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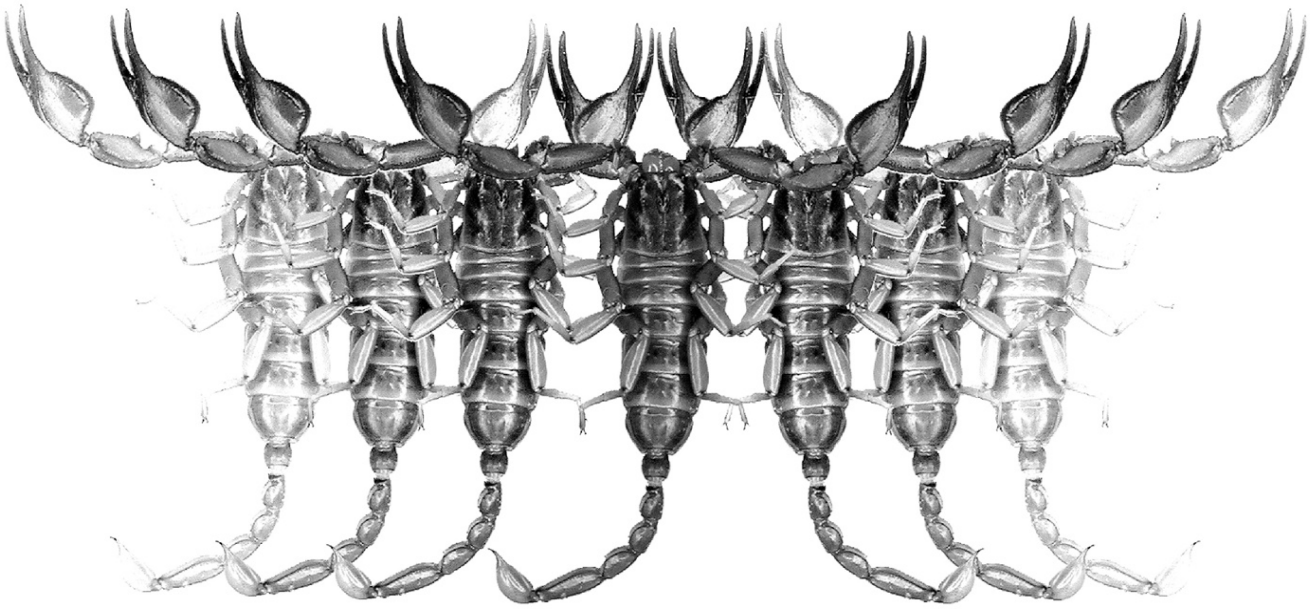

Non-aggressive competition between males of *Srilankametrus yaleensis* (Kovařík et al., 2019) (Scorpionidae), and other types of agonistic behavior observed in scorpions

Victoria Tang

January 2023 — No. 368

Euscorpius

Occasional Publications in Scorpiology

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The name ***Euscorpius*** Thorell, 1876 refers to the most common genus of scorpions in the Mediterranean region and southern Europe (family Euscorpiidae).

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Publication date: 28 January 2023

http://zoobank.org/urn:lsid:zoobank.org:pub:51052E5A-A2FB-4C14-BD10-5C378C762D8A

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Non-aggressive competition between males of *Srilankametrus yaleensis* (Kovařík et al., 2019) (Scorpionidae), and other types of agonistic behavior observed in scorpions

Victoria Tang

Zhangyang Rd. 200120, Pudong New District, Shanghai, China; email: jibril.flueqel@gmail.com

http://zoobank.org/urn:lsid:zoobank.org:pub:51052E5A-A2FB-4C14-BD10-5C378C762D8A

Summary

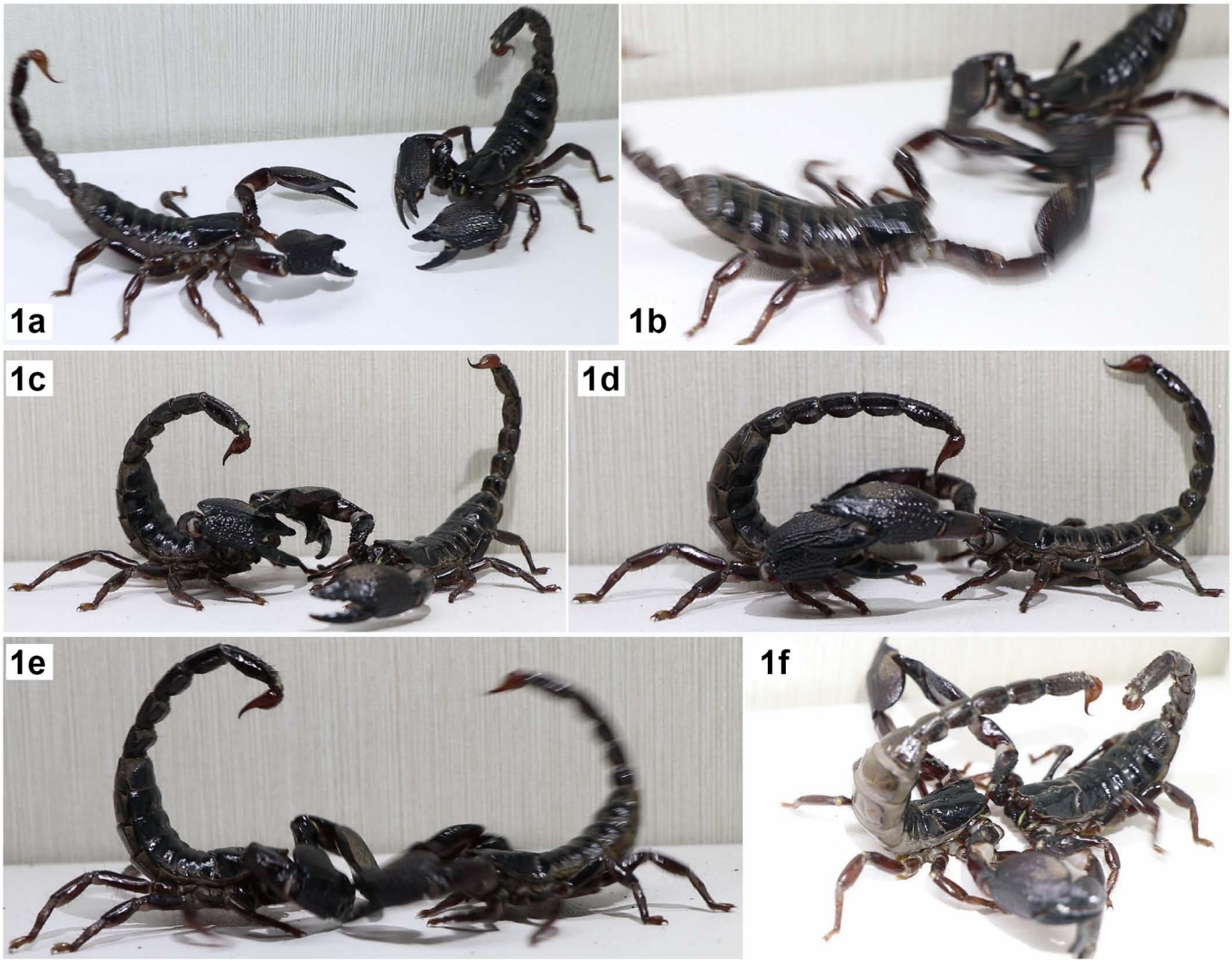
A peculiar intraspecific agonistic behavior involving a non-aggressive physical combat is reported between the adult males of *Srilankametrus yaleensis* (Kovařík et al., 2019) (Scorpionidae: Heterometrinae). The adult males were observed to resort to a ritualized and relatively gentle way for strength demonstration. The combat is characterized by lateral spreading of pedipalps, chelicerae-to-chelicerae collision, and entanglement of metasomal segments. This behavior is hereby considered a form of an intrasexual combat defined as the "arm-span competition". It is hypothesized to be beneficial for solving territorial and/or sexual competitions while avoiding unnecessary mortality which could pose adverse impact to the natural populations. Other Heterometrinae species that possess sexually dimorphic, elongate pedipalps in males were also found to display similar behavior. This may account for at least one potential reason for the evolution of such sexual dimorphism. Finally, this study supplements several other agonistic behaviors (intraguild or antipredatory) observed in scorpions, with special attention to the family Scorpionidae. Three basic types of behavior are defined for this family: aggressive response, shielding response, and arm-span competition. These types of behavior may have implications for the evolution of this family.

