



Interactions between woodpecker attack and parasitism by introduced parasitoids of the emerald ash borer

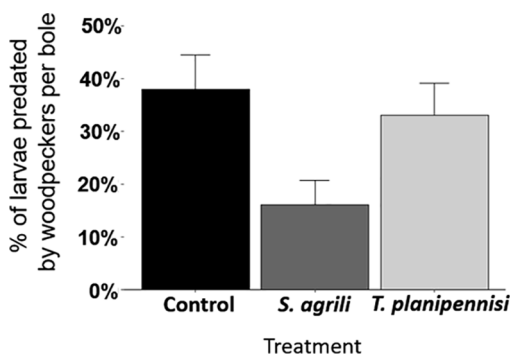
Theresa C. Murphy^{a,*}, Juli R. Gould^{b,1}, Roy G. Van Driesche^{c,2}, Joe S. Elkinton^{a,b,2}

^a Organismic and Evolutionary Biology, University of Massachusetts Amherst, MA 10003, United States

^b USDA-APHIS-PPQ, Buzzards Bay, MA 02542, United States

^c Department of Environmental Conservation, University of Massachusetts Amherst, MA 10003, United States

GRAPHICAL ABSTRACT



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ABSTRACT

Agrilus planipennis, the emerald ash borer (EAB), is an invasive forest pest causing significant economic and ecological impacts. EAB is attacked by some native natural enemies, the most significant being woodpeckers, which can remove between 30 and 95% of the EAB larvae in a tree. However, despite high woodpecker predation rates, EAB populations continue to grow. Management of EAB focuses on classical biological control, with the introduction of four parasitic wasps from Asia. Because both woodpeckers and larval parasitoids attack mature EAB larvae, their impacts overlap and potentially interact. This study examines the relationship between native woodpecker predation and parasitism by the introduced parasitoids *S. agrili* and *T. planipennisi*. We established a cohort of parasitized larvae on select ash trees and then used screening to exclude woodpeckers from some sections of the tree. We show that while woodpeckers had no effect on observed parasitism rates of individual trees, the presence of parasitized larvae changed woodpecker foraging behavior and resulted in significantly lower overall foraging by woodpeckers. We hypothesize these changes are due to these larval parasitoids being a lower quality food reward. Parasitism of EAB larvae could contribute to a decrease in patch quality for woodpeckers such that they would quit foraging sooner than expected if it were a high-quality, unparasitized patch. This study fills a gap in our understanding of the complex relationship between woodpecker

Abbreviations: EAB, emerald ash borer; DBH, diameter at breast height (approximately 1.4 m); USFS, United States Forest Service; USDA, United States Department of Agriculture

* Corresponding author at: 250 Natural Resources Road, Ag. Engineering Rm 115, University of Massachusetts, Amherst, MA 01003, United States.

E-mail addresses: theresa.c.murphy@aphis.usda.gov (T.C. Murphy), Juli.R.Gould@aphis.usda.gov (J.R. Gould), vandries@cns.umass.edu (R.G. Van Driesche), Elkinton@ent.umass.edu (J.S. Elkinton).

¹ USDA-APHIS-PPQ, 1398 West Truck Road, Buzzards Bay, MA 02542, United States.

² 160 Holdsworth Way, University of Massachusetts, Amherst, MA 01003, United States.

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mortality and parasitism mortality of EAB and our results demonstrate that this relationship may have broad implications for the EAB biological control program.

1. Introduction

Since its discovery in Michigan in 2002, the emerald ash borer (EAB), *Agrilus planipennis* Fairmaire (Coleoptera: Buprestidae), has spread to 32 states and three Canadian provinces, killing over a hundred million native ash, *Fraxinus* sp., trees (Herms and McCullough, 2014; Mercader et al., 2015; USDA Animal Plant Health Inspection Service). In North America it is estimated that it could damage or kill over 8 billion trees (Mercader et al., 2015) and cost over 10 billion dollars in urban areas alone to treat, remove, and replace infested ash (Kovacs et al., 2010). Eradication through removal of infested trees was tried initially but failed, while use of insecticides is considered economically prohibitive over large areas of forest (Herms and McCullough, 2014; McCullough and Mercader, 2012). Management of EAB currently focuses on classical biological control (the introduction of natural enemies from the pest's native range) to help reduce EAB population density (Bauer et al., 2008; Herms and McCullough, 2014). The EAB biocontrol program has introduced three larval parasitoids, *Spathius agrili* Yang, *Spathius galinae* Belokobylskij and Strazenac, and *Tetrastichus planipennisi* Yang, and one egg parasitoid, *Oobius agrili* Zhang and Huang (Yang et al., 2005; Zhang et al., 2005; Yang et al., 2006; Belokobylskij et al., 2012).

