

Biology and Control of Emerald Ash Borer



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CHAPTER 9: LIFE TABLE EVALUATION OF CHANGE IN EMERALD ASH BORER POPULATIONS DUE TO BIOLOGICAL CONTROL

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BACKGROUND

Emerald ash borer, *Agrilus planipennis* Fairmaire (EAB), is an invasive buprestid native to northeastern Asia that feeds on ash trees (*Fraxinus* spp.). First detected in North America (in Michigan, United States and Ontario, Canada) in 2002, EAB has spread rapidly, in part because of movement of infested nursery stock and untreated firewood (Cappaert et al., 2005a; BenDor et al., 2006; Poland and McCullough, 2006). As of January 2014, EAB was known in an additional 21 U.S. states and one Canadian province (USDA-APHIS, 2014), and it is expected to continue spreading to other parts of the continent with ash trees and a suitable climate (Sobek-Swant et al., 2012; Vermunt et al., 2012; DeSantis et al., 2013). Thus far, EAB has killed tens of millions of ash trees, with tree death generally occurring within 3-4 years of initial infestation by the beetle (Poland and McCullough, 2006). The treatment, or removal and replacement of landscape trees affected by this pest is projected to cost over \$10 billion in the United States in the coming decade (Kovacs et al., 2010). While insecticide treatments can be effective at reducing losses from EAB in urban settings, biological control might represent the most sustainable option for suppressing populations at the landscape level and in natural environments over the long term.

The primary risk factor for North American ash is their limited innate host resistance to EAB (Liu et al., 2003; Bauer et al., 2005; Gould et al., 2005; Rebek et al., 2008; Herms and McCullough, 2014). Another

cause of high ash mortality in North America is the lack of host-specific EAB natural enemies. In EAB's native range, however, parasitoids cause a considerable proportion of EAB egg and larval mortality, potentially regulating host population densities (Liu et al., 2003, 2007; Bauer and Liu, 2007; Wang et al., 2010; Duan et al., 2012a). In 2007, the USDA started the EAB Biological Control Program (Federal Register, 2007; Bauer et al., 2008), and began releasing three EAB parasitoids from China in the United States. These biological control agents are the larval ectoparasitoid *Spathius agrili* Yang (Yang et al., 2005, 2010), the larval endoparasitoid *Tetrastichus planipennisi* Yang (Liu et al., 2003, 2007; Yang et al. 2006; Duan et al., 2011a), and the egg parasitoid *Oobius agrili* Zhang and Huang (Zhang et al., 2005; Liu et al., 2007; Duan et al., 2011b; Duan et al., 2012b). Understanding the basic population dynamics of EAB will enable us to assess the effects of parasitism on EAB population growth and to more effectively target different life stages with biological control agents. One widely used approach to examining population dynamics is through life table analysis. Here, we briefly introduce some of the basic concepts of life tables, and then review some of the methods and results from life table analyses involving EAB.

LIFE TABLES

Life tables are constructed from data on the numbers of individuals that enter or die in different age or stage classes of populations over the course of a

generation (Van Driesche and Bellows, 1996; Stiling, 2012). Life tables have been used in ecology for over 65 years (Deevey, 1947), and they have provided insight into the population dynamics of a range of taxa including plants (Harcombe, 1987), fish (Cortes, 2002), mammals (Sherman and Morton, 1984), reptiles (Crouse et al., 1987), and insects (Hawkins et al., 1997). Early work in this field involved constructing life tables for the winter moth (*Operophtera brumata* L.) (Lepid.: Geometridae) (Varley and Gradwell, 1960; Buckner, 1969), and life tables have subsequently been employed widely in applied entomology for assessing the impact of pest control measures (Gould et al., 1992; Hoddle and Van Driesche, 1999; Kuhar et al., 2002; Nielsen et al., 2008). These effects can be examined either experimentally by manipulating certain sources of mortality in the field, or by modelling population

dynamics with and without factors of interest in the model. For a more detailed discussion of life tables in general see Bellows et al. (1992) or Southwood and Henderson (2000).

