



Biological Control of Southern Pine Beetle

Fred M. Stephen¹ and C. Wayne Berisford²

¹Professor, Department of Entomology, University of Arkansas, Fayetteville, AR 72701

²Emeritus Professor, Department of Entomology, University of Georgia, Athens, GA 30602

Abstract

Exotic invasive forest insects are frequently managed through classical biological control, which involves searching for, introducing, and establishing their exotic natural enemies. Biological control of native bark beetles, including the southern pine beetle (SPB), has been primarily attempted by conserving and manipulating their natural enemies. Knowledge of the role and biology of SPB natural enemies is increasing but is still limited, and is rarely well connected to coincident estimates of SPB host density. A rich complex of SPB native natural enemies exists, and these are discussed in greater detail in other chapters in this book. The cryptic nature of *Dendroctonus* species within phloem and bark, combined with the properties of many natural enemies (small size, highly aggregated distribution, lower density than their prey, and often acting late in the beetle's life cycle), results in challenging sampling problems that are difficult to overcome. Attempts to assess impact of natural enemies have often been presented as percent of mortality, but rarely do these assessments show variation in mortality. The manner in which mortality varies with host density is important in population regulation. Predators, parasitoids, and competitors of the SPB respond in varying degrees to SPB pheromones and tree volatiles during host selection. Variables such as bark thickness and SPB density influence parasitoid success. In making oviposition choices, parasitoids tend to select the host beetle and tree species from which they emerged. Short SPB generation times, continuous flight, and attack by SPB adults result in infestations containing all life stages of beetles and natural enemies. Opportunities for numerical response of parasitoids to epidemic population growth should be great but have not been confirmed. Manipulation efforts indicate that providing nutrients for parasitoid adults increases their longevity, stimulates production of additional eggs, and prevents resorption of existing eggs. Parasitoids do forage in canopies of both pine and hardwood trees, possibly to acquire honeydew as adult nutrition. Predators frequently are the most abundant and visible sources of SPB mortality, and their potential role as delayed density-dependent agents may be important in the cycles exhibited by SPB populations. Simulation models that experimentally remove mortality attributable to natural enemies show how rapidly infestations grow when natural enemies are absent. Experimental research on *Monochamus* spp. indicates that they can cause high mortality to SPB brood as competitors and predators, and field observations suggest that they may play an important role in the collapse of SPB epidemics.

Keywords

bark beetles
parasitoid competitors
population dynamics
predators
Scolytidae

28.1. INTRODUCTION

Infestations of southern pine beetle (*Dendroctonus frontalis* Zimmermann) (SPB) are a veritable hive of insect activity, and the majority of these insects are not SPBs. Observations from a field-based perspective of climbing hundreds of infested trees, sampling bark that contains different SPB life stages, and studying the multitudes of insect species searching on the bark surface and burrowing and developing within the inner bark and phloem, reveal the remarkable diversity of the SPB-associate complex. Many of these associated insects parasitize, prey upon, or compete for food and/or space with the SPB, and as such are considered natural enemies of the beetle. In five other chapters of this book detailed information is presented on SPB predators (chapter 10), parasitoids (chapter 8), competitors (chapter 12), and fungal and mite associates (chapters 9 and 11). Despite the extensive information that is known about SPB natural enemies, it is safe to say that we still know much less than we should about their roles and importance in suppressing SPB population density. The purpose of this chapter is to define the field of biological control as it relates to the SPB and to briefly summarize attempts made at SPB biological control.

28.2. BIOLOGICAL CONTROL

Human manipulation of natural enemies to effect reduction of pest populations has existed for millennia; however, the term “biological control” was first used by H.S. Smith (1919) to signify use of natural enemies, whether introduced or not, to control insect pests. Successful biological control of forest insects is well documented (Dahlsten and Mills 1999, Dahlsten and Whitmore 1989, Pschorn-Walcher 1977, Turnock and others 1976, Waters and others 1976), and biological control is today a primary tactic for management of many exotic forest insect pests.

28.2.1. Definitions

Natural control is a broad concept that encompasses the combined actions of abiotic and/or biotic environmental factors to maintain an organism’s more or less fluctuating population density, within certain definable upper and lower limits, over a period of time (DeBach 1964). Although the term “biological control” is used in many ways by different authors, the most accepted and in our view the

best definition is that of DeBach (1964), who considers biological control as a phase of natural control and defines it “as the action of parasites, predators, or pathogens in maintaining another organism’s population density at a lower average than would occur in their absence.” At its core, this definition implies that biological control is a natural process. The native complex of predators, parasitoids, and competitors associated with the SPB, for example, reduces to some extent SPB population density. This does not necessarily imply that natural enemies will maintain SPB population density below a level that is economically acceptable, but it does mean that without these natural enemies the SPB would be a more significant pest.

