

Improving trapping methods for buprestid beetles to enhance monitoring of native and invasive species

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Most of the current understanding of the orientation and communication of jewel beetles arose from research on the Asian emerald ash borer (EAB), *Agrilus planipennis*, which has become one of the most destructive invasive forest insect pests in history following its introduction to North America and European Russia. From a European perspective, a number of jewel beetles have a high invasive risk similar to that of the emerald ash borer, including the potential threat of the bronze birch borer *Agrilus anxius*, the goldspotted oak borer *Agrilus auroguttatus*, and the twolined chestnut borer *Agrilus bilineatus*. Native jewel beetles expanding their geographic range include the cypress jewel beetle *Ovalisia festiva* and the black-banded oak borer *Coraebus florentinus*. Other native species are increasing in their importance, including the flathead oak borer *Coraebus undatus*, the two-spotted oak borer *Agrilus biguttatus*, the flatheaded beech borer *Agrilus viridis* and *Agrilus cuprescens*. Commonly used prism and multi-funnel trap designs and other promising experimental trap designs have been tested and compared in the US and in Europe. One factor considered has been colouration, typically purple and green. Another is olfactory attraction, both to plant volatiles and extracts such as (Z)-3-hexenol, Manuka oil, Phoebe oil and Cubeb oil, and also to pheromones such as (Z)-3-lactone, for emerald ash borer. Field observations have been made of mating and host-finding behaviours of oak buprestids based upon visual stimuli in North America and Europe. By using pinned dead EAB models, visual mating approaches have been observed by males of *Agrilus biguttatus*, *Agrilus sulcicollis* and *Agrilus angustulus*, which is a behaviour similar to that previously observed in EAB. Green plastic-covered branch-traps significantly out-performed other trap designs and caught more *Agrilus* jewel beetles if an artificial visual decoy that copies a beetle body was included. A higher fidelity decoy offered the same distinctive light-scattering pattern as real resting EAB females and elicited the full sequence of stereotypical male mating flight behaviour of EAB and *A. biguttatus* from up to 1 m away. An optimization of visual, olfactory and other possible stimuli has likely not yet been achieved. More sophisticated trap designs could lead to more sensitive detection capabilities with increased selectivity.

Importance of Buprestidae from a European perspective

The jewel beetles (Buprestidae) are conspicuously colourful beetles with a characteristic shape. They can range from 2 to 85 mm in size (Muskovits and Hegyessy, 2002), and they constitute the eighth most diverse family of the order Coleoptera. According to the most generally accepted viewpoint, the family Buprestidae is divided into 13 subfamilies, 50 tribes and more than 500 genera and sub-genera (Bellamy, 1985). There are ~15 000 species of jewel beetles living throughout the world, mainly in

tropical regions. About 300 species live in Europe (Bellamy, 2002; Muskovits and Hegyessy, 2002).

Jewel beetles are exclusively phytophagous (Muskovits and Hegyessy, 2002). The larvae bore in tree trunks, branches and bushes mostly underneath the bark, less frequently inside the bark. The larvae of a few species live inside the soft stems, roots or leaves of herbaceous plants.

The genus *Agrilus* has more than 3000 valid taxa making it the most taxonomically diverse insect genera worldwide (Bellamy, 2002; Chamorro *et al.*, 2015; Jendek, 2016; Kelnarova *et al.*, 2019). However, this group of insects did not draw significant

attention before the accidental introduction of the Asian emerald ash borer, *Agrilus planipennis* Fairmaire (EAB) into North America (Haack *et al.*, 2002). During each local EAB outbreak, the typical pattern of forest decline includes mortality of green ash (*Fraxinus pennsylvanica* Marsh.), white ash (*Fraxinus americana* L.) and black ash (*Fraxinus nigra* Marsh.). Mortality exceeds 99 per cent after 15 years of the first infestation, leading to an orphaned cohort of saplings too small to be infested with EAB. Most trees (>60 per cent) die even earlier, over a 5 year period of time (Klooster *et al.*, 2018). By October 2018, EAB had been found in 35 states of the US, and in 5 provinces of Canada (Ontario, Quebec, New Brunswick, Nova Scotia and Manitoba) (<http://www.emeraldashborer.info>). The reports available to us and all personal communications indicate that all North American ash species encountered by EAB have been susceptible (Anulewicz *et al.*, 2008; EPPO, 2013; Poland *et al.*, 2015). According to Poland *et al.* (2015) EAB might be very efficient at locating host trees even when they are rare within mixed species stands. Thus, as described by Knight *et al.* (2013), the management strategy of reducing ash density is unlikely to protect the remaining ash trees.

EAB has also been accidentally introduced from Asia to the Moscow Region (Baranchikov *et al.*, 2008), expanding its range in all directions, but most noticeably southwards (Orlova-Bienkowskaja, 2014). By 2012, EAB reached the Smolensk Region bordering Belarus, and by 2013, the Voronezh Region bordering the Ukraine (Musolin *et al.*, 2017). It is known that the population density of EAB is high at the Ukraine border of Voronezh Region, where there are large areas with fully completely dead ash trees, and its presence in Ukraine has recently been confirmed (Drovalenko *et al.*, 2019). Earlier calculations by Orlova-Bienkowskaja and Bienkowski (2018) had estimated that the range of occurrence is likely to be restricted to Russia, with the probability of detection of the pest to be 15 %–40 % per cent in the east of Belarus, the Ukraine, Estonia, Latvia, and Lithuania by 2022.

