Journal of Insect Behavior, Vol. 10, No. 5, 1997

Functional Morphology of the Hind Legs as Weapons for Male Contests in *Leptoglossus australis* (Heteroptera: Coreidae)

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Accepted March 1, 1997; revised April 29, 1997

Functional morphology of the hind legs as weapons in male contests was analyzed in the leaf-footed plant bug, Leptoglossus australis Fabricius. Measurement of some metrical tratis of the hind femur and tibia indicated that the weapon was the hind femur. Sexual dimorphism in the femoral length and width, and in the number of spines on the lower side of the femur, indicated that these parts play a significant role in male contests. It was also suggested that the length from the base to the widest part of the femur had a functional significance for male-male combat behaviors of L. australis.

KEY WORDS: contest; femur; *Leptoglossus australis*; morphology; sexual selection; weapon.

INTRODUCTION

As a result of male contests for females certain sexually selected traits of males sometimes evolve as weapons (Andersson, 1994; Andersson and Iwasa, 1996), including horns, tusks, and spurs (e.g., Blum and Blum, 1979; Thornhill and Alcock, 1983; Andersson, 1994). In insects, it is well known that larger male beetles have larger horns than smaller ones (Palmer, 1978; Brown and Bartalon, 1986; Eberhard, 1979, 1982, 19878; Eberhard and Gutierrez, 1991; Siva-Jothy, 1987; Kawano, 1995a, b). However, why the larger individuals in a species possess relatively larger horns than smaller ones is a major unsolved problem of functional morphology (Otte and Stayman, 1979).

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The study of hind legs of males as weapons has been focused on coreid bugs (Mitchell, 1980; Fujisaki, 1980, 1981; Miyatake, 1995). The hind legs of males in coreid bugs show often large morphological variation (Miller, 1971), and a sexual dimorphism in femora of hind legs has been reported for three species, *Acanthocephala femorata* (F.) (Mitchell, 1980), *Acanthocoris sordidus* Thunberg (Fujisaki, 1980, 1981), and *Notobitus meleagris* F. (Miyatake, 1995). These sexual dimorphisms are considered to have evolved through male contests (Mitchell, 1980; Fujisaki, 1980, 1981; Miyatake, 1995). However, no study has analyzed in detail the dimensions of the hind legs in these coreid bugs.

Although many species of the genus *Leptoglossus* have hind legs with enlarged femur and dilated tibia (Allen, 1969), the function has not been studied (Miller, 1971). Miyatake (1993) showed that males of the leaf-footed plant bug, *Leptoglossus australis* F., fight for females by using their enlarged hind legs.

In this study, the hind femur and tibia of *L. australis* were measured to answer the question, which is the weapon for male contests, femur or tibia? The results are discussed in view of the relationship between aggressive behavior and functional morphology of hind legs in *L. australis*.

MATERIALS AND METHODS

A total of 56 adult males and 21 adult females was collected from the southern part of Okinawa Island, Japan, in 1983. After the body lengths were measured with calipers, right hind legs were removed from the bodies. The shapes of legs were drawn on paper with a ruler on the screen of a Nikon Profile Projector Model 6CT2. Thus, lengths and widths of the femur and tibia were measured with rulers, and the spines on the femur and tibia (Fig. 1) were counted. Linear and nonlinear regressions were used to analyze the relationship between body length and some dimensions of the hind legs (Snedecor and Cochran, 1967). Tests of significance of departure from linearity were also used (Snedecor and Cochran, 1967, p. 406). Spearman's rank test was used to analyze the relationship between the body length and the number of spines on the legs. To compare the number of spines on the hind legs between sexes, the Mann–Whitney *U* test was used.

RESULTS

Weapon for Male Contests

The relationships between body length and four leg measurements (A, femoral length; B, maximal femoral width; C, tibial length; and D, maximal tibial width) are shown in Fig. 2. The relationships between body length and

