# Facultative Intraguild Predation by Larval Cerambycidae (Coleoptera) on Bark Beetle Larvae (Coleoptera: Scolytidae)

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**ABSTRACT** Larvae of the Carolina sawyer *Monochamus carolinensis* (Olivier) (Cerambycidae) and bark beetle larvae (Scolytidae) often simultaneously feed in phloem of recently killed pine trees. Our investigations reveal that *M. carolinensis* larvae may act as facultative intraguild predators of bark beetle larvae. Phloem sandwiches were used in four experiments to examine inter- and intraspecific interactions. We discovered that all sizes of *M. carolinensis* larvae killed bark beetle larvae. Seventy-six percent of the killed bark beetle larvae were consumed by *M. carolinensis,* including 58% that were entirely ingested. Cannibalism in *M. carolinensis* occurred in every experimental trial. Based on this evidence, *M. carolinensis,* and possibly related cerambycid species associated with bark beetles, are facultative intraguild predators of larvae of other phloem inhabiting species. The consequences of this behavior may have important implications for bark beetle population dynamics.

**KEY WORDS** *Ips calligraphus, Ips, Monochamus carolinensis,* intraguild predation, Cerambycidae, Scolytidae

LARVAE OF CERAMBYCIDAE are normally considered phytophagous, feeding on most parts of living and dying plants and trees (Craighead 1923; Linsley 1958, 1959). However, larval cannibalism (Victorsson and Wikars 1996) and facultative predation on bark beetles (Hellrigl 1971) have been observed in several cerambycid species. Conifer-inhabiting cerambycids often rapidly colonize dying or dead trees attacked by scolytid bark beetles. Among the Scolytidae, bark beetle species, including *Dendroctonus brevicomis* LeConte (Stephen and Dahlsten 1976), *D. ponderosae* Hopkins (Dahlsten and Stephen 1974), *D. adjunctus* Blandford (Chansler 1967), and *D. frontalis* (SPB) Zimmermann (Overgaard 1968, Moser et al. 1971, Dixon and Payne 1979) all have cerambycids reported as associates. Release of pine host volatiles (Fatzinger et al. 1987, Schroeder and Weslien 1994a) and a kairomonal response (Billings and Cameron 1984) to bark beetle pheromones results in some cerambycids arriving on host trees coincident with or shortly following bark beetle attack. This leads to spatial and temporal coexistence of these two families in newly colonized host tree phloem.

Interactions between bark beetle and cerambycid larvae coexisting in the subcortical region of host trees typically have been described as competitive. Schroeder and Weslien (1994b) investigated competitive interactions occurring between *Acanthocinus aedilis* (L.) (Coleoptera: Cerambycidae) and *Tomicus piniperda* (L.) (Coleoptera: Scolytidae) and found the presence of cerambycids reduced production of bark beetle progeny by 78%. Coulson et al. (1976) described competition between the cerambycid *Monochamus titillator* (F.) and the scolytid *D. frontalis.* However, Flamm et al. (1989) later suggested that interactions occurring between *M. titillator* and *D. frontalis* might better be defined as commensalism. Miller (1984) reported that *M. titillator* competed for phloem resources with *Ips calligraphus* (Germar) (Scolytidae) and had a significant negative effect on some subcortical predators (Miller 1985).

Although competition has commonly been used as an explanation for bark beetle mortality, seldom have direct observations of interactions between phloem-feeding species been performed. Analysis of bark samples in which immature bark beetle density is compared with and without cerambycid foraging, or adult bark beetle emergence density is estimated as a function of cerambycid foraging, has been used to estimate bark beetle mortality. In these cases, mortality is usually attributed to competition (Coulson et al. 1976, 1980). We suggest an alternative, more complete explanation of mortality suffered by bark beetle larvae within phloem is that larger, more mobile cerambycid larvae may also function as facultative intraguild predators on bark beetle larvae.

Intraguild predation is a combination of predation and competition, where members of the same feeding guild prey upon each other (Polis et al. 1989). Examples of intraguild predation occurring in predaceous insects are common (Wissinger and McGrady 1993, Currie et al. 1996, Kester and Jackson 1996, Lucas et al. 1998, Phoofolo and Obrycki 1998); however, there are fewer examples of facultatively predaceous non-carnivorous insects (e.g., Wissinger et al. 1996).

