

Promiscuity and elongated sperm storage organs work cooperatively as a cryptic female choice mechanism in an earwig

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Female genitalia often show complex morphologies that cannot be explained by sperm reception and storage functions. However, our understanding of the forces underlying genital exaggeration in females is limited. Female earwigs, *Euborellia plebeja*, are promiscuous and their highly elongated sperm storage organs allow only partial removal and displacement of stored sperm by shorter male genitalia, resulting in only a 20% gain in paternity per copulation with a sperm-saturated female. This study examined the significance and optimality of restricted sperm displacement for females. A staged mating experiment with a paternity success analysis revealed that large males dominated male–male competition for burrows housing females, resulting in repeated copulations with the same female. Despite the low paternity gain per copulation, such repeated copulations resulted in a significant increase in paternity for larger males with higher resource-holding potential. A numerical simulation based on the relationship between male body size and copulation frequency showed that restricted sperm displacement (about 20% per copulation) is optimal for promiscuous females to accumulate sperm effectively from larger males. Because male body size is heritable in this species, females were estimated to benefit from a 1.4% increase in their sons' mating success. This genetic benefit disappeared when only a single copulation per male–female encounter was assumed. Since no measurable costs of mating for females have been detected in this species, the combination of promiscuity and restricted sperm displacement is best explained by the cryptic female choice hypothesis.

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In animals with internal fertilization, females often have specialized organs for storing sperm that are received during copulation for later oviposition. As with other components of male and female genitalia, these sperm storage organs show astonishing morphological diversity, even among closely related species, indicating their rapid evolutionary rate (reviewed by Eberhard 1985, 1996). Since the seminal paper by Waage (1979) on sperm removal behaviours of dragonflies, studies have documented that in many animal taxa, males manipulate the sperm of rival males that is held in storage organs (Birkhead & Møller 1998; Simmons 2001). However, the complex or exaggerated morphologies of sperm storage organs sometimes make it difficult for males to manipulate stored sperm completely. For example, male damselflies *Coenagrion scitulum* need to make repeated abdominal movements and perform repeated insemination to dilute and displace rival sperm (Cordero et al. 1995). Similar sperm removal behaviours have been reported for males of the damselfly *Mnais pruinosa* (Siva-Jothy &

Tsubaki 1989) and the cuttlefish *Sepia esculenta* (Wada et al. 2005). Furthermore, the morphology of female sperm storage organs sometimes does not permit male genitalia to gain access to stored sperm, rendering complete sperm manipulations physically impossible (reviewed by Córdoba-Aguilar et al. 2003 for examples in the Odonata). Thus, the shape of a sperm storage organ is an important determinant of postcopulatory sexual selection.

However, compared to explicit postcopulatory fitness benefits of sperm manipulation for males, it is usually unclear why females develop exaggerated morphologies in sperm storage organs that make sperm manipulation difficult for males. It may simply be a result of insufficient adaptation in male sperm manipulation behaviour, that is, females need large or elongated storage organs in which to house sperm, from which males cannot remove all of the stored sperm. Instead, incomplete sperm displacement itself may represent an adaptation in females. Polyandry with restricted sperm displacement may be an adaptive strategy for obtaining fresh young sperm (e.g. Lodesani et al. 2004; Tsuchiya & Hayashi 2010) while minimizing the risk of an infertile mating or mating with insufficient sperm supplies (Wedell et al. 2002; García-González 2004; South & Lewis 2011). Unless sperm from different males are completely separated, restricted sperm displacement

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results in mixed paternity. For species with paternal care by males, mixed paternity (or uncertainty in paternity) may be directly advantageous for females by inducing protection of offspring by males (e.g. Taub 1980; Hartley et al. 1995; Slatyer et al. 2012; cf. Arnqvist & Kirkpatrick 2005 for an opposing view). Alternatively, production of genetically diverse offspring may be advantageous in unpredictable environments. However, theories suggest that such genetic benefits (or indirect benefits) only arise under restricted conditions (very small populations or when genetically diverse offspring cooperate to increase their average performance; reviewed by Yasui 1998). The cryptic female choice (CFC) hypothesis provides another explanation for incomplete sperm manipulation by males. In many animals, females sometimes terminate mating before full insemination, eject or consume sperm after insemination and control the pattern of sperm usage, actively influencing paternity consequences (reviewed by Eberhard 1985, 1996). If there is heritable variation in male abilities to overcome such female-borne ‘trials’, polyandrous females ‘automatically’ gain genetic benefits by having sons that inherit the superior abilities of their fathers (sexy sons effects; Keller & Reeve 1995). In addition, when such abilities are positively and genetically correlated with other male or female fitness measures, further benefits arise (good-genes effects; Yasui 1997). In this paper, I adopt the broadest definition of CFC, that is, any female morphology or behaviour that works during or after copulation and increases the chances of having superior offspring. The definition here includes any indirect (following the definition by Wiley & Poston 1996) postcopulatory processes that lack any discriminative responses to sperm or sperm donors, but cause correlation between a focal female morphology/behaviour and obtained sperm quality. Partial sperm removal restricted by females can be considered such a female trait for gaining genetic benefits by CFC.