EAB generally has a one-year life cycle, but may require two years to complete development in cooler climates (Wei *et al.*, 2007; Tluczek *et al.*, 2011). The long drawn out flight period starts at ~250° days (from base 10°C, DD10), typically beginning in May and peaking in late June. Adults feed on the margins of ash leaves for at least 10–14 days before becoming sexually mature and mating (Rodriguez-Saona *et al.*, 2006; Ryall *et al.*, 2013). Females lay ~47 eggs on average (Rutledge and Keena, 2012), and hatch within two weeks. The emerging larvae feed in the inner phloem, outer xylem and cambium, creating serpentine-shaped galleries packed with frass (Poland *et al.*, 2015). After four developmental instars, larvae complete feeding in autumn and overwinter as mature larvae (pre-pupae) in pupal cells constructed in the outer bark or the outer sapwood. Pupation takes about three weeks, usually in April.

Relative to defoliators, wood borers and invasive pests have had larger negative impacts on net primary carbon production, with longer recovery times (Flower and Gonzalez-Meler, 2015). Using the USDA Forest Service forest inventory and analysis database, Flower *et al.* (2013) found that forest lands in the lower 48 US states hold ~8.7 billion ash trees and saplings, which represent ~2.5 per cent of the aboveground forest carbon mass. According to Klooster *et al.* (2018), disturbance

caused by ash mortality results in gap formation in forests and the accumulation of coarse woody debris, which has cascading impacts on forest communities. There have been impacts upon successional trajectories, increased growth of non-native invasive plants, changes to soil-dwelling and herbivorous arthropod communities and changes to bird foraging behaviour, abundance and community composition. Further, Kovacs *et al.* (2010) estimated the full cost of the treatment, removal and replacement of more than 17 million ash trees to be \$10.7 billion. These projections suggest that a substantial investment to slow the expansion of isolated EAB infestations and postpone the ultimate costs of ash treatment, removal and replacement may be worthwhile.

Other jewel beetle species may have the potential to cause similar impacts. This possibility might exist either when there is a new introduction to an area inhabited by evolutionarily isolated prospective hosts or when there are changes to the environment of already inhabited areas that are favourable to outbreaks and range expansion. For example, the bronze birch borer *Agrilus anxius* Gory, native to North America, may have the potential to threaten the birch trees (*Betula* spp.) of the entire Eurasian continent because they are not evolutionarily adapted to the North American pest (Muilenburg and Herms, 2012). Within North America, the goldspotted oak borer, *Agrilus auroguttatus* Schaeffer, native to Arizona, provides an example of a species that has undergone recent range expansion, and now is a pest in parts of southern California where it was previously unknown (Coleman and Seybold, 2011). Such a species could also be a threat to Europe.

In European oak forests (*Quercus* spp.), some jewel beetle species are considered severe forest pests of increasing importance. The black-banded oak borer *Coraebus florentinus* Herbst and the related flathead oak borer *Coraebus undatus* F. are primary pests of cork oak, *Quercus suber* L., in the Mediterranean region, which have caused great economic losses to the cork industry (Fürstenau *et al.*, 2012; Fürstenau *et al.*, 2015). *C. florentinus* is also reported to be a pest in Slovenia (Jurc *et al.*, 2009) and has become a forest pest of Central European oak forests in Hungary (Koltay and Leskó, 1991) and south-west Germany (Buse *et al.*, 2013), most probably due to the warm and dry environmental conditions of recent decades. Another thermophilic oak pest of increasing importance is *Agrilus biguttatus* Fabricius (Moraal and Hilszczanski, 2000), which has suspected links with acute oak decline in increased drought (Denman *et al.*, 2014; Brown *et al.*, 2015, 2017; Denman *et al.*, 2018).

Similarly, the establishment of populations of the cypress jewel beetle *Ovalisia festiva* L. northward in Europe from its endemic Mediterranean range has actually resulted in its status being changed from endangered to that of a pest in certain areas. In Hungary, there has been an observed increase in the abundance of this species in natural juniper forests, as well as in cypress and juniper ornamentals located in residential areas. Similar changes in the status of cypress jewel beetle have occurred in Romania and Slovenia. The damage to the health and aesthetic value of affected plants has resulted in the need for monitoring and plant protection measures (Razinger *et al.*, 2013; Nitzu *et al.*, 2016). The role of climate change in each of these individual cases remains to be fully supported by scientific data, but the trends in the expansion of buprestid habitats are obvious.

The flatheaded beech borer *Agrilus viridis* L. is a common species in Europe affecting a wide range of host plants and having pest status in common beech, *Fagus sylvatica* L. (Molnár *et al.*, 2010; Bruck-Dyckhoff *et al.*, 2019). *Agrilus populneus* Schaefer is a dangerous pest of hybrid poplar plantations in Central Europe (Szontagh, 1979). In the last twenty years, *Agrilus cuprescens* (Ménétriés) has become a significant pest in raspberries all over Europe, resulting in lower yields through the decrease of fruit bearing shoots (Gordon *et al.*, 1997; Véték and Péntes, 2008).

