

Observations on the Oak Twig Pruner, *Anelaphus villosus* (Coleoptera: Cerambycidae), in Michigan: Size of Twigs Pruned, Insect Survival, and Seasonality of Twig Drop

Robert A. Haack

USDA Forest Service, Northern Research Station, 2601 Coolidge Rd, Suite 206,
East Lansing, Michigan 48823 (Emeritus). (e-mail: robert.haack@usda.gov).

Abstract

The oak twig pruner [OTP; *Anelaphus villosus* (Fabricius)] is likely a species complex, with *A. parallelus* (Newman) recently recognized as a synonym. The *parallelus* form of *A. villosus* is considered the subject of this paper. In Michigan, OTP has a 2-year life cycle, with twigs pruned primarily in even-numbered years and adults emerging from the fallen twigs in odd-numbered years. During 1990 to 2011, I studied various aspects of OTP life history in southern Michigan (Ingham County). Based on measurements from over 300 infested oak twigs, they averaged 43.1 cm long, 9.4 mm in diameter at the pruned end, weighed 22.9 g (dry weight of woody material), and had 57 leaves. OTP adults emerged in 1991 from 15.9% of 290 pruned twigs that had fallen in 1990 and were left on the forest floor until December 1990 when placed in individual sleeve cages and later reared indoors in early 1991. Likely parasitoids of OTP emerged from 15.5% of these same 290 twigs. No linear relationship was found between the dry weight of OTP adults and the size or weight of the twigs in which they developed. During inspections along the same 1-km-long forest path from 1994 to 2011, recently-fallen pruned twigs were only found in even-numbered years, usually starting in late May to early June, peaking between late June to mid-July, and ending between August to December. The annual number of pruned twigs found along this same 1-km section of trail, varied from a low of 24 twigs in 2004 to a high of 168 in 2006. For all years combined, 89% of the recently fallen infested twigs collected on the ground in June had green foliage, compared with 52% of the twigs collected in July, 7.3% in August, and 2.6% in September.

Keywords: *Anelaphus parallelus*, Cerambycidae, longhorned beetle, wood borer, twig pruner, population cycles

Until recently, the scientific name of the beetle known as the oak twig pruner (OTP) was *Anelaphus parallelus* (Newman) (Coleoptera: Cerambycidae). However, *A. parallelus* is now considered a synonym of *Anelaphus villosus* (Fabricius) (Lingafelter 2020). Currently, there are 18 synonyms listed under *A. villosus*, including *A. parallelus* (Lingafelter 2020, Bezark 2023). Earlier, based on detailed rearing studies, Gosling (1978, 1981) reported that the “true” oak twig pruner in Michigan was *A. parallelus*, which oviposits on living host twigs, whereas typical *A. villosus* oviposits on already dead host material, and usually branches larger in diameter than the twigs infested by *A. parallelus*. When Lingafelter (2020) synonymized *A. parallelus* under *A. villosus*, he stated that he found no morphological features that could be used to consistently differentiate the two taxa. Although Lingafelter (2020) recognized that Gosling (1978, 1981) had shown differences in the biologies of *A. parallelus* and typical *A. villosus* in Michigan,

he felt that this could simply be an example of “intraspecific niche diversity” in the behavior of *A. villosus* in different parts of its range. Soon following Lingafelter’s (2020) revision, Brown et al. (2021) reported that *A. parallelus* and typical *A. villosus* could be separated by DNA barcoding as well as when using several morphological measurements together rather than just one or two. On BugGuide, Andrew (2021) summarized a conversation with S. W. Lingafelter, stating that the holotype of *A. parallelus* was actually a specimen of typical *A. villosus*, and that the form previously called “*parallelus*” may prove to be a distinct species. Considering that *A. villosus* is likely now a species complex, I will regard the insect discussed in the present paper to be the *parallelus* form of *A. villosus* as discussed in Gosling (1978, 1981), given that (1) all infested twigs in the current study were living at the time of oviposition, and (2) several of the adults reared in the present study were all confirmed as *A. parallelus* by David C. L. Gosling, with some

retained in his collection. When using the acronym OTP in the present paper, I will be referring to the *parallelus* form of *A. villosus*.