Evaluating the impact of natural enemies on pest population dynamics requires detailed quantification of the mortality factors in the system. Approaches to such studies include life tables (used for organisms like insects that have distinct life stage) or matrix models (used mainly for organisms like plants that lack clearly defined life stages) (Bellows et al., 1992; Caswell, 2001). Proper construction and interpretation of life tables or matrix models requires careful measurement of the rates of all important mortality factors in the study species' life system. This process can be complicated by interactions among competing mortality factors that affect a common stage and thus act contemporaneously. Quantifying the separate impacts of mortality factors that act contemporaneously depends on whether attack rates by one agent influence the observable attack rates of other agents (Royama, 1981; Elkinton et al., 1992).

Experimental studies are essential to understanding the true impacts of competing mortality agents (Campbell and Torgersen, 1983; Roland, 1990). Particularly relevant is whether the observable effectiveness of introduced biological controls will be affected by other factors already in the system. In North America, most emerald ash borer populations suitable for parasitoid release will likely experience significant woodpecker feeding, particularly in the winter (Jennings et al., 2015; USDA-

APHIS/ARS/FS, 2016). Woodpeckers present at our study sites that have been shown to feed on EAB included hairy woodpeckers (*Picoides villosus* L.), downy woodpeckers (*Picoides pubescens* L.) (Flower et al., 2014; Jennings et al., 2015) and red-bellied woodpeckers (*Melanerpes carolinus* L.) (Shackelford et al., 2000; Lindell et al., 2008). Woodpecker predation of EAB larvae in North America can be very high (30–95%) (Cappaert et al., 2005) in infested forests, and woodpecker predation can reduce larval densities in trees by 33–88% (Jennings et al., 2015). Woodpeckers have the potential to also consume the larvae, pupae, or even adults of the introduced larval parasitoids. Interactions between these two mortality agents (parasitoids and woodpeckers) will have important management implications for EAB (Jennings et al., 2013).

Selective predation and/or avoidance on parasitized versus non-parasitized larvae by generalist predators has been important in the population dynamics of other invasive species. The marginal attack rate is the proportion of individuals attacked by an agent if that agent acted alone; it is often called the true underlying mortality rate in the system (Royama, 1981; Buonaccorsi and Elkinton, 1990; Elkinton et al., 1992). This can differ from the apparent attack rate that researchers observe if two factors, such as predation and parasitism, overlap and do not act indiscriminately. Predators preferentially attacking un-parasitized pupae can result in higher observed parasitism rates and augment top-down control, e.g. winter moth pupae (*Operophtera brumata* L.) (Roland, 1990) and forest tent caterpillar (*Malacosoma disstria* Hübner) (Glasgow, 2006; Nixon and Roland, 2012). Few studies have examined predator-parasitoid relationships in the EAB system. Jennings et al. (2013) found a small but significant increase in parasitism between open trees (1.2% parasitism) and caged or woodpecker-exclusion trees (3% parasitism). However, this study only compared total fates and not observed parasitism or interactions between the two causes of death. Anecdotal evidence of half-eaten broods of parasitized larvae (personal observation) led us to hypothesize that parasitized larvae may be less preferred by woodpeckers, but this had not been investigated experimentally.

It was necessary to explore the relationship between woodpeckers and each parasitoid species separately because of their life-cycle differences. *Tetrastichus planipennisi* is a koinobiont endoparasitoid, while *S. agrili* is an idiobiont ectoparasitoid, which forms overwintering cocoons, and we believed that these differences might result in different interactions with woodpeckers. Both *T. planipennisi* and *S. agrili* oviposit from late spring through fall after beetle larvae reach a size suitable for attack (3rd to 4th instar) (Wang et al., 2007; Ulyshen et al., 2010a). EAB larvae continue feeding for about a week after parasitization by *T.*

Table 1
Study site locations and various characteristics.

Site	Coordinates	Date of initial EAB discovery	% Ash ¹	Site EAB Density Index ²	Egg Inoculation Density (Eggs/m ²)	Bole EAB Density (larvae/m ²) ³	Previous parasitoid releases & Initial date of release
N. Andover, MA	42.71 N, 71.12 W	2013	50	Medium	100	33.0	Yes; 2013
Dalton, MA	42.42 N, 73.19 W	2012	75	Medium	100	23.6	Yes; 2013
Pittsfield, MA	42.42 N, 73.27 W	2012	34	N/A	100	23.6	No
Cementon, NY	42.15 N, 73.92 W	2011	50	High	0	42.8	Yes; 2011
Catskill, NY	42.18 N, 73.91 W	2011	57	High	0	72.6	No
Saugerties, NY	42.12 N, 73.95 W	2011	50	High	0	95.4	No
Lake Katrine, NY	41.99 N, 74.00 W	2011	50	High	0	30.1	Yes; 2011

¹ Percentage ash by mature tree count (estimated).

² Low Density: EAB present but difficult to find. Nearly 100% of ash trees are healthy. Medium Density: Trees are beginning to show signs of EAB infestation (epicormic shoots, woodpeckering holes, bark splits, emergence holes) but > 75% of the trees are healthy and show no signs of EAB. High Density: > 25% of the trees show signs of EAB infestation.

³ Average density of mature (> 2nd instar larvae) in the peeled tree boles.

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