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Chapter 3

A MULTI-DISCIPLINARY APPROACH FOR DEVELOPING TOOLS TO MONITOR INVASIVE BUPRESTID BEETLE SPECIES

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ABSTRACT

Buprestid beetles (Coleoptera: Buprestidae), which were previously considered to be minor forest pests, have received substantial attention recently due to the widespread ash tree mortality associated with the North America introduction of the emerald ash borer, *Agrilus planipennis* from Asia. At the same time, geographic expansions of forest buprestid species associated with other hosts have been noticed, causing concern about potentially similar destructive outcomes. Attempts have been made to understand the host-finding and mating behaviors of these forest buprestids in order to develop detection and management tools, with a focus primarily on *A. planipennis*. A complex sequence of chemical and visual signals appears to mediate such behaviors, which has been difficult to mimic in an effective trapping approach. Both sexes appear to be attracted to the tree canopy as a result of host-produced volatile compounds. Once in the canopy, males visually seek and fly directly onto stationary females from a distance of up to 1 meter, an event which immediately precedes attempts to copulate. The subsequent copulation attempts by the males are mediated by sex-specific cuticular hydrocarbon signals. Similar visually-mediated approaches toward dead models have also been observed in other tree-dwelling buprestids such as *Agrilus cyanescens*, *A. subcinctus*, *A. biguttatus*, *A. sulcicollis*, and *A. angustulus*. While the extent of similarities of both visual and chemical signals shared by these species and *A. planipennis* has not been fully explored, it is becoming clear that the visual signal that induces attraction to a female is broadly tuned, exhibiting substantial cross-species attraction. Despite subtle differences in coloration patterns, all of these species generate an intense spectral signal using the refractive properties of repetitive layering of the elytral cuticle. Further investigation into both the means of generation and response to the visual signal, as well as the chemical ecology of these species, may provide advances in trapping technologies for the detection of all tree-feeding Buprestids.

1. INTRODUCTION

The eruptive outbreak of the emerald ash borer, *Agrilus planipennis*, in North America over the past decade has resulted in a serious threat to urban and forest ecosystems. The continuing spread of this insect has become an important model for understanding the ecology of invasive species. Furthermore, it has also highlighted the generalized potential threat of buprestid beetles (Coleoptera: Buprestidae), which like other invasive species have experienced host-range shifts because of human activities. Such impacts range from accidental introductions associated with travel or trade to climate-change-induced shifts in host susceptibility. The Buprestidae is a large and diverse family of insects, estimated to include 15,000 thousand species (Bellamy, 2008). Buprestids are typically associated with trees and shrubs, upon which eggs are laid in bark crevices. Larvae then tunnel into the inner bark where they feed to maturity and pupate before emerging from characteristic D-shaped exit holes as adults. The adults disperse and locate new hosts. In many cases they are known to intermittently feed and mate on the foliage of associated host plants. While this life history pattern is overwhelmingly common in buprestids, there are exceptions, such as leaf-mining in the genus *Brachys* (Turnbow and Franklin, 1981). Adult buprestids are also known for their bright, metallic coloring, which has long been implicated as a mechanism for mate attraction. Beer bottles having similar coloration and indentations as female *Julodimorpha bakewelli* were shown to evoke male mounting and copulation attempts (Douglas, 1980; Gwynn and Rentz, 1983).

The emergence of *A. planipennis* as a severe pest in North America has led to a renewed interest in research into the behavior and ecology of buprestids with the goal of developing methods for early detection of their infestations. Traditionally the impact of most buprestid populations has been assessed by examining damage done to host plants, which can be accomplished by observing the appearance of exit holes, branch dieback, or the presence of larval galleries under debarked logs and branches. The *A. planipennis* introduction to North America has provided a unique occasion in which a buprestid species has spread while infesting large numbers of healthy host trees within its host population, causing nearly universal mortality shortly after the appearance of physical symptoms of decline. In such a situation, detection of incipient infestations of healthy forests is crucial in order to maximize management options. Because there was no precedent for such a severe problem involving a buprestid species, little was previously known about the biology and ecology of any members of this group, let alone the emerald ash borer.

After approximately a decade since the initial identification of *A. planipennis* in North America (Haack et al., 2002), it is useful to review the progress of research and technological development aimed at its detection, while also identifying how such insights can be transferred to managing similar potential threats from other buprestid species. Here we will first present an overview of the buprestid species of greatest economic concern, and how their geographic ranges may be spreading. We will then focus on recent advances in knowledge of olfactory and visual mechanisms of host location and mating behavior in buprestids, with an emphasis on the well-studied *A. planipennis* model system. Finally, an assessment will be made of how current detection technologies are able to exploit such behavioral attributes of buprestids, with an exploration of how continued behavioral research will likely contribute to the development of improved traps.

2. BUPRESTIDS OF ECONOMIC CONCERN

a) The Emerald Ash Borer, *Agrilus Planipennis* Fairmaire

The emerald ash borer is a buprestid species native to North Eastern Asia (Jendek, 1994). It feeds primarily on ash trees (*Fraxinus* spp.), both in its native range (Yu, 1992), and in North America (Anulewicz et al., 2008).

The biology is typical of that described for other tree-feeding buprestids (Yu, 1992; Cappaert et al., 2005; Wang et al., 2010) The first positive identification of emerald ash borer in North America occurred near Detroit, Michigan, USA and Windsor, Ontario, Canada in 2002 (Haack et al., 2002). Soon after this identification, the beetle was found in other nearby Great Lakes states (Poland and McCullough, 2006). The beetle has now been detected in a much broader geographical range including Quebec, Canada and many northern U.S. states, which span the Mississippi River to Atlantic Coast regions, where the infestation is expected to continue to grow (MacFarlane and Meyer, 2005; Kovacs et al., 2010, 2011). Throughout its known range in North America, there have been widespread reports of overwhelming mortality of ash trees (Poland and McCullough, 2006).

It is believed that dispersal of *A. planipennis* has been assisted by the movement of infested firewood (Muirhead et al., 2006), in which the beetles are viable given typical handling procedures (Petrice and Haack, 2006). Quarantine efforts have thus focused on limiting the movement of firewood away from areas of known infestations. Within quarantine zones it has been estimated that infestations have spread at a rate of only 1km per year (Sargent et al., 2006), further underscoring the role of human assistance in the dynamics of the more widespread multi-state outbreak of this pest.