In Michigan, OTP has a two-year life cycle with most infested twigs being pruned by larvae and falling to the ground in even-numbered years and adults emerging from those twigs in odd-numbered years (Gosling 1978, 1981). OTP is native to eastern North America where it infests primarily oaks (*Quercus*), but also species of hickory (*Carya*) and walnut (*Juglans*) (Gosling 1978, Brown et al. 2021). A few other hardwood genera have been reported as OTP hosts by Linsley (1963) and MacRae and Rice (2007).

The genus *Anelaphus* was first proposed by Linsley (1936), with other generic designations over time being *Elaphidion*, *Elaphidionoides*, and *Hypermallus* (Casey 1912, Linsley 1963, Skiles 1985). Therefore, several scientific names can be found in the literature for species now in the genus *Anelaphus*. In the early literature, larval pruning of living twigs was credited primarily to typical *A. villosus*, with the *parallelus* form seldom mentioned (Clarkson 1885, Hamilton 1887, Packard 1890, Felt 1905, Chittenden 1910). This practice was followed by many later authors in the 1900s as well as Knull (1946), Craighead (1950), Duffy (1960), Linsley (1963), Baker (1972), Drooz (1985) and (Solomon and Payne 1986). One of the first authors to accept Gosling's (1978, 1981) distinction between the type of host material used for oviposition (living vs. dead) by the *parallelus* form and the typical form of *A. villosus* was Solomon (1995).

Many aspects of the OTP life cycle are relevant to the present study and are well described by Gosling (1978, 1981). Adult females oviposit in early summer, usually at the base of buds on short live twigs. During the first summer of development, the larva consumes most of the wood in the short twig and then tunnels into the node of the adjoining larger twig where it overwinters. Feeding is resumed the following spring in the larger twig, where it tunnels near the center for about 2–3 cm, proximad from the node where it had entered. At this point, usually in late June to early July in Michigan, the larva creates its pruning cut by removing a disk of wood through a series of gradually increasing arcs, leaving only the bark intact. The larva then plugs its tunnel at the pruning cut with shredded wood (Figs. 1A, 1B) and then continues to develop within the twig. The infested twigs break away from the tree soon after the pruning cut is made, often in response to strong wind. Adult emergence occurs the following summer, usually in June in Michigan. OTP adults are nocturnal and are attracted to UV-lights

(Yanega 1996) as well as certain lures (Miller et al. 2015, 2017).

The Dansville State Game Area (42.52° N, 84.32° W) is located in Ingham County, Michigan, and covers about 4800 ac (1942 ha). From 1987 through 2011, I walked our family dogs along the Game Area's trails multiple times monthly throughout every year. In early summer of 1990, I noticed several recently fallen oak twigs along the Game Area trails that were likely infested with OTP. I collected several of the pruned twigs in 1990 with the objective of characterizing them by size as well as attempting to rear adult beetles from the twigs in 1991. From 1994 through 2011, my objectives were to consistently record the seasonality of recently fallen, OTP-pruned twigs along a defined stretch of trail at the Game Area as well as record year-to-year variation in the number of OTP-pruned twigs. These observations add to our understanding of the life history of OTP in the northern portion of its geographic range and can serve as baseline data for future evaluation of possible "species" differences between the *parallelus* form and the typical form of *A. villosus*.

Methods

1990–1991 OTP-pruned twig study.

During July 1990, over 300 recently fallen oak twigs were collected along the trails at the Dansville State Game Area. Only twigs that appeared pruned by OTP were collected, as evidenced by the typical smooth pruning cut made by the larva at the end of the twig and the typical 2-mm-wide hole near the center of the pruned end that was usually plugged with shredded wood (Gosling 1978; Figs. 1A, 1B). In addition, a preference was given to those twigs that appeared to have all of their original current-year foliage intact. The selected twigs were taken to a woodlot behind the author's family home so they could be closely monitored (42.5481° N, 84.3189° W). This woodlot covered about 24 ha when neighboring properties were included and was largely mature northern hardwoods (beech-maple type, Cohen 2004) with several mature northern red oak (*Quercus rubra* L.) and white oak (*Quercus alba* L.) trees present (Haack 2020). The twigs were flagged and placed on the forest floor along the edge of a trail within the woodlot, which also had a known population of OTP present.

