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MATE CHOICE AND SEXUAL CONFLICT IN THE SIZE DIMORPHIC WATER SPIDER, *ARGYRONETA AQUATICA* (ARANEAE, ARGYRONETIDAE)

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ABSTRACT.   *Argyroneta aquatica* is the only spider that spends its entire life under water, and is one of the few spiders in which males are larger than females. In this paper we investigated size dependent mate choice to clarify whether intersexual selection may be partly responsible for the reversed sexual size dimorphism (SSD) in *A. aquatica*. We found that females that only copulated once could produce up to six viable egg sacs, although the number of offspring decreased with each egg sac produced. Males are the more active sex in mate acquisition and females prefer large males as mating partners. However, females fled more often from males larger than their own size (SSD > 1) than from relatively smaller males (SSD < 1), although small males approached females more often than large males did. We found that males of *A. aquatica* may cannibalize females, which to our knowledge is the first account of such reversed sexual cannibalism in spiders. The extent of SSD (m > f) determined the likelihood of females being cannibalized. Apparently, avoidance behavior of females towards the preferred, large mating partners is related to the higher risk of being cannibalized. In *A. aquatica*, intersexual selection may stabilize male size at an optimum instead of directionally selecting for large body size.

Keywords: Sexual size dimorphism, SSD, sexual cannibalism

In most web-building spiders, females are larger than males (Vollrath 1980; Head 1995). Recent studies suggest that selection pressures on male locomotory ability greatly influence optimal male body size. For terrestrial spiders, small male size has often been explained by mobility advantages (Foelix 1992). In some species, males are even able to balloon, similar to young spiderlings (Foelix 1992). Recently, Moya-Larano et al. (2002) proposed, with help of a simple biomechanical model, that smaller males are favored in species in which the male must climb to reach females in high habitat patches. They argued that the constraint imposed by gravity on climbing males is a selective factor in determining male dwarfism (Moya-Larano et al. 2002). In the water spider *Argyroneta aquatica* Clerck 1757, however, males are larger than females and larger males have mobility advantages over smaller ones when moving under water (Schütz & Taborsky 2003). Since the water

spider spends its entire life under water, large body size is favored in this species more in males, the more mobile sex, than in females

Mate choice and male-male competition.—There is evidence that female choice mechanisms may influence the evolution of male body size in some spiders. Elgar et al. (2000) demonstrated that females used cannibalism to choose their preferred mates in the orb-web spider *Argiope keyserlingi* Simon 1895, in which mature males are much smaller than mature females. Females that copulated with relatively smaller males delayed sexual cannibalism and prolonged the duration of copulation. Consequently, small males fertilized more eggs than large ones (Elgar et al. 2000). In the desert spider, *Agelenopsis aperta* Koch 1837, a species in which males and females are approximately the same size at maturity, heavy males were more likely to be accepted by females (Singer & Riechert 1995).

Intrasexual competition between males may also influence optimal body size in spider males. In some sheet-web spiders (Linyphi-

idae), where males are larger than females, the reversed sexual size dimorphism (SSD) probably depends on strong intrasexual selection through male-male competition for mating opportunities (Lång 2001). In contrast, male dwarfism may be the result of reduced intrasexual competition (Vollrath & Parker 1997). For example in *Nephila* spp., in which males suffer a much greater mortality risk than females due to active mate search and a higher mobility, intrasexual competition between males is strongly reduced and males are much smaller than females (Vollrath & Parker 1997).

Sexual conflict.—Mating patterns are often characterized by conflicts of interest between the sexes. Such conflicts may exist over the frequency of mating or the degree of parental investment (Warner et al. 1995; Henson & Warner 1997; Schneider & Lubin 1998; Johnson 2001). Since in spiders, males do not provide parental care and females can usually fertilize more than one clutch with a single copulation, the main conflict between the sexes in spider reproduction should be about the frequency of mating (Schneider & Lubin 1998).

Both sexes are selected to prevail in this conflict (Henson & Warner 1997; Shine et al. 2000; Eberhard 2002). In spiders, males may force copulations (Schneider & Lubin 1998) or develop adaptations that prevent the sperm of rival males from fertilizing the eggs of the female (sperm competition, Schneider & Elgar 2001). Females may reduce receptivity after one mating, they may respond aggressively towards approaching male, or they may have structures that enhance their control over mating (Schneider & Lubin 1998). Sexual conflict in spiders can even result in the death of one partner, usually when a female cannibalizes a male after, during or even before mating (Andrade 1996; Schneider & Lubin 1996; Schneider & Lubin 1998; Elgar et al. 2000).

