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Adaptations to an aquatic life may be responsible for the reversed sexual size dimorphism in the water spider, *Argyroneta aquatica*

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ABSTRACT

Argyroneta aquatica is the only spider that spends its whole life under water, and one of very few in which males are bigger than females. We hypothesized that the unusual ecology of the water spider is responsible for its exceptional sexual size dimorphism. If ecological parameters influence optimal body size for locomotion, the size of the more mobile sex (males) is expected to vary more between populations that vary in these ecological conditions than that of the other sex (females). Indeed, sexual size dimorphism differed significantly between four populations of *A. aquatica* studied at Vienna, and this variation depended more on variance in male size than in female size. We found that, apart from size, body shape and the relative length of the first pair of legs also differed significantly between the sexes.

In land spiders, among which females are usually larger than males, small male size has been attributed to the better mobility of smaller individuals, as generally males are the more mobile sex in spiders. In aquatic animals, larger individuals have mobility advantages over smaller ones. We therefore hypothesized that, in *A. aquatica*, large rather than small size may facilitate locomotion, and hence that males are better divers than females. This was confirmed by the results of diving experiments. It is probable that male diving superiority is mainly due to their longer first pair of legs. Female size determines fecundity to a large extent. We wished to determine which size constraints could prevent females from growing bigger. Female size may be limited by the costs of building air bells, which they use as a retreat and for brood care. In laboratory experiments, we found that females build larger air bells than males and that air bell size correlates with body size in females but not in males. Females need to collect air from the surface to refill their bells more often than males. We conclude that the need for males to move efficiently under water and the costs to females of building a retreat and breeding shelter may be important determinants of body size and morphology. Hence the reversed sexual size dimorphism in *A. aquatica* may be greatly influenced by mechanisms of natural selection.

Keywords: body size, diving behaviour, locomotion, natural selection, size costs and benefits.

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INTRODUCTION

In most web-building spiders, females are larger than males (Vollrath, 1980; Head, 1995). Head (1995) showed that, between species, the degree of sexual size dimorphism depends more on variation in female size than on variation in male size. He concluded that selection for early maturation in males and selection for fecundity in females may be the primary evolutionary causes of the extreme sexual size dimorphism found in some spider species. For example, in Bolas spiders of the genus *Mastophora*, the diminutive males mature about 2 months before females in temperate regions (Yeargan and Quate, 1997).

Vollrath and Parker (1992) developed a model to explain small body size in male spiders. They argued that dwarf size in male spiders is associated with a difference in adult mortality between the sexes. Males suffer a much greater risk than females. This applies in particular to species with sedentary females and roving males, where males are at a high risk of predation during mate search, which would bias the operational sex ratio towards females. Hence early maturation and consequent dwarfing is favoured in males to buffer the skew in the adult sex ratio. Vollrath and Parker (1992) concluded that, at least in some spiders (e.g. in *Nephila* ssp.), male dwarfism results from reduced intrasexual competition because of high differential adult mortality between the sexes. This view was challenged by Coddington *et al.* (1997), who showed that, in a comparative analysis, female nephilines are larger than their probable ancestors were and that males are the same size as, or slightly smaller than, their ancestors. Coddington *et al.* (1997) concluded that male nephilines are not dwarfs, but females are giants. Vollrath and Parker (1997) replied that 'the pertinent point of controversy of mini males versus giant females is that we desperately need more life-history data on unusual spiders, that is, species with extreme or absent sexual size dimorphism'.

In some sheet-web spiders (Linyphiidae), males are larger than females (Lång, 2001). This reversed sexual size dimorphism probably depends on intrasexual selection through male–male competition for mating opportunities (Lång, 2001). Perhaps the most unusual spider in terms of sexual size dimorphism is the water spider, *Argyroneta aquatica*, where males are on average nearly 30% larger than females (cephalothorax width; personal observation). *Argyroneta aquatica* is the only spider that spends its whole life under water (Wiehle, 1909; Crome, 1951; Bromhall, 1988; Grothendieck and Kraus, 1994) and, therefore, experiences ecological conditions that differ from those of all other spiders.

