

ARTICLE

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## Last-male paternity of *Euborellia plebeja*, an earwig with elongated genitalia and sperm-removal behavior

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**Abstract** Both sexes of the earwig *Euborellia plebeja* (Dermaptera: Anisolabididae) mate frequently. The elongated intromittent organs of males are as long as their bodies. Previous studies have revealed that this organ is used to remove rival sperm from the female sperm-storage organ (spermatheca), the length of which is twice that of the female body. The fitness benefit of sperm removal was quantified using two mating experiments with paternity analysis. As expected, given that the sperm-removal organ is shorter than the sperm-storage organ, males gained only about 20% of paternity per single mating with sperm-saturated females. The significance of frequent repeated matings with the same female by males is discussed.

**Key words** Anisolabididae · Earwigs · *Euborellia plebeja* · Last male paternity · Multiple matings · Sperm competition · Sperm displacement · Sperm storage

### Introduction

Sperm competition is the competition between the ejaculates of different males for the fertilization of a given set of ova, and it inevitably arises when females mate with multiple males (Parker 1970; Birkhead and Møller 1998; Simmons 2001). There are many examples of male behavioral, morphological, and physiological adaptations that mitigate or avoid the risk of sperm competition. These include guarding mates from competitors, deposition of copulatory plugs, transfer of antiaphrodisiac substances,

and removal of rival sperm (reviewed by Eberhard 1985, 1996). Elaborate male genitalia are sometimes devices for such mechanisms and thus influence the resultant paternity pattern (Birkhead and Møller 1998; Simmons 2001). In a promiscuous female, last-male paternity is the proportion of paternity achieved by the last male mate. It is determined by, and influences, the reproductive characteristics of both males and females. For example, females of the amphipod *Gammarus pulex* are incapable of sperm storage and accept matings only in a brief period after female molting. As a result, the first male monopolizes paternity and males compete for and guard pre-eclosion females (Birkhead and Pringle 1986). The opposite occurs in many odonates (dragonflies and damselflies), in which males use their genitalia to remove a considerable amount of rival sperm from female sperm-storage during mating. As is to be expected from situations resulting in high last-male paternity, males guard the mate from competitors (e.g., Corbet 1999). Furthermore, females can actively modulate sperm-storage and sperm-usage patterns, thereby biasing paternity (cryptic female choice or sperm choice). Female feral fowl eject sperm after coerced matings by subdominant males, reducing the likelihood of insemination (Pizzari and Birkhead 2000). Paternity pattern is therefore a key parameter in understanding sexual selection and sexual conflicts.

Females of the earwig *Euborellia plebeja* mate frequently with multiple males and lay egg batches of mixed paternity, indicating severe sperm competition (Baijal and Srivastava 1974; Kamimura 2003a, b). During mating, males use one of the pair of male intromittent organs (virgae), each of which is as long as the body, to remove rival sperm from the spermatheca, the fine-tubed female sperm-storage organ (Kamimura 2000, 2003a). The mechanism of sperm removal is as follows. First, a male inserts the virga deeply into the spermatheca without ejaculation. He then extracts the virga while ejecting semen from its tip and simultaneously removing rival sperm using a fringe-like projection on the virgal tip (Kamimura 2000). Because spermathecae are twice the virgal length, and the basal part of the virga lies in the common oviduct posterior to the spermatheca during mating (Kamimura 2000), one can predict that only a portion

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(less than 50%) of rival sperm is removed by a single mating. Therefore, we can predict that males gain only a minor share of the paternity per single mating when the female has a saturated sperm store. Knowledge of sperm-storage dynamics and resultant paternity patterns are crucial for understanding mating ecology and sexual selection in this promiscuous insect.

The aims of this study were to clarify the effects of multiple matings on the number of stored sperm and to quantify the last-male paternity of this promiscuous earwig. Based on the results, the significance of multiple matings for male *E. plebeja* is discussed.