Introduction

Competition among animals is an intra- or interspecific interaction in which the species compete for limited sources such as food, space, and mates, leading to either coexistence or exclusion (Hardin, 1960). It is considered as a crucial factor influencing the species diversity, guild structure and population dynamics, and is important in natural selection (Agrawal, 2007). Competition can be direct or indirect between different individuals; three major mechanisms are recognized: exploitation competition, interference competition, and apparent competition (Holomuzki et al., 2010). The former two share the similarity in competing for a limited source (e.g., food, water, territory, mates), while the third is manifested by competing survivorship between two species sharing a same predator (Hatcher et al., 2006).

Natural competition reported in scorpions mainly focused on the exploitation competition for a specific microhabitat, burrow site, or food (Polis & Sissom, 1990; Lira & Souza, 2014; Nime et al., 2016; McReynolds, 2020). These types of spatial competition become ubiquitous when the surface temperature is favorable for scorpions to leave their shelters. Polis & Sissom (1990) assumed that the preferable temperature acts as a physical cue suggesting food availability since the warm surface temperature is positively correlated with the prey abundance, and successively, the scorpion density (hence increasing the probability of intraguild contact). However, the use of different substrates could reduce the possibility of contact and subsequent interspecific conflicts (Warburg, 2000; Lira et al., 2013; Lira & Souza, 2014). Intraguild predation (direct competition), including cannibalism, is also widespread among scorpions, and may occur during the exploitation competition (Polis & McCormick, 1987; Toprak et al., 2022). Temporal differences of activity are present in various age groups of many scorpion species: generally, larger or adult individuals are more active in warm months or periods within a day (synchronized with prey abundance), whereas smaller or immature individuals tend to occur above ground more often in cooler months or periods (avoidance of adults and/or food competition) (Polis & Sissom, 1990; Polis & McCormick, 1987; Ramos, 2007). These differences may indicate a response to selective pressures such as the intraguild predation.

Intraguild competition (a paramount factor that determines the mortality among sympatric species, including intraguild predation) is hypothesized to be solved by different types of balance which decrease overlap and allow coexistence (Polis & Sissom, 1990): (1) exploitation competition for limited resources (food and space) is adjusted by the ecological divergence of different species in their use of these resources; (2) interference competition (aggression and territory) selects for subordinate species avoidance of more dominant species; (3) predation of the apparent competition can be restricted by environmental disturbance (e.g., periodic fires, storms, or



Figures 1a–**1f**. Developing from the initial stage to the confronting stage. **Figure 1a**. Initial stage, showing a defensive posture (left, A1, right, A2). **Figure 1b**. Initial stage, tentative pinching when mutually touched (left, A1, right, A2). **Figure 1c**. Initial stage, showing a shielding posture (left, B1, right, B2). **Figure 1d**. Initial stage, one trying to suppress the other (left, B1, right, B2). **Figure 1e**. Initial stage, shielding collision (left, B1, right, B2). **Figure 1f**. Spanning pedipalps, developing into confronting stage (left, A1, right, A2).

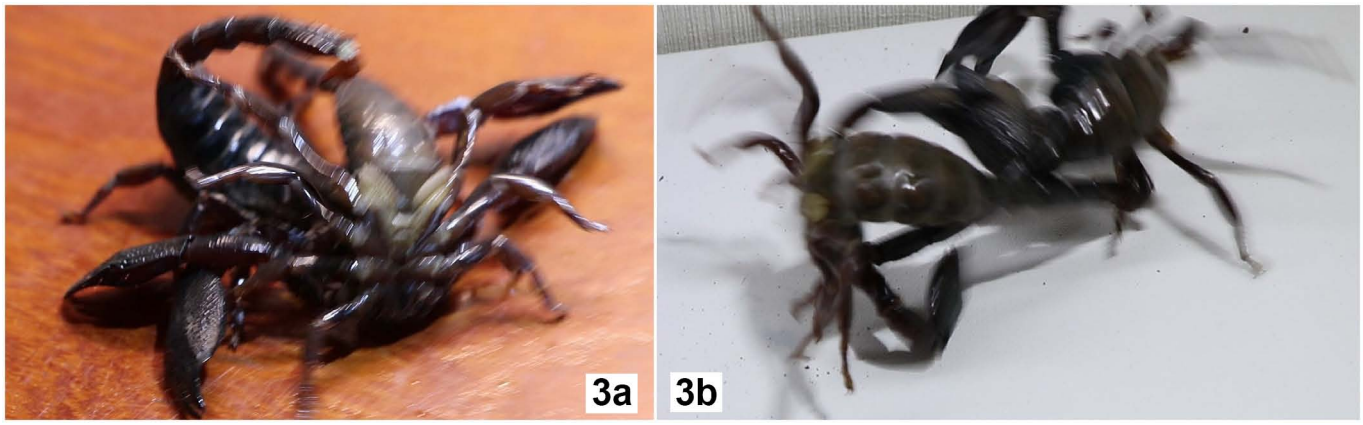
droughts) that prohibit excessive predation towards certain species. Scorpion affiliation is also balanced by temporal differences (including physiological adaptions towards different climates), microhabitat preferences (which are also manifested by ecomorphological adaptions), foraging modes (e.g., in vegetation, on the ground and at the burrow entrance), which can reduce negative interactions.

Although the ecological competition for food, space and mates has been well-studied among various scorpion taxa, the physical combat between adult male scorpions is rarely documented given a relatively low likelihood of spotting such an event in the wild. Physical combat (or fighting behavior) is another form of the interference competition apart from the intraguild predation that involves direct physical interactions between individuals; it is also a form of agonistic behavior (Scott & Fredericson, 1951). Sexual selection by male-male competition has been widely reported in some of the other arachnids, such as spiders, harvestmen (Opiliones), whip spiders (Amblypygi) and whip scorpions (Thelyphonida, or Uropygi *sensu stricto*) (e.g., Alexander, 1962; Weygoldt, 2002; Maklakov et al., 2004; Foellmer & Fairbairn, 2005; Willemart et al., 2009; Schütz & Taborsky, 2011; Tedore & Johnsen, 2012; Watari & Komine, 2016; Chapin & Reed-Guy, 2017); some of these types of behavior are not exhibited as direct physical combat (e.g., Christenson & Goist, 1979; Miyashita, 1993; Moya-Laraño et al. 2002; Moya-Laraño et al., 2009). Benton (1992) was probably the first and the only author to report the male physical combat in scorpions. In an introduced population of *Tetratrichobothrius flavicaudis* (De Geer, 1778) in Sheerness, Kent, England, males were found to stay in the same crack with females during the mating season. This was defined as the "mate guarding" behavior, usually involving a second-to-last instar female, or a parturient female (or while carrying offspring), and a mature male. When another male approached the crack, these two males would try to grasp each other with their chelae for only a few seconds before the

Figures 2a–**2f**. Confronting stage. **Figure 2a**. Spreading the pedipalps, lateral view (left, A2, right, A1). **Figure 2b**. Spreading the pedipalps, posterior view (distal, A1, proximal, C). **Figure 2c**. Metasoma of the two males entangling with each other (left, C, right, A1). **Figure 2d**. One being lifted up by the "metasomal hook" (left, C, right, A1). **Figure 2e**. Lifting, lateral view (left, A1, right, C). **Figure 2f**. Lifting, posterior view (proximal, A1, distal, C).

loser fled. In 2 of 140 contests which escalated into a fierce fight, it always involved a larger guarding male and a smaller intruding male. Normally, the larger or the original male won the contest (Benton, 1992).

