

Table 2. Type specific antigens of X-tropic viruses recovered from NIH Swiss and NZB mice. Neutralization tests were performed by exposing each virus to antiserum for 30 minutes at room temperature. The mixture was then diluted to give 30 to 90 MSV FFU or MLV XC plaque-forming units per plate and assayed on diethylaminoethyl-dextran treated NRK or NIH mouse embryo cells (5, 9). The number of foci or XC plaques were determined as described (1, 2, 6). Antiserums prepared in rats to the standard MLV were used at a final dilution of 1:40 (18). Rabbit antiserums to NZB MLV and NZB pseudotype virus were used at 1:10 and 1:40 dilutions, respectively.

| Antiserum against | Reduction (percent) in focus or plaque formation by these viruses: | | | | |
|----------------------|--|---------|-----------|----------------|----------------|
| | Harvey MSV | AKR MLV | Gross MLV | NZB pseudotype | NIH pseudotype |
| Moloney MSV | 100 | 18 | 10 | 28 | 27 |
| AKR MLV | 10 | 96 | 33 | 28 | 28 |
| Gross MLV | 0 | 97 | 100 | 10 | 15 |
| NZB MLV | 9 | 0 | 0 | 85 | 80 |
| NZB pseudotype virus | 8 | 10 | 0 | 90 | 90 |

exist. It militates against assuming that C-type particles observed in mice are the standard mouse-tropic types since either or both may be present. It encourages further virus assays with rat and human cells when mouse tissues containing gs antigen do not yield a mouse-tropic virus, and in those cases where both type viruses may be present.

The fact that this murine virus grows well in human cells offers a relatively easy method for its detection and isolation in preparations of other MLV and MSV, since passage through these cells would select for the X-tropic virus. Such a selection procedure probably accounts for the MSV described by Aaronson, which grows in rat and human cells (15), as well as the Rauscher MLV, which was "adapted" to propagate in human cells (16).

We have found the X-tropic virus in tissues from newborn NIH Swiss mice, but have not detected it in the embryos of NIH Swiss or other mice. However, its presence in every cell derived from NZB embryos may reflect a specific defect in NZB mice that has a relation to their development of autoimmune disease. In this regard, tissues from the immunosuppressed NIH Swiss mouse after cocultivation gave the highest titers of X-tropic pseudotype sarcoma virus (Table 1).

This unusual tropism of a mammalian C-type virus that we reported 3 years ago (1) is not now unique to mice. Certain feline C-type viruses propagate efficiently only in cells from animal species other than the host (17). It is likely that in many, if not all, animals, X-tropic viruses will be identified; and they must be true endogenous viruses of the host since horizontal infection is not likely. Similarly, in many different human tissues, C-type particles have been observed

which have not been propagated. These may be X-tropic human viruses that await identification after successful growth in correctly selected cells from animal species other than the host.

JAY A. LEVY

Cancer Research Institute,
University of California,
San Francisco 94143

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19. I thank Dr. E. R. Dirksen for the electron microscopy; Dr. Janet Hartley for providing the FMR, AKR, and Gross antiserums; Paul Hill (in Dr. Robert Huebner's laboratory) under whose supervision the complement-fixation testing for gs antigen was performed, and Patricia Kazan for technical assistance. Supported by a grant from the National Cancer Institute CA13086.

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Maternal Behavior in Wolf Spiders: The Role of Abdominal Hairs

Abstract. Newly emerged, juvenile wolf spiders do not settle on clothed or shaved areas of their mother's abdomen until after a period of days. Spiny, knobbed hairs, peculiar to adult female lycosids, apparently provide the stimulus and means for attachment by the inner layer of spiderlings. Innervated long, smooth hairs are mechanoreceptors which probably serve in other aspects of brood care.

After emerging from the egg sac, juvenile wolf spiders (Araneae: Lycosidae) immediately mass on the mother's abdomen (and posterior carapace, if a large brood) and are carried by her for a number of days. If brushed off, the spiderlings climb up the female's legs and settle again (1). Since coating the female's abdomen with certain chemicals did not repel the young whereas clothing it with various materials resulted in the young's settling on only nonclothed regions, Engelhardt (2) concluded that the spiderlings' aggregation resulted partly from tactile stimulation provided by the female's abdominal hairs. Graefe (3) has described

knob-tipped abdominal hairs as being peculiar to adult female lycosids and serving to reduce the abrasion of the egg sac, which he claimed would result from pointed hairs. Using experimental and morphological approaches, we have found that the knobbed hairs probably trigger the young's attachment behavior and are likely important in providing a grasping surface for the inner layer of spiderlings (4).

