

Could the European *Thanasimus formicarius* Outcompete the North American *Thanasimus dubius* (Coleoptera: Cleridae) if Introduced to North America?

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Abstract

A federal quarantine was enacted in the United States (US) in the fall of 1992 in response to discovery of the Eurasian pine shoot beetle, *Tomicus piniperda* (L.) (Coleoptera: Scolytinae), in July 1992 in Ohio. The quarantine regulated movement of pine products (e.g., Christmas trees, nursery stock, and logs) at the county level from infested to uninfested US states. A classical biological program was considered for *T. piniperda* starting in 1995, focusing on the Eurasian clerid beetle *Thanasimus formicarius* (L.) (Coleoptera: Cleridae), an important predator of *T. piniperda*. Concerns were raised in 1996 that if *Th. formicarius* were released in the US it possibly could outcompete the native clerid *Thanasimus dubius* (F.). We conducted a series of laboratory tests in 1996 to compare survival rates of *Th. formicarius* and *Th. dubius* larvae when added to bark beetle galleries on red pine (*Pinus resinosa*) bolts. Bolts were infested with one of three bark beetle species: *Ips grandicollis* (Eichhoff), *I. pini* (Say) or *T. piniperda*. The clerid species were added separately on some bolts or together on other bolts, sometimes at the same time or with *Th. formicarius* preceding *Th. dubius* by a week. For all treatments combined, 8.0% of *Th. dubius* larvae survived to adults compared to 4.4% of *Th. formicarius*. Survival of *Th. dubius* was higher than *Th. formicarius* on bolts infested with *I. grandicollis* and *I. pini*, but similar on bolts infested with *T. piniperda*. Overall, our results suggest that *Th. formicarius* would not outcompete *Th. dubius* if introduced. Although aware of our findings in 1997, USDA APHIS (United States Department of Agriculture, Animal and Plant Health Inspection Service) decided, based on the regulatory and pest status of *T. piniperda*, that release of *Th. formicarius* in the US was not warranted.

Keywords: Bark beetles, checkered beetles, biological control, survival, competition

Most members of the beetle (Coleoptera) family Cleridae are predacious as both larvae and adults (Opitz 2002, Chapman et al. 2025). Several clerid species prey on bark- and wood-infesting beetles in the families Bostrichidae, Buprestidae, Cerambycidae, and Curculionidae, the latter which includes bark beetles in the subfamily Scolytinae (Böving and Champlain 1920, Gosling 1980). Clerids in the genus *Thanasimus* Latreille are mostly predators of conifer-infesting bark beetles and are native to Asia, Europe, northern Africa, Central America, and North America (Person 1940, Opitz 2002, Schroeder 2003, Kim and Jung 2006, Li and Bai 2007, Löbl and Smetan 2007, Yuan et al. 2012, Chapman et al. 2025). *Thanasimus* adults utilize bark beetle pheromones and tree volatiles such as α-pinene and ethanol to locate their prey or trees where their prey will likely occur (Vité and Williamson 1970,

Bakke and Kvamme 1981, Herms et al. 1991, Poland and Borden 1997, Schroeder 2003, Miller 2023).

As of 2026, 582 species of Scolytinae are known to occur in North America north of Mexico, of which 66 were introduced from other continents (Atkinson 2026). The pine shoot beetle *Tomicus piniperda* (L.), a Eurasian bark beetle, is one of these 66 exotics, being first discovered in the United States in July 1992 in Ohio (Haack and Kucera 1993). Subsequent surveys found *T. piniperda* in several more locations in Ohio as well as in five nearby US states by the end of August 1992, indicating that it had been present and spreading for many years prior to its discovery. Subsequent DNA analyses suggested there had been at least two separate introductions of *T. piniperda*: one likely in Ohio at a maritime port on Lake Erie and the second at a port in Illinois or Indiana near

the southern tip of Lake Michigan (Carter et al. 1996).

The first specimens from Ohio were confirmed as *T. piniperda* by Dr. Stephen L. Wood, a scolytine expert at Brigham Young University. In his letter dated 16 July 1992, he wrote “this species is the notorious *Tomicus piniperda*, the second most destructive [bark beetle] in Europe and the most destructive on pine.” The discovery of *T. piniperda* along with Dr. Wood’s letter caused great alarm throughout the major pine-growing areas of the US, especially in the South and West. Starting in September 1992, several uninfested US states initiated quarantines on various pine products (e.g., pine logs, nursery stock, and Christmas trees) from the six infested states. However, in November 1992, USDA APHIS (United States Department of Agriculture, Animal and Plant Health Inspection Service) imposed a federal quarantine, that superseded all state quarantines, which regulated movement of pine host materials from regulated (infested) counties to unregulated (uninfested) counties within the US (USDA APHIS 1992).

Planning for a possible classical biological control program for *T. piniperda* was initiated in 1995 by individuals within three USDA agencies: APHIS, Agricultural Research Service (ARS), and Forest Service. Biological control was considered for various reasons. First, *T. piniperda* appeared to be spreading rapidly in the US, being found in 43 counties by the end of 1992, 92 by the end of 1993, 118 at the end of 1994, and 147 by the close of 1995 (Haack et al. 1997, Haack and Poland 2001). Second, although there had been no *T. piniperda* outbreaks in US forests during the early 1990s, many pine tree nurseries and pine Christmas tree farms reported high infestation levels throughout the regulated states. And third, because of *T. piniperda*’s relatively low threshold temperature for flight (10–12° C; Bakke 1968), field studies showed that *T. piniperda* adults became active 4–8 weeks earlier in spring than native pine-infesting bark beetles and their associated natural enemies in the Great Lakes region (Haack and Lawrence 1995a, 1995b; Bright 1996). As part of the planning process, a literature search was conducted for the natural enemies of *T. piniperda* in Europe and Asia. Some of the key papers reviewed were Hérard and Mercadier (1996), Mills (1985), Schroeder (1996), and Schroeder and Weslien (1994a, 1994b). In addition, several European and Asian forest entomologists that had experience with *T. piniperda* and its natural enemies were consulted, including Alf Bakke (Norway), Yuri Baranchikov (Russia), Bo Långström (Sweden), Martin Schroeder (Sweden), and

Jan Weslien (Sweden). The consensus was that *T. piniperda* populations were most impacted by the predators *Thanasimus formicarius* (L.) and *Rhizophagus depressus* (F.) (Coleoptera: Monotomidae). However, of these two predators, *Th. formicarius* was considered the most important natural enemy of *T. piniperda*, especially given that it has a similar low-temperature threshold for flight like *T. piniperda* (Hérard and Mercadier 1996, Schroeder 2003) and it can cause high levels of mortality to both *T. piniperda* adults and larvae (Schroeder 1996).

Once the decision was made to focus on *Th. formicarius*, collections began in France in 1995 by USDA ARS EBCL (European Biological Control Laboratory, Montpellier, France) entomologists Dominique Coutinot and Richard J. Dysart. They collected 199 adults in 1995 and 2,322 in 1996. The adult clerids were shipped in batches to the USDA ARS Beneficial Insects Introduction Research Unit in Newark, Delaware, headed by Roger W. Fuester and Lawrence R. Ertle, for initial screening and rearing. At first, the *Th. formicarius* adults were maintained at the quarantine facility in Newark, with their eggs and larvae shipped to the USDA APHIS biological control laboratory in Niles, Michigan. Later, many *Th. formicarius* adults from France were shipped to Niles soon after initial screening at Newark. A mass-rearing program for *Th. formicarius* was developed at Niles, led by David R. Prokrym. Initially, *Th. formicarius* larvae were reared on wax moth larvae, *Galleria mellonella* (L.) (Lepidoptera: Pyralidae), but soon laboratory colonies of the bark beetles *Ips pini* (Say) and *T. piniperda* were developed and used as prey.

Although no evidence of establishment exists now (2026), *Th. formicarius* was twice released in the US and *Th. formicarius* adults have been field collected at two locations in Canada. During 1892–1894, over 2,000 *Th. formicarius* adults and larvae from Germany were released at multiple locations in West Virginia to help control the scolytine *Dendroctonus frontalis* Zimmermann (Hopkins 1899). Again targeting *D. frontalis*, 200 *Th. formicarius* adults from the former Soviet Union were released in Mississippi in 1980 (Miller et al. 1987). Establishment of *Th. formicarius* has never been confirmed in either Mississippi or West Virginia. In Canada, one *Th. formicarius* adult was collected near Montreal, Quebec in the 1940s and two were collected in Halifax, Nova Scotia in 2001 (Webster et al. 2012). No additional *Th. formicarius* have been collected at either location, suggesting that establishment did not occur and that the beetles captured likely emerged from solid wood packaging associated with international cargo that arrived at the ports of Montreal and Halifax.

