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# Repeated Copulations Benefit of the Female in *Lethocerus deyrollei* Vuillefroy (Heteroptera : Belostomatidae)

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**Abstract** – The *Lethocerus deyrollei* male copulates repeatedly with the same female before and between ovipositions. Females stopped oviposition and waited for the next copulation when males were experimentally removed. This result suggests that females need to copulate before each oviposition bout. Since eggs fail to hatch without care of males, females have to detain males until the end of sequential ovipositions. Males assure their paternity with repeated copulations, and females can thus detain males.

*Lethocerus deyrollei* is a large predatory insect (body length 48–65 mm), which lives in still waters such as ponds and rice fields. Females lay egg-masses on emergent vegetation above water surface, as in the case of other *Lethocerus* (Hoffmann 1933; Rankin 1935; Tawfik 1969). Males of this species brood their eggs until hatching (Ichikawa 1985, 1988). This brooding behaviour has not been observed in other species of Lethocerinae. Oviposition is carried out at night. After copulating in the water, the female starts to oviposit on vegetation more than 10 cm above the waterlilne (Fig.1). She then copulates many more times with the same mate at an ovipositing site between ovipositions (Hirayama 1977; Ichikawa 1983).

Repeated copulations during 1 sequence of mating behaviour by an individual pair is known for Belostomatidae (Arimoto 1930; Smith 1979a,b). Sperm competition is common in insects, a result of multiple matings. Frequent copulation has been interpreted as an adaptation to reduce sperm competition (Parker 1970). Smith (1979a,b) showed that frequent copulation of paternal male water bugs is important in reducing the risk of cuckoldry. Tallamy (1984) pointed out that males which care for their young go to great lengths to assure paternity. These 2 hypotheses also may apply to the case of *L. deyrollei* males.

In general, the sperm competition avoidance mechanism requires time and energy and is costly to the female (Knowlton & Greenwell 1984). In some cases, however, females gain benefit from the sperm competition avoidance mechanism of males. During a prolonged copulation (2 to 3 days), the male love bug *Plecia nearctica* helps his mate to find food by aiding her movement from the emergence site to food. Females aided by males may produce more and /or better nourished eggs (Thornhill 1984).

Nobody, however, has described female benefit from repeated copulations of paternal brood caring water bugs ; my study does so.

## Insects and Method

Observations and experiments were carried out in an aquarium (90 × 45 × 45 cm, 10 cm depth), at night, in the summers of 1986–1988. Bugs were collected in the western part of Hyogo Prefecture in early summer. They were given small fishes for food.

Repeated copulations above water surface were observed 3 times for 3 mating pairs. A stick (30–40 cm long, 2 cm dia.) was provided as on ovipositing site. A 40 watt red bulb was set about 2 m away from the aquarium (under 10 lux). Since eggs of *L. deyrollei* are laid with bubbles, some drops of water were poured on the egg-mass between copulations for observation (B, C in Table 1). In these cases, a 40 watt white bulb light was used (over 200 lux) for counting eggs. Pairs had already copulated 1 to over 10 times under the water surface before copulations were recorded above water surface.

Experiments were carried out during 1 sequence of oviposition behaviour for 8 males and 9 females. Males were picked up and removed from the aquarium just when they climbed up the stick for the next copulation. The behaviour of females was then observed. Only 3 females were reunited with the removed males 30–60 min after removal. These males were placed 1 to 2 cm behind the egg-laying females. If copulation failed to follow, the process was repeated 1 or 2 more times (Fig. 2)

