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Female choice and spider genitalia

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RIASSUNTO

Vengono valutati due possibili tipi di scelta della femmina a livello dei genitali dei ragni, sulla base dei meccanismi di accoppiamento in un certo numero di specie. La scelta della femmina non è necessariamente determinante nell'evoluzione della specificità dei genitali dei ragni, mentre sembra verosimile che la femmina scelga semplicemente in base alla morfologia genitale. La pressione selettiva in questo caso non è costituita dal tipo di risposta fisiologica o comportamentale della femmina, ma dalla quantità di spermi trasferiti. Vengono infine proposte alcune ipotesi sulle implicazioni di un tale meccanismo nell'evoluzione dei genitali dei ragni.

Parole chiave: Genitali, Specie-specificità, Scelta della femmina.

SUMMARY

Based on the examination of copulatory mechanics in a number of spider species, two possible mechanisms of female choice at the level of genitalia are evaluated. Female choice by stimulations is doubted to be a dominant force in the evolution of species-specificity of spider genitalia, whereas there are indications that females simply choose by the morphology of their genitalia. The selective pressure in this case is not any female physiological or behavioural response but the number of sperm transferred. Some thoughts on the implications of such a mechanism for the evolution of spider genitalia are proposed.

Key words: Genitalia, Species-specificity, Female choice.

Female choice in spiders

In spiders, female control of paternity is likely to occur at several different levels. There is evidence for behavioural precopulatory control (e.g., in spiders with elaborate courtship, PECKHAM & PECKHAM, 1889), there are data that point to control during copulation, (e.g., by influencing the duration of copulation, JACKSON, 1980), and there are at least opportunities for postcopulatory control-mechanisms, e.g., by controlling the transfer of sperm to appropriate sites, or by remating or not.

Female choice and species-specificity of genitalia

This paper treats only one of these aspects: control during copulation. This mechanism of female choice is a cardinal point of one of the most interesting theories concerning genital morphology: in 1985 William Eberhard suggested species-specificity of genitalia to be a result of female choice. He proposed two mechanisms: (1) female choice by stimulations, i.e. physiological control, and (2) female choice by mechanical fit, i.e. morphological control. I will try to evaluate the significance of these two mechanisms in spiders.

The predictions

If females choose by stimulations, there should be selection towards optimized reception of the stimuli. It should not be enough to sense the mere presence of the male genital organ, but it should be crucial for the female to evaluate the minimal morphological variants that exist within a population. The only way to sense this is by mechanoreceptors. Apart from mechanoreceptive hairs, there should be slit sensilla in sclerotized parts and internal receptors in membraneous parts. The prediction is that at the contact zones, mechanoreceptors should be found in high density.

On the other hand, when there is female choice by mechanical fit, there need not be any mechanoreceptors. The prediction is that female contact zones should be highly sclerotized because membraneous pouches cannot discriminate between variants of the male genitalia. Another prediction is that the degree of mechanical fit should be correlated to the number of sperm transferred. This is the only mechanism of genitalic discrimination when there are no neurons and stimuli involved.

The methodical approach

A prerequisite for the evaluation of the significance of these two mechanisms in spiders is the detailed examination of the copulatory mechanics. Therefore, a new method has been applied that combines the freeze-fixation of copulating pairs with liquid nitrogen (-196° C) with the preparation of histological serial sections of the copulatory organs in functional contact (details see HUBER, 1994).

This method has provided many details of spider genital mechanics (e.g. HUBER, 1994, in press a, b, c; UHL, HUBER & ROSE, in press). The important aspect in the context of the female choice hypothesis is that the sections exactly show which female parts actually come into contact with the male structures during copulation.

Evidence against the stimulation hypothesis

A closer investigation of these contact zones in the scanning electron microscope revealed the surprising fact that there are no sensory hairs in these areas, whereas the remainder of female body surface is literally covered with various types of hairs. Also the search for slit-sensilla at the contact zones brought no positive result (in adjacent regions they occur in densities similar to all other body surfaces).

Internal receptors were not searched for, but these have until now only been found in membraneous joints of walking legs (FOELIX & CHOMS, 1979), and the contact zones of the female genitalia are not membraneous, although with a few exceptions.

