



Heritable variation in polyandry in *Callosobruchus chinensis*

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The evolution of polyandry remains controversial. Various hypotheses that account for its evolution assume heritable variation in polyandry. We compared the frequency of female remating in 10 strains of the adzuki bean beetle, *Callosobruchus chinensis*, then made crosses between populations of high and low remating frequencies to investigate the mode of inheritance of polyandry. We found significant heritable variation in polyandry between the strains. Lower levels of polyandry were found in populations derived from long-term laboratory cultures than in those from recently established ones, suggesting that a selection pressure favoured monandry in the laboratory cultures. F₁ offspring from reciprocal crosses between strains with high and low frequencies of female remating had frequencies similar to that of the strain with a high remating frequency, suggesting that polyandry is inherited with dominance in *C. chinensis*, unlike any other species reported to date. This study indicates that polyandry can evolve in response to selection in *C. chinensis*.

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Males can generally increase their reproductive success by mating with more females, whereas the reproductive success of females depends on the number of offspring produced (Bateman 1948). Theoretically, therefore, male fitness increases with mating frequency, whereas female fitness is maximized by one or the few matings necessary to ensure adequate fertilization (Arnqvist & Nilsson 2000). However, females of the majority of animal species mate multiply, usually with different males (Thornhill & Alcock 1983; Ridley 1988; Birkhead 2000). Since theoretical predictions and observations are at variance, the evolution of female multiple mating, or polyandry, is a salient subject in behavioural ecology (Thornhill & Alcock 1983; Yasui 1997, 1998; Arnqvist & Nilsson 2000).

Most studies on the evolution of polyandry have focused on various female benefits from multiple mating: direct, through increased productivity, and indirect, through genetically superior or diverse offspring (e.g. Thornhill & Alcock 1983; Yasui 1998; Jennions & Petrie 2000). Any hypotheses that suggest benefits to females to account for the evolution of polyandry assume a genetic basis of female mating frequency. Furthermore, sexual conflict over female mating frequency occurs as a consequence of males and females evolving their own mating strategies to maximize their reproductive success (Parker

1979, 1984; Hammerstein & Parker 1987; Arnqvist 1997). Sexual conflict has recently attracted attention in the study of sexual selection, where the evolution of female mating frequency has been discussed (Holland & Rice 1998; Chapman et al. 2003; Pizzari & Snook 2003). Only a few studies, however, have shown the requisite genetic basis of female mating frequency to argue its evolution. Female remating speed (female mating frequency) responds to artificial selection and has a genetic basis in *Drosophila melanogaster* (Pyle & Gromko 1981; Gromko & Newport 1988; Sgró et al. 1998) and in *D. ananassae* (Singh & Singh 2001). Female mating frequency shows heritable variation in crickets, *Gryllus integer* (Solymar & Cade 1990) and *Teleogryllus oceanicus* (Simmons 2003). In Lepidoptera, artificial selection shows heritable variation in female mating frequency in the beet army worm, *Spodoptera exigua* (Torres-Vila et al. 2001) and in female remating in *Lobesia botrana* (Torres-Vila et al. 2002); full-sib analyses show heritable variation in the female refractory period between matings (Wedell 2001) and in female lifetime mating frequency (Wedell et al. 2002) in the green-veined white butterfly, *Pieris napi*. To our knowledge, studies on the genetic basis of female mating frequency have been limited to these species.

A study using a small number of females from a single population has reported that female adzuki bean beetles, *Callosobruchus chinensis*, do not remate after the first mating (Takakura 1999). Recently, Miyatake & Matsumura (2004), using more females from two strains of this species, showed, however, that females of one strain derived from

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long-term laboratory culture do not remate, whereas some females of another strain recently established from the field do remate. These findings imply a broad range of heritable variation in the trait in *C. chinensis*. Numerous strains of *C. chinensis* have been maintained in the laboratory, some for many years (Shimada 1990; Kondo et al. 1999), since this species is widely used as material for the study of population ecology (e.g. Utida 1941a, b). Strains with genetically different female remating frequencies may be available for future studies on sexual conflict. In this study, we compared female remating frequency in various strains to investigate heritable variation in female remating; we then carried out crossing between different strains to examine the mode of inheritance of female remating in *C. chinensis*.

