Facultative Intraguild Predation of Red Oak Borer Larvae (Coleoptera: Cerambycidae)

V. L. WARE[1] AND F. M. STEPHEN

Department of Entomology, University of Arkansas, Fayetteville, AR 72701

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ABSTRACT In the Ozark National forests of Arkansas and Missouri, an outbreak of a native cerambycid beetle, the red oak borer, *Enaphalodes rufulus* (Haldeman), seems responsible for widespread oak mortality. The underlying reasons for this outbreak are being studied. Historically, a small portion of within-tree red oak borer mortality has been attributed to natural enemies (woodpeckers and nitidulid larvae), but the majority of mortality is from unknown factors. In four experiments, phloem sandwiches were used to observe inter- and intraspecific predation on red oak borer larvae. Our studies revealed that red oak borer was cannibalistic and that this behavior resulted in statistically significant weight gain. Observations were also made on predaceous behavior by associated insect larvae, specifically carpenterworms, elaterids, and nitidulids. We found that carpenterworms and elaterids will eat red oak borer larvae, but nitidulids exhibited no predaceous behavior. These observed behaviors may have important implications for red oak borer population dynamics because they identify potential mortality factors to red oak borer larvae.

KEY WORDS *Enaphalodes rufulus*, Cerambycidae, cannibalism, intraguild predation

EPIDEMIC POPULATIONS OF RED oak borer, *Enaphalodes rufulus* (Haldeman) (Coleoptera: Cerambycidae), were detected in the Ozark National Forest of Arkansas in 1999 (Stephen et al. 2001) and are associated with widespread oak mortality (Fierke et al. 2005b). Causes for this outbreak are uncertain. High insect population levels may result from migration (which is unlikely with this native species), increased natality (which has not been observed), or decreased mortality. Red oak borers spend the vast majority of their synchronous 2-yr life cycle in larval stages, with adults occurring for only a few weeks in summers of odd-numbered years (Hay 1969, Donley 1978, Fierke et al. 2005a). Woodpeckers, nitidulid larvae, and ants have been identified as predators of red oak borer larvae, but the majority of larval mortality is from unknown factors (Hay 1969, 1974, Feicht and Acciavatti 1985, Galford 1985).

Red oak borer adults are nocturnal, do not feed on twigs or foliage, and live for ~3 wk (Solomon 1995). Females oviposit an average of 119 eggs singly in bark crevices or under lichens (Donley 1978). Eclosion occurs in 10–13 d, and larvae chew through bark to initiate phloem galleries (Solomon 1995, Fierke et al. 2005a). Larvae begin their first overwintering period in mid-November (Hay 1969, Fierke et al. 2005a). In the subsequent June, larvae continue to feed in phloem and eventually move into heartwood, forming 15- to 25-cm vertical galleries where they become quiescent during the second winter (Hay 1969, Fierke et al. 2005a). The following spring, pupation occurs and adults emerge in late June (Hay 1972, Fierke et al. 2005a).

Red oak borer, as a member of the long-horned beetle family Cerambycidae, is phytophagous, feeding in the tissues of woody plants (Craighead 1923, Linsley 1958, 1959). As within-tree populations increase, the potential for intraspecific interactions increases. In this high-density environment, larvae that are normally noncarnivorous may act opportunistically and exhibit cannibalistic behaviors (Dodds et al. 2001, Hanks et al. 2005).

Elgar and Crespi (1992) defined cannibalism as the killing and consumption of intraspecific individuals and suggest that it is widespread in the animal kingdom. There are many potential benefits from this behavior that include acquisition of nutrients needed for growth and development, decrease in intraspecific competition for food and space, and elimination of future reproductive competitors. Potential costs include high energy expenditure, especially when prey are of similar size, potential wounding/death from counterattacks, and risk of parasite or pathogen transmission (Elgar and Crespi 1992).

Polis et al. (1989) described intraguild predation as a combination of two interactions, competition and predation, by organisms using the same food and space. This behavior is relevant to cannibalism as each organism must choose to consume individuals of the same or differing species (Shausberger 2003). Intra-

[1] Corresponding author, e-mail: vware@uark.edu.

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guild predation is ubiquitous among predaceous insects (Phoofolo and Obrycki 1998, Zheng et al. 2004, Snyder et al. 2004) and is not uncommon among phytophagous insects (Goyer and Smith 1981, Wilson et al. 1996, Wissinger et al. 1996, Dodds et al. 2001).