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The cerambycid *Monochamus carolinensis* colonizes weakened and dying pine trees in the southeastern United States (Baker 1972) and is often found in association with bark beetles (Moser et al. 1971). *Monochamus carolinensis* develop in phloem of host trees for ≈3–4 wk before entering sapwood to construct U-shaped galleries in which pupation will later occur (Pershing and Linit 1986). During construction of sapwood galleries, larvae frequently return to the phloem and feed near their entrance hole. Larval length of *M. carolinensis* ranges from 2 mm at hatching to ≈4 cm before pupation occurs.

*Ips calligraphus* is a multivoltine polygynous bark beetle found throughout eastern North America, where it inhabits most species of pine (Baker 1972). Freshly killed or injured trees are usually colonized by *I. calligraphus* but in drought years living trees may also undergo attack. In the southern United States, *I. calligraphus* is often found inhabiting phloem of trees killed and also colonized by *D. frontalis* (Paine et al. 1981, Wagner et al. 1985). Eggs of *I. calligraphus* are deposited in galleries created within phloem of host trees. Larvae develop, feed, and pupate in the phloem region of host trees; those larvae developing in phloem range in length from 1 to 4 mm.

Larvae of *Monochamus carolinensis* and *I. calligraphus* often simultaneously occupy and feed in phloem of recently killed pine trees. Because the newly created phloem resource is subject to rapid colonization by an extensive and predictable complex of insects, mites, and fungi (Stephen et al. 1993), the ability to act as a facultative intraguild predator could provide *M. carolinensis* with additional nutrition in an area where competition for resources may be high. As an additional advantage, predation may eliminate present or future competitors and thus help to ensure that resources remain plentiful.

Our initial observations of interactions occurring between *M. carolinensis* and *I. calligraphus* suggested the possibility of a predator-prey interaction between these two phloem feeding species. Preliminary laboratory experiments demonstrated that a high frequency of bark beetle larvae were killed and consumed by cerambycid larvae. Additionally, response to bark beetle larvae seemed to be dependent on the size of cerambycid larvae. If predation is frequent, then it is possible that cerambycid species may play a more significant role in the population dynamics of bark beetles than previously believed. The objective of the research reported here is to better define the nature and frequency of this phenomenon. Intraspecific interactions of cerambycids were also made and are here reported.

## Materials and Methods

Larvae of *Monochamus carolinensis* were obtained from infested logs originating from a laboratory colony held by M. J. Linit at University of Missouri, Columbia. Larvae were ≈25 d old when our experiments were initiated, and varied in length from 1.0 to 2.6 cm. Larvae had not begun to create sapwood galleries and were still feeding in phloem tissue when they were removed from bolts. Third and fourth stage larvae of *Ips calligraphus* were obtained from a laboratory colony at University of Arkansas, Fayetteville.

Phloem sandwiches were made using disposable polystyrene petri dishes (100 by 15 mm). A disk of phloem (≈8 cm in diameter) was cut to fit into the top half of the petri dish. The smaller bottom half of the petri dish was placed so that its outer surface pushed the phloem sample flat. Parafilm was wrapped around the dish to maintain a seal and keep phloem pressed flat between the petri dish halves. All surfaces, including the petri dishes and phloem samples, were sterilized using a weak bleach solution (≈0.05%).

Before placement in the phloem sandwich, cerambycids were slightly flattened between clean petri dishes and measured from the tip of the mandibles to the most posterior point of the abdomen using calipers. To introduce cerambycids into the phloem, a small (1.5 cm diameter) cork borer was used to make a circular hole into the phloem. In all experiments, cerambycid larvae were placed in the hole where the phloem was removed and held for 24 h until feeding was initiated and they had become established.

**Experiment 1: Predaceous Behavior of *M. carolinensis* Larvae.** Experiment 1 tested the hypothesis that larvae of *M. carolinensis* were predaceous on larval *Ips calligraphus.* Ten cerambycid larvae were used in daily experiments over a 6-d period leading to a total of 60 trials. Each day, larva of one *I. calligraphus* was added to phloem sandwiches and interactions were observed for 1 h. Each larva of *I. calligraphus* was placed in the cerambycid gallery, as far away from the cerambycid larva as possible. Phloem sandwiches were resealed and an attempt was made to minimize disturbance to cerambycid galleries. Results of interactions of cerambycid larvae with *I. calligraphus* larvae were noted and recorded at 10-min intervals.