There have also been a few erroneous reports of *Th. formicarius* releases in the US. For example, Opitz (2002) correctly stated that *Th. formicarius* was released in the US in the 1890s but incorrectly stated that it was again released in the late 1900s. Opitz was likely referring to the present study, where *Th. formicarius* was brought into the US but never released. Webster et al. (2012), citing Opitz (2002), repeated this incorrect assertion. A similar error was made by Klimaszewski et al. (2017), stating that *Th. formicarius* occurred in Delaware, Florida, and Michigan based on Haack et al. (1997) and Leavengood (2008). Although Haack et al. (1997) stated that *Th. formicarius* was shipped from France to Delaware and then to Michigan, they also stated that any decision to release had been postponed. In Leavengood's (2008) thesis on the clerids of Florida, his only references to *Th. formicarius* pertained to individuals released by Hopkins in the 1890s. But Hopkins released clerids in West Virginia not Florida.

Although the life cycle of *Th. formicarius* is better synchronized with *T. piniperda* than the North American clerid *Thanasimus dubius* (F.), concerns were raised that if *Th. formicarius* were released it could potentially outcompete and possibly replace *Th. dubius* over time (Haack et al. 1997, Haack and Poland 2001). This concern was first raised during an informal meeting of several researchers who attended the North American Forest Pest Work Conference that took place in San Antonio, Texas, during 8–12 April 1996 (Billings and Nebeker 1996). In response, we conducted a series of laboratory tests in 1996 to evaluate survival of these two clerids when added as larvae in various combinations to pine bolts infested with bark beetles. Our main objectives were to (1) compare survival rates of *Th. formicarius* and *Th. dubius* larvae when *Th. formicarius* was added to bark beetle galleries several days before *Th. dubius* or on the same day, and (2) determine if clerid survival rates varied when introduced into the gallery systems of three different bark beetle species: *Ips grandicollis* (Eichhoff), *I. pini*, and *T. piniperda*. The findings from this study were made available to APHIS in 1997, but the details of the study have not been previously published.

Materials and Methods

Collection and preparation of pine bolts. During late May and early June 1996, several red pine (*Pinus resinosa* Sol. ex Aiton) trees were cut in a young pine plantation at Michigan State University's W. K. Kellogg Forest Experiment Station (Kalamazoo County, MI; 42.36° N, 85.36° W).

Tree diameters at breast height (1.4 m above groundline) were 16–19 cm. Bolts, averaging 45-cm-long, were cut from the trunks of the trees down to a minimum trunk diameter of 10 cm. Areas of the trunk with branches or large knots were avoided. More than 100 bolts were cut. The bolts were transported within a day of cutting to our laboratory on the Michigan State University campus in East Lansing, Michigan. The bolts were taken indoors and allowed to air dry for 3–4 days, labelled on the cut ends, and then end-dipped in melted paraffin wax to reduce desiccation.

Sources of *Ips* adults. Starting in summer 1995, we initiated separate laboratory colonies of *I. grandicollis* and *I. pini*, using beetles that had been field collected in Michigan. The *Ips* beetles were reared at room temperature (ca. 22–27° C) on red pine bolts held in cardboard rearing tubes (ca. 20–25 cm diameter and 66 cm long; Michigan Can and Tube, Saginaw, MI) with plastic lids that had attached collection cups (for more details see Petrice and Haack 2006, Haack and Petrice 2022). The bolts, 43–48 cm long, were cut from small diameter red pine trees growing at Kellogg Forest. The colonies were maintained by using some of the progeny adults from the most recent generation as parent adults to initiate the next generation of bark beetles. When *Ips* adults were needed as parent adults in the present study, newly emerged adults were collected from the tubes, sexed, and then placed, several at a time, in 1-quart (ca. 0.95 l) plastic containers with lids that had screened ventilation holes. The containers had strips of red pine inner bark and moistened brown paper towels to provide nourishment and substrates to walk on. The containers were kept in an environmental chamber at ca. 10° C until needed.

Sources of *Tomicus piniperda* adults. We used two methods to obtain *T. piniperda* parent adults. The first method involved placing recently cut red pine logs at various sites in southern Lower Michigan that had relatively high populations of *T. piniperda*. Log placement in the field was staggered from March through May 1996. This provided a steady supply of newly infested logs that we would transport to the laboratory and debark to obtain parent adults from their galleries.

The second method involved live-trapping *T. piniperda* adults in α -pinene-baited, 12-unit Lindgren funnel traps (Phero Tech Inc, Delta, BC) at multiple sites in southern Michigan during spring 1996. We placed strips of brown paper towels in each collection cup to provide a surface for the trapped insects to walk on. The traps were emptied regularly into individual 1-pint (473 ml)

labelled cardboard food containers with tight-fitting lids. The containers were placed in chest coolers, returned to the laboratory, and stored in a refrigerator until sorted, which typically occurred within one day. As with the *Ips* adults, *T. piniperda* adults were sexed, placed several at a time in plastic containers with strips of inner bark and brown paper towels, and stored at 10° C until needed.

Sources of *Thanasimus formicarius* adults and larvae. As stated above, collections of *Th. formicarius* adults were made in France in 1995 and 1996 and then shipped to the USDA ARS facility in Newark, DE. From there various life stages of *Th. formicarius* were shipped to the USDA APHIS facility in Niles, MI. For our study, *Th. formicarius* eggs were shipped in coolers twice a week by overnight mail from Niles to East Lansing, MI, during May and the first half of June 1996. The eggs were placed in labelled and dated Petri dishes with moistened filter paper and checked daily for newly eclosed larvae.

Sources of *Thanasimus dubius* adults and larvae. Starting in late April 1996, we added racemic ipsdienol lures to the funnel traps that were already baited with α -pinene to increase their attraction to *Th. dubius* adults. We collected *Th. dubius* through May 1996. As described above for *T. piniperda*, traps were emptied multiple times per week, with all insects returned to the laboratory in the cardboard containers and soon sorted. The recovered clerid adults were sexed and then single pairs (1 female and 1 male) were placed in individual 1-quart plastic containers as described above. Mating usually took place soon after both beetles were placed in a container. Moistened and crumbled brown paper towels were added to each container to serve as an ovipositional substrate. The male clerids were removed after 1–2 days and maintained separately but were reintroduced for a day every 2 weeks in case multiple matings were required for females to maintain laying fertile eggs. Each adult clerid was given four adult bark beetles per day as prey through mid-June, using both *I. grandicollis* and *T. piniperda* as prey. This number of prey allowed *Th. dubius* females to maintain a high rate of egg production (Haack and Lawrence 2026). Daily, we removed the 1-day-old paper towel and inserted a new one. Areas of the towel with clerid eggs were cut and placed in a labelled and dated Petri dish with moistened filter paper. The eggs were checked daily for newly eclosed larvae.

Introduction of bark beetle adults into bolts. When introducing *T. piniperda* or either *Ips* species into the bolts, we tar-

geted an attack density of 50 egg galleries per square meter of bark surface area. This value is within the range of attack densities commonly reported for these three bark beetles but lower than the maximum values of 200–400 attacks/m² that have been reported (Hertel et al. 1969, Långström 1984, Haack and Lawrence 1995a, Steed and Wagner 2004). Based on the length and diameter of each bolt, and our target attack density, we introduced 7–14 female bark beetles per bolt (mean $\pm$ SE: 9.1 ± 0.2 , $N = 108$ bolts). The method used to introduce the adults varied by species because *T. piniperda* is monogynous with female-initiated galleries, while *Ips* species are harem polygynous with male-initiated galleries and multiple females per male that each bore separate egg galleries (Kirkendall 1983). Therefore, separate entrance holes were initiated for each *T. piniperda* female. By contrast, for the *Ips* species, we introduced two females into each male-initiated gallery (i.e., nuptial chamber).

We made “starter holes” on the bark surface while the bolts were positioned horizontally on the laboratory countertop. The starter holes were made through the outer bark at an oblique angle with a 2-mm-diameter awl so that frass would fall easily from the galleries. We spaced the starter holes so that they would be no closer than 10 cm from each other or the cut ends of the bolts. Only adults that had emerged or been collected during the previous two days were used as parent adults. In addition, only adults that appeared healthy were used, i.e., those that had all six legs, both antennae, and could walk up the sides of the containers were used. Depending on the bark beetle species, we placed either a single male or female adult in the long section of a size 00 gelatin capsule that had been pierced at the end for ventilation and contained a rolled section of paper for footing. The capsule with a single beetle was then placed over the starter hole and held in place with a ring of Duxseal sealing compound. After about 24 hours, a single male was introduced into each *T. piniperda* gallery by placing it in the gel capsule and resealing it over the starter hole. Similarly, for each *Ips* gallery, a single female was introduced into each gallery after the male had about 1 day to construct the nuptial chamber. About 2–3 hours later a second female was added to each *Ips* gallery. All gel capsules were examined the following day and if any bark beetle was present in the capsule, rather than in the bolt, they were replaced. On the day after the last bark beetle was introduced, each bolt was placed individually in a cardboard rearing tube and in the same position as it had been on the countertop. Prior to placing each bolt

Table 1. Descriptions and codes used in Figures 1–3 for nine treatments that were tested when introducing larvae of *Thanasimus formicarius* (F) and *Thanasimus dubius* (D) into galleries initiated by *Tomicus piniperda* (Tp) females or galleries initiated by *Ips grandicollis* (Ig) or *Ips pini* (Ip) males. Two females of the same species were introduced into each *Ips* male gallery.