Srilankametrus yaleensis (Kovařík et al., 2019) was initially described in the genus *Heterometrus* Ehrenberg, 1828, from the southern region (Yala National Park, Southern Province) of Sri Lanka, and subsequently moved to genus *Srilankametrus* Couzijn, 1981 by Prendini & Loria (2020). This species is an obligatory burrower (it constructs oblique, 30 to 50 cm long burrows once or twice curved, situated in open terrain (Kovařík et al., 2019)). Obligatory burrowers (fossorial species) in scorpions exhibit a generally low surface activity; immatures never occur above ground except when they are dispersing away from their maternal burrows, while adults usually only come to the surface during the mating season (Polis & Sissom, 1990). According to Polis & Sissom (1990), among the adults wandering on surface, most are adult males in search of females. Consequently, this leads to a high possibility of male-male encounter. Mortality of male scorpions is generally higher than that of females, which is basically attributed to the behavioral differences between sexes during the mating season (Polis & Sissom, 1990). Vagrancy in males predisposes them to a higher incidence of cannibalism, intraguild predation and the predation by vertebrates (Polis & Sissom, 1990). Prolonged movement on the surface also makes the males more likely to experience starvation and thermal death (Polis & Sissom, 1990).



Figures 3a–3b. Comparison of aggression between arm-span competition and stinging fighting behavior. **Figure 3a**. No fighting occurred after one was pulled over (left, A1, right, C). **Figure 3b**. Violent fighting occurred at the initial stage when both individuals were infuriated (left, A1, right, B1).

Figure 4. Escaping stage (right male (A2) fled).

The studied species, *Srilankametrus yaleensis*, also displays the chelal shielding behavior (lifting the pedipalp with two chelae positioned next to each other as a shield; below, termed as a "shielding response"; Fig. 10b) under predatory pressure (simulated by artificial stimuli; Tang, pers. obs.) apart from the stridulation (Alexander, 1959). Such shielding response is prevalent in many Scorpionidae with rounded and powerful chelae (e.g., Heterometrinae, Opistophthalminae and Pandininae; Tang, pers. obs., Table 1). At least in some species, those chelae are also utilized for sealing the entrance of a burrow, preventing intrusion from potential adversaries (e.g., in *Scorpio fuscus* (Ehrenberg, 1829); Polis & Sissom, 1990).

The present study reports a peculiar intraspecific physical combat behavior (below, defined as the "arm-span competition") between males of *Srilankametrus yaleensis* that is assumed to be beneficial in avoiding unnecessary mortality, while at the same time, guarantees the balance of food and space resources for each individual in the wild populations, and possibly, the beneficial genetic traits to be passed down through generations.

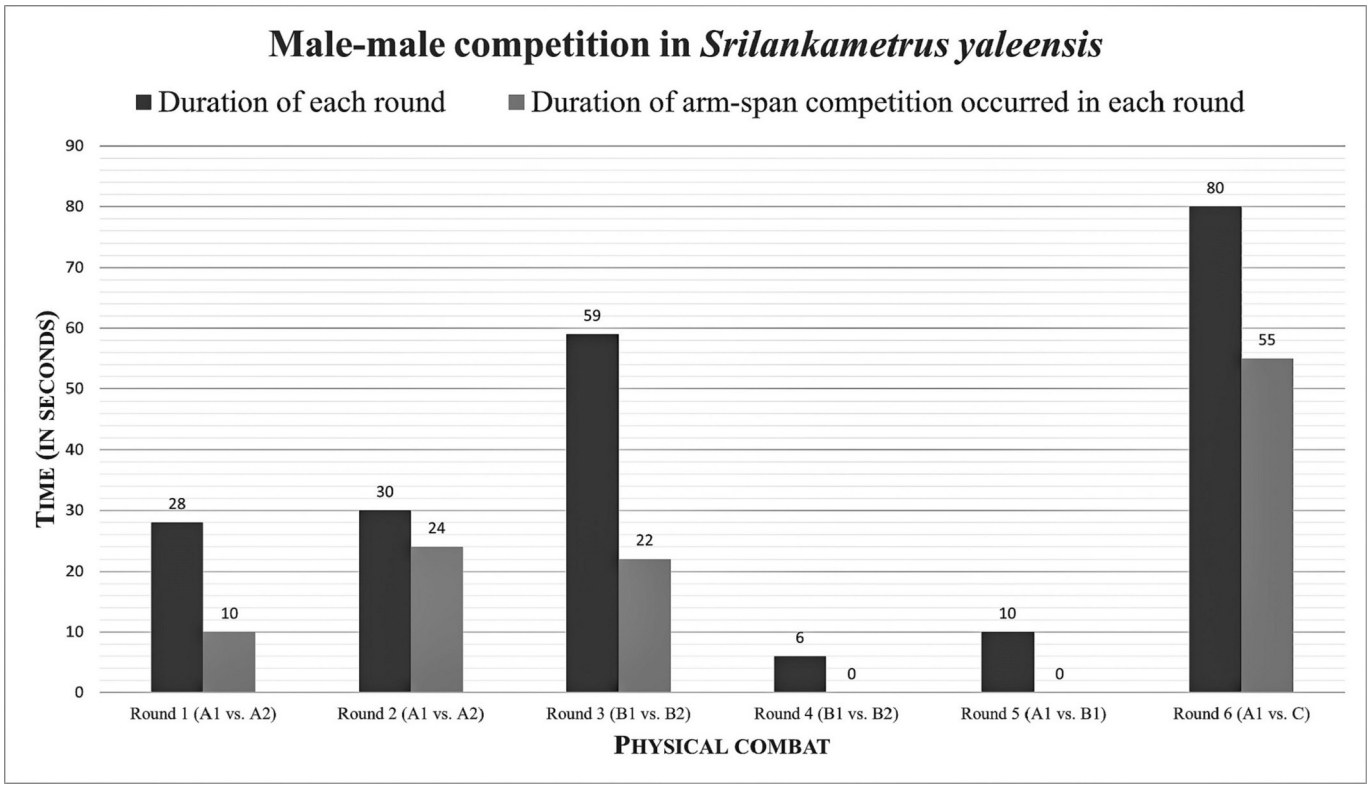


Figure 5. Duration of each round and that of arm-span competition occurred in each round (in seconds).

