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Fighting Performance of Female Chinese Wolf Spiders in Cannibalistic Contests in Relation to the Battlefield Size

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Abstract

Game theory models suggest that both the forms (ritualized display and real fighting) and outcome of animal contest can be influenced by the relative body size, fighting experience, and hunger level of contestants. However, whether a factor determining the outcome of a contest exhibits similar effects in different forms of the contest has not been highlighted. In a cavity-nesting predator, the Chinese wolf spider *Lycosa sinensis (Araneae: Lycosidae)* that frequently carries out cannibalism on the Tibetan Plateau, we addressed this question in female cannibalistic contests by designing three series of experiments (the first between large and small opponents, the second between experienced and inexperienced opponents, and the last between satiated and hungry opponents). By repeatedly performing these experiments in large and small artificial battlefields, we revealed that battlefield size determined whether these three factors came into play in the cannibalism of spiders. In asymmetric contest, big spiders always defeated their opponents in real fights. But the battlefield size determined whether a contest can be escalated into real fights. Experienced or satiated spiders can successfully escalate the contest into real fights by enhanced aggressiveness; however, they were unlikely to defeat their inexperienced or hungry opponents in a real fighting. This battlefield size effect may be a reason for Chinese wolf spiders to excavate a cave with themselves proportionally accommodated. Therefore, this effect of battlefield size needs to be considered in future studies of animal contests, especially for the spiders that cannibalism frequently occurs in natural environments.

Keywords: *Lycosa sinensis*; Cannibalism; Battlefield size; Nest-cave character

Introduction

Real fights are the extreme form of animal contests for limited resource, such as food, shelter, mate, and territory [1-7]. Evolutionary game theory suggests that both the form and outcome of animal contest can be influenced not only by the relative fighting power of contestants, which is often indexed by the relative body size [8,9], but also by the fighting motivation [10-12] and strategy [13,14]. By contrast to ritualized display, real fighting to each contestant generally means paying a greater price in the contest and enduring a higher risk of being injured [15,16], even for the winner. Thus, each contestant should have made the best choice about whether to escalate the contest intensity [8]. For example, in an asymmetric contest, the larger contestant usually defeats its smaller opponent in real fighting because larger body size usually associates with greater strength and higher ability to inflict injury [17-19]. However, asymmetric contests in most cases are terminated by ritualized display because smaller contestants generally avoid escalating the contest intensity after self-assessment [20,21], although larger contestants show aggressiveness in the contest [22]. Then, a question raises, whether a factor determining the contest outcome in the form of ritualized display also exhibits similar effect in the form of real fighting?

Beside the relative body size [20,23], several other factors may also influence the choice of each contestant about the contest form, including fighting experience [24,25], and hunger [2,26]. The self-assessment hypothesis suggests that fighting experience, particularly winning experience, can help a contestant establish self-confidence in its fighting ability and assess the fighting ability of its opponents accurately [24,27]. Thus, experienced contestants tend to escalate the contest intensity [28]. Since a hungry contestant will value the same amount of food higher than does a satiated one [29], different hunger levels may result in distinct contest desire, with hungry contestants often increasing aggressiveness in a contest [26] whereas satiated contestants avoiding escalating the contest because defeating an aggressive, hungry opponent is uneconomical for them [30,31]. Apparently, both fighting experience and hunger increase the aggressiveness of a contestant, but whether the enhanced aggressiveness could increase the success of a contestant in real fights remains undetermined [18,25].

Cannibalism is a special type of animal contest that occurs between intraspecific individuals mostly in arthropods, such as spiders [32-34]. Unlike in other contests for external resources, individuals in cannibalistic contests are usually killed if they lose the contest [15]. This great cost of cannibalism will prevent opponents from retreating from real fighting. Thus, we assume that i) relative body size determines whether a cannibalistic contest is terminated in the form of ritualized display or real fighting; ii) experience and hunger facilitate a cannibalistic contest to escalate into real fighting but they do not influence the outcome of the real fighting because no one will actively retreat; iii) relative body size solely determines the outcome of cannibalism if it is escalated to real fighting.

