while a greater proportion of higher frequencies (8- to 22-Hz) predicts slower rates of learning. To our knowledge, this is the first demonstration that a neurophysiological measure taken before training can predict the subsequent behavioral rate of learning. The result is consistent with consolidation studies showing a positive relationship between amount of theta in the posttraining EEG and subsequent retention performance (*10, 15*), and with studies reporting changes in hippocampal frequency during training that are correlated with the degree of learning (*7*). This result also seems relevant in the context of mathematical learning theories (*19*), in that a physiological measure can increase precision in estimating acquisition rate parameters. Our data support the hypothesis that the hippocampus has a critically important role in learning and raise the possibility of manipulating learning with independent variables influencing hippocampal RSA. Although some studies have indicated that massive lesions of either the hippocampus or the septum do not impair NM conditioning (*20*), more selective disruption of hippocampal activity by stimulation or making lesions of discrete afferent pathways significantly retards the rate of learning (*21*). Finally, the data presented here support the general notions that "behavioral state" plays an important role in learning (*22*) and that hippocampal EEG is a potentially powerful index of behavioral state (*3, 22*).

STEPHEN D. BERRY
RICHARD F. THOMPSON
Department of Psychobiology,
University of California, Irvine 92717

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Mating Behavior and Related Morphological Specialization in the Uropodine Mite, *Caminella peraphora*

Abstract. *Sperm transfer in* Caminella peraphora *is closely associated with secretion and construction of a female-associated structure, the signet ring. The ventral portion of the ring serves as an external spermatheca early in mating. Although sperm assimilation occurs prior to development of the dorsal ring elements, male participation is instrumental in successful ring completion.*

Caminella peraphora Krantz and Ainscough (*1*) is a nematophagous uropodine mite that has been recovered only in moist to semiaquatic habitats on two neighboring mountains in the Coastal Range of western Oregon. Unlike other known acarines, females of *C. peraphora* carry a large, noncellular, saclike structure dorsally, fused to a ring of similar material which girdles the body behind coxae IV (Fig. 1, D to F). It was suggested (*1*) that this "signet ring" might be a flotation mechanism which aided in dispersal of eggs or larvae, and that formation of the ring probably occurred prior to the last nymphal molt. Later, Ainscough (*2*) speculated that the ring was an external spermatheca, and observed that it developed after ecdysis.

As with most uropodines, the life cycle of *C. peraphora* includes egg, larval, protonymphal, deutonymphal, and adult stages. Oviposition is sporadic under laboratory conditions (*3*), but viable eggs are produced throughout the life of the female. An average of 68 days was required for newly oviposited eggs ($N = 3$) to reach the deutonymphal instar. Laboratory-cultured deutonymphs failed to attain adulthood, although specimens survived for up to 37 days in this stage. Field-collected deutonymphs occasionally would molt successfully and mate, but often only after several weeks in captivity. The average developmental time observed for each life stage was: egg to larva, 22 days (21 to 23, $N = 5$); larva to protonymph, 24 days (22 to 32, $N = 5$); protonymph to deutonymph, 21 days (19 to 25, $N = 3$).

Female deutonymphs of *C. peraphora* are attractive to males shortly before female ecdysis. A single male "courts" each deutonymph, remaining by her side until she molts. In those instances where other males attempt to intervene, a brief, nonaggressive contact between the defending male and encroaching individuals is sufficient to disperse would-be suitors. Mating proceeds soon after female emergence, with the male approaching the female from the posterior and mounting her dorsum. Mounting occurs swiftly, with no further courtship being observed. The female begins a lateral rocking which may persist for 30 minutes or more. After this time, the male reverses his position on the female dorsum so that he is facing posteriorly (Fig. 1A). The male then initiates a later-

