Sound Production by Nearctic Wolf Spiders: A Substratum-Coupled Stridulatory Mechanism

Abstract. *High-speed films of sound-producing male* Lycosa *and* Schizocosa *spp. show that their palps are not "drummed," as previously assumed, but rapidly oscillate at the tibio-tarsal joint. A new type of spider stridulatory organ is located on hidden surfaces of this joint. Coupling to the substratum via tarsal spines increases the communicatory effectiveness of this apparatus.*

For nearly a century there have been reports of "drumming spiders" that occur in the Nearctic region (*1*). These usually refer to the male *Lycosa gulosa*, which can be heard by humans up to 6 m away when it performs on dry leaf litter (*2*). Various workers have enlarged the list of lycosid sound producers (*3*); and others have recorded and analyzed some of the signals (*2, 4, 5*). By playback techniques I demonstrated the sounds' communicatory function during courtship and agonistic displays in male *L. rabida* (*4*). All the investigators have regarded such sounds as being solely percussive—a tapping or scraping of the palps against the substratum to produce a "buzz" or "purr." High-speed film analysis now has revealed the location of a stridulatory organ within each palp that is involved in generating acoustic signals.

I filmed displaying male *L. rabida*, *Schizocosa crassipes*, and *S. saltatrix* at 200 frames per second (*6*). Subsequent viewing of the slowed palpal movements showed that these appendages are not used percussively in the *Schizocosa* spp. The only palpal movement is an anterior-posterior oscillation with maximum displacement at the tibio-tarsal joint that results from alternating, low-amplitude flexions and extensions. In *L. rabida* a similar movement again is the predominant feature during sound production, but several palpal taps or scrapes may also be included (Fig. 1A).

Examination of the tibio-tarsal joint revealed a well-hidden stridulatory organ in the medio-dorsal region (*7*). This apparatus can be seen by flexing the joint and peering into the space between the opposing segmental surfaces (Fig. 1, B and C), although best viewing requires removal of the tarsus. A file (pars stridens) is present within a sclerotized, arch-shaped cuticular projection of the distal tibia (Fig. 1, D and E). Protruding from the base of the tarsus into the bowl of the file is a scraper (plectrum), consisting of a sclerotized lip of cuticle with a single crest (Fig. 1F). I surveyed the known sound-producing members of *Lycosa* (six species) and *Schizocosa* (three species) and found this organ at the same location in all of the males (*8*). Penultimate (immature) males and adult females lacked any such device (*9*). Expanding Legendre's classification for spider stridulatory organs (*10*), I propose calling this "type h," in which the file and scraper are on opposing segmental surfaces of a joint within a single appendage.

To gain a preliminary determination of the effect of restraining the stridulatory mechanism during display behavior, I anesthetized (CO_2) five male lycosids and placed paraffin casts around the tibio-tarsal joints of both palps of each spider (*11*). Sound production had been recorded prior to treatment in these individuals (*12*). Monitoring the amplified sounds during the subsequent observations of these treated males, I heard "rattle" sounds roughly resembling those of normal males in *L. rabida*. High-speed film analysis revealed that a series of scraping and tapping movements had replaced the normal tibio-tarsal oscillations of the palps (*13*). In *S. crassipes* occasional "taps" resulting from striking of the substratum by the body or legs were present as in normal males; however, the characteristic "purr" component was lacking. In *S. saltatrix* the prolonged "buzz" that is the main feature of courtship was absent. (Abdominal vibrations and stereotyped foreleg movements indicated that display was occurring.) Physical analysis of sounds produced by normal as compared to treated male lycosids will indicate in some cases the relative contribution of the stridulatory mechanism to the total acoustical output. In cases like that of *L. rabida* another method of shutting off the stridulatory organ (ablation?) must be developed.

During sound production by normal males the palpal tarsus did not contact the substratum directly but via a group of stout spines (macrosetae) present in all nine species surveyed. These spines projected above the chemosensitive hairs (Fig. 1, G and H). (Penultimate males and