Figure 1. The five buprestid species used as decoys for attracting European oak buprestids *Agrilus planipennis* (8–15 mm), *A. biguttatus* (10–14 mm), *A. sulcicollis* (6–8.5 mm), *A. cyanescens* (4.5–7.5 mm), and *A. angustulus* (4–6.5 mm). List includes range of lengths (Muskovits and Hegyessy, 2002). Reproduced from Domingue et al., 2011.

b) The Bronze Birch Borer, *Agrilus anxius* Gory

The bronze birch borer is a pest of trees in the genus *Betula* in North America. Normally only stressed or diseased trees are seriously affected, as a result of better larval performance in these conditions (Ball and Simmons, 1986). *A. anxius*-related birch decline has been shown to be correlated with stresses from temperature and precipitation changes (Jones et al., 1993). There is also strong evidence that susceptibility to this pest differs among birch species, with exotic tree species experiencing greater infestation, damage, and mortality rates than native species (Miller et al., 1991; Nielsen et al., 2011).

c) North American Oak Borers

The gold spotted oak borer was originally considered to include the single species, *A. coxalis* Waterhouse, which has recently been separated into sister species, *Agrilus auroguttatus* Schaeffer and *A. coxalis* (Hespenheide and Bellamy, 2009). The borers are native to the southwestern United States and Central America, feeding on oak trees within that range. Severe infestations of *A. auroguttatus* have been implicated in widespread tree mortality of coast live oak in California, after a likely recent migration of the species from Arizona (Coleman and Seybold, 2008, 2011). The susceptibility of coast live oak to attack and mortality from this species is not related to stress conditions, underscoring the likely severity of this impending threat (Coleman et al., 2011).

The two-lined chesnut borer, *Agrilus bilineatus* (Weber) is another pest of oak that is found in the eastern United States and Canada. The biology is similar to that of other tree-feeding buprestids described here (Cote and Allen, 1982), with attacks having been noticed to be prevalent on stressed trees, beginning high in the upper branches, and proceeding downward until the tree is killed (Haack and Benjamin, 1982). The prevalence of two-lined chesnut borers and associated oak tree mortality has been linked to defoliation events caused by the Gypsy moth, *Lymantria dispar* (Muzika et al., 2000)

d) European Oak Borers

Among several buprestid species known to feed on European oaks (Muskovits and Hegyessy, 2002), *Agrilus biguttatus* Fabricius (Figure 1B) is considered to be the greatest threat. It will sometimes attack larger diameter stems and branches, causing oak decline and mortality (Moraal and Hilszczanski, 2000; Vansteenkiste et al., 2005). Warm, dry summer weather encourages its growth and reproduction (Schlag, 1992). Mass occurrences of this species are often recorded 1–2 years after outbreaks of defoliating insects such as *Lymantria dispar*, causing further decline of weakened trees (Csóka and Kovács, 1999; Csóka and Hirka, 2006; McManus and Csóka, 2007).

Agrilus sulcicollis Lacordaire (Figure 1C), and *A. angustulus* Illiger (Figure 1E), are examples of smaller species not as strongly associated with oak decline (Schopf, 1992). They attack smaller branches and the upper parts of stems and smaller trees (Kolk and Starzyk, 1996; König, 1996; Csóka and Kovács, 1999; Muskovits and Hegyessy, 2002). *A. sulcicollis*, has recently been identified in North America (Haack et al., 2009; Jendek and Grebennikov,

2009), prompting concern that there may be a pathway by which the more aggressive *A. biguttatus* might also reach the forests of North America.

e) Other Forest Systems Affected by Buprestids

Although the above examples provide some of the more serious pest management concerns regarding buprestids, there are diverse buprestids common throughout all known forest ecosystems. When other species have emerged as threats of interest, the potential deleterious impacts have always included either drought stress of trees, or the accidental exotic introduction of the buprestid species. Outbreaks of the beach splendor beetle, *Agrilus viridis* Linnaeus, were reported in Germany corresponding to a severe drought in 2003 (Lakatos and Molnár, 2009). Likewise, *A. difficilis* Gory, a known buprestid pest of honeylocust in North America, is more successful on drought-stressed trees (Wescott, 1973; Akers et al., 1986). *Agrilus subrobustus* Saunders is an Asian buprestid species that has recently been found in the southeastern United States (Hansen et al., 2010; Hoebeke et al., 2011). It is a pest of Mimosa or silk tree, *Albizia julibrissin*, which itself was originally imported to North America approximately 200 years ago.

f) Agricultural Pests

There are also buprestids of economic concern that are pests of fruit-bearing trees and shrubs in plantation settings. In such circumstances mortality is not necessary to cause significant damage to the crops produced by affected plants. The flatheaded apple tree borer, *Chrysobothris femorata* Olivier, a widespread species, and a related species, the pacific coast borer, *Chrysobothris mali* Horn, are sources of such damage for several fruit and nut trees in North America (Burke, 1919). Particularly vulnerable to such attacks are newly transplanted trees (Johnson and Lyon, 1991). A number of other buprestids are known to affect berry plants, often causing galls in the woody stems. For example, the rednecked cane borer, *Agrilus ruficollis*, causes galls in blackberry bushes that have been linked to reduced berry counts (Johnson and Mayes, 1989; Johnson, 1992). *Agrilus rubicola* is a species native to Europe that has long been noted as a pest of agricultural crops such as raspberries (Davis and Raghuvir, 1964).

3. EXPLOITABLE BEHAVIORS OF BUPRESTIDS: AN ECOLOGICAL PERSPECTIVE

The species listed above clearly share many biological attributes, such as similar life history patterns and a tendency to cause greater damage to drought-stressed or non-native trees. However, little is known about several of the critical behavioral attributes of buprestids that might be exploited for management purposes, especially the development of detection and monitoring tools. Detection tools are perhaps most critical for identifying introductions of

exotic buprestids, which are unpredictable events that may go unnoticed until substantial tree damage and mortality has already occurred.