The physical principles of aquatic locomotion differ from those of moving on land or in air (Withers, 1992). Water is a more dense medium than air and hence yields higher resistance. Even more importantly, animals of terrestrial origin that still breathe air face the potential problem of buoyancy force. Even though aquatic animals are slightly denser than water, any gas volume transported under water that exceeds 5–8% of body volume causes a buoyancy force that the animal must compensate to stay under water (Withers, 1992). Since water spiders are bound to carry large quantities of air under water for breathing and filling their air bells, diving in open water is probably very costly for them. If possible, water spiders move preferentially by holding on to subaquatic structures or spider thread that they spin between structures (personal observation). If optimal body size for moving under water is influenced by the costs of locomotion and by habitat characters (e.g. plant density, quantity of wood and debris), the size of the sex that is more mobile (males) should be affected to a greater extent by differences in habitat than the size of the less mobile sex (females). If this is the case, habitat differences should affect the degree of sexual size dimorphism between populations. We therefore studied the extent and natural variation of sexual size dimorphism in *A. aquatica* among four populations from different habitats in Vienna. We compared various body measures between males and females to quantify morphological differences, and compared body sizes between populations for both sexes. To examine differences in activity and behaviour between males and females, we recorded their behaviour in standardized laboratory experiments.

We proposed two hypotheses to explain the sexual size dimorphism of *A. aquatica* by mechanisms of natural selection. Generally in aquatic animals, larger individuals can move more rapidly than smaller ones (for a comparison of the maximum speed of animals in different media, see Azuma, 1992). Additionally, smaller animals have a higher energy cost of transportation than larger ones (Azuma, 1992). Therefore, we hypothesized that the more mobile males are better divers than females because of their larger size, longer legs or different body shape. In laboratory experiments, we examined whether the sexes differ in their diving abilities, and whether and how body measures relate to this ability. Secondly, because females would clearly benefit from larger size due to increased fecundity, we assumed that female size may be constrained by some factor related to subaquatic life. Females are more sedentary than males and usually stay in air bells, where they also raise their broods. Air has to be brought from the surface into these bells, which is risky, time-consuming and probably energetically costly. Therefore, we hypothesized that female size may be limited by high costs of maintaining air bells under water. In laboratory experiments, we measured and compared air bell sizes between the sexes, and examined whether bell size relates to body size within each sex.

THE BIOLOGY OF *A. AQUATICA*

Argyroneta aquatica is a solitary, territorial spider (Heinzberger, 1974), which is distributed over 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 is specifically adapted to life under water. For digesting their prey, moulting, depositing eggs and sperm, copulating and raising offspring, they construct air bells under water, which are usually built between water plants and fixed with spider thread to plants or stones (see Wesenberg-Lund, 1939; Heinzberger, 1974). The abdomen and legs bear hairs that maintain an air bubble around the body to help to transport air from the surface down to the air bell and to breathe under water (Ehlers, 1939). The respiratory system of *A. aquatica* differs from that of other spiders, as the lamellae of the book lung are reduced in number to about 20, and a large and complex tracheal system compensates for this rather rudimentary organ (Moore, 1976).

The body of water spiders appears to be poorly adapted to life under water (Engelhardt, 1989). *Argyroneta aquatica* is not a good diver, as it struggles to compensate buoyancy when moving under water (Schollmeyer, 1913). Males are less sessile than females; they rove around more often and catch their prey mainly by active hunting (Crome, 1951). Females spend most of their time inside their air bell. They catch prey mainly from there when detecting vibrations caused by prey touching the underwater net. Females take care of their brood and the young spiderlings moult four times in their natal bell (27.0 ± 2.6 days, personal observation; see also Hamburger, 1910; Stadler, 1917; Crome, 1951). Thus, males and females have different 'life-styles', which may select for different body sizes.

METHODS

The sexual dimorphism of *A. aquatica* and its natural variation in the field

From August to October 1999 and from July to September 2000, we collected more than 160 water spiders (45 adult females, 35 adult males and > 80 subadults) from four populations in Vienna with small fishing nets (Lobau, Mauthnerwasser, bomb crater in the Prater, pool at KLIVV; size of bodies of water = 25–500 m^2, depth = 0.5–1.0 m). These water bodies included an artificial pool, a small stream, a bomb crater and a backwater of the River Danube. We kept individuals from the four populations separately, with adults held isolated in glass jars and subadults held in groups in aquaria. We measured the width of the cephalothorax, the total body length and body weight of each spider. We calculated the ratio [body weight/(cephalothorax width)^3] as a measure of condition and the ratio [cephalothorax width/total length] as a measure of body shape, and compared these ratios between the sexes. Unless otherwise stated, we only included adult spiders (i.e. after the last moult) in the analysis of differences between the sexes.

