

Seasonal Emergence, Egg Gallery Characteristics, and Natural Enemies of the Eastern Ash Bark Beetle, *Hylesinus aculeatus* (Coleoptera: Curculionidae: Scolytinae), in Michigan

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Abstract

Hylesinus aculeatus Say (Coleoptera: Curculionidae: Scolytinae) commonly infests the trunks and limbs of recently dead, dying, or cut ash (*Fraxinus* spp.) trees in eastern North America. In the Great Lakes region, *H. aculeatus* is univoltine, overwinters as adults, breeds in late spring and early summer, and constructs transverse biramous egg galleries. I sampled trunk and branch sections from three small-diameter white ash (*F. americana* L.) trees that were cut in April 1986 in Ingham County, Michigan, and then naturally infested by *H. aculeatus* and associates. Bolts cut from these trees and placed in an outdoor rearing cage in late June 1986 yielded *H. aculeatus* brood adults, adults of three hymenopteran braconid parasitoids [*Coeloides scolytivorus* (Cresson), *Dendrosoter* sp. and *Spathius* sp.], and one predatory clerid beetle [*Enoclerus nigripes* (Say)]. *Hylesinus aculeatus* brood adult emergence began in July, peaked in early August, and ended in early October. Of 590 egg galleries measured on bolts collected from the study trees in autumn 1986, 4% had one arm and 96% had two arms (biramous). On average, the biramous egg galleries measured 36 mm long and had 32 egg niches and 23 larval mines each. Average nearest-neighbor distance between entrance tunnels was 29 mm. For bolts that had retained all their original bark, survival from egg (= number of egg niches) to adult (= number of *H. aculeatus* exit holes) averaged 52.7%. Mean percent parasitism was estimated at 2.4%.

Keywords: *Leperisinus*, *Fraxinus*, life history, attack density, percent parasitism

The eastern ash bark beetle, *Hylesinus aculeatus* Say (Coleoptera: Curculionidae: Scolytinae) occurs throughout the range of ash (*Fraxinus* spp.) in eastern North America, extending west to the Rocky Mountains (Solomon 1995, Atkinson 2026). *Hylesinus aculeatus* is univoltine in the Great Lakes region (Dodge 1938) and Canada (Ives and Wong 1988) but may complete two generations per year in North Carolina (Beal and Massey 1945) and three in Mississippi (Blackman 1922). After overwintering, adults initiate egg galleries as early as late March in Mississippi (Blackman 1922), but not until May or June in the Canadian Prairie Provinces (Ives and Wong 1988). *Hylesinus aculeatus* typically infests recently dead, dying and cut ash trees (Beal and Massey 1945, Solomon 1995). *Endo*-Brevicomin and *exo*-Brevicomin appear to be pheromones of *H. aculeatus* as well as many other *Hylesinus* species (Schönherr 1970, Rudinsky and Vallo 1978, Rabaglia 2002, Shepherd et al. 2010). In much of the early literature, *H. aculeatus* is discussed under the synonym *Leperisinus aculeatus* (Say).

Female *H. aculeatus* adults initiate egg-gallery construction by making a short tunnel through the outer bark to the cambial region. This tunnel serves as a turning niche as well as a nuptial chamber where mating occurs (Beal and Massey 1945). Each female typically constructs a transverse, biramous (2 arms) egg gallery, perpendicular to the wood grain (Wood 1982, Kirkendall et al. 2015). The females appear to extend both arms at roughly similar rates, often alternating between them as described for *Hylesinus californicus* (Swaine) (Langor and Hergert 1993). Eggs are deposited singly in niches on both sides of the egg galleries. After hatching, larvae construct galleries that tend to follow the wood grain and therefore are mostly perpendicular to the egg gallery. The egg galleries and larval galleries of *H. aculeatus* score deeply into both the outer sapwood and bark and have a very uniform appearance (Knaus 1886, Chamberlin 1939, Beal and Massey 1945, Solomon 1995). Pupation occurs at the end of the larval galleries. Brood adults tunnel directly through the bark from their pupation sites without any apparent maturation feeding in the natal tree (Blackman 1922). Adults overwinter in

short tunnels constructed in the bark of living ash trees or recently cut logs (Blackman 1922, Dodge 1938, Beal and Massey 1945). After overwintering, *H. aculeatus* adults likely conduct maturation feeding in the bark of branches and twigs of ash trees as reported for *H. californicus* by Langor and Hergert (1993). Various parasitoids, especially in the families Braconidae and Eurytomidae (Hymenoptera), have been reared from *H. aculeatus*-infested ash material (Hoffmann 1938, Beal and Massey 1945).