In one series of tests we used peripherally placed dabs of paraffin to attach a rectangle of chiffon cloth to the female's dorsal abdomen. Unlike Engelhardt's (2) nearly complete covering, our treatment left the lateral and ven-

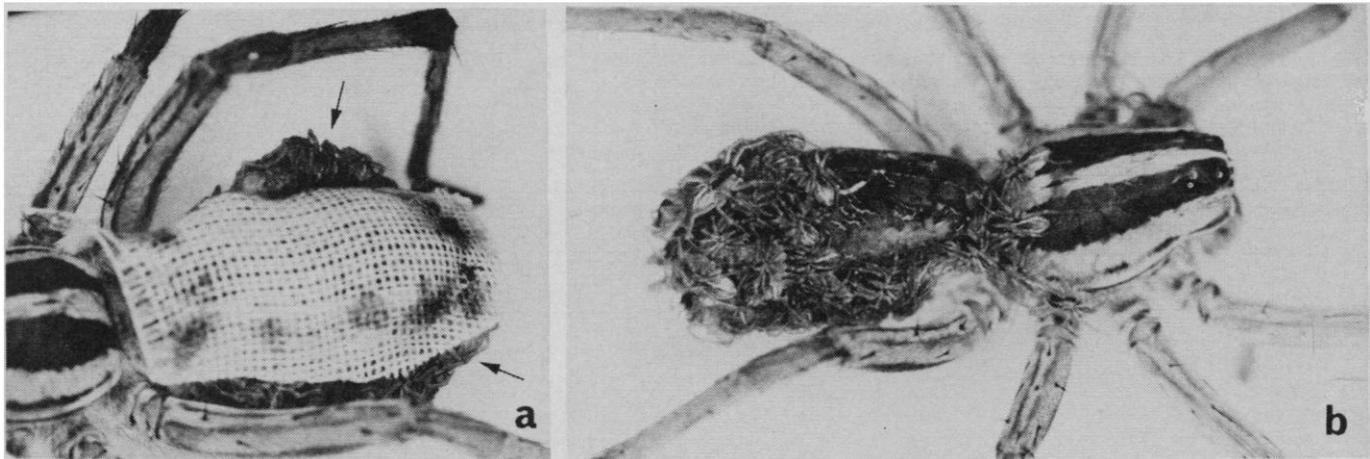


Fig. 1. Experimentally modified female *Lycosa rabida* with broods. (a) Dorsal abdomen covered with cloth; young are visible at the edges (arrows). (b) Anterior-dorsal abdomen shaved; young are found only on the hairy regions, including the carapace.

tral surfaces exposed. Five females were treated prior to the young's emergence, and five were treated 1 day after the young's emergence. The brushed-off spiderlings from the females treated 1 day after the emergence of young were allowed to remount after the female had recovered from CO₂ anesthesia. Spiderlings did not begin to settle on the altered surface until after a mean of 5.8 days (5). During these initial days, spiderlings settled only on the untreated surface of the abdomen and crowded tightly up to the edges of the cloth (Fig. 1a). Some settling on the posterior carapace also occurred.

Since there was a possibility that covering the abdominal hairs with an artificial substratum might have introduced disturbing factors (physical or chemi-

cal) for the settlement of the spiderlings, we performed a second series of tests, this time removing the hairs rather than covering them. The anterior-dorsal abdominal surfaces of ten female spiders were shaved with surgical blades; five were treated prior to the emergence of the young and five were treated 1 day after the young's emergence. Newly emerged young did not begin to settle on the shaved area until after 4.0 ± 2.0 days (mean \pm standard deviation). During these initial days they covered the remaining abdominal surface and sometimes the posterior carapace (Fig. 1b). On the other hand, four of the five broods that had had 1 day of experience on the mother settled on the shaved area during the day on which they remounted her (6).

All 20 broods eventually showed settlement on clothed or shaved areas; settlement may have been related to the increased amount of silk deposited by young crossing these areas during periods of wandering and drinking (7). The dragline threads eventually form a layer over the surface and probably provide a good means of attachment for the spiderlings (Fig. 2c).

