Sexual Selection in the Water Spider: Female Choice and Male–Male Competition

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Abstract

The water spider *Argyroneta aquatica* is the only spider spending its whole life under water, and one of the few spider species in which males are larger than females. Previous studies indicated that males can cannibalize females, which is uncommon among spiders. Here we aimed to further test for a potential influence of sexual selection on male body size. We examined the importance of female choice by testing whether females prefer the larger of two simultaneously presented males as mating partners. Further, we examined the influence of male–male competition by comparing the fighting behaviour between large and small males when alone or when together with a female, and we determined the outcome of fights. We found that females approach and choose large males as mating partners, despite the risk of male cannibalism. Additionally, males intensively compete for females, and large males clearly win against smaller ones. Hence sexual selection seems to be important for the evolution of the peculiar sexual size dimorphism of water spiders, as large size is beneficial for males in both the intra- and intersexual context. Previous studies have suggested an important role of natural selection in the sex-specific body size of water spiders, but natural and sexual selection mechanisms apparently work in the same direction, favouring large male size.

Introduction

When selection acts differently on the body size of males and females, their adult sizes may diverge. The resulting sexual size dimorphism (SSD) covers an astounding range across taxa, with extreme examples in both directions (see Fairbairn et al. 2007). Generally, in most sexually reproducing animals, females are the larger sex (Andersson 1994; Fairbairn et al. 2007), which is mainly explained by fecundity selection (Darwin 1874). The most extreme female-biased SSD (measured in weight) known among animals is exhibited by the blanket octopus *Tremoctopus violaceous*, where females are up to 4×10^4 times heavier than males (Jones & Avise 1997). The most extreme male-biased SSD known is by far not as spectacular and is shown by the shell-brooding cichlid *Lamprolo-gus callipterus*, where nest males are on average more than 12 times heavier than females (Schütz & Taborsky 2000). There is an apparent trend of finding extreme SSDs in aquatic environments and in association with highly skewed mating ratios, where only the larger sex accumulates multiple mates (Fairbairn 2007).

Sexual size dimorphism primarily reflects the adaptation of males and females to their different reproductive roles, as body size determines reproductive success typically through fecundity selection in females and mating success in males (Fairbairn 2007). Whereas large females produce bigger clutches and sometimes larger offspring or eggs (Darwin 1874), large body size of males may increase their mating success through an advantage in male–male competition or female choice (Andersson

1994). For example, large males may exclude smaller ones from their mating territories (e.g. Le Boeuf & Mesnick 1991) or females may choose large males for mating because male body weight may affect the fitness of their offspring, for instance through genes determining body weight (Jiggins et al. 2000). On the other hand, SSD may also reflect adaptations of the two sexes to different ecological conditions and constraints when males and females occupy different ecological niches (Schütz & Taborsky 2003; Fairbairn 2007).

Spiders exhibit a large range of SSDs, from male-biased to extremely female-biased examples (Foellmer & Moya-Laraño 2007). They are easy to keep in the laboratory for controlled experiments and are therefore an optimal group to study the mechanisms and selective forces driving SSD. In the majority of spider species, females are the larger sex (Vollrath & Parker 1992; Head 1995; Prenter et al. 1998; Vollrath 1998; Foellmer & Moya-Laraño 2007). Almost invariably, males are the searching sex, and they often stop feeding and building prey-catching webs after the final moult (Foellmer & Moya-Laraño 2007; for an exception see Aisenberg et al. 2007, 2009). The different ways of catching prey (with or without webs) have consequences for male and female mobility and for the mating system, which in turn affects the direction and extent of SSD. In species without prey-catching webs such as jumping spiders (Salticidae) and wolf spiders (Lycosidae), both sexes roam about and actively hunt their prey. These species show no or only little SSD (Foellmer & Moya-Laraño 2007). Exceptional among non-web building spiders are some crab spiders, where females can be 100 times heavier than males (Legrand & Morse 2000). On the other hand, in web- or nest-building spiders, females are more sedentary than males, and the latter are searching and competing for them. In the vast majority of these species, females are the larger sex (Foellmer & Moya-Laraño 2007) with the exception of kleptoparasitic spiders of the genus Argyrodes (Theridiidae; Elgar 1998).