Trapping approaches have usually targeted the reproductive behavior of insects. After the first insect sex pheromone was identified (Butenandt et al., 1959) the discovery of pheromones of agricultural and forest pests soon began to intensify (Silverstein et al., 1966; Roelofs and Arn, 1968; Roelofs et al., 1969; Tumlinson et al., 1969; Bierl et al., 1970), leading to the discovery of a dizzying array of chemical signaling pathways in a diverse number of insect orders and families. The identification of such insect pheromones has since made an overwhelmingly large contribution to the development of pest management tools, which have come to include detection, mating disruption, and mass trapping (recently reviewed, Baker, 2009).

Scolytid bark beetles fill a quite similar ecological niche to the buprestid beetles described above, with both groups feeding on the inner bark of trees. Scolytids were among the first insects for which pheromones were identified (Rudinsky, 1966; Silverstein et al., 1966, 1968; Pitman et al., 1968; Wood et al., 1968). From the family Scolytidae, the website pherobase.com lists the pheromones of 72 species from 21 genera, most of which involve long-range attraction. However, there are currently no known long-range pheromones for any buprestid species. Here we propose that this lack of reporting of buprestid pheromones is not due to a failure of chemical ecologists to isolate them, but rather is more likely to reflect their lack of existence. Despite the similar use of the inner bark as the nutritive source for larval development in scolytids and buprestids, differences in particular behavioral and life history traits make long-range pheromone use advantageous for scolytids, but disadvantageous for buprestids.

The advantages to each individual scolytid bark beetle in emitting a pheromone signal that will attract an aggregation of conspecifics have been well described (Berryman et al., 1985). Scolytid adults enter the bark after dispersing. They then emit their pheromones from under the bark, where mating subsequently occurs, followed by female excavation of galleries for laying eggs. It is advantageous for the survival of each individual adult bark beetle attempting to enter the bark to broadcast an aggregation pheromone, because they are otherwise likely to be overwhelmed by the tree defenses if they are not joined by large numbers of other beetles (Raffa and Berryman, 1983). Furthermore, the bark provides some protection from predators and parasitoids, which are known to eavesdrop on pheromone signals (Bakke et al., 1981; Billings et al., 1984).

In contrast, adult buprestids do not enter the bark. Instead, each female beetle potentially lays a multitude of eggs on the bark, which will emerge as larvae that will later attempt to enter the bark and overwhelm any defenses produced by the tree. Once a suitable host has been found, there is a substantial disadvantage in broadcasting a chemical signal that intraspecific or interspecific competitors or predators might be able to exploit. In buprestids, there thus should be a strong selective pressure in females to develop the ability to locate favorable oviposition sites in stressed trees (Carlson and Knight, 1969). For males, finding suitable hosts would also be advantageous if it helps them locate females. In such a scenario it is not requisite for mating to occur directly at the oviposition sites on preferred hosts. Indeed female *A. planipennis* appear to be most commonly approached for mating when they are feeding on leaves (Lelito et al., 2007), indicating a spatial separation of oviposition and mating behavior. Thus the location of females by males after they have located such preferred hosts may be assisted by other intermediate to short range chemical or visual cues.

As in many pest management scenarios, fully exploiting all possible dispersal and mate-searching behaviors is needed to develop a trap that most effectively functions at very low population densities. Regardless of the reproductive capability of the target species, such low population densities will exist at the earliest stages and advancing margins of outbreaks of invasive species. Given the context of the life history characteristics of buprestids described above, it is clear that exploiting male mating behavior will be most effective for trapping. One reason males should be easier to detect at low densities is that unlike females, they are expected to continue to move about in the environment searching for mates among different favorable host trees throughout their adult lifespan. Females, on the other hand, are likely to become less mobile once favorable oviposition sites have been located. Secondly, male mating behavior has a point-source orientation towards its target of a receptive female. Female host selection has an inherently weaker directional component, with orientation to stress-induced volatiles at a much larger spatial scale (the whole tree). Furthermore, it is not necessarily clear that stress volatiles used by females to locate trees will always emanate from the tissues where oviposition occurs. Thus, as we review the literature that is now available on host location and mating behavior in buprestids, we will focus on the development of technology for detection of males.

4. THE ROLE OF STRESS-INDUCED VOLATILES IN HOST LOCATION

With the observation that tree stress is associated with buprestid infestations, experiments have been performed to attempt to increase attraction to trees by manipulating stress levels and volatile production of trees likely to be affected by buprestid pests. For *A. bilineatus*, approaches such as artificially girdling trees (Dunn et al., 1986a; Haack et al., 1982) or adding cut logs and ethanol (Dunn and Potter, 1991) have proved effective in attracting adult beetles. Furthermore, steam distillates from stressed oak logs were also used to attract more *A. bilineatus* to traps (Dunn et al., 1986b). A similar and more detailed exploration has been undertaken of the attraction of *A. planipennis* to stress-induced volatiles, which has been demonstrated to occur after girdling of ash trees (McCullough et al., 2009). Crook et al. (2008) identified several ash bark sesquiterpenes that were also antennally active to male or female *A. planipennis*. All but one of these compounds are found in commercially available manuka oil, a steam distillate of the manuka tea tree *Leptospermum scoparium*. All of the desired compounds are found in phoebe oil from the Brazilian walnut, *Phoebe porosa* (Crook et al., 2008; Cossé et al., 2008). Crook et al. (2008) were able to capture *A. planipennis* at an elevated rate when manuka oil or phoebe oil was added to traps at a variety of doses.

These oils have proven most effective when presented with stand-alone traps. For example, when manuka oil was added directly to trees, capture of *A. planipennis* was not elevated over control trees and was lower than in girdled trees (McCullough et al., 2009). However, when purple prism-panel traps were used near ungirdled trees with phoebe or manuka oil being added, trap captures were better than if similar unbaited traps were hung near girdled trees (Marshall et al., 2010).

Although sex ratio varies significantly within different trapping events in different studies, there has been no evidence that manuka or phoebe oil affects sex ratio. Studies

employing manuka oil have shown enhancement of trap capture on purple prism traps versus controls without altering sex ratios (Grant et al., 2010; Silk et al., 2011; Lelito, 2009). Phoebe oil added to green prism traps similarly increases trap captures versus controls without substantially changing the sex ratio (Grant et al., 2011; Lelito, 2009).