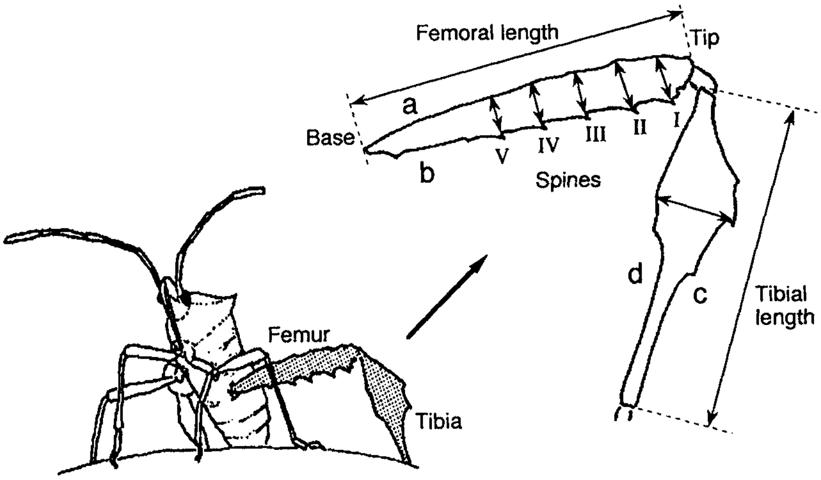

Fig. 1. An adult male of the leaf-footed plant bug, *Leptoglossus australis* (drawn from a photograph by Futoshi Kawamura), and the right hind leg used for male contests. Several parts for measurement are shown. Femoral upper and lower sides are labeled a and b, respectively. Tibial upper and lower sides are labeled c and d, respectively.

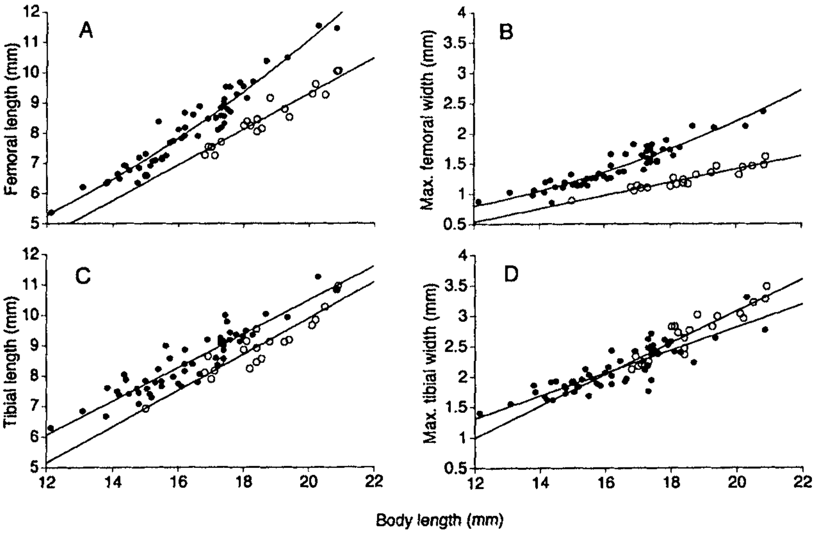

Fig. 2. Relationships between body length and femoral length (A), maximal femoral width (B), tibial length (C), and maximal tibial width (D). Filled and open circles show males and females, respectively. Linear and nonlinear regression lines are shown.

femoral length (Fig. 2A), and between body length and femoral maximum width (Fig. 2B) deviated significantly from linearity in males (femoral length, $F = 3.75$, $P < 0.01$; maximal femoral width, $F = 7.00$, $P < 0.01$), and their curvilinear regressions were as follows: femoral length; $Y = 1.78 + 0.03X + 0.02X^2$, $r^2 = 0.929$; and maximal femoral width; $Y = 0.77 - 0.10X + 0.01X^2$, $r^2 = 0.877$. In females, however, linear relationships characterized femoral length (Fig. 2A; $F = 0.97$, n.s.) and maximal femoral width (Fig. 2B; $F = 1.25$, n.s.), with the following linear regressions: femoral length, $Y = -2.46 + 0.59X$, $r^2 = 0.929$; and maximal femoral width, $Y = -0.77 + 0.11X$, $r^2 = 0.886$.

Relationships between body length and tibial length (Fig. 2C) and maximal tibial width (Fig. 2D) showed no significant deviation from linearity in either sex (tibial length in male, $F = 1.47$, n.s.; tibial length in female, $F = 1.35$, n.s.; maximal tibial width in male, $F = 0.25$, n.s.; maximal tibial width in female, $F = 0.22$, n.s.), and their linear regressions were as follows: tibial length in male, $Y = -0.58 + 0.55X$, $r^2 = 0.855$; tibial length in female, $Y = -1.97 + 0.59X$, $r = 0.861$; maximal tibial width in male, $Y = -0.94 + 0.19X$, $r^2 = 0.743$; and maximal tibial width in female, $Y = -2.12 + 0.26X$, $r^2 = 0.863$.