In early December 1990, the twigs were briefly taken indoors to my laboratory on the Michigan State University campus to make various measurements. Several aspects of each twig were evaluated and recorded: (1) maximal twig length (cm), by following the branch from the pruning cut to the tip of the longest twig; (2) twig diameter (mm) at the

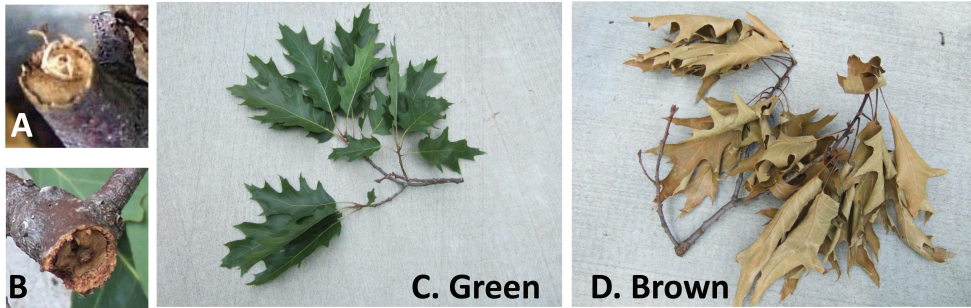


Figure 1. Examples of OTP-pruned red oak twigs that had recently fallen to the forest floor, showing (A) the end of a pruned red oak twig with the central larval tunnel plugged with long pieces of shredded wood, (B) the end of another pruned red oak twig where the larval tunnel is plugged with shredded wood that is not exerted much beyond the wood, (C) a twig with green foliage that indicates it fell soon after the larva made its pruning cut, and (D) a twig with brown foliage that indicates the twig fell to the forest floor several days after the larva made the pruning cut.

pruned end of the twig, including the outer bark; (3) whether or not the plug of shredded wood was present; (4) diameter of the side twig (mm) in which the larva initially bored, measured near its base where it joined the next larger twig that was eventually pruned; (5) distance (mm) from the base of initial side twig to the pruning cut; and (6) total number of leaves per twig. Soon afterwards, all leaves and acorns were removed from each twig and most side branches were cut off and dried to a constant weight (g), using a drying oven set at about 60 °C. The remaining central portion of each twig, which was not initially weighed and likely contained an OTP life stage, was bagged individually in a labelled, fine-mesh nylon sleeve-cage that was closed at both ends and then stored outdoors in a screen house.

In February 1991 (exact date not recorded) the bagged twigs were taken indoors and laid flat on countertops in my laboratory at Michigan State University. The bags were checked at least three times weekly for OTP adults and other insects that were likely natural enemies (e.g., Diptera and Hymenoptera). The day of collection was recorded for each. Several of the newly emerged OTP adults were dried to a constant weight, which later were used in regression analyses with various twig parameters. After adult emergence had stopped for about five weeks the twigs were dissected in June 1991 to record any insects still present inside the larval gallery, their life stage, and if they appeared alive or dead. After an insect had emerged from a twig, or once the twig was dissected, all woody material from each twig was collected and dried to a constant weight. Later, the dry weights of both the initial side twigs that had been removed in December 1990 and the main twig from 1991 were

added together to estimate the total woody biomass of each pruned twig.

