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A preliminary analysis of mate choice in a bush cricket (*Poecilimon laevissimus*: Tettigoniidae) suggests virginity is more important than body size

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Abstract

Insects are predicted to prefer larger partners for a number of reasons relating to fitness. In species where males provide an expensive nuptial gift, male and female preferences for a larger partner are likely to be more pronounced. In nuptial-feeding insects however, models of sperm competition and female choice predict that males and females should also prefer virgin partners. Here we test the relative importance of size *vs* virginity in a Greek bushcricket, *Poecilimon laevissimus,* in which males offer typically large nuptial gifts during mating. While only a small number of replicates could be implemented, and there is a clear need for further analysis, we found that all males and females preferred to mate with virgins, despite the fact that nearly 90% of the virgins were smaller in size than the nonvirgins offered. In terms of mate choice, virginity therefore appears more important than body size in *P. laevissimus*.

Key words

body mass, mate choice, *Poecilimon laevissimus*, sperm competition, virgin, nuptial gift, spermatophore

Introduction

With respect to mating success, body size is arguably the most prevalent measure of fitness documented in the literature. Males are predicted to prefer larger females because they are generally more fecund (*e.g.* Gwynne 1981, 1984, 1985; Thornhill & Alcock 1983; Simmons & Bailey 1990; Honek 1993; Vincent & Lailvaux 2006), and females are predicted to prefer large males, as body size is associated with several direct and indirect measures of fitness (for a review see Wedell & Ritchie 2004). Such measures include: disease and parasite load (Simmons 1994, Lehmann & Lehmann 2000a, for a review see Zuk & Stoehr 2004), intrasexual competition (Thornhill & Alcock 1983, Simmons 1988), male vigor (*e.g.*, Reid & Roitberg 1995), sperm vigor (*eg.*, Reinhardt & Siva-Jothy 2005) and good genes (*e.g.*, Beck & Powell 2000, Wedell & Ritchie 2004).

In many insects, males donate a nuptial gift during mating which is costly and typically positively associated with a male's body size (Heller & Reinhold 1994, Vahed & Gilbert 1996, Wedell 1997, McCartney *et al.* sub. ms.). Bushcricket males, for instance, produce an often expensive nuptial gift (*e.g.*, Dewsbury 1982, Heller & Helversen 1991, Vahed 2007) in the form of a gelatinous spermatophore which functions in a dose-dependent manner, to optimize male fertilization success, and in some cases, offspring fitness (for reviews see Vahed 1998, Gwynne 2001). Sexual conflict resulting in mate choice is predicted to occur when male and female investment optima differ, such as, for example, when males invest heavily in spermatophores and have a high confidence of paternity (Knowlton & Greenwell 1984, Parker 1984). As a result, males are predicted to discriminate against females if they pose a threat of cuckoldry and females are predicted to detect males with greater investment ability and discriminate accordingly (Dewsbury 1982, Simmons *et al.* 1993, Gwynne 2001). Mate choice in spermatophore-producing bushcrickets is therefore likely to be strong because of the benefits that females potentially receive in the form of fertilisation and nutrients, and the expected returns that males may receive, in the form of greater fecundity, from mating with a larger female.

On the other hand, the cost of spermatophore production for males and the subsequent benefits that this may have for females should also result in selection for a preference by both sexes for virgin partners. Males may be expected to seek virgins in order to avoid sperm competition (*e.g.*, Simmons & Achmann 2000, Simmons 2001) or to take advantage of young females that produce eggs at a greater rate or of better quality than older females (*e.g.*, Rutowski 1982). Females may be predicted to prefer virgin males as they are normally younger and less affected by factors negatively affecting spermatophore size, such as parasites and disease (for reviews see, Lehmann & Lehmann 2000b, Zuk & Stoehr 2002). Younger males may also produce higher quality sperm (*e.g.*, Reinhardt & Siva-Jothy 2005) and, at least in the case of fruit flies, higher quality offspring (Price & Hansen 1998).

Despite the likely benefits of mating with virgins and larger partners, there is surprisingly little documentation showing a direct preference for either in bushcrickets. *Requena verticalis*, for example, showed an initial preference for virgins over nonvirgins, although this advantage was lost when nonvirgins had oviposited (Lynham *et al* 1992). Later it was found that males prefer youth, not virgins *per se*, and ultimately larger females were preferred over virgins (Simmons *et al.* 1993, Simmons *et al.* 1994).

