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OVIPOSITION BIOLOGY OF *ACANTHOCINUS NODOSUS* (COLEOPTERA: CERAMBYCIDAE) IN *PINUS TAEDA*

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ABSTRACT

Oviposition biology of *Acanthocinus nodosus* was examined on southern pine beetle (SPB), *Dendroctonus frontalis*, infested loblolly pine trees in Alabama, U.S.A. Components of oviposition biology, including oviposition pit description, colonization period, average number of eggs laid per oviposition pit, use of bark beetle entrance or ventilation holes as oviposition sites, and pit density were described. *Acanthocinus nodosus* oviposition pits were easily differentiated from *Monochamus titillator*, another cerambycid species that also inhabits SPB-killed trees. Colonization of trees by *A. nodosus* began within 2 days of initial SPB attack and lasted for 8 to 14 days. Females laid an average of 3.33 (SE ± 0.48) eggs per oviposition pit and 99% of the pits occurred on SPB entrance and ventilation holes. All pits were on the lower bole between 18 and 163 cm above the ground. Oviposition pit density ranged from 0.22 to 0.45 pits per cm^2 of bark surface. Potential interactions with other phloem inhabiting species were noted.

Key Words: *Acanthocinus nodosus*, *Monochamus titillator*, *Dendroctonus frontalis*, oviposition, Cerambycidae, Scolytidae

RESUMEN

Se examinó la biología oviposicional de *Acanthocinus nodosus* sobre arboles de pino (*Pinus taeda* L.) infestados con el escarabajo de pino sureño (SPB), *Dendroctonus frontalis*, en Alabama, U.S.A. Se describen los componentes de la biología oviposicional, incluyendo la descripción del hoyo de oviposición, el período de colonización, el promedio de huevos puestos por hoyo de oviposición, el uso de la entrada del escarabajo de la corteza o los hoyos de ventilación como lugares de oviposición, y la densidad de los hoyos. Se distinguen facilmente los hoyos de oviposición de *Acanthocinus nodosus* de los de *Monochamus titillator*, otra especie de cerambícido que habita los arboles matados por el SPB. La colonización de los arboles por *A. nodosus* empezó dentro de 2 dias del ataque inicial de SPB y duró por 8 a 14 dias. Las hembras pusieron un promedio de 3.33 (SE ± 0.48) huevos por hoyo de oviposición y 99% de los hoyos occurian en la las hoyos de entrada de SPB y los hoyos de ventilación. Todos los hoyos fueron sobre el parte abajo del trunco entre 18 y 163 cm de encima de la tierra. La densidad de los hoyos de oviposición varia de 0.22 a 0.45 hoyos por cm^2 de superficies de corteza. Se notaron la interacciones potenciales con otras especies que habita la floema de la planta.

Acanthocinus nodosus (F.), (Coleoptera: Cerambycidae) is a frequent associate of the southern pine beetle (SPB), *Dendroctonus frontalis* Zimmermann (Coleoptera: Scolytidae) in southern U.S. forests (Overgaard 1968; Moser et al. 1971; Dixon & Payne 1979). By attacking and killing living pine trees, SPB provides extensive phloem resources that can be utilized for reproduction by *A. nodosus*. Upon arrival at host trees, adult *A. nodosus* chew pits in the bark or enlarge bark beetle ventilation holes for use as oviposition sites (Beal 1952; USDA 1985). While mining in the phloem, *A. nodosus* larvae often compete with and/or destroy bark beetle brood (Beal 1952). *Acanthocinus nodosus* is usually found in the thick-barked lower portion of the tree bole (Savely 1939) and is reported to complete one generation per year (USDA 1985). *Acanthocinus nodosus* is found throughout the eastern United States in dead and dying pines (Yanega 1996).

Little research has been conducted on *A. nodosus*, however, Schroeder (1997) investigated the reproductive biology of *A. aedilis* (L.) on pine bolts in a Swedish forest. He found that 55% of *A. aedilis* oviposition on cut bolts occurred in bark beetle holes and reported a mean egg density of 3.7 eggs per pit.