Test	<i>Tomicus piniperda</i> (Tp)	Tp code	<i>Ips grandicollis</i> (Ig) and <i>Ips pini</i> (Ip)	Ig code	Ip code
1	Tp only	Tp	Ig or Ip only	Ig	Ip
2	2F per Tp female	2F/Tp♀	4F per Ig or Ip male	4F/Ig♂	4F/Ip♂
3	1F per Tp female	1F/Tp♀	2F per Ig or Ip male	2F/Ig♂	2F/Ip♂
4	(1F + 1D) per Tp female (same time)	(1F+1D)/Tp♀	(2F + 2D delayed 1 day) per Ig or Ip male	(2F+2D)/Ig♂	(2F+2D)/Ip♂
5	(2F + 2D) per Tp female (same time)	(2F+2D)/Tp♀	(4F + 4D delayed 1 day) per Ig or Ip male	(4F+4D)/Ig♂	(4F+4D)/Ip♂
6	(1F + 1D delayed 1 wk) per Tp female	1F+(1D)/Tp♀	4F per male in half the galleries and 4D per male in the other half of galleries per bolt (same time)	(4F or 4D)/Ig♂	(4F or 4D)/Ip♂
7	(2F + 2D delayed 1 wk) per Tp female	2F+(2D)/Tp♀	8F per male in half the galleries and 8D per male in the other half of galleries per bolt (groups of 4F or 4D were added on two consecutive days)	(8F or 8D)/Ig♂	(8F or 8D)/Ip♂
8	1D per Tp female	1D/Tp♀	2D per Ig or Ip male	2D/Ig♂	2D/Ip♂
9	2D per Tp female	2D/Tp♀	4 D per Ig or Ip male	4D/Ig♂	4D/Ip♂

into the cardboard tube, we removed the gel capsules and Duxseal and then circled the starter holes with a permanent marker pen.

Treatments and introduction of clerid larvae. Nine treatments were tested for each bark beetle species (Table 1). The treatments were the same for the two *Ips* species but differed somewhat for *T. piniperda*. Four bolts were selected randomly for each bark beetle-treatment combination, for a total of 108 bolts. Average room temperature during the main study period (June through September) was 27° C. The laboratory room lacked windows. At first, the room lights were on for about 12 hours per day, but later when the bolts were in the rearing tubes a nearby bank of lights was left on continuously to attract emerging beetles to the collection cups.

The treatments varied from testing each bark beetle species without clerids (control), to others with either *Th. formicarius* or *Th. dubius* alone or in various combinations. When both clerids were introduced into bolts with *T. piniperda*, one treatment

involved adding *Th. dubius* larvae a week after *Th. formicarius* had been introduced to simulate what happens in early spring when *Th. formicarius* adults become active much sooner than *Th. dubius* adults. In another treatment with *T. piniperda*, the *Th. formicarius* and *Th. dubius* larvae were introduced on the same day to simulate what could happen in late spring when both clerid species are active and some *T. piniperda* parent adults reemerge from their first galleries and initiate a second gallery (Sauvard 1993), or when both *Ips* species are active. With the later timing of gallery initiation by *Ips* species, only late spring scenarios were tested when both clerids were introduced into bolts with one of the *Ips* species (Table 1). Those late spring scenarios with *Ips* included adding both clerid species into the same galleries similar to bolts with *T. piniperda* (treatments 4 and 5), as well as adding *Th. formicarius* larvae in half the *Ips* galleries and *Th. dubius* in the other half on each bolt (treatments 6 and 7).

Given that two *Ips* females were introduced into each male-initiated *Ips* gallery system (= starter hole), we added twice as many clerid larvae per gallery system for the *Ips* galleries compared to the *T. piniperda* galleries. Admittedly, when we introduced two, four, or eight clerid larvae into a single *Ips* gallery system, we do not know how the clerid larvae partitioned themselves. That is, did they divide themselves evenly between the two *Ips* egg galleries, or did all clerid larvae enter a single gallery?

We introduced the clerid larvae six days after the bark beetles had been introduced into each bolt, and then again depending on the assigned treatment (Table 1). We removed nine bolts at a time from the cardboard tubes that had all been infested with the same bark beetle species. Each bolt was then randomly assigned to one of the nine treatments and labeled accordingly. A similar label was placed on the tube where each bolt had resided. The bolts were placed horizontally on the benchtops in the same position that they were situated in the tubes. Beforehand, we prepared several pierced gelatin capsules each with a ring of Duxseal that would be used to seal the clerid larvae over each starter hole. We generally used clerid larvae that had eclosed from eggs during the previous day but no more than 2 days earlier. Only clerid larvae that were actively walking in the Petri dishes were used. Clerid larvae were hand-transferred one at a time to the starter holes with a trimmed and wetted paint brush. In most cases, the larvae quickly entered the starter holes, after which the gel capsule was attached. In cases when a larva failed to enter immediately, it was placed in the gel capsule and then attached over the starter hole. We recorded the time and species when each clerid larva was introduced into each starter hole. When several clerid larvae were placed in the same starter hole on the same day, we waited at least one hour before introducing the next larva. Similarly, when multiple larvae of both species were introduced into the same starter hole, the clerid species were alternated.

The collection cups were checked for beetles nearly every day from June through September, and usually every 2–3 days through October. The number and species of all beetles collected were recorded daily for each bolt. Occasionally clerid larvae were found in the collection cups. When this occurred, the clerid larvae were placed back into their respective rearing containers.

The study ended in October 1996. Over the next few weeks all bolts were debarked and examined. We recorded the number of clerids and bark beetles found within each container, as well as any found during de-

barking. In addition, we recorded the total length of all egg galleries made by the parent females that were introduced into each bolt.

Data analyses. We used one-way ANOVA when comparing various mean values on a per bolt basis given that the means were based on more than 30 bolts for each species of bark beetle. A two proportion *z* test was used when comparing various proportions between the two clerid species or at times between two of the bark beetle prey species. For the above analyses, the data were $\log_{10}(x + 1)$ transformed prior to analysis to reduce heteroscedasticity. Linear regression was used to explore relationships between the number of clerid larvae introduced per bolt and the number of bark beetle brood adults that emerged. The non-parametric Mann-Whitney U test was used to compare means between two variables such as development time and percent survival between the two clerid species. Similarly, the non-parametric Kruskal-Wallis rank sum test followed by Dunn's test for post-hoc pairwise comparisons were used to compare means of three or more variables such as the mean survival values for all treatments in which *Th. formicarius* had been introduced for each bark beetle species, and again separately for all treatments in which *Th. dubius* had been introduced. These nonparametric tests were selected because the data were usually skewed and thus not normally distributed. We used the online R-based calculators at <https://www.statskingdom.com> and an alpha level of 0.05 for all analyses.

Results

Bolt dimensions and infestation levels. Although the bolts were roughly similar in size there were significant differences in average bolt length, diameter, and surface area for the bolts provided to each of the three bark beetle species (Table 2). Overall, average surface area of the bolts provided the two *Ips* species (18.8 and 19.5 dm²) were larger than the bolts used for *T. piniperda* (17.1 dm²). Given that the initial infestation level for each bolt was based on its surface area, more females of each *Ips* species were introduced into the bolts (342 and 349 total females) compared with *T. piniperda* (311). Nevertheless, the mean number of female bark beetles introduced per bolt did not vary significantly among bark beetle species (Table 2). As expected, about twice as many *T. piniperda* males were introduced per bolt compared to the two *Ips* species, given that *Tomicus* bark beetles are monogynous whereas both *Ips* species are harem polygynous.

Bark beetle summary data. Bark beetle parent adults constructed galleries

Table 2. Summary data for (a) the number of scolytine parent adults and clerid (*Thanasimus formicarius* and *Th. dubius*) larvae introduced and the number of scolytine brood adults and clerid adults that emerged for all 36 red pine bolts tested for each of the three scolytine prey species tested (*Ips grandicollis*, *I. pini*, and *Tomicus piniperda*), and (b) mean ($\pm$ SE) bolt dimensions as well as various mean scolytine parent adult, brood adult and egg gallery values.