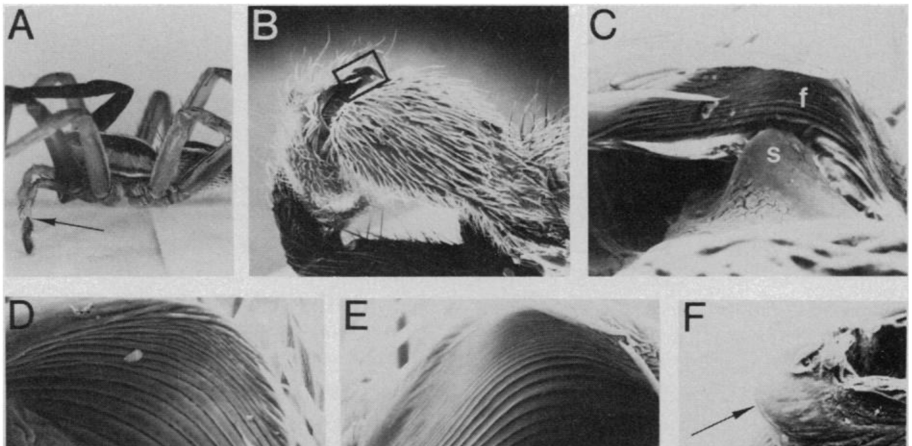

Fig. 1. (A) Lateral view of male *Lycosa rabida* during production of the courtship sound (× 2). The arrow indicates the tibio-tarsal joint of the palp. (B to I) Scanning electron micrographs. The right palp of the male is shown in all views but (E). (B) Palp of male *Schizocosa saltatrix* (× 22). The stridulatory organ is located within the enclosed area. (C) Enclosed area of (B) at higher magnification (× 190). The file is labeled *f*; the scraper, *s*. (D) File of *S. saltatrix* (× 220). Such views are obtained after removal of the tarsus. (E) File (left palp) of *L. gulosa* (× 220). (F) Scraper (arrow) on medio-dorsal surface of the base of a tarsus removed from *L. carolinensis* (× 95). (G) Spines (arrow) on dorsal surface of tarsal tip in *L. rabida* (× 95). (H) Spines (arrow) on ventral surface of tarsal tip in *L. gulosa* (× 95). (I) Spines (arrow) on tarsal tip in *S. saltatrix*, apical view (× 48).

adult females lacked such spines, possessing instead a single claw.) The shape, relative size, and number of spines varied among the species (*14*); however, their distribution usually was along the anterior-posterior axis within a roughly elliptical boundary when the tarsus was viewed apically (Fig. 1I). These spines probably serve as holdfasts by catching onto irregularities in the substratum and thus prevent or reduce slipping of the palp during oscillations of the tibio-tarsal joint. Their anterior-posterior distribution supports this idea. During attempted sound production on glass surfaces the male's palps repeatedly slide posteriorly. Temporary attachment of the palp may be essential for obtaining maximum pressure by the tarsal scraper against the tibial file.

By coupling the tarsus to the substratum, the spider increases the communicatory effectiveness of the stridulatory apparatus since solid-borne vibrations are conducted directly into the substratum (*15*). Playback experiments suggest that female wolf spiders orient better to substratum vibrations than to airborne sounds (*4*). Coupling may incorporate the substratum into the system as a sounding-board, thereby increasing the loudness of the airborne component. The airborne sound probably plays a role (for example, reduces the prey-capture tendency of the female) prior to the time that both spiders are located on the same substratum during the final phase of precopulatory display. Both the loudness and the regularity of the fine structure of the sounds produced by male lycosids such as *L. gulosa* (*2*) can be understood on the basis of this substratum-coupled stridulatory device. Clearly, "percussion" no longer denotes correctly the primary mechanism used by most sound-producing male wolf spiders (*16*).

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References and Notes

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2. J. B. Harrison, *Anim. Behav.* **17**, 14 (1969).
3. H. Prell, *Zool. Anz.* **48**, 61 (1916); W. S. Bristowe and G. H. Locket, *Proc. Soc. Zool. London* **1926**, 317 (1926); L. Chopard, *Bull. Soc Zool. France* **59**, 132 (1934); B. J. Kaston, *Entomol. Am.* **16**, 97 (1936); H. Hallander, *Oikos* **18**, 145 (1967).

→ J. S. Rovner, *Anim. Behav.* **15**, 273 (1967).