5. LEAF- AND BEETLE- PRODUCED COMPOUNDS RELEASED WHEN ADULTS FEED

The observation of feeding by adult buprestids on the leaves is common, and for female *A. planipennis* precedes mating (Lelito et al., 2007). Thus this behavior provides the possibility for both the induction of host volatiles and the release of sex pheromones. It has been found that both *A. planipennis* feeding and the application of methyl jasmonate to Manchurian ash seedlings induce similar increases in volatile emissions from leaves, but with a different qualitative profile (Rodriguez-Saona et al., 2006). Several of these volatile compounds were also found to be antennally active to males and females by GC-EAD analysis (Rodriguez-Saona et al., 2006; deGroot et al., 2008). Initial lab bioassays indicated that only females were behaviorally active in response to such compounds (Rodriguez-Saona et al., 2006). However, subsequent testing of these compounds in the field revealed a strong male bias in trap capture increases in response to (*Z*)-3-hexenol, the only consistently effective green leaf volatile (deGroot et al., 2008; Grant et al., 2010, 2011). The discrepancy between lab and field behavior may be explained by the subsequent field observations that males are always flying in search of mates when they are in a position where they would be exposed to such volatile compounds (Lelito et al., 2007, 2011; Domingue et al., 2011), whereas the laboratory bioassays involved walking approaches.

A possible sex pheromone was inferred from a study involving *A. bilineatus* where males were attracted to caged females provided with leaves for feeding (Dunn and Potter, 1988). This attraction occurred regardless of whether or not cut logs were included with the females. It was not clear if other visual or auditory signals could have also caused this attraction of males. In laboratory experiments, *A. planipennis* were able to locate females at close range when their eyes had been blocked by paint, but not when their antennae were blocked (Pureswaran and Poland, 2009). Other natural environmental cues necessary to elicit visual mate finding were absent in this experiment, such as direct sunlight and host leaves, likely precluding the observation of visual-mate finding when the eyes of males were uncovered. Thus, while the relative importance of visual versus chemical attraction could not be assessed in this experiment, there was nevertheless likely a cue perceived by the antennae at short-range that promoted mating.

The nature of the chemical cue operating in this experiment by Pureswaran and Poland was not determined, but a prospective volatile pheromone for *A. planipennis* has been isolated from females feeding from ash leaves (Bartelt et al., 2007). The compound was (*3Z*)-dodecen-12-olide, a macrocyclic lactone that was shown to evoke antennal responses in both males and females (Bartelt et al., 2007). It was later discovered that exposure to sunlight causes isomerization of this compound to (*3E*)-dodecen-12-olide, which is also antennally active (Silk et al., 2011). Field trapping has shown that both of these isomers can enhance the capture of male *A. planipennis*, but only when acting synergistically with (*Z*)-3-hexenol.

Thus, while further research is needed to determine the optimal release rates for all possible effective green leaf volatiles and pheromone components, there is now good evidence that female *A. planipennis* provide males with an exploitable attractive chemical cue while they are feeding on the foliage.

6. VISUAL MATE-FINDING

Although intermediate-to-short-range semiochemical signals produced by feeding females may play a role in male mate-finding, there is substantial evidence that such signals are not necessary to elicit mating approaches by males, which can occur solely due to visual signals. Using dead pinned *Agrilus planipennis* beetles as models on ash leaves, Lelito et al. (2007) were able to demonstrate highly repeatable male flights directly onto the decoys from 30 -100 cm above (Figure 2). The term “paratrooper copulation” was used to describe this behavior as it was often immediately followed by vigorous attempts to copulate with the model, which involved the extension of the feral male’s aedeagus.

It was quite clear that the visual image of the beetle alone is capable of evoking this response in the field, because the rate of male paratrooper flights was nearly identical if either male or female models were used and regardless of whether or not all potential chemical cues had been washed off of the models with organic solvents (Figure 3, Lelito et al., 2007). Also determined to be important was the wing position of the models approached. To induce male mating flights, the wings of the model needed to be held flatly, fully covering the abdomen.

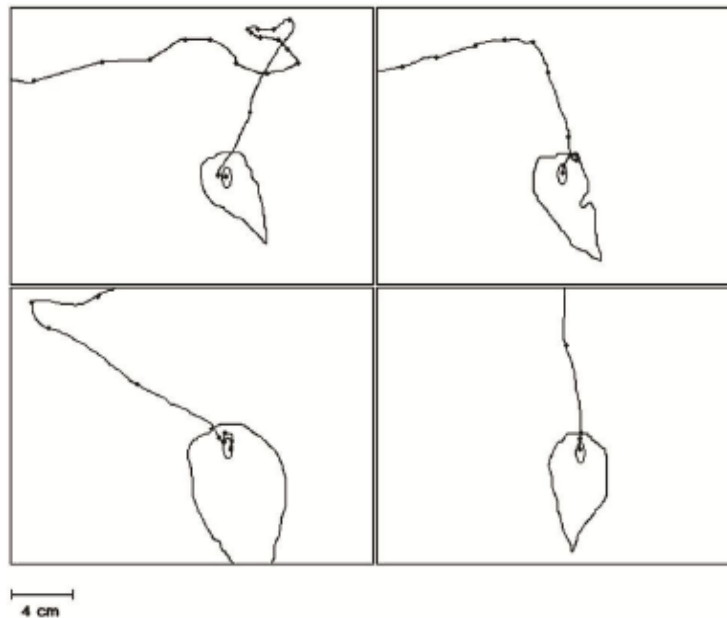


Figure 2. Various approach flight-tracks, transcribed from video, of feral male *Agrilus planipennis* descending rapidly onto pinned, closed-elytra decoys on leaves. The scale bar at left indicates 4 cm in each frame. The small oval on each depicted leaflet is the position of the pinned *A. planipennis* on the leaf. The span of time between each dot is 1/16 s. Reproduced from Lelito et al., 2007.