As reported previously, while residing in southern Lower Michigan for many years starting in the 1980s, I often reared bark- and wood-boring insects from recently dead or cut trees found in the family woodlot (Haack 2020, 2021, 2023). The present paper deals with insects reared from white ash (*Fraxinus americana* L.) trees that were primarily infested with *H. aculeatus*. The objectives of the current study were to (1) record the emergence pattern of *H. aculeatus* brood adults and their associates, (2) make various measurements of the egg and larval galleries, and (3) estimate infestation densities and percent parasitism of *H. aculeatus*.

Materials and Methods

Study site. The study was conducted in a 24-ha, mature beech-maple woodlot near Dansville, Ingham County, Michigan (N 42.5481° Lat, W 84.3189° Long) as described in Haack (2020). The dominant tree species were sugar maple (*Acer saccharum* Marshall) and American beech (*Fagus grandifolia* Ehrh.). Other common tree species included yellow birch (*Betula alleghaniensis* Britton), bitternut hickory [*Carya cordiformis* (Wangenh.) K. Koch], shagbark hickory [*Carya ovata* (Mill.) K. Koch], white ash, black cherry (*Prunus serotina* Ehrh.), northern red oak (*Quercus rubra* L.), white oak (*Quercus alba* L.), American basswood (*Tilia americana* L.), and slippery elm (*Ulmus rubra* Muhl.).

Host material. On 19 April 1986, I cut three small-diameter (10–16 cm diameter at breast height) white ash trees in the woodlot. The trees were cut near the ground and left upright by leaning them against the lower crown branches of nearby trees. The trees were left to undergo natural infestation by bark beetles and other borers, and their natural enemies. The bark along the lower trunk was inspected for frass on multiple occasions in late April and early May to verify that the trees were undergoing infestation by bark beetles such as *H. aculeatus*. In addition, a single bolt (26–42 cm long) was cut from the trunk of one of the ash trees at 2-week intervals from early May to early July to monitor brood development. The length and height of

each bolt were recorded as well as the number of egg galleries, the length of each egg gallery, the distance to the next closest egg gallery when measuring between entrance tunnels, and the length of the longest larval gallery emanating from each egg gallery.

Outdoor rearing. In late June 1986, prior to emergence of the bark beetle brood adults, three 30-cm-long bolts from each of the three study trees were cut and placed in a rearing cage within a covered shed. The three bolts from each tree represented samples taken from the lower, mid, and upper trunk. The remaining trunk sections were left in the woodlot and left leaning upright against the trunks of nearby trees. The rearing cage was ca. 60 cm wide, 45 cm deep, and 45 cm tall. The cage had a wood floor, a sliding Plexiglas front panel, and fine screening on the three other side walls and the upper surface. The cage was placed on a counter within the shed, which had double doors at opposite ends that remained open to allow air flow. The shed received direct sunlight during the early morning hours but otherwise was shaded by large trees, and therefore the temperatures inside the shed were considered similar to ambient conditions. The cage was usually checked, and insect collected, every 1–2 days from late June through mid-October 1986. All bark beetle emergence had ceased by early October. On each collection day, one or more vials were used to collect all insects that were seen in the cage, either walking on the bolts or on the screen walls. All vials were placed in a single, labelled zip-lock plastic bag and frozen. Later, the individual insects were separated into morphospecies and identified by experts: William F. Barr (University of Idaho) identified the Cleridae (Coleoptera), Paul M. Marsh (USDA, Systematic Entomology Laboratory, Beltsville, MD) identified the Braconidae, and Stephen L. Wood (Brigham Young University) identified the Scolytinae. Once identified, the insects were totaled by species and emergence date. Specimens of each species were retained by the identifiers in their personal or institutional collections.

Gallery measurements. In October 1986, several bolts were cut from the trunk and major branches of each of the three study trees and taken to the USDA Forest Service, Insect Unit laboratory on the Michigan State University campus in East Lansing, MI. Each bolt was labelled by tree and trunk location. The length and diameter (inside bark) of each bolt was recorded. On a few bolts that still had nearly all their original outer bark, the number of “exit holes” were counted on the bark surface before debarking. The larger exit holes (ca. 1 mm wide; Solomon 1995) were considered to be made by *Hylesinus* bark beetles, while the

Table 1. Summary data for *Hylesinus aculeatus* egg and larval galleries in bolts cut during May through July 1986 from the trunk of a single white ash tree that was felled on 19 April 1986 and allowed to undergo natural infestation in a woodlot in Michigan. One bolt was cut on each sampling date.