METHODS

Comparison of Remating Frequencies

We compared the female remating frequency in 10 strains of *C. chinensis* collected from different localities in Japan. Table 1 gives the year of collection, locality and number of founder females for each strain. The mgC98, kkC98 and mrC98 strains have been maintained as several isofemale lines (Kondo et al. 1999, 2002); for the present study we used offspring populations obtained by crossing two isofemale lines within each strain. The isC strain (Yanagi & Miyatake 2003) and the yoC02, smC02 and akC02 strains were established with numerous females collected in the field. All rearing and subsequent experiments were conducted in a chamber maintained at 25°C and 50% relative humidity under a photoperiod cycle of 14:10 h light:dark.

Virgin beetles were randomly collected from each stock culture, kept in separate-sex groups of up to 10 adults in plastic cups (2.8 cm high, 7 cm in diameter) and given water and adult food (1:2 yeast extract:sugar). At the age of 2–5 days, one virgin female and one virgin male were placed in a glass vial (4.4 cm high, 1.7 cm in diameter) and mating was observed for 1 h. We measured the duration of copulation, then removed the male. Female remating was scored on days 1, 3 and 5 after the first mating. To determine the willingness of the female to remate, we

placed another virgin male from the same strain into the glass vial, and observed them each day until females either remated once or 1 h had passed. Remated females were not observed further.

Crosses

We made reciprocal crosses between strains with high and low remating frequencies to investigate the mode of inheritance of the trait. We used the isC and jC-S strains, which had cumulative frequencies of female remating on day 5 after the first mating of 38.4 and 8.8%, respectively (Table 2). We refer to these as the high and low strains, respectively. The frequency of female remating in the offspring was examined as described above. We used two experimental designs. In design 1, we determined the remating frequency of female offspring from reciprocal crosses by pairing a female with a virgin male derived from the same cross. Interstrain variation in female remating can be caused by a female trait, a male trait or both: for example, the female's receptivity to remating or the male's ability to induce nonreceptivity to remating in the female or to seduce or coerce the mated female into remating. The results of design 1 might confound genetic components of female traits with those of male traits. In design 2, therefore, with the aim of restricting the study to genetic components of female remating traits that would exclude male traits, we used virgin males from the specific (high-remating) strain as mates for female offspring from all crosses.

Statistical Analyses

The sequential Bonferroni method (Rice 1989) was applied after the *G* test using Williams's correction (Sokal & Rohlf 1995) to compare the frequencies of female first mating and remating among strains or crosses. No female in the mC strain remated on day 1 after the first mating, and thus we substituted '1' for the value zero, because the *G* test cannot be applied to observed frequencies that include zero (Table 2). We used the Scheffé method (SAS Institute 1998) to compare copulation durations of strains, the two-tailed Mann–Whitney *U* test (SAS Institute 1998) to compare the female remating frequencies of strains

Table 1. The rearing history of each strain of *Callosobruchus chinensis* used in this study

Strain	Collection year	Locality of population (latitude, longitude)	Number of founder females
mgC98	1998	Mino, Gifu (35°33' N, 136°54' E)	2‡
isC	1997	Ishigaki, Okinawa (24°22' N, 124°10' E)	More than 100
yoC02	2002	Yoshii, Okayama (34°55' N, 134°05' E)	9
smC02	2002	Izumo, Shimane (35°21' N, 132°45' E)	More than 10
akC02	2002	Sanyo, Okayama (34°45' N, 134°01' E)	More than 50
jC-F*	1936	Kyoto, Kyoto (34°59' N, 135°46' E)	†
kkC98	1998	Kasukabe, Saitama (35°58' N, 139°45' E)	2‡
jC-S*	1936	Kyoto, Kyoto (34°59' N, 135°46' E)	†
mrC98	1998	Maruoka, Fukui (36°08' N, 136°16' E)	2‡
mC	1960s	Morioka, Iwate (39°42' N, 146°11' E)	†

*The jC-F strain was reared at Tsukuba University and the jC-S strain at Tokyo University.

†No available information.

‡Two isofemale lines were crossed.

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