There are many potential insect predators, both facultative and active, that share the phloem resources of red oak borer and inhabit the galleries that they construct in heartwood tissue. Two species of carpenterworms (Lepidoptera: Cossidae), *Prionoxystus robiniae* (Peck) and *P. macmurtrei* (Guerin), are phytophagous, but they are also known to be antagonistic and frequently occupy heartwood galleries of red oak borer (Hay 1974). Sap flow from active red oak borer phloem galleries attracts nitidulid beetles (Coleoptera: Nitidulidae), that inoculate galleries with bacteria, fungi, and yeast (Hay 1974). It has also been suggested that nitiduilid beetles may be capable of facultative predation (McCoy and Brindley 1961, Hay 1974). Eyed click beetle larvae, *Alaus oculatus* L. (Coleoptera: Elateridae), are also potential red oak borer predators because they are aggressive predators of wood-boring larvae (Craighead 1950).

The objectives of our research were (1) to determine if red oak borer larvae exhibit cannibalistic behavior, and if so, the frequency of this behavior; (2) to determine if red oak borer larvae will actively seek/consume other red oak borers when initially placed in separate arenas; (3) to determine if cannibalism results in significant weight gain compared with controls; and (4) to determine the nature/frequency of carpenterworm, elaterid, and nitidulid predation on red oak borer larvae.

Materials and Methods

Red oak borer larvae were collected from northern red oak, *Quercus rubra* L., in the Ozark National Forest in areas of known infestation. A majority of collections were made from May through July in 2004, which is early in the second active life stage of the red oak borer life cycle (Fierke et al. 2005a), meaning larvae were 10–12 mo old, ≈2.5 cm in length, and had not begun to form heartwood galleries. To obtain these larvae, bolts were cut from felled trees and returned to the laboratory, and outer bark and phloem were removed using a drawshave.

Potential intraguild predators were collected simultaneously with red oak borer larvae. The exceptions were nitidulid larvae, which were hand-collected from oozing red oak borer attack sites in the spring of 2004. Because of difficulty in finding larvae and to increase the number of replicates involving potential predators, additional red oak borer larvae, carpenterworm, and elaterid larvae were collected from heartwood galleries using a wood splitter at the end of the second quiescent period (Fierke et al. 2005a) in the spring of 2005.

Phloem sandwiches were created according to techniques developed by Dodds et al. (2001). Phloem from northern red oak was removed from the cambium using a reciprocating saw (Milwaukee Sawzall model 6524–21 Milwaukee. Brookfield, WI.) and sanded flat. A disk of phloem was cut using a band saw to fit into the top half of a disposable polystyrene petri dish (diameter = 9 cm). Phloem disks were sterilized in a weak bleach solution (≈0.05%) to prevent fungal growth. The outside of a small, bottom half of a petri dish was inverted to push the phloem sample flat. Parafilm was wrapped around the sandwich to create a seal and to prevent desiccation.

Cerambycid larvae were weighed to the nearest milligram using an electronic scale before being introduced into the phloem sandwiches. Circular holes in the center of the phloem, ≈2–4 cm in diameter and 1–2 cm in depth, were made using sterilized cork borers to create arenas in which larvae could establish their galleries. Phloem sandwiches were stored in the dark at 29°C and observed daily for 1–2 wk, depending on the time needed for interactions to be "completed." Interactions were completed when one larva cannibalized another or when "unattacked" larvae established separate galleries.

If a larva directly encountered another larva but no aggression was observed, the larva was considered "unattacked." If one red oak borer larva was partially eaten, the larva was considered to be "partially consumed." "Complete consumption" occurred when one larva completely ate the other larva. When appropriate, data were analyzed using Student's unpaired *t*-tests ($\alpha = 0.05$), and measurements of error are presented as SEM (SAS Institute 2003).

Cannibalistic Behavior of Red Oak Borer in Same Arena. This experiment was conducted to determine if red oak borer larvae exhibited cannibalistic behavior. Two larvae of comparable size were simultaneously placed together in a phloem arena that was of appropriate size to force interaction. Fifty replicates were completed.

Cannibalistic Behavior of Red Oak Borer in Adjacent Arenas. The purpose of this experiment was to determine if red oak borer larvae would actively seek and consume other red oak borer larvae as they bore through phloem. Two larvae were introduced into adjacent arenas that were a minimum of 1.5 cm apart. Thirty-three replicates were completed.