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## Materials and methods

Eight adult inseminated females of *E. plebeja* were collected in Kawasaki, Kanagawa Prefecture, central Japan, in May 2001 and reared in the laboratory. The rearing methods have been described in detail by Kamimura (2003a); in brief, the animals were kept at  $23 \pm 1^\circ\text{C}$  (14 h light:10 h dark) with unlimited amounts of water and commercial cat food. Earwigs used in this study were either F1 or F2 generation derived from these founders. Each generation was maintained at high numbers (>100) and systematically bred to avoid sib-matings. Owing to mixed paternity, the genetic relatedness among offspring produced by a wild-caught female is very low (ca. 0.2; Kamimura 2003b). The study stock, therefore, must have been more genetically diverse than would normally be expected from the small number of founders. To promote subsequent egg laying, F1 animals were kept at low temperature ( $7^\circ\text{C}$ ) and short photoperiod (10 h light:14 h dark) for 50 days and were then subjected to gradual changes of temperature and photoperiod.

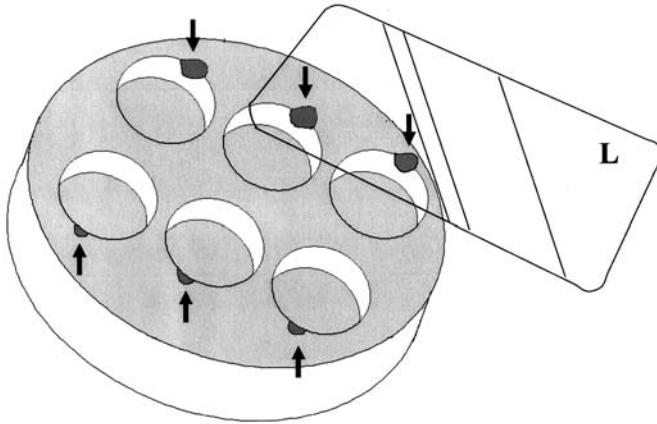
Experiment 1 was designed to examine the effect of multiple matings on the number of stored sperm in females. In this experiment, 29 virgin male–female pairs (4–26 days old) were each placed on a separate plastic dish (3 cm in diameter) with a plaster-of-Paris floor. They were kept together for a set period [0.5 h ( $n = 7$ ), 1 h ( $n = 8$ ), 6 h ( $n = 7$ ), or 24 h ( $n = 7$ )] and allowed to mate freely. A video camera (NV-S100, Matsushita Electric Industrial Co. Ltd., Osaka, Japan) and a time-lapse video cassette recorder (AG-6720A, Matsushita Electric Industrial Co. Ltd., Osaka, Japan) were used to record behaviors. Pairs that cohabited for 24 h first experienced 14 h of light, followed by 10 h of darkness, while the other pairs were observed in darkness with dim red light. Mating duration was quantified to the nearest second from video recordings and was defined as the duration of rigid contact of male and female subgenital plates. Based on previous studies (Kamimura 2000, 2003b), only rigid contact of male and female subgenital plates sustained for >1.5 min was considered as a successful copulation, with sperm transfer. Immediately after video recording, pairs were anaesthetized by cooling and killed by freezing. Sperm counts were conducted following established protocols (Kamimura 2003b). Briefly, spermathecae or seminal vesicles (male sperm-storage organs) were dissected in insect

Ringer's solution. After grinding these organs in liquid nitrogen, an adequate volume of distilled water was added. For ten 1- $\mu\text{l}$  drops of each sperm suspension, sperm number was determined under a fluorescence microscope after DAPI staining. Because sperm of *E. plebeja* are rather long (0.94 mm total length, unpublished data) and may easily be entangled, squashing of the sperm-storage organs was essential for accurate numbers estimation, although the procedure damaged sperm nuclei to some degree. To avoid overestimation, only sperm nuclei longer than 1  $\mu\text{m}$  were counted, corresponding to about 50% of the intact length. Sperm accumulation in females and sperm depletion in males was analyzed by plotting the number of sperm in either spermathecae or seminal vesicles against the mating frequency or total mating duration. Because of problems with dissection, only 21 of 29 males were analyzed for sperm storage.

