*J. Ethol.* 11 : 63–65, 1993 *Short Communication*

# Male-male Aggressive Behavior is Changed by Body Size Difference in the Leaf-footed Plant Bug, *Leptoglossus australis*, Fabricius (Heteroptera: Coreidae).

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Maynard Smith & Price (1973) introduced the theory of games to the issue of animal conflict. In the prediction of the theoretical models (e.g. Maynard Smith & Parker 1976; Maynard Smith 1982), size is often a good predictor of resource holding power (RHP) (Parker 1974), leading to prediction that the larger animal of the 2 opponents should win. When 2 contestants differ in fighting ability or RHP, this asymmetry, if perceived by both contestants, should be used to settle contests. Escalated fighting should occur when the difference in size of contestants is small.

In 2 species of the coreid bug, *Acanthocephala femorata* (Mitchell 1980) and *Acanthocoris sordidus* (Fujisaki 1980, 1981), males fought with each other for access to females. These 2 species have sexually dimorphic hind legs, that is, only males have enlarged hind femora used for male-male combat. These studies showed that male-male combat for females exists, and that territorial males tended to be larger than non-territorial males. The study of *Acanthocoris sordidus* (Fujisaki 1981) clarified that size was a reliable measure of RHP, and that males evaluate their opponent's RHP during wrestling. However, the study did not show the relationship between size differences of contestants and the type of male-male aggressive behaviors.

In this study I examined the relationship between male-male aggressive behaviors and size differences of the males in the leaf-footed plant bug, *Leptoglossus australis*, a species in which males have enlarged hind femora but females do not.

## Materials and Methods

Interactions between 2 males were observed in a laboratory. Adult bugs were collected from fields of sponge gourd, *Luffa cylindrica*, on Okinawa Island in 1983. Four adult males which were individually marked with quickly drying paints (Mitsubishi Paint Marker®) were simultaneously introduced into a small cage (25 × 25 × 30 cm). A sponge gourd fruit was hung from the ceiling of the cage as a site for male-male combat, since all matings (n=9) observed in the field were on sponge gourd fruit (Miyatake unpubl.). Experiments were carried out for 8 days between 1000 and 1700 using 3 cages. I recorded the outcomes of interactions only after the first encounter for each male pair. After the observation, the body lengths of males were measured with calipers to the nearest 0.05 mm.

## Results and Discussion

A total of 49 aggressive encounters were observed on fruit after introduction of males (Fig. 1). A male on fruit responded immediately to the presence of another male by raising up a hind leg toward his opponent. I defined this behavior as "Threat". If the opponent did not retreat from "Threat", the first male displayed a second behavior, "One-side attack". In "One-side attack", 2 types of behaviors were observed. In one type, a male tried to hook and pull his opponent's thorax by his forelegs, simi-

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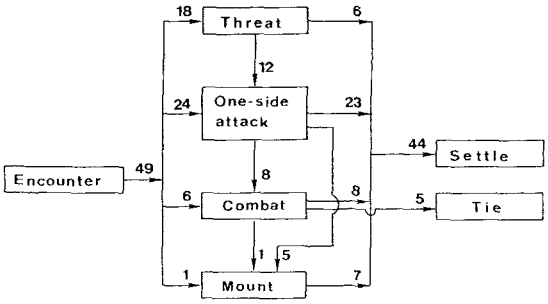


**Fig. 1.** The sequence of aggressive behaviors of the leaf-footed plant bug.

lar to that of a courtship behavior in this species (Miyatake unpubl.). In the other type of "One side attack", a male beat his opponent with 1 hind leg. If the opponent did not retreat, the male spread his hind legs widely apart and turned his abdomen toward his opponent. The opposing male responded in the same way, so that 2 males were positioned tail to tail with hind legs in contact. Sometimes the males escalated the battle and a tactile fencing match ensued, in which each bug attempted to wrap his hind legs around the abdomen of the opponent. This behavior was defined as "Combat", similar to the combat of *Acanthocephala femorata* (Mitchell 1980) and to the wrestling of *Acanthocoris sordidus* (Fujisaki 1981). After "One-side attack" and/or "Combat", a male sometimes tried to exhibit dominance by mounting his opponent's back. I defined this behavior as "Mount". Loser males showed no resistance to mounting, escaping from the mounter immediately after release.

Thus aggressive behaviors were divided into 4 types of behavior, i.e. "Threat", "One-side attack", "Combat" and "Mount". Figure 1 shows the sequence of 4 types of male-male fighting behaviors and an overview of all encounters. Forty-nine encounters resulted in 18 "Threat", 24 "One-side attack", 6 "Combat" and 1 "Mount" behaviors. In 6 out of 18 "Threat" cases, the interactions were settled, but the remaining 12 cases advanced to "One-side attack". In 23 out of 36 "One-side attack" cases, the interactions were settled, but the remaining 13 pairs progressed to "Combat" or "Mount". In 8 out of 14 "Combat" cases, the interactions were settled. In the remaining 5 cases, however, the outcomes were tied: 2 contestants stopped their combat and separated from each other. "Mount" occurred in a total of 7 cases. "Mount" always resulted in settlement ('Settle').

Given that a retreating or mounted male was the loser, larger males won 39 of 44 interactions ($\chi^2 = 26.27$, $P < 0.001$). There was a significant difference in body length of male pairs advancing to the 4 aggressive behaviors (Table. 1). Non-parametric multiple comparisons showed that "Mount" tended to occur more often in cases where larger body size differences were present, as compared to other aggressive behaviors. Furthermore, there was also a significant difference in body size difference between pairs where a male retreated and where males tied during "Combat"; i.e. 'Settle': mean ± SD = 1.19 ± 0.66, n = 8; and 'Tie': mean ± SD = 0.44 ± 0.21, n = 5 (Mann-Whitney's *U*-test, $P < 0.05$). 'Tie' were cases in which males did not settle even after "combat".

These results are consistent with the game

Table 1. Size difference of male pairs advanced to each aggressive behavior. (Kruskal-Wallis test, $P < 0.01$ for all four comparisons)

| Behaviors | N | Size difference: mean±SD (mm) | Multiple comparisons* |
|---|---|---|---|
| Threat | 6 | 0.80±0.74 | A |
| One-sided attack | 23 | 1.02±0.82 | A |
| Combat | 13 | 0.90±0.64 | A |
| Mount | 7 | 2.31±0.94 | B |

*Letters indicate significant difference at the 5% level in non-parametric multiple comparisons (Conover, 1980).

theory prediction, that is, size relative to the opponent was a good predictor of contest outcome (the larger individual tends to be the winner). Male-male aggressive behaviors were influenced by body size difference. "Mount" always resulted in a winner and a loser. After "Mount", no further encounter was observed. Thus "Mount" may be the behavior that results in settlement of contests.

In this study, the influences of the resource value for contestants (Austad 1983; Verrell 1986; Wells 1988; Jackson & Cooper 1991) and the contest duration (Verrell 1986; Wells 1988) on the outcome of male-male interactions were not examined. In this species the resource value for a male may change due to the presence of a female on the fruit. It would be worthwhile to examine whether this factor affects the aggressive behavior of *L. australis*.

*Acknowledgements* — I thank O. Iwahashi for critical review of the manuscript and B.E. Spix and E. Jang for their helpful comments.

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(Received 21 Aug. 1992; Accepted 19 Nov. 1992)