Giant brides and dwarf grooms – sexual size dimorphism in spiders

For years, one of the most challenging and yet unlocked secrets of nature has been sexual size dimorphism, known in almost every group of animals. Sexual dimorphism means the existence of physical differences between males and females of the same species, other than differences in the sex organs. These can be differences in body parts used in fights or courtship displays, such as horns or elaborate ornamentation in males, often to such an extent that males and females may even look like different species.

Figure 1. Male and female of the ladybird spider (*Eresus cinnaberinus*) from Central Asia.

Sexual dimorphism also includes body size differences, from moderate to extreme, referred to as sexual size dimorphism. This phenomenon is widespread among spiders.

In spiders, females are usually larger and have a bulkier body. Roaming hunters, such as wolf or jumping spiders, usually display little size dimorphism, with males approximately 10-20% smaller than females but with comparatively longer legs. Far more impressive are extreme cases of sexual dimorphism where the male is dramatically smaller than the female, on average £50% of female size (Figures 2-6). Numerous hypotheses have been proposed to explain the factors that may give rise to size dimorphism in spiders. Some of them are briefly discussed in the Table. In this article, we shall consider several possible explanations in order to understand how such size disparity can evolve.

Giant females – fertile and attractive

In general, spider females are larger because the physical demands and accompanying energy requirements to produce webs and broods are far greater than in males.

Figure 2. A tiny male of the crab-spider (*Thomisus sp.*) from the Gambia sits on the abdomen of the female waiting to mate.

Once mature, a males' only function is to mate. The most spectacular cases of sexual size dimorphism occur in the orb-weaving spiders, where dwarf males of some species can be 10 times smaller and 100 times lighter than the females (Figures 3-4). It is believed that size dimorphism in orb spiders is the result of females becoming giants rather than males becoming dwarfs. In the evolutionary history of spiders, such size dimorphism seems to have appeared at least six times, usually amongst close relatives.

Figure 3. A mating couple of the black-widow spider (*Latrodectus dahli*) from the Middle East; tiny male is on top.

However, what factors were responsible for such extreme variation in female body size is poorly understood. Why have females of some spider species grown into giants, whereas females of others have not?

Figure 4. The giant orb-web spider (*Nephila fenestrata*) from the Gambia, displaying typical sexual size dimorphism: females are huge (some 35 mm long), while males are tiny.

The most common explanation is that large size in females could be driven by selection on female fecundity (= the potential reproductive capacity), acting to increase the number of offspring produced. In spider species with giant females, size dimorphism is thought to reflect fecundity selection favouring large female size, since larger females can produce more eggs and hence more young. With the high level of juvenile mortality, the production of larger numbers of offspring is crucial for survival of the species. However, additional factors should be considered. Larger fecund females may be more attractive to males as mates, having better chances for successful mating. Mating success (= number of mates) is different from fecundity and is driven by sexual selection (see Table). Larger females can provide better parental care for their brood. Being bigger also means that females may outgrow their enemies or be themselves more effective predators. Both factors will increase their survival, reflecting processes of natural selection. Whatever the potential benefits of being large may be, female giantism can result from more than one mechanism, which may be a balanced mixture of sexual, fecundity and natural selections. Although fecundity selection is a common explanation for larger females, there are problems with this idea. For example, the growth of females to a larger adult size will take more time and energy and may decrease their survival. Therefore, in order to fully understand why females become giants, both survival and fecundity advantage in relation to body size need to be considered.