Parameter	Bolt information by colonizing bark beetle			ANOVA results
	<i>Ips grandicollis</i>	<i>Ips pini</i>	<i>Tomicus piniperda</i>	
Total No. bolts	36	36	36	
No. bolts that received clerid larvae	32	32	32	
No. bolts that produced clerid adults	20	12	23	
Total No. female bark beetle introduced	342	349	311	
Total No. male bark beetle introduced	173	175	311	
Total No. brood adults that emerged	7492	3283	4048	
Total No. <i>Th. formicarius</i> larvae introduced	330	318	313	
Total No. (%) <i>Th. formicarius</i> adults emerged*	10 (3.0%)	2 (0.6%)	30 (9.6%)	
Total No. <i>Th. dubius</i> larvae introduced	338	334	303	
Total No. (%) <i>Th. dubius</i> adults emerged	38 (11.2%)	16 (4.8%)	24 (7.9%)	
Mean bolt length (cm)	44.0 $\pm$ 0.2 b	45.9 $\pm$ 0.2 a	45.4 $\pm$ 0.2 a	$F = 11.6$; $df = 2,105$; $P < 0.0001$
Mean bolt diameter (cm)	13.5 $\pm$ 0.2 a	13.5 $\pm$ 0.4 a	12.0 $\pm$ 0.3 b	$F = 6.8$; $df = 2,105$; $P < 0.0001$
Mean bolt surface area (dm ²)	18.8 $\pm$ 0.3 a	19.5 $\pm$ 0.6 a	17.1 $\pm$ 0.5 5b	$F = 7.0$; $df = 2,105$; $P = 0.0014$
Mean No. bark beetle males introduced per bolt	4.6 $\pm$ 0.2 b	4.7 $\pm$ 0.2 b	8.6 $\pm$ 0.2 a	$F = 160.2$; $df = 2,105$; $P < 0.0001$
Mean No. bark beetle females introduced per bolt	9.0 $\pm$ 0.3 a	9.5 $\pm$ 0.3 a	8.6 $\pm$ 0.2 a	$F = 2.8$; $df = 2,105$; $P = 0.0663$
Mean No. brood adults emerged per bolt	208.1 $\pm$ 14.8 a	91.2 $\pm$ 11.3 b	112.4 $\pm$ 10.8 b	$F = 25.1$; $df = 2,105$; $P < 0.0001$
Mean total egg gallery length per bolt (cm)	93.7 $\pm$ 3.5 a	60.5 $\pm$ 4.2 b	46.3 $\pm$ 3.8 c	$F = 40.2$; $df = 2,105$; $P < 0.0001$
Mean No. brood adults per cm of egg gallery per bolt	2.3 $\pm$ 0.2 a	1.5 $\pm$ 0.2 b	2.4 $\pm$ 0.2 a	$F = 10.5$; $df = 2,105$; $P < 0.0001$

*Of the 42 *Th. formicarius* individuals collected, 39 were adults and 3 were prepupae found when the bolts were debarked at the end of the study.

Table 3. Summary data for the number of clerid adults that emerged per bolt for all treatments and both clerid species (*Thanasimus formicarius* and *Th. dubius*) combined by bark beetle prey species.

No. clerid adults produced per bolt	No. bolts that produced clerids by bark beetle host species			
	<i>Ips grandicollis</i>	<i>Ips pini</i>	<i>Tomicus piniperda</i> *	All bark beetle hosts combined
0	12	20	9	41
1	3	8	8	19
2	10	3	8	21
3	3	0	3	6
4	4	1	2	7
5	0	0	0	0
6	0	0	1	1
7	0	0	1	1
Total clerids	48	18	54	120
Percent of bolts that produced clerids (N = 32 bolts per prey species)	62.5%	37.5%	71.9%	57.3%

* Data for *T. piniperda* includes the three *Th. formicarius* prepupae recovered during bolt dissections at the end of the study.

and produced brood adults in all bolts. On average, about 100 to 200 brood adults emerged from each bolt, with the most emerging from bolts infested with *I. grandicollis* (Table 2). There was no significant linear relationship between the total number of clerids introduced to each bolt and either the total number of brood adults produced per bolt ($F = 0.68$; $df = 1,106$; $P = 0.410$) nor the average number of brood adults per centimeter of gallery ($F = 0.88$; $df = 1,106$; $P = 0.348$). Similarly, when comparing average brood production per bolt among the nine treatments for each of the three prey species, no significant differences were found for *I. grandicollis* ($H = 7.5$; $df = 8$; $P = 0.479$), *I. pini* ($H = 9.4$; $df = 8$; $P = 0.311$), nor *T. piniperda* ($H = 3.5$; $df = 8$; $P = 0.901$). On average, total egg gallery length was greatest on bolts infested with *I. grandicollis*, intermediate for *I. pini*, and lowest for *T. piniperda* (Table 2). Similarly, average brood production per bolt was significantly higher for *I. grandicollis* than either *I. pini* or *T. piniperda*. However, when considering the average number of brood adults that emerged per centimeter of egg gallery, average values per bolt were significantly higher for *T. piniperda* and *I. grandicollis* compared with *I. pini*.

General clerid summary data. Overall, 78 *Th. dubius* adults were recovered in the study, 64 during the rearing process when the clerid adults entered the collection cups (82%) and 14 at the end of the study (all were dead) when the rearing tubes were cleaned and the bolts dissected. By contrast, only 12 *Th. formicarius* adults (31% of 39 adults recovered) were found in

the collection cups with 27 adults (all dead) and 3 last-instar larvae (prepupae, all alive) were recovered in the rearing tubes and during bolt dissections. The three prepupae found during bolt dissections were all in bolts that had only received *Th. formicarius* larvae initially and therefore were considered *Th. formicarius* with confidence. In addition, because these larvae were alive and appeared to be prepupae, we assumed they would eventually become adults and thus were classified as “adults” in all subsequent analyses. When considering all clerid larvae introduced into the 96 test bolts that received clerids, *Th. dubius* survival (78 adults from 975 larvae or 8.0% survival) was greater than *Th. formicarius* survival (42 of 961 larvae or 4.4%) ($z = 3.3$; $P = 0.001$).

At least one clerid adult emerged from 55 of the 96 bolts (57%) that received clerid larvae (Table 3). Generally, only one or two clerids emerged per bolt, but as many as six clerids emerged from one bolt and seven from another (Table 3). These latter two bolts were both infested with *T. piniperda*. The bolt that produced six adult clerids, all of which were *Th. dubius*, had been assigned to treatment 7 (Table 1) in which 16 *Th. formicarius* larvae were initially added to the bolt and then 16 *Th. dubius* larvae were added one week later. For the bolt that produced seven adult clerids, all of which were *Th. formicarius*, it had been assigned to treatment 3 in which 10 *Th. formicarius* larvae were initially added.

After combining data for the two clerid species, more bolts produced adult clerids if they were infested with either *I. grandicol-*

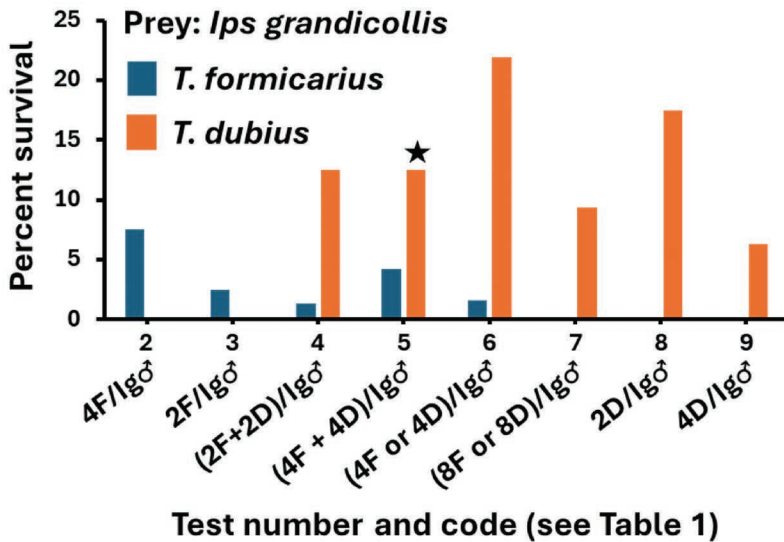


Figure 1. Mean *Thanasimus formicarius* (F) and *Thanasimus dubius* (D) larva-to-adult survival on red pine bolts infested with *Ips grandicollis* by treatment (N = 4 bolts per treatment). The Kruskal-Wallis test indicated no significant differences in average clerid survival among the six treatments in which *Th. formicarius* larvae were introduced ($P = 0.959$) nor among the six treatments in which *Th. dubius* larvae were introduced ($P = 0.931$). The Mann-Whitney U test indicated that *Th. formicarius* and *Th. dubius* survival values were significantly different in test 5 ($P = 0.025$; denoted by star) but not in test 4 ($P = 0.161$), test 6 ($P = 0.408$), nor test 7 ($P = 0.163$).

lis ($z = 2.0$; $P = 0.045$) or *T. piniperda* ($z = 2.8$; $P = 0.006$) compared with *I. pini* (Table 3). By contrast, the proportion of bolts that produced at least one clerid of either species was similar between bolts infested with *I. grandicollis* and *T. piniperda* ($z = 0.8$; $P = 0.423$). Considering the bolts infested with the three bark beetle species separately, a higher proportion of *Th. dubius* emerged compared with *Th. formicarius* from bolts infested with *I. grandicollis* ($z = 4.1$; $P < 0.001$) or *I. pini* ($z = 3.3$; $P = 0.001$), whereas the proportions were similar in bolts infested with *T. piniperda* ($z = 0.7$; $P = 0.456$) (Table 2).