When individuals died, we also measured the lengths of the four left legs, the chelicerae (basic part and claw) and pedipalps, the length of the cephalothorax and the length and width of the ventral prosoma. The width of the cephalothorax is generally used as a measure of body size, because it is easy to take and it has been shown to be highly reproducible (see Foelix, 1992; Lång, 2001). Therefore, in this paper, the term ‘body size’ refers to this measure. All other body measures taken correlated significantly with body size (log regression with 12 linear measures, $P < 0.001$; after Lång, 2001).

To determine whether body appendages differ in relative size between the sexes, we calculated the residuals of legs, pedipalps and chelicerae on cephalothorax width and compared them between the sexes. For determining the volumetric weight (= weight/volume) of the spiders, we measured their volume using a kathedometer. Body weight was determined to the nearest 0.01 mg.

Differences in behaviour between the sexes

In laboratory experiments, we assessed the activity, spacing, locomotion, interaction and breathing behaviour of males and females. The bottom of a 10 litre tank was covered with 3 cm of small gravel; then, 10 plants (*Cryptocoryne* sp.) consisting of only one leaf were placed in a row at the front of the tank to allow behavioural observations. Each experiment lasted 2 days. In 14 experiments, we placed one male and one female together in a tank. Twice a day we noted the location of each spider, and continuously recorded their behaviour on videotape with a time lapse recorder, so that 48 h were condensed into 3 h (sixteen-fold time compression). The video recordings were analysed in two ways, with instantaneous scan sampling and continuous all occurrences sampling (Lehner, 1996). As a measure of mobility, every 5 min during the first hour of the experiment we recorded whether the spiders were (i) walking on a leaf, (ii) walking on gravel or (iii) swimming or diving in the water column (frequency of behaviours recorded out of 13 recordings per hour). These recordings were repeated for 1 h after breaks of 3 h without recording (i.e. recordings were made during hours 1, 5, 9, 13, etc.). Throughout the experiment, we continuously recorded which spider approached the other. To determine whether males and females differ in the frequency of breathing or bringing air into the bell, we continuously recorded when spiders swam up to the surface and when they brought air into their bells. We compared the mean behaviour frequencies between males and females using paired *t*-tests except when stated otherwise, as the data distributions were not different from normal (Kolmogorov-Smirnoff one-sample tests, $P > 0.1$).

The potential influence of natural selection on sexual size dimorphism

Hypotheses

We proposed and tested two hypotheses to explain the reversed sexual size dimorphism in *A. aquatica*. First, size or body shape may influence mobility under water. Water spiders have to compensate for buoyancy because, with an air bubble around their abdomen, they are much lighter than water (see Withers, 1992). If males are more mobile than females (see Crome, 1951), they may be under stronger selection to optimize diving ability. A result of this selection pressure may be the evolution of larger body size, an elongated body shape and longer first legs in males. In laboratory experiments, therefore, we examined whether the sexes differ in their diving abilities, and whether certain measures of size and shape relate to this ability.

Secondly, female size may be more limited than male size because females need to invest more in air bell construction and maintenance under water. They are less mobile than males and spend most of their time inside their air bell (unpublished data). To obtain rough estimates of the relative costs of air bell construction for both sexes, we examined differences in air bell size between the sexes, and related body size to bell size within the sexes. We also assessed the potential influence of body size on female fecundity.

Diving ability

In an experiment testing the diving abilities of males and females, we determined the diving speed along a structure in a 1000 ml glass cylinder. The cylinder was covered with black plastic foil, leaving just a small strip clear for observations. At the start of each replicate, we placed one spider into the cylinder, which was lit from the top with a 20 W halogen lamp, about 15 cm from the surface of the water. Since water spiders flee from bright light, all spiders attempted to dive down the cylinder immediately after the light was switched on. In the middle of the cylinder, there was a vertical cord running from the surface to the bottom of the cylinder, which was marked at 1 cm intervals. Using a stopwatch we determined the time it took the spiders to move down the cord (minimum criterion > 12 cm) and calculated diving speed. Each of 8 males and 15 females was tested five times in a row. Between successive tests, we briefly removed the spiders from the cylinder. We examined whether the sexes differ in diving speed, and whether body size, condition, shape or length of first leg is related to diving speed. Since we were not able to measure leg length in living spiders, we estimated the length of first legs of each spider from its cephalothorax width using the sex-specific regression of leg length on cephalothorax width obtained from dead individuals. To determine the relationship between body measures and diving ability, we pooled the data of males and females, because we also included subadult individuals in the diving experiments so that the size ranges of males and females overlapped completely in both experiments [experiments with structures: male body size = 3.3 ± 0.5 cm, female body size = 3.2 ± 0.4 cm; experiments without structures (see below): male body size = 3.4 ± 0.6 cm, female body size = 3.3 ± 0.5 cm; mean ± standard deviation].