Moreover, the vast majority of work seems to have been done on male preferences for females (for a review see Jennions & Petrie 1997) and there seems to be no documentation on the preference of females for virgin males over body mass in bushcrickets. In *Poecilimon*, larger males produce larger spermatophores (*e.g.*, McCartney *et al.* submitted manuscript) and larger females are likely to hold more eggs, but virgin males are likely to contain larger reserves of spermatophore material and virgin females can offer high assurance of paternity to males. Here we present a preliminary analysis of mate preference shown by males and females in a spermatophore-bearing bushcricket, *Poecilimon laevissimus,* for small virgin or larger nonvirgin partners.

Methods

P. laevissimus (Figs 1,2) is a Greek bushcricket (Tettigoniidae) of medium size; male body mass ≈ 781 mg (n=50, McCartney &

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Heller, sub. ms.), female body mass ≈ 848 mg (n = 50, McCartney & Heller unpub. data). It is considered a foliovore and is nocturnal, semelparous, and has a univoltine life-cycle with an obligate diapause. The spermatophore ranges in size from 6 to 11% of male body mass in this species (McCartney *et al*. sub. ms.), and consists of a large proteinaceous spermatophylax, which protects the ejaculate contained in the associated ampulla from premature removal as it passes into the female.

The experiment was conducted in a natural population in north Ilia, Erimanthos Valley, east of the village Koumani (lat 37°48′N, long 21°47′E), Peloponnese, Greece, during June and July, 1997. Age was kept approximately constant by ensuring that all bushcrickets used in the experiment were taken on a single day as subadults and all pairings occurred within a single day. Furthermore, adult populations of *P. laevissimus* only survive for a few weeks (McCartney & Heller in prep.) and therefore should all have been similar in age. Males and females were kept separately in field cages until they had reached adulthood, and had sufficient time to attain reproductive maturity. Fresh leaves and flowers, taken from the site of the local population, and water, were supplied *ad libitum*. All individuals were then numbered with an indelible pen on their pronota. The nonvirgin mating partners were taken from the field population on the same day and otherwise handled in a similar fashion as the virgin mating partners. The only difference was that they had mated once or twice previously and been allowed at least five days recovery to ensure they were fully receptive.

The experiments were conducted in mesh cages of approximately 35 × 20 × 20 cm. Each subject was placed in a separate cage with a smaller virgin and a larger nonvirgin of the opposite sex. Four male and five female bushcrickets (nine replicates) were placed with two partners that were matched for mass (to the nearest 1 mg), so that the virgins weighed less than the nonvirgins. In one additional male test, the virgin female was longer than the mated female. When a mating took place, the pairs were observed until the pair had uncoupled. Two of the ten replicates, one male and one female, resulted in no mating attempt. Following mating, the spermatophore was carefully removed from the female with watchmakers forceps and weighed. Each individual was then weighed and the spermatophore mass from the resulting mating added to the male's current weight.

Results and discussion

In all successful matings, over both male and female treatments, virgins were chosen over nonvirgins, despite their smaller size. Virgin males in the female-choice treatment were on average 17% (mean weight = 0.59 g, range = 0.52 – 0.66g, n = 4) smaller than nonvirgins (mean weight = 0.71 g, range = 0.59 – 0.80 g, n = 4). Virgin females (mean weight = 0.93 g, range 0.84 – 1.1 g, n=3) in the male-choice treatment were on average 9% smaller than the nonvirgins (mean weight = 1.027 g, range = 0.87 – 1.219 g, n=3). In the additional test where the virgin female (weight = 0.873 g) was larger than the nonvirgin female (weight = 0.652), the virgin was also chosen.

There is evidence that in other bushcrickets, males discriminate in favor of virgin females, yet further analysis reveals that it is normally a preference for youth, not virgins *per se*, and ultimately body mass is likely preferred over virginity (*e.g.*, *Requena verticalis*, Lynham *et al.*1992, Simmons *et al.* 1993, Simmons *et al.* 1994). A strong preference for young females (and virgins) is understandable in *R. verticalis* because the first male to mate has a high confidence of paternity and subsequent mating males are thus likely to have their nutrient investment cuckolded (Gwynne 1988).

In the Botswana armored ground cricket, *Acanthoplus discoidalis* (Tettigoniidae), males prefer females with a lower mass and reject nonvirgins more often. This, however, was also interpreted as a preference for younger females, not virgins *per se*, because virgins were significantly younger than the nonvirgins tested (Bateman & Ferguson 2004). While it may be preferable for males to detect virgins, more proximate cues used to detect virginity may not exist in these species and youth may serve as the best proxy. *A. discoidalis* seemed to use cues, such as small size, to detect youth (Bateman & Ferguson 2004), so the apparent preference in *P. laevissimus* males for virgin females may actually be a preference for small females, rather than the larger, nonvirgin females or virgins *per se*. However, our single female that was larger than the nonvirgin female was also chosen, consistent with virgin status, and not size, being more important: this needs to be investigated in future studies.