Types of Life Tables

Two main types of life tables are utilized used in ecology: horizontal (cohort) and vertical (static) life tables (Van Driesche and Bellows, 1996; Stiling, 2012). Horizontal life tables follow a given cohort of same-aged individuals from birth throughout their lives, while vertical life tables use data from a population at one particular point in time. Vertical life tables often are used when study organisms are long-lived and it is not practical to follow them throughout their lives, and vertical life tables are

Table 1. Life table for an experimentally established EAB cohort at Legg and Central Parks, Meridian Township, Michigan in 2010.

Life stage	l_x	m_x	d_x	d_i	Mortality factor	q_x	q_i	q
(egg)	229	0	69		Infertility/predation/parasitism by <i>Oobius agrili</i>	0.300	0.300	0.300
L1-L2	160	0	34	34	Killed by tree resistance	0.213	0.557	0.149
L3	126	0	22	15	Killed by tree resistance	0.175	0.119	0.066
				3	Undetermined disease/other		0.024	0.013
				4	Parasitism (<i>Atanycolus</i> spp.)		0.068	0.018
L4	104	1	32	4	Undetermined disease/other	0.308	0.038	0.018
				7	Killed by tree resistance		0.067	0.031
				18	Parasitism (<i>Atanycolus</i> spp.)		0.173	0.079
				1	Parasitism (<i>Balcha indica</i>)		0.010	0.004
				2	Woodpecker predation		0.019	0.009
JL	71	9	52	52	Woodpecker predation	0.732	0.732	0.228
Adult exit hole observed	10	9	1	1	Undetermined disease/other	0.000	0.100	0.004
(Overwintered L4/JL-pupae)	10	-	3	3	29% additional overwintering woodpecker predation	0.290	0.290	0.013
(Emerging adults)	16	-	1	1	5% adult mortality from disease and predation	0.050	0.050	0.004
(Females)	8	-	-		1:1 sex ratio			
(F_1 eggs)	812	-	-		101.5 eggs per female			
R_0	3.6	-	-					

more suited for continuously breeding organisms with overlapping generations. Either method may be used for EAB, but given that we are able to create experimental cohorts of larvae, the horizontal (or stage-specific) life table may be more suitable.

Life Table Parameters

Several different parameters are used in life tables, and here we follow the general methods and column definitions described in Southwood and Henderson (2000). Table 1 is presented as an example of a stage-specific life table for EAB constructed from data collected in Michigan. Column headings are l_x = number of live EAB entering each stage (based on reverse calculation of the different stages of EAB observed at the sampling time, and with l_0 representing the number of eggs estimated to start the life table); m_x = number of live EAB observed at sampling time, d_x = number of dead EAB observed in each stage; q_x = apparent (stage-specific) mortality rate (d_x/l_x); d_i = number of EAB dying in association with the specific factor observed, q_i = apparent mortality rate because of the specific biotic factor d_i/l_x ; q = real mortality (d_x or d_i/l_0), R_0 = net reproductive rate, calculated as the ratio of l_0 divided by l_{F_1} (the number of eggs produced by surviving adults). R_0 can be interpreted as follows: if $R_0 = 1$, the population is constant; if $R_0 > 1$, the population is growing; and $R_0 < 1$, the population is declining.

Apparent Mortality

Expressing the number of individuals dying in a stage as a percentage of the number entering the stage generates the estimate of apparent mortality (Van Driesche and Bellows, 1996). Apparent mortality can subsequently be used to calculate k-values, as $k = -\log(1 - \text{apparent mortality})$. Apparent mortality is generally used to estimate a single source of mortality within an individual life table, while k-values are additive over several mortality factors within a given life table and can be used to identify the key mortality factor for a population if life tables are available for a series of generations.