In a second experiment, we determined the vertical diving ability of water spiders without structures that would help them to descend. We tested 12 males and 11 females in the same way as described for the first experiment. In this second experiment, each spider was tested three times for 3 min. The spiders tried to reach the bottom of the cylinder or to dive as deeply as possible by continuous swimming movements, and we determined whether the frequency of reaching the bottom (0, 1, 2 or 3 times) differed between the sexes and between size classes (large *vs* small). For further analysis, we divided the diving cylinder into upper and lower halves, and compared how much time each spider spent in the lower half of the cylinder (average time of three dives, as a percentage). The percentages of time spent in the lower half of the cylinder were transformed (arcsin $(\sqrt{p})$) to obtain a normally distributed variable. We examined whether males and females differed in the time they spent in the lower half of the cylinder, and whether this time related to the spiders' body size, condition, shape, or length of first leg.

Female reproductive success and potential costs of bell size to females

We determined the reproductive success of differently sized females by counting all independent spiderlings when they left the cocoon after about 25 days of brood care (data obtained only from the first cocoon built by each female after catching them in the field). The females were measured at the same time, and the number of offspring was related to female body size.

To determine whether female size may be more limited than male size due to sex-specific requirements of air bell construction, we measured the sizes of air bells built by 23 males and 22 females and related them to their body size. We determined volumes of air bells by sucking out the air of the bells with a syringe. The web was then destroyed and removed; 1 week later, the volume of the replacement bell was measured. We examined at least three bells built in succession by each spider following this manipulation, and used their mean size in the statistical analyses.

RESULTS

The sexual dimorphism of *A. aquatica* and its natural variation in the field

Adult males were significantly larger ($t = 5.926$, $P < 0.001$, $n = 48$ males and 50 females; Fig. 1a) and heavier ($t = 2.693$, $P < 0.01$, $n = 33$ males and 48 females; Fig. 1a) than females, but had a poorer body condition (i.e. less weight per structural size; body weight/(cephalothorax width)^3: $t_{78} = -6.798$, $P < 0.001$). The sexes also differed in body shape: the ratio of cephalothorax width to total length was smaller in males than in females ($t_{95} = -2.172$, $P < 0.05$). In comparison to body size, males had longer first legs and chelicerae than females (first leg: $t_{24} = 4.048$, $P < 0.001$; chelicerae basal part: $t_{26} = 2.819$, $P < 0.01$; chelicerae claw: $t_{28} = 2.964$, $P < 0.01$; see Fig. 1b). No difference between the sexes was found for the other three legs and the pedipalps (*t*-tests, all $P > 0.1$). The average density (body weight/body volume) of water spiders was 0.727 ± 0.197 (mean ± standard deviation of 8 male and 9 female spiders, including subadults), which shows that the spiders are much lighter than water (density of about 1). A canonical discriminant analysis containing only cephalothorax width and first leg length revealed significant differences between the sexes ($n = 19$ males, $n = 7$ females, $\chi^2_2 = 15.0$, $P < 0.001$). When comparing spiders from the four different populations, we found that the variation in body size and body weight was greater between than within populations for males but not females (Table 1, Fig. 1c).