Studies with butterflies, fruit flies, weevils, grasshoppers (see Simmons *et al.* 1994 and references cited therein), and at least two bushcrickets (Wedell 1992, Wedell 1998) all show that males distinguish virgin from nonvirgin partners, apparently because of their greater fecundity and associated increased certainty of paternity; there is no evidence at this stage to indicate that this may be otherwise in *P. laevissimus*.

Female *P. laevissimus* actively selected virgin males despite their smaller size. Female *Ephippiger ephippiger* (Tettigoniidae) mate with younger males, as youth in this species indicates mating history and males with fewer matings produce larger, more nutritious spermatophores with more sperm (Wedell & Ritchie 2004). Spermatophore size in *Poecilimon* is closely related to body size (McCartney *et al*. sub. ms.), so it seems unlikely that females select smaller, albeit virgin, males if they require nutritional investment from males. Sperm number however, is not related to body size in *Poecilimon*, and compared to other *Poecilimon* species, *P. laevissimus'* spermatophylax mass is lower in relation to the sperm number (McCartney *et al.* sub. ms.). So female *P. laevissimus* may select virgin males in order to receive greater sperm loads. Other data from *P. laevissimus* suggest that females rarely contain more than 50-75% of the sperm that males offer in one spermatophore, further suggesting preferences for multiple mating and a higher sperm load (McCartney & Heller in prep.).

Intrasexual competition may be an important factor influencing mate choice in *P. laevissimus*. Virgin female *Poecilimon* may respond phonotactically to male calls faster than nonvirgins, and virgin males may produce calls or pheromones that are more attractive to females. Furthermore, males may directly interfere with copulating pairs in order to dislodge the copulating male (pers. obs.). The choice made in our treatments therefore may not be a result of mate choice *per se*, but instead of the virgin from each trial showing more concupiscence than the nonvirgin and so ultimately winning access. However, female *P. laevissimus* respond acoustically to male calls, and males respond to this by moving toward the female (Heller & Helversen 1986). *P. laevissimus* are therefore more likely to interpret mating status from the mating call and, as with other bushcrickets (*e.g.*, *E. ephippiger*, Wedell & Ritchie 2004), discriminate accordingly. Furthermore, no males in the female choice experiment were observed 'wrestling' for access to females, so it is likely that the females similarly used sound or pheromone cues to discriminate.

While the influence of intrasexual interactions on *P. laevissimus* mate-choice needs further investigation, both sexes of *P. laevissimus*

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showed a consistent preference for smaller virgins and there is no direct evidence to suggest any interaction between the virgin and nonvirgin individuals during any of the trials.

It is important to state that given the sample size, the evidence presented here is compelling yet not definitive. Further study is needed for all combinations of virginity, size and age in both sexes before we can state with certainty that *P. laevissimus* prefer virgin over large partners. However, our evidence is important in that there is little indication in the literature showing a preference in spermatophore-bearing bushcrickets toward virgin partners over larger partners.

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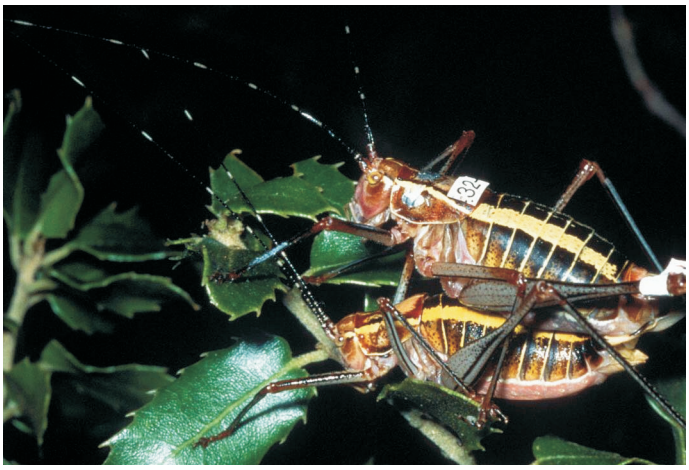


Fig. 1. *Poecilimon laevissimus* mating pair. Erimanthos valley, Peloponnese, Greece, 1997. Photo by J. McCartney. See Plate III.



Fig. 2. *Poecilimon laevissimus* bearing engorged eutrombiid mites. Erimanthos valley, Peloponnese, Greece, 1997. Photo by J. McCartney. See Plate III.

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