5. D. J. Buckle, *Blue Jay* **30**, 110 (1972).
6. Cine-8 Super-8-mm high-speed camera, model SP-1 (Visual Instrumentation Corp., Burbank, Calif. 91502).
7. After being examined under a dissecting microscope, some of the material was coated with gold (without prior dehydration) and immediately examined with an Hitachi HSS 2R scanning electron microscope.
8. The stridulatory organ components were largest relative to the size of the palp in *S. crassipes* and *S. saltatrix*. They were relatively smaller but still well developed in *L. aspersa, L. carolinensis, L. gulosa, L. punctulata, L. rabida*, and *S. avida*. The small, narrow file in *L. Helluo* was rather difficult to detect. Sounds have been recorded from males of all these species [(*2, 4, 5*); also J. S. Rovner, unpublished data].
9. Although lacking morphological adaptations for sound production, adult female *Lycosa* spp. produce faint sounds by scraping the tarsal claw against the substratum during agonistic displays (J. S. Rovner, unpublished data).
10. R. Legendre, *Ann. Biol.* **2**, 371 (1963). The stridulatory devices described previously in spiders involved three basic forms: the abdomen rubbing against the prosoma or pedicel (types a and b), one appendage rubbing against another (types c to f), or one appendage rubbing against the abdomen (type g). The only stridulatory organ heretofore reported in a lycosid was of type g and occurred in *Pardosa fulvipes* (Palearctic) [T. Kronestedt, *Zool. Scripta* **2**, 43 (1973)].
11. Two *L. rabida*, two *S. crassipes*, and one *S. saltatrix*. Placing both palps in a human hair sling with its ends attached to the middle of the carapace prevented the spiders from "chewing" off the paraffin casts prior to testing, at which time the palps were freed from the sling. This precaution was necessary only for *L. rabida*; the others courted soon after the casts were applied.
12. Solid-borne sounds were detected with a high-sensitivity vibration pickup system (type 1560-P14, General Radio, West Concord, Mass. 01781) connected to a sound-level meter (type 1551-C, General Radio), whose output was fed into a tape recorder. The same paper substratum was used during all recordings.
13. When all palpal movement is prevented (by attaching the palps to the prosoma with paraffin), a very faint "whirring" sound still occurs during display in *L. rabida*. It apparently arises from the simultaneous vibrations of the forelegs and abdomen. The intensity of this sound was reduced but not eliminated after attachment of the abdomen to the prosoma by a paraffin bridge.
14. The presence of such spines in illustrations of male palps in taxonomic reports treating various species of *Lycosa* and *Schizocosa* (including other than Nearctic forms) suggests that the sound-producing mechanism described here may be found in most (or all) species in these genera.
15. This would be most effective if it is the file that is setting the tarsal scraper into vibration, as could be the case [B. Dumortier in *Acoustic Behaviour of Animals*, R. G. Busnel, Ed. (Elsevier, Amsterdam, 1963), p. 279)].
16. A few male lycosids do rely on percussion. According to O. von Helversen (personal communication) the male *Hygrolycosa rubrofasciata* (Palearctic) taps dry leaves with its abdomen, whose ventral surface has a sclerotized plate for this purpose. Male *Alopecosa pulverulenta* (Palearctic) [Bristowe and Locket (*3*)] and *A. aculeata* (Nearctic) (*5*) also are reported to use abdominal and palpal percussion as a mode of sound production.
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Lymphocytes of the Toad *Xenopus laevis* Have the Gene Set for Promoting Tadpole Development

Abstract. *Nuclear transplantation experiments show that differentiated cells, such as lymphocytes, from the adult frog can express the genes necessary for tadpole development. The transplanted cells were proven to be lymphocytes by immunological methods. The origin of the tadpoles that developed after lymphocyte nuclei injections was ascertained by a karyotypic marker.*

A better knowledge of the genetic content of a "pre-committed" lymphocyte is needed for understanding the mechanism of antibody formation. Moreover, the lymphocyte can be used for investigating whether such differentiated cells have the full gene set needed for promoting development of normal individuals in nuclear transplant experiments.

Nuclei of embryonic amphibian cells can give rise to normal frogs when injected into enucleated amphibian eggs (*1*). Several reports suggest that development could occur after nuclear transplantation of differentiated normal cell nuclei (*2*). Convincing evidence has been provided by the experiments of Gurdon *et al.* (*3*) where both the differentiation state of the cells that were injected into enucleated eggs and the genetic origin of the developing embryos were established. Here, we report on the development after transplantation of adult *Xenopus laevis* lymphocyte nuclei.

Table 1. Genetic origin of the clones of serial transfers, as followed by the nucleolar marker. One to four individuals per clone were checked. Chromosome numbers were derived from 6 to 20 metaphases per individual; nucleolus numbers were ascertained from squash preparations under the phase contrast microscope.

Number of clones	Number of chromosomes	Number of nucleoli	Origin of the clones
6	36	1	Lymphocyte
2	~ 72	3	Unclear
1	32	2	Unclear

Individuals of *Xenopus laevis* one nucleolar (1-nu) mutant (*4*) were immunized by one injection of 2,4-dinitrophenyl (DNP)-hemocyanin from the keyhole limpet. The spleens of the *Xenopus* were removed 7 to 15 days later and teased in Wolf and Quimby culture medium; the resultant cell suspensions were washed twice in the same medium. The spleen cells obtained in this way were then placed on nylon grids to which DNP had been coupled according to the Kiefer modification (*5*) of a method of Edelman *et al.* (*6*). To show that the cells coupled to the grid were differentiated immunoglobulin-bearing cells, we assayed the inhibition of binding after treatment with antiserum to immunoglobulin. The lymphocyte population was treated with antiserum to immunoglobulin of defined specificity (*7*); the lymphocytes were then exposed to the grid. Under these conditions, only 49 cells bound to the grid, although we counted 2390 binding cells in the control preparation (pooled data of