Using the number of days from when clerid larvae were introduced into each bolt until adults were found in the collection cups of the rearing tubes as a proxy for development time, it appears that *Th. dubius* developed faster than *Th. formicarius*. For example, mean ($\pm$ SE) development time from larva to adult for *Th. dubius* was 61.7 ± 1.5 days for the 64 adults found in the cups compared with 114.8 ± 7.0 days for the 12 *Th. formicarius* adults found in cups.

Clerid survival on bolts infested with *Ips grandicollis*. Adult *Th. formicarius* emerged from 7 of 24 *I. grandicollis*-infested bolts (29%) in which they were introduced. By comparison, *Th. dubius* emerged from more of the bolts (16 of 24 bolts; 67%) in which it had been introduced ($z = 2.6$; $P = 0.008$). Considering the individual treatments listed in Table 1, there were no significant differences in average clerid survival among the six treatments in which *Th. formicarius* larvae were introduced ($H = 1.0$; $df = 5$; $P = 0.959$) nor among the six treatments in which *Th. dubius* larvae were introduced ($H = 1.3$; $df = 5$; $P = 0.931$) (Fig. 1). Among the four treatments where both clerid species were introduced to the same bolts (treatments 4–7), average survival was always higher for *Th. dubius* than *Th. formicarius* in absolute terms, but the averages were significantly different only in treatment 5 where four larvae of each clerid species were introduced into each gallery system ($U = 0$; $z = 2.2$; $P = 0.025$) (Fig. 1). We recognize that at times the average survival values shown for individual treatments in Figs. 1–3 appear much different between clerid species but were not found to be “significantly” different. This usually occurred because some bolts in nearly all treatments produced no adult clerids. For example, for treatment 6 in Fig. 1, no adult clerids emerged from two of four bolts that received *Th. dubius* nor

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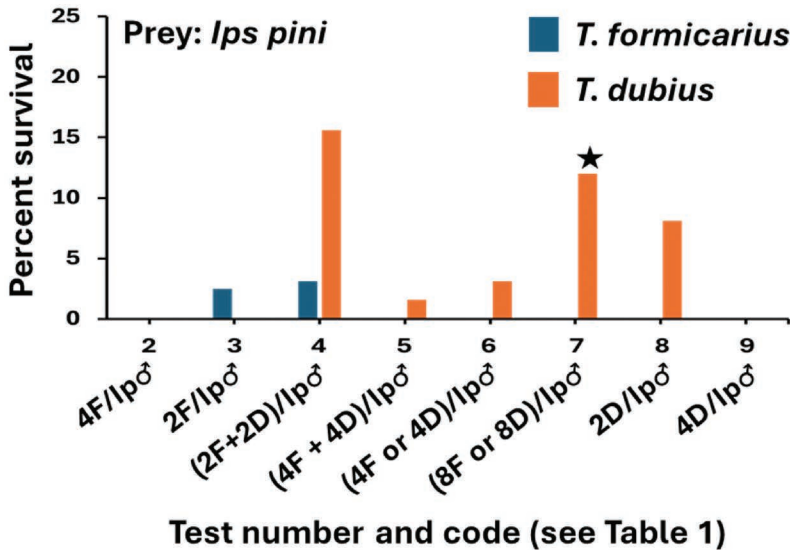


Figure 2. Mean *Thanasimus formicarius* (F) and *Thanasimus dubius* (D) larva-to-adult survival on red pine bolts infested with *Ips pini* by treatment (N = 4 bolts per treatment). The Kruskal-Wallis test indicated no significant differences in average clerid survival among the six treatments in which *Th. formicarius* larvae were introduced ($P = 0.523$) nor among the six treatments in which *Th. dubius* larvae were introduced ($P = 0.115$). The Mann-Whitney U test indicated that *Th. formicarius* and *Th. dubius* survival values were significantly different in test 7 ($P = 0.021$; denoted by star) but not in test 4 ($P = 0.408$), test 5 ($P = 0.453$), nor test 6 ($P = 0.453$).

from three of four bolts that received *Th. formicarius*.

Clerid survival on bolts infested with *Ips pini*. Adult *Th. formicarius* emerged from 2 of 24 *I. pini*-infested bolts (8%) in which they were introduced. By contrast, *Th. dubius* adults emerged from 11 of 24 bolts (46%) ($z = 3.0$; $P = 0.002$). As for the individual treatments, there were no significant differences in average clerid survival among the six treatments where *Th. formicarius* larvae were introduced ($H = 4.2$; $df = 5$; $P = 0.523$) nor among the six treatments where *Th. dubius* larvae were introduced ($H = 8.9$; $df = 5$; $P = 0.115$) (Fig. 2). Among the four treatments where both clerid species were introduced to the same bolts, *Th. dubius* always had greater survival than *Th. formicarius* in absolute terms, but the differences were significant only in treatment 7 where the larvae of each clerid species were introduced into separate gallery systems on each bolt ($U = 0$; $z = 2.3$; $P = 0.021$).

Clerid survival on bolts infested with *Tomicus piniperda*. Adults of *Th.*

formicarius emerged from 15 of the 24 *T. piniperda*-infested bolts (63%) compared with 14 of 24 bolts (58%) for *Th. dubius* ($z = 0.4$; $P = 0.723$). As for the individual treatments where *Th. formicarius* was introduced, *Th. formicarius* survival was significantly higher on treatments 2 and 3 (where only *Th. formicarius* larvae were introduced) compared with treatments 5–7 (which all had introductions of *Th. dubius* as well) ($H = 13.3$; $df = 5$; $P = 0.021$) (Fig. 3). However, in the case of *Th. dubius*, no significant differences in average clerid survival were found among the six treatments where larvae were introduced ($H = 9.1$; $df = 5$; $P = 0.103$). Among the four treatments where both clerid species were introduced to the same bolts, *Th. dubius* had greater average survival than *Th. formicarius* in three of the four treatments in absolute terms, but only in treatment 6 (where one *Th. formicarius* larva was added and then one *Th. dubius* larva was added a week later to each gallery) were the differences significant ($U = 1$; $z = 2.1$; $P = 0.036$).

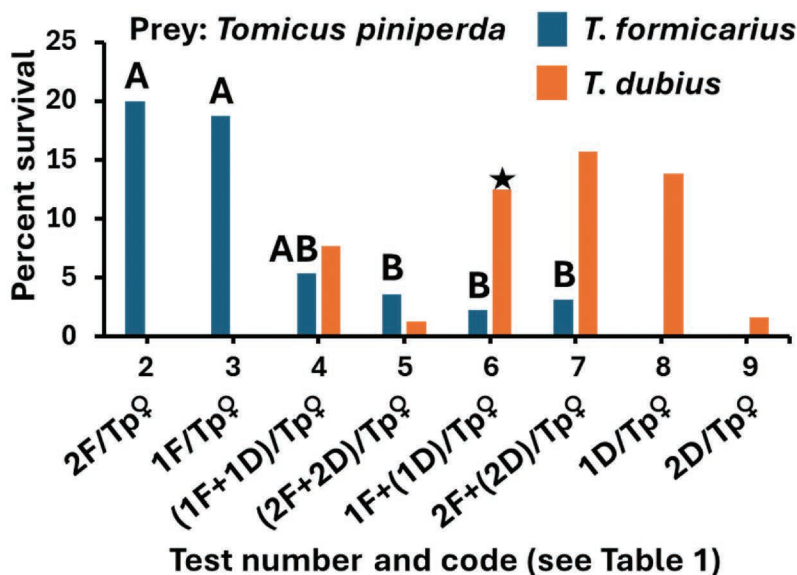


Figure 3. Mean *Thanasimus formicarius* (F) and *Thanasimus dubius* (D) larva-to-adult survival on red pine bolts infested with *Tomicus piniperda* by treatment (N = 4 bolts per treatment). The Kruskal-Wallis test indicated significant differences in average clerid survival among the six treatments in which *Th. formicarius* larvae were introduced ($P = 0.021$; bars with the same letter are not significantly different.) but not among the six treatments in which *Th. dubius* larvae were introduced ($P = 0.103$). The Mann-Whitney U test indicated that *Th. formicarius* and *Th. dubius* survival values were significantly different in test 6 ($P = 0.036$; denoted by star) but not in test 4 ($P = 0.757$), test 5 ($P = 0.620$), nor test 7 ($P = 0.106$).