Interaction results were categorized as "unattacked," "attacked," "killed," "ingested," or "consumed." If a cerambycid larva encountered an *I. calligraphus* larva directly, but no aggressive reaction was observed, the *I. calligraphus* was considered "unattacked." If a larva was "attacked," and the *I. calligraphus* larva was still mobile and no damage to its cuticle could be detected, it was considered "not killed." The *I. calligraphus* larva was recorded as "killed" only if visceral contents could be clearly identified oozing around the attacked larva and all movement had ceased. "Ingestion" was said to take place if the *I calligraphus* larva had been noticeably reduced in size or if *M. carolinensis* larva grasped the *I. calligraphus* larva in its mandibles and chewing motions were observed for >1 min. The larva was classified as "completely consumed" only if the entire larva was eaten during the 1-h observation period.

**Experiment 2: Effects of *M. carolinensis* Larval Size on Predaceous Behavior.** Experiment 2 tested the hypothesis that length of larval cerambycids affected their response to bark beetle larvae. To determine if cerambycid larval size affected aggressive behavior, logistic regression of frequency of trials on larval

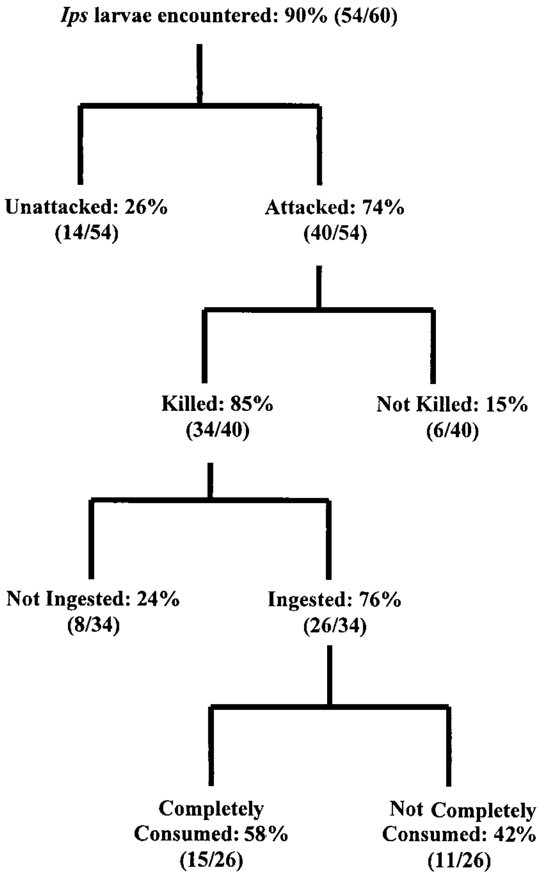

**Fig. 1.** Predatory behavior of cerambycid larvae in response to the presence of one *I. calligraphus* larvae added to arena gallery. Raw numbers are shown in parentheses. Flow chart begins with 60 trials (10 individuals observed daily for 6 d).

length was performed (SAS Institute 1996). Larval instar determination was not possible, although judging from molting patterns, the size categories most probably reflected two different instars. Larval sizes fell within the range that is found in the field in association with bark beetle broods (Graber 2000).

**Experiment 3: Cannibalistic Behavior in *M. carolinensis* Larvae.** Experiment 3 was conducted to determine if larvae of *M. carolinensis* were cannibalistic. Two *M. carolinensis* larvae, matched according to their size, were simultaneously placed at opposite margins from one another in petri dishes. Five replicates were conducted and results of interactions determined after 24 h of exposure.

## Results

**Experiment 1: Predaceous Behavior of *M. carolinensis* Larvae.** Illustrated in Fig. 1 is a dichotomous flow chart showing the outcome of 60 interactions between *M. carolinensis* and *I. calligraphus* larvae. In 10% of the trials, the cerambycid failed to notice or ignored the bark beetle larva. *Monochamus carolinensis* attacked the other larvae in 74% of the trials. Eighty-five percent of those attacks resulted in immediate mortality to *I. calligraphus* larvae, and 76% of the larvae were at least partially ingested. Fifty-eight percent of those larvae that were ingested were entirely consumed.