Furthermore, in western Russia, a large number of *Agrilus convexicollis* Redtenbacher specimens were collected from younger branches of declining green ash trees (planted as ornamentals), which were also infested with EAB (Orlova-Bienkowskaja, 2015; Orlova-Bienkowskaja and Volkovitch, 2015). *A. convexicollis* is a common species all over continental Europe (Muskovits and Hegyessy, 2002). Thus with the inevitable spread of EAB, the monitoring of *A. convexicollis* might gain importance because it develops in living but weakened hosts, and contributes to overall decline in tree vigour.

Finally, the twolined chestnut borer *Agrilus bilineatus* (Weber) has been recorded for the first time in Europe (Hizal and Arslanogundogdu, 2018), when two specimens were collected at the south-eastern border of Europe at Istanbul, Turkey. It has also been recorded in Asia Minor in the Anatolian Part of Turkey (Jendek, 2016). The twolined chestnut borer could potentially achieve pest status in European oak and chestnut forests. It is already considered to be a pest in its native North America, where it attacks trees stressed by drought or other abiotic or biotic factors and is associated with extensive mortality in the eastern deciduous forests (Millers *et al.*, 1989; Haack and Petrice, 2019). Each of the above mentioned species has a high invasive risk to other continents, thus to maximize management possibilities, it will be essential to assess and improve the ability to monitor such *Agrilus* species and other buprestid populations with effective trapping systems.

The challenge of jewel beetle detection

It was demonstrated by Siegert *et al.* (2014) that EAB populations are often established in a local area well before they are detected. From such unnoticed populations, there can arise a remarkable capacity for rapid population growth and geographic expansion. Early detection of EAB and other jewel beetles would provide more time to develop a management strategy and implement activities to reduce the impacts of infestations. Effective methods to detect new infestations and monitor low density populations are therefore critical aspects of managing the pests in urban, residential and forested settings (McCullough and Poland, 2017).

The above examples draw our attention to the need of developing sufficiently efficient sampling methods for jewel beetles in Europe and elsewhere. However, adult jewel beetles are typically small, swift flyers with just a short active mating period. At the same time, the larvae of most species develop hidden under the bark of trees and shrubs, or inside the stems and roots of herbs, making their presence difficult to visually detect (Muskovits and Hegyessy, 2002; Chamorro *et al.*, 2015). Thus, early infestations are extremely difficult to detect due to

cryptic larval feeding when there is still a lack of obvious signs or symptoms of initial attack.

Within the buprestids, EAB has the only identified sex pheromone, and the deployment of this compound and an analogue have been successfully researched (Bartelt *et al.*, 2007; Ryall *et al.*, 2012; Ryall *et al.*, 2015; Silk and Ryall, 2015). However, this compound is not very volatile and thus is not likely active at longer distances, limiting its ability to increase trap captures and improve detection at lower densities. Furthermore, an optimal combination of all possible olfactory and visual stimuli suitable for monitoring purposes may not have been found yet. These limitations make detection of EAB presence and monitoring changes in their population dynamics very difficult, especially when there is interest in whether they have become established at sites with high invasion risk.

When EAB was first described in North America, Haack *et al.* (2002) describe the lack of specific tools for the monitoring of EAB, which we believe persists and applies to other potentially important jewel beetle species. Infestations are insidious in that they often go undetected during initial colonization. The recognition of characteristic D-shaped adult exit holes (typical for *Agrilus* and *Coraebus* spp.) is not particularly useful when checking ring porous hardwoods (like ash, chestnut and oak) where infestations often start in the canopy and move downward along the trunk in succeeding years. Exit holes only become noticeable at ground level when they begin to occur lower on the trunk of the ring porous hardwood trees and the larvae have already significantly damaged the tree (Haack and Benjamin, 1982; Haack *et al.*, 1983). On the contrary, diffuse-porous hardwoods (like aspen and birch) are more likely to benefit from the examination of the lower trunk sections before mass damage to the crown occurs (Muilenburg and Herms, 2012). Another concern is that the patchy distribution of host trees and small number of heavily-infested 'brood trees' can significantly delay the time of detection of the goldspotted oak borer (Haavik *et al.*, 2015).

Girdling for detection purposes

The detection and sampling of EAB infestations include using girdled trap-trees to increase attraction to adults followed by subsequent examination of larval densities (Ryall, 2015), which is still one of the most effective means of detecting very low densities of EAB (McCullough *et al.*, 2009a, b; Mercader *et al.*, 2013). Ash trees are girdled in spring to attract ovipositing females then debarked in the autumn to assess larval presence and density. Targeting the 8–12 cm diameter section of the trap tree stem keeps the amount of the tree peeled at less than 45 per cent, while more than 50 per cent of EAB larvae within the tree are encountered in this targeted section (Marshall *et al.*, 2011). Probability of detection using a single detection tree was >50 per cent when density proxies for the area were <5 larvae per detection tree, while the probability of detection with purple prism traps baited with Manuka oil that were placed in the same area was <35 per cent, even when density proxies exceeded 25 larvae per detection tree (Mercader *et al.*, 2013). At very low densities of <5 EAB larvae per detection tree, using three detection trees would increase detection probabilities to 90 per cent, while five artificial traps would increase the detection probability only to

40 %. Using another approach, which involves placing sticky bands on girdled trees, a higher density of EAB beetle captures may be possible (i.e. McCullough *et al.*, 2008). Furthermore, debarking girdled trees can be labour-intensive and locating suitable trees for girdling can be difficult, especially in urban or residential areas or when surveys must be conducted for multiple years (Mercader *et al.*, 2013).