The reversed SSD in the water spider may lead to a different outcome of sexual conflict with respect to rates of mating when the water spider is compared to other spiders. Due to their relatively large size it may be easier for *A. aquatica* males to overcome resistance of the female, and female cannibalism of males may be difficult.

The study species.—*Argyroneta aquatica* (Clerck 1757) is a solitary, aquatic spider (Heinzberger 1974) distributed in northern and middle Europe, in Siberia up to 62° latitude north, and in central Asia (Crome 1951). It is active mainly during the night (Stadler 1917; Heinzberger 1974; Masumoto et al. 1998) and shows specific adaptations to the life under water. For digesting their prey, molting, copulating, depositing eggs and raising offspring, males and females separately construct air bells under water, which are usually built between water plants and fixed with spider thread to plants or stones (Wesenberg-Lund 1939; Heinzberger 1974). The abdomen and legs bear hairs that keep an air bubble around the body to help transport air from the surface down to the air bell, and to breathe under water (Ehlers 1939). Adult males were significantly larger (males: 3.8 ± 0.67 mm, females: 3.2 ± 0.29 mm, mean $\pm$ SD) and heavier (males: 0.15 ± 0.08 g, females: 0.10 ± 0.039 g) than females (data in Schütz & Taborsky 2003).

Water spiders appear to suffer from certain constraints from their life under water (Engelhardt 1989). *Argyroneta aquatica* is not a good diver as it struggles hard to compensate for buoyancy when moving under water (Schollmeyer 1913). Males are more mobile than females. They rove around more often, actively searching for females and catching their prey mainly by active hunting (Crome 1951). Females spend most of the time inside their air bell, where they also raise their broods. They are ambush predators catching prey mainly when detecting vibrations caused by prey touching the underwater net, which surrounds their air bell. Thus, males and females have different ''life styles'', which may select for different body sizes (Schütz & Taborsky 2003).

In a previous study we found that *A. aquatica* males (i.e. the more mobile sex) are better divers than females, as measured by the vertical diving ability in a 1000 ml glass cylinder with and without structures to grasp. It is possible that ecological constraints select for a body size that is optimal for underwater locomotion in males much more than in females. We further found that females built larger air bells than males and that air bells size correlated with body size in females, but not so in males. Thus female size may be limited by the costs of building air bells (Schütz & Taborsky 2003). In the present study, we

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investigated how this unusual direction of SSD relates to mate choice and sexual conflict in *A. aquatica*. Do females choose mates according to size, and do males compete for access to females?

METHODS

Study subjects.—All spiders used for this study were wild caught animals from four adjacent populations near Vienna, Austria, or their offspring. In 1999 and 2000 we collected more than 160 water spiders (45 adult females, 35 adult males and > 80 subadults) with small fishing nets and kept each adult spider isolated in a glass jar. Whole broods and smaller subadults were held in groups in small aquaria, and all spiders were fed twice a week with living *Assellus aquaticus* or *Gammarus pulex*. The prey also survived very well in the small aquaria, so that the spiders had access to ad libitum quantities of living food. For each spider, we determined the cephalothorax width as a measure of body size (see Foelix 1992; Lång 2001). After we could determine the sex of subadult spiders, we measured their cephalothorax width when they were mature. Voucher specimens (two females) have been deposited in the Natural History Museum of Berne.

Due to very dense aquatic vegetation in the field it was impossible to observe the water spiders' behavior there and to measure population parameters such as longevity of males and females, sex ratios or spider and nest densities. From continuous size monitoring of individual spiders that were born in the lab (cephalothorax width), we found that under standardized conditions, females grew faster than males. After 200 days, females were significantly heavier than males (T-test, $T = 2.226$, $P = 0.035$, $n = 13$ males and 15 females). Lab born females survived significantly longer than lab born males (T-test, $T = 2.226$, $P = 0.035$, males: 358.9 ± 72.9 days, mean $\pm$ SD, $n = 13$, females: 479.7 ± 84.6 days, $n = 15$). In the field, females and males that are born late in the season have probably two mating seasons, with females laying several clutches per season. Much about the life history of this species remains unknown because of the difficulties of studying them in their natural habitat.