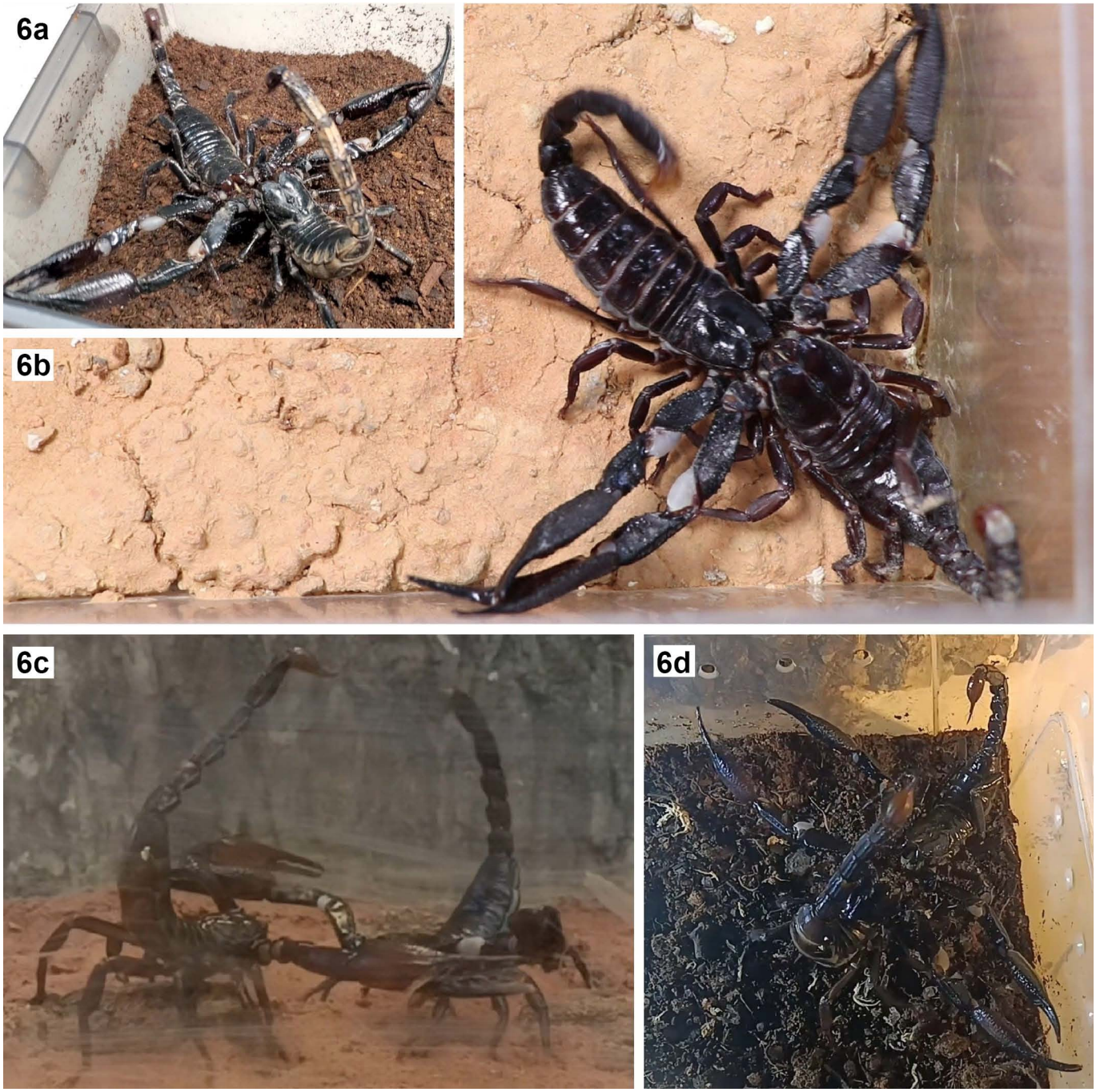
Heterometrinae species	ASC	SR	AR_C	AR_P
Chersonesometrus madraspatensis	?	+	-	-
Chersonesometrus tristis	+	+	-	-
Gigantometrus swammerdami	-	+	+	-
Gigantometrus titanicus	-	+	+	-
Heterometrus laoticus	-	-	+	+
Heterometrus longimanus	+	-	-	+
Heterometrus minotaurus	+	-	-	+
Heterometrus silenus	-	-	+	+
Heterometrus spinifer	+	-	-	+
Heterometrus thorellii	+	-	-	+
Javanimetrus cyaneus	?	-	?	+
Srilankametrus yaleensis	+	+	-	-

Table 1. Records of three types of behavior among several Heterometrinae species based on personal observations. Abbreviations: ASC (arm-span competition between adult males), SR (shielding response towards predatory stimuli), AR_C (*only* aggressive response against competitors) and AR_P (*only* aggressive response against predators); all scorpions are capable of counterattacking (aggressive response) under a certain degree of pressure. Symbols: + (observed), - (not observed), ? (unknown).

Methods & Abbreviations

Studied species

Srilankametrus yaleensis (Kovařík et al., 2019) is a fossorial and pelophilous species, inhabiting the open savanna formation with a sandy-loam substrate in the southern region of Sri Lanka (Kovařík et al., 2019; Prendini & Loria, 2020). Little is known about the physiology and life history of this species; as a member of the subfamily Heterometrinae (under family Scorpionidae), it is expected to be having a relatively long development and gestation period and life expectancy. (The author's observation of juveniles revealed a very low metabolic rate in this species: these scorpions could live healthily consuming no food for a couple of months as long as the moist soil/adequate humidity is provided). In this study, all the individuals (5 adult males) were bought from a Chinese online shopping website (Xian Yu; https://goofish.com/) as



Figures 6a–**6d**. Examples of similar behavior observed between two adult males in other Heterometrinae species. **Figure 6a**. *Heterometrus minotaurus* (above) and *Heterometrus thorellii* (below) (photo: V. Tang). **Figure 6b**. *Chersonesometrus tristis* (photo: V. Tang). **Figure 6c**. *H. thorellii* (photo: Gentia). **Figure 6d**. *H. thorellii* (below) and *Heterometrus longimanus* (above) (photo: Gentia).

pets (labelled in the name "耶鲁异蝎" or "耶鲁异距蝎") in 2019 when the author was an amateur as a scorpion keeper. This species has become a common pet in China since its import from Sri Lanka, and many captive individuals are sold online (price ranging from 400 to 3000 CNY depending on the age and sex). The collector, who had once provided photos of habitat to the author, is no longer contactable. With the guidance of the local scorpion hunters he successfully found the scorpions, but he did not provide exact coordinates for the specimens. The animals had been acclimatized under captive conditions (quarantined in their respective plastic containers with soil substrate and crickets as food) for two months. However, they were directly introduced into the experiment arena and allowed to meet their competitor without fully familiarizing with the environment.

Procedure and setup

The trials or cases were either carried out deliberately or happened unexpectedly. The observations were all conducted in captive environment with wild caught individuals. The first

Figures 7a–**7d**. Examples of physical combat in other scorpions. **Figure 7a**. Adult females of *Androctonus gonneti* Vachon, 1948 aiming at each other with their metasoma (the accompanied juddering behavior cannot be illustrated by the figure). **Figure 7b**. A pair of adult *A. gonneti*, the female is controlling the telson of the male. **Figures 7c**–**7d**. Adults of *Hottentotta salei* (Vachon, 1980) controlling the telson of the opponent: female and male (c), and two males (d).

deliberate trial was performed in the afternoon on 21 December 2020. Animals were introduced onto wooden desks next to a wall with the surface coated with baking finish. The margin of the desk was blocked to prevent falling but the arena was sufficiently spacious for the animals to complete the entire process. In the deliberate trials, six rounds were conducted, involving five adult males. Those males were assigned to three groups (2, 2, 1 individual in each). The combat in the first two groups was conducted twice between each pair (2 rounds each), and the winners of either groups were allowed to continue the fight in round 5. Successively, the winner of the fifth combat was introduced to the single male in the third group and finished the final round (sixth) of combat. The two adult males in the first group are termed as A1 and A2, and those in the second group as B1 and B2. The single male in the third group is termed C.