Monitoring and trap design

The most commonly used trap designs and some alternatives that have only been deployed in research settings are discussed below.

Prism traps: sticky and coloured three-sided (35 × 60 cm) prism traps were a substantial improvement in trap design (Francese *et al.*, 2010a, b) and provided the first standard monitoring method for EAB. Prism traps fabricated from coloured corrugated plastic are widely used in survey activities in the US and Canada (Francese *et al.*, 2011; McCullough and Poland, 2017). According to APHIS (2018) ~12 000 purple prism traps are used yearly, which forms the basis of EAB monitoring system in the US. European examples of prism traps being used for trapping include *A. convexicollis* and *A. viridis* in beech (*Fagus* spp.) and poplar forests (*Populus* spp.) in Slovakia (Rhainds *et al.*, 2017), *A. biguttatus* and *A. sulcicollis* Lacordaire in oaks (*Quercus* spp.) in the UK (Brown *et al.*, 2017) and *C. undatus* in cork oak in Spain (Fürstenau *et al.*, 2015).

Branch traps: small sticky branch traps (two 5 × 9 cm sticky sheets) were used to test beetle decoys in an oak forest in Hungary (Domingue *et al.*, 2013) and in an ash plantation in Pennsylvania (Domingue *et al.* 2016a). Both of these studies suggested that the use of particular semiochemical treatments could improve trap designs, including in the latter case the lactone pheromone. Such designs have not been further explored for evaluation at low densities or with additional design and lure improvements.

Double-decker traps. These traps have also been designed for the goal of early detection of EAB (Poland *et al.*, 2016; McCullough and Poland, 2017). They consist of two corrugated plastic prisms, one green (baited with (Z)-3-hexenol) and one purple, attached to a 3 m tall polyvinyl chloride (PVC) pipe supported by a T-post. These double-decker traps have twice as much surface area (14 400 cm²) as the individual prism canopy traps (7200 cm²) and 30 per cent more area than the combined surfaces of all 12 funnels of a Lindgren funnel trap (11 160 cm²). In contrast to baited prism traps hung from the branch of an ash tree, double-decker traps are designed to be placed in open areas near ash trees.

Multi-funnel (Lindgren) traps: more recently these traps were developed to address the demand for a reusable, user-friendly trap expressed by program managers, surveyors and researchers (Francese *et al.*, 2011). Multi-funnel traps are fitted with wet collection cups filled with 150–200 ml of propylene glycol, used as a surfactant and preservative. The contents are filtered at inspections. Both purple and green multi-funnel traps have been evaluated to have similar or better efficacy in comparison to the current standard purple prism traps. Larger sized (12- and 16-unit) multi-funnel traps caught more beetles than their

smaller-sized (4- and 8-unit) counterparts (Francese *et al.*, 2013). Green traps coated with untinted (white) Fluon caught almost four times as many adult EAB as Rain-X and tinted (green) Fluon-coated traps, and almost 33 times more beetles than untreated control traps. Thus, the slippery surface provided by the Fluon coating is more conducive to trapping the insects. The sex ratio was not affected by the trap coating (Francese *et al.*, 2013). In later experiments, trap catches have been shown to be consistently greater in Fluon-coated green Lindgren multi-funnel traps versus purple prism traps (Crook *et al.*, 2014). In Europe, Lindgren 8-unit funnel traps have been used for trapping the *C. undatus* in cork oak in Catalonia, Spain (Fürstenau *et al.*, 2015), where it was reported to be less suitable than prism traps.

Electrocution traps. Nano-bioreplicated decoys were created with electroconductive features. This property allowed for the creation of traps where beetles alighted onto the decoys and were stunned, killed and collected in a container (Domingue *et al.*, 2014). This electrocution-based funnel trap has been tested for targeting EAB in an ash plantation in the US and other jewel beetles in an oak forest in Hungary. Similar to the multi-funnel traps, the design features allow for the capture of greater numbers of individual beetles without the saturation of the trap with each additional capture. Such trap saturation and labour associated with servicing traps are a typical disadvantage of the sticky designs commonly used for catching jewel beetles.

Non-sticky trap designs can make the determination of the captured jewel beetle specimens far easier (i.e. Domingue *et al.*, 2013). Furthermore, they are more suitable for quantitative comparisons (Wall, 1989). In an oak forest, a Fluon-coated light green multi-funnel trap design (MULTz) was tested on buprestids (Imrei *et al.* unpublished; Figure 1). Both this trap and 23 × 36 cm sticky sheets of the same colour caught similar numbers of *Agrilus obscuricollis* Kiesenwetter, *A. graminis* Laporte et Gory, *A. angustulus* (Illiger), *A. laticornis* (Illiger) and *A. convexicollis*. Both coloured traps had significantly more of the same species as compared with the transparent control. The lightweight design applies no fluid but an insecticide strip only in its catch container, which simplifies its operation and the handling of the insects caught.

