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Authors: Castillo, Raúl Cuevadel, and Núñez-Farfán, Juan

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The evolution of sexual size dimorphism: the interplay between natural and sexual selection

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Raúl Cueva del Castillo and Juan Núñez-Farfán

(RCC)Laboratorio de Ecología, UBIPRO; Facultad de Estudios Superiores Iztacala, Universidad Nacional Autónoma de México. Apartado Postal 314, Mexico 54090, Estado de México, México. E-mail: rcueva@ecologia.unam.mx
(JN-F) Laboratorio de Genética Ecológica y Evolución, Departamento de Ecología Evolutiva, Instituto de Ecología, Universidad Nacional Autónoma de México. Apartado Postal 70-275, Mexico 04510, Distrito Federal. E-mail: farfan @ servidor.unam.mx

Abstract

Sexual size dimorphism (SSD) in animal species can result from the interplay between natural and sexual selection. In this paper we review the impact of sexual and natural selection on grasshopper body size and the evolution of SSD. Mate choice by females, and natural selection on female fecundity could explain an evolutionary trend to increase SSD in species in which females receive nutritional benefits during mating. In general, sexual selection is stronger in males than females. However, when females receive nutritional resources from males during mating, selection could be stronger in females than males. These resources constitute high energetic costs to males and it is expected that this promotes an increment in male mate selectivity. Higher female-biased SSD might evolve as a result of polyandry in species where males transfer nutritional benefits in the ejaculate. This hypothesis is testable at both macro- and micro-evolutionary levels. Finally, we discuss the relationship between body size and mate-guarding duration and its evolutionary implications and propose future studies to analyze the evolution of SSD and mate-guarding duration in grasshoppers.

Key words

Orthoptera, katydid, grasshopper, sexual size dimorphism, evolution, body size, sexual selection, mate-guarding, nuptial gift

Evolution of sexual size dimorphism: effects of natural and sexual selection

The direction and magnitude of selection on body size may differ between sexes and generate sexual size dimorphism (SSD). SSD may result from an interplay between sexual and natural selection (Slatkin 1984, Hedrick & Temeles 1989, Shine 1989, Fairbairn 1997). In insects, body size in both males and females is a target of directional selection. Large females generally have higher fecundity (because of larger clutches), and thus natural selection may favor large female body size (Ridley 1983, Fairbairn 1997). On the other hand, large males often have advantages in male-male competition and female choice (Thornhill & Alcock 1983). If females are larger than males, this suggests that natural selection for high female fecundity could be stronger than sexual selection on males (Ridley 1983, Wiklund & Karlsson 1988). Such differences in selection between males and females can produce SSD. However, the magnitude of SSD is expected to be smaller in those insect taxa where sexual selection favors large males (see Fairbairn & Preziosi 1994). Nevertheless, in insect species where females are larger than males, female size in many cases increases proportionally more as male body size increases (*i.e.*, in different populations or different rearing conditions), thus augmenting SSD (see Teder & Tammaru 2005 for a review).

Why does SSD increase as body size increases in some clades, but decrease in others? Some hypotheses can be offered to explain such observations (Fairbairn 1997, Blanckenhorn & Demont 2004, Fairbairn 2005, Teder & Tammaru 2005, Cueva del Castillo & Gwynne 2007), and these are based on the relative magnitude of sexual selection on females and males. Male fitness is generally related to the number of copulations, whereas female fitness is limited by the amount of resources that can be devoted to produce eggs (Trivers 1972, Andersson 1994). However, male resource investment can alter the intensity of sexual selection pressures on the sexes (Trivers 1972). Thus, food stress can increase sexual selection on females for increasing size; here, selection might occur through female to female competition for access to nurturant males and through male mating preferences, when costly nutrient contributions limit male mating frequency (Rutowski 1982, Gwynne 2004).

Because nutritional resources represent energetic costs to males, it is expected that males will show mate choice, rejecting low-quality females and competing for access to high-quality females (Bonduriansky 2001). The extreme situation can be found in species where there is sex-role reversal. In the katydids *Anabrus simplex* and *Kawanaphila nartee*, a reduction in food availability causes both a decrease in the number of males that are able to produce high quality spermatophylax meals (Gwynne & Simmons 1990; Gwynne 1993, 2001), and an increase in hungry females looking for these mating meals. Females fight for access to males and males prefer large females, rejecting smaller ones (Gwynne 1984, 1993; Simmons & Bailey 1993). Female quality may be "assessed" through body size which is correlated with fecundity. Large females are more fecund (Ridley 1983, Honëk 1993) and may have a higher mating success than smaller ones (Ridley 1983, Bonduriansky 2001, Cueva del Castillo & Núñez-Farfán 2002).

