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Effects of Male Cohabitation on Female Reproduction in the Bean Bug, *Reptortus clavatus* THUNBERG (Heteroptera: Alydidae)¹

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In recent studies of female mating systems, much attention has been given to clarifying the effects of males on female reproduction. RIDLEY (1988) showed that in polyandrous insect species, females that mated more than once usually had higher fecundity and fertility than those that mated only once. Through repeated matings, they may gain nutrient materials from the males which enhance reproductive output (e.g., THORNHILL, 1976; BOGGS and GILBERT, 1979; GWYNNE, 1981, 1984) or may replenish inadequate sperm supply and thus ensure higher fertility (e.g., GROMKO and PYLE, 1978; GROMKO et al., 1984). In these insects, isolation from males after the first mating would cause a reduction in the females' fitness.

On the other hand, females can suffer costs by

male cohabitation: (1) the time and energy costs devoted to mating; (2) the time and energy costs required to repel unwanted suitors; and (3) increased risks of predation during multiple matings (THORNHILL and ALCOCK, 1983).

In the bean bug, *Reptortus clavatus*, it was observed that females mated repeatedly when they were reared with males under laboratory conditions. However, females were unwilling to copulate with males for 15 to 20 days after the first mating (SAKURAI, in press). In this study, to investigate the benefit and cost of multiple mating, I experimentally examined the effect of male cohabitation on female fitness components.

MATERIALS AND METHODS

Experiments were carried out with *R. clavatus* taken from laboratory-stock cultures which had been established from a soybean field in Nagoya City, from June to August in 1990. The stock cultures were maintained under diapause-preventing conditions ($25 \pm 1^\circ\text{C}$, 16L:8D, NUMATA and HIDAKA, 1982) with sufficient water and dried soybeans. Newly molted adults were taken from the cultures daily and individually reared in 200 ml plastic containers with water and soybeans.

Adult females matured within seven days after emergence (NUMATA and HIDAKA, 1982). Therefore, to investigate the effect of male cohabitation on female reproduction, females on the 7th day after adult emergence were divided into the following three experimental groups. Lifetime paired group (LPG, $n = 11$): Single males were introduced into plastic cups (200 ml) containing single females and were reared in pairs throughout their lives. When the male

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Fig. 1. Changes in oviposition rate of females in the lifetime paired group (LPG, $n = 11$), those of the single mated group (SMG, $n = 25$) and those of the unmated group (UMG, $n = 17$). Females in the former two groups copulated with a virgin male on the 7th day after emergence. Circles and squares represent averages ($\pm$ SE).

died during the experiment, another male of almost the same age was introduced (4 of 11); Single mated group (SMG, $n = 25$): Males were removed from females after they mated once; Unmated group (UMG, $n = 12$): Females were kept virgin. In the former two groups, all males mated with females within the day of introduction.

Small pieces of cotton were placed in the containers as oviposition substrates. The numbers of oviposited and hatched eggs were recorded every seven days.

Data were analyzed by a one-way ANOVA, followed by SCHEFFÉ's F test and a repeated measures ANOVA, and percentages were normalized by arcsin-root transformation before calculation.

RESULTS AND DISCUSSION

In *R. clavatus*, as in many other insects, copulation promoted egg production by females. The number of eggs laid by females during their lifetime differed significantly among the three groups (LPG: 372.6 ± 133.4 ; SMG: 215.7 ± 84.3 ; UMG: 103.9 ± 78.0 , one-way ANOVA, $F = 27.1$, $p < 0.0001$; SCHEFFÉ's F test,

LPG vs. SMG: $F = 10.5$, $p < 0.001$; SMG vs. UMG: $F = 7.1$, $p < 0.01$; UMG vs. LPG: $F = 27.0$, $p < 0.0001$). The number of hatched eggs in LPG was also significantly greater than that in SMG (former: 176.4 ± 116.4 ; latter: 104.4 ± 62.9 , one-way ANOVA, $F = 5.8$, $p < 0.05$). That in UMG was zero because no eggs were fertilized.