Optimal trap placement

Horizontal placement and exposure to sun

Francese *et al.* (2008) found significant differences in EAB trap catches along a transect gradient from wooded to open field conditions, with most beetles being caught along the edge, or in open fields, 15–25 m outside an ash woodlot. It is generally recognized that EAB adults are much more likely to colonize trees grown in the open versus shaded trees, while they also prefer branches within trees exposed to sunlight (McCullough and Siegert, 2007; Francese *et al.*, 2008; McCullough *et al.*, 2009a, b; Mercader *et al.*, 2013). In addition, more EAB were captured in (Z)-3-lactone pheromone compound and (Z)-3-hexenol baited traps when they were placed in the more strongly sun-exposed southern versus northern aspect of the crown (Ryall *et al.*, 2015). All traps designed for using visual decoys have been deployed at the southern exposed sides of trees (Domingue *et al.*, 2011, 2016a) after earlier observations that visually guided mating behaviour



Figure 1 Non-sticky MULTz trap design by the authors (Imrei *et al.* unpublished) and tested in Hungary.

occurs in direct sunlight (Lelito *et al.*, 2007), often intensifying as the time period with no cloud cover lengthened (Domingue *et al.*, 2016b).

Proximity of multiple point source attractants in double decker traps and other designs

Guidelines for EAB detection surveys in the US require individual prism traps to be suspended from a mid-canopy branch in an ash tree growing along a road or the edge of a wooded area (APHIS, 2018). In theory, this should ensure that at least one panel of the prism is exposed to sunlight. Operationally, however, prism traps may be partially shadowed by overhead branches or by adjacent or nearby trees according to McCullough and Poland (2017). Thus, an advantage of the double-decker traps is that they allow placement of the trap in open areas near ash trees, rather than relying on placement in the trees themselves. Furthermore, not only is the open area better exposed to sun, but traps do not have to compete with compounds emitted by live ash trees surrounding the trap. Hence, the unique placement of double-decker traps and their doubling of the size of the sticky-coloured surface compared with standard prism traps might be reasons why a greater percentage of the traps were reported to have positive detections, when compared with prism traps or multi-funnel traps in ash tree canopies.

Other studies also suggest that employing multiple interacting stimuli can have an enhancing effect. For example, when deploying (Z)-3-lactone and (Z)-3-hexenol, the traps resulted in significantly greater increases in EAB male captures when the pairs of traps were placed on the same tree compared with traps placed on adjacent trees (Ryall *et al.*, 2015). These results not only suggest that the (Z)-3-lactone may be more active at close range, but may draw attention to the importance of several point sources strengthening each other in the effective communication of EAB. However, there is an indication that in combining visual and chemical cues, precise point source synchronization of signal transmission may not be necessary. In experiments with decoy-baited traps for EAB, it did not affect trap captures whether or not odour lures had been placed on the traps versus simply in the same tree (Domingue *et al.*, 2013).

Trap height

Jewel beetles seem to be more abundant in the tree canopies, which results in typically greater catches when traps are placed higher in the canopy, especially in tall trees. In one study, more EAB males were captured at 4 m height compared with traps placed at 2 m (Lelito *et al.*, 2008). In another study, traps at the mid-canopy level of 13 m caught significantly more beetles than those operating at ground level (Francese *et al.*, 2008; Francese *et al.*, 2010b). EAB catches also increased when the height of traps were raised in a 5–8 m tall stand (Ryall *et al.*, 2012). Furthermore, in the UK, traps at a height of 10 m caught significantly more *A. laticornis* than those at 3 m, while *A. biguttatus* and *A. sulcicollis* showed no clear preference in catches at these heights (Brown *et al.*, 2017).

Trap development: colour

North America

The first traps exploiting colour cues for detecting EAB were developed following its occurrence in North America (Francese *et al.*, 2005). Retinal sensitivity of EAB was examined with an objective to improve trap efficacy for the beetle (Crook *et al.*, 2009). Electroretinogram (ERG) recordings showed maximum spectral sensitivity at UV (340 nm), violet/purple (420–430 nm), blue (460 nm) and green (540–560 nm) regions of the spectrum. Females were also particularly sensitive to red regions of the spectrum (640–670 nm), whereas males were not. The regions identified by these ERG recordings correlate with the purple and green colours successfully used in prism traps.

Francese *et al.* (2008) confirmed that there is high attraction at wavelengths similar to the peak sensitivities of the ERG recordings. More EABs are caught on purple prism traps than on red or white traps. Furthermore, green plastic multi-funnel traps caught significantly more beetles than black or purple ones (Francese *et al.*, 2011). In an unbaited trapping study, significantly more adults were caught on green prism traps by decreasing the reflectance of traps from 67 % to 49 % to create a darker green (Francese *et al.*, 2010a). In a direct comparison of the behavioural activity of green and purple hues, any tested shades of purple generally attracted much lower numbers of the EAB adults than green traps. This was independent of whether they were tested in

prism or Lindgren multi-funnel trap designs or with regard to the trap height or surface coating of the non-sticky traps (Francese *et al.*, 2010b, 2013).