Calendar date in 1986	Julian day	Bolt surface area (dm ²)	No. egg galleries per dm ²	Mean total egg gallery length (mm)	Mean distance to nearest neighbor (mm)	Mean length of longest larval gallery per egg gallery (mm)
11 May	131	4.3	13.1	39 ± 2 a*	21 ± 1 b*	7.1 ± 0.4 c*
25 May	145	9.5	8.9	41 ± 2 a	23 ± 1 a	18.6 ± 0.9 b
7 June	158	7.4	9.7	43 ± 2 a	23 ± 1 ab	2.5 ± 2.3 a
21 June	172	6.5	8.3	42 ± 2 a	24 ± 1 a	36.2 ± 3.1 a
5 July	186	6.8	7.8	44 ± 2 a	23 ± 1 ab	44.2 ± 7.3 a

* Means followed by the same letter (within columns) are not significantly different: mean egg gallery length, $H = 4.01$; $df = 4$; $P = 0.405$; mean distance to nearest neighbor, $H = 11.7$; $df = 4$; $P = 0.020$; and mean longest larval gallery, $H = 48.0$; $df = 4$; $P < 0.0001$.

smaller ones were considered to be made by parasitoids. Tracing back some of the exit holes from the bark surface to the sapwood surface confirmed that the two size classes of exit holes were consistently made by either *Hylesinus* bark beetles or parasitoids. After removing the outer bark from each bolt, several measurements were made on each egg gallery present on the sapwood surface. These included (1) number of egg gallery arms, (2) length of each arm, (3) number of egg niches, (4) number of larval mines, (5) approximate average length of the larval galleries, and (6) distance to the nearest egg gallery, measuring between entrance tunnels.

Data analyses. The non-parametric Kruskal-Wallis rank sum test followed by the Dunn’s test for post-hoc pairwise comparisons were used to compare means of three or more variables such as mean egg gallery length and mean larval gallery length by sampling date in spring 1986. Similarly, the non-parametric Mann-Whitney U test was used to compare means with two variables such as between (1) egg gallery systems with one vs. two arms, and (2) the left arm vs. the right arm for egg galleries with two arms. These nonparametric tests were selected because the data were usually skewed and thus not normally distributed. In addition, the data were $\log_{10}(x + 1)$ transformed prior to analysis to reduce heteroscedasticity. Linear regression was used to explore the relationship between the total number of eggs niches per gallery and total gallery length. Analyses were conducted using an alpha level of 0.05 and the online calculators at <https://www.statskingdom.com>, which uses the R programming language.

Results

Initial egg gallery construction and larval development. On 26 April 1986, a week after the three ash trees were cut, hundreds of frass piles were observed on the bark surface of each tree. Twelve galleries were exposed by cutting with a knife and in all cases two scolytine adults were found in each gallery and assumed to be one female and one male. Most females had already started constructing two egg-gallery arms on opposite sides of the entrance tunnel. Most arms were under 5 mm in length, but a few were already 10 mm long. The two arms of the same egg gallery were usually similar in length (e.g., 6 and 7 mm long) but a few showed distinct differences (e.g., 4 and 10 mm).

Mean egg gallery length (both arms combined) was 39 mm on the first dissection date (11 May) and did not increase significantly during any of the next four sampling dates through 5 July (Table 1). Average lengths of the right and left arms on each egg gallery ($N = 39$) were not significantly different on 11 May: 19.3 ± 1.5 mm for the left arm and 20.3 ± 1.3 mm for the right arm ($U = 665$; $z = 0.96$; $P = 0.339$). Although mean arm lengths did not differ significantly, the actual lengths of the two arms of the same egg gallery differed from 0 to 32 mm, averaging 8.7 ± 1.3 mm. With respect to mean length of the longest larval gallery in each gallery system, values increased significantly from 11 May to 25 May and again from 25 May to 7 June (Table 1).