Last-male paternity was estimated using controlled (experiment 2) and non-controlled (experiment 3) mating experiments. For the purposes of this study, last male paternity ( $P_{\text{last}}$ ) was defined as the average paternity gain arising from a single mating with females having a saturated sperm store. In experiment 2, six F2 families fixed at either the fast (F) or slow (S) allele of a tetrazolium oxidase (*Tzo*: E.C. not specified) locus were used. The males in this experiment had been used in another 1-day pairing experiment, which will be reported elsewhere, whereas the females were virgins. After cohabitation of a female (whose genotype in the *Tzo* locus was FF or SS) with an FF (SS) male for 24 h in the pairing vessel, she was mated once or twice to another male of genotype SS (FF). This procedure was repeated twice for each of 19 male pairs by reciprocating male roles. Thus, if an FF male loaded sperm and an SS male displaced it in trial 1, then SS and FF males served as sperm-loader and displacer, respectively, in trial 2. This procedure yielded 38 treated females in total. In nine randomly chosen cases, displacers were allowed to mate only once in trial 1 and twice in trial 2. In the other cases, the opposite procedure was applied. Females were then individually maintained in plastic vessels (8 cm in diameter, 4.5 cm high); after 10 days, 24 of them had laid eggs. Female *E. plebeja* intermittently lay batches of about 40 eggs (iteroparity) and care for them for about 2 weeks until hatching (Kamimura 2003b). The *Tzo* genotype of 7- to 9-day-old hatchlings (10–20 individuals per female) was electrophoretically determined using the methods described in Kamimura (2003b). Although the mating frequency of sperm loaders was not recorded in this experiment, the results of experiment 1 showed that 24-h cohabitation was sufficient to fill the sperm-storage organ of females (see Results). Confidence limits (CLs) of 95%, for last-male paternity gain (proportion of the offspring sired by sperm displacers), were calculated by 10,000-iteration bootstrapping (simple percentile CLs; Manly 1997).

Experiment 3 was designed to estimate last-male paternity under conditions in which the mating order of two competing males was not controlled. Mating trials using two males plus one female ( $n = 23$ ) were conducted. Earwigs used in this experiment were virgin adults (4–33 days old) of the F2 generation, collected from nine families known to

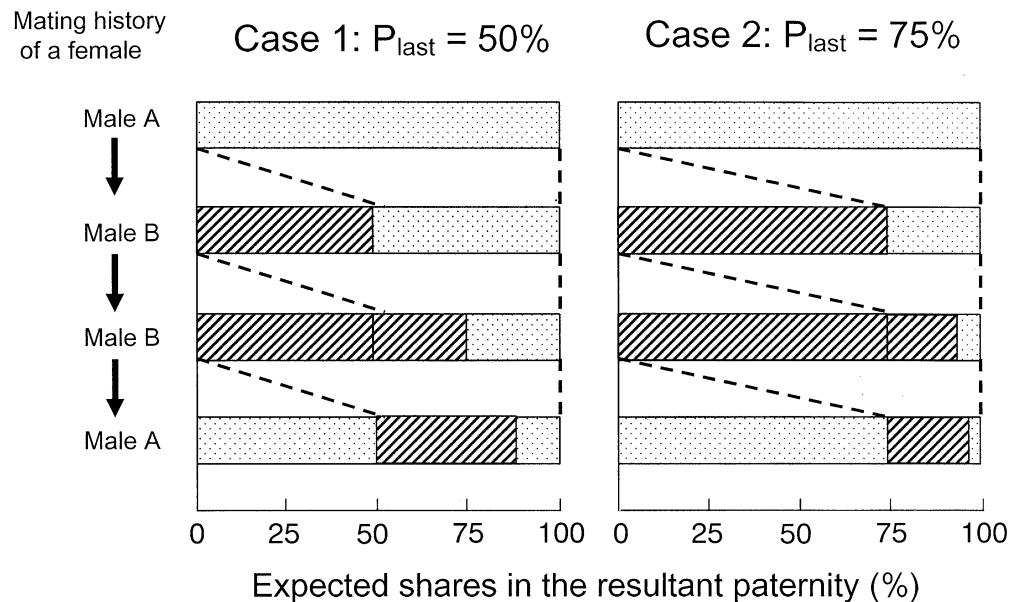
be fixed for either the F or S allele in *Adh* (alcohol dehydrogenase; E.C.1.1.1.1) or *Tzo* allozyme loci. One of the pair of males was randomly chosen and marked with a small spot of yellow paint on the prothorax. A mating arena (8.7 cm in diameter) had six small burrows (2 cm in diameter) covered with a transparent plastic board (Fig. 1). Since adult *E. plebeja* are about 1–1.5 cm in body length, the