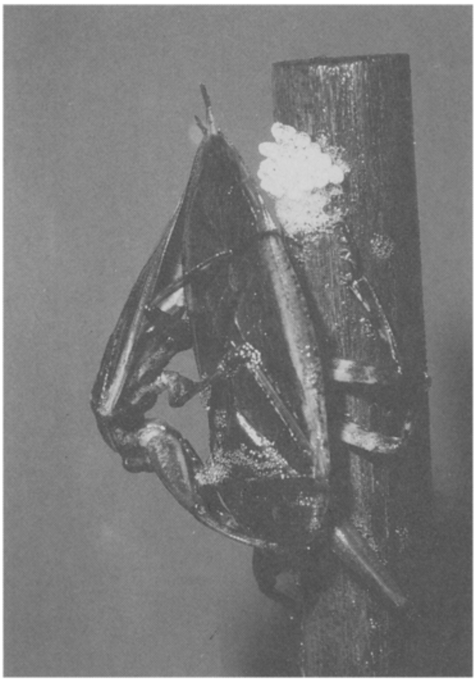

**Fig.1.** Copulation at ovipositing site.

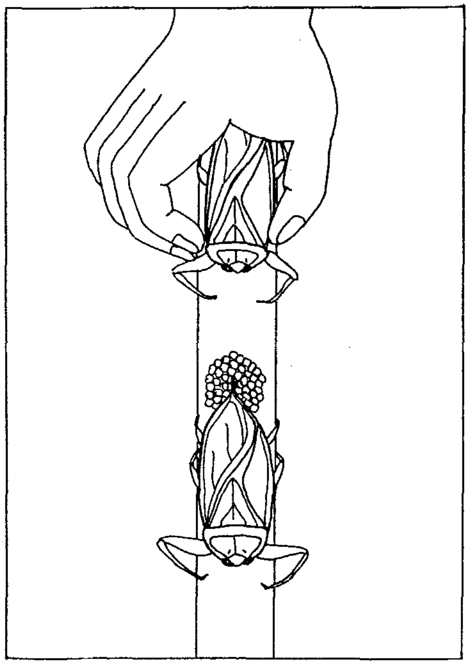

**Fig.2.** The removed male was replaced behind the same former female partner.

Table 1 Repeated copulations above water surface.

| Observation (date) | A:(1986.7.6) | | B:(1988.6.28) | | C:(1988.8.10) | |
|---|---|---|---|---|---|---|
| Copulation | begin | end | begin | end | begin | end |
| 1st | 21:28 | 21:31 | 23:57 | 0:06 | 21:59 | 22:08 |
| 2nd | 21:34 | 21:39 | 0:09 | 0:16 | 22:20 | 22:28 ( 1) |
| 3rd | 21:40 | 21:43 | 0:23 | 0:28 | 22:41 | 22:48 ( 4) |
| 4th | 21:45 | 21:47 | 0:30 | 0:34 ( 1) | 22:49 | 22:55 ( 7) |
| 5th | 21:49 | 21:51 | 0:36 | 0:39 ( 3) | 22:56 | 23:00 (10) |
| 6th | 21:52 | 21:54 | 0:42 | 0:45 ( 6) | 23:02 | 23:05 (14) |
| 7th | 21:56 | 21:57 | 0:49 | 0:52 (11) | 23:07 | 23:10 (18) |
| 8th | 22:00 | 22:02 | 0:56 | 1:00 (17) | 23:12 | 23:14 (23) |
| 9th | 22:03 | 22:06 | 1:04 | 1:07 (22) | 23:16 | 23:18 (33) |
| 10th | 22:08 | 22:10 | 1:10 | 1:14 (28) | 23:21 | 23:23 |
| 11th | 22:12 | 22:14 | 1:22 | 1:25 (37) | 23:25 | 23:26 |
| 12th | 22:16 | 22:18 | 1:30 | 1:34 | 23:28 | 23:30 |
| 13th | 22:21 | 22:23 | 1:40 | 1:43 (55) | 23:32 | 23:34 |
| 14th | 22:25 | 22:26 | | | 23:36 | 23:38 |
| 15th | 22:29 | 22:31 | Observation was | | 23:40 | 23:42 |
| 16th | 22:34 | 22:35 | stopped at 1:45. | | 23:45 | 23:47 |
| 17th | 22:38 | 22:41 (59) | | | 23:51 | 23:52 |
| 18th | | | | | 23:57 | 23:58 |
| 19th | The male was removed | | | | 0:03 | 0:04 |
| 20th | from the aquarium at | | | | 0:09 | 0:11 |
| 21th | 22:42 for experiment. | | | | 0:14 | 0:16 (88) |

Figures in parentheses are cumulative number of eggs laid.
Only observation (C) was continued until the end of the whole oviposition sequence.