As different evolutionary pathways have lead to SSD in spiders, it is unlikely that a general mechanism can explain its origin and maintenance (Hormiga et al. 2000). Fecundity selection has been suggested as a major factor contributing to the evolution of SSD in spiders (Coddington et al. 1997; Foellmer & Moya-Laraño 2007), but in many species, large size renders advantages also to males in intrasexual competition for mates (Leimar et al. 1991; Schmitt et al. 1992; Enders 1993; Faber & Baylis 1993; Hack et al. 1997). Female choice may

also select for larger male size, e.g. in the primarily monogamous desert spider Agelenopsis aperta, where heavy males are preferred as mating partners (Singer & Riechert 1995). In contrast, early maturation and dwarfism of males are favoured when competition over access to females is reduced, which may occur either because males suffer a high mortality risk during mate search (Kasumovic et al. 2007) or because of a low probability that several males will reach a female owing to low population densities (Ghiselin 1974; Vollrath & Parker 1992). Redback spider males were found to rapidly adjust their development in response to pheromonal cues of females and to male density (Kasumovic & Andrade 2006). When females are absent, males grow slowly and attain large size and high body condition; larger males in better condition are more likely to survive mate searching and direct competition when females are sparse. In contrast, males develop rapidly and remain small when females are present, which can provide a head start in competition for virgin females. An alternative explanation for male dwarfism in spiders is that small males might benefit by lower costs to overcome gravity when searching for females, which includes climbing (Moya-Laraño et al. 2002). A third hypothesis assumes that small males might benefit from greater agility, which enables them to better escape female attacks; however, no evidence was found for this 'cannibalism hypothesis' in recent studies (Foellmer & Fairbairn 2004; Foellmer & Moya-Laraño 2007).

Reversed SSD where males are larger than females is only found in very few spider species. In the sheet web spider Linyphia triangularis, males grow 10% larger than females (Lång 2001). Selection for large male size seems to be greater than selection for large female size, resulting in a faster growth rate of males despite distinct protandry (Lång 2001). In the sand-dwelling wolf spider, Allocosa brasiliensis, males are also the larger sex and they spend great reproductive effort by building and providing females with a secure place for oviposition (Aisenberg et al. 2007). In this species, the typical courtship pattern is also reversed, with males being the choosy sex while females locate males and initiate courtship (Aisenberg et al. 2007, 2009).

The water spider Argyroneta aquatica (Cybaeidae), the only spider that spends its whole life under water, belongs to the few spider species where males are larger than females (Foelix 1996; Schütz & Taborsky 2003). For animals with a body adapted to terrestrial life, movement and behaviour under water is more costly than on land, as water is much denser

and more viscous than air. Therefore, the selection pressures on the body sizes of the two sexes may differ in *A. aquatica* compared with other spiders. Both sexes build air bells under water to digest prey, moult and copulate, and the building and maintenance of these bells impose high costs (Schütz & Taborsky 2003). Females are more stationary than males and spend most of their time inside their large living bells, where copulations usually take place. Males build smaller, temporary air bells for specific functions, and they rove around more often than females to actively hunt their prey and search for mates (Schütz & Taborsky 2003).

In previous studies we found that in addition to fecundity selection in females, important determinants of the reversed SSD in this species may be that males must be able to move efficiently under water, which is facilitated by large size (Schütz & Taborsky 2003). Females need to reduce the costs of building a retreat and breeding shelter, which increase with body size (Schütz & Taborsky 2003). Mating costs appear to be higher for females than for males, as cannibalism of females by males does occur in this species (Schütz & Taborsky 2005a), just like in the wolf spider *A. brasiliensis* (Aisenberg et al. 2009). Furthermore, we observed intrasexual competition between males, which sometimes resulted in the death of the smaller male, and found indications that females might prefer large males as mating partners (Schütz & Taborsky 2005a). In the latter study, males were more active than females and approached them more often than *vice versa*. However, in this situation females had no choice between males as only one female and one male were combined in a tank (Schütz & Taborsky 2005a).