Typical mating behavior.—We observed over 50 pairings of the water spider in a variety of settings in the laboratory, and from these observations have developed a general description of a "typical" mating.

Number of young produced in successive broods after one copulation.—To find out whether females need to copulate repeatedly to fertilize subsequent clutches, we took 31 females that had matured in the lab (and thus we knew they were virgins), mated them in the lab, then held the females separately in glass jars for one year, and counted all offspring in successive egg sacs.

Mate choice and male-male competition experiments.—In a mate choice experiment in the lab we studied which sex is more active in mate acquisition and whether either sex chooses particular individuals as mating partners. In a male-male competition experiment we tested whether males compete for access to females and whether sexual cannibalism occurs and depends on the direction and extent of SSD. The test females were mature and had laid three successive egg sacs without copulating in between before they were used in these experiments. They were kept in 2 liter holding tanks before and between experiments for at least three weeks to ensure that they were ready to mate at the beginning of each experiment. Each female was used in both experiments, with a different partner in each experiment. Each male was tested twice in both experiments, with at least two weeks between trials.

For both experiments, the bottom of each 10 liter tank was covered with 3cm of small gravel (grain size $\leq$ 2mm), and ten one-leaf plants (*Cryptocoryne* sp.) were put in a row in the front part of the tank, so that the spiders had the opportunity to build a diving bell between two plants or between one plant and the glass wall of the tank. The whole tank was videotaped, and the behavior of the spiders was recorded with a time lapse recorder so that 48 h were condensed into three h, and recorded on a 180 min video tape.

In the mate choice experiment, we tested for behavioral differences (i) between males and females, (ii) between large and small males and (iii) of males towards large and small females. In 20 replicates, half of the test females were presented first with a small male for two days and then with a large male for two days; in the other ten females the sequence was reversed. Large males were on av-

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erage 4.6 ± 0.5 mm (cephalothorax width, mean ± SD, range: 4.05–5.8 mm), small males 3.5 ± 0.35 mm (range: 2.95–3.91 mm), and females 3.2 ± 0.26 mm (range: 2.71–4.24 mm). Each mate choice trial lasted for four days, in which the female was together with either of the two males for two days each.

The video recordings were analyzed in two ways: (A) Instantaneous time sampling: in the first hour and then every fourth hour of the experiment, we noted every five minutes real-time whether the male and female are together, either inside or outside of the female air bell. From this we calculated the percent of time each pair stays together during 48 hours and compared these times between large and small males. For females we also noted whether they built an egg sac. (B) Continuous recording: during the whole experimental period we continually recorded which spider approached the other, fled from the other, and which spider cannibalized the other. For each spider we calculated the frequency of approaching and fleeing within 48 hours, and compared these frequencies between (i) males and females, (ii) smaller and larger males, and (iii) males towards the larger and towards the smaller females. We also analyzed whether females fled more often or spent more time together with either of the two males. From 14 videos we could analyze the first experimental pairing of the female with a male, and from 12 of these 14 videos we were able to analyze the experimental pairing of the female also with the second male.

We noted the location of each spider twice a day (between 10.00–11.00 and between 17.00–18.00) in the mate choice experiment, whether a male and female were together, whether they showed courtship behavior (e.g., the male chasing the female outside of the bell or both spiders swimming around until they meet again in the bell) or mating behavior (i.e. copulations or when the two spiders are in an entangled position), and whether females built egg sacs. When the female courted, mated or built an egg sac only with one male, we interpreted this as "preference" for this male. When a female showed any such preference with the first male on days 1 and 2, we left her in the tank to observe encounters with the second male on days 3 and 4, and to see whether females re-mate in dependence of the relative sizes of the two partners.

In the male-male competition experiment, two differently-sized males were released in one tank on the first day and kept together for two days. For the following two days a female was added. Sixteen replicates were performed each with different individuals. The daily recordings were similar to the female choice experiments, and we analyzed whether females preferred to copulate with either of the two males.