Analyses. Of the 311 twigs collected, 282 were from red oaks and 26 from white oaks based on their foliage. There were three pruned twigs that had no foliage when collected. Summary statistics were produced for each measured twig variable using Excel's statistical toolpak. Initial analyses (*t*-test) of the measured twig parameters found no significant differences between red oaks and white oaks for most measured twig parameters (twig diameter, $P > 0.16$; number of leaves per twig, $P > 0.45$; twig dry weight, $P > 0.20$; but not for average twig length with red oaks being significantly longer (44.2 cm) than white oaks (33.1 cm), $P < 0.013$). Given that the pruned twigs of the red and white oaks were mostly similar the data were combined for both oak species. The twig data were usually complete for all twigs but occasionally some had missing parts (e.g., the side twig used by the larva in its first year was at times broken off). Linear regression was used to explore relationships between OTP dry weight and twig length, twig dry weight, twig diameter at the pruned end, and number of leaves per twig. Similar linear relationships were explored among the measured twig variables themselves. The *z*-test was used to compare two population proportions for various insect and tree variables. An alpha level of 0.05 was used for significance in all tests. In addition, the number of twigs from which insects emerged or where insects were found inside upon dissection were summarized.

1994–2011 seasonal twig drop study. Starting in 1994 and going through 2011, detailed notes were taken on the number and condition of OTP-infested

twigs found along the same ca. 1-km-long section of trail at the Dansville State Game Area. This trail section was bordered by trees along nearly its entire length, passing through mostly mature hardwood forest of the dry-mesic (oak-hickory) type found in southern Michigan (Lee 2007). There were 41 red oak trees and 9 white oak trees of various sizes that had some of their crown branches overhanging this section of trail. Some of the other tree species along the trail, but not counted, were American basswood (*Tilia americana* L.), black cherry (*Prunus serotina* Ehrh.), black walnut (*Juglans nigra* L.), eastern cottonwood (*Populus deltoides* W. Bartram ex Marshall), and shagbark hickory [*Carya ovata* (Mill.) K. Koch]. Site visits usually occurred 3-6 times monthly from March through November, and usually at least twice monthly during the winter months of December through February. During each visit, the number of recently fallen, OTP-pruned twigs along the path was recorded by tree species and general color of the foliage (green vs. brown; Figs. 1C, 1D). Green foliage was considered to indicate a twig that had recently been pruned by the larva and soon fell to the ground from the parent tree, while brown foliage indicated a twig that had been pruned by the larva sometime earlier but remained in the crown for considerable time before falling to the ground. Only twigs within about 2 m of either side of the trail and with the typical OTP larval pruning cut were counted. After the twig data were recorded, the twigs were tossed about 4–6 m to the side of the trail on the forest floor so they would not be counted again. In addition, the twigs were not removed to any other location so as not to influence the local OTP population.

Data analyses. For each year, the number of infested twigs were summed by month and year. Similarly, the percentage of twigs with either green or brown foliage was calculated by month for all years combined. The z-test was used to compare proportions of various variables.

Results

1990–1991 OTP-pruned twig study.

Twig data were generally complete for over 300 OTP-pruned twigs. Frequency diagrams are shown in Figs. 2 and 3 for four of the measured twig variables. Overall, twigs averaged 43.1 cm long, had a dry weight of 22.9 g for the woody portion (no leaves or acorns), and had 57.3 leaves each (Figs. 2A, 2B, 3B). For a subsample of these twigs (N = 57; all red oaks) there was an average of 2.5 acorns per twig (range 0–23, of which 38 twigs had no acorns). These 57 red oaks twigs were the first twigs processed in December 1990 after which all acorns were simply removed but

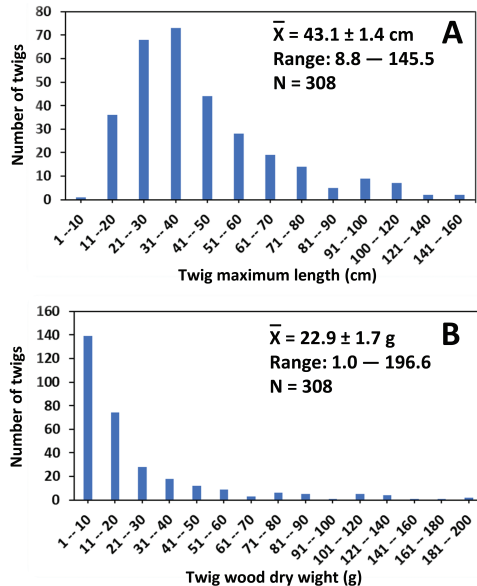


Figure 2. Frequency diagrams and descriptive statistics for OTP-pruned oaks twigs (red and white oaks combined) collected in summer 1990 in Ingham County, Michigan, including (A) maximal twig length (cm) measured from the pruning cut to the tip of the longest twig, and (B) twig dry weight (g) of the woody portion but not including leaves or acorns.