Marginal Attack Rates

For situations in which there are multiple contemporaneously acting mortality factors (e.g., predators consuming prey, some of which have already been parasitized), calculating the marginal attack rate is an improvement over apparent mortality (Elkinton et al., 1992). A marginal attack rate is the proportion of individuals entering a stage that are subject to attack by a given factor (A), even if some other factor (B) ends up actually killing some individuals previously attacked by factor A. It can be calculated using the following equation: $m_i = 1 - (1 - d)d_i/d$. This may be especially important with EAB because it is likely that some EAB larvae are stung by parasitoids but later consumed by woodpeckers or other insectivorous birds before immature parasitoids complete their development and kill their host.

CONSTRUCTING LIFE TABLES FOR EAB

EAB Life Cycle

Constructing life tables for EAB requires detailed knowledge of the species' life cycle (see Chapter 1). EAB females generally produce about 100 eggs (Wei et al., 2007; Wang et al., 2010), which are laid underneath small bark flakes or in crevices on ash trees. In Michigan, EAB's peak oviposition period occurs during late spring through summer (Poland and McCullough, 2006), and this appears to be the case throughout most of its North American range. Upon hatching, larvae burrow into the cambium and feed on the phloem and outer sapwood. Larvae develop through four instars in summer and fall, form a pupal chamber or cell (see Chapter 1), and overwinter in an obligatory diapause as mature 4th instar larvae. Under some circumstances, larvae require two years to complete development (Cappaert et al., 2005a,b) (see further discussion of this below). Adults begin emerging from ash trees in late spring or early summer (Brown-Rytlewski and Wilson, 2005) and feed on ash foliage throughout their lives. EAB adults mate within days of emerging, and oviposition typically begins after another week or two depending

on weather conditions (Cappaert et al., 2005a).

Given the cryptic nature of wood-boring insects, the life cycles of beetles such as EAB present many challenges for the construction of life tables. For instance, because EAB's eggs are laid between layers of bark and in bark crevices, they are not easily counted by observers. Furthermore, the majority of the EAB life cycle takes place as larvae feed, develop, and pupate inside host trees. This effectively prohibits repeated sampling as larval fates can only be determined by debarking trees, making it impossible to determine exactly when individuals might have died (although using stage-specific life tables can circumvent this). Additionally, wild EAB populations can be either univoltine (one-year generation time) or semivoltine (multi-year generation time), which appears to be influenced by climate, host tree condition, and oviposition date (Cappaert et al., 2005a,b). Having populations with mixed generations presents problems because individuals may not be exposed to a specific mortality factor for the same length of time or during the same season. For example, semivoltine larvae developing over two growing seasons will have a longer period of exposure to parasitoids than univoltine larvae that complete develop after one growing season.

Life table analyses for EAB have been conducted in Maryland, Michigan, and New York. In Michigan, a life table approach was used to assess the effectiveness of biological control agents released over three generations of EAB (Duan et al., 2010; Duan et al., 2014). In Maryland and New York, a life table approach was used by Jennings et al. (2013), primarily to explore the effect of woodpecker predation on EAB populations, although parasitism rates from biological control agents were also quantified.

Establishing Experimental Cohorts

Several methods have been created to establish experimental cohorts of EAB in ash trees, which subsequently enabled accurate quantification of their population dynamics. For example, Duan et al. (2010) used two methods to establish EAB cohorts in Michigan. Their first method involved the placement of laboratory-reared EAB eggs directly onto the tree. To achieve this, EAB adults were first induced to

lay eggs underneath strips of ribbon on small ash logs in the laboratory (the ribbon simulating loose bark crevices found naturally on ash trees). Using a utility knife, small bark flakes (to which at least one egg was attached) were then cut from the logs and taken to the field. Bark flakes were inserted under bark flaps cut into ash trunks with knives, and the flaps were then pinned to the tree to offer protection from predators but still allow enough space so as not to crush the eggs. This method is labor intensive as it requires the production of eggs in the laboratory, and resulted in rates of EAB larval establishment of 14-26% (Duan et al., 2010). On the positive side, this method may retain some of the contact pheromones from EAB females, and it allows for placement of precise numbers of eggs in the field.