We analyzed aggressive behavior between males and whether cannibalism (intra- and intersexual) occurred. If it happened, we analyzed whether its occurrence depended on the degree and direction of SSD. For this we pooled the data from the mate choice and male-male competition experiments. From the mate choice experiment we included the cases in this analysis in which the female was combined with the larger of the two males ($n = 20$). In the male-male competition experiments the females were together with two males simultaneously. We only included the SSDs between the female and the larger male in this analysis ($n = 16$), because due to the male-female size difference only the larger males were candidates for sexual cannibalism.

Statistics.—Data distributions were tested for normality (Kolmogorov-Smirnoff one-sample tests, $P > 0.1$). Non-parametric statistics were used if significant differences from normal distributions were found ($P < 0.1$), and when the sample size was too low to test reliably for normality. Otherwise we used parametric statistics. All tests were two-tailed.

RESULTS

Typical mating behavior.—A typical mating in *A. aquatica* starts with the male approaching the female in her living bell (see also Braun 1931). Once in the bell, the male chases the female out of the bell and both spiders swim around for a short while until they meet again in the bell, a behavior called "courtship swimming". Once they are back in the bell, the female accepts the male, they chase each other around the air bell and after a short period they start copulating. Copulation takes place in the female's living bell, where the male transfers the sperm to the female, and the spiders remain in an entangled position for some seconds. Copulations take place several times, and after the last one the pair remains together in the bell for some min-

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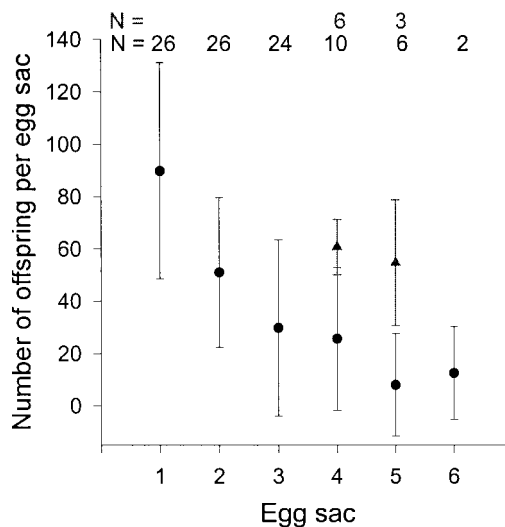
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Figure 1.—Number of spiderlings per egg sac produced in successive egg sacs by *Argyroneta aquatica* without copulation between successive broods (dots) and with copulation after the third egg sac was produced (triangles, means and standard deviations).

Figure 2.—Frequency of approaching and fleeing from each other in males and females during 48 hours (means and standard deviations).

utes, while the female starts building an egg sac (see also Braun 1931). Producing an egg sac took a few hours. The female cares for the brood alone (27 ± 2.61 days in the first broods of each female in this study, $n = 23$; see also Hamburger 1910; Stadler 1917; Crome 1951). When the female does not accept the male, she tries to chase the male out of her bell, but often looses the conflict by loosing her bell and sometimes even her life (see below), and then the male stays in the bell.

Number of young produced in successive broods after one copulation.—Of the 31 females that were known to have mated only once, 26 produced at least three successive egg sacs. A few females produced up to six egg sacs while they were isolated in single glass jars for a year. The number of spiderlings per egg sac decreased significantly with increasing egg sac number (Spearman correlation, $r = -0.943$, $P = 0.005$, $n = 6$, Fig. 1). A pairwise comparison of the numbers of spiderlings per egg sac in the first and second egg sacs revealed that females raised significantly more young in the first eggs sac than in the second (paired T-test, $T = 5.611$, $n = 26$ females, $P = 0.001$). Females that copulated a second time after producing the third egg sac produced significantly more offspring
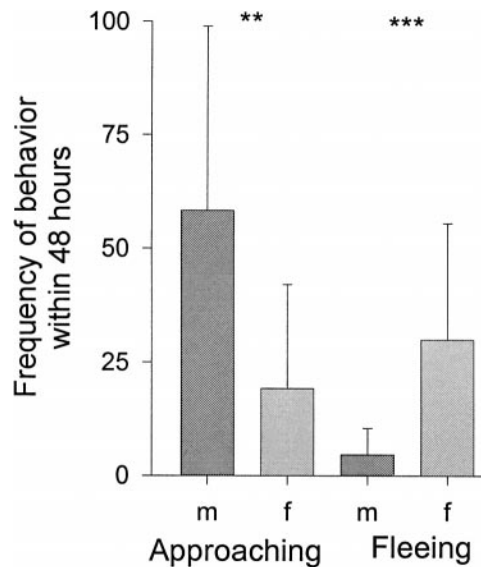
in the fourth egg sac (Mann-Whitney-U-test, $Z = -2.284$, $n = 6 + 10$, $P = 0.022$) and in the fifth egg sac (Mann-Whitney-U-test, $Z = -2.263$, $n = 3 + 6$, $P = 0.024$) than females that did not copulate after the third egg sac (see Fig. 1).