28.2.2. The Field of Biological Control

Biological control of insect pests can be considered an applied discipline; however, its foundations are based in ecological theory. Thus knowledge of insect ecology and ecosystem interactions is usually key to successful biological control. Although much is known, we still do not have sufficient knowledge to enact successful biological programs against the SPB. Biological control as a discipline is often separated by the origins of pests and of their natural enemies and by the approaches used to maximize the effectiveness of the natural enemies. These approaches can be distinguished as follows: 1. classical biological control – the importation and establishment of exotic natural enemies to control exotic or native pests; and 2. manipulative biological control – techniques that manipulate natural enemies to augment or enhance their effectiveness, or techniques that manipulate the environment to benefit and conserve existing natural enemies. Examples of these approaches in relation to the SPB are explained and discussed below. Disruption of naturally occurring biological control through human intervention can and does occur. This knowledge should further stimulate our efforts to gain more knowledge of forest / bark beetle / natural enemy interactions. Because successful biological control must be based on the fundamentals of scientific knowledge, it is essential to subsequently evaluate the reasons for success or failure of biological control programs.

Importation (Classical Biological Control)

The importation of natural enemies to control exotic (introduced) pests is by far the most

common approach to biological control of forest insects (Dahlsten and Mills 1999). Invasive insects or other organisms that are accidentally or intentionally introduced from geographically distant areas into a new locale such as North America may reproduce without mortality from natural enemies or host resistance that normally evolves through generations of insect-plant interactions. The search for natural enemies of the pest in its native area, coupled with their importation, quarantined rearing to eliminate secondary parasitoids or diseases, in concert with release, establishment, and control of the pest in its new environment constitutes classical biological control (DeBach 1964). In forest systems, classical biological control should be considered as an essential management tool, particularly in light of the increasing numbers of invasive exotic pest species that are being discovered. If eradication of these exotic species fails, then management of their populations with classical biological control should be fully explored. Although there are many famous and successful biological control projects of forest pests that have involved importation and establishment of natural enemies (Dahlsten and Mills 1999, Huffaker and Messenger 1976, Pschorn-Walcher 1977, Turnock and others 1976, Waters and others 1976), for bark beetles the number of successful examples is quite limited.

A related approach that derives from the principles of classical biological control has been proposed (Hokkanen and Pimental 1984, Pimental 1963). These authors suggest that because host-parasitoid relationships often tend to become less virulent over evolutionary time, new associations of natural enemies selected from species related to a particular pest may be advantageous. Pschorn-Walcher (1977) reports that this approach has not worked in forests, but suggests it should not be disregarded without more exploration. Indeed, predator introductions that are discussed below, *Thanasimus formicarius* (L.) (Coleoptera: Cleridae) and *Rhizophagus grandis* (Gyllenhal) (Coleoptera: Rhizophagidae), are both natural enemies of European bark beetles related to North American genera, and are thus illustrations of the new associations strategy.

Manipulation (Augmentation and Conservation)

Classical biological control may be an essential approach for managing invasive exotic pest species; however, manipulation by augmenting

and conserving natural enemies is for native pests a strategy more important and more likely to succeed. Humans can act to augment numbers of natural enemies, and they can manipulate their habitats so as to increase natural enemy survival and effectiveness. Actions that manipulate insects themselves can theoretically be considered distinct from actions that alter the environment in which the insects live; however, in practice it can be difficult to distinguish the two (Rabb and others 1976). Conservation of natural enemies may be an approach that is highly appropriate in forest ecosystems, as they are longer lived, suffer fewer disruptions, and are generally more complex than agricultural systems (Dahlsten and Mills 1999).

Study

The phrase, “know your enemy,” would seem to be essential to any commander of a military campaign, and may be an appropriate cliché in biological control programs. Successful biological control depends on knowledge of the biology and ecology of target hosts, natural enemies, and the ecosystems in which they will exist together. Although multiple lists of SPB natural enemies have been prepared (Berisford 1980, Franklin 1969, Goyer and Finger 1980, Linit and Stephen 1983, Moser and others 1971, Overgaard 1968, Stephen and others 1993), detailed information on their biology and impact is woefully lacking. There are many reasons for this circumstance. Bark beetles are difficult to observe. They spend most of their life cycle in phloem and bark tissues, and most of their natural enemies are also found in this cryptic environment. It is challenging to rear the SPB in the laboratory. Creating experiments with both the SPB and its natural enemies is even more difficult. Few controlled studies have succeeded in replicating environmental conditions encountered by the SPB and its associated species in the field. Sampling to estimate density of natural enemies is challenging, owing to their occurrence within bark and phloem tissue many meters above the ground in standing pine trees, their aggregated patterns of dispersion within trees in regard to their bark beetle hosts (Stephen and Taha 1976), and the timing of their arrival and development in relation to the SPB life cycle (Camors and Payne 1973, Dixon and Payne 1979b). Natural enemy abundance and distribution also varies seasonally (Goyer and Finger 1980, Stein and Coster 1977) and as a function of infestation age and size (Stephen and others 1989).

28.3. NATURAL ENEMIES OF SOUTHERN PINE BEETLE

Published literature that supports the importance of natural enemies in suppressing SPB populations traces its roots to A.D. Hopkins in the late 19th century (Hopkins 1899). Since then many other scientists have noted the abundance of natural enemy species and surmised that at times they must be extremely important mortality agents even if their overall importance in regulating SPB populations is unclear.