Documentation

Behavior was recorded through photography or videos in order to review and extract key information, using *ad libitum* sampling (Altmann, 1984), allowing the observer to note information freely without systematic constraints on what should be recorded and when. The duration of each round of combat is defined as a time period between the first moment when two animals touched each other and the moment when one of them started to escape. The arm-span competition (the duration of which is defined as time period during which the scorpions spread their pedipalps and confronted each other; i.e., ended when they separated) does not have to occur during each round. Duration of each round of combat and that of the arm-span competition was recorded (Fig. 5); however, the time of the interval between each combat was not recorded.

A video recording of a section of competition between two adult male *Srilankametrus yaleensis* is available as a Supplementary file to this publication.

Result

I. Initiation stage

Two vigilant males were artificially introduced into the "arena". They displayed a defensive posture, elevating their metasomas and shielding the prosomas with pedipalps (Fig. 1a). After several slight instances of punching and pinching, at the moment when their fingers touched (Fig. 1b), the two males gradually spread their pedipalps to lateral sides and approached each other (Fig. 1f). Sometimes, the pinching may be violent and may even escalate into a fierce but short-term fight. However, this was considered as a consequence of immediate contact during the period when the scorpions were still alert after they were introduced in the "arena", as they were previously infuriated by artificial stimuli. One of the males may also try to use its chelae (Fig. 1c-d) for suppressing the pedipalps of another male if those were within its pedipalp span range, although this would nonetheless subsequently develop into the next phase, instead of violently fighting with each other. In addition, shielding response with transient collisions (Fig. 1e) may not be followed up by punching or pinching.

II. Confronting/challenging stage

The two males moved their legs at small paces, with their metasomas stretched forward towards the opponent (Fig. 2a). Movements within a small range by small steps continued throughout this phase, and both males kept seeking the opportunity to move to the lateral side of the opponent. Some males surrendered and fled soon after this stage. The pedipalps of each male may not always be opposed; the pedipalps of the stronger male may soon be able to bypass that of the weaker male and reach the lateral sides of its mesosoma. If both males were bellicose, they will extend the metasoma towards the opponent's body (Fig. 2b), occasionally scraping on the tergites or other parts, but never intended to give an actual sting. More interestingly, if the telson and fifth metasomal segment of these males were crossed, these two segments would form a "hook" and allow each male to wrench his opponent by leaning backwards and unbalancing the opponent (Fig. 2c–d). Often, one of the males was pulled over and lost it balance, fell onto the opponent, or both of them were well-matched in strength and fell backwards (Fig. 2e–f). Surprisingly, the steady male would not pinch or sting the fallen male when it was pulled over (Fig. 3a); instead, it would wait patiently until the other male regained its balance. The two males continued their competition, until one lost its fighting will. In the fourth trial, the loser from the previous trial attempted to escape as soon as it sensed its component, while its component was ready for the arm-span competition. In the fifth trial, the two males did not display any arm-span competition, but violently fought with each other employing stinging behavior (Fig. 3b). In the sixth trial, six arm-span competitions were recorded, with variable duration (13, 3, 8, 10, 14, 7, respectively, in seconds).

III. Escaping/surrendering stage

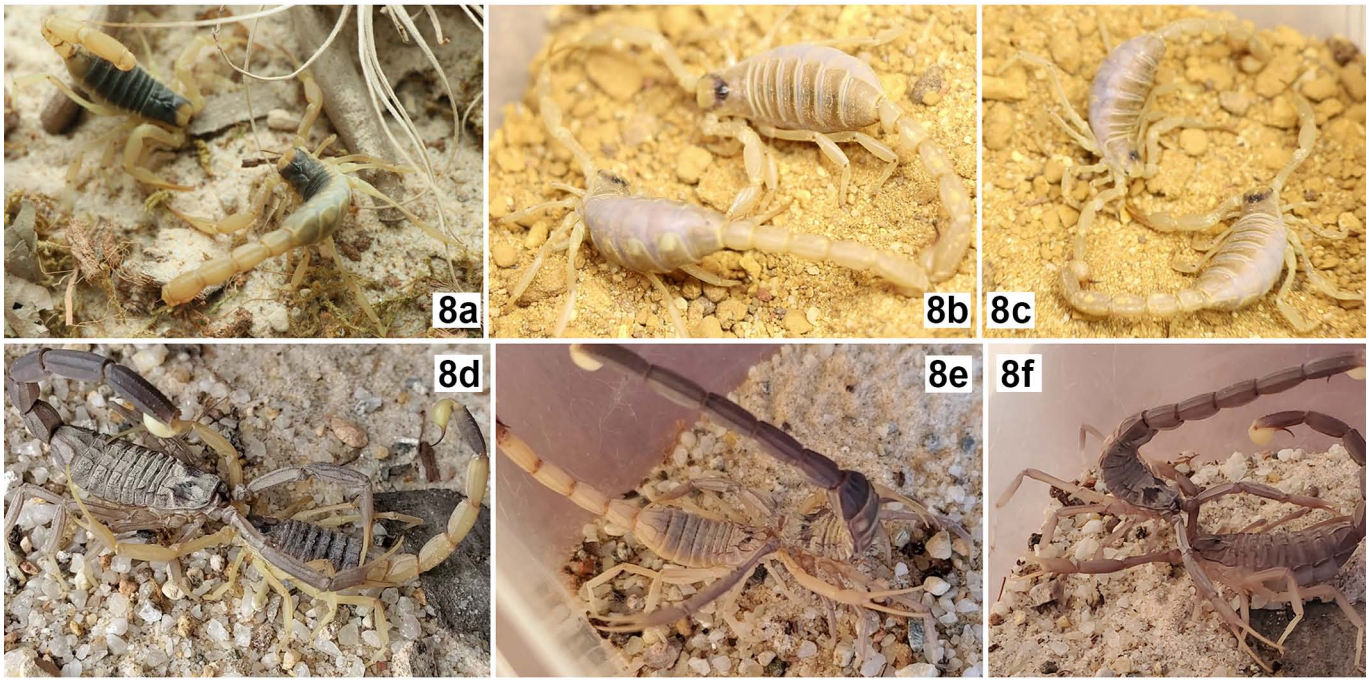
The loser would run away after it felt powerless, but the fleeing velocity varied among individuals. This fleeing behavior was always found in the loser in the second round of each pair soon after the combat started, as the interval between the two rounds was short. Intriguingly, although the winner may chase the loser for a short distance (at low velocity), it was not aggressive at all and never attempted to punch or even kill the loser, but still maintained the previous posture: stretching the metasoma forward and the pedipalps anterolaterally (Fig. 4).

Discussion

Agonistic behavior in scorpions

Agonistic behavior involves both attack (i.e., physical combat/direct fighting behavior) and defense, and the defensive behavior of scorpion seems to be dependent on the target. Most scorpions attempt to sting in response to threat stimuli, while others may resort to their thick, powerful pedipalp chelae that can be used for pinching and punching (thanatosis, fleeing and other non-aggressive behaviors triggered by threat stimuli are not considered herein, e.g., Triana et al., 2022). Under laboratory condition, some deterrent behaviors, such as stridulation (e.g., *Androctonus*, *Heteroctenus*, *Parabuthus*, Opistophthalminae, Pandininae and Heterometrinae), venom squirting (e.g., *Parabuthus* and *Hadrurus*) and chelal shielding in front of or above the prosoma (e.g., Opistophthalminae, Pandininae and Heterometrinae) have hardly been observed between scorpions (Tang, pers. obs.), but often happened due to artificial stimuli, which may be recognized by these scorpions as a predatory signal from vertebrates. (However, in Heterometrinae, stridulation may still be triggered when two scorpions are fighting violently, but is never applied as a phonic warning signal against the opponent prior to the fight.).