not counted. The twig diameter at the pruned end averaged 9.4 mm (Fig. 3A). In addition, the mean ($\pm$ SE) basal diameter of the side twig that was tunneled by the larva in its first year of development was 5.2 ± 0.1 mm (range 1.5–12.0 mm, N = 212 twigs where the smaller twig was not broken), and the mean distance from the twig's pruned end to where the first-year twig joined averaged 25.8 ± 1.5 mm (range 2–210 mm; N = 222 twigs).

There were 35 twigs from which OTP adults emerged that had both complete twig data and adult beetle dry weight. In the following analysis, all beetles were combined because male and female *Anelaphus* adults are similar in size (Skiles 1985, Lingafelter 2020). For these 35 twigs (4–18.5 mm diameter at the pruned end), no significant linear relationships were found between adult dry weight (77–237 mg) and maximal twig length ($P > 0.32$), twig dry weight ($P > 0.048$), twig diameter at the pruned end ($P > 0.26$), and number of leaves ($P > 0.70$).

As for the twig data, all measured variables were highly correlated with each other. For example, for the 307 twigs with complete data, there were highly significant ($P < 0.0001$) linear relationships between

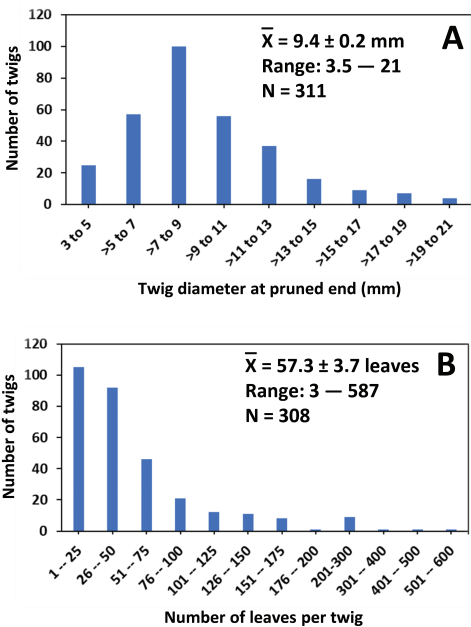


Figure 3. Frequency diagrams and descriptive statistics for OTP-pruned oak twigs (red and white oaks combined) collected in summer 1990 in Ingham County, Michigan, including (A) twig diameter (mm) at the pruned end, including the outer bark, and (B) the total number of leaves per twig.

the number of leaves per twig and maximal twig length ($R^2 = 0.35$), twig dry weight ($R^2 = 0.63$) and twig diameter at the pruned end ($R^2 = 0.42$).

There were 290 twigs that were suitable to include in the survival summary, of which 265 twigs were from red oaks and 25 from white oaks (Table 1). Considering all 290 twigs together, a single OTP adult emerged from about 16% of the twigs, while another 17% contained a single dead OTP larva, pupa, or adult. Parasitoids were reared from about 16% of the twigs, of which about 5% were Diptera (Tachinidae) and 11% Hymenoptera (Ichneumonidae) (Table 1). No twigs produced both an OTP adult and parasitoids. Unfortunately, these parasitoids were not identified to species. No OTP life stages were reared from or found inside the larval galleries of the remaining 52% of the twigs when dissected. The presence or absence of the shredded-wood plug was recorded on 210 of these 290 twigs. Of these 210 twigs, 121 still had the plug present when inspected in December 1990, while 89 twigs did not. Insects (OTP or parasitoids, either emerged or found dead during twig dissection) were found significantly more often in twigs with plugs present (40.5%), than in twigs with no plugs (24.7%; z -test: $z = 2.3882$, $P < 0.017$). As an indication of the order of seasonal adult emergence, using those insects with accurate dates of emergence from the twigs held in the laboratory during spring 1991, the mean ($\pm$ SE) Julian day of emergence was 95.6 ± 0.8 (range: 88–109; $N = 46$) for OTP, 98.2 ± 1.8 (range: 91–126; $N = 25$) for the ichneumonids, and 117.5 ± 8.5 (range: 109–126; $N = 2$) for the tachinids.