Differences in behaviour between the sexes

The patterns of locomotion differed between the sexes. Males spent more time walking on leaves than females ($t_{12} = 2.378$, $P < 0.05$; see Fig. 2a), and males approached females more often than the other way round ($t_{13} = 3.064$, $P = 0.01$). There were no differences between the sexes in the frequencies of diving ($t_{12} = -1.405$, $P > 0.1$) and walking on gravel ($t_{12} = 1.315$, $P > 0.1$). Males and females did not differ in frequency of taking air from the surface ($t_{12} = 0.101$, $P > 0.1$); however, males took the air to their bell in only 13% of

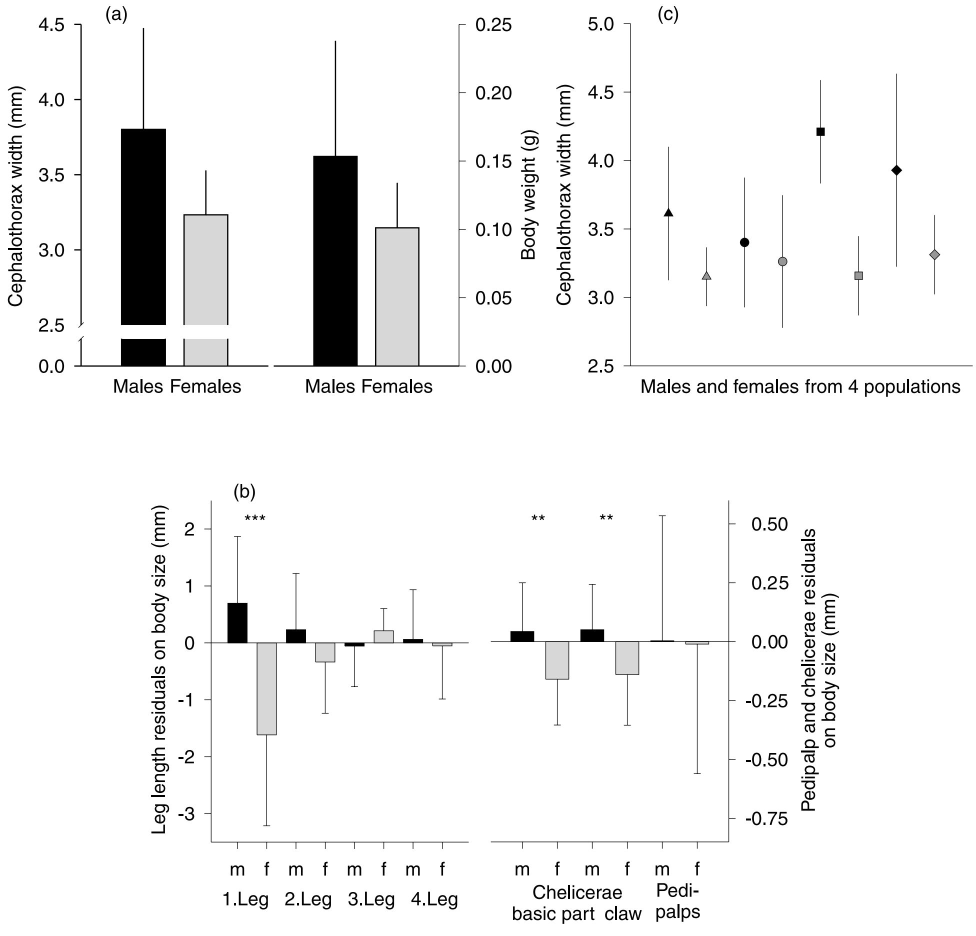

Fig. 1. (a) Body size (cephalothorax width) and weight of adult males and females sampled in four populations (mean and standard deviation). (b) Residuals of lengths on cephalothorax width for the four legs, the chelicerae and the pedipalps of males (m) and females (f). ** $P < 0.01$; *** $P < 0.001$. (c) Body sizes of males and females separated for the four different populations (mean and standard deviation). Black bars and symbols represent male sizes, and grey bars and symbols female sizes.

Table 1 One-way analysis of variance of the body size of males and females between and within populations

	Between populations		Within populations			
	Variance	d.f.	Variance	d.f.	*F*	*P*
Cephalothorax width						
Males	1.042	3	0.352	49	2.962	0.041
Females	0.107	3	0.082	51	4.516	0.285
Body weight						
Males	0.017	3	0.004	28	1.299	0.011
Females	0.000	3	0.001	41	0.32	0.811

Note: d.f. = degrees of freedom.

visits to the surface, whereas females did so in almost 30% of visits ($\chi^2_1 = 6.936$, $P < 0.01$; Fig. 2b).