In the present study we aimed to test for the influence of female choice on effects of male body size of water spiders by providing females with the opportunity to choose between two differently sized males simultaneously present in a tank. In laboratory experiments we investigated which sex would initiate interactions with conspecifics and the approach to potential partners. We compared female behaviour towards large and small males, and the behaviour of large and small males towards the female. Further we examined the influence of male body size on male–male competition. Apparently, fights are very costly in these spiders, as fatal injuries may occur and the spiders need to surface to renew the air in their bells between fighting bouts (own observations). Therefore, we compared the fighting behaviour between large and small males when alone or together with a female and determined the outcome of fights.

Methods

Ethical Concerns

In our experimental design we attempted to eliminate potential causes of stress and mortality for the test individuals. We put water plants into the experimental tanks to serve as shelters for fleeing spiders to hide when being attacked. Following the ABS/ASAB guidelines and the policy of research granting agencies, we used the smallest number of animals possible to accomplish our research goals in accordance with expected effect sizes, to avoid unnecessary suffering and waste of animals. *Argyroneta aquatica* is regarded as highly threatened in Germany and Central Europe (Binot et al. 1998). We could not prevent individual spiders killing others in the experiment, as the variation in body size and the direct interaction between animals were of essence to this study. However, killing conspecifics and cannibalism are very common among *A. aquatica* and other spider species also under natural conditions (see Elgar 1992 for review).

Subjects

All spiders used in this study were wild-caught animals from four adjacent populations near Vienna, Austria, or their F1 offspring (see Schütz & Taborsky 2005a for collecting and holding conditions). For each adult test spider, we determined the cephalothorax width as a measure of body size at the beginning of the experiments (cf. Foelix 1996; Lång 2001). Each female was used only once, and each male was tested twice with a different rival male, but in the same role (large or small), with at least 2 wk between trials. It was necessary to use males twice because the water spider is regarded to be endangered (Binot et al. 1998), and therefore, we had to minimize the number of individuals used in the experiments. Some males of our stock could not be used because they were smaller than females, or they showed no or little reproductive behaviour in the holding tanks. These males were not used for the experiments, and hence the remaining suitable males were each tested twice to obtain the intended number of replicates, and their data were pooled. According to Leger & Didrichsons (1994) who analysed four data sets, both simulated and real, and in their pooled and unpooled form, pooling does not bias results provided that the sample sizes are equal.

This is the case in this study. Also, it is worth noting that the degree of pooling in our data was very low, because only two values of the same individual males measured in different social settings (i.e. with a different male competitor and a different female) were used in the analysis.

Of the male spiders that were available, two groups containing males with different body sizes were created using the natural variation in size to allocate large males into one experimental group and small males into the other. The average cephalothorax width of large males was 4.5 ± 0.3 mm (mean $\pm$ SD), of small males 3.8 ± 0.4 mm, and of females 3.3 ± 0.2 mm. The large male was always larger than the two other spiders in the experimental tank and the small male was larger than the female except in one case, where he was smaller than the female by 0.05 mm.

Experimental Setup

The experiments were performed at the Konrad Lorenz-Institut für Vergleichende Verhaltensforschung in Vienna (KLIVV) in summer 2000 during a period of 3 mo. Before the experiments, the spiders were kept singly in their holding tanks with water plants and *ad libitum* food at a water temperature of 25°C. In standardized laboratory experiments (for details see Schütz & Taborsky 2005a), we compared courtship, aggressive and mating behaviours between two differently sized males and a female.

Here we build on a previous study in which we had tested the behaviour of females towards a large and a small male successively (Schütz & Taborsky 2005a). Twenty test females had been presented either first with a small male and then with a large male or *vice versa*, each for 2 d. We tested which sex is more active in mate acquisition and whether there are apparent mating preferences. Data showed that males were more active than females in mate acquisition, and the latter fled more often from the approaching spider than *vice versa*. Small males approached the female more often than large males did, but females performed reproductive behaviour (courtship, mating and egg sac building) only with the latter, which hinted at a female preference for large males. In a second experiment we tested aggression and cannibalism propensities in the absence of a female. In 16 replicates we kept two differently sized males in a tank for 2 d, which revealed very high aggression levels, resulting in the death of the smaller male in three cases (Schütz & Taborsky 2005a).