We test this assumption in a cavity-nesting predator, the Chinese wolf spider *Lycosa sinensis (Araneae: Lycosidae)* that exhibits sexual size dimorphism (female: 19-30 mm, male: 15-21 mm). Owing to relatively smaller size, male spiders are more vulnerable to low temperature, starvation, water scarcity and intra-species competition

than females [35]. Consequently, population sex ratios are often biased toward female (male:female, 1:4-1:7, Hu 2001). Chinese wolf spiders have two hunting strategies. One is ambushing passing preys such as beetles, noctuid, acridid and muscid by hiding at the entrance of a cave, which they excavate themselves [36]; the other is running after subaerial insects outside the cave [37].

In this study, we design three series of experiments to evaluate the effects of relative body size, fighting experience, and hunger on female performance in cannibalistic contests. These experiments were repeated in big and small artificial battlefields. We mainly address whether 1) larger spiders are more likely to defeat their smaller opponents, 2) experienced and hungry spiders are more likely to defeat their inexperienced and satiated opponents, and 3) the battlefield size influences the fighting performance of female contestants.

Methods

Study area and population

We performed this study at the Gahai-Zecha National Natural Reserve on the northeastern Tibetan Plateau (34°14' N, 102°20' E). This region has a mean annual temperature of 1.2°C and annual precipitation of 782 mm. The vegetation is characterized by alpine *Kobersia* meadow. Dominant plants include *Elymus dahuricus Turcz, Deschampsia caespitosa, Carex tristachya, Potentilla anserina* and *Polygonum viviparum*. The growth cycles of plants start at late April and end in mid-September. Larvae of herbivorous insects, including Coleoptera and Lepidoptera, begin to resuscitate from overwintering status at the end of April and adults are widely detected in mid-June.

Chinese wolf spiders thaw out of hibernation at the end of March when the weather gets warmer. The density of spider caves in a study area of 4 ha reached 4/sq. m. Most caves were excavated in the previous year. However, in some cases, we witnessed that the spider excavated the cave in March, mainly from 10:00 a.m. to 12:00 noon on a sunny day. The dietary items mainly consisted of herbivorous insects, such as beetles, flies, noctuid species, and locusts. Chinese wolf spiders exhibited high frequency of cannibalism in March and April, probably because of lack of food. Consequently, nearly 90% of the caves we examined were inactive because the owner had been killed or eaten.

Cave measurement

Both males and females of Chinese wolf spiders dug cave for nocturnal roosting. The architectural structure of a cave consists of 4 sections (Figure 1). We measured 5 parameters: the vegetable coverage of the entrance (the proportion of plants covering a range of 0.25 m in radius from the entrance), the long and short diameters of the entrance (l and s), slant height of the cave (SH), and total length of the cave (TL, Figure 1). On the basis of these data, we calculated the entrance area ($1/4 \times \pi \times l \times s$) and the capacity ($1/4 \times \pi \times l \times s \times$ TL) of the cave.

Capture of candidate spiders

By contrast to other geographic populations where Chinese wolf spiders forage at night [37], they are diurnal in our study area because of the extremely low temperature at night. We captured spiders from the cave. If the spider retreated back into the cave, we placed a small knife at the entrance and waited for the spider to come out again. The knife was diagonally inserted into the cave to prevent the spider from retreating. The spider was captured by placing a glass bottle (3 cm in diameter and 6 cm in height, with a lid for ventilation) in front of it and then driving it inward. All captured spiders were marked (denoted by Arabic numerals on the back of the abdomen for individual identification), sexed (males having palpal organs on the palpus, and females having an epigynum on the abdomen), and finally maintained individually inside the glass bottles. We maintained these bottles at 15°C. Only female spiders were used in subsequent experiments because few males were captured and males seldom carried out fights.

