shorter than that of females (male: 4 s; female: 10 s) and the success rates of males were higher than those of females at their first attack (male: 61%; female: 36%) although these differences were not statistically significant. It seems that males are more effective hunters than females against flightless prey, suggesting that *M. gisti* male diets may be biased towards flightless prey as compared to females. This is because long chelicerae make males less efficient at feeding winged prey. In addition, feeding on the eggs of other spiders is an important feeding method in all *Myrmarachne* species that have been studied so far, and there was an apparent advantage of the males' larger chelicerae for preying on other spiders' eggs compared to females' normal chelicerae (Jackson 1986, 1994). Further studies are needed to investigate whether *Myrmarachne* males in nature prey on eggs more than females.

We found no evidence of a trade-off that would be evident from a phenotypic correlation between chelicera length and any of the neighboring structures measured in *M. gisti* males. Instead, we found that the sizes of all four neighboring traits (i.e., palp length, leg I length, anterior middle eye width (AME), and anterior eye row width (AEW)) were positively correlated with male chelicera length. These results indicate that those males investing more in their chelicera growth also invest heavily in the growth of these neighboring traits. Like other *Myrmarachne* species (Jackson 1986, 1994), in male contests, *M. gisti* usually display with legs I erected and always in conjunction with spread chelicerae. Together with spread chelicerae, erecting legs I is also used as a threat device in the earlier phase of male contests, which may provide reliable information about the male size and perhaps strength as in other spiders and harvestmen (Eberhard et al. 2018). Furthermore, visual prowess is often limited by the size of the eyes. Larger anterior middle and lateral eyes and a wider front eye row in males with longer chelicerae may improve the focal length for seeing better and detecting motion beyond the length of the chelicerae from a distance during contests. Nevertheless, we cannot rule out the possibility that the lack of a negative correlation between chelicera length and the neighboring structures does not necessarily indicate the absence of a trade-off between traits, given that there are likely variations in resource acquisition amongst individual males. An experimental or genetic approach should be used to test for such a trade-off in future studies. Furthermore, it would be of interest to test the hypothesis about the trade-off between weapons and testes, which is commonly found in animals (Simmons and Emlen 2006).

Another explanation for the positive correlations between weapon traits in *M. gisti* is that increased size of legs I and anterior eyes (AME and AEW width) may compensate for costs associated with increased chelicera size. Producing and

wielding weapons can be costly, and the exaggerated weapons may thus carry costs unrelated to sexual selection, which natural selection would act to reduce (Andersson and Iwasa 1996). However, given that compensation through correlated growth acts to reduce costs, it is difficult to detect the pure costliness of the trait/weapon in question. By increasing the length of palps, legs I, and anterior eyes, it is possible that some *M. gisti* males have compensated for bearing relatively large chelicerae for their body size, while suffering no costs to mobility. Therefore, weapons may be developmentally associated with other structures to enable males to wield them more effectively during contests or courtship (Tomkins et al. 2005; Okada and Miyatake 2009).

We also found a positive phenotypic correlation of chelicera length with size of all neighboring traits in females in *M. gisti*. This indicates that, similarly to males, those females that invest heavily in their chelicerae for their body size also invest heavily in these traits. However, our results show that while both palp length and legs I were positively correlated with their chelicera length in both males and females, it seems that females need to invest more heavily in palp length and legs I with a small increase in chelicera length than males. This pattern is not observed for the relative anterior eye size in both males and females as there was no significant difference between males and females in the relationships of chelicera length with AME width and AEW. These traits are thus under correlated selection in both males and females, but there are differences in ways that males and females compensate for increasing palp length and legs I, not for relative anterior eye size in *M. gisti*. Further studies are needed to explore the developmental mechanisms responsible for such a difference.

Sexually selected exaggerated traits may incur other types of costs. In our study, we did not test the performance costs of male locomotion while carrying large chelicerae. It has been reported in fiddler crabs (*Uca pugilator*) that the removal of the major claw (comprising on average 30% of total body mass) does not result in faster sprint speeds for males, but the mass-specific metabolic rates are higher and endurance capacity is lower for males bearing an exaggerated claw compared with those without (Allen and Levinton 2007). In the future, it would be interesting to measure metabolism when spiders are at rest and while active (O'Brien et al. 2019; Somjee et al. 2021). In addition, we may test other types of prey, such as those with large body size and hard cuticle to examine the locomotion economics of the elongated chelicerae during foraging. Moreover, the elongated chelicerae may incur unwanted attention from predators (Nelson and Jackson 2006), since the exaggerated chelicerae may render the morphology of ant-mimicking salticid spiders a deviation from the model ants they mimic, and probably make them slower at escaping predators as the chelicerae constitute a large proportion of body mass. Future studies should thus investigate the relationship between chelicera length and the risk of predation, that is, the potential long-term cost in terms of survival rates, with regard to their effect on myrmecomorphy. Finally, even if we can demonstrate that a sexually selected weapon directly causes fitness costs, it is not enough (Kotiaho 2001; McCullough and Emlen 2013). Unfortunately, we did test whether the potential costs, if any, of the exaggerated chelicerae reduce male survival in *M. gisti* in this study.

In summary, in contrast to one of the most basic assumptions of sexual selection theory that exaggerated traits are expensive to produce and wield, we found that sexually

selected chelicerae in males of the ant-mimicking jumping spider, *M. gisti* do not necessarily carry substantial costs in terms of prey-capture efficiency. If our results from *M. gisti* are typical for *Myrmarachne* and other jumping spider lineages, and exaggerated chelicerae are indeed not expensive to produce and wield, then chelicerae may be free to diverge in size and form. However, to understand the differences in chelicera morphology among species, future studies are needed to investigate whether particular chelicera design may perform better than others depending on how they are used (i.e., the fighting style).

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Conflict of Interest Statement

The authors have no relevant financial or non-financial interests to disclose.

Author Contributions

D.L., H.Z.L., C.J.P., G.C.Y., and S.C.Z. conceived and designed the study. H.Z.L., G.C.Y., and Z.T.Z. collected the data. D.L., H.Z.L., C.J.P., G.C.Y., L.Y., and S.C.Z. analyzed the data. All authors contributed critically to the drafts and gave final approval for publication.

Availability Accessibility

All supplementary tables are available in Supplementary Material. All data and R codes used in this study are available from the Mendeley Data (doi: [10.17632/7dp7v8gmsy.1](https://doi.org/10.17632/7dp7v8gmsy.1)).

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