The potential influence of natural selection on sexual size dimorphism

Diving ability

Males and females did not differ in their ability to dive down along a cord in the diving cylinder. All spiders were able to reach the bottom, and males and females did not differ in their diving speed ($t_{21} = -0.757$, $P > 0.1$; Fig. 3a). Neither body size (Pearson correlation

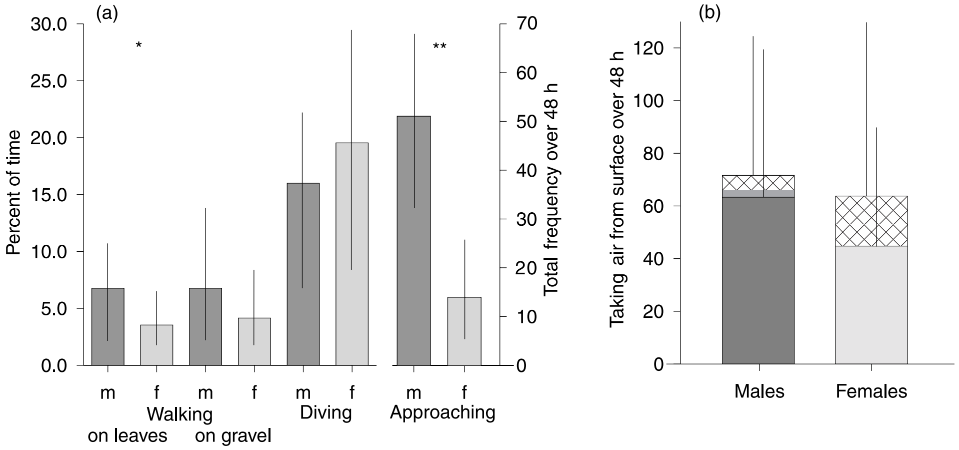

Fig. 2. Behavioural differences between males and females. (a) Percent of time spiders spent walking on leaves, on gravel or diving in the free water, and frequency of approaching the opposite sex over 48 h (medians and quartiles). $*P < 0.05$; $**P < 0.01$. (b) Total number of times air taken from the surface over 48 h (mean and standard deviation). Darker bars = males, lighter bars = females; cross-hatched sections of bars indicate the frequency of bringing air into the bell.

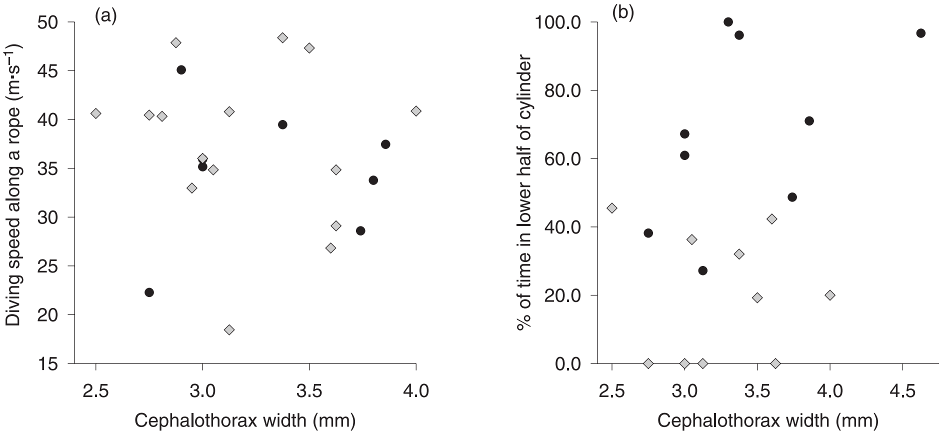

Fig. 3. Diving ability of males (●) and females (◆) of different sizes. (a) Diving speed ($\mathrm{m \cdot s^{-1}}$) along a cord (Experiment 1). Two male data points overlap (cephalothorax width 3.0 mm) and, therefore, cannot be separated in the graph. (b) Percent of time in lower half of cylinder (Experiment 2).

analysis, $r = -0.098$, $n = 23$, $P > 0.1$), length of first leg ($r = -0.135$, $n = 23$, $P > 0.1$) or body shape ($r = -0.023$, $n = 20$, $P > 0.1$) correlated significantly with diving speed. There was a tendency for body condition to correlate positively with diving speed ($r = 0.421$, $n = 21$, $P = 0.057$).