**Fig. 1.** Mating arena (87 mm in diameter) with six burrows (20 mm in diameter, 6.5 mm in depth). The base of the arena was made of plaster of Paris containing charcoal powder. For simplicity, a surrounding wall (55 mm high) of transparent plastic sheet is not illustrated. The burrows were covered by the transparent plastic lid (L), and earwigs entered the burrows through the entrance (indicated by the arrows) made by cavities in the plaster

burrows could not accommodate two individuals (a male and a female) without body contact. Under natural conditions, copulating *E. plebeja* are found in small hollows, under shelters such as stones and wood fragments (unpublished data). The mating arena therefore simulated a complicated semi-natural habitat. Trials commenced at 1800 hours and ended at 0900 hours the next day, during which the first 10 h and the remaining 5 h were dark and light periods, respectively. For acclimation, females were released into each arena 30 min before the trial, while males were introduced immediately before the start of observation. Male–male and male–female interactions were recorded on video, as in experiment 1.

After the mating observation, females were reared in individual plastic vessels for egg production for up to 2 months, as in experiment 2. Hatchlings 7–9 days old (6–20 per brood, 17.6 on average) were used for genotyping. The complete record of mating sequence and resultant paternity success allowed estimation of  $P_{\text{last}}$ , based on the criterion of least squares. For example, if  $P_{\text{last}} = 0$ , the first male is expected to sire all offspring of the mate. If there is complete sperm precedence for the last male ( $P_{\text{last}} = 1$ ), all offspring of the female must be fathered by the last mate. To calculate predicted paternity shares for all other possible values of  $P_{\text{last}}$  (in the calculation, random values extracted from a uniform distribution between 0 and 1), it was assumed that the female sperm store is saturated by the first mating, and that sperm in spermathecae are thoroughly mixed between consecutive matings (Fig. 2). Males were therefore assumed to remove not only rival sperm but also



**Fig. 2.** Calculation of predicted paternity shares based on a value of the last male paternity gain ( $P_{\text{last}}$ ) and the record of mating sequences. The scheme illustrates a case in which a virgin female mates with two males (male A and male B) in the sequence of A, B, B, A. After the female's first mating, the expected paternity of male A and male B is 100 and 0%, respectively. When  $P_{\text{last}} = 0.5$  (case 1), male B is expected to gain 50% of the paternity by the female's second mating. Under the assumption of thorough sperm mixing between consecutive matings, the expected paternity of male B increases to 75% after the female's

third mating. In this mating, male B is assumed to randomly remove 50% of the sperm in the spermatheca, regardless of whether it is A or B sperm. After the fourth mating, male A gains 50% of the paternity by sperm removal, while only 25% of the remaining "non-removed paternity" is A's. Therefore, the predicted paternities of male A and male B after the fourth mating are 62.5% ( $50\% + 50\% \times 25\%$ ) and 37.5% ( $50\% \times 75\%$ ), respectively. In a similar way, one can calculate the predicted paternity shares of males given the complete mating sequence and a  $P_{\text{last}}$  value. Case 2 shows an example in which  $P_{\text{last}} = 0.75$