Discussion

The impetus for the present study was the concern that if *Th. formicarius* were introduced to eastern North America it could potentially outcompete the native clerid *Th. dubius* and thereby destabilize the normal balance between native conifer-infesting bark beetles and their natural enemies (Haack et al. 1997, Haack and Poland 2001). Although the results of the present study were not summarized until December 1996, a teleconference was held on 9 September 1996 between APHIS staff and key State Plant Health Regulators from five US states where *T. piniperda* was most widely found: Indiana, Michigan, New York, Ohio, and Pennsylvania (Haack and Poland 2001). During that teleconference it was decided that APHIS would postpone any releases of *Th. formicarius* until 1998 at the earliest. The main reasons for this decision were (1) *T. piniperda* has not yet caused any significant damage in unmanaged pine forests in the US, and (2) there was still insufficient information available on the potential non-target impacts of such a release. Although the general findings from the

present study were made available to APHIS and the *T. piniperda*-infested states by early 1997, it was later decided by July 1997 that APHIS would cancel all plans to release *Th. formicarius* in 1998 and beyond. As a result of that decision, all *Th. formicarius* colonies at USDA facilities in the US were destroyed by late 1997.

Another factor that influenced the decision by the infested states to not support release of *Th. formicarius* was the approval in 1996 of a compliance management program for managers of pine Christmas tree farms and tree nurseries in *T. piniperda*-infested counties to ship their pine products to markets outside the quarantine zone (USDA APHIS 1996). The program, which began in 1997, was called the "Pine Shoot Beetle Compliance Management Program," and was largely based on research conducted at Michigan State University and Purdue University (McCullough and Sadof 1996, 1998). Producers enrolled in the program were required to conduct a series of management activities throughout the year, and in so doing be (almost) guaranteed that they would be able to ship their pine products to markets

outside the quarantine zone. The management requirements included (1) destruction of brood material (e.g., pine stumps and cut trees), (2) spring trapping of *T. piniperda* parent adults, (3) insecticide applications, (4) monitoring trees for evidence of shoot feeding by *T. piniperda*, and (5) record keeping.

Although the main concern of releasing *Th. formicarius* in the US was that it might outcompete the native clerid *Th. dubius*, our results indicated that this scenario was not likely to occur. That is, *Th. formicarius* survival was generally higher when it was introduced by itself to *T. piniperda* galleries, but it performed less well in galleries of the two North American *Ips* species. Moreover, when the two clerid species were present on the same bolts, regardless of the timing of their introduction, survival was generally higher for *Th. dubius* than *Th. formicarius* in absolute terms (Figs. 1–3). These findings suggest that if *Th. formicarius* had been released in the US it would have had its greatest impact on *T. piniperda*, and that *Th. dubius* would continue being the main clerid predator of the native *Ips* bark beetles. Such a situation currently occurs in parts of Europe where the two clerids *Th. formicarius* and *Thanasimus femoralis* (Zett.) coexist. As mentioned above, *Th. formicarius* initiates flight in early spring similar to *T. piniperda*. By contrast, *Th. femoralis* adults begin their flight season later in spring at about the same time as spruce bark beetle, *Ips typographus* (L.), its main prey species (Schroeder 2003).

We do not know what caused the high mortality of the clerid larvae that we introduced into the bolts. Possibly some clerids were killed by parent-adult bark beetles when the clerid larvae entered the egg galleries. Or perhaps many were killed by other clerid larvae within the same gallery system where they were introduced or possibly in other galleries on the same bolt given that the clerid larvae were free to move among gallery systems once the bolts were placed back in the rearing tubes. Cannibalism is known to occur among both *Thanasimus* adults and larvae (Mignot and Anderson 1969, Öunap 1992, Weslien and Regnander 1992, Reeve 2011). In bolts where both *Th. dubius* and *Th. formicarius* were introduced, perhaps the higher survival of *Th. dubius* reflects a greater ability by *Th. dubius* to avoid parent-adult bark beetles or that *Th. dubius* larvae killed or outcompeted *Th. formicarius* larvae when individuals of the two species met.

Another factor that could have contributed to higher survival rates in *Th. dubius* compared with *Th. formicarius* relates to differences in their preferred pupation sites.

For example, *Th. dubius* larvae often pupate in the outer bark near where they fed as larvae, although some larvae will emerge and then crawl downward on the bark surface and select pupation sites along the lower trunk where the outer bark is thicker (Mizell and Nebeker 1981). By contrast, *Th. formicarius* larvae typically move to the base of the trees in which they developed and there construct pupal cells in the thicker bark (Ye 1998). Therefore, some *Th. formicarius* larvae may have died because they did not locate areas on the bolts where the bark was sufficiently thick to construct pupal cells.

It is also possible that survival rates of the two clerid species would have been different if we had delayed the timing of clerid introduction. For example, we introduced the clerids six days after the bark beetles had been introduced. Six days is often sufficient time for the first eggs laid by *Ips* and *Tomicus* bark beetles to eclose (Schenk and Benjamin 1969, Schmitz 1972, Ye 1994, Cognato 2015). However, if we had waited say 10–14 days, the egg galleries would have been longer and there would have been many more bark beetle eggs and larvae available to the clerid larvae. Perhaps the significantly higher average survival of *Th. dubius* over *Th. formicarius* in test 6 for *T. piniperda* ($P = 0.036$), and nearly so in test 7 ($P = 0.106$; Fig. 3), reflects that *Th. dubius* larvae in those two tests were introduced a week after *Th. formicarius* larvae (i.e., on day 13 vs. day 6 after introduction of *T. piniperda*).

Again, the six-day scenario best reflects mid-spring conditions when *T. piniperda* adults are making their sister broods and *Ips* bark beetles are just starting to colonize host material. However, in early spring, when both *T. piniperda* and *Th. formicarius* adults first become active, *Th. formicarius* females do not yet have mature eggs (Schroeder 2003). In Sweden, *Th. formicarius* often feed for about two weeks before starting to oviposit (Schroeder 1999). Similarly, newly emerged *Th. dubius* adults need to feed before becoming sexually mature but can start ovipositing in less than a week after emergence, and in as little as 3–4 days at 20° C (Mignot and Anderson 1969). This time difference likely reflects cooler spring conditions in central Sweden where average daily high temperatures increase from about 7 to 13° C during April (<https://weatherspark.com/>), which is the month when *Th. formicarius* usually becomes active in central Sweden (Schroeder 1999, 2003).

It is interesting to note that we found no significant relationship between the number of clerid larvae introduced on a bolt and the eventual number of scolytine brood adults that emerged. Again, this may reflect

that we introduced most clerid larvae just six days after the bark beetles had been introduced, and the low clerid survivorship in many of the test bolts. By contrast, in many other studies, both in the field and laboratory, *Thanasimus* species have been shown to reduce brood production in various bark beetle species (Mills 1985, Schroeder and Weslien 1994b, Weslien 1994, Schroeder 1996, Aukema and Raffa 2002).

It is also important to mention that our study only focused on interactions between larvae of the two clerid species, not the adults. Competition for prey could also occur on the bark surface between *Th. dubius* and *Th. formicarius* adults as they search for prey on the same trees. Our finding that *Th. dubius* adults emerged after an average of 62 days compared with 115 days for *Th. formicarius* suggests that development time is much shorter for *Th. dubius*. However, given that 27 of the 39 (69%) *Th. formicarius* adults recovered were found dead in the rearing tubes at the end of the study indicates that many individuals had transformed to adults much earlier but for some reason did not enter the collection cups. By contrast, only 14 of the 78 (18%) *Th. dubius* adults recovered were found dead in the rearing tubes. The shortest and longest periods of time for adult clerids to enter the collection cups after being placed on the bolts as larvae was 47 and 104 days for *Th. dubius* and 69 and 140 days for *Th. formicarius*. In studies conducted in North Carolina by Mignot and Anderson (1969), *Th. dubius* completed larval and pupal development in about 53 days on average in the field and 62 days in the laboratory at 25° C. In other studies, a prolonged prepupal period has been reported for *Th. dubius*. For example, Nebeker and Purser (1980) reported that at 27° C, *Th. dubius* larval development was completed in about 30 days but the prepupal and pupal periods together lasted an average of 81 days. Similarly, at room temperatures of 20–25° C, Lawson and Morgan (1992) reported an average development time of 42 days for *Th. dubius* larvae and 56 days for the combined prepupal and pupal periods. In a laboratory study at 25° C in Norway, Ye and Bakke (1997) reported average larval and pupal development time of 32 and 15 days for *Th. formicarius*, respectively, as well as prepupal periods that ranged from 42 to 56 days. Given the above, it is possible that the *Th. dubius* larvae we used had a very short prepupal period or none at all, while the *Th. formicarius* required a longer prepupal period. In addition, a two-year life cycle or possibly an extended period of diapause has been also reported for both *Th. dubius* (Reeve et al. 1996) and *Th. formicarius* (Schroeder 1999).