Mate choice and male-male competition experiments.—*(i) Differences between males and females:* In order to assure data independence, for this analysis we only included the first experimental pairing of the female with either of the two males in the mate choice experiments. Males approached females more often than vice versa (Paired t-test, $T = 3.064$, $df = 13$, $P = 0.009$, Fig. 2), and females fled more often from males than vice versa (Paired t-test, $T = -4.017$, $df = 13$, $P = 0.001$, Fig. 2).

(ii) Behavior of large and small males towards females: In the first experimental pairing of each female with a male in the mate choice experiments, small males approached the female more often than large males did (Pearson correlation, $r = -0.624$, $n = 14$, $P = 0.017$, Fig. 3).

(iii) Male behavior towards females of different sizes: We tested with pairwise comparisons whether males behaved differently towards large and small females when they were tested with differently sized partners. There

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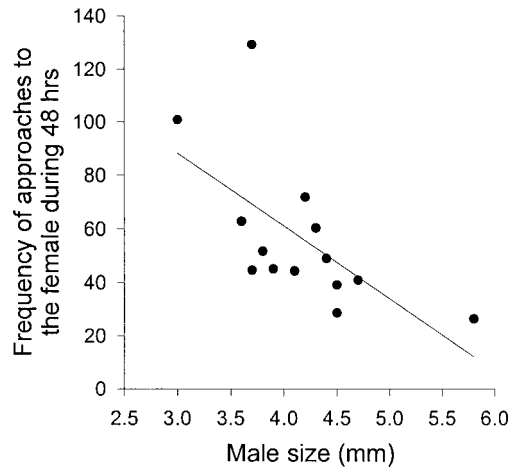

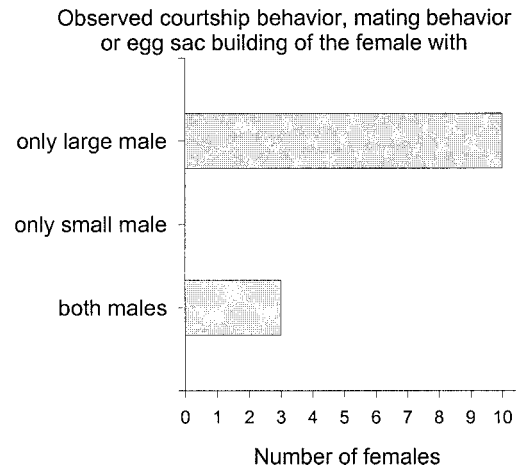Figure 3.—Frequency of approaches of males of different sizes to the test female.

Figure 4.—Number of females courting, mating or building an egg sac with only the large male, only the small male or both males.

was no difference in the behaviors measured (Wilcoxon tests, $n = 11$, all $P > 0.15$, see methods for behaviors).

In three instances, females mated with both males. From 20 females in the mate choice experiments, 10 showed a preference because they performed reproductive behavior, i.e. courtship behavior ($n = 4$), mating behavior ($n = 3$) or egg sac building ($n = 3$) with only one of the two males. Nine females did not show a preference (Fig. 4; one female was killed during the experiment), because they performed reproductive behavior with both ($n = 3$) or with neither of the males ($n = 6$). When the test-females preferred one male, they showed reproductive activity with the larger of the two males (Binomial test, $n = 10$, $P = 0.002$), despite the fact that small males approached females more often than large males (see above). In both cases in which a female showed reproductive behavior with the smaller male first, she repeated this with the larger male, but in only one of six cases when a female showed reproductive behavior with a larger male first, did she again show reproductive behavior with the smaller male.