The objectives of this study were to describe the oviposition pit of *A. nodosus* and aspects of its oviposition biology including egg density, area of infestation on tree boles, duration of oviposition, and some interactions with SPB.

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Materials and Methods

Study Site

Research was conducted between July 28 and August 16, 1998, in a mixed hardwood-pine forest on the Oakmulgee Ranger District of the Talladega National Forest, Alabama. Several species of pine were present including loblolly, *Pinus taeda* (L.), longleaf, *Pinus palustris* (Mill.), and shortleaf, *Pinus echinata* (Mill.). Three loblolly pines, trees A, B, and C, were used to investigate *A. nodosus* oviposition biology. Additional egg samples were removed from two *P. taeda* in the same SPB infestation.

Oviposition Pit Description

Oviposition of three female *A. nodosus* was observed. After oviposition was completed, pits were removed with a 2.54 cm arch punch and egg placement and egg characteristics were noted. These oviposition pits were compared to known *Monochamus titillator* (Fab.) pits to establish differences between the two species.

Arrival Period

Trees were examined for evidence of oviposition pit construction over a 20-day period. After detecting a new SPB attack, trees were checked to determine presence of existing *A. nodosus* ovipositional pits. If no pits were detected, sampling commenced. The first day of SPB attack was the beginning of our first sample interval. Every other day (one sample interval) sample trees were checked for new oviposition pits. Pits were either marked with a permanent felt tip pen, or removed to determine egg densities. Trees were checked until no new pits were located for two successive sample intervals. Previous observations of *A. nodosus* oviposition indicate that once oviposition ceased for more than 3 days, trees were not further colonized.

Egg Densities and SPB Interactions

Egg density was determined by removing bark and phloem immediately surrounding an oviposition pit. A 2.54 cm arch punch was hammered through the bark and phloem, stopping at sapwood, and pits were removed. Bark samples (n = 97) were then dissected by peeling the phloem back from the bark and locating the eggs. Total number of eggs was recorded for each pit. Each sample was then examined to determine if a SPB ventilation or entrance hole had been used for oviposition by *A. nodosus*. If the ventilation or entrance hole was the only hole present in the pit and ended in an SPB gallery, then it was concluded that *A. nodosus* was using an SPB hole for an oviposition site.

Area of Infestation

After oviposition by *A. nodosus* was complete, the height of each pit above the ground was measured. Measurements were grouped to create a histogram depicting pit frequency at heights from 0 to 200 cm above the tree base.

Results

Acanthocinus nodosus oviposition pits are elliptical to round with steeper walls than *M. titillator* and contain a noticeably round hole at the bottom of the pit (Fig. 1). Eggs of *A. nodosus* were oviposited as a group at one margin of the pit, apparently chosen at random, as if the ovipositor had been inserted once and all eggs deposited. Eggs were found directly in SPB galleries as well as in the phloem surrounding the SPB hole.

Colonization of host trees by *A. nodosus* ranged from 8 to 14 days after initial SPB attack, with an average of 11.3 (SE ± 1.8). On average, 80% of oviposition pits on sample trees occurred during the first five sampling intervals following initial SPB attack. Average number of *A. nodosus* pits on host trees was 41.3 (SE ± 10.6) and ranged from 27 to 62 (Table 1). Average pit number per 100 cm^2 of bark surface was 0.30 (SE ± 0.08).

Egg numbers per oviposition pit varied considerably. Mean number of eggs was 3.33 (SE ± 0.48), with a range of 0 to 33 (Fig. 2). Among 97 pits removed for sampling, over 35% contained 0 eggs, 11% contained 3 eggs, 10% contained 1 egg, and 9% contained 2 eggs. Almost all (96 of 97) *A. nodosus* oviposition pits were found at the site of SPB holes. The one pit that did not use a SPB hole was located within a *M. titillator* oviposition pit.