The earwig *Euborellia plebeja* (Dermaptera: Anisolabididae) is an excellent candidate for studying exaggerated morphology in female sperm storage organs that allow only incomplete manipulation of sperm by males. Both males and females of the species are highly promiscuous (Bajjal & Srivastava 1974; Kamimura 2003a, b, 2005). Under laboratory conditions, females mate several to dozens of times during 15 h (Kamimura 2005). The mode of sperm displacement and resulting paternity gains are well understood in this species. Several (usually fewer than three) copulations are enough to saturate an elongated spermatheca, the fine-tubed female sperm storage organ (Fig. 1). The spermatheca in this species is twice the length of the female body (on average 33.6 mm; Kamimura 2000, 2005). After saturation, females continue to copulate repeatedly with males, which cannot be explained as a mere sperm supply function (Kamimura 2005). Flash-fixation experiments of mating pairs have revealed that males use one of their paired intromittent organs (virgae), which are as long as their bodies (on average 15.8 mm), to remove rival sperm from the spermatheca (Kamimura 2000, 2003a). The mechanism of sperm removal is as follows. First, a male inserts the virga deeply into the spermatheca without ejaculating. He then extracts the virga while ejaculating semen from its tip and simultaneously removing rival sperm using a fringe-like projection on the virgal tip (Kamimura 2000). As predicted from the considerable difference in their lengths, males can remove only a portion of stored sperm (Kamimura 2000), and a paternity analysis experiment revealed that the paternity gain is only about 20% (mean \pm SD = 0.193 ± 0.182) for a single copulation with a female whose sperm storage organ has been saturated by a rival male (Kamimura 2005; in this study, the paternity gain from a single copulation with a sperm-saturated female was termed last-male paternity, P_{last}). Another experiment, in which the mating order of two males was not controlled, also showed that the best fit between the predicted and realized paternity success is obtained when assuming $P_{last} = 0.22$

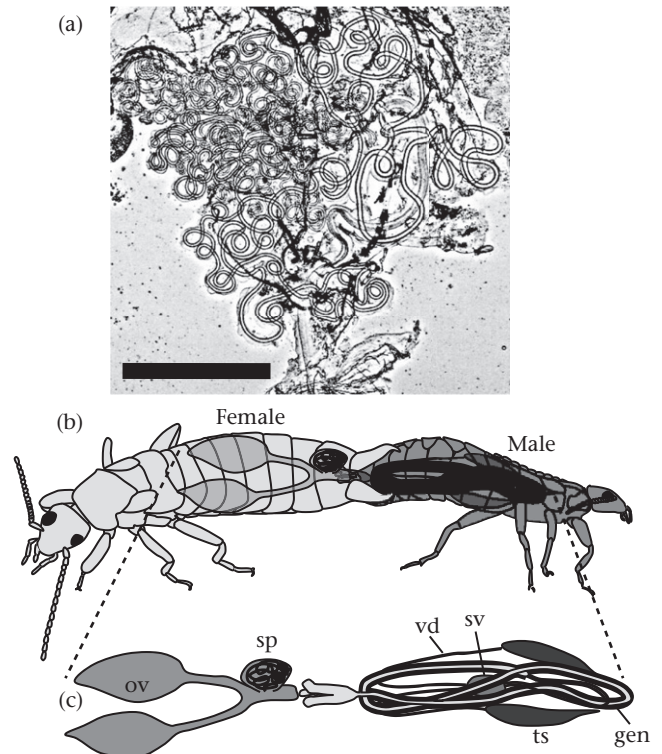


Figure 1. (a) A spermatheca and (b, c) schematic drawings of a mating pair of *Euborellia plebeja*. Male and female internal reproductive organs and genitalia (c) are overlaid on (b) as silhouettes. Paired virgae, one of which is inserted into the spermatheca for sperm transfer, are encased in the elongated male genitalia. gen: male genitalia (sensu stricto); ov: ovary; sp: spermatheca; sv: seminal vesicle; ts: testis; vd: vas deferens. Scale bar in (a) = 500 μ m.

(Kamimura 2005). Females oviposit repeatedly (approximately 40 eggs) at intervals of about 27 days (Kamimura 2003b), and thus are likely to collect sperm from several to dozens of males before depositing each clutch. Field-caught females lay egg batches with low genetic relatedness as a result of mixed paternity, clearly showing that female promiscuity and incomplete sperm displacement are not laboratory artefacts (Kamimura 2003b).

This study was composed of two parts. First, a staged mating experiment and allozyme-based paternity analysis were conducted to clarify the relationship between male mating success and resultant paternity in *E. plebeja*. Male–male combat and male mating success were observed under conditions that simulated the terrestrial habitats occupied by this flightless earwig species. Second, based on the results of the staged mating experiment and the previous genetic study of male body size, a simulation study was conducted to examine the relationships between the number of female mates, P_{last} values and expected offspring quality (body size of offspring) to test the hypothesis that promiscuity and restricted sperm displacement work cooperatively as a cryptic female choice mechanism in this species.

MALE MATING SUCCESS AND PATERNITY

Methods

A staged mating experiment was designed to clarify the relationship between male mating success and paternity. Mating trials involving two males and one female ($N = 53$) were conducted in a rearing room at a controlled temperature of 23 °C with a photoperiod of 14:10 h light:dark. The earwigs used in this experiment

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