1994–2011 seasonal twig drop study. Of the 492 OTP-pruned twigs collected along the 1-km-long trail section

Table 1. Survival data for the oak twig pruner (OTP) and associated parasitoids from 290 oak twigs that were collected in Ingham County, Michigan, in July 1990, maintained unprotected on the forest floor until December 1990, then bagged individually in a fine-mesh sleeve cage and stored in an outdoor screenhouse until February 1991 when brought indoors for rearing, and later dissected in June 1991 if no insects had emerged. Data are presented for red oak twigs and white oak twigs separately and combined. See Methods for more details.

Insect Data	Red oak		White oak		All oaks	
	Number of twigs	Percent	Number of twigs	Percent	Number of twigs	Percent
Emerged OTP adults	45	17.0 %	1	4 %	46	15.9 %
Dead OTP adults	4	1.5	1	4	5	1.7
Dead OTP pupae	3	1.1	1	4	4	1.4
Dead OTP larvae	38	14.3	2	8	40	13.8
Diptera parasitoids	13	4.9	1	4	14	4.8
Hymenoptera parasitoids	27	10.2	4	16	31	10.7
Nothing found in gallery	135	50.9	15	60	150	51.7
Total	265		25		290	

Table 2. Summary data for the annual number of OTP-pruned twigs collected along the same 1-km-section of trail at the Dansville State Game Area, Ingham County, Michigan from 1994 through 2011, and when twig drop began, peaked, and ended in each year. Data are only shown for the even-numbered years because no OTP-pruned twigs fell along the trail in the odd-numbered years.

Year	No.	Timing of twig drop		
		Start	Peak	End
1994	106	Late May	Mid-July	August
1996	138	Early June	Late June	Mid-Sept
1998	61	Mid-June	Mid-July	Early Sept
2000	31	Early June	Late June	Early Oct
2002	57	Mid-June	Early July	Mid-Sept
2004	24	Early June	Late June	Early Sept
2006	168	Early June	Late June	Early Dec
2008	119	Mid-June	Early July	Early Nov
2010	32	Mid-June	Mid-July	Mid-Sept

during 1994 through 2011, all twigs fell to the ground in even-numbered years. In addition, although exact twig counts were not made during 1988–1993 along the same trail, field notes indicated that newly fallen OTP-infested twigs were only observed in the even-numbered years of 1988, 1990, and 1992. The number of OTP-pruned twigs that fell along the trail during each even-numbered year varied from as few as 24 twigs in 2004 to as many as 168 in 2006 (Table 2). Twig drop usually began between late May and mid-June, peaked between late June to mid-July, and ended between mid-August to early December (Table 2, Fig. 4). For all years combined, 89% of the twigs collected in June had green foliage, compared to 52% of the twigs collected in July, 7.3% in August, and 2.6% in September (Fig. 4). Of the 492 pruned twigs, 385 were from red oaks, 93 from white oaks, 2 from shagbark hickories, and 12 from black walnut trees. Considering only the oaks, the proportion of twigs from red oaks ($80.5\% = 385/478$) was not statistically different than the proportion of red oak trees with branches over the trail section that was monitored as mentioned above in the methods (82% ; 41 of 50 oaks trees were red oaks; z -test: $z = -0.2481$, $P > 0.802$).