Infested bole length varied slightly between sample trees (Table 1). Average infested bole length was 135.3 cm (SE ± 4.8), with tree C having the longest infested bole (145 cm) and tree B the shortest (130 cm). On average, infestation ranged from 23 cm (SE ± 2.9) to 158.3 cm (SE ± 2.6) from the base of the tree. Tree B had the largest area of infestation (1.56 m^2), followed by tree A (1.39 m^2) and tree C (1.15 m^2). For tree A, the greatest number (19%) of pits occurred between 100-120 cm, with 40% occurring between 100-160 cm (Fig. 3A). On tree B, 68% of oviposition pits occurred at heights above 80 cm, with 42% of the total pits concentrated in the 100-160 cm range (Fig. 3B). In contrast to the other sample trees, 63% of the oviposition pits on tree C were located below 100 cm (Fig. 3C). The highest density of pits on tree C occurred between 120-140 cm and 20-40 cm from the base of the tree.

Discussion

Arrival of SPB associates, especially parasitoids and predators, has been investigated by several authors (Camors & Payne 1973; Dix &

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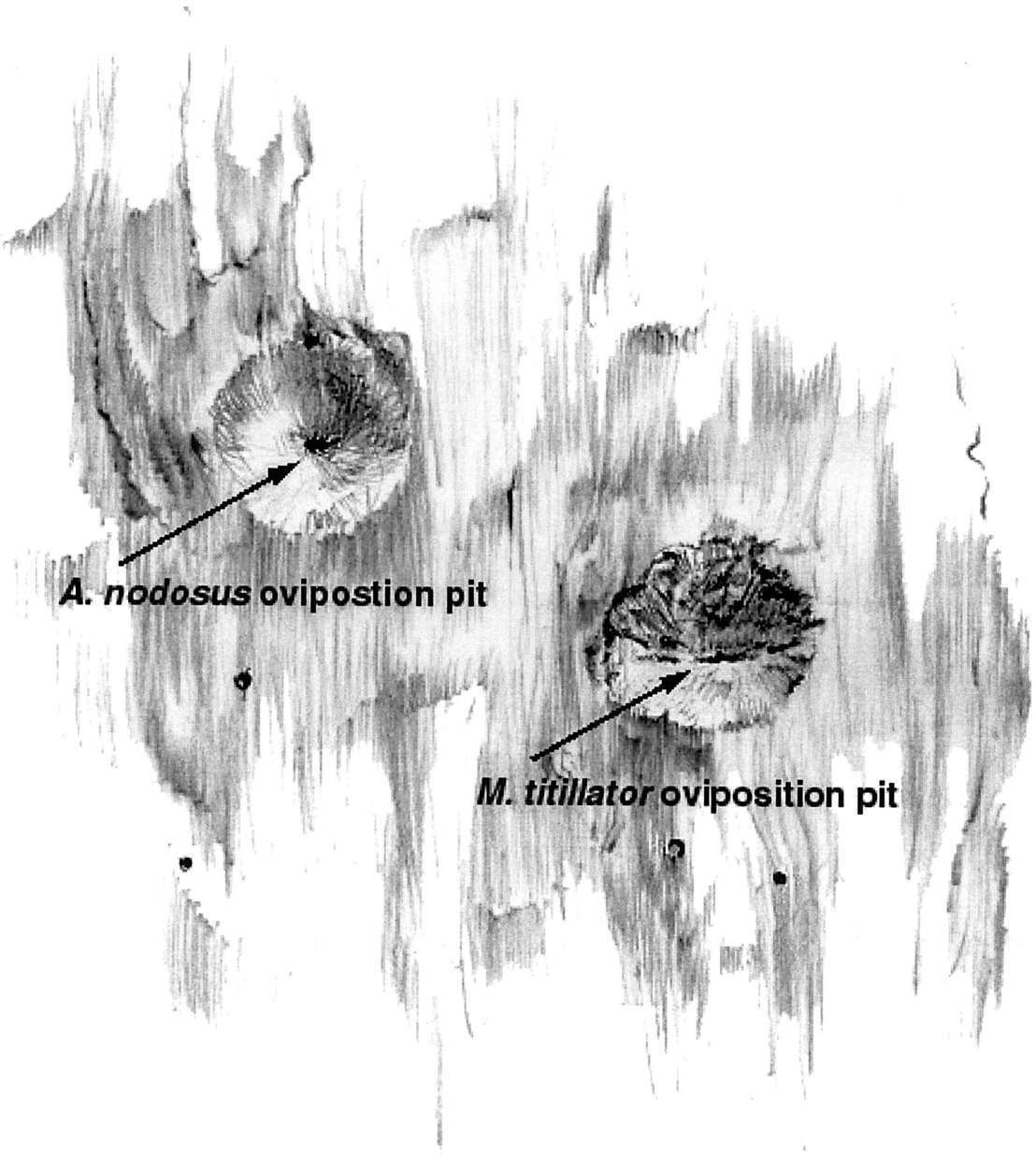


