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On the Fore Legs of Seed Bugs (Heteroptera: Lygaeidae): Aggression and Allometric Scaling in *Scolopostethus affinis* Schilling

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ABSTRACT: Males and females of the seed bug *Scolopostethus affinis* used their fore legs with modified femora in intra-sexual aggression. Males were smaller than females, but had larger fore femora. Allometric scaling of the fore femora on body size was similar in both sexes. This argues against hypotheses that the often spiny and enlarged fore legs of seed bugs serve to move seeds or to aid in movement in confined spaces. Instead, they may function primarily in aggression.

The fore legs of many seed bugs (Lygaeidae), especially among the Rhyparochrominae, are strikingly modified with enlarged and spiny femora (Schuh and Slater, 1995) so that they seem raptorial (Borror et al.,1992). This is puzzling for bugs which are primarily herbivorous (Sweet, 1979; Schuh and Slater, 1995), and two main hypotheses have been proposed as explanations: that the fore legs are used to manipulate seeds along irregular substrates (Sweet, 1964a), or that they aid in movement within enclosed spaces (Schuh and Slater, 1995). However, another possibility is that the modified legs of these bugs are used in aggressive contests, as for example in coreid bugs with their hind legs (Mitchell, 1980; Miyatake, 1993, 1997; Eberhard, 1998).

There are some descriptions of fights involving the fore legs in seed bugs. Males of *Neacoryphus bicrucis* grapple to defend patches of their host plant (McLain, 1984). Sweet (1964a, b) reported fights in *Neopamera bilobata*, (see also Rodríguez S., 1998), *Pseudopachybrachius basalis*, *Sisamnes contractus*, *Ligyrocoris diffusus*, *Scoloposthetus diffidens*, *S. atlanticus* and *S. thomsoni*. Although Sweet (1964a) interpreted this behavior as seed defense against conspecifics, with occasional occurrences in sexual contexts, he viewed the main function of the modified fore legs of seed bugs as moving seeds.

Here I describe a case in which the fore legs of both sexes are used in aggressive interactions, in *Scolopostethus affinis* Schilling (Rhyparochrominae: Drymini), and I present data on the allometric scaling of the fore femora on body size. These data support the idea that the modified fore legs of seed bugs may function primarily in aggression.

Materials and Methods

I collected *S. affinis* on a patch of strawberries during June and July 1998, on semi-rural Pfuhl, Neu-Ulm, Bayern, Germany. They were on the ground, on strawberries that had fallen to the ground, and on the plants themselves, especially the roots. I kept bugs in individual Petri dishes with a wet napkin and halved sunflower seeds.

I observed interactions under a dissecting microscope. I placed bugs in Petri dishes containing dried bits of strawberries, in the following combinations: two males, two females, and two males with 1–2 females. I measured the width of the pronotum and the right fore femur of 50 males and 36 females with an optical grid attatched to a dissecting microscope.

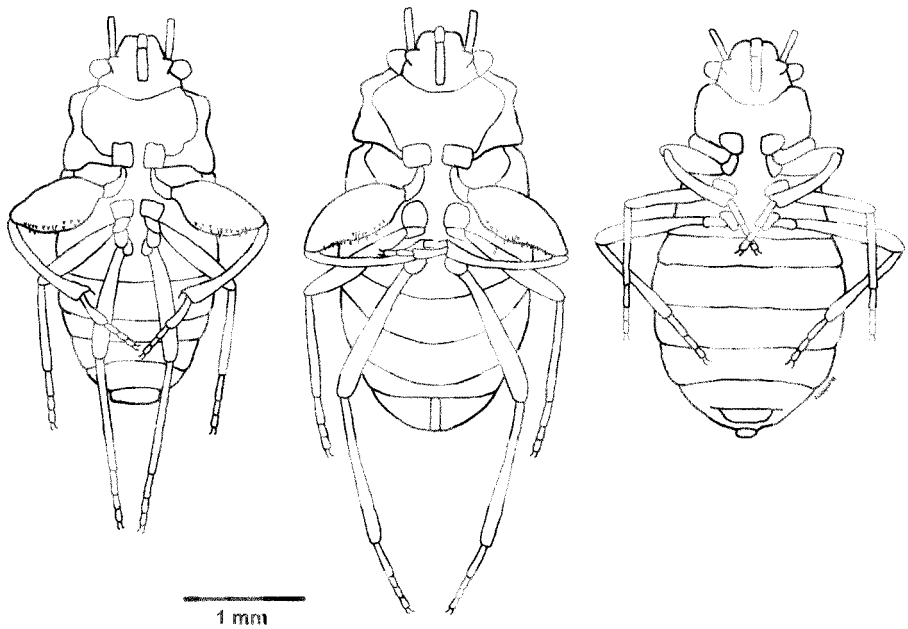

Fig. 1. Sketch of a male (left), female (middle) and last-instar nymph (right) of *S. affinis*, showing their fore femora. Note also the curved fore tibiae, which had bumps along the ventral side (not shown).

Results

BEHAVIOR: Interactions were not very common in the Petri dishes. I observed one aggressive stance and one fight between males out of 17 instances in which I put males and females together. There were two aggressive stances in the five cases in which I put only males together. Most male encounters consisted only of brief antennation followed by separation. There were aggressive stances all three times that I put only females together.

In aggressive interactions the bugs assumed an "aggressive stance" such as described by Sweet (1964a, b), in which they stood on the mid and hind legs, raised the head and thorax, extended the fore legs horizontally, and vibrated the antennae.