In the male-male competition experiment, when two differently sized males and one female were combined in one tank on days three and four, the larger male copulated with the female five times, but the smaller male never copulated with the female (Fisher's exact test, $0.05 < P < 0.1$).

In mate choice experiments with SSD > 1 (male:female, males 1.28 ± 0.13 times larger than females, $n = 22$) females fled more often from the males than in experiments with SSD < 1 (males = 0.85 ± 0.03 times female size, $n = 3$; Mann-Whitney-U-test, $Z = -2.174$, $P = 0.03$, Fig. 5). We found no significant differences in the percent of time females spent together with the larger or smaller males (Wilcoxon matched-pairs signed-ranks test, $Z = 0.0$, $n = 12$, $P = 1.0$), either inside the air bell (Wilcoxon test, $Z = -0.677$, $n = 12$, $P = 0.498$), or outside of it (Wilcoxon test, $Z = -0.7$, $n = 12$, $P = 0.944$).

Cannibalism occurred in two of 40 pairings in the mate choice experiments. In one of the 20 pairings where the female was together with the larger of the two males, the male killed the female. This was in the experiment with the highest SSD (m:f) among all experiments (SSD = 1.72:1). In the replicate in which the largest of all test females was combined with the smaller of the two males assigned to her, the female killed this male (SSD = 0.87:1). Video analysis revealed that when one spider killed another one, the killer ate the victim thereafter.

Male-male competition experiments revealed that aggression between males was very high. During the days one and two of these experiments, when two differently sized males were kept in one tank without a female, in three out of 16 experiments, aggression re-

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sulted in the death of the smaller male (= 18.75%). There was no significant difference in the size disparity between the two males in cases with or without cannibalism (Mann-Whitney-U-test, $Z = -1.144$, $n = 3 + 13$, $P = 0.296$).

On days three and four of the male-male competition experiments, when two differently sized males and one female were kept in one tank, the larger male killed the female in three trials and the larger male killed the smaller male in one trial. It never happened that a female killed a male in the male-male competition experiments, or that the smaller male killed another spider.

By comparing the cases in which male cannibalism of females occurred with those in which this did not happen, the extent of SSD (m > f) was greater when cannibalism occurred (Mann-Whitney-U-test, $Z = -2.074$, $n = 4 + 22$, $P = 0.037$, see Fig. 6).

DISCUSSION

Our results show that, although the number of offspring per egg sac decreased, females that only copulated once could produce up to six viable clutches. Test females that copulated a second time after producing three successive egg sacs had a higher reproductive success in their fourth and fifth clutches than females that did not copulate again. This suggests that sperm depletion occurs in females and shows that it is to the females' advantage to mate repeatedly when producing a series of clutches.

Our experiments suggest that in addition to the natural selection acting on sexual dimorphism (Schütz & Taborsky 2003), both inter- and intrasexual selection mechanisms may be involved in the evolution of large male size in *A. aquatica*. As is usual in spiders (Foelix 1992), *A. aquatica* males are more mobile and they are the more active partners in mate acquisition. In controlled experiments they approached the females more often than vice versa, and females fled from males more often than vice versa. Females chose large males preferably as mating partners. Since small males approached females more often than large males did, female preference for large males cannot be due to a lack of contact with small males. Males did not show a preference for females of a certain size.

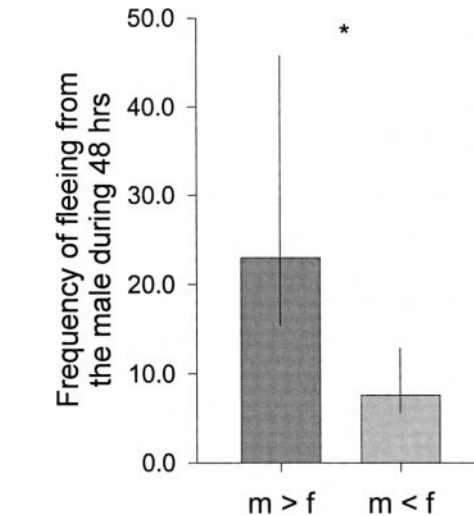Aggression between males was very high

Figure 5.—Frequency of fleeing in females when the male is larger (m > f) or smaller (m < f) than the female (medians and quartiles).

and sometimes resulted in the death of the smaller male. These results suggest that in males, large size is favored by intersexual and intrasexual selection mechanisms in *A. aquatica*. Males are also the better divers in this spider, so the necessity of moving under water efficiently appears to be an important determinant of large male body size as well (Schütz & Taborsky 2003).