Dwarf males – rushing off to females

In order to overcome the aforementioned problem various models based on ecological causation for size dimorphism have been proposed (see Table). The most famous of its kind is the differential mortality model. This hypothesis uses life-history data to illustrate the evolution of sexual size dimorphism in spiders with large sedentary females and dwarf roaming males (Figures 3-6). Usually, these spiders live at low population density. In such groups, mature males are involved in scramble competition over first finding a fecund female, because males that mate first with a female will sire most or all of her offspring. Due to contrasting life-styles of adult males and females, males suffer higher levels of mortality. This leads to a non-proportionally large number of adult females in the population and, as a result, a reduced intensity of male-male competition. At the same time, selection continues to favour the males that arrive first, which seems to be a selection parameter that favours a high growth rate and attaining sexual maturity of males earlier than the females. The advantage lies not so much in the small size itself, as in the shorter ontogeny of males (i.e., their shorter development from the fertilized eggs to mature forms). Males mature in fewer moults than females. This model generally predicts not an absolute selection for the reduction of male size, but for the relative sizes of the two sexes.

Figure 5. A couple of South African tarantulas (*Augacephalus junodi*); tiny male is on the left.

According to the differential mortality model, sedentary spiders should be more dimorphic than actively hunting ones. This prediction is not always fulfilled. However, there are excellent examples confirming the idea that the high sexual size dimorphism in spiders with sedentary females is likely to result from selection acting on small male size (= male dwarfism). For instance, true dwarf males occur in certain tarantulas and large burrowing wolf-spiders (Figures 5-6), living in hazardous habitats characterized by high seasonal aridity and extreme summer temperatures or periodic flooding. In such environments, the burrowing females are safe in their burrows and less at risk than the roving males, which are subject to higher adult mortality. Small males can easier avoid hostile conditions. The reduction of male size could be one of the major adjustments in adapting to such high-mortality habitats. If so, male dwarfism may result from natural rather than sexual selection. Some scientists also speculated that reduced size increases the agility and maneuverability of males and hence increases their search efficiency. However, experimental evidence that the agility of males affects their mating success is lacking. Yet, small males can be less at risk of sexual cannibalism from the larger and stronger females.

Figure 6. Museum specimens of sexually dimorphic burrowing wolf-spiders (*Zyuzicosa baisunica*) from Central Asia; female on the left, male on the right.

Growing up dwarf or giant

Developmental aspects (i.e., details of ontogeny and sex-specific selection factors during growth) are essential in revealing the mechanisms underlying the evolution of sexual size dimorphism. Differences in body size of adult spiders can be produced by two kinds of growth patterns: growth rate (the rate at which growth occurs) and growth duration (the number of juvenile instars). In spiders, the size of adults mainly depends on growth duration. For example, males of the crab spider Thomisus onustus mature after 3-5 moults whereas females mature after 6-9 moults. As a result, the sexes exhibit extreme size dimorphism (Figure 2).

There is great variability in number of moults, developmental rate, juvenile survival, adult size and fecundity, even within single spider species. The range of this variability is determined genetically, but its expression can increase under stress and poor growing conditions. For instance, growth patterns depend on temperature and feeding regime (such as feeding rate and nutrient composition of diet) during ontogeny. In the burrowing wolf-spiders Lycosa tarantula, males reared under food shortage showed a significant sexual size dimorphism, being much smaller than females. Well-fed males were roughly of the same size as females. Thus, food shortage may be a selective factor for smaller males (see Table: marginal habitats).
Unfortunately, the physiological mechanisms responsible for the number of moults in spiders remain poorly understood. Furthermore, studies analyzing causative factors of sexual size dimorphism in spiders (such as sex-specific developmental regulators and modifiers known in vertebrates and plants) in relation to environmental conditions have not been conducted.

In summary, the extreme sexual size dimorphism in spiders is the end result of a complex interplay of various selective pressures. No single hypothesis can fully explain this phenomenon. Each pattern requires its own explanation. Body size is subject to several selection factors operating simultaneously. Some of these may act differently on males and females. We need more life-history and developmental data on dimorphic spider species in order to solve the puzzle of extreme sexual size dimorphism.