Seasonal emergence of adult insects. One species of bark beetle (*H. aculeatus*), three species of braconid parasitoids [*Coeloides scolytivorus* (Cresson), *Dendro-*

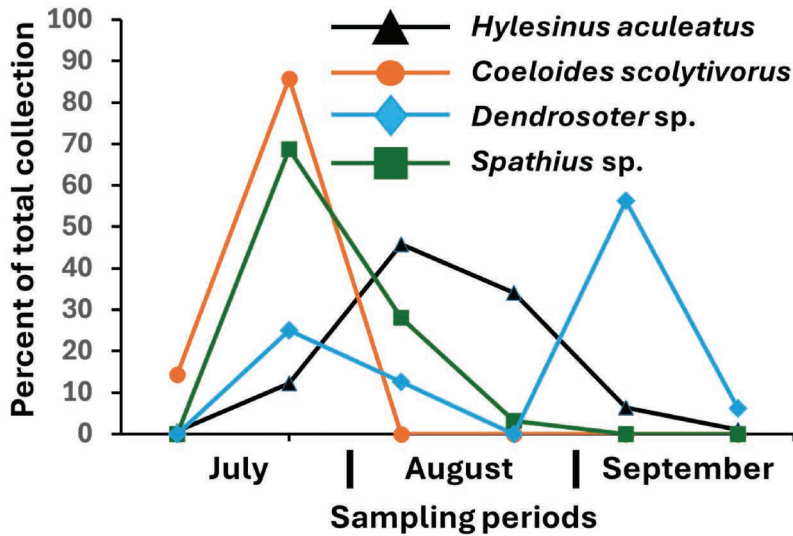


Figure 1. Seasonal emergence in 1986 of adult *Hylesinus aculeatus* bark beetles and three braconid parasitoids (*Coeloides scolytivorus*, *Dendrosoter* sp., and *Spathius* sp.) in Michigan reared from white ash bolts from trees cut in April 1986 and allowed to undergo natural infestation until late June when selected bolts were cut from the trees and placed in an outdoor rearing cage through mid-October. Emergence data were pooled for the first half and second half of each month during July through September by species.

soter sp., and *Spathius* sp.], and one clerid (Coleoptera) predatory beetle [*Enoclerus nigripes* (Say)] were identified from the specimens submitted for identification. No other bark- or wood-boring insects were collected. Notes from Paul Marsh that accompanied the braconid identifications in 1986 stated that the *Dendrosoter* specimens represented an apparently undescribed species and that actual host information was needed to make more precise determination of the *Spathius* specimens. At the time I submitted the *Spathius* specimens collected in the present study in 1986, they were combined with other *Spathius* specimens, as well as other parasitoids, that I had reared from shagbark hickory and slippery elm (Haack 2020), and also tamarack [*Larix laricina* (Du Roi) K. Koch] (Haack and Blank 2023). Moreover, both the parasitoids and the bark- and wood-boring beetles from the above four tree species were mailed to the identifiers at about the same time in late 1986 and therefore the identities of the likely host beetles were not provided to the parasitoid identifiers.

Overall, 1,091 *H. aculeatus* adults were collected from the bolts in the rearing cage in 1986, starting on 6 July and ending on 2 October. Similarly, 55 braconid parasitoids were collected from the rearing cage,

including seven *C. scolytivorus* during 6–28 July, 16 *Dendrosoter* sp. during 26 July to 16 September, and 32 *Spathius* sp. during 25 July to 16 August. Peak emergence of the *H. aculeatus* adults occurred in early August. By contrast, peak emergence of *C. scolytivorus* and *Spathius* sp. adults occurred in late July, while *Dendrosoter* sp. showed peaks during both late July and early September (Fig. 1). Three *E. nigripes* adults were reared from the ash bolts: one was collected on 22 September and two on 29 September.

Gallery measurements. Detailed measurements were made on 11 bolts from the three study trees that varied in diameter from 3–12 cm. The combined total length of all 11 bolts was 3.7 m. Of the 590 *H. aculeatus* galleries measured on all 11 bolts, 23 (3.9%) had only one distinct arm, while 567 (96.1%) had two distinct arms. As expected, galleries with two arms vs. those with one arm were significantly longer and had more total eggs and larvae per gallery on average (Table 2). However, one-arm and two-arm galleries were similar in average number of eggs and larvae per centimeter of gallery, larval gallery length, percent egg-to-larval survival, and distance to the next closest entrance tunnel. Mean values for various gallery measurements are also presented in Table 2 for all 590 galleries combined. Linear

Table 2. Summary data for *Hylesinus aculeatus* egg and larval galleries in bolts sampled in fall 1986 that were obtained from white ash trees cut in spring 1986 and allowed to undergo natural infestation in a woodlot in Michigan.