Discussion

The life cycle of OTP reported herein is similar to Gosling’s (1978) observations in that OTP exhibited a 2-year life cycle in Michigan, with twigs dropping primarily in even-numbered years and adults emerging in odd-numbered years. In support of this synchronous 2-year life cycle, Gosling (1978) summarized museum collection records for field-collected OTP adults from Michigan and showed that 91% of 227 museum specimens were collected in odd-numbered

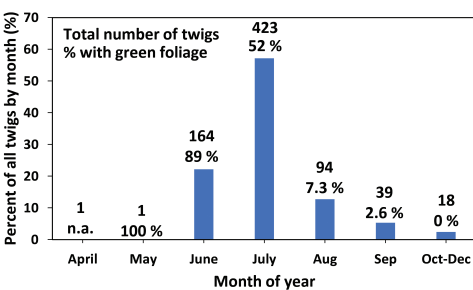


Figure 4. Percent of all recently fallen OTP-pruned twigs collected along the same 1-km section of trail at the Dansville State Game Area in southern Michigan from 1994 through 2010 by month of collection. Above each bar is the total number of twigs collected during the 1994–2010 period as well as the percent of those twigs that had green foliage when they fell to the forest floor and were collected. The one twig collected in April fell before the leaves flushed.

years between 1891 and 1977. In addition, Gosling (1978) showed a similar pattern of collection data for 53 typical *A. villosus* specimens in Michigan museums (87% collected in odd-numbered years between 1913 and 1977). The average size of the OTP-pruned oak twigs recorded by Gosling (1978) was also similar to the values reported here. For example, Gosling (1978) reported that infested twigs were about 10 mm in diameter near the pruned end (vs. an average of 9.4 mm reported here; Fig. 3A) and that the base of the twig used during the larva’s first year of development was generally within 20–30 mm of the pruning cut (vs. an average of 25.8 mm reported here). Similarly, for twig collections made in New York and Pennsylvania, Brown et al. (2016) reported that

OTP-infested oak twigs averaged 9.3 mm in diameter at the pruned end.

The lack of any significant linear relation between OTP adult size (mass) and the various measured twig parameters could indicate that nearly all twigs selected for oviposition were highly suitable for larval development. That is, given that OTP adults and last larval instars are about 3 mm wide [estimated from Gosling (1978) and Brown et al. (2019)], OTP larvae would have had little difficulty tunneling in any of the twigs pruned in the present study that ranged from 3.5 to 21 mm in diameter at the pruned end (Fig. 3A).

Several parasitoids have been reared from OTP-infested twigs in past studies, including the Braconidae (Hymenoptera) *Eubazus denticulatus* (Martin), *Iphiaulax eurygaster* (Brulle), *Meteorus tibialis* Muesebeck, a species of *Atanycolus*, a species of *Digonogastra*, and an unidentified species near *Pambolus*; the Ichneumonidae (Hymenoptera) *Agonocryptus discoidaloides* (Viereck), *Dolichomitus irritator* (Fabricius), and *Helcostizus annulicornis* (Walsh); and the Tachinidae (Diptera) *Zelia* (*Minthozelia*) *ruficauda* (Reinhard) (Gosling 1978, Krombein et al. 1979, Brown et al. 2016, Brown and Dombroskie 2019). It is possible that the parasitoids reared in the present study were some of the species listed above given that two of the ichneumonid wasps (*A. discoidaloides* and *H. annulicornis*) and the one tachinid fly have all been reared from OTP in Michigan by others (Gosling 1978, Krombein et al. 1979). Parasitism apparently occurs after twig drop, given that Gosling (1978), working in Michigan, reported parasitism in twigs that remained on the forest floor until October but not in twigs caged soon after twig drop. Similarly, in New York, Brown and Dombroskie (2019) reported higher rates of OTP adult emergence from bagged twigs compared with unbagged twigs that were placed on the forest floor or suspended in a hedge until October before moved indoors. In the present study, the OTP-pruned twigs were not removed from the forest floor and bagged until December 1990, so there was ample time for parasitism and predation to occur in the field.