Prior to the experiments, spiders in captive were fasted for two days to stimulate their appetite by starvation. The two-day fasting caused no adverse effects on the spiders.

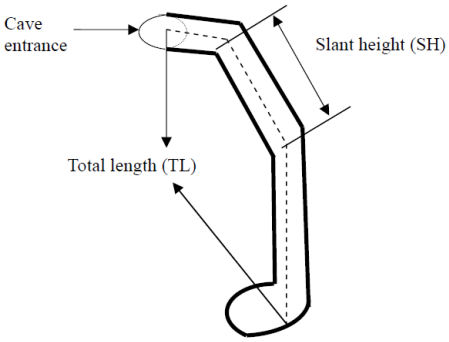

Figure 1: Diagram of the cave of the Chinese wolf spiders, consisting of 4 sections (I to IV) and showing the entrance, slant height, and total length of the cave. The owner often sits in the first section of the cave (I). When there is a danger sign outside the cave, it will retreat to the fourth section (IV).

Experimental design

We designed three types of experiments to evaluate the effects of relative body size, fighting experience and hunger level on the fighting performance of spiders. All of the experiments were repeated in two different-sized battlefields. The first was conducted in a cylindrical container (15 cm in diameter and 15 cm in height, with 1 cm of soil at the bottom) and the second in a glass bottle (3 cm in diameter and 6 cm in height). The former battlefield is similar to the outside of the cave where both contestants had sufficient space to execute an attack or retreat and the latter battlefield is similar to the inside of the cave where both contestants have no room for maneuver when they encounter.

To evaluate the effect of relative body size on the fighting performance of females, we randomly paired two contestants in the first type of experiments. All bottles containing female spiders were mixed in a black bag and then randomly took two battles out of the bag. Each spider was weighed to the nearest 0.01 g, which was used as the index of body size. When two contestants differed by more than 10% in body size, the contest was asymmetric [4]; otherwise, it was symmetric. In the large container, we put 2 bottles on the soil and removed the lid simultaneously. After two spiders crawled out of the bottle, we started the timer to record the fighting and terminated it after five minutes. In the small bottle, two spiders were taken out of their respective bottle and put into a third bottle. Similarly, we recorded the fighting for five minutes. The fighting was first recorded

by a digital camcorder (ZX1, Eastman Kodak Co. Rochester, NY, USA), then analyzed by playing the videos back on the computer. We finally performed 44 rounds of asymmetric fights (31 in the large container and 13 in the small bottle) and 35 rounds of symmetric fights (24 in the large container and 11 in the small bottle).

Within five minutes, if a spider killed or hurt its opponent, it was considered as "winner" and its opponent was labelled "defeated". In Chinese wolf spiders, an individual performing a cannibalistic contest aimed to obtain "food". If small spiders do not escalate the ritualized display, large spiders cannot capture the opponent and obtain the "food" at the end. So, if no real fighting occurred or both contestants separated after five minutes without injury, the outcome of contest was considered as "draw".

To evaluate the effect of fighting experience, we used the winner spiders in the first type of experiments as experienced contestants in the second type of experiments. The defeated spiders were eliminated because they were injured. The winner spiders were allowed to eat their opponents only within the stipulated five minutes to regain physical power. Thereafter, they were fasted again for one day. The winner spider was matched against a new spider that never fought and was fasted 2 days in captive. We ensured that the body weight of experienced spider was 5% to 10% heavier than its inexperienced opponent to control the effect of body size on fighting performance. In the end, we witnessed 28 rounds of fights between experienced and inexperienced contestants in large container and 18 in small bottles.