Parameter	Galleries with one arm (N=23) Mean ± SE (range)	Galleries with two arms (N=567) Mean ± SE (range)	Mann-Whitney U test results	All galleries (N = 590) Mean ± SE
Total gallery length (mm)	20.4 ± 3.6 (5–71)	36.3 ± 0.7 (7–113)	$U = 2096; z = 5.52; P < 0.0001$	35.6 ± 0.7
Total eggs (= egg niches) per gallery	18.2 ± 3.4 (3–60)	32.2 ± 0.7 (2–131)	$U = 2856; z = 4.57; P < 0.0001$	31.7 ± 0.7
Total larvae (= larval mines) per gallery	15.4 ± 3.3 (2–56)	23.4 ± 0.6 (0–108)	$U = 3630; z = 3.61; P < 0.001$	23.1 ± 0.6
Larval gallery length (mm)	13.8 ± 1.2 (4–25)	12.8 ± 0.2 (0–30)	$U = 7422; z = 1.13; P = 0.260$	12.8 ± 0.2
Eggs per cm of gallery	8.8 ± 0.7 (3–15)	8.8 ± 0.1 (1–21)	$U = 6680; z = 0.20; P = 0.844$	8.8 ± 0.1
Larvae per cm of gallery	7.0 ± 0.7 (2–15)	6.3 ± 0.1 (0–15)	$U = 6900; z = 0.47; P = 0.637$	6.3 ± 0.1
Distance to next closest entrance tunnel (mm)	26.0 ± 2.3 (12–48)	28.8 ± 0.7 (3–148)	$U = 6237; z = 0.35; P = 0.724$	28.7 ± 0.7

regression analysis for all 590 galleries found a significant positive relationship between total egg-gallery length and total number of eggs (= egg niches) per gallery (Fig. 2).

For the 567 two-arm egg galleries, average (± SE) length of the left arm (18.7 ± 0.5 mm, range 2–95 mm) did not differ significantly from the right arm (17.6 ± 0.4 mm, range 2–58 mm) ($U = 164,512; z = 0.75; P = 0.494$). Although average length of the two arms did not differ significantly, only 23 of the 567 galleries (4%) had arms of equal length, while 38% and 65% had no more than a 5- or 10-mm difference in total length, respectively (Fig. 3). At the extremes, the left arm of one gallery was 79 mm longer than the right arm, while in another gallery the right arm was 49 mm longer than the left arm.

Infestation and emergence densities. On average, considering the 11 bolts used for egg gallery measurements, there were 7.7 ± 1.2 egg galleries / dm² of bolt surface area (range: 2.4–12.7), 218 ± 28 egg niches / dm² (82–341), and 160 ± 21 larval

mines / dm² (29–258). Emergence densities could only be calculated from five bolts, which had retained all their original bark and thus exit holes could be counted with confidence. These five bolts originated from two of the three study trees and varied from 3 to 9 cm in diameter and had a combined total length of 1.9 m. When making the emergence calculations for each bolt, the number of *H. aculeatus* galleries was subtracted from the total number of bark beetle “exit holes” counted, because the entrance holes of *H. aculeatus* galleries were similar in size to the true exit holes made by *H. aculeatus* brood adults. Using this approach, mean densities were 109 ± 31 exit holes / dm² of bolt surface area (range: 13–197) for *H. aculeatus* brood adults and 4.3 ± 1.8 exit holes / dm² (0.1–10.1) for all parasitoids combined.

Survival estimates. Mean percent egg (egg niches) to larval (larval galleries) survival, based on data for each of the 11 bolts used for egg gallery measurements, was 72.4 ± 4.3% (range: 35.7–88.6%). Similarly, for the five bolts used to count exit holes, average *H. aculeatus* egg (egg niche) to adult