Fig. 1. *Acanthocinus nodosus* and *Monochamus titillator* oviposition pits. *Acanthocinus nodosus* pits tended to be more rounded than *M. titillator* and contain a distinct round hole at the bottom. The hole at the bottom of the pit was most likely the result of ovipositing on a bark beetle entrance or ventilation hole.

Franklin 1978; Dixon & Payne 1979). Unfortunately, fundamental knowledge concerning the basic biology of many associates, especially those that do not assume a direct beneficial role (i.e., parasitoids or predators) is lacking. This study explored the oviposition biology of *A. nodosus*, one of those poorly studied associated insect species.

We were able to easily differentiate the oviposition pits of *A. nodosus* from *M. titillator*. While *M. titillator* pits were elliptical with a small horizontal line at the bottom (Webb 1909), *A. nodosus* pits tended to be more rounded in shape and contained a distinct round hole at the bottom. In our study, the round hole at the bottom of the oviposition pit was most likely a result of the bark beetle entrance or ventilation hole. Another difference between *A. nodosus* and *M. titillator* oviposition pits was placement of the eggs. *Acanthocinus no-*

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TABLE 1. *ACANTHOCINUS NODOSUS* INFESTATION DATA FOR SAMPLE TREES A, B, AND C.

Sample tree	DBH (cm)	Height at base of infest. (cm)	Height at top of infest. (cm)	Length of infest. (cm)	Area of infested bole (m^2)	Total *A. nodosus* pits	No. of pits per 100 cm^2 of bark
A	29.5	23	154	131	1.39	62	0.45
B	32	28	158	130	1.56	35	0.22
C	24.5	18	163	145	1.15	27	0.23
Mean	28.7	23	158.3	135.3	1.4	41.3	0.30
SE	2.2	2.9	2.6	4.8	0.12	10.6	0.08

dosus eggs were placed as a single group, usually oriented in one direction. In comparison, *M. titillator* placed eggs in a distinct circular pattern around the center of its oviposition pits (Webb 1909). Eggs of *A. nodosus* were creamy-white in color compared to the yellowish color of *M. titillator* eggs.

Acanthocinus nodosus was common on the trees we sampled and had a close association with SPB. After successful initiation of SPB attack, *A. nodosus* arrived and began oviposition. *Acanthocinus nodosus* oviposition activity lasted from 8 to 14 days and occurred during the egg-oviposition stage of SPB activity. Interestingly, *A. nodosus* pits were found that had fresh resin flowing from them. It is reported that *A. nodosus* use bark beetle exit holes as oviposition sites (USDA 1985). The findings of our study, however, suggest that colonization occurs much sooner. We found *A. nodosus* ovipositing while SPB adults were making galleries and depositing eggs. Also, SPB entrance holes are typically filled with resin and frass and slant in relation to the bark surface, while ventilation holes are horizontal and filled with frass only (Stephen & Taha 1976). In our study, we did not differentiate between the types of bark beetle holes. However, it was noted on several occasions that fresh resin was in the SPB hole that was used as an oviposition site by *A. nodosus*. Due to the presence of SPB adults constructing galleries and resin in the egg samples, it can be assumed that *A. nodosus* were using SPB entrance holes