For the purpose of the present study, we added a female to the two males on the third day of this experiment to check for (1) female choice when test females had access to two differently sized males simultaneously, (2) male–male competition in the presence of a female, and (3) the behaviour of males in comparison between periods with and without a female present. This experimental sequence ensured that the males had accustomed to the experimental tank environment and behaved normally when a female was added. Males are more agile than females (Schütz & Taborsky 2003), and it takes longer until they settle in a new tank than the more stationary females that usually build an underwater air bell soon after being introduced to a new tank.

When the female was added exactly 48 h after the males had been introduced into the tank (between 14.00 and 16.00 h), the two males were mobile and kept moving around during the whole observation period. Usually males built a small underwater bell when they caught prey to digest it, but they spent most of their time outside bells. The females therefore could choose between two males moving around actively, which resembles the natural situation (Schütz & Taborsky 2003, 2005a). We used young mature females that already had bred successfully once to ensure that they were capable of breeding and motivated to reproduce. They were kept isolated in 2-l holding tanks before the experiments for at least 3 wk to ensure that they were ready to mate at the beginning of each replicate.

The whole experimental tanks were videotaped continuously for all 4 d (with and without female present), starting with the introduction of the two males, to be able to compare male behaviour before and after the female was added. The time-lapse video recorder was set to 90 frames/min so that 48 h were condensed into 3 h.

Video Analysis

We analysed the behaviour of the spiders from 12 h before to 48 h after the female was added to the tank. For each interaction between two or three spiders, we recorded the following behaviours: (1) Instantaneous Contacts, when two spiders met haphazardly during moving around in the tank and one spider or both fled immediately after having physical contact. (2) Approach, when one spider actively moved towards another spider. After an active approach, we noted the exact time and duration of the behaviour that followed, and who was fleeing or leaving after the encounter. (3) Fight, when wres-

tling occurred between two spiders. (4) Joint Residence, when the position of the female was within 5 cm of a male, which was used as an estimate of mate guarding. When one male and the female stayed in joint residence, we recorded whether and when the second male disturbed the residence and whether and who was expelled after the interference. (5) Palpation, when one male and the female tapped each others' first pair of legs. (6) Copulation, when the male inserted his pedipalps into the females' genital opening. As copulations always took place in an under-water air bell built between the plants, it was not always possible to clearly identify copulations. Therefore, the frequencies of copulations recorded are probably an underestimate. (7) Unclear Behaviour, which consisted mainly of two spiders moving around each other or two males staying in joint residence without any interaction. Unclear behaviour was not analysed further.

Behavioural Analyses and Statistics

In three of the 16 trials, the small male was killed by the large male before introduction of the female, in one case he disappeared, and in two trials the female was killed by the large male after 1 and 20 h, respectively. These six replicates were not used for further data analyses because either they did not provide any data or the data did not suffice for analysis. In another replicate, the female was killed by the large male after 37 h, and in one case, the female escaped from the tank after 34 h. These two replicates were included in the analyses because sufficient data had been obtained already before these incidents to enable data inclusion. Therefore, the sample size for the further analyses was 10.

To determine the influence of male size on female choice, we analysed for the 48-h period after introducing the female (1) which sex would approach the other more often when a female had access to two males simultaneously, (2) whether females approached males independently of their size, and (3) how competing males of different sizes performed in mate acquisition. We also tested for behavioural reactions, in particular for differences in (4) the reaction of large and small males to female approaches towards them, (5) the reaction of the female to approaches of large and small males towards her, (6) the total and average time large and small males spent in joint residence with the female, (7) frequencies of large and small males disturbing joint residence of the other male with the female and (8) the rates of successful expulsions of

the female by a large or small male from joint residence with the other male. All tests used were two tailed. Test statistics reported in the Results are z- and p-values attained by Wilcoxon matched-pairs signed-ranks tests unless stated otherwise, using the statistical package SPSS 13.0, SPSS Inc., Chicago, IL, USA.