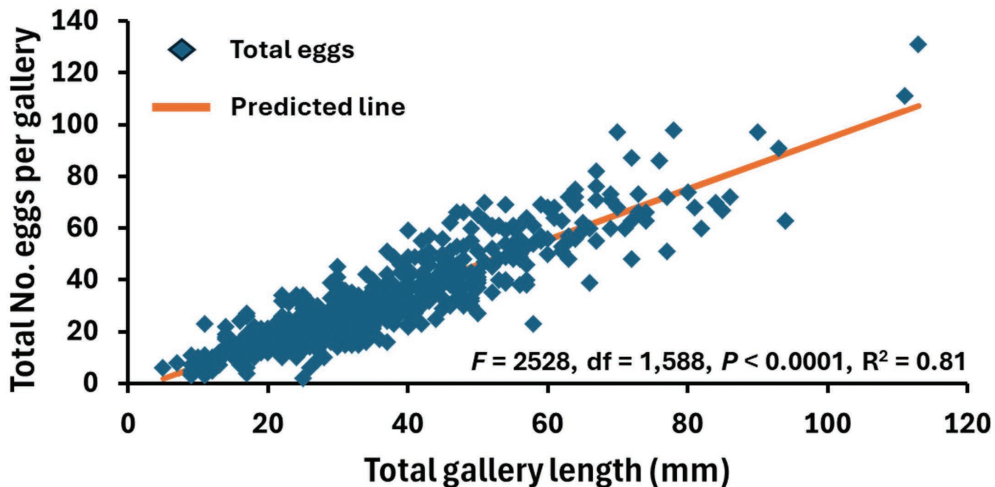


Figure 2. Scatter diagram of total number of eggs (egg niches) per gallery vs. total gallery length for 590 *Hylesinus aculeatus* galleries measured on bolts cut from naturally infested white ash trees in Michigan. Statistical results and predicted straight line curve are shown based on linear regression.

(exit hole) survival was $52.7 \pm 12.9\%$ (range: 11.3–88.6%). Mean percent parasitism of *H. aculeatus* based on exit hole data for the same five bolts was $2.4 \pm 0.9\%$ (range: 0–5.7%).

Discussion

The emergence pattern of *H. aculeatus* brood adults recorded in the current study i.e., starting in early July, peaking in August, and ending in early October, appears credible given that rearing was done in a well-ventilated outdoor shed. The only other account of *H. aculeatus* brood emergence from a northern location was by Dodge (1938) in Minnesota, who simply stated that brood adults emerge in “midsummer.” In studies of the western ash bark beetle, *Hylesinus californicus*, near Calgary, Alberta (Lat. 51° N), Langor and Hergert (1993) noted that field populations of brood adults emerged from 26 July to 5 September 1990.

In Chamberlin’s 1939 treatise on the bark and ambrosia beetles of North America, he wrote admiringly about the gallery systems of *H. aculeatus* as follows: “Of all the scolytid mines known to us, no species excavates a more uniform set of galleries than does this species. Given a plain surface in which to work they are not only exceedingly regular but are almost always exact duplicates of one another, hardly varying in size or arrangement.” Although the galleries appear very uniform, the present study found that total egg gallery length varied from 5 to 113 mm (Table 2). Others have reported similar

ranges in total egg gallery length for *H. aculeatus*: 25–100 mm by Knaus (1886) and Felt (1905), 20–60 mm by Blackman (1922), and 10–98 mm by Hoffman (1938). In *H. californicus*, Langor and Hergert (1993) reported that egg galleries averaged 5.5 cm in length (range: 2–10 cm), and that 5% of the galleries only had one arm. In the European ash bark beetle, *Hylesinus varius* (Fabricius) [or its synonym *H. fraxini* (Panzer)], egg galleries averaged 4.6 cm in length (range 1.0–8.5 cm - estimated from their Fig. 2) (Lukášová and Zimová 2015). Variation in egg gallery length for members of the same bark beetle species is common, often reflecting variation in infestation densities, and when any particular adult beetle arrives on the host plant during colonization. That is, early colonizers, but not necessarily the initial pioneer beetles that may confront strong host tree defenses, often face less competition for phloem resources and thus construct longer egg galleries and have higher reproductive success compared to late arrivers (Wagner et al. 1982, Haack et al. 1987, Anderbrant 1990, Latty and Reid 2010).

It should be noted that of all the reports that I have read on *H. aculeatus*, Felt’s (1905) account was the only one suggesting that each arm of an individual *H. aculeatus* egg gallery is constructed by a different female. Chamberlin (1939) disagreed with Felt (1905), but neither author presented evidence to support their argument. In the case of *H. californicus*, Langor and Hergert (1993) stated that each gallery is initiated by a single female who is soon joined by