Relationships between body lengths and the number of spines on the femur and tibia are shown in Fig. 3. There were significant rank correlations between the body length and the number of spines on the upper and lower sides of the femur and tibia of both sexes (femoral upper side—male $r_S = 0.7$, $P < 0.001$, and female $r_S = 0.7$, $P < 0.001$; femoral lower side—male $r_S = 0.7$, $P < 0.001$, and female $r_S = 0.5$, $P < 0.05$; tibial upper side—male $r_S = 0.3$, $P < 0.05$, and female $r_S = 0.5$, $P < 0.05$; and tibial lower side—male $r_S = 0.7$, $P < 0.001$, and female $r_S = 0.5$, $P < 0.05$).

There was no significant difference between sexes in the number of spines on the femoral upper side, tibial upper side, and tibial lower side [femoral upper side—male, 1.82 ± 1.63 (mean ± SD), and female, 1.24 ± 1.37; tibial upper side—male, 2.71 ± 0.68, and female, 2.76 ± 0.83; tibial lower side—male, 1.07 ± 1.48, and female, 0.62 ± 0.92]. However, the number of spines on the lower side of the femur was significantly larger in males than in females (male, 5.70 ± 1.06; female, 4.62 ± 1.20; $z = 3.942$, $P < 0.001$), indicating sexual dimorphism in the number of spines in this location.

Functional Morphology of the Femur

The change in femoral size and shape with an increase in body size is shown in Fig. 4 in relation to the development of spines on the lower side of the femur. As the body length increased, the femoral length and width and the number of spines also increased, and new spines appeared on the lower side of

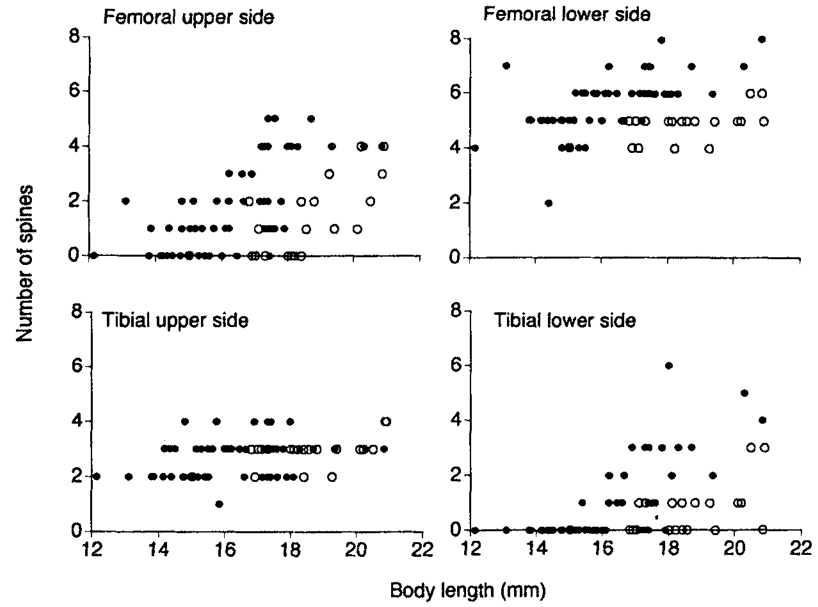

Fig. 3. Relationships between the body length and the number of spines on the femur and tibia. Filled and open circles show males and females, respectively.

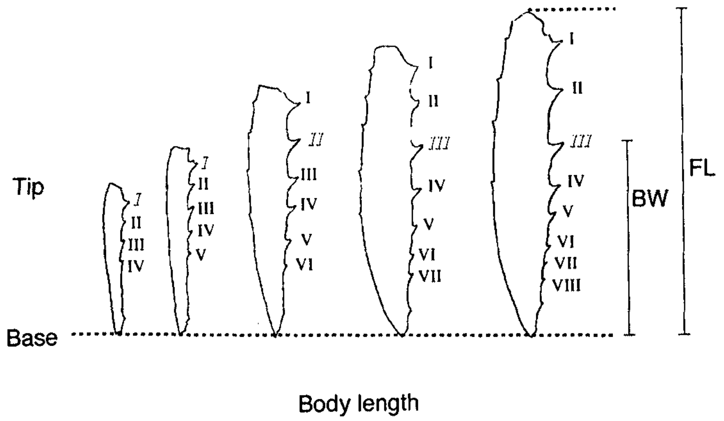

Fig. 4. Morphological change of the femur in relation to increasing body length. FL, femoral length; BW, length from the base to the widest part (shown as hollow slanted numbers) of the femur.