The third type of experiments was used to evaluate the effect of hunger level, in which one spider was satiated and the other was hungry. Some candidate spiders (six individuals) were the winners in the first type of experiments that were allowed to eat their opponents. Their opponents were the winners in the first type of experiments but were not allowed to eat their opponents. This matching method controlled the potential influence of fighting experience. Other candidate spiders were newly captured individuals. Some of them were fed on the muscid and their opponents were fasted for two days. The body weights of two contestants in the third type of experiments differed less than 10% to control the effect of relative body size. We got 18 rounds of fights between satiated and hungry contestants in large container and 12 in small bottles.

All procedures on animals were performed under the Wildlife Conservation Law Legislated by the tenth National People's Congress of China (20040828).

Statistical analysis

The body sizes and the cave parameters of male and female spiders were compared using independent samples t-tests. The variation of cave parameters with female body weight was regressed with curve estimation. The fighting outcomes in the three types of experiments were compared by chi-squared tests. Statistical analysis was performed using SPSS (version 19.0, IBM, Armonk, NY, U.S.A.). Descriptive data are presented by mean ± SE. Null hypotheses were rejected when $P_{\text{two-tailed}} < 0.05$. Before the *t*-tests, we checked both the normality and Levene variance equality of the data. If both preconditions were satisfied, we used the results of parameter tests; otherwise, we used the results of non-parameter tests.

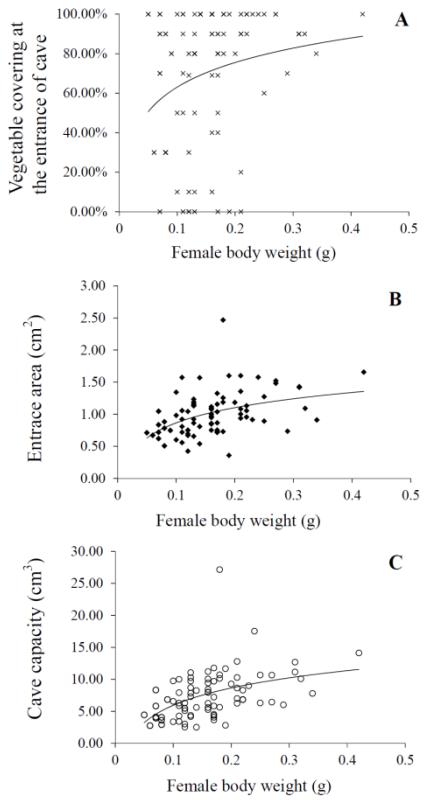

Figure 2: A-C) Variation of three architectural parameters of spider cave with the female body weight. The curves represent the result of regressions.

Results

Cave parameters in relation to body size of spiders

Females of Chinese wolf spiders (0.178 ± 0.008 g, n = 70) were significantly larger than males (0.072 ± 0.002 g, $n = 20$; non-parameter *t*-test: $t_{81} = 13.02$, P<0.001). Accordingly, the caves of females had significantly larger entrances (1.04 ± 0.04 cm^2) and capacities (7.95 ± 0.45 cm^3) than those of males (entrance area: 0.75 ± 0.03 cm^2, $t_{76} = 5.48$, P<0.001; capacity: 4.70 ± 0.39 cm^3, $t_{71} = 5.44$, P<0.001). No differences in the vegetable coverage at the entrance were discovered between the caves of males (70.96 ± 4.15%) and of females (62.00 ± 3.217.87%, $t_{88} = 1.02$, $P = 0.313$). All three architecture parameters of female cave–the vegetable coverage of entrance ($R^2 = 0.10$, $F_{1,68} = 7.35$, $P = 0.008$; Figure 2A), the entrance area ($R^2 = 0.12$, $F_{1,68} = 9.52$, $P = 0.003$; Figure 2B), and the capacity ($R^2 = 0.14$, $F_{1,68} = 10.65$, $P = 0.002$; Figure 2C)-increased significantly with the body weight of females, indicating that females with larger body size constructed larger caves to accommodate themselves.