The second method utilized by Duan et al. (2010) was to cage gravid EAB females on trees (along with males and ash leaves), which forced oviposition to occur within a specific region of the tree. Cages were constructed from ventilated, rectangular containers (10 cm long x 7 cm wide x 4 cm deep) that were fastened to the trees, with the open side facing the trunk. One female and one male were placed into each cage. Benefits of this method were that it again allows for the retention of any contact pheromones from adult beetles, and it allows EAB females to oviposit naturally onto the bark. This method resulted in a higher rate of establishment in comparison with insertion of eggs into bark flaps, with ~75% of eggs producing established larvae (Duan et al., 2010). This method can be problematic, however, because quantifying the exact number of eggs produced is challenging, as some eggs may be overlooked or damaged during sampling via debarking. Furthermore, because of the variation in the number of eggs produced by females and consequently in larval density, statistical comparisons among trees can be difficult.

A third method, used by Jennings et al. (2013), modified the approach from Duan et al. (2010) that involved grafting individual EAB eggs directly onto the tree (Abell et al., 2012). For this method, eggs were first laid on a coffee filter paper substrate by EAB females in the laboratory. Strips of filter paper containing 1-3 fertilized eggs (as indicated by



Figure 1. Method for establishing experimental cohorts of EAB on ash trees. Shown are: (a) attaching eggs to bark, (b) covering eggs with cotton balls, (c) protecting eggs further with tree wrap, and (d) repeating on tree as desired, ensuring that bands of eggs are evenly distributed to avoid overlapping galleries (Photo credit: David Jennings, University of Maryland)

brownish color) were then cut and transported to field sites. Once suitable trees were identified at field sites, small patches of bark were shaved flat using a draw knife. Egg strips were then glued flush to the bark using standard wood glue, taking care to ensure that no glue came into contact with the eggs (Fig. 1a). To reduce the chances of galleries overlapping, a maximum of three eggs were placed on any one bark patch. Once the egg strip had been attached, a cotton ball was glued over the eggs, to reduce the risk of predation (Fig. 1b). This was replicated until there were six eggs at a particular height on the tree (a “band”). Once a band was completely inoculated with eggs, it was covered in tree wrap to limit predation (Fig. 1c). This process was repeated until there were five bands, each containing six eggs, on the tree for a total of 30 eggs (Fig. 1d). This method allows for a more precise number of eggs to be deposited on each experimental tree section. However, it appears to lower the rate of eggs transferring into established larvae, with estimates of establishment being ~54% (Jennings et al., 2013). Producing the eggs for this method is also labor intensive as it again requires the production of eggs in the laboratory, and care is needed when cutting the filter paper into strips. Additionally, this method precludes predation on the eggs themselves, removing this mortality factor from the life table. However, anecdotal evidence suggests that use of uncovered egg strips results in extremely high egg mortality, likely from predation.

Wild Populations

Life tables can also be constructed by directly sampling survival of life stages in wild populations of EAB (Jennings et al., 2013; Duan et al., 2014) by debarking sections of the tree and following the same process for identifying sources of mortality as with the experimental populations described above. However, several key caveats must be acknowledged when using wild populations for life table construction. The most obvious is that it is not possible to be certain how many eggs were laid on a tree in that year, given the difficulty associated with locating every egg on a tree and dating them. One approach to provide an estimate of the number of eggs per tree could be to search a given area of a tree and then extrapolate those findings for the rest of the tree. Additionally, it is not possible to state with certainty whether populations being studied are univoltine or semivoltine. The latter is strongly suggested if debarking of trees in the fall reveals many early instar larvae (likely being young of the sample year, whereas older larvae would have originated in the previous year and hence belong to a different generation). Despite these problems, constructing life tables for EAB in heavily infested areas can still provide valuable information on population dynamics. At such areas, it might not be possible to determine the fate of experimental cohorts given the high density of other galleries, and monitoring wild populations may be the most effective option at present.

Assigning Individuals to EAB Life Stages

Eggs. EAB eggs are around 1 mm in diameter and change color from white to brown a few days after being laid (Bauer et al., 2004; Wang et al., 2010). Such eggs found between layers of ash bark are presumed to be those of EAB.