In grasshoppers and other orthopterans, males can transfer nutritional fluids that may increase egg-laying (see Friedel & Gillot 1977, Butlin *et al*. 1987, Muse 1992, Pardo *et al*. 1995, Tregenza & Wedell 1998, Reinhardt *et al*. 1999, Wagner *et al*. 2001), and females can increase their reproductive success by mating repeatedly (see Arnqvist & Nilsson 2000). The potential interaction between natural selection on female fecundity and sexual selection due to male mate choice may explain the results found by Teder and Tammaru (2005) (but see Blanckenhorn & Demont 2004). The six orthopteran species included in Teder and Tammaru's (2005) review show higher intraspecific female-biased SSD, as body size increases across different populations or environments (rearing conditions). Higher female-biased SSD might evolve as a result of polyandry in species where males transfer nutritional benefits in the ejaculate (see Cueva del Castillo & Gwynne 2007).

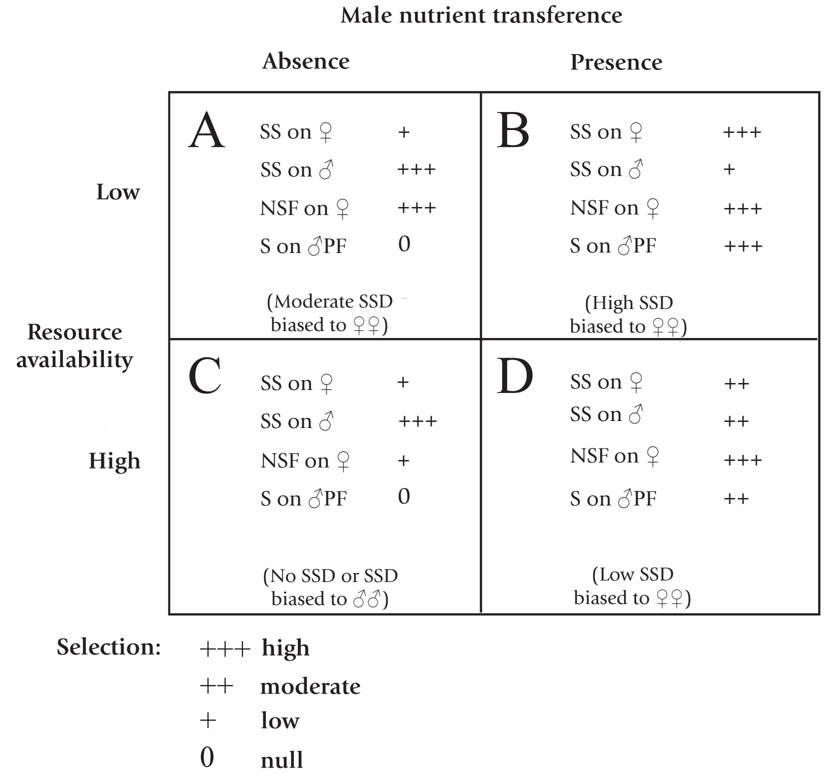

Fig. 1. Four ♂♀ potential scenarios for the evolution of sexual size dimorphism (SSD). Taken into consideration are: NSF= natural selection on fecundity; SS = sexual selection on ♀♀ and ♂♂; S on ♂PF = selection on males promoting (female) fecundity. Selection occurs in a variable environment regarding food-resource availability and whether or not males transfer nutritional resources to females during copulation. Predicted SSD are in parentheses.

This hypothesis can be tested at both macro- and microevolutionary scales. For this, it is necessary to compare the evolution of SSD in species where polyandry increases female fecundity *vs* those species where polyandry does not increase female fecundity. It is also possible to compare the magnitude of natural and sexual selection on body size in males and females. The differences in the intensity of sexual selection on females' and males' body size can vary dramatically between them. For instance, Jann *et al*. (2000) found that in the dung fly *Scathophaga stercoraria*, selection on male body size was more than twice the magnitude of selection on female body size; however, we do not know if females receive direct benefits due to mating. In the grasshopper *Leptysma argentina*, sexual selection was stronger on male femur length than on female femur length, but selection on thorax length was stronger in females than in males (Colombo *et al.* 2004). In the grasshopper *Eyprepocnemis plorans*, somatic condition (body size and somatic mass) and reproductive condition (gonad mass) were positively correlated to female, but not to male, mating success (Martín-Alganza *et al.* 1997). In *S. purpurascens* the magnitude of selection on body size was similar in both sexes (Cueva del Castillo & Núñez-Farfán 1999, 2002). In this latter species, mating duration increases female fecundity, but apparently polyandry does not (Lugo-Olguín & Cueva del Castillo 2007).