After 28 years, USDA APHIS rescinded the federal quarantine for *T. piniperda* in 2020 (Haack 2020, USDA APHIS. 2020). This decision was based largely on observing no more than minimal damage to pine trees in natural forest settings in the 20 US states that were infested in 2020 and the relatively high cost of compliance by both Christmas tree producers and nursery managers to the National Pine Shoot Beetle Compliance Management Program. Given this outcome, it now appears that releasing *Th. formicarius* in the US would not have been warranted. However, if *Th. formicarius* had been released and become established, our results suggest that it would not have outcompeted and displaced *Th. dubius*. Nevertheless, the methods used in the present study to evaluate the interactions between exotic and native predators when presented with exotic and native prey species may prove useful when designing future biological control programs.

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Literature Cited

- Atkinson, T. H. 2026. Bark and ambrosia beetles of the Americas. Available from: <https://www.barkbeetles.info/>.
- Aukema, B. H. and K. F. Raffa. 2002. Relative effects of exophytic predation, endophytic predation, and intraspecific competition on a subcortical herbivore: consequences to the

- reproduction of *Ips pini* and *Thanasimus dubius*. *Oecologia* 133: 483–491.
- Bakke, A. 1968.** Ecological studies on bark beetles (Coleoptera: Scolytidae) associated with Scots pine (*Pinus sylvestris* L.) in Norway with particular reference to the influence of temperature. *Meddelelser fra det Norske Skogforsøksvesen* 21: 447–593.
- Bakke, A. and T. Kvamme. 1981.** Kairomone response in *Thanasimus* predators to pheromone components of *Ips typographus*. *Journal of Chemical Ecology* 7: 305–312.
- Billings, R. F. and T. E. Nebeker (eds). 1996.** Proceedings: North American Forest Insect Work Conference; April 8–12, 1996. San Antonio, TX. Texas Forest Service Publication 160. 228 pp.
- Böving, A. G. and A. B. Champlain. 1920.** Larvae of North American beetles of the family Cleridae. Proceedings of the United States National Museum 57: 575–650.
- Bright, D. E. 1996.** Notes on native parasitoids and predators of the larger pine shoot beetle, *Tomicus piniperda* (Linnaeus) in the Niagara region of Canada (Coleoptera: Scolytidae). Proceedings of the Entomological Society of Ontario 127: 57–62.
- Carter, M. C. A., J. L. Robertson, R. A. Haack, R. K. Lawrence, and J. L. Hayes. 1996.** Genetic relatedness of North American populations of *Tomicus piniperda* (Coleoptera: Scolytidae). *Journal of Economic Entomology* 89: 1345–1353.
- Chapman, E. G., J. M. Leavengood, and J. R. Dupuis. 2025.** The Cleridae and Thanaerocleridae of eastern North America, with illustrated keys, updated distributions, and special emphasis on the Kentucky fauna. *Zootaxa* 5639: 1–88.
- Cognato, A. I. 2015.** Biology, systematics, and evolution of *Ips*. Pages 351–370 in: F. E. Vega and R. W. Hofstetter (eds), *Bark beetles*, Academic Press, London.
- Gosling, D. C. 1980.** An annotated list of the checkered beetles (Coleoptera: Cleridae) of Michigan. *The Great Lakes Entomologist* 13: 65–76.
- Haack, R. A. 2020.** Where have all the pine shoot beetles gone, long time passing? The 1992 PSB federal quarantine is coming to an end. Newsletter of the Michigan Entomological Society 64(2): 1–3.
- Haack, B. and D. Kucera. 1993.** New introduction-common pine shoot beetle, *Tomicus piniperda* (L.). USDA Forest Service, Northeastern Area Pest Alert NA-TP-05-93.
- Haack, R. A. and R. K. Lawrence. 1995a.** Attack densities of *Tomicus piniperda* and *Ips pini* (Coleoptera: Scolytidae) on Scotch Pine logs in Michigan in relation to felling date. *Journal of Entomological Science* 30: 18–28.
- Haack R. A. and R. K. Lawrence. 1995b.** Spring flight of *Tomicus piniperda* in relation to native Michigan pine bark beetles and their associated predators. Pages 524–535 in F. P. Hain, S. M. Salom, W. F. Ravlin, T. L. Payne, and K. F. Raffa (eds), *Behavior, population dynamics and control of forest insects*, Proceedings of the joint IUFRO conference for Working Parties S2.07-05 and S2.07-06, Maui, Hawaii, 6–11 February 1994. Ohio State University, Wooster, Ohio.
- Haack R. A. and R. K. Lawrence. 2026.** Fecundity of *Thanasimus dubius* (Coleoptera: Cleridae) rebounds after a period of prey scarcity. *The Great Lakes Entomologist* 59: 25–36.
- Haack, R. A. and T. R. Petrice. 2022.** Mortality of bark-and wood-boring beetles (Coleoptera: Buprestidae, Cerambycidae, and Curculionidae) in naturally infested heat-treated ash, birch, oak, and pine bolts. *Journal of Economic Entomology* 115: 1964–1975.
- Haack, R. A. and T. M. Poland. 2001.** Evolving management strategies for a recently discovered exotic forest pest: the pine shoot beetle, *Tomicus piniperda* (Coleoptera). *Biological Invasions* 3: 307–322.
- Haack, R. A., R. K. Lawrence, D. G. McGullough, and C. S. Sadof. 1997.** *Tomicus piniperda* in North America: an integrated response to a new exotic scolytid. Pp. 62–72. In: Grégoire, J.C., Liebholt, A.M., Stephen, F.M., Day, K.R., and Salom, S.M. (eds): *Proceedings: Integrating cultural tactics into the management of bark beetle and reforestation pests*. General Technical Report NE-236, USDA Forest Service, Northeastern Forest Experiment Station, Radnor, Pennsylvania.
- Hérard, F. and G. Mercadier. 1996.** Natural enemies of *Tomicus piniperda* and *Ips acuminatus* (Col, Scolytidae) on *Pinus sylvestris* near Orléans, France: temporal occurrence and relative abundance, and notes on eight predatory species. *Entomophaga* 41: 183–210.
- Hermes, D. A., R. A. Haack, and B. D. Ayres. 1991.** Variation in semiochemical-mediated prey-predator interaction: *Ips pini* (Scolytidae) and *Thanasimus dubius* (Cleridae). *Journal of Chemical Ecology* 17: 1705–1714.
- Hertel, G. D., F. P. Hain, and R. F. Anderson. 1969.** Response of *Ips grandicollis* (Coleoptera: Scolytidae) to the attractant produced by attacking male beetles. *The Canadian Entomologist* 101: 1084–1091.
- Hopkins, A. D. 1899.** A report on investigations to determine the cause of unhealthy conditions of the spruce and pine from 1880–1893. *West Virginia Agricultural and Forestry Experiment Station Bulletin* 56: 197–461.