Larvae and pupae. EAB larvae create characteristic serpentine galleries (Bauer et al., 2004; Lyons et al., 2004). Because the gallery size of EAB larvae changes over time, it can be used to estimate the stage the larva was in when it died, for example <2 mm wide for 1st to 2nd instars, 2-3 mm wide for 3rd instars, and >3-4 mm wide for 4th instars. Larvae then chew a pupation chamber in the outer sapwood or bark before folding into a J-shape for overwintering. These mature 4th instar larvae are termed J-larvae (Duan et al., 2010), but are sometimes referred to as prepupae (Chamorro et al., 2012) (see Chapter 1 for clarification).

Adults. For the purposes of life tables, EAB can be assigned as adults if there is evidence that they have successfully emerged from their pupal chamber, as indicated by a D-shaped exit hole in the bark. Adults are generally <10-13 mm in size and bright metallic green in color, and can live for 3-6 weeks after emergence (Cappaert et al., 2005a; Parsons, 2008).

Estimating Fecundity

Estimating fecundity from experimentally established cohorts or wild populations is extremely difficult, and thus far EAB life table studies have used fecundity data collected from laboratory-reared females. However, one problem with using estimates from laboratory-reared females is the high variation in the number of eggs produced. While some estimates have suggested that EAB females produce about 100 eggs (Wei et al., 2007; Wang et al., 2010), other data from laboratory-reared EAB showed an average of 74 eggs (range of 1 to 307 eggs per female (EPPO, 2013)). Given the optimal rearing conditions in laboratories, it is possible that these are overestimates compared to field conditions. Alternatively, when logistically possible, sections of trees where EAB cohorts have been placed could be caged to trap and collect

emerging adults. These adults could then be reared in the laboratory to obtain direct estimates of fecundity. However, cages would need to be checked frequently to minimize adult mortality.

Assigning Deaths in EAB Life Stages to Particular Mortality Factors

Eggs. Several methods have been developed to assess egg mortality under field conditions. One simple method involves searching for EAB eggs between thin layers of bark, typically for a set period of time, which then avoids problems associated with tree size (Duan et al., 2011b; Bauer et al., 2012; Duan et al., 2012b). Alternatively, estimates of egg mortality can be obtained through the use of egg sentinel logs (ESL). ESLs can be created in the laboratory using small logs with EAB eggs either laid directly onto the log surface by females or, if eggs have been laid on filter paper, attached artificially to the log. ESLs can then be suspended from trees in the field. Eggs exposed in this manner, however, often suffer high levels of predation unless protected with screening or ribbon.

Another method for assessing rates of egg parasitism in the field is carried out by scraping off outer sections of bark from ash trees and returning bark removed from delineated areas of the trunk to the laboratory (Bauer et al., 2012). There, samples are first placed in incubators for several weeks to allow live parasitoids time to emerge. Next, the bark scrapings are passed through standard window screening (~1 mm x 1 mm mesh) and the material passing through the screen is examined under a microscope to detect eggs and determine their fate (live, dead, dead parasitoid, emerged parasitoid, emerged EAB larvae, infertile egg). Eggs that have been parasitized often turn darker in color and contain droplets of meconium inside the egg shell, and parasitoids leave characteristic round exit holes. These two sources of information (emerged parasitoids and eggs found in screened material) are combined to estimate of parasitism. This procedure provides the best available estimate of parasitism, but it does not capture any estimate of predation rates on eggs. Predation (potentially by taxa such as ants or thrips) is indicated by large, jagged holes in the

eggs, and can potentially obscure previous parasitism (Duan et al. 2011b). Separate sampling methods are needed to estimate the extent of egg predation under field conditions.