**Experiment 2: Effects of *M. carolinensis* Larval Size on Predaceous Behavior.** Whether or not an *I. calligraphus* larva was attacked ($P > 0.36$) or was killed ($P > 0.33$) was not significantly related to cerambycid larval size. Although there was a trend to feed upon *I. calligraphus* larvae more frequently, this was not significant ($P > 0.11$). Larger *M. carolinensis* larvae were significantly more likely to consume bark beetle larvae, however ($P > 0.01$). Small cerambycids were never seen consuming *I. calligraphus* larvae completely, and often ignored bark beetle larvae once they had been attacked and killed.

**Experiment 3: Cannibalistic Behavior in *M. carolinensis* Larvae.** In all five replicates of this experiment, one cerambycid larva attacked, killed, and at least partially consumed the other once an encounter occurred. Encounters did occur in all replicates within 5 d of initiating the experiment.

## Discussion

Our experiments clearly demonstrate that *M. carolinensis* is a facultative predator of bark beetle larvae and thus should be considered an intraguild predator during periods of its subcortical development. Facultative predation is not uncommon in phytophagous insects (Girault 1908, China 1953, Gangwere 1961, Lavigne and Pfadt 1964, Bowden and Phipps 1967, Cooke 1968, Root and Chaplin 1976, Whitman and Orsak 1985, Root 1986, Trichilo and Leigh 1986, New 1991, Wilson et al. 1996) and has been reported with other bark beetle associates (Parker and Davis 1971, Goyer and Smith 1981). To our knowledge, however, with the exception of a brief comment by Hellrigl (1971), facultative predation by Cerambycidae has not been previously described.

We consider the aggressive behavior exhibited by *M. carolinensis* to be predator-like, although it is probably facultative rather than active. *Monochamus carolinensis* usually ignored *I. calligraphus* larvae in galleries unless close contact was made. Occasionally, even if *M. carolinensis* had direct contact with *I. calligraphus* larvae, no attacks were observed. Cerambycid larvae actively pursuing *I. calligraphus* larvae in the phloem was rare, although we observed one larva enlarging an established *I. calligraphus* gallery in pursuit of its prey. Although phloem sandwiches used in this study were small, we believe that ample phloem was available for cerambycid feeding throughout the study period. We also believe it is unlikely that the small size of the arena resulted in an artificially high probability of contact between the two beetle species.

The majority of *I. calligraphus* larvae encountered by *M. carolinensis* in experiment 1 were attacked and killed, supporting our hypothesis that the cerambycid would prey upon larvae of bark beetles. Seventy-six percent of *I. calligraphus* larvae killed were consumed to some degree. Of the *I. calligraphus* larvae ingested, roughly half were completely consumed by *M. carolinensis.* Predator satiation may explain why more *I. calligraphus* larvae were not fed upon. In some instances, *M. carolinensis* larvae were preparing to molt when *Ips* larvae were introduced and in these cases, cessation of feeding had already taken place.

*Monochamus carolinensis* may incur multiple benefits from ingestion of *I. calligraphus* larvae. Intraguild predation, a combination of competition and predation, offers many advantages (Polis et al. 1989). First, *M. carolinensis* may gain nutrition by ingesting animal material if phloem resources are limited or if phloem nutrient content is low. Insect bodies contain between 6.6 and 12.0% dry weight nitrogen, while phloem contains 0.1–2.2% dry weight nitrogen (Slansky and Scriber 1985). In circumstances when densities of phloem feeding species are high, phloem resources may subsequently become less available. Furthermore, phloem thickness has been shown to influence performance of phloem-feeding species (Haack and Slansky 1987) and by feeding on other phloem inhabiting larvae cerambycids may gain essential nutrients when phloem resources are of poor quality.

It has been demonstrated that improved nutritional quality may have an adaptive advantage for cerambycid larvae by shortening development time. Hellrigl (1971) found that another cerambycid species *Monochamus sartor* F. grew three times faster when fed bark beetle larvae than when fed phloem alone. Evidence also exists that feeding cerambycids on an artificial diet shortens development time substantially (references in Haack and Slansky 1987). It is likely that *M. carolinensis* develops faster as a result of feeding on *I. calligraphus* larvae, but this remains to be tested.