Fighting behaviour of Chinese wolf spiders

Generally, one round of spider fighting was composed of 3 consecutive steps, with the intensity escalating from pre-contact ritualized display to attacking, and finally to aggressive wrestling. Once

two contestants crawled out of the captive bottles, they generally made an immediate circuit in the large container, but not in the small bottle. Subsequently, they slowly approached the opponent, with the 1-3 former legs shifted to display (the first step). During this process, the larger spider moved toward its opponent (42 of 44 cases, $\chi1^2$ = 36.36, P<0.001). The other spider responded depending on its relative body size to the approaching initiator. If it was significantly smaller than the initiator, it always receded at the same speed; otherwise, it also approached the initiator slowly. Once two contestants located themselves within a short distance, attacking started. The initiator decidedly jumped at the opponent, combining a series of actions, including a take off by two pairs of hind legs, a 180-degree turn by the second pair of former legs, and lifting the cephalothorax of the opponent with the first pair of legs. If these actions were completed successfully, the third step would begin; otherwise, the initiator would repeat these actions. In the third step, if the initiator touched the venter of its opponent and bit into the coxa of the second leg (15 of 79 cases), it could roll itself and turn over the opponent by taking advantage of body size. Being bitten on the vital part and pressed reversely, the spider would completely lose offensive capability. If the initiator could not beat its opponent in the first act of jumping, two contestants tussled with each other by opening all their eight legs to hold the opponent. In 9 of 31 cases, one spider bate the vital organ of its opponent and win the fighting. In other cases, both could not bite the opponent and disengaged themselves in less than five seconds (22 of 31 cases).

Depending on the opponent encountered, a spider spent different lengths of time to execute the three steps. In the large container, spiders in a symmetric contest spent less time in ritualized display (114.6 ± 16.3 s, n = 24) and attacking (10.0 ± 2.0 s) but more time in wrestling (129.1 ± 15.0 s) compared with those in an asymmetric fight (ritualized display: 199.2 ± 21.9 s, n = 31; t_{53} = 2.94, P = 0.005. Attacking: 34.6 ± 9.4; t_{53} = 2.26, P = 0.028. Wrestling: 61.5 ± 18.4 s; t_{53} = 2.73, P = 0.009; Figure 3A). In the small bottle, spiders in a symmetric fight spent more time in ritualized display (54.0 ± 9.4 s, n = 11) and attacking (11.5 ± 2.3 s) but less time in wrestling (220.5 ± 19.2 s) compared with those in an asymmetric fight (ritualized display: 5.4 ± 1.2 s, n = 13; t_{22} = 5.57, P <0.001; attacking: 5.8 ± 0.6; t_{22} = 2.62, P = 0.016; wrestling: 288.8 ± 1.2 s; t_{22} = 3.88, P = 0.001; Figure 3B).

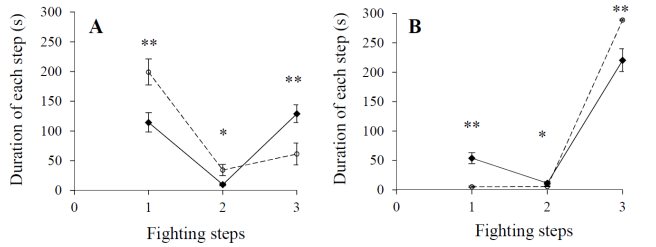

Figure 3: Duration (mean ± SE) of each step in the symmetric (diamonds and solid lines) and asymmetric fight (circles and dashed lines) in large (A) and small (B) battlefields. Means are compared using independent samples t-tests. One star indicates a significant difference at the level of P<0.05; and two stars indicate an extremely significant difference.