A repeated measures ANOVA was performed on female fecundity in the three groups, with copulatory status and adult age as the main effects (Table 1). Copulatory status, adult age and interaction all differed significantly. Figure 1 shows the changes in oviposition rate as a function of days after emergence for the three groups. Shortly after the first mating, the oviposition rate in SMG increased and the maximal rate was higher than that in LPG. Females in SMG laid significantly more eggs than those in LPG during the first 14 days after emergence (former: 45.2 ± 20.7 ; latter: 30.6 ± 11.3 , one-way ANOVA, $F = 4.2$, $p < 0.05$) and also during 21 days (former: 95.5 ± 42.5 ; latter: 67.2 ± 20.0 , one-way ANOVA, $F = 4.4$, $p < 0.05$). However, the oviposition rate in SMG began to decrease from the 21st day, although females in

Table 1. Repeated measures ANOVA performed to test for differences in fecundity between LPG, SMG and UMG

Source	df	MS	<i>F</i>	<i>p</i>
(1) Copulatory status	2	21500.1	37.7	< 0.0001
Error (1)	50	570.6		
(2) Adult age	7	5319.0	52.7	< 0.0001
Interaction (1) × (2)	14	1897.8	18.8	< 0.0001
Error (1) × (2)	350	100.9		

Table 2. Repeated measures ANOVA performed to test for differences in hatchability between LPG and SMG

Source	df	MS	<i>F</i>	<i>p</i>
(1) Copulatory status	1	18214.2	10.8	< 0.01
Error (1)	34	1684.8		
(2) Adult age	6	9865.8	43.6	< 0.0001
Interaction (1) × (2)	6	3159.3	14.0	< 0.0001
Error (1) × (2)	204	226.4

Fig. 2. Changes in hatchability (%) of eggs laid by females per week of females in the lifetime paired group (LPG, $n = 11$) and those of the single mated group (SMG, $n = 25$). Circles represent averages ($\pm$ SE).

the other groups continued to lay almost the same number of eggs constantly. This shows that an interaction between copulatory status and adult age exists, because the decrease in the oviposition rate was much larger for old females in SMG than for those in other groups.

A repeated measures ANOVA was also performed on hatchability, with copulatory status and adult age as the main effects (Table 2). Copulatory status, adult age and interaction all differed significantly. Al-

though hatchability in LPG remained constant, that in SMG decreased with female age (Fig. 2).

In this species, there were no significant differences in female life span among the three groups (SMG: 77.4 ± 20.3 days; LPG: 89.1 ± 14.7 days; UMG: 90.2 ± 34.4 days, one-way ANOVA, $F = 1.6$, NS).

These results indicate that the effects of male cohabitation on female reproduction change with the passage of time: during the first 21 days after emergence, females in SMG laid more eggs than females

in LPG, but lifetime fecundity and hatchability were higher for LPG than for SMG.

Multiple mating, as RIDLEY (1988) argued, may be generally necessary for females to achieve total fecundity and hatchability in insects in which females normally mate more than once (e.g., THORNHILL, 1976; GROMKO and PYLE, 1978; BOGGS and GILBERT, 1979; GWYNNE, 1981, 1984; GROMKO et al., 1984, but see WALKER, 1980; DRUMMOND, 1984; HALLIDAY and ARNOLD, 1987). On the other hand, several studies have shown a decline in the reproductive success of females which are confined with males all their lives, either because of the time cost of multiple mating or because of sexual harassment by courting males (e.g., NIELSON and TOLES, 1968; GERBER and CHURCH, 1976). In *R. clavatus*, the lower productivity during the early oviposition period in LPG may be caused by mating or mounting behavior of courting males. Females are often unwilling to copulate with males during the first 15 to 20 days after the first mating (SAKURAI, in press). By rejecting the males, which interrupt their oviposition with prolonged copulation (for ca. 2.5 h), they might avoid the cost of remating (i.e., reduction of reproduction).

It follows from what has been described above that the time cost may cause a refractory period before remating in *R. clavatus* females, and the females should accept further matings if the costs of reduced oviposition rate and hatchability outweigh the costs of remating.

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