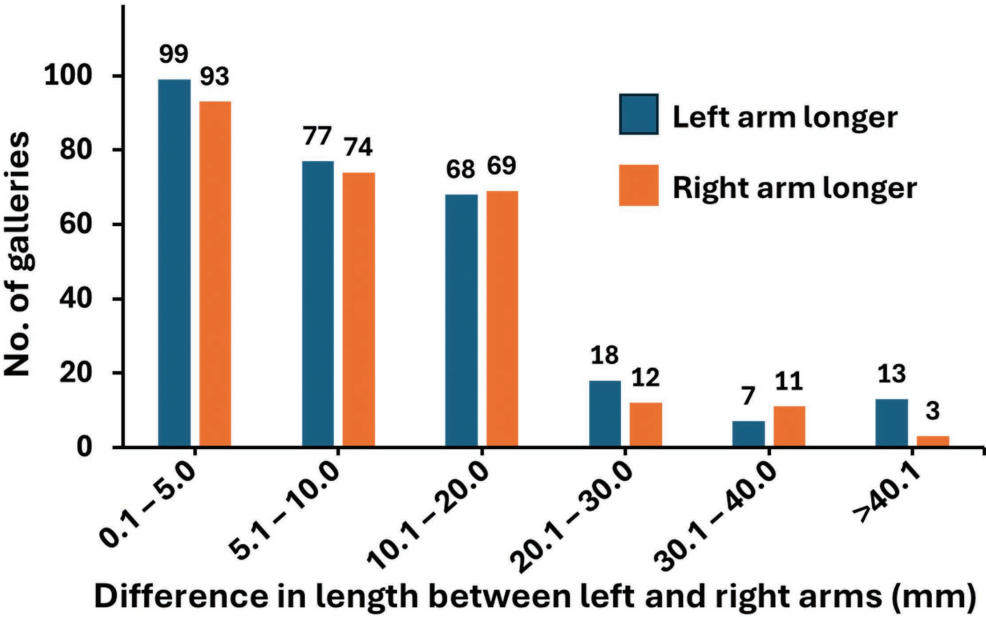


Figure 3. Comparison of arm-length difference in *Hylesinus aculeatus* egg galleries with two arms (N = 567). Egg galleries were measured in bolts cut from white ash trees that were naturally infested in Michigan after brood emergence had ended. Of the 567 galleries, 23 had arms of equal length. The value above each bar is the number of galleries within each arm-length difference category.

one male. Similar scenarios are presented by Solomon (1995) for *Hylesinus criddlei* (Swaine), and by Shepherd et al. (2010) for *Hylesinus pruinosus* Eichhoff. In the present study, careful notes were taken only during late April on the number of *H. aculeatus* parent adults in each gallery, and that is when a single pair of adults was found in each of 12 galleries dissected. In Europe, Rudinsky and Vallo (1978) stated that *H. varius* egg galleries are initiated by one female, but later a second female may enter the same gallery, especially when the parent-adult male has left the gallery. In follow-up studies, Lukášová and Zimová (2015) never found two *H. varius* females in the same egg gallery in more than 350 galleries inspected, whereas Løyning and Kirkendall (1999) found two females in 4 of 114 galleries. Given the above, it is possible that two *H. aculeatus* females were present in some of the egg galleries measured in the present study.

With respect to the number of *H. aculeatus* larvae per gallery, Hoffman (1938), working in New Jersey, recorded an average of 35 larval galleries per egg gallery (range: 2–95), compared to 23 in the present study (Table 2). This difference likely reflects, in part, that the egg galleries measured

by Hoffman (1938) averaged 45 mm long compared to 35.6 mm in the present study. Based on data in Table 2, nearly 9 eggs are laid on average per centimeter of gallery, so if adjusted to equal gallery lengths the number of larval mines would have been more similar between the two studies. Other possibilities for more larval mines per gallery occurring in the Hoffman (1938) study include: (1) more eggs were laid per unit length of gallery, (2) fewer egg niches lacked eggs, and (3) a higher percentage of the eggs hatched in the Hoffman study.

In other *Hylesinus* species, Langor and Hergert (1993) reported that *H. californicus* females laid an average of 21.3 eggs per gallery. Their value is based on actual eggs found, not egg niches, given that they noted that 12% of the egg niches lacked eggs. In the case of *H. varius*, Løyning and Kirkendall (1999) reported an average of 43.7 eggs per gallery where galleries averaged 38.7 mm long. By contrast, Lukášová and Zimová (2015) reported 63.6 eggs per *H. varius* gallery where galleries averaged 46.3 mm long.

With respect to attack density, Hoffman (1938) reported an average value of 9.9 galleries / dm² of bark surface area based on an examination of about 0.7 m² of bark from

a single tree. That value compares somewhat closely with the average value of 7.7 galleries / dm² of bolt surface area reported in the present study. By contrast, Lukášová and Zimová (2015) reported a relatively low average attack density of 1.2 galleries / dm² for *H. varius* infesting European ash (*Fraxinus excelsior* L.).