To test for the influence of male body size on male–male competition, we analysed the frequencies of active and haphazard approaches between the two males for the 12-h period before introducing the female. For each male, we analysed the proportion of active approaches resulting in escalated fights, and we compared these frequencies and the fight durations between the periods with and without females using Wilcoxon matched-pairs signed-ranks tests. With Friedman ANOVAs we compared the frequencies of fleeing after being involved in an escalated fight between all three spiders. Differences between pairs of treatments were subsequently tested with Friedman post hoc multiple-comparison tests ($\alpha = 0.01$; Conover 1980).

Results

Do Females Approach Males More often than *vice versa* when Given a Choice Between Mates?

Females approached males more often than *vice versa* ($z = -1.988$, n = 10, p = 0.047). They actively approached large males more often than small ones ($z = 2.073$, n = 10, p = 0.038; Fig. 1a), whereas males of both sizes did not differ in their frequencies
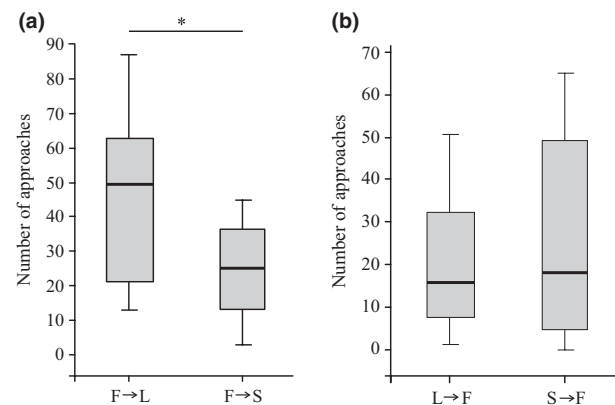

Fig. 1: Number of approaches between two spiders during 48 h, averaged between trials (medians [bold lines], quartiles, minima and maxima). L, large male, S, small male, F, female; A → B: A approaches B. (a) Female approaches towards large and small males, *p < 0.05. (b) Approaches of large and small males towards the female.

	Reaction (means/48 h)	Sample size, N	Test value, z	p-value
(a) Reaction of large vs. small males to female approaches				
Fight	L (12.48) < S (23.49)	10	−2.429	**0.015**
Joint residence	L (40.71) > S (22.52)	10	2.497	**0.013**
Copulation	L (3.74) > S (1.38)	10	2.201	**0.028**
(b) Female reaction to large vs. small male approaches				
Fight	L (9.22) < S (20.36)	9	−2.1	**0.036**
Joint residence	L (27.74) > S (16.23)	10	2.1	**0.036**
Copulation	L (0.39) ≈ S (0.35)	9	4.447	0.655

Table 1: Wilcoxon test statistics of (a) the reaction following female approaches towards the large or small male, and (b) female reaction following large or small male approaches towards her. The numbers denote the per cent of active approaches resulting in a specific behavioural reaction
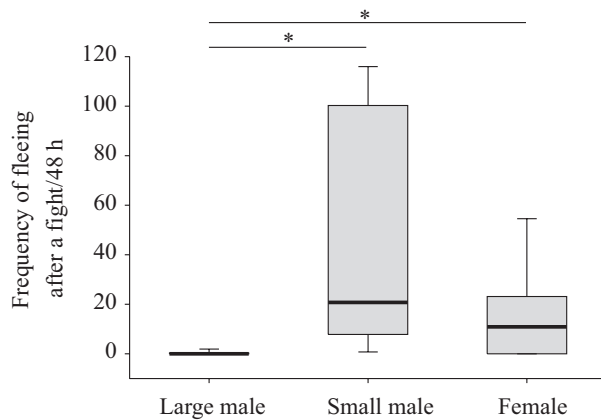
L, large male, S, small male and F, female.
Significant p-values are highlighted in bold (p < 0.05).

of approaching the female ($z = -0.56$, n = 10, p = 0.575; Fig. 1b).

Do Interactions Between Females and Males Depend on Male Size?