In diving experiments without structures, males were able to reach the bottom more often than females (Mann-Whitney *U*-test, $U = 27.5$, $z = -2.506$, $P < 0.05$), but there was no difference in reaching the bottom between large and small individuals ($\chi_1^2 = 1.5$, $P > 0.1$). Males managed to spend more time in the preferred, lower part of the glass cylinder than females [*t*-test with $\arcsin(\sqrt{p})$ transformed data, $t_{21} = 4.518$, $P < 0.001$; Fig. 3b]. Overall, length of the first legs correlated positively with the time spent in the lower part of the cylinder ($r = 0.599$, $n = 19$, $P < 0.01$). Neither body size ($r = 0.312$, $n = 19$, $P > 0.1$), condition ($r = 0.45$, $n = 12$, $P > 0.1$) or body shape ($r = 0.246$, $n = 17$, $P > 0.1$) correlated significantly with the time in the preferred, lower part of the glass cylinder.

Female reproductive success and potential costs of bell size to females

The number of independent spiderlings produced in the first cocoon after collection from the field increased with increasing female body size ($r = 0.680$, $n = 27$, $P < 0.001$; Fig. 4a). The air bells of females were significantly larger than those of males ($t = -2.798$, $n = 23$ males and 22 females, $P < 0.01$). For females but not males, average bell size correlated significantly with body size (males: $r = 0.183$, $n = 22$, $P > 0.1$; females: $r = 0.587$, $n = 22$, $P < 0.01$; Fig. 4b).

DISCUSSION

The sexual dimorphism of *A. aquatica* and its natural variation in the field

All body measures were sexually dimorphic, with males exceeding females except in body condition. The body shape of males was more elongated than that of females, as derived

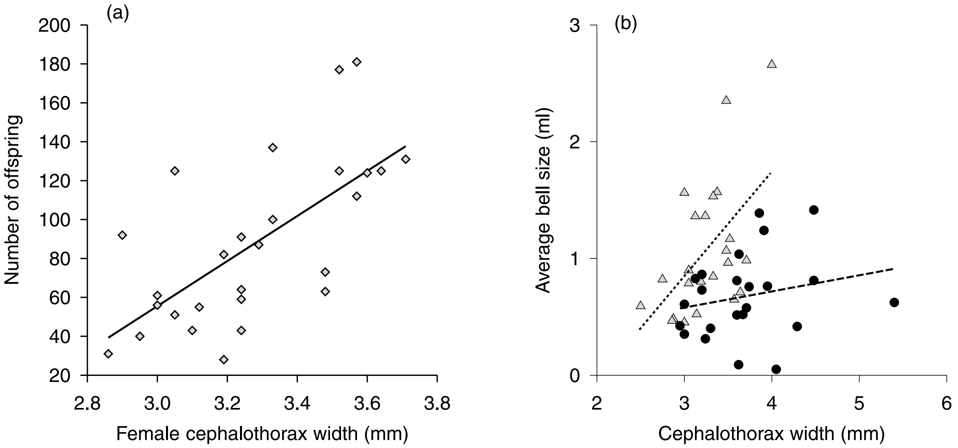

Fig. 4. (a) Female body size and numbers of independent spiderlings produced. Solid line = regression line. (b) Body sizes (cephalothorax width) of males (●) and females (▲) and average bell sizes with corresponding regression lines.

from the ratio of body length to cephalothorax width. In relation to body size, the first legs and the chelicerae were longer in males than in females, which hints at different selection pressures on these structures between the two sexes. The difference in first leg length may reflect a sex-specific ecological adaptation, because males are more mobile than females and individuals with longer first legs are better divers than those with shorter ones. The difference in chelicerae length between the sexes suggests intrasexual selection, as the sexes do not differ in feeding ecology and males attack and sometimes kill each other with their chelicerae (unpublished data).

An interspecific comparison of terrestrial spiders revealed that the extent of sexual size dimorphism depends mainly on variation in female size; Head (1995) concluded that selection for increased size in females is the probable cause of variation in sexual size dimorphism between species. Our population comparison of *A. aquatica* showed that, within this species, the extent of sexual size dimorphism depends on variation in male size. Female body size varied little between populations, suggesting that selection for increased male size may be the main reason for variation in sexual size dimorphism in this species. Unfortunately, it was not possible to quantify habitat differences between the four water bodies where we collected the spiders. The subaquatic structures were variable, but mostly dense and fragile, and attempts to quantify these structures led usually to their immediate destruction.