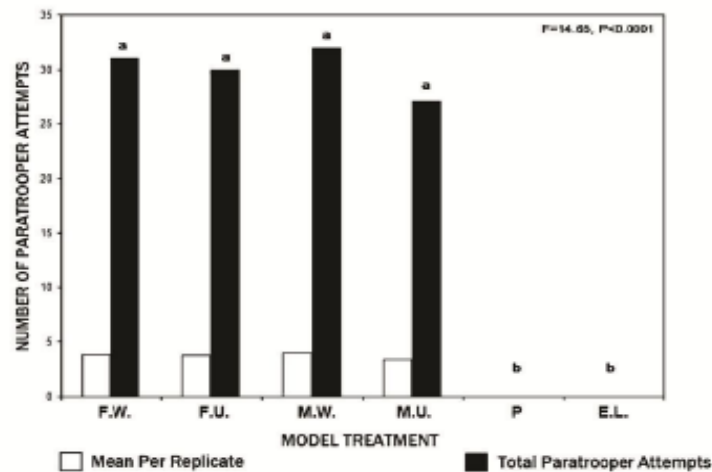


Figure 3. Mean number of *Agrilus planipennis* paratrooper copulation attempts observed per replicate (black bars) and the total number of paratrooper attempts (empty bars) observed in response to the different models during the eight replicates of our experiment. F.W. washed female; F.U. unwashed female; M.W. washed male; M.U. unwashed male; P leaflet with pin; E.L. empty leaflet. Eight replicates of this experiment were conducted, each lasting for 2 h. The number of feral males observed near any of the four types of beetle models is not statistically different (ANOVA, $F=0.47$, $p=0.7024$) but all four of the decoys had significantly more males than either of the two controls (ANOVA, $F=14.65$, $p<0.0001$). Reproduced from Lelito et al., 2007.

Spreading the wings of the models to reveal the abdomen reduced the rate of these approaches. Additional experiments determined that the use of only two excised elytra placed in parallel could also induce the paratrooper approaches at a high frequency (Lelito, 2009).

Subsequently, similar behaviors have been documented in other tree-dwelling buprestids when field populations have been presented with such visual decoys. Both *Agrilus cyanescens* Ratzeburg and *A. subcinctus* Gory were observed performing similar paratrooper flights toward pinned conspecific models (Lelito et al., 2011). *A. cyanescens* is a native European species that is now found in North America and specializes on honeysuckle (*Lonicera*) host plants. *A. subcinctus* is a native North American species that feeds on ash trees. Figure 1D shows the relatively smaller size of *A. cyanescens* in comparison to *A. planipennis*. *A. subcinctus* are even smaller, approximately similar in length to the *A. angustulus* pictured in Figure 1E. As was previously determined for *A. planipennis*, washing with solvent did not affect the frequency of aerial approaches to decoys for either species.

Attempts to assess the species-specificity of male aerial approaches to visual decoys have revealed a surprisingly degree of promiscuity. When examining the mating behavior of *A. cyanescens* it was found that the iridescent elytra of tiger beetles (*Cicindela*) could elicit male approaches at a frequency as great as conspecific decoys (Lelito et al., 2011; Figure 4). Field observations of the three sympatric species of European oak buprestids, *A. biguttatus*, *A. sulcicollis*, and *A. angustulus*, again revealed visually mediated mating approaches from distances up to 1m above pinned decoys (Domingue et al., 2011). Furthermore, in this experiment the feral beetles observed were presented with the choice of decoys of five different species (all of those shown in Figure 1). *A. biguttatus*, *A. sulcicollis*, and *A.*

angustulus all responded to the decoys presented with a great deal of cross-species attraction, despite some indications of preferences for certain decoys (Figure 5).

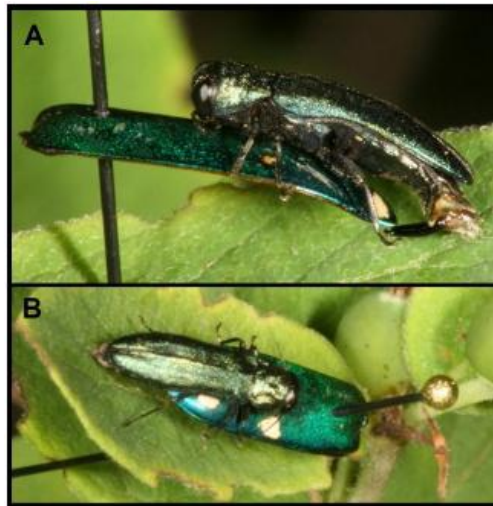


Figure 4. A live male *Agrilus cyanescens* attempting copulation with a *Cicindela sexguttata* elytron treated with female *A. cyanescens* cuticular extract, lateral (A) and dorsal view (B). Reproduced from Lelito et al., 2011.

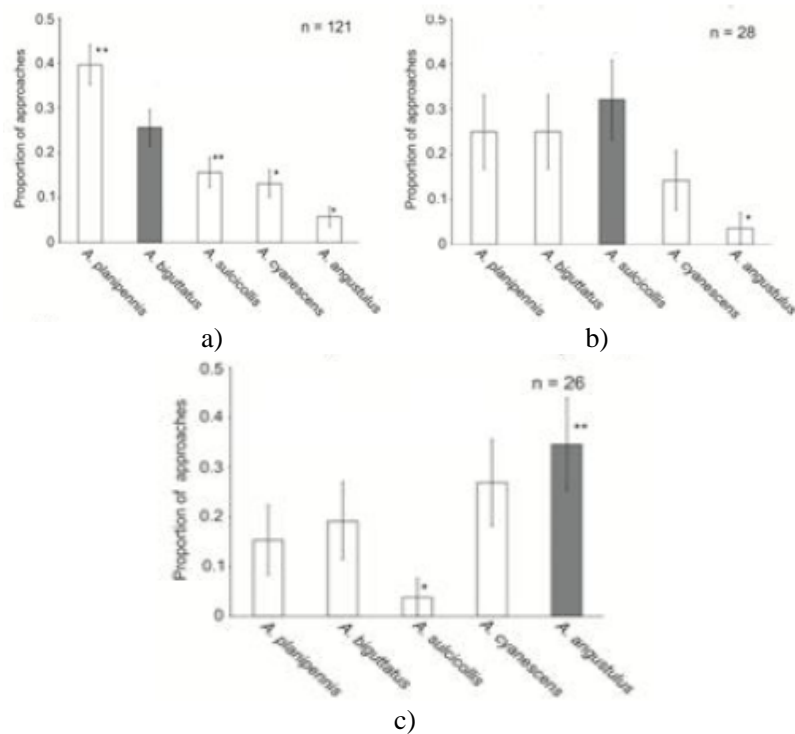


Figure 5. Mean (\pm SE) proportion of paratrooper approaches to each of the five decoys, by A) *Agrilus biguttatus*, B) *A. sulcicollis*, and C) *A. angustulus*. Significantly different proportion of paratrooper approaches in comparison to the conspecific decoy indicated (Fisher's exact test: * $P < 0.05$, ** $P < 0.1$). Reproduced from Domingue et al., 2011.