Therefore, the prediction of the stimulation hypothesis does not seem to be fulfilled. However, it cannot be concluded that the occurence of genitalic stimulation in spiders is definitely disproved. There might be undiscovered internal receptors in certain membraneous parts, and females could sense the male genital organs with slit sensilla far away from the copulatory organ.

However, as already pointed out, it is not enough only to sense the male genitalia, but in order to be able to exert a selective pressure, the female must be able to discriminate between minimal morphological variants. It may be doubted that this is possible with sensory organs far away from the contact-zones.

Evidence in favour of the mechanical fit hypothesis

What about the predictions of the mechanical fit hypothesis?

Are the contact zones sclerotized and thus able to discriminate mechanically, and is there evidence that the degree of mechanical fit is correlated to the number of sperm transferred?

As an example, the sheet-web spider *Neriene montana* may serve to answer these questions. As shown by van HELSDINGEN (1969, 1972) the spirally wound male terminal apophysis is inserted into the female genital cavity during copulation. In accordance with van HELSDINGEN, histological sections (unpublished) have revealed that the male apophysis almost exactly closes the open spiral groove in the female genital cavity which is highly sclerotized.

The predictions of the mechanical fit hypothesis are apparently fulfilled: the female contact zones are highly sclerotized and a misfitting of the male structures inevitably results in a loss of sperm out of the open female spiral groove.

Until now, 19 spider species from ten families have been investigated with respect to these questions (partly in press, see references, rest unpublished) and results all point to the same direction: genitalic stimulation cannot be definitely disproved but appears to be a doubtful mechanism in spiders, whereas there are good indications that females exert control of paternity simply by the morphology of their genital organs.

Female choice by mechanical fit and the evolution of spider genitalia

One thorny issue with the mechanical fit hypothesis is the difficulty to explain a runaway process basing on this mechanism. EBERHARD (1985) proposed convincing arguments for a runaway process based on stimulations and female preferences for supernormal stimuli. But there is no indication in his book about how mechanical fit results in rapid and divergent evolution of genitalia. I would like to propose some thoughts on this problem.

The crucial point probably is that genitalia will never fit absolutely but somewhat less well. There are two reasons for this: there will always be some small variation in the morphology of the genitalia within a population (= there are slightly varying female "preferences" for slightly varying male traits). Secondly, there will be selection towards genitalia that fit a maximum number of the genitalic variants of the opposite sex.

Two conclusions can be drawn from this, concerning the evolution of spider genitalia:

(1) Evolutionary divergence will never stop since there is always variation in the morphology of genitalia. If this variation results in different numbers of sperm transferred, and if the number of sperm transferred is correlated with the number of offspring (an assumption that remains untested), then there will be selection in favour of those genitalia that ensure optimal sperm transfer. In contrast to the evolutionary runaway process of FISHER (1930) this need not necessarily result in evolution with accelerating rapidity. A continuous divergence, together with the relative independence of genitalic evolution from other organ systems (GRASSHOFF, 1975), may be the principal causes of species-specificity in spider genitalia.

(2) Supposing that genitalia are selected towards fitting a great number of genitalic variants of the opposite sex, evolutionary divergence can take two different directions (which can certainly occur several times convergently): first, towards simplification of the genitalia (a simple pyriform bulb can theoretically be introduced into nearly every female "lock"). Secondly, towards increasing complexity, if males with additional clasping and locking structures can successfully copulate with a bigger number of female genitalic variants. Both evolutionary trends have apparently occurred in spiders: The most primitive, east-Asian liphistiids have medium-complex genitalia (KRAUS, 1978). From such a situation we can derive the mygalomorph and haplogyne spiders which have rather simple genitalia, and on the other hand the entelegyne spiders with partly very complex genitalia.

Concluding, morphological female control of paternity may be responsible for two evolutionary processes concerning spider genitalia: for continuous (not necessarily accelerating) divergence resulting in species-specificity of genitalia and for evolution towards increasing complexity or simplicity due to the reaction of male genitalia to varying female preferences.

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