Pertaining to the intraguild combat, various scorpion species resort to various forms of agonistic behavior, and some of which could be fatal and end in intraguild predation (including cannibalism). Some types of agonistic behavior are ritualized aggression (threatening behavior involving physical display of either individual) without a physical contact unless necessary. Species with a relatively potent venom and strong metasoma, like those of *Androctonus* and *Parabuthus*, often frighten and/or expel their opponents by causing vibrations on the substrate through juddering, positioning laterally with metasoma facing towards the opponent in order to produce a powerful strike (Tang, pers. obs.; e.g., Fig. 7a). Similar postures have also been found in *Hadrurus* species (Tang, pers. obs.; e.g., Fig. 8a–c); however, those scorpions often open their pedipalps while facing the enemy, forming smaller angles at IV–V metasomal articulation and rising their mesosoma laterally while keeping the metasoma curving downward (sometimes the end of the metasoma will rub the substrate), probably to make themselves look larger by increasing the front-viewed width (from the tip of one chelal finger to the tip of the anal arch at the opposite end). However, if those types of preliminary behavior, expressed as warning by physical means (e.g., changes of air current caused by swaying of



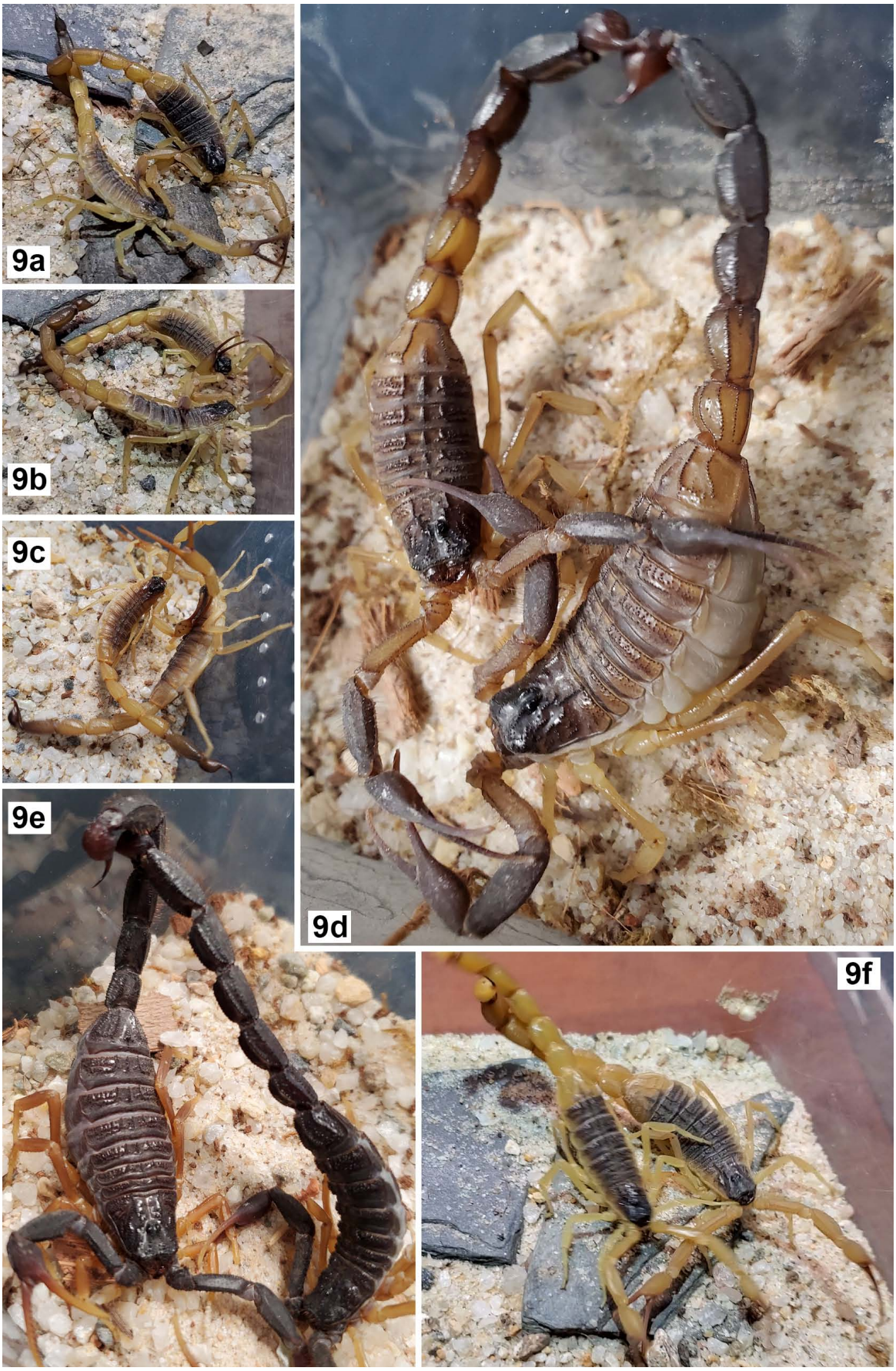
Figures 8a–**8f**. Examples of physical combat in other scorpions. **Figures 8a**–**8c**. Juveniles of *Hadrurus arizonensis* Ewing, 1928, performing the typical deterrent posture. **Figures 8d**–**8f**. *Leiurus* spp., performing the intimidation behavior: adult males of *Leiurus jordanensis* Lourenço et al., 2002 and *L. haenggii* Lowe et al., 2014 (d), adult males of *L. jordanensis* and *L. quinquestriatus* (Ehrenberg, 1828) (e), and an adult pair of *L. jordanensis* (f; male on the left).

metasoma (or perhaps spreading hormones), or substrate vibrations induced by juddering; Brownell & Hemmen, 2001; Lira et al., 2019), are not effective, direct physical contacts take place. Medium to large sized *Hottentotta* species have been found to form their telson, metasoma and mesosoma in a sublinear position, and to rub each other while standing side by side (Tang, pers. obs.; e.g., Fig. 9a–f)—an enigmatic behavior still needs to be clarified. Aggressive combat involving hostile stinging behavior may also be accompanied by telson seizure: a scorpion uses its chela to control metasomal movement of the opponent by crossing and fastening its fingers between the segments (e.g., Fig. 7b–d). Death may occur during intraspecific combat; however, scorpions are known to tolerate their own venom: e.g., Shulov and Levy (1978) demonstrated that *Leiurus quinquestriatus* (Ehrenberg, 1828) is resistant to its own venom, with the lethal dose of conspecific venom worth about 18 stings. *Leiurus* species have also been observed to perform a distinctive behavior of physical combat (Tang, pers. obs.; e.g., Fig. 8d–f): the competitors stretch their pedipalps forward and constantly pinch each other on the mesosoma and/or legs with a low force; their metasoma is leaned toward the opponent but no actual stinging takes place. This is assumed to be a relatively safe way of strength demonstration.