For example, *A. biguttatus* actually preferred the larger *A. planipennis* decoys to conspecific decoys, while they approached the other smaller species, *A. sulcicollis*, *A. cyanescens*, and *A. angustulus* less often. Both *A. sulcicollis*, and *A. angustulus* showed similar attraction to the other decoys presented, with the exception of reduced attraction to each other.

Another pattern emerging from these studies is the observation that the smallest species, *A. subcinctus*, and *A. angustulus*, while dropping downward toward decoys from 1m above them like the larger species, did not usually land directly on their targets. Instead they tended to land 1-2 cm away and then approached the decoys, often antennating them (Lelito et al., 2011; Domingue et al., 2011). Perhaps the smaller beetles simply experience a more turbulent path dropping through the air toward their targets than the larger beetles.

Considering the prevalence of paratrooper approaches in buprestid males, the bizarre spectacle of buprestids attempting to mate with beer bottle pieces observed by Gwynn and Rentz (1983) was perhaps reflective of a universal inherent tendency of particular visual cues to induce the release of a strong mating response. These observations suggest a possible common visual template for male mate-attraction, which would be highly desirable to better understand for the further development of more effective and sensitive traps. Such a template would not preclude the ability for both the emitter and receiver of the visual signal to modify characteristics and preferences so as to allow certain species-specific information to be conveyed. Perhaps elytral spots, lines, or subtle color variations might provide information that modifies the response. One conceivable need for a modification of the general visual template might be to facilitate the avoidance of heterospecific mating with a competing sympatric species, which is consistent with the preference patterns observed for the distinctly colored *A. sulcicollis* and *A. angustulus*.

A further understanding of both the production and response to the visual signals produced by buprestids is needed to begin to test such hypotheses and develop the technical capacity to duplicate the signal in a reliable fashion for trapping purposes. Currently it is known that the metallic aspect of buprestids and many other metallic-colored beetles such as cicindelids, is structurally produced by alternating uncolored and melanized cuticle layers (Figure 6) (Durrer and Villinger, 1972; Schultz and Rankin, 1985). This one quarter wavelength-stacked structure is highly effective for creating a strongly spectral color in sunlight, with little background emission of light of other wavelengths. Furthermore, the wavelength of light reflected from such a structure may vary with the angle of incidence, creating an iridescent effect. Such structurally produced colors are also often known to be accompanied by a dimpled or pitted coarse structure, which can be microscopically viewed for Buprestids (Figure 7). It has been suggested that such structures can obscure the different spectral colors emanating from the cuticle when viewed from a distance by predators (Seago et al., 2009). A more detailed examination of the structural coloration produced by a wider array of buprestid beetles may be useful for understanding which aspects of their coloration elicit the intense male mating responses that have been observed. Ultimately the nanofabrication of such structures could be used to create artificial beetle decoys to be incorporated in trapping designs aimed at more fully exploiting male mating behavior.

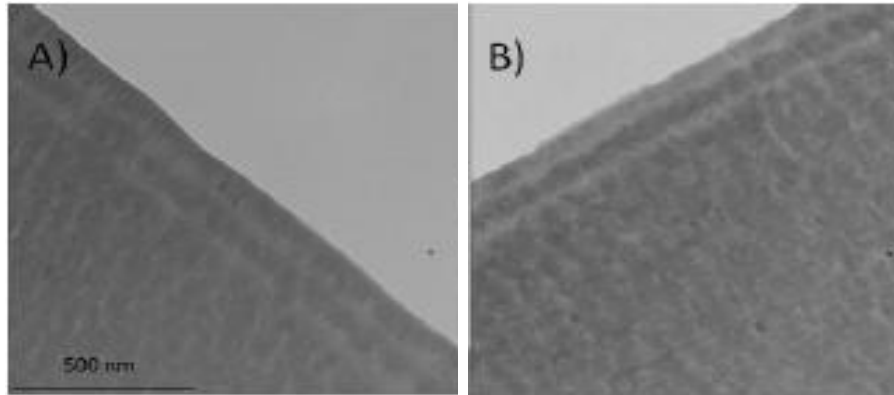


Figure 6. TEM image of the elytra of *A. biguttatus* (left) and *A. sulcicollis* (right) showing regular layering of the epicuticle.

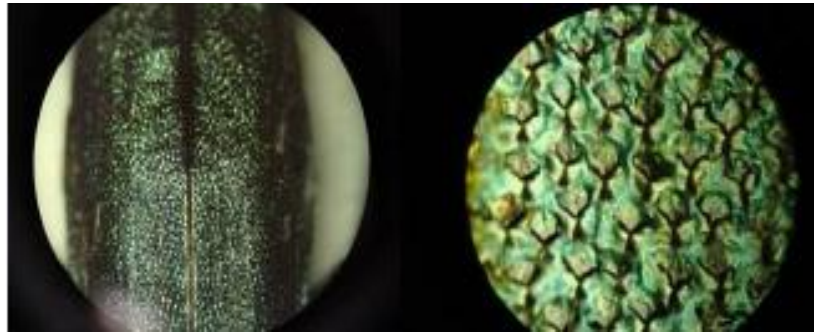


Figure 7. *Agrilus sulcicollis* under a light microscope revealing irregularities of the elytral surface structure.