Effect of battlefield and body sizes on fighting performance

Females exhibited completely different fighting performance in large and small battlefields (Table 1). In asymmetric contests, large females in the large container ended in a draw in 25 rounds, won 5 rounds and lost 1 round ($\chi2^2$ =32.00, P < 0.001); meanwhile, those in small bottles won 12 rounds and ended in a draw in 1 round ($\chi1^2$ =9.31, P = 0.002). These results indicated that large spiders were more likely to defeat their small opponents in small battlefield but only ended in a draw in large battlefield. In symmetric contests, both contestants ended in a draw in 19 rounds and either won or lost in 5 rounds in the large container ($\chi1^2$ = 8.17, P = 0.004); they ended in a draw in 10 rounds and either won or lost in 1 round in the small bottle ($\chi1^2$ = 7.36, P = 0.007). These results indicated that two matched contestants were more likely to end in a draw in both large and small battlefields.

Fighting outcome	Asymmetric fight		Symmetric fight	
Battlefield	Win/loss	Draw	Win/loss	Draw
Large container	5/1	25	5	19
Small bottle	12/0	1	1	10

Table 1: Effects of body size on the fighting performance of female Chinese wolf spiders in large and small battlefield. The total number of observations was 55 in the large container (including 31 asymmetric fights and 24 symmetric fights) and 24 in the small bottle (including 13 asymmetric fights and 11 symmetric fights), respectively, which are represented by the values in the table.

Effect of experience and hunger level on the fighting performance

In the second type of contests, experienced spiders often initiated the attacking (24 of 28 cases in the large container: $\chi1^2$ = 14.29, P <0.001; 14 of 18 cases in the small bottle: $\chi1^2$ = 5.56, P = 0.018). However, they cannot always win their inexperienced opponents. In the large container, they won 9 rounds, lost 11 rounds, and ended in a draw in 7 rounds ($\chi2^2$ = 0.93, P = 0.629; Table 2). In the small bottles, they won 4 rounds, lost 6 round and ended in a draw in 8 cases ($\chi2^2$ = 1.33, P = 0.513; Table 2).

Fighting outcome	Experienced *vs.* inexperienced			Satiated *vs.* hungry		
Battlefield	Win	Loss	Draw	Win	Loss	Draw
Large container	9	11	7	4	6	8
Small bottle	9	3	6	7	2	3

Table 2: Effects of fighting experience and hunger level on the fighting performance of female Chinese wolf spiders in large and small battlefields. The total number of observations was 45 in the large container (including 27 between experienced and inexperienced contestants and 18 between satiated and hungry contestants) and 30 in the small bottle (including 18 between experienced and inexperienced contestants and 12 between satiated and hungry contestants), respectively, which are represented by the values in the table.

In the third types of contests, satiated spiders always initiated the attacking (16 of 18 cases in the big container: $\chi1^2$ = 10.89, P = 0.001. 10 of 12 cases in the small bottles: $\chi1^2$ = 5.33, P = 0.021). They won 9

rounds, lost 3 rounds and ended in a draw in 6 rounds in the large container ($\chi 2^2 = 3.00$, $P = 0.223$; Table 2), and won 7 rounds, lost 2 rounds and ended in a draw in 3 rounds in the small bottle ($\chi 2^2 = 3.50$, $P = 0.174$; Table 2). It seemed that satiated spiders were unlikely to win a fight against hungry opponents, although they were more likely to escalate the contest into a real fighting.

Discussion

In the cannibalism between female Chinese wolf spiders, we found that large spiders were more likely to defeat their small opponents; but this effect only occurred in small battlefield. In large battlefields, the contests probably ended in a draw because small spiders avoid escalating the ritualized display into real fighting. Moreover, experienced and satiated spiders exhibited higher aggressiveness, but they cannot defeat their inexperienced and hungry opponents.

Female Chinese wolf spiders engage in cannibalism to acquire food

Cannibalism of spider species has attributed to the competition for limited resources, such as food, mate, or nesting sites [12,38,39]. In the Chinese wolf spiders, we prove that cannibalistic contests may be an important strategy for females to get food in March and April. This strategy is beneficial for females to survive food lacking.