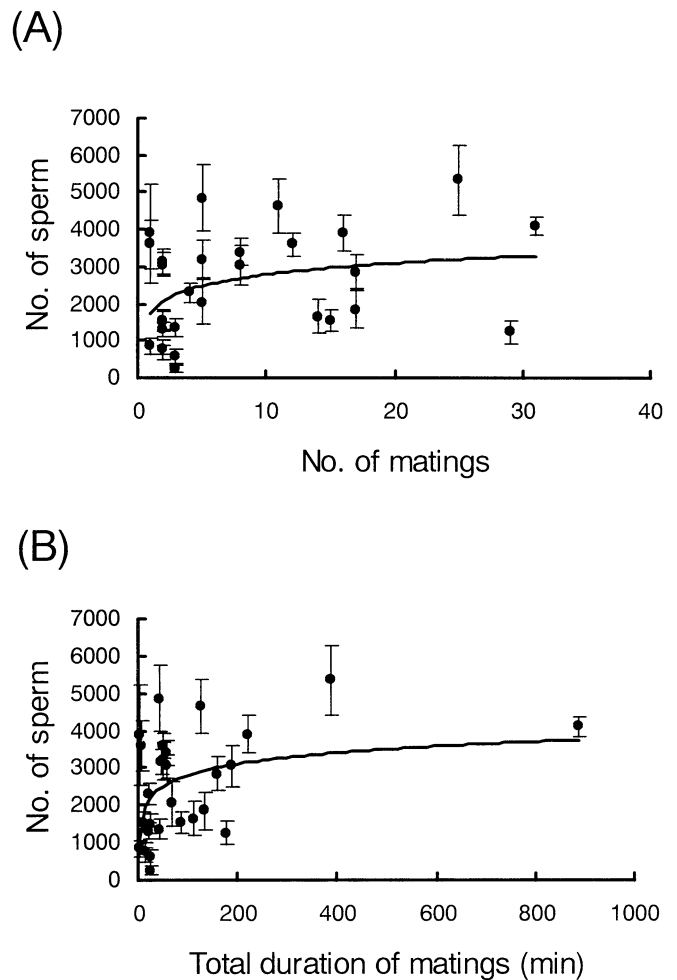
their own sperm, loaded by previous matings, according to numerical representations in female sperm storage. The realized values of the resultant paternity shares were linearly regressed on the expected values to calculate the sum of squares of vertical deviations. This procedure was iterated 2,000 times, exploring the most likely value of  $P_{\text{last}}$  that minimizes the sum of squared deviations. Experiment 3 was conducted as part of a larger experimental setting designed to study the determinants of male reproductive success. Here I report only the estimated  $P_{\text{last}}$ . More details of mating and paternity success of males in this species will be reported elsewhere.

## Results

In experiment 1, allowing pairs to mate freely for 0.5, 1, 6, or 24 h produced large variations in mating frequency (1–31 times), and in total mating duration (1.9–888.9 min). The number of sperm in females rapidly increased with the number and total duration of matings (although the effect of the number of matings was marginal) in a saturating manner. That is, one or several matings corresponding to a total mating duration of <30 min seemed sufficient to fill spermathecae with sperm (Fig. 3a, b). In contrast, the number of sperm stored in males did not decrease with mating frequency (log-transformed,  $r^2 = -0.017$ ,  $F_{1,19} = 0.686$ ,  $P = 0.425$ ) or with total mating duration (log-transformed,  $r^2 = 0.0047$ ,  $F_{1,19} = 1.095$ ,  $P = 0.309$ ,  $n = 21$ ). Furthermore, males that mated more than ten times ( $n = 9$ ) still possessed large quantities of sperm (mean  $\pm$  SE = 2,861  $\pm$  769), equivalent to those in sperm-saturated females (Fig. 3a, b). Thus, saturation in female sperm storage is not likely to be caused by sperm depletion in the paired male; rather, it indicates that saturation is determined by the storage capacity of the females.

The controlled mating experiment (experiment 2) revealed that  $P_{\text{last}}$  values were moderate to low under these conditions. Although displacer males that were mated twice gained higher paternity [mean  $\pm$  SD (95% CLs) = 0.275  $\pm$  0.154 (0.183–0.369),  $n = 9$ ] than those that mated only once [0.193  $\pm$  0.182 (0.110–0.289),  $n = 15$ ], this difference was not statistically significant, as shown by highly overlapping 95% CLs. When these two groups were combined, the last-male precedence incurred by one or two matings with females with saturated sperm-storage capacity was 0.224  $\pm$  0.174 (0.159–0.295,  $n = 24$ ). In both once- and twice-mated groups, the total mating duration of sperm displacers was not significantly correlated with the resultant paternity proportion (data not shown).