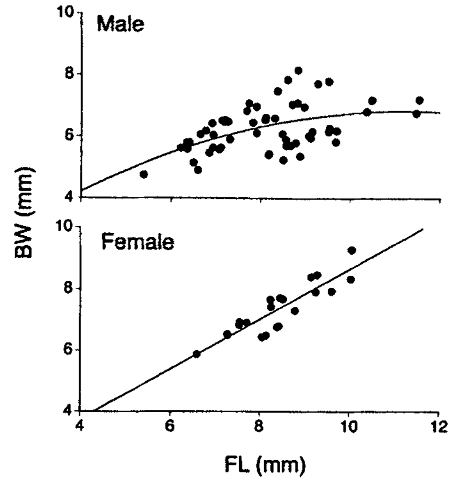

Fig. 5. Relationships between the femoral length (FL) and the length from the base to the widest part of femur (BW) for both sexes.

the femur forward of the base (Fig. 4). Each spine was numbered I to VIII in order from the tip to the base of the femur. The length from the base to the widest part of the femur is abbreviated BW. In 56 males measured, the numbers of individuals having the widest part of the femur at the position of spines I, II, and III were 19 (34%), 17 (30%), and 20 (36%), respectively. In contrast, the number of females having femurs with the widest part at spines I and II were 13 (2%) and 8 (38%), respectively. No females had the widest part of the femur at spine III.

The relationship between femoral length (FL) and BW deviated significantly from linearity in males (Fig. 5) ($F = 1.65$, $P < 0.05$), and the curvilinear regression was $Y = 0.55 + 1.12X - 0.05\ X^2$ ($r^2 = 0.265$). In females, however, the relationship did not deviate from linearity ($F = 0.51$, n.s.), and the linear regression was $Y = 0.50 + 0.82X$, $r^2 = 0.783$ (Fig. 5). This means that there is a difference between sexes in the pattern of morphological change of the femur as body size increases, and it suggests a functional significance of the femur (BW) for male contests.

DISCUSSION

The coreid *L. australis* exhibits sexual dimorphisms in femur length, femur width, and number of spines on the lower side of the femur, indicating that its hind leg femur is used as a weapon in male contests. The sexual dimorphisms suggest that the femur structure has been influenced by sexual selection.

Male–male contest behaviors in *L. australis* are divided into four patterns, i.e., "threat," "one-side attack," "combat," and "mount" (Miyatake, 1993). In "threat," a male raises up a hind leg toward his opponent. In "one-side attack," a male beats his opponent's body with a hind leg. The most escalated fighting behavior, "combat," occurs when the difference in body size of two fighting males is small (Miyatake, 1993). In "combat," two 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 male attempted to wrap his hind legs around the abdomen of the opponent (Miyatake, 1993). This behavior is also seen in other coreid bugs (Mitchell, 1980; Fujisaki, 1981; Miyatake, 1995).

There was a sexual difference in the pattern of morphological change of femur as size increased. The relationship between FL and BW was linear in females but nonlinear in males (Fig. 5). This suggests a possibility that an absolute optimal length in BW for male-male "combat" exists. In "combat" the spines on the lower side of the femora come in contact with the opponent's abdomen. Thus, BW should have a functional significance for male-male "combat."

The number of spines on both sides of the femur and tibia increased as the body length increased (Fig. 3). However, there was sexual dimorphism only in the number of spines on the lower side of the femur. Why the number of spines on the tibia and the other side of the femur also should increase as body length increased is not clear, as these structures appear to have no functional significance for fighting. These might be caused by allometric growth of the increase in spines on the lower side of the femur.

Even in females which did not show "combat" behavior (Miyatake, unpublished data), the number of spines on the femur and tibia increased as the body length increased. This may be due to either or both of two reasons: (1) the spines of females might develop by a genetic correlation between sexes (Lande, 1980; Falconer, 1989), and (2) the spines might develop due to "one-side attack," which is shown by females when they compete for feeding sites (Miyatake, unpublished data).

The posterior tibiae are strongly foliaceous in the genus *Leptoglossus*, and the purpose of these extravagant modifications in form is not known (Allen, 1969; Miller, 1971). In this study, no significance of the tibia in male contests was found. Foliaceous tibiae may be evolved for other purposes, for example, defense against predators or camouflage against natural enemies.

There are many coreid species having enlarged femora (Allen, 1969; Miller, 1971), some of which have been evolved as weapons for male contests (Mitchell, 1980; Fujisaki, 1980, 1981; Miyatake, 1995). Comparative studies of femoral shapes in coreid bugs may be worthwhile to clarify the evolution of weapons.