Three basic forms of agonistic behavior in Scorpionidae

Based on personal observations and photographs from the internet and previous publications, three basic forms of agonistic behavior in Scorpionidae are recognized: aggressive response, shielding response, and arm-span competition (Fig. 10a–c). The employment of these types of behavior varies according to the species and target (intraguild, antipredatory, or both). Among these, the aggressive response is the most common response that occurs in all scorpions. Species under Scorpionidae are usually less toxic and possess powerful chelae. This leads to a preference between stinging behavior and pinching/punching behavior, and the latter is generally preferred. Pinching/punching behavior can be often accompanied by stinging behavior based on certain species. An aggressive response can always be triggered against either the intraguild competitors or potential predators; however, in some species, this is the only response they exhibit in both cases. Pinching behavior is defined as crushing any physical parts of an opponent which may last for several seconds, while punching behavior is a more rapid attack presented as waving the pedipalp towards an opponent. Punching behavior can be followed by a brief pinch. Stinging behavior acts as a chemical attack apart from the physical attack accomplished by forceful chelae. Stinging is often more common between intraguild competitors, but species of the subfamily Scorpioninae (e.g., *Scorpio palmatus* (Ehrenberg, 1828); Tang pers. obs.) may also be more likely to sting a potential predator compared to the other subfamilies. During an intraguild physical combat, species with a longer metasoma are more likely to be threatening to the opponent of a of similar body size, as they can reach a greater distance for stinging.

Shielding response is the second common behavior in Scorpionidae; it appears to be used only toward potential predators. This behavior can be easily recognized: a scorpion stands up to elevate itself (if the threat stimulus comes from above, e.g., a finger touch), lifting the pedipalps with two chelae positioned next to each other forming a shield in



Figures 9a–**9f**. Examples of physical combat in genus *Hottentotta* Birula, 1908. **Figures 9a**–**9c**. Adult males of *H. minusalta* Vachon, 1959. **Figure 9d**. An adult pair of *H. jayakari* (Pocock, 1895). **Figure 9e**. An adult pair of *H. franzwerneri* (Birula, 1914). **Figure 9f**. An adult pair of *H. buchariensis* (Birula, 1897).

front of or above its prosoma and stretching its metasoma towards the stimuli, or simply raising it up. However, there is a difference in the performance among the four subfamilies of Scorpionidae. Within Scorpioninae, which is the most basal (ancestral) subfamily, this behavior seems to be more general. Although all the *Scorpio* species have rounded pedipalp chelae, when exhibiting the shielding behavior, their chelae are not positioned closely to each other but are spaced allowing their prosoma to be accessed (e.g., iNaturalist obs. ID = 16356314, 53393403, 93400171, 120806051). Additionally, their fingers are always open and ready to pinch (e.g., *S. palmatus*, Tang pers. obs.). Shielding response is harder to be triggered in *Scorpio palmatus*, as the scorpion often tends to attack the enemy in an aggressive response. In the species pf remaining three subfamilies, however, the fingers are not always open or open for attack only; open fingers increase the range of protection. In Opistophthalminae, the second ancestral subfamily, displays a similar positioning of chelae. They do lift their chelae, but they may be just flanking the prosoma without actually covering all of it (e.g., iNaturalist obs. ID = 141185652, 139356290, 136848704, 102346356). Nevertheless, they can still withstand the adversaries coming from the front and they do not abandon this posture and convert into aggressive response unless necessary. Thus, the shielding response appears to be more evolved in this subfamily than in Scorpioninae. Furthermore, species of this subfamily often just rise their metasoma, forming a sublinear curve along the body axis, instead of pointing at the threat stimuli. Both Pandininae and its more derived sister subfamily Heterometrinae present a well-established shielding response. Although more elaborate in general, some Pandininae, with their less rounded or flattened pedipalp chelae (e.g., *Pandipalpus* Rossi, 2015) exhibit similar posture to Opistophthalminae (e.g., iNaturalist obs. ID = 36827950, 16786786, 5056439). Wider chelae allow a scorpion to protect the most of its prosoma, as observed in genera *Pandinoides* Fet, 1997, *Pandinopsis* Vachon, 1974 and *Pandinus* Thorell, 1876 (e.g., iNaturalist obs. ID = 5490689, 35850136, 22042114). The remaining genera of Pandininae may also exhibit similar posture, although no definite photographs are known but only indicated (e.g., one *Pandinurus kmoniceki* from Kovařík et al., 2017: 10, fig. 44, not fully triggered). In Heterometrinae, however, this behavior is restricted to a few genera (Table 1); species of *Gigantometrus* Couzijn, 1978 perform a highly evolved posture (chelae often closely or fully adjoined; e.g., iNaturalist obs. ID = 134039988, 89501002, 50225495, 49561304, 31538992, 20284850). Members of all these three subfamilies can stridulate while performing the shielding response, and appears to be common in adults (not observed in young juveniles). Interestingly, although their metasoma may be pointed at a threat stimulus, it is often not used and is more likely functions for enlarging the visual size of the individual.

Arm-span competition is so far only observed in Heterometrinae, the most derived subfamily in Scorpionidae (Loria & Prendini, 2020), and it only occurs between intraguild competitors. The combat is characterized by the lateral spreading of pedipalps with two antagonistic adult males colliding with each other, face to face. This collision is often accompanied by the touching between each opposing pair of pedipalp presented as the respective swaying of pedipalp. Entangling of metasoma is only observed in *S. yaleensis*, while other species normally just sway their metasoma when they meet an opponent as the deterrent signal. This behavior is further discussed below.

Arm-span competition in *Srilankametrus yaleensis*

A peculiar behavior that is documented in the present study can be interpreted as a direct physical combat but much less aggressive as it does not cause injury. This kind of agonistic behavior also occurs amongs some of the other Heterometrinae species (Tang, pers. obs.; e.g., Fig. 6a–d), even interspecifically, including *Chersonesometrus tristis* (Henderson, 1919), *Heterometrus longimanus* (Herbst, 1800), *H. minotaurus* Plíšková et al., 2016 and *H. thorellii* (Pocock, 1892). All these four species exhibit a prominent sexual dimorphism with adult males possessing relatively narrower and elongate pedipalps (especially the chelae). Ecological function of the elongated pedipalps is usually interpreted as an adaption for predation and navigation in the crevices (or subterranean caves; Prendini, 2001; Prendini et al., 2021), and perhaps, handling a female during the courtship. However, the first function is not sex-dependent as both sexes of the same species dwell in the crevices (or subterranean caves). Longer pedipalps may aid in male's manipulation and perception of the female during the initiation stage of the courtship. Males have been observed to constantly touch the body of the female, gently pinching its metasoma and legs when they first meet (provided that the female is receptive rather than aggressive). This behavior may help the male to evaluate the size of the female, as well as to calm down the female in order to accomplish a safe and successful mating. As a result, long pedipalps may assist a male to reach a greater distance for a better overall control over a female when they confront each other.

On the contrary, the behavior reported in the current study indicates another ecological role of a long pedipalp; that is, for neither predation nor courtship, but for intrasexual competition. In certain species, the length of the pedipalp of an individual is correlated to the body length of that individual, which is roughly equivalent to the body size/weight. As a result, the arm span demonstrates the size, and possibly, the strength, of an individual. When the two males are facing each other with their pedipalps stretched laterally, they could judge which of them is larger, perceived by the tips of chelal fingers. This behavior is hereby defined as the "arm-span competition". Another personal observation recorded between two adult males of *Chersonesometrus madraspatensis* and *C. tristis* showed that although the arm span does function as a useful indicator of body size for intimidation, the final winner is decided by strategy and a better command of timing. A male *C. tristis* managed to suppress a male of *C. madraspatensis* during most of the process but eventually failed to overcome its opponent,

Figures 10a–**10c**. Examples of three types of behavior observed among several species of Heterometrinae. **Figure 10a**. Arm-span competition (*Chersonesometrus tristis*). **Figure 10b**. Shielding response (strictly defined as an easily triggered response; *Heterometrus* species do exhibit similar posture but happens only when their pedipalps are suppressed; *Srilankametrus yaleensis*). **Figure 10c**. Aggressive response (here shows a pre-posture before "pinching" or "punching"; *Heterometrus spinifer*).