Female approaches towards the large male resulted in significantly fewer fights between male and female, more joint residences and more copulations than female approaches towards the small male (Table 1a). Conversely, large male approaches towards the female also resulted in significantly fewer fights and more joint residences than approaches of the small male towards the female (Table 1b).

Females stayed longer in residence with the larger (median = 97.01 min/48 h, interquartile range (IQR) = 36.55–1269.07) than with the smaller male (median = 14.93 min/48 h, IQR = 3.22–55.95; $z = 2.09$, n = 10, p = 0.037). In all 10 replicates, the female stayed in joint residence with the larger male at some stage, which was disturbed by the smaller male at least once in eight replicates. In eight of the 10 replicates the female stayed in joint residence also with the smaller male, which was always disturbed by the larger male. In absolute terms, the small male disturbed the joint residence of the other male with the female more often than the large male did ($z = 2.38$, n = 10, p = 0.017). However, if 'disturbance of joint residence' is corrected for 'time of joint residence with the female', there is no difference between the two males ($z = 0.652$, n = 10, p = 0.515).

The female left the joint residence with the small male after disturbance by the large male in all cases (100%), whereas she left the joint residence with the large male only in 38.6% of cases when the small male disturbed. In the remaining 61.4% of cases, the small male was expelled by the large male and the female stayed in joint residence with the latter. This difference in response to disturbance was significant ($z = -2.375$, p = 0.018; in 2 (1) cases, the smaller (larger) male did not disturb joint residence of the other male, therefore, n = 7).

Male–Male Aggression with and without Female

When the female was present, more approaches of the large male towards the small male resulted in escalated fights than when no female was present ($z = -2.666$, n = 9, p = 0.008), which was not the case for approaches of the small male towards the large male ($z = -1.599$, n = 9, p = 0.11). With female presence, fights between the two males lasted significantly longer (mean ± SD = 15.15 ± 9.54 s) than when no female was present (mean ± SD = 7.12 ± 4.63 s; $z = 2.429$, n = 10, p = 0.015). All fights except one were won by the larger male, and the frequency of withdrawals after a fight differed significantly between the three spiders (Friedman test, $\chi^2 = 12.056$, n = 10, p = 0.002): after a fight, the larger male withdrew significantly less often than the small male and the female (Friedman post hoc multiple-comparison tests, p < 0.01, Fig. 2).

Discussion

When given a choice between potential partners, females were more active in mate search than males and they preferred and actively chose large males for mating. However, despite this preference, they did not exclusively mate with them. In one replicate, for example, where both males had a diving bell, the female alternately approached the large male five times and the small male three times to copulate with them in their bells. It is unknown which sensory information female water spiders use to judge the quality or size of males, but it is possible that they use water movement for orientation at a distance. Once they are in direct body contact, tactile

Fig. 2: Frequencies of fleeing after a fight; box-plots and symbols as in Fig. 1.

information might be used: When male and female met, they seemed to 'examine' each other by palpation (see Methods section).

Our results differ from those of a previous study where males had been more active than females and approached them more often than *vice versa* (Schütz & Taborsky 2005a). However, in that study females could not choose between two simultaneously present males, because only one female and one male were combined in a tank. The different results therefore suggest that females are actively approaching and choosing males when more than one potential mate is available. In this situation, which may resemble high population densities in nature, they seem to compare the males, and visit, stay with, and copulate more frequently with larger than with smaller males.

To the observer, the behaviour shown in response to active approaches between different spiders in our experiment resembled that in the natural situation (own obs.). It might be argued that the difference between female and male activity was affected by the period during which the males acclimatized to the tank without female presence. However, this would not explain why females are choosy and take such an active role in visiting and interacting with the different males. Obviously, female activity was also not brought about by enhanced search for a place to construct an air bell, because there was ample space for building a bell between the plants and the walls of the tank. Therefore, we think it is safe to conclude that in *A. aquatica,* females are actively choosing and preferring large over small partners. An active role of females in mate choice has been observed also in wolf spiders (Kotiaho et al.

1996), but females are the larger sex in these species.