The fight between males consisted of three brief encounters and occurred in the presence of a dead female, which may have been incidental. One male assumed the aggressive stance and clamped his fore legs over the other male, which had all legs on the substrate and his side facing the aggressor. The encounter lasted less than 10 s and ended in separation of the males. In the second encounter the same aggressive male trapped the other male's antenna between his fore femur and tibia, and the other male walked backwards and pulled free. Finally, the aggressive male trapped the other male's thorax with both his fore legs, one over and the other under the thorax, and flipped him over. This has not been previously reported: fights usually involve the males simply striking each other with horizontal movements (Sweet, 1964a, b; Rodríguez S., 1998). On subsequent encounters in the following 30 min, the aggressive male assumed the aggressive stance and the other male walked away.

All three aggressive interactions between females involved one single aggressive female and three "submissive" females, observed in sequence. The aggressive fe-

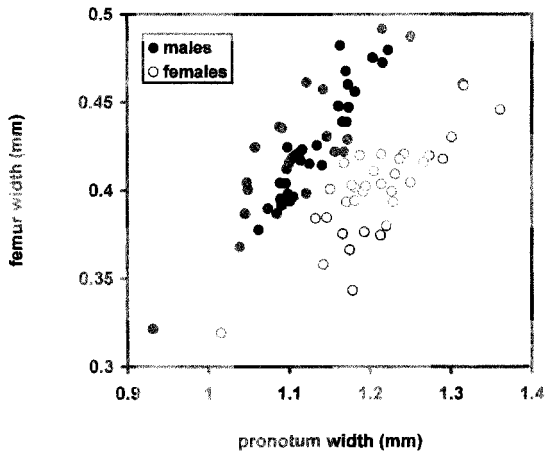

Fig. 2. Males had significantly wider fore femora than females ($t = 3.7$, $P = 0.0004$) although their pronotum width was significantly lower ($t = -6.2$, $P < 0.0001$). But the log-log slopes of fore femur width on pronotum width were not significantly different between males and females (male slope = 1.4, $N = 50$; female slope = 1.1, $N = 35$; $F_{1,81} = 0.04$, $P > 0.75$).

male assumed the aggressive stance, tapped the submissive female with her antennae and approached, at which point the submissive female retreated. In one encounter the aggressive female stood on her mid and hind legs and dropped on top of the other female. Finally she approached the other female again, briefly trapped one of her antennae between her fore femur and tibia, climbed on top of her and there assumed the aggressive stance!

I did not observe *S. affinis* move seeds with their fore legs. Instead, they carried them on the rostrum, which was directed anteriorly at about 45° with the horizontal. This was the case even when I made two males walk on an irregular surface while carrying seeds, and then lightly prodded them with a forceps. The irregular surface consisted of sand and small branches placed on the Petri dish, to imitate the obstacles of Sweet (1964a) that should favor the use of the fore legs in moving seeds. However, I observed two males that appeared to be trying to move a dead female around by climbing on her body, and in this case all the males' legs were brought into action.

MORPHOLOGY: Adult males had a significantly wider fore femur than females, although they were significantly smaller (Figs. 1, 2). However, the slopes of fore femora on body size did not differ between males and females (Fig. 2). The fore tibia was curved (Fig. 2) and had small bumps along its ventral side, which seems well suited for aggressive interactions, especially trapping the body of the opponent between fore femur and tibia. Nymphs of *S. affinis* did not have the enlarged fore femora of the adults (Fig. 1).

Discussion

My observations suggest that the fore legs of *S. affinis* function in aggression. If they served mainly to move seeds or to aid in movement in confined spaces, one would expect nymphs to also have enlarged fore femora, which was not the case in

S. affinis. However, other seed bugs do have nymphs with enlarged fore femora (J. A. Slater, pers. comm.), although this may sometimes be incidental to development for the adult stage.

Behavioral observations to evaluate the prevalence of aggression are neccesary to determine whether it explains the modified fore legs of seed bugs or not. Estimates of sexual dimorphism alone may be misleading because, as in the present case, different methods may yield different answers and both sexes may engage in aggression. However, it may be common that the sexes engage in aggression to different degrees or with different structures. For example, males of *Acanthocephala declivis* and *Leptoglossus australis* (Heteroptera: Coreidae) have modified hind femora that are larger and scale differently on body size than in females, and use them for delivering squeezes in male-male contests (Miyatake, 1993, 1997; Eberhard, 1998), whereas female *A. declivis* have hind tibiae with a modified plate that is wider and scales differently on body size than in males, and use them in aggressive displays between females (Eberhard, 1998).

Another prediction of the aggression hypothesis is that it should be more common in species of seed bug with modified fore legs. For example, the coreid bug *Leptoglossus phyllopus* is monomorphic in hind leg structure, and the males did not engage in aggression (Mitchell, 1980). However, males of the seed bug *Neacoryphus bicrucis* do not have modified fore femora, but did engage in aggression with other males (McLain, 1984).

Aggression may occur in several contexts, such as intra-specific competition for food, mates or other resources, or competition when several species co-occur on a temporarily plentiful resource (J. A. Slater, pers. comm.). For example, males of *N. bicrucis* aggressively defend patches where the buds of their host plant are in high density against other males (McLain, 1984), but also against several hemipteran and coleopteran species (McLain, 1981). My observations are not sufficient to identify the main context of aggression in *S. affinis*. However, the frequency of contests within and between species, and in the presence of seeds, mates and other resources, may serve as an indicator of the strength of selection that the different contexts and resources impose on the bugs.

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