Although finding 52% of the OTP-pruned twigs collected in the 1990–1991 study were empty of insects was at first surprising, others have reported similar findings. For example, in one rearing trial by Gosling (1978), he reported that 31% of the twigs that had been left on the ground until October had been opened by red squirrels, *Tamiasciurus hudsonicus* (Erxleben), and another 40% of the twigs showed no evidence of vertebrate feeding but also lacked any

OTP life stage or natural enemy. Gosling (1978) suspected ant (Formicidae) predation as the cause for these empty twigs. Others have speculated that many larvae are dislodged when the twig breaks and falls from the tree or that birds remove the larvae after twig drop (Townsend 1886, Chittenden 1910). Packard (1890) reported that about 75% of the fallen twigs lacked larvae and suggested that many larvae were likely dislodged if the twig broke early while the pruning cut was being made or the larvae were eaten by birds after the twig fell to the ground. Similarly, Solomon (1985), working in the southern United States, reported that larvae of the cerambycid branch pruner *Psyrassa unicolor* (Randall), which is similar to OTP in adult size, were found in only 29% of 121 recently fallen hickory branches that had been pruned by this cerambycid.

The trend that foliage color of recently fallen twigs shifted from mostly green during early summer to mostly brown in late summer (Fig. 4) indicates that most larvae made their pruning cuts during early summer with most twigs falling soon thereafter (i.e., those with green foliage) while others did not fall for several weeks (i.e., those with brown foliage). Similar observations were made by Brown and Dombroskie (2019) in New York, who noted that some pruned twigs became lodged in other canopy branches as they fell and at times remained suspended for several weeks or even months.

As reported here and by Gosling (1978), OTP requires 2-years to complete one generation in Michigan. Moreover, OTP populations are mostly synchronous in Michigan as well as in many other northern states, with twig drop occurring primarily in even-numbered years. For example, in the recent studies in New York and Pennsylvania by Brown et al. (2016) and Brown and Dombroskie (2019), the authors collected recently fallen OTP-pruned twigs in 2010, 2012, and 2014. This same pattern appears to have been dominant over a century ago given that early accounts of large numbers of OTP-pruned twigs, which was sometimes described as damage by the typical form of *A. villosus*, were reported falling in several northern states from Maine and New Jersey west to Michigan and Kansas on only even-numbered years from 1878 through 1910 (Clarkson 1885, Townsend 1886, Packard 1890, Chittenden 1910). The reason for such synchrony is unknown, but perhaps at some earlier time there was a regionwide stress event that negatively affected one population (e.g., first-year larvae that overwinter in twigs in the canopy) more than the other (e.g., second-year larvae that overwinter on the ground in fallen twigs). Although most OTP adults likely emerge in

odd-numbered years in the northern United States and Canada, some adults do emerge in even-numbered years. As evidence, consider that recent research-grade photos on BugGuide.net and iNaturalist.org of OTP from the northern United States and Canada were taken in both odd- and even-numbered years. Note that as of this writing (August 2023), both BugGuide and iNaturalist have accepted Lingafelter's (2020) synonymy and placed all former *A. parallelus* records under *A. villosus*.

Although a 2-year life cycle is typical for OTP in the northern United States and Canada, it may be univoltine in the southern United States (Solomon and Payne 1986). In a study by Miller et al. (2017) in Georgia, where cerambycid adults were captured in baited traps at the same field site in 2012 and 2013, similar numbers of beetles identified then as *A. parallelus* were collected each year (226 adults in 2012 with 40 traps and 219 adults in 2013 with 48 traps). Such collection records suggest a stable population of OTP in this Georgia study area but do not clarify if the beetle is univoltine in Georgia or has a 2-year life cycle with individuals evenly split between even- and odd-numbered years. Using data from SCAN-bugs.org (SCAN 2023) for research quality observations from iNaturalist.org for both *A. parallelus* and *A. villosus*, which were still kept separate as of August 2023, I found that photos of adults that were usually observed at lights were taken most often in March in five southern states (Alabama, Florida, Georgia, Mississippi, and Texas; range December to May, $N = 91$ observations) compared with mostly in July in four northern states (Maine, Michigan, Minnesota, and New York) and two Canadian provinces (New Brunswick and Ontario; range May to September, $N = 21$). With peak adult emergence occurring about three months earlier in the southern portion of the beetle's range, it is likely that both the *parallelus* and typical forms of *A. villosus* can complete their life cycle in a single year in the southern United States; however, such a generalization needs confirmation with further data across the southern states.

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