- Kim, J. I. and B. H. Jung. 2006.** Taxonomic review of the Cleridae (Coleoptera) in Korea (Part 1): Clerinae Latreille, 1802. *Entomological Research* 36: 6-15.
- Kirkendall, L. R. 1983.** The evolution of mating systems in bark and ambrosia beetles (Coleoptera: Scolytidae and Platypodidae). *Zoological Journal of the Linnean Society* 77: 293-352.
- Klimaszewski, J., D. W. Langor, A. B. T. Smith, E. R. Hoebeke, A. Davies, G. Pelletier, H. B. Douglas, R. P. Webster, C. Bourdon, L. Borowiec, and G. G. E. Scudder. 2017.** Synopsis of adventive species of Coleoptera (Insecta) recorded from Canada. Part 4: Scarabaeoidea, Scirtoidea, Buprestoidea, Byrrhoidea, Elateroidea, Derodontoidea, Bostrichoidea, and Cleroidea. *Pensoft Series Faunistica* 116: 1-215.
- Långström, B. 1984.** Windthrown Scots pines as brood material for *Tomicus piniperda* and *T. minor*. *Silva Fennica* 18: 187-198.
- Lawson, S. A. and F. D. Morgan. 1992.** Rearring of two predators, *Thanasimus dubius* and *Temnochila virescens*, for the biological control of *Ips grandicollis* in Australia. *Entomologia Experimentalis et Applicata* 65: 225-233.
- Leavengood J. M. 2008.** The checkered beetles (Coleoptera: Cleridae) of Florida. M.S. thesis, University of Florida, Gainesville, FL.
- Li, C. D. and Y. Q. Bai. 2007.** Taxonomic review of Cleridae (Coleoptera) in Heilongjiang Province with one new record species from China. *Journal of Forestry Research*, 18: 147-148.
- Löbl I. and A. Smetan (eds.). 2007.** Catalogue of Palaearctic Coleoptera Volume 4: Elateroidea - Derodontoidea - Bostrichoidea - Lymexyloidea - Cleroidea - Cucujoidea. Apollo Books, Stenstrup, Denmark. 935 pp.
- McCullough D. G. and C. S. Sadof. 1996.** Pine shoot beetle compliance program for Christmas trees: a manual for Christmas tree growers. Michigan State University Extension, East Lansing, Michigan, USA. *Extension Bulletin E-2615*. 15 pp.
- McCullough D. G. and C. S. Sadof. 1998.** Evaluation of an integrated management and compliance program for *Tomicus piniperda* (Coleoptera: Scolytidae) in pine Christmas tree fields. *Journal of Economic Entomology* 91: 785-795.
- Mignot, E. C. and R. F. Anderson. 1969.** Bionomics of the bark beetle predator, *Thanasimus dubius* Fab. (Coleoptera: Cleridae). *Entomological News* 80: 305-310.
- Miller, D. R. 2023.** Coleopteran predators of bark and woodboring beetles attracted to traps baited with ethanol and α -pinene in pine (Pinaceae) forests of the southern United States of America. *The Canadian Entomologist* 155: e5.
- Miller, M. C., J. C. Moser, M. McGregor, J. C. Gregoire, M. Baisier, D. L. Dahlsten and R. A. Werner. 1987.** Potential for biological control of native North American *Dendroctonus* beetles (Coleoptera: Scolytidae). *Annals of the Entomological Society of America* 80: 417-428.
- Mills, N. J. 1985.** Some observations on the role of predation in the natural regulation of *Ips typographus* populations. *Zeitschrift für angewandte Entomologie* 99: 209-215.
- Mizell, R. F. and T. E. Nebeker. 1981.** Within-tree distribution of the pupae of *Thanasimus dubius* (Coleoptera: Cleridae), a predator of the southern pine beetle (Coleoptera: Scolytidae). *The Canadian Entomologist* 113: 387-394.
- Nebeker, T. E. and G. C. Purser. 1980.** Relationship of temperature and prey type to developmental time of the bark beetle predator *Thanasimus dubius* (Coleoptera: Cleridae). *The Canadian Entomologist* 112: 179-184.
- Opitz, W. 2002.** 73. Cleridae Latreille 1804. Pages 267-280 in R. H. Arnett Jr., et al. (eds), *American Beetles. Volume 2. Polyphaga: Scarabaeoidea through Curculionoidea*. CRC Press, Boca Raton, FL.
- Õunap, H. 1992.** Predators of bark beetles (Coleoptera: Scolytidae). *Proceedings of the Estonian Academy of Sciences. Biology*. 41: 131-140.
- Person, H. L. 1940.** The clerid *Thanasimus lecontei* (Wolc.) as a factor in the control of the western pine beetle. *Journal of Forestry* 38: 390-396.
- Petrice, T. R. and R. A. Haack. 2006.** Effect of cutting date and outdoor storage conditions on survival of *Agrilus planipennis* (Coleoptera: Buprestidae) in firewood logs. *Journal of Economic Entomology* 99: 790-796.
- Poland, T. M. and J. H. Borden. 1997.** Attraction of a bark beetle predator, *Thanasimus undatulus* (Coleoptera: Cleridae), to pheromones of the spruce beetle and two secondary bark beetles (Coleoptera: Scolytidae). *Journal of the Entomological Society of British Columbia* 94: 35-42.
- Reeve, J. D. 2011.** Predators of the southern pine beetle. Pages 153-160 in: R. N. Coulson and K. D. Klepzig (eds), *Southern pine beetle II. General Technical Report SRS-140*. USDA Forest Service, Southern Research Station, Asheville, NC.
- Reeve, J. D., J. A. Simpson, and J. S. Fryar. 1996.** Extended development in *Thanasimus dubius* (F.) (Coleoptera: Cleridae), a predator of the southern pine beetle. *Journal of Entomological Science* 31: 123-131.

- Sauvard, D. 1993.** Reproductive capacity of *Tomicus piniperda* L. (Col., Scolytidae) 2. Analysis of the various sister broods. *Journal of Applied Entomology* 116: 25–38.
- Schenk, J. A. and D. M. Benjamin. 1969.** Notes on the biology of *Ips pini* in central Wisconsin jack pine forests. *Annals of the Entomological Society of America* 62: 480–485.
- Schmitz, R. F. 1972.** Behavior of *Ips pini* during mating, oviposition, and larval development (Coleoptera: Scolytidae). *The Canadian Entomologist* 104:1723–1728.
- Schroeder, L. M. 1996.** Interactions between the predators *Thanasimus formicarius* (Col.: Cleridae) and *Rhizophagus depressus* (Col.: Rhizophagidae), and the bark beetle *Tomicus piniperda* (Col.: Scolytidae). *Entomophaga* 41: 63–75.
- Schroeder, L. M. 1999.** Prolonged development time of the bark beetle predator *Thanasimus formicarius* (Col.: Cleridae) in relation to its prey species *Tomicus piniperda* (L.) and *Ips typographus* (L.) (Col.: Scolytidae). *Agricultural and Forest Entomology* 1: 127–135.
- Schroeder, L. M. 2003.** Differences in responses to α -pinene and ethanol, and flight periods between the bark beetle predators *Thanasimus femoralis* and *T. formicarius* (Col.: Cleridae). *Forest Ecology and Management* 177: 301–311.
- Schroeder, L. M. and J. Weslien. 1994a.** Interactions between the phloem-feeding species *Tomicus piniperda* (Col.: Scolytidae) and *Acanthocinus aedilis* (Col.: Cerambycidae), and the predator *Thanasimus formicarius* (Col.: Cleridae) with special reference to brood production. *Entomophaga* 39: 149–157.
- Schroeder, L. M. and J. Weslien. 1994b.** Reduced offspring production in bark beetle *Tomicus piniperda* in pine bolts baited with ethanol and α -pinene, which attract antagonistic insects. *Journal of Chemical Ecology* 20: 1429–1444.
- Steed, B. E. and M. R. Wagner. 2004.** Importance of log size on host selection and reproductive success of *Ips pini* (Coleoptera: Scolytidae) in Ponderosa pine slash of northern Arizona and western Montana. *Journal of Economic Entomology* 97: 436–450.
- USDA APHIS (US Department of Agriculture, Animal and Plant Health Inspection Service). 1992.** 7 CFR Part 301—pine shoot beetle. Federal Register, 19 November 1992, 57(224): 54492–54499.
- USDA APHIS. 1996.** Pine shoot beetle compliance management program. USDA APHIS, Plant Protection and Quarantine, Domestic and Emergency Programs, Riverdale, Maryland, 24 pp.
- USDA APHIS. 2020.** 7 CFR Parts 301 and 319—Deregulation of pine shoot beetle. Federal Register, 1 October 2020, 85(191):61806–61809.
- Vité, J. P. and D. L. Williamson. 1970.** *Thanasimus dubius*: prey perception. *Journal of Insect Physiology* 16: 233–239.
- Webster, R. P., J. D. Sweeney, and I. DeMerchant. 2012.** New Coleoptera records from New Brunswick, Canada: Trogossitidae, Cleridae, and Melyridae, with an addition to the fauna of Nova Scotia. *ZooKeys* 179: 141–156.
- Weslien, J. 1994.** Interactions within and between species at different densities of the bark beetle *Ips typographus* and its predator *Thanasimus formicarius*. *Entomologia Experimentalis et Applicata* 71: 133–143.
- Weslien, J. and J. Regnander. 1992.** The influence of natural enemies on brood production in *Ips typographus* (Col. Scolytidae) with special reference to egg-laying and predation by *Thanasimus formicarius* (Col.: Cleridae). *Entomophaga* 37: 333–342.
- Ye, H. 1994.** Influence of temperature on the experimental population of the pine shoot beetle, *Tomicus piniperda* (L.) (Col., Scolytidae). *Journal of Applied Entomology* 117: 190–194.
- Ye, H. 1998.** Life cycle of *Thanasimus formicarius* (Coleoptera: Cleridae) in southern Norway. *Entomologia Sinica* 5: 55–62.
- Ye, H. and A. Bakke. 1997.** Development and reproduction of *Thanasimus formicarius* (L.) (Coleoptera: Cleridae) at three constant temperatures. *The Canadian Entomologist* 129: 579–583.
- Yuan, F., Y.-Q. Luo, J. Shi, and K. Heliövaara. 2012.** Different attractive effects and EAG responses of *Ips subelongatus* (Coleoptera, Scolytidae) and its predator *Thanasimus substriatus* (Coleoptera: Cleridae) to ipsilures. *Scientia Silvae Sinicae* 48(6): 89–94.