Dr Dmitri Logunov,
Manchester Museum,
University of Manchester, UK

Table

Some of the major hypotheses explaining the evolution of sexual size dimorphism in spiders

N	Hypothesis	Proposed mechanism
1	Sexual selection	Based on the assumption that the occurrence of competition among males for access to female mates favours those traits that provide no benefit to survival but that increase male's mating success. These traits are called 'secondary sexual characteristics' and include: 'weapons' (horns, spurs, etc.) driven by '*male competition*' (males compete for territory or access to females), and/or 'ornaments' (conspicuous colour, etc.) driven by '*mate choice*' (female mating preferences based upon elaborate ornamentation or male behaviours). Sexual selection usually results in escalation of large male size (common in vertebrates). In spiders, only a few species have males of a larger size than females. Such size difference is referred to as reverse sexual size dimorphism.
2	Fecundity selection	See the main text.
3	Ecological divergence	Based on the assumption that sexual size differences evolve because of differing ecological adaptations of males and females (sex foraging specialization, specific nutritional requirements, habitat preferences, etc). It is also assumed that the direction of dimorphism in body size is determined by sexual selection, but its degree is driven by ecological factors.
4	Marginal habitats	Based on the assumption that smaller males could be selected in marginal habitats where food resources are less than optimal. Usually, maturation time of males depends on a feeding regime, with less food causing an earlier maturation of males at a smaller size.
5	Low population density	Based on the assumption that in spider species living at low densities, the congregation of males around receptive females does not happen and thus selection for larger males due to sexual selection is relaxed. Instead, selection by scramble competition favours males with special traits and/or strategies that enable them to reach females faster. An early maturation of males at a smaller size is advantageous because by maturing earlier fewer male juveniles are killed. Moreover, the quicker they mature, the better their chance of mating.
6	Differential mortality	See the main text.
7	Gravity selection	A biomechanical model based on the assumption that in spiders that live high off the ground, males must climb to reach their female partners. Males will be selected to have smaller body size and mass, because they would have an advantage in scramble competition by reaching females faster, or because they escape predators more effectively by running faster on vertical surfaces.
8	Developmental aspects	See the main text.

Further reading:

Andersson, M. (1994). Sexual Selection. Princeton: Princeton University Press.

Coddington, J. A. *et al.* (2000). Giant female or dwarf male spiders? Nature, **385:** 687-688.

Sexual dimorphism (Wikipedia), online at: http://en.wikipedia.org/wiki/Sexual_dimorphism

Feedback

The ASAB education newsletter

Feedback ISSN 2042-5724

Issue 51 **Autumn 2011**

In this issue

Association for the Study of Animal Behaviour

Note from the editor

Dear Colleague,

Here is the 51st Edition of Feedback. We are still working very hard to ensure that most of our resources will soon be freely downloadable from our exciting new website - details will follow.

You can also keep track of our progress via our facebook page. Just search for ASAB education and 'like' us – in return you will find interesting links and up to date news.

Inside this edition you will find previous questions by Michael Dockery and a showcase of some of our available resources. A selection of which were beautifully displayed at the ASAB Summer Meeting.

The Association for Science Education (ASE) Conference will be very exciting this year. The conference runs between the 4th and 7th of January 2012 and is being hosted by the University of Liverpool. Look here for more information: http://www.ase.org.uk/conferences/annual-conference/

Our very own Rob Thomas – ASAB's Education Secretary - will be giving the 2012 ASAB lecture as part of the 'Biology in the Real World' lecture series. This year the series has an Olympic theme and the title of ASAB's contribution is 'The race to reproduce' expect tales of sex, violence and underhand tactics… Rob's talk will be on Friday 6th of January at 2pm.

The ASAB education committee will be part of 'The Biology Stand' in the exhibition hall at the conference, alongside some other learned societies, including The Society of Biology, The British Ecological Society, and The Biochemical Society. Please come, say hello and pick up some free resources.

ASAB Education Officer,
Charlotte Evans

E-mail:
behaviour@cardiff.ac.uk

ASAB education website is:
http://asab.nottingham.ac.uk/