7. CONTACT PHEROMONES

After buprestid males have visually located and approached females, there are additional cues known to facilitate copulation and prolonged mating contact. When presenting solvent-washed or unwashed beetle decoys, Lelito et al. (2007) found that feral *A. planipennis* males would stay on top of unwashed females for much longer periods than on washed models of either sex or unwashed males. The cuticular hydrocarbons 3-methyl-tricosane (Lelito et al., 2009) and 9-methyl-pentacosane (Silk et al., 2009) were later implicated in causing this prolonged mating contact. Although no contact pheromone components have been identified for other buprestids, similar behavioral evidence was found for them in *A. cyanescens* and *A. subcinctus*, which both had greater durations of copulatory contact when presented with unwashed females versus other treatments (Lelito et al., 2011). *A. biguttatus* males spent more time on *A. planipennis* dead female decoys than on conspecifics, suggesting that if *A. biguttatus* does use a contact pheromone, it is likely similar to that of *A. planipennis* (Domingue et al., 2011). There have not yet been any attempts to employ contact pheromones in trapping designs.

8. DETECTION OF BUPRESTIDS OF ECONOMIC CONCERN

a) Visual Detection Methods

In many cases a high incidence of buprestid damage can be observed by various types of visual surveys of trees that might be expected to be infested by beetles. Such detection methods tend to be labor intensive and are usually most effective if used in an area where stressed or vulnerable trees exist. In some cases this approach has consisted simply of peeling back bark (Wargo, 1977). The characteristic D-shaped emergence holes of buprestids can also be used to estimate the presence and size of infestations. For example, binocular surveys of emergence holes at the edge of an outbreak of *A. planipennis* proved capable of predicting crown thinning rates (Smitley et al., 2008). Another highly effective technique for capturing buprestids is the use of trap trees. This technique involves girdling trees and allowing them to be colonized by the buprestids (McCullough et al., 2009; Marshall et al., 2011). Some studies have placed a sticky band around the trunk of a girdled tree to detect beetles (Dunn et al., 1986a). Girdling is highly effective for attracting buprestids, but is of course also destructive. Finally, it has been shown that early infestations of *A. planipennis* in at-risk areas can be detected in a high percentage of trees by removing and sampling 6 inch branches (Ryall et al., 2011). Such a technique provides a minimally destructive approach for identifying large numbers of individually infested trees for treatment or removal, before they can serve as sources of continuing population expansion.

The visual survey, girdling, and branch sampling techniques described above are most effective for urban situations where areas of infestation are known and it is of interest to characterize and simultaneously mitigate the extent of the problem. For a highly invasive species such as *A. planipennis* there is also a need to survey larger geographic areas to determine where new infestations are emerging, often in areas that can be quite distant from known infestations when human-assisted emigration has occurred. For such an application, traps are desirable that can be easily fabricated and distributed to monitor large geographic areas. The following sections discuss recent progress toward developing such traps for buprestids.

b) Sticky Traps

A number of different techniques have been used to attempt to capture adult buprestids using natural or artificial surfaces coated with sticky material that will entangle them. One such approach for trapping buprestids has been to employ sticky card surfaces (Wargo and Montgomery, 1983). For *A. planipennis* it was initially demonstrated that purple panel traps made of corrugated plastic were more effective in capturing beetles when compared to a large array of similar traps using other colors (Francese et al., 2005). To provide a large trapping surface, this basic trap design was later modified to include a three-panel “prism trap”. This trap, with each side being approximately 35 X 60 cm (Francese et al., 2008), has subsequently become the trap used in most *A. planipennis* detection programs. Francese et al. (2008) also found that more beetles were caught if traps were placed higher in the canopy and near open, sunlit areas.

The purple version of the prism trap was developed in response to the operational success of the materials employed, rather than to any particular biological principles. Thus, attempts to understand the behavioral attributes of buprestids being exploited by these traps have occurred subsequent to their original development. Crook et al. (2009) performed electroretinogram recordings on *A. planipennis* to wavelengths of light within the visual spectrum. He found generally broad responsiveness to all wavelengths, with a modest increase in sensitivity to red wavelengths in females. Crook et al. (2009) went on to speculate that the preference for purple colored traps might be linked to this greater response to the higher wavelengths of visible light in females, and perhaps also indicative of attraction to the red abdomen of *A. planipennis*. Alternatively, the same authors later proposed that the attraction to purple traps might arise from attraction to host bark (Francese et al., 2010a). The second explanation seems more plausible given that greater proportions of females have been documented for beetles on purple traps (Francese et al., 2010a), and for beetles observed on ash tree trunks and branches (Lelito et al., 2007). Furthermore, revealing the red abdomen of visual decoys actually severely reduced the attraction of males to the decoys (Lelito et al., 2007). In addition there is no known behavioral attraction of females toward conspecifics, let alone specifically to the abdomen.

It was also later found that a green version of the prism traps could often be more effective than the purple traps. Additional effort has been made to identify the optimal wavelength and reflectance of green traps used (Francese et al., 2010a). It has also been found that green traps perform better the higher they are placed in the canopy (Francese et al., 2010b). As described above, researchers investigating the effects of the green leaf volatile (*Z*)-3-hexenol and the prospective lactone pheromone (3*Z*)-dodecen-12-olide, have had greater success when using these green prism traps high in the canopy (Grant et al., 2010, 2011; Silk et al., 2011). The male-biased sex ratio observed in these studies suggests that these traps may be evoking some aspects of male mate-finding, which involves persistent flight through the canopy while actively searching for prospective mates. These attributes include the green color of leaves and the chemical emanations of leaves being fed upon by females when they become accessible for mating approaches.

c) Multi-Funnel Traps

In an attempt to find an alternative to the large sticky prism traps, Francese et al. (2011) developed modified multi-funnel traps, based on existing designs developed for scolytid bark beetles (Lindgren, 1983). Such traps function by inducing beetles to land on their sloped surfaces where they slip and fall into a collection cup below. These traps were customized using the green and purple colors employed for prism traps. They were effective at catching similar numbers of *A. planipennis* as prism traps if coated with substances such as Rain-X or Teflon. These traps provide the potential advantage of avoiding the difficulty of working with the sticky glue material used for the prism traps. It is not yet known how effectively the semiochemical lures developed for *A. planipennis* work with this trap design. However, they seem to operate using similar principles as the prism trap, providing a large surface of a color that is presumably attractive to the beetles because of some biological function, such as oviposition or maturation feeding.