Larvae and pupae. Larvae and pupae are relatively easy to locate in comparison to the other EAB life stages. To begin with, when using experimentally established cohorts created from eggs laid on filter paper, hatching success can be ascertained by inspecting the paper for signs that the larvae chewed through it. If larvae do successfully emerge from eggs, four general sources of mortality can then be assigned to EAB larvae and pupae: 1) disease, 2) killed by tree resistance, 3) parasitism, and 4) predation (Fig. 2). Disease can be assigned by examining the cadaver for signs and symptoms of entomopathogenic fungi or other disease-causing pathogens (Liu and Bauer, 2006) (Fig. 2a). However, because diagnostic tests for pathogens are not done, however, this category also includes EAB killed by starvation or cannibalism. Tree resistance, which typically affects early (1st and 2nd) larval instars, can usually be identified by callous formation around the larval gallery (Fig. 2b).

There are several approaches used to detect parasitism, which is most often identified in late (3rd and 4th) larval instars and pupae. These methods include examining galleries for meconium left by parasitoid larvae, or finding parasitoid larvae, pupae, adults, or parasitoid pupal exuviae in galleries (Fig. 2c). In addition to detecting introduced parasitoids, the same approach also detects several native parasitoids that attack EAB in North America, and those parasitoids should also be considered in life table analyses, including *Atanycolus* spp., *Balcha indica* Mani and Kaul, *Spathius floridanus* Ashmead, and *Phasgonophora sulcata* Westw. (Bauer et al., 2005; Duan et al., 2009; Duan et al., 2012c; Duan et al., 2013a). Even if there are no obvious signs of parasitism, any live larvae or pupae collected when debarking trees should be found and maintained in incubators for adult emergence and identification. Live larvae damaged during sampling should be immediately dissected to detect possible immature parasitoids. This may also be preferable even for the live undamaged larvae because many such larvae



Figure 2. Examples of the four main mortality factors affecting EAB. Shown are: (a) disease/intraspecific competition; (b) killed by tree resistance; (c) parasitism, and (d) predation. (Photo credit: Jian Duan, USDA-ARS, and David Jennings, University of Maryland)

die of fungal diseases during the prolonged rearing period required for them to complete their life cycle (Bauer et al., 2012).

Predation from insectivorous birds such as woodpeckers generally occurs on late (3rd and 4th) larval instars and pupae (Cappaert et al., 2005c; Lindell et al., 2008; Jennings et al., 2013; Koenig et al., 2013). Woodpecker damage can be identified on the outside of the bark before peeling, and then galleries can be traced underneath to the point of attack (Fig. 2d). Because parasitism and predation both occur on late larval instars, there is a possibility that some evidence of parasitism could be lost through predation. Presently there does not appear to be any evidence that woodpeckers preferentially feed on parasitized or unparasitized larvae, but the number of parasitized larvae has been found to be significantly higher when woodpeckers were excluded from trees with experimentally established

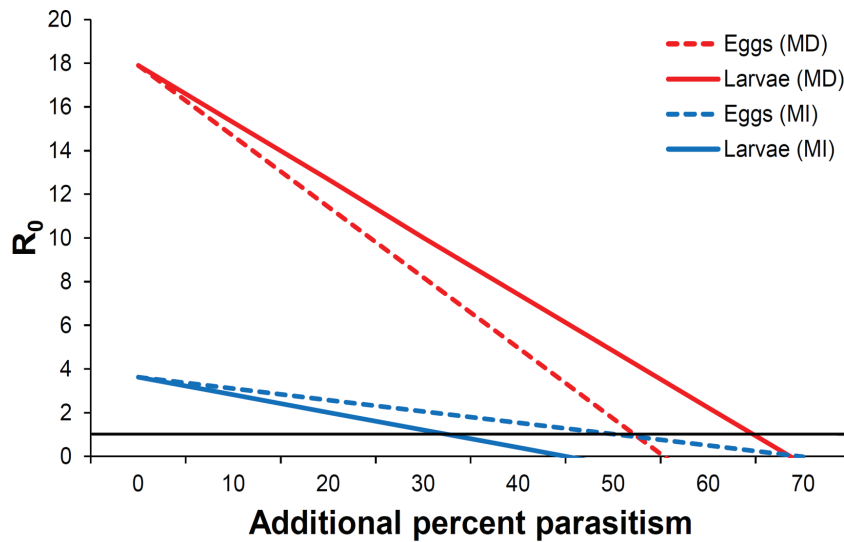


Figure 3. Simulated additional parasitism rates required to reduce EAB R_0 to <1 in Maryland (red lines) and Michigan (blue lines) (based on experimental cohorts at Legg and Harris Nature Center Parks in 2010). Solid lines represent larval parasitism, dashed lines represent egg parasitism. Black line represents $R_0 = 1$, beneath which EAB population growth would be declining.

cohorts of EAB (Jennings et al., 2013), suggesting that parasitized larvae are taken.