Figure 11. *Dinorhax rostrumpsittaci* (Simon, 1877), two males in threatening condition.

not exhibiting enough aggression after it was frightened off for the first time. This gave the male of *C. madraspatensis* time to regain courage and become more determined in defeating an indecisive enemy (*C. tristis*, a species which performs a gentler way for male-male competition). The male *C. madraspatensis* continued its victorious pursuit and scared off a larger *C. tristis* for good (video recording available as an additional supplementary file).

In *Srilankametrus yaleensis*, however, the sexual dimorphism in the pedipalp chelae is not so prominent, although male chelae are relatively narrower. Consequently, this peculiar behavior in this species cannot be assigned to the possession of elongated pedipalps; alternatively, this could simply be a case of convergent evolution. Notably, *Heterometrus spinifer* (Ehrenberg, 1828) is also a species that displays such a behavior, but it again does not show extreme sexual dimorphism in the pedipalp chelae as do its congeners (e.g., *H. longimanus* and *H. thorellii*). It is still unclear how many other species in Heterometrinae may resort to this form of physical combat, but in the species with relatively robust pedipalp chelae, e.g., *H. laoticus* Couzijn, 1981 and *H. silenus* (Simon, 1884), the competition is much fiercer. Bellicose males will fight violently when they meet a conspecific competitor, wielding their muscular chelae to crush the body of an opponent, or simply showing their strength by thumping the opponent (Tang, pers. obs.). Surprisingly, in *Gigantometrus swammerdami* (Simon, 1872), a species with relatively flattened chelae resembling that of the *Chersonesometrus tristis*, the combat is nonetheless aggressive (Tang, pers. obs.).

A possible explanation for these Heterometrinae species to adopt a gentler way of combat may lie in them avoiding unnecessary death. Generally, the survivorship and average longevity of males appear to be lower than for females, while the mortality rate for adult males is much higher than for adult females, which produces the heavily skewed sex ratio observed for many species of scorpion (Polis & Sissom, 1990). Males are often more vagrant and mobile during the mating season, while the females usually stay in their burrows. This behavioral difference between sexes leads to the differential mortality in males that results from cannibalism and predation. Although several species of Heterometrinae have been observed to live in colonies formed of different developmental stages (e.g., *Chersonesometrus fulvipes* (C. L. Koch, 1837), *Gigantometrus titanicus* (Couzijn, 1981), *Heterometrus longimanus* and *H. silenus*; Prendini & Loria, 2020), intraspecific competition between males nonetheless happens as is proved by the current observation (including other personal observations). Thus, rather than fighting to death, a ritualized demonstration of strength can minimize the casualty that could be detrimental to the natural population, while achieving the goal of territorial or sexual competition. However, this hypothesis will only be authenticated through long-term field investigation demonstrating that those animals

indeed experience various environmental pressures in their natural habitats, such as predation and natural disasters (e.g., flooding, although many Heterometrinae species are capable of staying beneath water surface for a long time, and sometimes they walk into the water voluntarily; Tang, pers. obs.). Another reason may be ascribed to the relatively long gestation period and developmental time in at least some of these species; it appears that in most scorpionids, these periods are longer than those of the buthids (Polis & Sissom 1990). Additionally, the litter size is usually smaller in Scorpionidae when compared with other families (e.g., Buthidae, Bothriuridae and Chactidae; Polis & Sissom 1990). Conclusively, the underlying interpretation accounting for the evolution of this behavior could be multifaceted.

The combat behavior in *Srilankametrus yaleensis* is more likely to be a part of sexual competition, rather than food and/or space competition. Obligatory burrowers like this species usually employ the "sit-and-wait" hunting strategy, indicating that they have their own burrows where they spend most of the time inside, and the prey is not encountered by active foraging. However, other species that display the similar behavior are energetic hunters (e.g., *Heterometrus longimanus* and *H. spinifer*); hence, this behavior may function as a safe intraguild competition contingently. Females often favor males with larger body size or greater weight. A better body condition is usually demonstrated by more vigorous and efficient courtship; thus, it offers males with a mating advantage and represents as an indicator of courtship performance (Olivero et al., 2016). Traits that enhance the success of courtship are the indicators of males carrying with better genes, which could be beneficial for offspring fitness. Usually, females are the decisive sex to choose reproductive partners on account of their extreme parental investment asymmetry in offspring care. As a result, a pre-exclusion of weaker males within a certain region could save time for the entire population during the mating season. The male-male competition in scorpions is not likely to be supervised by a nearby female as in other visual animals; conversely, this competition may just be aimed at expelling competitors to delimit territories where females may occur. Although the violent fighting was also observed, I speculate that an "emotional state" of a scorpion decides the choice of either fighting or arm-span competition (i.e., whether the individual has been infuriated by human touch).

Interestingly, McLean et al. (2019) proposed that the longer raptorial pedipalps in a male whip spider, *Damon variegatus* C. L. Koch, 1850, evolved for display contest rather than fierce fighting. Chapin & Reed-Guy (2017) documented the male contest in *Phrynus longipes* (Pocock, 1894) and provided videorecordings of experiment animals (available at: https://www.youtube.com/watch?v=Nj0gCtFXEgI&t=14s). This is similar to the hypothesis made in this study for the sexual dimorphism in some Heterometrinae species with more slender pedipalps present in adult males in that it could be associated with sexual selection through intrasexual competition (however, in amblypygids the display contest may also be used for territorial competition for food and space). In amblypygids, most of display contests of pedipalp length do not escalate to fatal combat and cannibalism is rare, which agrees with the current knowledge of the similar behavior in Heterometrinae species. Nevertheless, should this competition become an aggressive combat, body mass is a more reliable predictor of the winner rather than the length of pedipalps. This could prove true for those Heterometrinae although no cannibalism is known for this behavior, and further investigations in this regard may shed light on the behavioral convergent evolution among arachnids. The unique occurrence of this behavior in this subfamily may have certain implications for the evolution and phylogeny of the entire family. Finally, in a camel spider species, *Dinorhax rostrumpsittaci* (Simon, 1877) (Arachnida: Solifugae), an apparently similar behavior was also observed between males (Fig. 11). The pedipalps of both males were open, with the tips (suctorial organs) in contact. The males opened their chelicerae, rubbing their own pairs by rotating their prosoma to left and right sides. Cheliceral rubbing also functions as a threatening signal towards predatory stimuli (e.g., *Galeodes caspius* Birula, 1890; Tang, pers. obs.) and in some species this is accompanied with phonic signal, similar to the stridulation of *Opistopthalmus* (e.g., *Galeodes granti* Pocock, 1903, pers. obs. by the author's friend Maxwell Wang with videorecording). Sexual dimorphisms regarding the more gracile pedipalps and chelicerae in male camel spiders have been previously discussed along with their potential roles, but often related to the mate-searching behavior of males and the intersexual behaviors (e.g., McLean et al., 2018). In their exhaustive description of the reproductive biology of Solifugae, Peretti et al. (2021) did not document any observations concerning the male interactions. However, it is yet premature to determine this behavior as the "arm-span competition". All these similarities in behavior may facilitate a better understanding of the evolutionary relationships between these arachnids.

Acknowledgments

I am grateful for Dr. André F.A. Lira for his review and for Dr. Rolando Teruel for his information on the male competition in scorpions. I also would like to thank Gentia (nickname of my friend) for his provision of the two photos. I thank two anonymous reviewers for their comments.

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