Traps with a green hue at peak reflectance of 49 per cent had EAB catches skewed towards males (Francese *et al.*, 2010a). Proportions of male beetles captured were generally much higher on green traps than on purple traps, regardless of height or the trap types (Francese *et al.*, 2010b, 2013). On the contrary, purple traps were found to be more attractive to females than males, correlating with the above-mentioned female-specific sensitivity in the red regions of the spectrum at 640–670 nm (Francese *et al.*, 2010a, 2013).

Europe. Green plastic-covered branch-traps significantly outperformed other trap designs for *A. angustulus*, *A. sulcicollis*, *A. obscuricollis*, *A. laticornis* and *A. graminis*, in an oak forest in Hungary (Domingue *et al.*, 2013). *A. laticornis* was also confirmed to be attracted to green colour in field experiments with prism traps carried out in the UK (Brown *et al.*, 2017). The ash and poplar-infesting *A. convexicollis* was almost exclusively captured on green prism traps in Slovakia (Rhainds *et al.*, 2017), whereas purple traps attracted 2–3 times more adults of the beech-infesting *A. viridis*, with high (>95 %) female ratios as compared with green traps in the same study. Further, purple prism traps caught *A. biguttatus* and *A. sulcicollis* in oak forests in the UK (Brown *et al.*, 2017) and *C. undatus* in a cork oak forest in Spain (Fürstenau *et al.*, 2015).

To summarize, in Europe, purple and green colours seem to be highly attractive stimuli with some obvious colour preferences species by species, which should be considered in future trapping studies. It may also be worthwhile to investigate electroretinogram (ERG) sensitivities or additional aspects of colour preferences in field-trapping, since these attributes for each species may diverge from the results observed for EAB highlighted above.

Trap development: odor

North America

Lures containing (Z)-3-hexenol were the most effective amongst all tested green leaf volatiles (GLVs) in increasing EAB trap catches and were more attractive to males than females, especially when deployed alongside green prism traps (de Groot *et al.*, 2008; Grant *et al.*, 2010, 2011). Catches with (Z)-3-hexenol-baited light green sticky prism traps showed a significant male bias, and these traps caught significantly more males than the unbaited controls at both sites (Grant *et al.*, 2011).

A lactone, (Z)-3-dodecen-12-olide, has been extracted from EAB females feeding on ash foliage (Bartelt *et al.*, 2007), and this lactone has been shown to synergistically increase the attraction toward green prism traps when co-emitted with (Z)-3-hexen-1-ol (Bartelt *et al.*, 2007; Silk *et al.*, 2011; Ryall *et al.*, 2012, 2013). Male catches were increased with the application of (Z)-3-lactone and (Z)-3-hexenol in the traps (Ryall *et al.*, 2012). A 3.0 mg/septum dose of (Z)-3-lactone in combination with (Z)-3-hexenol was found to be more attractive towards EAB than the lower 0.001, 0.1 and 1.0 mg/septum doses or (Z)-3-hexenol alone (Ryall *et al.*, 2015). Furthermore, its saturated analogue, dodecan-12-olide, was similarly active in both olfactometer and trapping bioassays in green traps with (Z)-3-hexenol (Silk *et al.*, 2015).

Oils

Because bark samples taken from girdled trees were seen to have elevated sesquiterpene levels, which are not commonly available as synthetic compounds, natural sources have been used in trapping applications (Crook and Mastro, 2010). Manuka oil is a steam distillate from the New Zealand Manuka tea tree, *Leptospermum scoparium* J. R. and G. Forst (Myrtaceae), while Phoebe oil is a steam distillate from Brazilian walnut *Phoebe porosa* Mez. (Lauraceae), which grows in the Araucaria forests in southern Brazil. In a series of behavioural field studies using baited purple traps, Manuka oil-baited traps caught significantly more of both sexes of EAB adult beetles as compared with unbaited traps (Crook *et al.*, 2008; Grant *et al.*, 2010), whereas catches on light green sticky prism traps baited with Phoebe oil showed a significant female bias (Grant *et al.*, 2011), despite an opposite male bias being typical of the green colour itself, as discussed above. Phoebe oil-baited traps caught significantly more beetles than either Manuka oil baited traps or unbaited traps. Furthermore, Ryall *et al.* (2013) found that significantly higher proportion of females caught on traps baited with Phoebe oil had mature development of eggs when compared with females collected on traps baited with (Z)-3-hexenol. Crook *et al.* (2008) hypothesized that the improved attraction of Phoebe oil to EAB over Manuka oil was caused by the presence of the antennally active sesquiterpene, 7-epi-sesquithujene, a bark volatile of fully girdled (stressed) green ash.

Europe

Trapping approaches developed for EAB were adapted for European oak buprestid species in experiments by Domingue *et al.* (2013). The addition of semiochemical lures, including Manuka oil, (Z)-3-hexen-1-ol and (Z)-9-tricosene, gave a tendency of increased catches, with significant effects of these odour treatments for total pooled *Agilus* spp., and specifically for *A. angustulus* and *A. sulcicollis*.

Purple coloured prism traps baited with a mixture of (E)-2-hexenal (93 mg), (E)-2-hexenol (100 mg), 1-hexanol (51 mg), (Z)-3-hexenyl acetate (66 mg) and n-hexyl acetate (11 mg) in a similar ratio to that found in headspace volatiles from the freshly cut branches of the host, cork oak, were the most effective combination to catch female *C. undatus* (Fürstenau *et al.*, 2015). This result suggests that GLVs play an important role in the host and/or mate finding behaviour of females of this species.