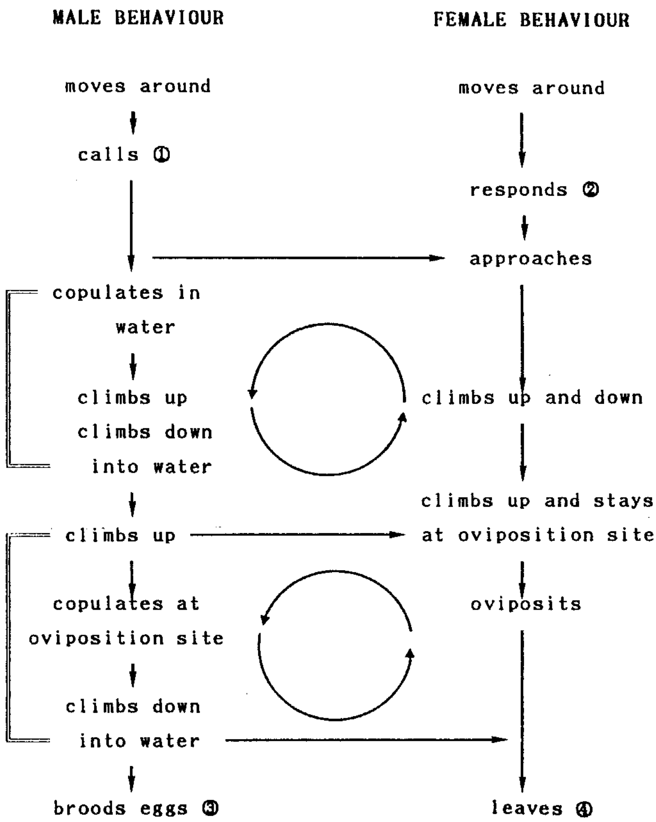


**Fig.3.** A sequence of mating behaviour of *Lethocerus deyrollei.*
①② A male makes waves by bending joints, but sometimes a female does not respond.
③ He frequently climbs up to the egg-mass from the water, and supplies the eggs with moisture.
④ She jumps down directly into the water (not along the vegetation) after confirming her mate's ascent, and leaves the egg-mass.

## Results

Results of observation about the sequence of mating behaviour are shown in Fig.3, and those about repeated copulations are shown in Table 1. Repeated copulations of 3 pairs were observed. Observation was continued until the end of oviposition for 1 pair. This pair copulated 21 times, and the female laid 88 eggs in the sequence of oviposition.

Table 2 shows results of experiments. Females stopped laying eggs at 4.75−5.5 min after removal of males and stopped moving. When removed males were replaced behind females, they resumed copulations, with females ovipositing thereafter. When males were not replaced, 3 females climbed down the stick into the water 42−77 min after removal of males and did not climb up again. One of these females was dissected. There were 33 eggs in her ovaria, no eggs in the oviduct and some spermatozoa in the spermatheca. The abdomen of 1 female, from which her mate had been removed, adhered to the egg-mass with a glue-like substance which bubbled from the ovipositor with the eggs. This female could not copulate again.

## Discussion

A pair of *L. deyrollei* copulated 21 times in sequent oviposition. The female laid 3−10 eggs after each copulation bout. Smith (1979a, b) showed repeated copulations with the same mate in *Abedus herberti* (Belostomatinae). Female bugs in this subfamily lay eggs on the backs of males, and males brood them until hatching. Smith (1979a, b) interpreted this repeated copulation as a paternity assurance tactic of males because the last male to mate sires almost all eggs.

Table 2 Female behaviour after removing male during oviposition.

| Number of eggs laid | Time (min) female waited (a) | Resultant female behaviour |
|---|---|---|
| A: The male was removed. | | |
| 8 | 42 | Climbed down into the water. |
| 20 | 90 | Abdomen adhered to stick. |
| 38 | over 60 | In the water next morning. |
| 46 | 70 | Climbed down into the water. (b) |
| B: The male was reintroduced 30–60 min after removal. | | |
| 21 | 30 | Oviposition, resumed. |
| 29 | 60 | " " |
| 59 | 45 | " " |

(a) The time females waited at oviposition site until they climbed down into the water or until males were reintroduced.

(b) This female was dissected. Thirty three eggs remained in the ovary, as did some spermatozoa in the spermatheca.

Copulated *Diplonychus major* (Belostomatinae) multiply with plural mates in an egg-mass loading sequence to the male's back in an aquarium (Ichikawa 1989). Some female bugs aggegated near a male to aggressively lay eggs on one another. Density of adult *D. major* in the field is high ($19/m^2$), unlike that of *A. herberti*. A male *D. Major* should therefore have eggs from many females on his back in the field. Male bugs of this species always tried to copulate before every oviposition. Repeated copulations may be useful to assure their paternity.

Male bugs of *D. major* always tried to copulate before each oviposition bout, but females sometimes laid an egg on the back of the male without copulation (Ichikawa 1989). This suggests that females of *D. major* do not need to copulate before every oviposition. There may be little benefit to *D. major* females in repeated copulations. However, the present study showed no occurrence of solitary oviposition in *L. deyrollei* after removal of males. If males were experimentally removed, females stopped oviposition and waited for their mates, strongly suggesting female benefit from repeatd copulations.

What is the benefit to females? After finishing oviposition, females jump down directly into the water and leave their egg-masses if they can confirm that males come up for brooding (Hirayama 1977; Ichikawa 1983). The males, which are left alone, brood eggs until hatching. Ichikawa (1988) reported that *L. deyrollei* eggs failed to hatch without male care both in still water and dry air. In this behavioral process, males and females must have opposing parental obligation roles. Females succeed in "initiating" male brooding of eggs, but must be able to reciprocate and detain males near eggs until the conclusion of oviposition. Repeated copulations assure males of their paternity and is the mechanism with which females detain partners. After confirming the presence of males by copulation females proceed to oviposit. According, they stop oviposition if males are absent, thereby saving eggs.

Repeated copulation of *L. deyrollei* is assumed to have evolved under the pressure of mutual benefit for both sexes.

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