The phylogenetic relationship of *A. aquatica* supports the conclusion that the unusual sexual size dimorphism resulted from an increase in male body size rather than a reduction in female size. *Argyroneta aquatica* is the only species in the genus *Argyroneta*, which belongs to the family Cybaeidae together with the genus *Cybaeus* (Nentwig *et al.*, 2001). In *Cybaeus* species, males are much smaller than in *A. aquatica* (4.5–7.0 mm total length *vs* 7.8–18.7 mm in *A. aquatica*), but females are of a similar size to *A. aquatica* females (6–10 mm total length *vs* 7.8–13.1 mm in *A. aquatica*; Nentwig *et al.*, 2001; personal observations).

Differences in behaviour between the sexes

As in spiders in general, *A. aquatica* males are more mobile than females (Foelix, 1992). This was confirmed in our standardized laboratory experiment, in which males were more active than females, spending more time walking on leaves and approaching females more often than the other way round. After rising to the surface to collect air, females transported the air into their air bell more often than males. These different activity patterns reflect the different 'lifestyles' of males and females in the wild. In contrast to females, males actively hunt their prey under water (Heinzberger, 1974) and apparently actively search for the more sessile females. Prey availability is probably equal for males and females because they feed on the same prey (water asellus and water fleas).

The potential influence of natural selection on sexual size dimorphism

Diving ability

Small male size in land spiders has often been explained by the greater mobility of the male sex (Foelix, 1992). In some species, males are even able to fly with their own web, just like young spiderlings (Foelix, 1992). Under water, small body size does not help in locomotion, because there larger animals have a mobility advantage over smaller ones and lower energy costs than the latter (Azuma, 1992). This is especially important when diving or swimming in the free water column. In diving experiments in which spiders could move along a cord, there was no relationship between sex or any body measure with diving speed, except that spiders in better condition tended to dive more quickly; this could suggest an energetic cost of diving. However, in diving experiments without structures, males were better divers than females, independent of size. In part, this could result from the longer first legs of males, or from their more elongated body shape. In the water column, *A. aquatica* moves by paddling intensely with its legs. The drag force on parts of the body results in thrust, propelling the animal forward (see Withers, 1992). It is possible that this is the result in particular of longer first legs, because by their backward stroking movements they may be more efficient than the other legs. Longer first legs may also be advantageous when moving between subaquatic structures, but we did not test for this in our experiments. In contrast to our expectations, body shape did not correlate with diving performance. Predation risk may be higher for males than for females because of their greater mobility. When escaping predators, better diving abilities may also be advantageous, thus favouring large size in males.

Sexual size dimorphism in sea snakes, where males are also larger than females, has been explained by different selection pressures on locomotive abilities in the two sexes due to different lifestyles (Shine and Shetty, 2001). Sea snakes are amphibious and male sea kraits move faster than females, especially on land (Shine and Shetty, 2001). Mate-searching males were found to be much more active on land than females, and hence may be under stronger selection for terrestrial locomotion (Shine and Shetty, 2001).

Female reproductive success and potential costs of bell size to females

Female reproductive success clearly increased with increasing body size, which raises the question of why females are not bigger. Are there size constraints related to the ecology of females?

We found that females build larger air bells than males and that air bell size increases with body size in females, but not in males. The females' living bells were up to 2.7 ml in size, while the maximum bell size of males was only half that. Additionally, behaviour analyses showed that females surface more often than males to bring fresh air into their bells. It is apparently very difficult for spiders to compensate buoyancy when they dive down from the surface to transport fresh air. They do this by holding the hind legs backwards around the abdomen, which enlarges the air volume around the abdomen. We assume, therefore, that the building of large bells, and the exchange of air in large bells, is energetically costly. Bell volume increases approximately with a power of 3 with body size, which may limit female body size and act against fecundity selection in the water spider. High energetic costs for maintaining sufficient air exchange in breeding bells may also limit the number of offspring a female can raise in a clutch.

Our results suggest that adaptations to an aquatic life via mechanisms of natural selection may play an important role in the evolution of reversed sexual size dimorphism in *A. aquatica*. The influence of natural selection on sexual size dimorphism was also suggested in mustelids (Gliwics, 1988) and snail-breeding cichlids (D. Schütz and M. Taborsky, submitted). Differences between males and females that are the result of ecological divergence (food use) have been shown in hummingbirds (Temeles *et al.*, 2000) and mosquitoes (Proctor *et al.*, 1996). Additional reasons for larger male size in *A. aquatica* may be female choice of larger males or strong intrasexual competition in males. We will address this possibility in another study.

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