d) Visual Decoy-Based Traps

Agrilus planipennis can be trapped by applying Tanglefoot glue to leaves with pinned visual decoy beetles, an assemblage that was given the name “sticky leaf trap” (Figure 8A; Lelito et al., 2007, 2008). Further attempts to use *A. planipennis* decoys on plastic cards were also successful in capturing other *A. planipennis*, but not as successful as the natural leaf and decoy combination (Lelito et al., 2008; Lelito, 2009). It was also demonstrated that the use of manuka oil or phoebe oil can increase captures on such traps (Lelito, 2009). Whenever in the above-cited studies a visual lure was employed, and the sexes of beetles captured were identified, a heavy male bias was reported. Furthermore, leaves without decoys captured fewer beetles without displaying a male bias. Thus, it is clear that decoy-baited traps are positively exploiting the male visual mate-finding behavior described as “paratrooper” approaches.

It is impractical to use sticky leaves for sustained field trapping over large geographic areas due to the degradation of the leaf surface over time. More recently it was shown that green plastic cards were proficient at catching the European oak borers *A. biguttatus*, *A. sulcicollis*, and *A. angustulus* if presented on a horizontal surface located on branches to replace the foliage (Figure 8B; Domingue, 2011). Furthermore the addition of *A. planipennis* decoys further increased trap captures of European oak borers, as did concomitant baiting with manuka oil and Z-(3)-hexenol. To further improve usability of such traps, it would be desirable to develop an artificial decoy that is capable of being affixed to the traps before deployment.

e) Biological Detectors

It has been noted that a solitary digging wasp, *Cerceris fumipennis*, hunts buprestids, using them to provision their nests (Evans, 1971). A wide diversity of buprestids has been reported from samples of their nest sites (Marshall et al., 2005). Furthermore, researchers have been able to use these wasps to successfully capture *A. planipennis* near infestation sites (Careless and Marshall, 2010).

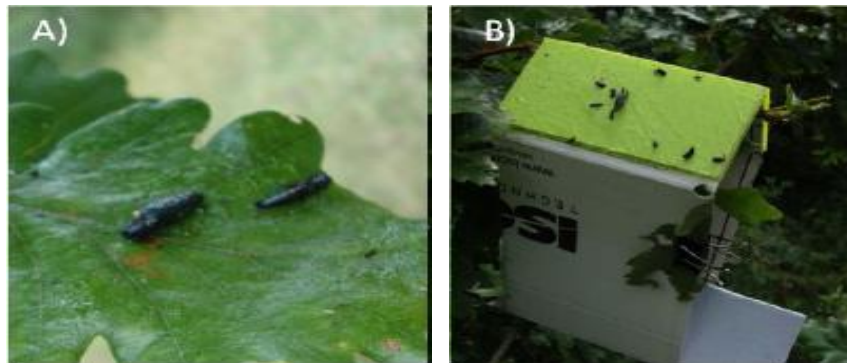


Figure 8. Visual decoy-based trapping designs: A) *Agrilus planipennis* on sticky leaf captures an *A. sulcicollis* male; B) *A. planipennis* on green plastic surface captures multiple small buprestids.

The potential for using *Cerceris fumipennis* as a detection tool is intriguing, and researchers are now implementing the monitoring of a large geographic area using a network of volunteers at research institutions (Careless and Marshall, 2010). Regardless of the success of such endeavors, we also believe that further research into the visual attributes of this wasp may eventually produce insights into how male buprestids themselves are able to find mates. The wasps appear to be able to recognize universal characteristics of buprestids. As described above, the high degree of visual cross-attraction among buprestids suggests a common visual template for mate attraction. Thus, *Cerceris fumipennis* wasps may also be highly tuned to the essential visual attributes of buprestids that characterize this general template, which if duplicated may lead to a highly effective generic trap for buprestids.

CONCLUSION

We currently envision the further refinement of both the multi-funnel and the visual decoy-based trapping approaches. Unfortunately the two approaches are not likely to be compatible to employ within the same design. The surfaces of funnel traps slope downward and inward, and are thus inherently oriented away from sunlight. The presentation of decoys in full sunlight, however, appears to be a key component of visual-decoy-based trapping approaches. Nevertheless, the multi-funnel traps have the distinct advantage of allowing captures of large numbers of buprestids without entangling them in sticky material, thus allowing substantial improvement in the collecting, handling, and identification of insects found in these traps. Because they appear to operate using similar biological principles as prism traps, we envision that they will be optimized by expanding upon similar lines of research, and become the most convenient and effective tool for monitoring the sizes of buprestid populations in areas of known or likely infestations.

However, because long-range pheromone signaling does not seem to exist in buprestids, such traps may continue to experience difficulty attracting and capturing beetles from very small populations. The visual decoy trapping has a greater potential in this respect because it manipulates the strongest behavioral tendency yet observed in buprestids, the paratrooper landing of the highly vagile males onto prospective mates after their wide-ranging scanning of the tree canopies. These traps require further development for widespread usability, including the fabrication of artificial visually-attractive decoys. It would also be desirable to develop traps based on this principle that circumvent the use of sticky material. If these engineering challenges can be met, visual-decoy traps are likely to be well suited for distribution across large geographic areas for early detection of unexpected populations of buprestids.

Given that the host location, pheromone signaling, and visual mate-finding behaviors of *A. planipennis* potentially contributing to optimal trap design are not yet fully understood, applying such trap technologies to other buprestid species will also be another substantial challenge. All of the less thoroughly researched buprestids have tended to show similar biological properties and ecological interactions as those observed for *A. planipennis*. However, most of the details of these interactions are not yet known. For example, will most species use similar chemical cues when responding to stressed hosts? Do additional intermediate-range pheromones similar to (3Z)-dodecen-12-olide exist in other species? If so,

are they relatively more or less important in comparison to the visual mating response of males in those cases? Ultimately it will be desirable to develop multifunnel and visual-decoy traps that will work generically for many buprestids species, but that can also be tuned to focus on particular species of interest when needed.

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