A synthetic blend of three sessile oak-related (*Quercus petraea* (Matt.) Liebl.) leaf volatiles, including (Z)-3-hexenal, (Z)-3-hexen-1-ol and (Z)-3-hexenyl acetate evoked strongly positive behavioural responses in olfactometer studies with virgin *A. biguttatus* females and males, although fresh leaf material was more effective than this synthetic blend (Vuts *et al.*, 2016). Another blend, comprising of a five-component mixture made up of bark volatiles including *p*-cymene, 1,8-cineole, (E)-ocimene, γ -terpinene and (R/S)-camphor, proved to be as behaviourally active for gravid females as bark tissue. The field performance of these blends remains to be investigated.

A. viridis was attracted to Cubeb oil, an essential oil from tailed pepper, *Piper cubeba* L. (Piperaceae) (Singh *et al.*, 2007), which performed optimally in purple sticky prism traps in Slovakia

(Rhainds *et al.*, 2017). In general, for most European experiments, odours have shown weak activity in the field, which draws attention to the need of gaining sufficient species-specific basic knowledge. This perspective increases the value of approaches such as that illustrated by Vuts *et al.* (2016) concerning the choice of optimal formulations of odorant lures.

Jewel beetles as visual decoys

The bright, metallic colour of jewel beetles derives from the physical properties of the cuticle that cause light interference and reinforcement of particular reflected wavelengths, rather than from pigmentation caused by molecules produced at the cellular level (Seago *et al.*, 2009; Sharma *et al.*, 2009; Stavenga *et al.*, 2011; Domingue *et al.*, 2014). The outermost layers of the cuticle of jewel beetles consist of thin transparent refractive layers. The various metallic colours are produced as light is reflected through these layers, with the predominant wavelengths sometimes varying with the viewing angle.

North America

According to Lelito *et al.* (2007), EAB males search the tree during flight and attempt to copulate with females resting on the foliage in bright sunlight, after descending rapidly straight down on them from a distance of 30 to 100 cm. Dead beetles of both sexes pinned to leaves elicited similar behavioural response, which suggested that males find potential mates predominantly by exploiting visual cues. Both *Agrilus cyanescens* Ratzeburg and *Agrilus subcinctus* Gory (Lelito *et al.*, 2011) were similarly confirmed to use visual signals to mediate direct approaches of conspecifics.

In the initial study of EAB adult mating behaviour, Lelito *et al.* (2007) found that equal numbers of feral males approached dead male and female beetles, although they spent considerably more time attempting to copulate with dead females compared with males. However, when all chemical cues were washed from dead male and female beetles, there was no longer a sexually dimorphic effect upon the contact time exhibited by approaching males. Furthermore, feral males spent significantly more time in contact with these washed specimens compared with unwashed males and less time compared with unwashed females. These observations demonstrated that contact pheromones are used with respect to the copulation behaviour, components of which were later identified (Lelito *et al.*, 2009; Silk *et al.*, 2009).

Agrilus cyanescens, a species similar in colour to EAB but smaller in size, showed a strong response to blue-coloured sticky traps to which dead male EAB had been affixed with adhesive. This was amongst the first studies suggesting a general use of visual cues in the mating systems of other buprestids beyond EAB and cross-species compatibility of the signal (Lelito *et al.*, 2008).

Europe

The research initiated in the US on the orientation and communication of EAB (Lelito *et al.*, 2007; Crook and Mastro, 2010; Silk and Ryall, 2015) preceded and facilitated similar research approaches concerning some buprestid species that typically exist at far lower population densities in Europe (Domingue *et al.*, 2011). In a European oak forest, five jewel beetle species, EAB,

A. biguttatus, *A. sulcicollis*, *A. cyanescens* and *A. angustulus*, were used as dead visual decoys in a mating observation experiment (Domingue *et al.*, 2011). *A. sulcicollis* was of particular interest, because the species has already been introduced to North America (Haack *et al.*, 2009; Jendek and Grebennikov, 2009). In this experiment, mating approaches by males of *A. biguttatus*, *A. sulcicollis* and *A. angustulus* were observed (Domingue *et al.*, 2011). *A. biguttatus* and *A. sulcicollis* nearly always landed directly on female models, similar to EAB and *A. cyanescens* in North America (Domingue *et al.*, 2011; Lelito *et al.*, 2011). However, *A. angustulus* usually landed on the leaf surface adjacent to the model, before subsequently walking toward and antennating it, similar to the behaviours observed for male *A. subcinctus* in North America (Domingue *et al.*, 2011; Lelito *et al.*, 2011).

Males of *A. sulcicollis*, *A. angustulus* and *A. subcinctus* most often chose conspecific models in the presence of other *Agrilus* spp. models (Lelito *et al.*, 2007; Domingue *et al.*, 2011). However, *A. biguttatus* seemed to prefer specimens based upon their size, rather than species identity, with the largest EAB models preferred over males of other species. Furthermore, *A. angustulus* was shown to prefer certain colours amongst similarly sized EAB colour morphs presented to them in the field, indicating possible species-specific colour affinities (Domingue *et al.*, 2016b).