In both types of experiments a small cluster of young, sometimes more than one layer deep, was occasionally found in the center of an otherwise clear, treated area of the abdomen. That the young packed tightly together rather than spread evenly over the available surface supports Engelhardt's (2) suggestion that during this period juvenile lycosids possess an aggregation tend-

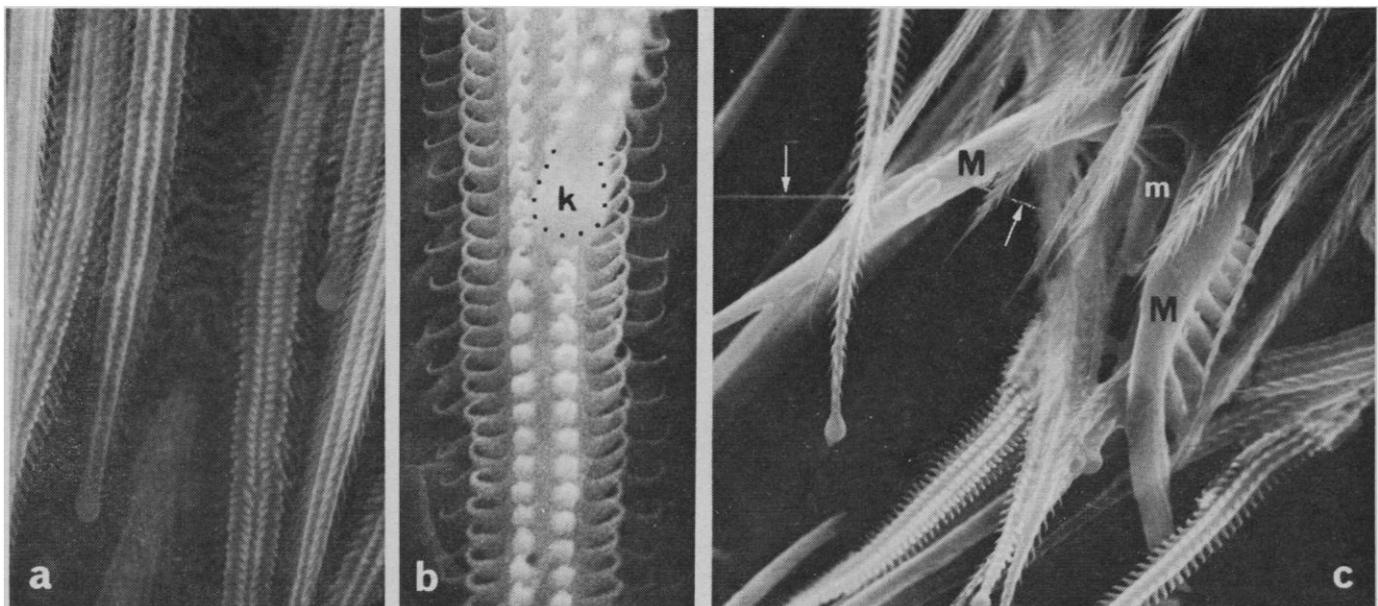


Fig. 2. Scanning electron micrographs of dorsal abdominal hairs of female lycosid spiders (the bottom of the photograph is toward the posterior of the animal). (a) Knobbed hairs, *Lycosa punctulata* ($\times 1000$); (b) detail of knobbed hair with superimposed knobbed tip (*k*) of another hair, *L. punctulata* ($\times 3000$); (c) tarsal main claws (*M*) of spiderling grasping knobbed hairs on the carapace of the mother, *Schizocosa avida*. The short middle claw (*m*) hooks onto a silk thread (arrows) ($\times 1000$).

ency, independent of the response to the mother's surface, which contributes to the normal massing of young on the female (8).

Examination of the body surface of an adult female *Lycosa punctulata* with a scanning electron microscope (9) revealed the presence of at least two different types of hairs on the abdomen and posterior carapace. Relatively few long, smooth hairs project rather steeply above a dense layer of shorter hairs with knobbed tips (Fig. 2a), the latter corresponding to Graefe's "knobbed hairs" (3). Prominent longitudinal rows of curved spines run the length of the knobbed hairs (Fig. 2b). Examination of an adult male *L. punctulata* revealed no knobbed hairs, although some spiny but sharp-tipped hairs occur. Males possess primarily short, smooth hairs, which are rare on the abdomen of adult females.

Histological preparations of the female abdomen (10) indicated that the knobbed hairs were not innervated, nor did their structure suggest any secretory function. The few long, smooth hairs are triply innervated and exhibit the same ultrastructure as other spider mechanoreceptors (11). They probably play a role in maternal care, since the climbing of young onto the female's abdomen provides a mechanical stimulus which triggers the dropping of the egg sac and inhibits prey capture behavior in the mother during the period of brood care (2).