Another potential importance of cannibalism is to regulate the population size and sex ratio [40-42]. In the Chinese wolf spiders, all cannibalistic fights we observed in the wild occur between females. When two males encountered, they performed only a ritualized display and quickly retreated from the site, similar to the jumping spider *Phidippus clarus* [12]. Moreover, females never performed cannibalism on males, although they have larger body size compared with males. This pattern of cannibalism in Chinese wolf spiders may help maintain the number of males. After all, if the number of males decreases in a female-biased population [37], females will have difficulty in obtaining a mate in the upcoming reproduction.

Battlefield size determines the effect of relative body size on the fighting performance of Chinese wolf spiders

In asymmetric contests, larger contestants can defeat their opponents either in the form of ritualized display due to the retreat of smaller contestants [43-45] or when the contest escalates into real fighting [17]. In the cannibalism of Chinese wolf spiders, we found that relative body size solely determined the outcome of a cannibalistic contest if it was escalated into real fights (in symmetric fights, two matching contestants more likely ended in a draw; whereas in asymmetric fights, larger spiders more likely defeated their small opponents). But, if the contests cannot be escalated into real fights, larger contestants failed to achieve the goal of cannibalism, to get "food". Under the condition, battlefield size plays a key role in determining the outcome of asymmetric contest. In small battlefield, such as the bottle in our experiments or the cave in the wild, small spiders have no adequate space to retreat from the contest. Thus, they are forced to engage in real fights. By contrast, in large battlefield, such as the container in our experiments or outside of the spider cave, small spiders can quickly flee from the attacking range of large opponents (they possessing an obvious advantage in the speed of movement), thus avoid escalating into real fights.

Battlefield size does not influence the effects of experience and hunger

Fighting experiences can increase the aggressiveness of an individual because of the accumulation of skills and self-confidence in their fighting abilities [24,27,28]. Similarly, hungry individuals also exhibit aggressiveness in competing for food [26]. In the Chinese wolf spiders, experience but not hunger can increase the aggressiveness of a contestant. Interestingly, satiated individuals are more likely to escalate the contest. In the real fights, neither the experienced nor satiated contestants showed absolute advantage in defeating their opponents. Apparently, the great cost of cannibalistic contest [40] drives each contestant to fight to the end, regardless of the battlefield size. So, it is the nature of cannibalism that determines whether fighting experience and hunger level can determine the outcome of cannibalistic contests.

A cave protects its owner

For cave-nesting animals, the cave provides the owner not only the advantage of heat conservation [46,47] but also the protection from predators [48,49]. On the Tibetan Plateau, Chinese wolf spiders do not seem to use the cave to conserve their body temperature because their caves range from 3.7 cm to 13.4 cm in depth, which is significantly shallower than those excavated in low-altitude regions (30-50 cm, Dong 1990). Such a shallow cave cannot prevent spiders from freezing at night. Given that each spider precisely designed its cave in accordance with its own body size (Figure 1), the cave may be used as a protection of its owner. As shown above, larger spiders can defeat their small opponents in a small battlefield. If a large spider can enter the cave of a smaller spider, it can undoubtedly seize the small spider and eat it. However, the large spider has difficulty in entering the narrow cave of a smaller spider because the case only fits its smaller owner.

For the small spiders, they will be safe if they stay within their caves because large spiders cannot enter their caves. However, if a small spider wants to get food, it has to take the risk of entering into other spiders' cave. Under the condition, its fate depends largely on the body size of other spiders it encounters. In fact, many small spiders have been killed and eaten in other spiders' caves.

In conclusion

By investigating cannibalistic contests in females of the Chinese wolf spiders, we reveal that relative body size of contestants determines the outcome of the contest if it escalates into real fight; however, the battlefield size determines whether the contest can escalate into real fight. Both the fighting experience and satiation can enhance the aggressiveness of a contestant but not its probability of winning the real fight. This battlefield size effect can significantly influence the outcome of animal contests; hence, it needs to be considered in the future studies of animal contests, especially for the spiders that cannibalism frequently occurs in natural environments.

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