In addition to possible nutritive benefits, *M. carolinensis* may reduce competition for limited food resources and simultaneously minimize numbers of predators within the phloem by acting as an intraguild predator. Intraguild predation to reduce competition has been documented in marine arthropods (Ambrose 1984), ants (Rosengren 1986), termites (Leving and Adams 1984), and parasitoids (Askew 1971). Miller (1985) reported that foraging by *M. titillator* reduced numbers of natural enemies in pine bolts colonized by *I. calligraphus.*

The effectiveness of *M. carolinensis* as a facultative predator, or intraguild predator, may be size dependent and may change through its developmental periods in phloem of host trees. Unfortunately, there is no known technique for distinguishing instars of *M. carolinensis* (Pershing and Linit 1989), although body length appears well correlated with developmental stages (C.G., unpublished data).

Preliminary laboratory experiments indicated that *M. carolinensis* size influences the behavioral outcome of interspecific encounters. Smaller cerambycids did not consume *I. calligraphus* larvae as frequently as larger ones. Larger cerambycid larvae often consumed some portion of *I. calligraphus* larvae provided during the experiment. In experiment 2, the number of *I. calligraphus* larvae consumed exhibited significant size dependence. Possibly, a pivotal point during development may exist where larvae will switch to more predator-like behavior, however, aggressive or protective behavior, as shown by the number of attacks and kills, appears to lack size dependence.

Because predator-like behavior was so prevalent in our initial trials, experiment 3 was conducted to examine the possibility of cannibalism in this species. Cannibalism has been documented previously in a laboratory experiment with a European cerambycid *Monochamus sutor* (L.) (Victorsson and Wikars 1996), and evidence for cannibalistic behavior in *M. titillator* larvae has been observed in the field (K.J.D., unpublished data). Rose (1957) also found that several stages of *M. scutellatus* (Say) were cannibalistic in logs of *Abies balsamea.*

In experiment 3, *M. carolinensis* killed and at least partially consumed conspecifics within phloem sandwiches; however, they frequently tended to avoid each other in these arenas until resources became scarce. This observation suggests that risking the chance of a cannibalistic encounter may be advantageous only in high density circumstances. The advantages of cannibalism would probably be similar to those derived from interspecific predation.

The probability of cannibalism may have been exaggerated by creation of small arenas where cerambycids were more likely to encounter each other, however, the subcortical region of pine trees is a similarly closed system where high densities of cerambycids may crowd residents to a comparable degree. The size-dependent component of intraspecific predation was not examined for *M. carolinensis*, although this effect may be similar to laboratory trials conducted with *M. sutor* in which larger larvae cannibalized smaller ones in most cases (Victorsson and Wikars 1996).

Analysis of bark beetle population fluctuations in the southern United States has resulted in different opinions as to factors responsible for the observed changes that occur. Although density-independent factors including climate and rainfall affect bark beetle populations (King 1972, Michaels 1984), recent research supports the importance of density dependent factors, particularly predation (Turchin et al. 1991, 1999; Reeve 1997).

In the southern United States, *M. titillator* populations are often found associated with *D. frontalis* in bark beetle killed trees (Overgaard 1968, Moser et al. 1971, Dixon and Payne 1979). *Dendroctonus frontalis* flight and reproduction is continuous throughout much of the year in the South. It is an aggressive bark beetle, which during outbreaks kills large numbers of pine trees in discrete groups. Adult cerambycids that are present in *D. frontalis* infestations rapidly respond and colonize the freshly killed trees, continually breeding and numerically increasing in these bark beetle infestations. Because *M. titillator*'s life history is so similar to *M. carolinensis*, it is highly probable that they are facultative predators on *D. frontalis* larvae in phloem of host trees. Polis et al. (1989) suggest that intraguild predation can drastically reduce or eliminate local populations of prey items and that may be important in the decline of *D. frontalis* populations following density-dependent intraguild predation by several generations of *M. titillator.*

Quantitative surveys of cerambycid populations in areas of active *D. frontalis* outbreaks may be required to investigate the impact of intraguild predation by *Monochamus* spp. on *D. frontalis* and other bark beetle population fluctuations. Because cannibalistic interactions are often self-regulating on populations (Walker 1984), the ubiquity of cannibalistic interactions within this system may limit the effect of increasing cerambycid densities on bark beetle mortality. Additional research exploring interactions among bark beetle associated insects in phloem of host trees appears important if we are to increase our understanding of bark beetle population dynamics.

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