Weight Gain of Red Oak Borer. This experiment was conducted to determine if red oak borer cannibalism resulted in significant weight gain compared with larvae that only consumed phloem. Larvae were randomly assigned to treatment and control groups. Two treatment larvae (n = 32 pairs) were placed together in a phloem arena, and one control larva (n = 37) was placed in a phloem arena. All larvae were marked with a permanent marker for identification. Larval weights were measured to the nearest milligram after 1 wk, and means of treatment and control groups were compared using Student's unpaired *t*-tests (SAS Institute 2003).

Predaceous Behavior by Other Insects. Red oak borer larvae were paired with elaterid larvae (n = 15), carpenterworm larvae (n = 15), or nitiduilid beetle larvae (n = 5) and introduced into the same arena.

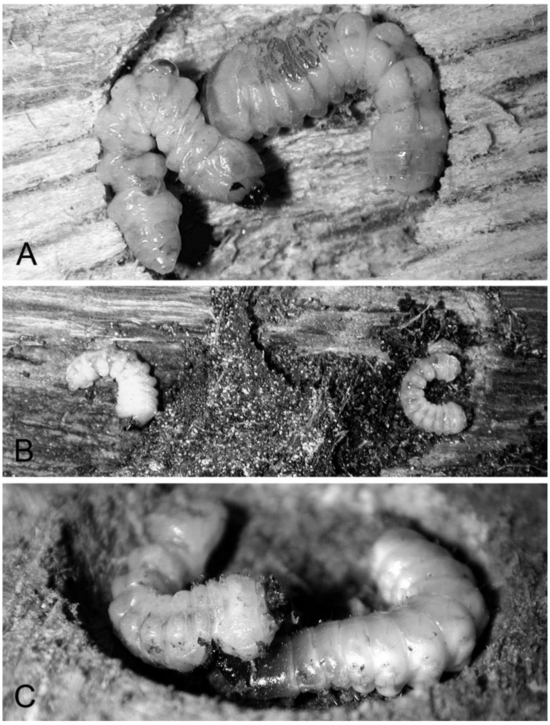

Fig. 1. (A) Marked red oak borer larvae exhibiting aggressive intraspecific behavior. (B) Wall building by red oak borer larvae. (C) Elaterid larva eating red oak borer larva.

Replicates were limited by availability of potential predators.

Results

Cannibalistic Behavior of Red Oak Borer. Eighty-four percent of potential encounters resulted in consumption of one larva (20% partial and 64% complete; Fig. 1A). Sixteen percent of larvae were unattacked, which led to eventual partitioning of the arena by construction of frass walls (Fig. 1B). These behaviors were observed in <4 d after the introduction of larvae within phloem.

Cannibalistic Behavior of Red Oak Borer in Adjacent Arenas. All larvae that encountered other larvae by boring into the adjacent arena (55%) exhibited aggressive behaviors that resulted in consumption (12% partial and 43% complete). Fifteen larvae (45%) did not invade adjacent arenas. These behaviors were observed within 1 wk on introduction of larvae within phloem.

Weight Gain of Red Oak Borer. Larvae exhibiting cannibalism gained significantly more weight (10 ± 2 mg) than larvae feeding only on phloem (2 ± 1 mg; df = 64; $P = 0.001$).

Predaceous Behavior by Other Insects. Fifteen trials with elaterid larvae resulted in 27% partial consumption and 73% complete consumption of red oak borer (Fig. 1C). Fifteen trials with carpenterworm resulted in 40% partial consumption and 54% complete consumption of red oak borer by carpenterworm. Six percent ($n = 1$) of these encounters resulted in partial consumption of carpenterworm by red oak borer. All larvae remained unattacked in the five trials between red oak borer and nitidulid larvae.

Discussion

Although the primary food of red oak borer is red oak phloem and xylem, our experiments showed that red oak borer will exhibit cannibalistic behavior under laboratory conditions. Cannibalistic behavior has been reported among other cerambycids including *Monochamus sutor* L., a European cerambycid (Victorsson and Wikars 1996); *M. alternatus* (Hope), an Asian cerambycid (Togashi 1990); and *M. carolinensis* (Olivier), the Carolina sawyer (Dodds et al. 2001). Dodds et al. (2001) reported similar results in laboratory conditions in which *M. carolinensis* exhibited both cannibalistic and avoidance behaviors. He suggested that the risk of a cannibalistic encounter may be advantageous only in high density circumstances; however, because phloem does not seem to be a limiting resource for red oak borer larvae, cannibalism may function more opportunistically as the perceived benefits may outweigh the potential detriments.