Even in the mating arena with six burrows (simulating complicated habitats with lower encounter rate) used in experiment 3, both males and females mated frequently: one to 41 times for males (mean  $\pm$  SD = 6.8  $\pm$  7.0,  $n = 46$ ) and 4–42 times for females (13.6  $\pm$  8.7,  $n = 23$ ). The total mating duration of females varied from 13.8 to 481.7 min (173.3  $\pm$  123.5 min,  $n = 23$ ) and was positively correlated with the number of matings ( $r = 0.74$ ,  $P < 0.0001$ ). Matings



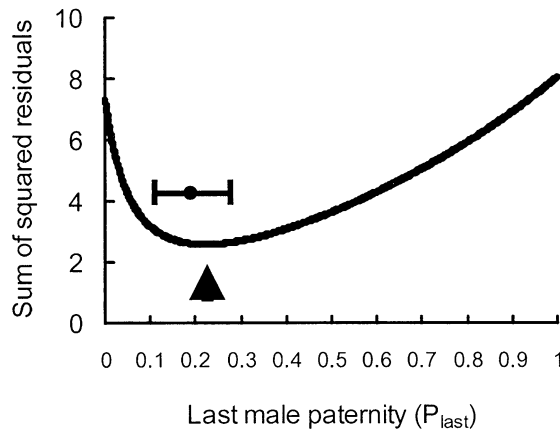
**Fig. 3a,b.** Sperm number in spermathecae of female *Euborellia plebeja* in relation to **a** the number of matings [ $y = 450.3 \ln(x) + 1756.7$ ,  $r^2 = 0.084$ ,  $F_{1,27} = 3.553$ ,  $P = 0.073$ ] or **b** the total duration of matings [ $y = 429.7 \ln(x) + 834.0$ ,  $r^2 = 0.141$ ,  $F_{1,27} = 5.587$ ,  $P = 0.025$ ]. Error bars show standard errors in the number of sperm

were frequently repeated (up to 19 times) during a cohabitation of the same male–female pair in a small burrow.

Realized paternities of males were determined by allozyme analysis of a total of 471 offspring from 23 females. Based on mating sequence data, the expected paternities were calculated for 2,000 possible values of  $P_{\text{last}}$ , ranging from 0 to 1. The best fit (the minimum sum of deviation squares) between predicted and realized paternity success was obtained when  $P_{\text{last}}$  was assumed to be 0.22 (Fig. 4). Further details of mating and paternity patterns will be reported elsewhere.

## Discussion

This study revealed the following characteristics of reproduction by *E. plebeja*: (1) both males and females mate multiple times, including frequent repeated matings between the same pair; and (2) one to several matings are



**Fig. 4.** Relationship between supposed values of last-male paternity ( $P_{\text{last}}$ : 0–1.000) and sum of squared deviations between realized and expected proportions of paternity. Expected values were calculated from mating sequences and  $P_{\text{last}}$  values (see Fig. 2 for examples). The least sum of squared deviations was obtained when  $P_{\text{last}} = 0.22$  (indicated by the arrow). The closed circle and its error bars indicate the mean  $\pm$  95% CLs of last-male paternity estimated by a controlled mating experiment (experiment 2). See text for details

sufficient to achieve saturation of female sperm-storage capacity, from which a male can gain only about 20% of the paternity per mating.

The low  $P_{\text{last}}$  values revealed in this study are in accordance with the prediction that males can physically remove only <50% of rival sperm stored in the spermatheca per mating (see Introduction). Furthermore, field-caught female *E. plebeja* lay egg batches of low within-brood relatedness (ca. 0.2; Kamimura 2003b), which must result from promiscuous matings, combined with low  $P_{\text{last}}$ . Walker (1980) pointed out that among non-social insects there is a general tendency for high last-male sperm precedence values in species with tubular or elongated spermathecae, and low or absent values in those with spherical spermathecae (but see also Ridley 1989). The deviation by *E. plebeja* from this general rule may be due to relatively quick sperm mixing in the thin spermathecae, which hampers the stratification of sperm derived from several males. Sperm can move from the opening to the distal tip of fine-tubed spermathecae within 30 min (unpublished data). Female *E. plebeja* lay clutches, intermittently, at approximately 27-day intervals (Kamimura 2003b), which must be sufficient for thorough sperm mixing in the spermathecae.