Competition between males was very intense in our experiment, sometimes resulting in the death of the smaller male. Males also competed for captured prey and fought regularly when there was no female in the tank. Fights about prey mainly occurred after one male caught and killed a prey that was not immediately consumed but attached to a plant or the substrate before taking it into a diving bell for digestion. If the other male tried to steal the prey fights might ensue, which were always won by the larger male regardless of who had caught it. Such interactions are probably costly as water spiders have to work against buoyancy constantly when moving under water, and they are oxygen limited, needing to surface regularly to replace the air in their diving bells and around their bodies (Schütz et al. 2007).

When a female was present, the number and duration of fights between males increased significantly, which illustrates the potential of intrasexual selection for the evolution of large male body size. The larger males won all fights except one. Also in male bowl and doily spiders *Frontinella pyramitela* male fighting escalates more easily in the presence of a female, which may again lead to disablement or even fatal injury in extended fights (Austad 1982, 1983). However, even in species where males are much smaller than females (e.g. *Nephila edulis*), larger males may be better at fighting off smaller males (Elgar et al. 2003), but this clear advantage in male size did not lead to male-biased SSD.

Our experiments showed that large male size also pays when males interfere with mating pairs. The joint residence between male and female was regularly disturbed by the other male attacking the pair. The large male was successful every time he disturbed the joint residence of the small male, as either the female, the small male, or both left their joint residence in response. In contrast, only 38.6% of the disturbances by the small male resulted in the female leaving her joint residence with the large male, whereas in the majority of cases she stayed in residence with him. This again illustrates the potential advantage of large body size in male–male competition for mates.

In an earlier study, we found evidence that the unusual ecology of the water spider is important for the evolution of its exceptional SSD (Schütz & Taborsky 2003). The degree of SSD differed significantly between four adjacent populations of *A. aquatica*, which depended more on variance in male size than in female size. This suggests that ecological

parameters influence optimal body size for locomotion, as males are generally the more mobile sex in *A. aquatica* (Schütz & Taborsky 2003). In terrestrial animals, smaller individuals have generally a mobility advantage over larger ones and hence small size may facilitate locomotion (Withers 1992; Azuma 1992; for an exception see Bauwens et al. 1995). In contrast, in the water spider, large individuals have a mobility advantage over smaller ones, as (large) males were better divers than (small) females in a diving experiment (Schütz & Taborsky 2003). Female size might be limited by the costs of building air bells, which they use to raise their broods. Therefore, SSD in *A. aquatica* seems to be influenced also by natural selection mechanisms, as the necessity to move efficiently under water and the costs of building air bells may limit the body size of both sexes in opposite directions (Schütz & Taborsky 2003).

In this study, we found that females show a clear preference for large males despite the risk of male cannibalism (see Schütz & Taborsky 2005a). When males attacked females in our experiment, one could argue that they might have confused them with a male, especially as males were together without a female before the latter was introduced. However, in an earlier experiment in which two spiders were introduced into the tank simultaneously, large males killed smaller females and smaller males alike, apparently merely contingent on the direction and extent of the size difference. This suggests that cannibalism in *A. aquatica* might follow the simple rule 'Large eats Small' (Schütz & Taborsky 2005a).

In addition we found here that males strongly benefit from large size in intrasexual encounters, especially when competing for a mate. Hence, sexual selection is probably important for the evolution of the unusual SSD of water spiders in addition to natural selection, as both intra- and intersexual selection seem to favour large male size (Hunt et al. 2009). This resembles the situation in the cichlid fish *Lamprologus callipterus*, where also natural and sexual selection are important determinants of SSD, which is the most extreme male-biased size dimorphism known in animals (Schütz & Taborsky 2000, 2005b; Schütz et al. 2006). In spiders, it has been suggested that the evolution of female size may be more important for generating SSD than the evolution of male size (Foellmer & Moya-Laraño 2007). This seems to be different in the water spider, which might be due to different selection pressures acting under water than on land. In water spiders natural and sexual selection pressures work in the same direction in males and strongly favour large body size, suggesting that selection on male size may be more important for generating and maintaining the reversed SSD than selection on female size. This supports the conjecture also in spiders that deviating or extreme SSDs are often associated with aquatic environments (Fairbairn 2007).

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