Adults. Estimating the mortality of EAB adults can be challenging. Natural sources of mortality likely include predation from insectivorous birds and disease, but these are difficult to quantify under field conditions. For the purposes of life table construction, the most effective way may be to use data collected from laboratory studies to parameterize the models. Such an approach was utilized by Duan et al. (2014), who assigned a mortality rate of 5% to EAB adults.

EFFECTS OF BIOLOGICAL CONTROL ON EAB POPULATIONS

In areas where EAB parasitoids have been released for several years there is evidence that some species (particularly *T. planipennis*) are establishing and increasing in population size (Duan et al., 2013b). With few published studies examining the effects of these parasitoids on EAB population growth using a life table approach, it is difficult to make generalizations from the results. However, using the data available, we can manipulate life tables and

investigate how EAB populations are projected to change under different scenarios. Specifically, we can use the data from published life tables to model what rates of egg and larval parasitism would be sufficient to reduce EAB population growth to non-pest levels.

In Maryland, EAB first arrived in 2003 from EAB-infected ash nursery stock shipped from Michigan and sold in Maryland and Virginia. Despite an attempt to eradicate EAB in this region, EAB was considered established in Maryland in 2006 and Virginia in 2008 (see Chapter 1). In Maryland, EAB populations from experimental cohorts were found to have R_0 values of 17.9 when woodpeckers were present and 19.2 when woodpeckers were excluded using caging (Jennings et al., 2013). Both of these growth rates are high, and they suggest that woodpecker predation does not contribute greatly to mortality at sites with a low to moderate EAB infestation. The main source of mortality at these newly colonized sites was tree resistance, and while parasitism was detected it was at relatively low levels. However, in New York (at study sites where EAB was established longer in comparison to those used in Maryland), where neither parasitism nor tree resistance were significant sources of mortality, R_0

values for wild populations were much higher (29.8 and 50.5 when woodpeckers were able to feed on EAB stages and when woodpeckers were excluded, respectively) (Jennings et al., 2013). This suggests woodpecker predation can significantly reduce EAB population growth only at sites where EAB densities are high.

In Michigan (at sites where EAB has been established for several years), life tables constructed by Duan et al. (2014) found that in the first generation of EAB studied R_0 values were similar to those in Maryland (16 for experimental cohorts and 19.4 for wild populations). However, a large drop in R_0 was seen in the second generation (4.6 and 4.7 for experimental and wild cohorts, respectively), which coincided with an increase in the level of parasitism detected. Mortality was greater in later larval stages than in early ones, primarily because of parasitism from *Atanycolus* spp. and *T. planipennisi*. Host tree resistance and disease remained important for early larval stages, while woodpecker predation was the largest mortality factor for J-larvae. The results also suggest that experimental and wild cohorts of EAB may be used comparably for population studies if certain adjustments are made to account for potentially overlapping generations.

Models using data from experimental cohorts at some of the sites in Maryland and Michigan suggest that if egg and larval parasitism can be increased then there is the potential to reduce EAB population growth to more manageable levels (Fig. 3). These models were constructed by increasing parasitism in increments of 10%, while re-adjusting the stage-specific mortality rate to keep it at the originally observed proportions. Results suggest that in Michigan, ~30% additional larval parasitism would be sufficient to cause a decline in EAB populations, while in Maryland it would take ~65%. An increase in egg parasitism of ~50% would be sufficient to reduce $R_0 < 1$ in both locations. While these models are simplistic, they serve to illustrate the utility of life table analyses.

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