There were observations of *A. cyanescens* showing a strong response to dead male EAB decoys on blue-coloured sticky traps, suggesting cross-species attraction (Lelito *et al.*, 2008). Similarly, *A. biguttatus* males attempted to copulate with both *A. biguttatus* and EAB models, remaining with them for several minutes afterwards (Domingue *et al.*, 2011). *A. biguttatus* males also spent more time on EAB models than on conspecific models, proving that there is substantial cross-species attraction in not only the visually mediated mating approaches, but also the copulation behaviour. In further experiments in Europe (Domingue *et al.*, 2013), it was shown that on small branch-traps with green plastic surfaces (4 cm × 9 cm), the presence of the visual decoy of EAB increased catches of *A. sulcicollis*, *A. obscuricollis*, *A. graminis*, *A. biguttatus* and *Anthaxia* spp., which is a further indication of a generally high level of cross-species attraction in *Agrilus* mating behaviour.

In all of the three European buprestid species studied intensively (*A. biguttatus*, *A. sulcicollis* and *A. angustulus*), there were visually mediated approaches toward dead, pinned beetle models similar to the North American species. In all cases, the male visual location of females feeding on foliage or placed on a green plastic background was critical to the mate-finding behaviour. Thus, it appears that a broadly tuned visual behavioural template for mate attraction may be common in buprestids or at least amongst *Agrilus* species. It is reasonable to conclude that optimized artificial decoys could be useful additions to the efficacy of trap designs that also replicate the background colour of the leaves with the appropriate green colour stimulus. There is no indication from any published studies that beetles placed on purple traps create a similar template for attraction.

Trap development: artificial decoy

In general, in contrast to the extensive efforts for the identification of chemical cues in insect communication, the identification

of visual cues linked to insect behaviour in natural environments is lagging far behind. There is also evidence that the behavioural template for male visual mate attraction may not require the precise shape of a dead jewel beetle. For example, in North America, the frequency of responses of EAB to the elytra of tiger beetles (*Cicindela sexguttata* F.) (Coleoptera, Cicindelidae), which represent a different insect family, was not different from that to conspecific models (Lelito *et al.*, 2011).

A better understanding of the stimuli involved has been achieved by the description of the surface of jewel beetles at a nanometre scale, which was replicated with the necessary fidelity to evoke behavioural responses (Domingue *et al.*, 2014). In general, this has been an underexplored field. A nanoscale replication of the female EAB exoskeleton evoked stereotypical mate-finding behaviour from *A. biguttatus* males (Domingue *et al.*, 2014). The behavioural response would only occur when the spicules and spines that scatter light into intense strands were replicated in the artificial decoys with enough fidelity to replicate those observed in the outer cuticular surface of the beetle's elytra. Other plastic models with similar colouration and shape did not elicit the behaviour. The successful replication of the light scattering pattern in the artificially bioreplicated specimens was verified by comparing their projection when illuminated by a white laser to that of real *Agrilus* specimens. The nanometre-level replicated artificial decoys evoked the complete attraction and landing sequence of *A. biguttatus* males. In contrast, *A. biguttatus* males made brief flying approaches toward the artificial decoys without these features, but diverted away before alighting on them. The nanometre-level replicates were electroconductive, which allowed the creation of a prototype electrocution trap to attract, stun, kill and collect jewel beetles. The prototype was successful at collecting a number of jewel beetle species in the field, including EAB and *A. biguttatus*.

Combination of stimuli and their relative importance

Crook *et al.* (2012) found that in the attraction of EAB beetles, the relative importance of light or dark green visual stimuli is more important than the olfactory stimulus of (Z)-3-hexenol. Similarly, Crook *et al.* (2014) noted that independent of the plant volatile and pheromone combinations used, detection rates on green Fluon-coated 12-unit multi-funnel traps were comparable with glue-coated purple prism traps in areas with low EAB population densities. These studies continue to suggest that visual stimuli are more crucial than olfactory ones. Ryall *et al.* (2015) concluded that the optimal EAB trap design and protocol would use dark green colour, baited with 3.0 mg (Z)-3-lactone and (Z)-3-hexenol, being deployed in the south aspect of the canopy. Using branch traps, Domingue *et al.* (2016a) reported that EAB male attraction was synergized by a combination of the decoy with (Z)-3-hexenol or (Z)-3-hexenol and (Z)-3-lactone, pheromone compound. Female captures were not affected by the visual decoys, but odours did influence captures, with the (Z)-3-hexenol plus lactone treatment catching the greatest number of females. Thus, unlike many insect groups of economic importance, a complex orientation and communication system is used by jewel

beetles in which visual stimuli have an important role (Gwynne and Rentz, 1983; Lelito *et al.*, 2007; Crook *et al.*, 2009). In future research projects, the focus should be on not only novel species-specific cues, but also on understanding the synergistic effects of the complex visual and semiochemical cues produced by both buprestids and their host plants. Each of these factors seems to play a role in mate finding and host location. A combination of visual, olfactory (specific plant volatiles and/or pheromones) and possibly other stimuli in more sophisticated trap designs could lead to more sensitive detection methods with increased selectivity.

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