ACKNOWLEDGMENTS

I am grateful to Paula Levin Mitchell (Winthrop University, USA), Malte Andersson (University of Göteborg, Sweden), and an anonymous reviewer for critical review of the manuscript and for correcting grammatical errors. I also thank Osamu Iwahashi (University of the Ryukyus, Japan) and Kenjiro Kawasaki (National Institute of Sericultural and Entomological Science, Japan) for useful comments on an early version of the manuscript.

REFERENCES

Allen, R. C. (1969). A revision of the genus *Leptoglossus* Guerin. *Entomol. Am.* **45:** 35–140.

Andersson, M. (1994). *Sexual Selection*, Princeton University Press, Princeton, NJ.

Andersson, M., and Iwasa, Y. (1996). Sexual selection. *Trends. Ecol. Evol.* **11:** 53–58.

Blum, M. S., and Blum, N. A. (1979). *Sexual Selection and Reproductive Competition in Insects*, Academic Press, New York.

Brown, L., and Bartalon, J. (1986). Behavioral correlates of male morphology in a horned beetle. *Am. Nat.* **127:** 565–570.

Eberhard, W. G. (1979). The function of horns in *Podischnus agenor* (Dynastinae) and the other beetles. In Blum, M. S., and Blum, N. A. (eds.), *Sexual Selection and Reproductive Competition in Insects*, Academic Press, New York, pp. 231–258.

Eberhard, W. G. (1982). Beetle horn dimorphisms: Making the best of a bad lot. *Am. Nat.* **119:** 420–426.

Eberhard, W. G. (1987). Use of horns in fights by the dimorphism males of *Ageopsis nigricollis* (Coleoptera, Scarabeidae, Dynastinae). *J. Kans. Entomol. Soc.* **60:** 504–509.

Eberhard, W. G., and Gutierrez, E. E. (1991). Male dimorphism in beetles and earwigs and the question of developmental constraints. *Evolution* **45:** 18–28.

Falconer, D. S. (1989). *Introduction to Quantitative Genetics*, 3rd ed., Langman, London.

Fujisaki, K. (1980). Studies on the mating system of the winter cherry bug, *Acanthocoris sordidus* Thunberg (Heteroptera: Coreidae). I. Spatio-temporal distribution patterns of adults. *Res. Popul. Ecol.* **21:** 317–331.

Fujisaki, K. (1981). Studies on the mating system of the winter cherry bug, *Acanthocoris sordidus* Thunberg (Heteroptera: Coreidae): II. harem defense polygyny. *Res. Popul. Ecol.* **23:** 262–279.

Kawano, K. (1995a). Horn and wing allometry and male dimorphism in giant rhinoceros bettles (Coleoptera: Scarabaeidae) of tropical Asia and America. *Ann. Entomol. Soc. Am.* **88:** 92–99.

Kawano, K. (1995b). Habitat shift and phenotypic character displacement in sympatry of two closely related rhinoceros beetle species (Coleoptera: Scarabaeidae). *Ann. Entomol. Soc. Am.* **88:** 641–652.

Lande, R. (1980). Sexual dimorphism, sexual selection, and adaptation in polygenic characters. *Evolution* **34:** 292–305.

Miller, N. C. E. (1971). *The Biology of the Heteroptera*, E. W. Classey, London.

Mitchel, P. L. (1980). Combat and territorial defense of *Acanthocephala femorata* (Hemiptera: Coreidae). *Ann. Entomol. Soc. Am.* **73:** 404–408.

Miyatake, T. (1993). Male-male aggressive behavior is changed by body size difference in the leaf-footed plant bug, *Leptoglossus australis*, Fabricius (Heteroptera: Coreidae). *J. Ethol.* **11:** 63–65.

Miyatake, T. (1995). Territorial mating aggregation in the bamboo bug, *Notobitus meleagris*, Fabricius (Heteroptera: Coreidae). *J. Ethol.* **13:** 185–189.

Otte D., and Stayman, K. (1979). Beetle horns: some patterns in functional morphology, In Blum, M. S., and Blum, N. A. (eds.), *Sexual Selection and Reproductive Competition in Insects*, Academic Press, New York, pp. 259–292.

Palmer, T. J. (1978). A horned beetle which fights. *Nature* **274:** 583–584.

Siva-Jothy, M. T. (1987). Mate securing tactics and the cost of fighting in the Japanese horned beetle, *Allomyrina dichotoma* L. (Scarabeidae). *J. Ethol.* **5:** 165–172.

Snedecor, G. W., and Cochran, W. G. (1967). *Statistical Methods*, 6th ed., Iowa State University Press, Ames.

Thornhill, R., and Alcock, J. (1983). *The Evolution of Insect Mating Systems*, Harvard University Press, Cambridge, MA.