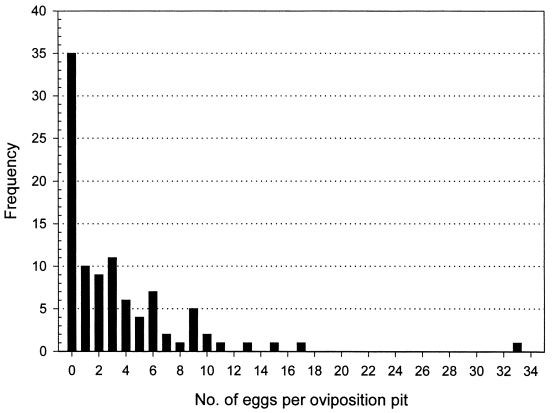


Fig. 2. Frequency distribution of egg numbers in *A. nodosus* oviposition pits.

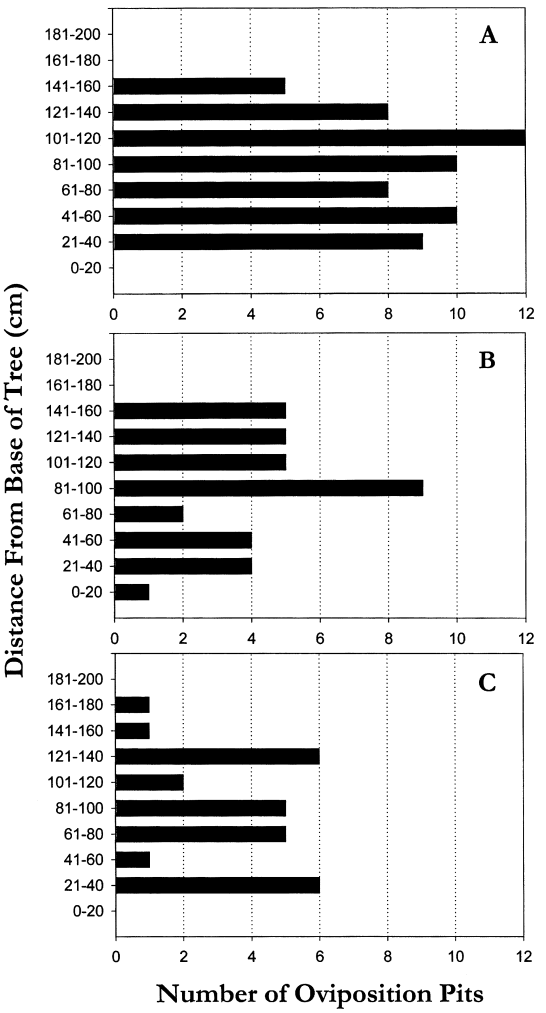


Fig. 3. Histogram depicting the distribution of number of *A. nodosus* oviposition pits at different heights below 2 m on trees A, B, and C.

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and ventilation holes for oviposition sites. Discrepancies between *A. nodosus* usage of SPB hole types in our study and the previously recorded observations (USDA 1985) could be a factor of *A. nodosus* oviposition timing and SPB density. In our study, SPB mass attack density was low and rate of colonization appeared slow in our sample trees. For example, during the entire time *A. nodosus* were ovipositing, SPB were constructing galleries and depositing eggs.

There are a number of possible explanations to account for the wide range of egg numbers found in *A. nodosus* pits (0-33). First, the large number of zero egg counts could be a result of predation by egg predators (e.g., Histeridae). Because SPB ventilation or entrance holes are used for oviposition by *A. nodosus*, predators have easy access to eggs. On several occasions, histerid beetles were found in the presence of *A. nodosus* eggs. Because histerids are known SPB egg predators (Moser et al. 1971), it seems probable that they would consume *A. nodosus* eggs. Second, some cerambycid species need a period of maturation before oviposition commences (Linsley 1961). Walsh and Linit (1985) found that some *M. carolinensis* (Olivier) females chewed oviposition pits before reaching sexual maturity. At the other extreme, the large numbers of eggs found in some oviposition pits could be explained as multiple oviposition events by female *A. nodosus*. Because *A. nodosus* displays opportunistic behavior by using SPB holes, it also seems possible that females may oviposit in existing pits created by their own species. A similar habit has been noted in female Eucalyptus borers, *Phoracantha semipunctata* F., where up to 100 eggs have been found in the same area under bark or in crevices of eucalyptus trees (L. M. Hanks, pers. comm.). Mean number of *A. nodosus* eggs was similar to estimates in Sweden by Schroeder (1997) who found an average of 3.7 *A. aedilis* eggs per pit.