Mean percent parasitism was relatively low in the current study (2.4%), when compared to other studies. For example, Blackman (1922) stated that in one case as much as 90% of the *H. aculeatus* brood was killed by hymenopteran parasitoids, while Hoffman (1938) reported 32% parasitism in his study. In the studies of *H. californicus* by Langor and Hergert (1993), they estimated that parasitism caused about 17% of the egg-to-adult mortality, and that late-instar larvae and pupae were the primary prey.

Regarding the three parasitoid species reared in the present study, Hoffman (1938) also reared *C. scolytivorus* and a species of *Spathius*, as well as a species of *Eurytoma* (Hymenoptera: Eurytomidae) in New Jersey. Similarly, Beal and Massey (1945), working in North Carolina, reared *C. scolytivorus* and *Eurytoma* sp. from white ash infested with *H. aculeatus*. The *Spathius* species reared in the present paper, as well as those by Hoffman (1938), could have been *Spathius laflammei* Provancher (= *Spathius benefactor* Matthews, and some *Spathius canadensis* Ashmead), which has been reared from *H. aculeatus* and other bark beetles of hardwood trees (Marsh and Strazanac 2009). As for the *Dendrosoter* specimens reared in the present study, I have no information if they were ever described as a new species. One possibility is that they were *D. protuberans* (Nees), a European species first released in Michigan and elsewhere in the 1960s for biological control of the smaller European elm bark beetle, *Scolytus multistriatus* (Marsham) (Kennedy 1970, Truchan 1970, Truchan and Butcher 1970). In Europe and North Africa, *D. protuberans* has been reared from several hardwood-infesting scolytines, including *H. varius* and *Hylesinus taranio* (Danthoine) [= *H. oleiperda* (Fabricius)] (Mendel 1986, Campos and Lozano 1994, Jardak et al. 2002). *Dendrosoter* species native to North America use conifer-infesting bark beetles and weevils as prey (Marsh 1979). In Alberta, Langor and Hergert (1993) reared various species of Braconidae, Eurytomidae, and Pteromalidae from *H. californicus*.

The clerid *E. nigripes* is native to much of North America east of the Rocky Mountains (Chapman et al. 2025). This clerid is a known predator of many bark- and wood-boring weevils and bark beetles on both conifers and hardwoods, including

ash [Böving and Champlain 1920 (reported as *Enoclerus quadriguttatus* Olivier, which is now a synonym of *E. nigripes*), Gosling 1980, Chapman et al. 2025]. In Mississippi, Blackman (1922) noted numerous *E. nigripes* (reported as *E. quadriguttatus*) adults on the bark surface of ash trees that were being colonized by *H. aculeatus*.

Cognato et al. (2009) recognized three species of *Hylesinus* as occurring in Michigan: *H. aculeatus*, *H. criddlei*, and *H. pruinosis*. A fourth species of *Hylesinus* was reported for Michigan by Rabaglia et al. (2019): *H. fasciatus* LeConte. Ash is the host tree for all four of these *Hylesinus* species. Although the specimens that I submitted to Stephen L. Wood in 1986 were identified as *H. aculeatus*, it is possible that other *Hylesinus* species were present on one or more of the study trees, but inadvertently not collected or not submitted for identification. However, in Ohio, where at least three ash-infesting *Hylesinus* species occur (Rabaglia et al. 2019, Atkinson 2026), *H. aculeatus* was the only *Hylesinus* species collected in ash branches sampled in Ohio by Ulyshen et al. (2012).

There are still many unanswered questions about *H. aculeatus* and many other *Hylesinus* species. For example, is maturation feeding required by *H. aculeatus* adults when they become active in spring and where does it occur? Likewise, if multiple species of *Hylesinus* infest the same tree, do they partition themselves vertically to any degree along the trunk and branches? And thirdly how has the widespread mortality of ash trees throughout North America caused by the exotic emerald ash borer, *Agrilus planipennis* Fairmaire (Coleoptera: Buprestidae) impacted the various North American *Hylesinus* species? Various authors (Gandhi and Herms 2010, Wagner and Todd 2015, 2016) have stated that the North American *Hylesinus* species, along with many other invertebrates that are ash-specialists, are at risk of extirpation due to widespread ash mortality caused by *A. planipennis*.

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