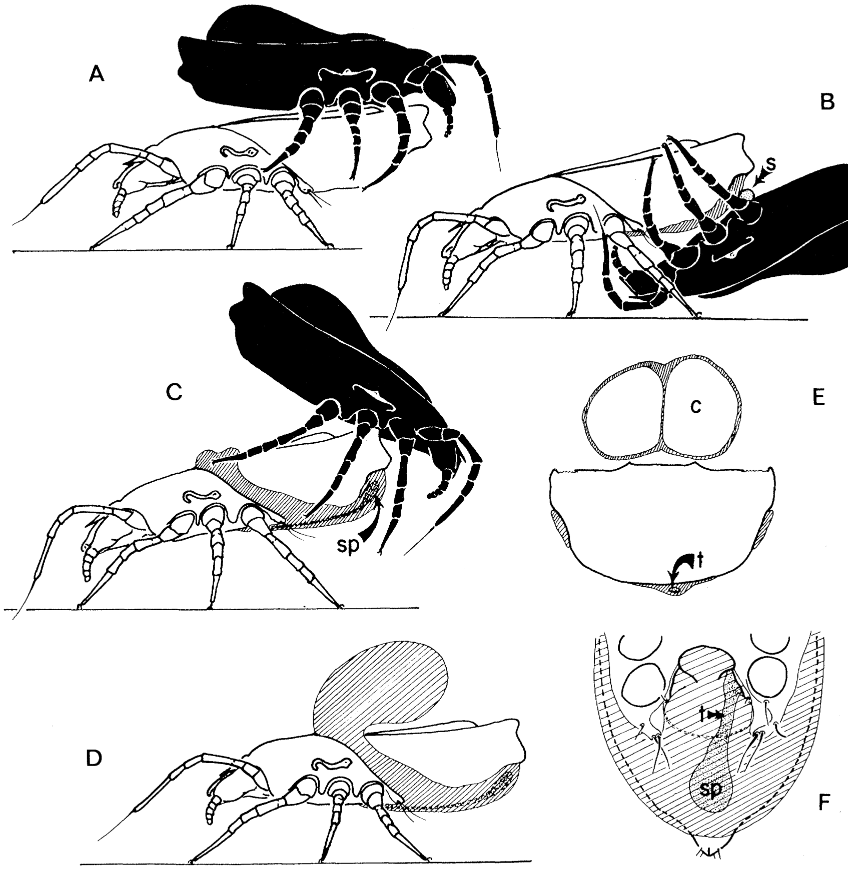

Fig. 1. (A to C) Sperm transfer and signet ring construction in *C. peraphora*. (A) The male (black) faces posteriorly on dorsum of female (white) and initiates a lateral rocking motion. (B) The male moves ventrally and deposits a globular sperm packet (*s*) into the ring material mass (diagonally lined) secreted by the female. (C) The male moves to dorsum of female and manipulates ring material with pretarsi IV. Spermatheca (*sp*) and anterior tubular extension are stippled for clarity. (D) Lateral aspect of female *C. peraphora* showing completed signet ring. (E) Cross-section of female *C. peraphora* just behind coxae IV, showing tubular extension of spermatheca (*t*) and dorsal signet ring chambers (*c*). (F) Ventral aspect of signet ring showing external spermatheca (*sp*) and tubular extension (*t*).

al rocking motion which may continue for up to 9 hours. During this period the female begins the secretion of the material from under the epigynial shield which eventually will be formed into a signet ring structure.

After the female has covered the posterior third of her ventrianal shield with an amorphous mass of ring material, the male moves posteriorly and ventrally, establishing contact between his genital valves and the ring material mass. The male then secretes a sperm packet (Fig. 1B, *s*) which is pressed into and enveloped by the ring material in the preanal concavity of the female, thus forming a ventral external spermatheca (Fig. 1, C and F, *sp*). Sperm were observed in the spermatheca only during the period prior to further ring development. An anterior tubular extension for sperm transport joins the spermatheca to the anterolateral margin of the epigynial shield (Fig. 1F, *t*). The chelicerae of the male may play a role in spermathecal construction, but observations at this stage were inconclusive. Using pretarsi IV, the male manipulates the developing lateral bands which are generated from the ring material mass adjacent to the spermatheca and which finally encircle the female. The male begins this task while still in a posteroventral position, but he soon moves to the female dorsum where he continues to manipulate the developing bands with the pretarsi of legs IV (Fig. 1C). The lateral bands elongate as fluid ring material is extruded apically, then meet and fuse at the dorsal midline of the idiosoma. After fusion, the dorsal portions of the band expand and harden to form paired chambers (Fig. 1E, *c*) which extend posteriorly over the idiosoma (Fig. 1D). If the male is disturbed prior to chamber completion, he abandons the female who subsequently develops nonfused, abnormal chambers. The time required for successful mating and chamber formation may range from 24 to 48 hours. Females are fertilized for life, and produce only one signet ring.

Sperm packet deposition on the anterior margin of the epigynial shield, and subsequent sperm passage into an internal spermatheca beneath the epigynial shield, have been reported to occur in various uropodine species (*4*). However, the sperm packet of *C. peraphora* is placed near the anal opening, so that the sperm must be transported to the epigynial shield margin by means of the tubular extension mentioned earlier.

The mechanics of tube formation and sperm transport are unclear, but reasons for this complex adaptation may be found in certain habitat considerations. The semiaquatic milieu in which *C. peraphora* commonly occurs places certain constraints on a sperm transfer method entailing external placement of a fluid sperm mass by the male. The secretion of ring material and subsequent embedding of the sperm packet in the preanal concavity of the female may be a strategy for protecting the packet from water. The formation of a sequestered spermatheca reduces water film problems created by close venter-to-venter contact, and confers a degree of protection from packet dislodgment during sperm transfer.

The signet ring of *C. peraphora*, then, serves as a temporary external spermatheca, but it may also relate to a function which has no direct bearing on reproduction. The expanded dorsal compartments which are formed after uptake of sperm by the internal spermatheca do not appear necessary for successful egg production inasmuch as field-collected females with gaping holes in the dorsal chambers lay viable eggs, as do females which have completely lost the easily removed ring. Remarkably, the male is intimately involved with dorsal chamber construction, even though sperm deposition and transport are completed before the chambers are formed.

G. L. COMPTON, G. W. KRANTZ
Department of Entomology, Oregon State University, Corvallis 97331

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