In terrestrial spiders, often small males have locomotor advantages over larger males (e.g. see Moya-Larano et al. 2002), i.e. natural selection acts against sexual selection, which is a minor selective force in some spider species (see Vollrath & Parker 1997). Therefore, the difference in locomotor advantages of differently sized males on land and under water, together with intra- and intersexual selection mechanisms, may explain the reversed SSD of the water spider in comparison to many terrestrial spiders. In females, large size is favored by fecundity selection, but female size is apparently limited by the high costs of building air bells under water (Schütz & Taborsky 2003). This may be an additional cause of the reversed SSD in water spiders.

Sexual conflict was very obvious in our experiments and sexual contact sometimes resulted in the death of the female. To our knowledge, this reversed sexual cannibalism (i.e. males cannibalizing females) has not been reported before in any spider species. In

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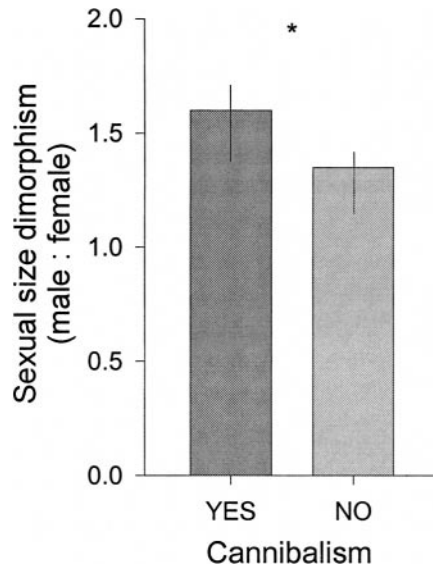SCHÜTZ & TABORSKY—SEXUAL CONFLICT IN THE WATER SPIDER

Figure 6.—Median SSDs when the male cannibalized the female and when it did not (medians and quartiles).

A. aquatica, the extent of SSD determined the likelihood of females to be cannibalized. The SSD was greater in cases when the male cannibalized the female than when he did not.

There are two main hypotheses to explain female cannibalism in spiders (see Johnson 2001; Schneider & Elgar 2002). The adaptive nutritional-advantage hypothesis postulates that sexual cannibalism is an economic, adaptive foraging strategy on the part of the adult female (Newman & Elgar 1991; Schneider & Elgar 2002). The aggressive-spillover hypothesis postulates that precopulatory sexual cannibalism is misplaced aggression favored in previous life history phases (Arnqvist & Henriksson 1997; Schneider & Elgar 2002), so it would be neutral or maladaptive. It is conceivable that these hypotheses could explain male cannibalism as well, even though the potential benefits appear to be smaller for males than for females. However, our results do not allow us to distinguish between these hypotheses for the explanation of sexual cannibalism in *A. aquatica*. In our experiments large males killed smaller females and small males, apparently dependent mainly on the direction and extent of the size difference. Sexual cannibalism in *A. aquatica* seems to follow the simple rule ''Large eats Small''.

An aspect of particular interest is the ob-served preference of females for large males, despite the risk of cannibalism. There is an apparent conflict between attraction and avoidance as females often flee from large males. Sexual cannibalism by otherwise preferred, large males might select for large female size, in addition to fecundity selection. However, female size is apparently limited by the energetically costly and risky air bell building and maintenance, which is size dependent in females but not in males (Schütz & Taborsky 2003).

In contrast to other species, mate choice in *A. aquatica* may select for an ''optimal male size'' instead of directional selection for large size. Usually, natural selection constrains SSD against the action of sexual selection by limiting the evolution of extreme body size in one of the two sexes. For example, a comparative study of North American passerines suggested that sexual selection for increased male size is balanced by energetic constraints of paternal care (Hughes & Hughes 1986; see also Cabana et al. 1982; Saether et al. 1986; Joensson & Alerstam 1990). In *A. aquatica* intersexual selection may stabilize male size without a necessary limitation imposed by natural selection, with sexual cannibalism being the constraining factor.

ACKNOWLEDGMENTS

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