Simmons (2001) compiled  $P_2$  values (the proportion of eggs fertilized by the second male to mate in a controlled double-mating trial) reported for 133 non-social insect species. Among these, only 15 species (11.2%) had average  $P_2$  values of <0.4. These studies used experimental designs in which each of two males mated only once with a female and, consequently, the  $P_{\text{last}}$  values calculated in the present study are not directly comparable to those that have been reported for other insect species (see below). Nevertheless, the existing data suggest that *E. plebeja*, with its low  $P_{\text{last}}$ , is unusual among insects. In addition to mean values of last-male paternity, intraspecific variation is also important for

elucidation of mechanisms and consequences of sperm competition. In several insect species (especially lepidopterans) such as *Pseudophilus includens* (Mason and Pashley 1991), a high frequency of failed insemination causes a bimodal distribution of  $P_2$ , with two modes at 0 and 1. Thus, the average  $P_2$  value of these species is mainly stochastically determined by the failure rate. The SDs of last-male paternity estimated in the present study (0.154–0.182) are rather low, in comparison with the SDs of  $P_2$  values that have been reported for other insect species. This characteristic is especially noteworthy, given the demonstrated negative correlation between means and SDs of  $P_2$  values among insect species (Simmons and Siva-Jothy 1998; Simmons 2001). The processes of sperm displacement in *E. plebeja* (see Introduction for mechanisms of sperm removal) may, therefore, be rather stereotyped and robust to stochastic events.

Almost identical low  $P_{\text{last}}$  values (about 0.2) were obtained under controlled mating (experiment 2) and non-controlled mating (experiment 3) conditions. Although  $P_2$  is the most commonly used measure of last-male precedence in insects, misleading predictions of resultant paternity shares can be obtained when more than two males participate (e.g., Zeh and Zeh 1994). A possible reason for this inconsistency may be changes in sperm-displacement dynamics before and after the female sperm storage is saturated. In this study, we used the results of experiment 1 (in which female spermathecae were saturated by one to several matings) to justify the assumption that female sperm storage was saturated by the first single mating, when calculating the most likely value of  $P_{\text{last}}$ . Rapid sperm mixing in the spermatheca between consecutive matings was also assumed, as discussed above. The remarkable match in estimates of the  $P_{\text{last}}$  in experiments 2 and 3 indicates that these assumptions are useful for the highly promiscuous species *E. plebeja*. This figure implies that in each repeated mating, male *E. plebeja* remove 20% of their own sperm that is already occupying the female spermatheca.

An important point verified in this study is that male *E. plebeja* will repeatedly mate with the same female during cohabitation in a small burrow. Low  $P_{\text{last}}$  values would be crucial for the evolution of repeated matings by males with the same female. Figure 5 schematically depicts this prediction as an analog of Parker's (1978) model of optimal mating duration. Let us consider the situation that a male encounters a female whose spermatheca is filled with rival sperm. If the male gains a considerable portion of paternity by one mating owing to nearly complete sperm removal (e.g.  $P_{\text{last}} = 0.9$  in Fig. 5), additional mating with the same female will only slightly increase paternity (to 0.99, assuming complete sperm mixing between the first and second matings) while incurring costs in terms of energy, time, or sperm transferred (Wedell et al. 2002). In *E. plebeja*, fragile virgae can be broken by disturbance during matings (Kamimura and Matsuo 2001), and this risk could be considered a kind of mating cost. If a certain cost (such as time or energy) is also incurred in searching for new females ( $C$  in Fig. 5; measured in the same unit as the mating cost), the optimal mating frequency per encounter is estimated to be one, as this value maximizes the tangent ( $B_1/Ct_1$ ), that is, the