No oviposition pits of *A. nodosus* occurred above 163 cm and only one tree contained pits below 20 cm. There could be several reasons for *A. nodosus* not ovipositing in areas higher on the tree bole. First, by ovipositing lower on the tree bole, *A. nodosus* avoids competing with high densities of other phloem inhabiting species (e.g., SPB, *M. titillator*). In addition, *A. nodosus* is reported to pupate in the bark of host trees (USDA 1985) and may be confined to the lower bole where thick bark provides adequate pupation sites. The highest density of pits per 100 cm^2 occurred on tree A, which had the second highest infested bole area. The lowest density of pits occurred on tree B, which had the greatest infested bole area. However, on trees B and C pits were marked and removed for egg counts, while not removed on tree A. Release of host volatiles, combined with bark removal from tree B and C could have negatively impacted oviposition behavior of *A. nodosus*. The negative effect on *A. nodosus* oviposition behavior on trees B and C seems surprising since the removal of bark surface would likely increase host volatiles, perhaps increasing the attractiveness of the tree to cerambycids. Although there has been no work conducted on the effect of host volatiles on *A. nodosus*, Schroeder and Weslien (1994a) found *A. aedilis* was attracted to alpha-pinene and 95% ethanol. It is likely that *A. nodosus* exhibits a similar behavioral response to host volatiles.

Our study provides basic observations of *A. nodosus* oviposition behavior and its interactions with SPB. Because both SPB and *A. nodosus* coexist in time and space with other bark beetle and cerambycid species, competition or intraguild predation among these species is probable. Schroeder and Weslien (1994b) investigated interactions between *A. aedilis* and *Tomicus piniperda* (L.) (Coleoptera: Scolytidae) and found that the cerambycid species significantly impacted bark beetle reproduction. Coulson et al. (1980) reported that *M. titillator* competed for food resources with SPB, reducing SPB brood by 14% when the two species occurred concurrently in the same tree. Further, Dodds et al. (2001) concluded that *Monochamus carolinensis* larvae were facultative intraguild predators of *Ips calligraphus* larvae (Germar). Because *A. nodosus* feeds in the same manner as *M. titillator*, but in the lower portion of the bole, competition or intraguild predation between SPB and *A. nodosus* is probable in that area of the tree. However, the overall impact of *A. nodosus* foraging on SPB survival may be less than that caused by *M. titillator* since the latter inhabits much more tree surface area than *A. nodosus*.

Bark beetle species that share the same tree are typically partitioned along the length of the bole to minimize competition (Paine et al. 1981; Flamm et al. 1987). Like the stratification that occurs in bark beetle species, a similar type of resource division might occur among cerambycid species arriving on SPB infested trees. For example, it is known that *M. titillator* primarily inhabits the middle and upper portions of infested tree boles (Hennier 1983), while *A. nodosus* occurs in the lower portion. *Arhopalus rusticus obsoletus* (Randall), another cerambycid species occurring in SPB infestations, is limited to the base and roots of dead and dying pines (Knull 1946; Linit et al. 1983). *Xylotrechus sagittatus sagittatus* (Germar) occurs concurrently with the above cerambycids, but may avoid direct competition for phloem resources by feeding primarily in the sapwood (Gardiner 1957).

Further studies into cerambycid biology, including *A. nodosus*, and other SPB associates are needed. A more developed knowledge of interspecific interactions of the phloem inhabiting guild associated with SPB may lead to a more complete understanding of bark beetle population dynamics.

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