Our experiments also showed that red oak borer larvae may invade neighboring larval galleries and consume the inhabiting larva. Densities of galleries in the current generation are 10 times higher in 2002 and 2003 than previously reported (Hay 1974, Donley and Rast 1984), with first year phloem galleries ranging from 142 to 1,244 per tree (mean, 599 ± 50) (Fierke et al. 2005a). These high population numbers could create an environment in which cannibalism may be occurring frequently enough to be an important mortality factor. Akbulut et al. (2004) found that only 12% of a *M. carolinensis* cohort from reared logs survived to adulthood and attributed this mortality to intraspecific competition and cannibalism.

Because immature red oak borer are cryptic, it is difficult to determine what factors cause larval mortality. More larval phloem galleries than larvae have been observed during intensive and extensive sampling of red oak borer larvae in naturally infested logs (Fierke et al. 2005a). These larval galleries were often intersecting with two larvae in proximity or coalescing with one or two larvae remaining (unpublished data). These observations, in conjunction with the data we present here, suggest that cannibalism may be an important mortality factor at the high population levels we have recently encountered.

Our experiments indicated that larvae exhibiting cannibalistic behavior gained significantly more weight than larvae feeding only on phloem. Phloem is relatively nitrogen poor (0.1–2.2% dry weight) compared with insect bodies (6.6–12.0% dry weight) (Slansky and Scriber 1985). Therefore, cannibalism would be beneficial both nutritionally and energetically, which could translate into increased growth, faster development, and greater survival. Hellrigl (1971) also showed that carnivory favors growth. He found that *Monochamus sartor* F. larvae grew three times faster when supplemented with bark beetle larvae than those fed solely phloem.

We are not aware of any other research documenting interactions of larvae within subcortical tissues of oaks. Although replication of interspecific predation experiments was limited, our results suggest that insects associated with red oak borer phloem and xylem galleries may be important mortality factors of red oak borer larvae. Craighead (1950) found that individual *A. oculatus* larvae consumed >200 cerambycid larvae during development in caged studies. Our experiments corroborate these findings as encounters with elaterid larvae resulted in 100% red oak borer larval mortality.

Hay (1974) reported that carpenterworms were facultative predators of red oak borer larvae, causing 3–9% of red oak borer larval mortality. Furthermore, he reported that 96% of carpenterworm larvae gained entrance into the tree through openings created by other agents, with the majority (66%) being created by red oak borer attacks. These findings indicated that the likelihood of these two insects interacting is high. Our experiments also indicated that carpenterworms are facultative predators of red oak borer larvae, with 84% of encounters resulting in red oak borer mortality. In one instance, a carpenterworm was consumed by a larger red oak borer; therefore, the outcome of this interaction may be dependent on the life stage of each respective insect as they have differing developmental rates and accompanying sizes.

Hay (1974) and McCoy and Brindley (1961) suggested that nitidulids may be capable of actively killing red oak borer larvae; however, we did not observe any aggressive behavior by nitidulid larvae. Rather, red oak borer became moribund or flacid (as observed in the field by Hay 1974) after ~5 d after nitidulid larvae were introduced. This suggests that observed field mortality may be the result of fermentation or associated bacteria and yeasts (Hay 1974). Further research is needed to verify the role of nitidulid larvae in relation to red oak borer mortality.

Other potentially important mortality agents of red oak borer larvae that were not included in these experiments include formicid ants, *Aphaenogaster flemingi* (Smith) and *A. treatae* (Forel), and various carpenter ants, *Camponotus* species. There have been some anecdotal observations of ant predation on red oak borer reported (Hay 1974, Donley 1984, Feicht and Acciavatti 1985, Galford 1985), but little experimental research has been conducted on ants as predators of red oak borer. Ants were not included in our experiments because our specific experimental design would be unable to assess their role as predators. Ants have been noted as potentially very important predators of other forest insect pests (Campbell and Torgersen 1982, Torgersen et al. 1983, Young and Campbell 1984) because of their abundance within forest environments. We recognize the potential importance of these insects as predators of red oak borer, but future research is needed to confirm this assertion.

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