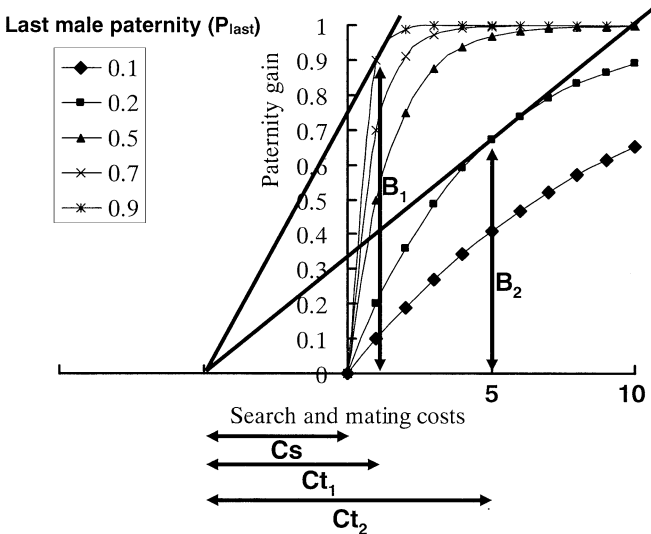
benefit of paternity ( $B_1$ ) divided by the total cost ( $Ct_1$ ). In other words, the relative benefit of searching for new females should increase rapidly with repeated matings to the same female. This prediction can provide an evolutionary explanation of the Coolidge effect – the progressive decline in the propensity of a male to mate with a female over successive inseminations combined with sexual interest in a novel female (Dewsbury 1981). Males of species with similar searching costs and lower  $P_{last}$  values should mate more times with every female encountered to maximize lifetime paternity success (five matings per female maximize  $B_2/Ct_2$  when  $P_{last} = 0.2$ ; Fig. 5). Although it is difficult (almost impossible) to quantify search and mating costs for males under natural conditions, this simple model gives a prediction that repeated matings with the same female are likely to evolve when the paternity gain per mating is low. Comparable systems have been reported for several insect species such as the leaf beetle *Labidomera clivicollis* (Dickinson 1986, 1988), the scorpion fly *Hylobittacus apicalis* (Thornhill 1976), and the yellow dung fly *Scatophaga stercoraria* (Parker 1978). In these insects, mating duration rather than mating frequency is critical for sperm loading and paternity success. Under these circumstances the rate of sperm accumulation in spermathecae may influence the optimal copulatory duration for males (Parker 1978).

Because male and female interests in mating are not necessarily coincident, it is also necessary to consider the mating characteristics of *E. plebeja* from the female perspective. Firstly, because coerced matings by males are not feasible in *E. plebeja* (Kamimura 2000), females would be important determinants of mating frequency, and repeated matings with multiple mates would suggest the accumula-

tion of (material or genetic) benefits for females (Zeh and Zeh 1996, 1997, 2001; Yasui 1997, 1998; Arnqvist and Nilsson 2000; Jennions and Petrie 2000). Secondly, the enormously elongated spermathecae of females, which lead to incomplete sperm removal and mixed paternity of the brood (Kamimura 2003b), may be a female adaptation for enhanced ability to control fertilization processes (sperm choice). Possible benefits for females of promiscuity, coupled with low last-male paternity gain, will be discussed elsewhere, with analyses of the relationships between male traits and fitness.

This study depicted the mating characteristics of *E. plebeja* on the basis of its population averages. Although relative sizes of male and female genitalia seem important in determining values for last-male paternity in promiscuous *E. plebeja*, both spermathecae [ $33.6 \pm 5.7$  mm ( $\pm$ SD),  $n = 40$ ] and male virgae ( $15.8 \pm 0.11$  mm,  $n = 43$ ) show large phenotypic variation in their length (Kamimura 2000). These variations may result in individual differences in paternity gain per mating. Detailed analysis of individual variation would bring deeper insights into the evolution of genitalia and mating systems of this animal.

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**Fig. 5.** A marginal value theorem model for the optimal frequency of repeated mating by male animals. Curves represent relationships between frequency of repeated matings by males and paternity calculated for each value of last-male paternity ( $P_{last}$ ), assuming rapid and thorough sperm mixing in the female sperm storage between consecutive matings. See text for details.  $B$  Benefit of paternity,  $Cs$  search cost,  $Ct$  total cost

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