Since the knobbed hairs are found on female lycosids only after the final molt and are absent in females of the closely related family Pisauridae (3), it is likely that they are associated with the brood care behavior peculiar to the Lycosidae. Our experiments indicated that newly emerged spiderlings would not settle on a denuded abdominal surface for a period of days. As the most abundant of the two protruding structures on the surfaces chosen for settlement, the knobbed hairs probably trigger the attachment response of the young which form the inner layer of the brood. Indeed, the structure of the knobbed hair suggests an important role in attachment itself, the interstices between the spines providing good grasping sites for the tarsal claws of the spiderlings. Scanning electron microscope examination of young lycosids mounted on their mother (12) indicated such a relationship (Fig. 2c). Since the welfare of the outer layers of the brood ultimately depends on the ability of the innermost layer of spiderlings to hold

tightly to the mother, the need for a grasping surface is obvious. Conceivably, knobbed hairs also facilitate the subsequent attachment of silk draglines by the spiderlings.

JEROME S. ROVNER
GAILE A. HIGASHI

Department of Zoology,
Ohio University, Athens 45701

RAINER F. FOELIX
Research Division, North Carolina
Department of Mental Health,
Raleigh 27602

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4. We used the large wolf spider *Lycosa rabida* for the experimental portion of our study. Spiders were collected as immature individuals and, when adult, mated in the laboratory. Emergence of young occurred about 1 month after egg sac construction.
5. When tested by the Mann-Whitney U test, the difference in data between young with and without 1 day of prior experience on the female was not significant ($P = .075$). However, the group of young without 1 day of prior experience on the female did not settle on the cloth until after 9.4 ± 7.7 days, whereas the group of young with 1 day of prior experience on the female showed initial settlement after 2.2 ± 1.5 days.
6. It may be that remounting spiderlings lay draglines as they wander over the abdomen, which would then serve for attachment in the shaved area. Newly emerged young, having settled in hairy regions, may not have wandered extensively over the shaved areas during the first few days, since they had never been forced to vacate their original sites.
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8. We also noted alternating periods of settlement and absence of young on the cloth substratum; that is, either a mass of young were present on the cloth or no young at all were present. This finding constitutes further indication that the aggregation tendency plays a role in determining site selection.
9. The carapace and abdomen were exposed to glutaraldehyde and osmium vapors for several days. They were then coated with gold (without prior dehydration) and immediately examined with a JEOL JSM 2 or a JSM 50-A scanning electron microscope.
10. Small pieces of the dorsal abdomen of female *Lycosa punctulata* were fixed in cold, cacodylate-buffered glutaraldehyde, then fixed in OsO_4 and embedded in Epon. Thick sections stained with methylene blue were used for light microscopy; thin sections were contrasted with uranyl acetate and lead citrate for electron microscopy.
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12. Female lycosids with young were immersed in liquid nitrogen or kept in a freezer (-20°C) for several days. They were then processed as described in (9).
13. We thank I-W. Chu-Wang for collaboration on the scanning electron microscope, C. H. Page for valuable discussions, and R. Braun for assistance in obtaining G. Graefe's unpublished dissertation. Supported in part by NSF grant GB-35369 to J.S.R.

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Trigeminal Deafferentation and Feeding in the Pigeon: Sensorimotor and Motivational Effects

Abstract. *The role of oral sensations in the control of hunger and thirst in the pigeon was studied in birds in which the trigeminal sensory nerves had been sectioned bilaterally. Trigeminal deafferentation, although it does not impair drinking, disrupts both the neurosensory and the motivational control of feeding behavior. These two types of deficit may be experimentally dissociated.*

It has been suggested that, in mammals, oropharyngeal sensations are not essential either for the arousal of hunger and thirst or for the regulation of body weight (1). This generalization is derived primarily from experiments with a combination of intragastric feeding techniques and operant conditioning procedures (2) rather than from studies of feeding behavior in surgically deafferented animals. The location and peripheral distribution of the pigeon trigeminal nerves permits deafferentation of the oral region without affecting motor function. I found that trigeminal deafferentation in the pigeon not only disrupts the consummatory response of eating but also affects motivational processes underlying the arousal of hunger and the regulation of body weight, and has these effects without impairing drinking.

Anatomical and electrophysiological

studies indicate that the trigeminal nerve in the pigeon innervates the orbit, beak, and buccal cavity, exclusive of the tongue (3, 4). Section of one or more trigeminal sensory branches was done under a dissecting microscope. In ophthalmic and mandibular denervations, sections approximately 10 to 15 mm long were removed, whereas maxillary sections were somewhat less extensive. Control surgical procedures were identical in all respects except for actual nerve section.

In the first experiment, deafferentation effects on the consummatory response of eating were studied in a group of eight food-deprived birds maintained at 80 percent of their free-feeding weight to ensure a constant level of responsiveness to food during testing. Birds were tested three times weekly in an observation chamber con-