Body size, mate guarding and sperm competition

Sperm competition is thought to be common in insects and relevant in determining male reproductive success. In katydids, larger males allow more time for ejaculate transfer and thus achieve more fertilizations (Leimar *et al.* 1994, Vahed 1998). However, there are few studies in grasshoppers in relation to sperm competition (see Simmons 2001). Grasshoppers tend to be polygamous, and pre- and postcopulatory mate-guarding behavior has been documented in some species (Parker & Smith 1975, Wickler & Seibt 1985, Muse & Ono 1996, Cueva del Castillo *et al.* 1999, Zhu & Tanaka 2002). Anecdotic reports of extraordinary female-male guarding periods suggest that long-duration guarding could be a phylogenetically inherited trait in the Pyrgomorphidae (see Descamps & Winterbert 1966). In four species, *Zonocerus elegans*, *Atractomorpha lata*, *Sphenarium purpurascens*, and *Sphenarium magnum* — males can spend long periods mounted on females (*Z. elegans*: up to 45 d, Wickler & Seibt 1985; *A. lata*: up to16 h, Muse & Ono 1996; *S. purpurascens*: up to 18 d, Cueva del Castillo *et al*. 1999; and *S. magnum*: up to 21 d Cueva del Castillo, pers. obs.). In *S. purpurascens*, the duration of guarding and the number of copulations are positively related to female body size (Cueva del Castillo 2003). Interestingly, *A. lata* is the smallest of the four species and has the shortest guarding duration, whereas *Z. elegans* is the largest species and has the longest guarding duration. Moreover, it seems that males might change their guarding duration according to the potential risk of sperm competition and paternity payoff. For instance, males of *S. purpurascens* invest more time guarding and copulating with large females or females that have been previously mated by other males (see Cueva del Castillo 2003, Lugo-Olguin & Cueva del Castillo 2007). However, before accepting this interpretation, it is necessary to know to what extent guarding behavior is related to the likelihood of paternity in pyrgomorphids.

Long-duration guarding could be adaptive from the female's perspective if during the association, as result of multiple copulations, there is a transference of nutritional resources that increase females' longevity and/or fecundity (see Butlin *et al.* 1987; Muse 1992, 2002). Perhaps larger males contribute more to female fecundity, transferring larger nutritional donations than smaller ones. Nevertheless, this hypothesis remains to be tested as well.

Guarding duration can be affected by several factors, including: i) energetic and predation costs for each sex, ii) operational sex ratio, and iii) body size (see Alcock 1994). The prolonged guarding periods in some members of the Pyrgomorphidae open an opportunity to study in detail, the energetic and predatory costs of guarding. For instance in *S. purpurascens*, males can feed only in an opportunistic way during guarding (*e.g.*, if they get positioned close to plant leaves and no potential rival males are nearby). Furthermore, because optimal guarding duration can differ between females and males, it may give rise to a conflict of interest between sexes.

Future studies

Several topics of the evolution of mating systems deserve further study in grasshoppers. A complete understanding of the evolution of body size and SSD requires the simultaneous analysis of the impact of sexual and natural selection on female and male body size (Fairbain *et al*. 2007). Particularly interesting is the study of the consequences of 1) the availability of environmental resources, and 2) the presence/absence of the transference of nutritional resources during copulation, on the evolution of body size and SSD. Considering a discrete variation in resource availability (low and high), four potential scenarios can be analyzed to predict the evolution of SSD (Fig. 1). In the A scenario, the reproductive cost is higher in females than males and selection to increase fecundity is expected to be greater than sexual selection on males; here, moderate SSD biased toward females is expected. The B scenario is very interesting because the low availability of resources promotes sex-role reversal, with female-female competition, selection on female fecundity and male mate choice; accordingly, high SSD biased to females is expected. In the C scenario, sexual selection on males is higher than sexual selection on females and selection on female fecundity; very low or even no SSD biased toward females is expected but SSD biased toward males is possible. Finally, in D scenario reciprocal sexual selection plus selection on females' fecundity predicts moderate SSD biased toward females (Fig. 1).

Finally, much of the information regarding mating system evolution and SSD in grasshoppers has derived from Holartic species. In contrast, the diverse contingent of tropical grasshopper species is still poorly known. Due to their diversity and abundance, tropical grasshopper species remain as potential and valuable models to test these evolutionary hypotheses.

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