28.3.1. The Natural Enemy Complex

The complex of insect natural enemies that is associated with the SPB is extensive and may reach 150 species (Berisford 1980, Dixon and Payne 1979b, Franklin 1969, Goyer and Finger 1980, Linit and Stephen 1983, Moser and others 1971, Overgaard 1968, Stephen and others 1993). Organisms other than insects may also be key agents of mortality, and can include birds, particularly woodpeckers (Kroll and Fleet 1979), mites (Klepzig and others 2001a, Moser 1975, Moser and Roton 1971), fungi (Barras 1970, 1973; Bridges 1983; Hofstetter and others 2006a; Klepzig and others 2001a, Paine and Stephen 1988), and nematodes (MacGuidwin and others 1980, Moore 1971, Sikorowski and others 1979). Other chapters in this text on SPB population dynamics within trees (chapter 4), SPB competitors (chapter 12), SPB parasitoids (chapter 8), SPB predators (chapter 10), and SPB mites and fungi (chapter 11) address details of mortality to SPB from this diverse group of enemies.

28.3.2. Natural Enemy Impact Assessment

Evaluating the impact of mortality caused by natural enemies has been varied and often innovative. Basic approaches to assessing the importance of natural enemies are often through some variation of either excluding them or adding them to an experiment, then comparing the resultant mortality to control situations. Adding predators and manipulating SPB host density showed that *T. dubius* can influence SPB attack density (Reeve 1997). Exclusion studies, both in the laboratory and field, provide estimates of mortality to the SPB by natural enemies (Linit and Stephen 1983, Miller 1984, Reeve and others 1998, Riley and Goyer 1986). Estimates of mortality or percent of parasitism obtained by rearing bark beetles and natural enemies are common, but provide very rough

estimates. Correctly attributing mortality to a particular species, obtaining accurate density estimates, timing of tree felling, or caging, all contribute to errors in estimation. A life table approach to sampling on trees, where density of all bark beetle life stages can be found, and corresponding amount of stage-specific mortality by known natural enemies is a remarkably difficult and expensive operation, and rarely conducted. Experiments with direct observation of natural enemy / host interactions can be obtained using the valuable technique of phloem sandwiches (Dodds and others 2001, Kinn and Miller 1981). Trapping with the synthetic aggregation pheromone frontalin and turpentine can be used to estimate ratios of the SPB to its predator *T. dubius*, yielding predictions for SPB population trends but not impact from predation (Billings 1988).

Measured Impact

Linit and Stephen (1983), by sequential, on-tree exclusion studies, estimated within-tree mortality caused by the SPB natural enemy complex at 23-28 percent; this is certainly sufficient to be considered as potentially important in population regulation, particularly as much of it comes late in the SPB life cycle. Multiple factors are involved in determining natural enemy effectiveness. The success of eight species of SPB parasitoids was studied in relation to bark thickness and SPB host density (Gargiullo and Berisford 1981). In regions of thinner bark all species were found at higher densities, illustrating the importance of this variable to parasitoid success. These authors also determined that in seven of the eight species studied, parasitism increased as SPB host density increased.

During a 4-year period in Arkansas, Stephen and others (1989) sampled within-tree populations of the SPB and their natural enemies during years when overall SPB population levels were increasing (1975), epidemic (1976), and collapsing (1978). Over those years they found that egg density increased; however, numbers of eggs per attack remained fairly constant at about 28-30 (Table 28.1). Numbers of natural enemies increased 3 fold, and the proportion of natural enemies to late-stage immatures increased in a similar manner, from 0.18 to 0.57. Percent of mortality, calculated as the percentage of change in density from eggs to late-stage immatures, rose from 67 percent to 82 percent, suggesting that natural enemies were important in the collapse of this outbreak.

Table 28.1 — Changing relationships among SPB within-tree life stages and natural enemies as overall SPB population levels increase to epidemic status and then collapse. Data adapted from Stephen and others (1989)

Year (pop. level)	SPB attacks/dm ²	SPB eggs/dm ²	Late stage Eggs/attack	Late stage larvae/pupae/dm ²	Natural enemies (NE)/dm ²	Proportion NE	Percent mortality egg-larvae/pupae
1975 (increasing)	3.7	107.7	29.1	35.1	6.2	0.18	67.4
1976 (epidemic)	5.7	157.4	27.6	43.2	12	0.28	72.6
1978 (collapsing)	5.7	172.8	30.3	31.9	18.3	0.57	81.5

Larvae of the SPB guild and *Monochamus* spp. are commonly found together in phloem of SPB-attacked trees. Quantitative evaluations of mortality resulting from interactions between *Monochamus* and the SPB were investigated in the 1970s in East Texas, and interspecific competition was confirmed (Coulson and others 1976a, 1980a). They found that foraging by *Monochamus* reduced bark beetle survival when both co-existed, but that frequently the timing of their occurrence, coupled with the tendency of the SPB to move to the outer bark to form pupal chambers, often diminished that interaction. They further concluded that the observed levels of mortality had a significant influence on within-tree SPB survival, averaging 14 percent on a per tree basis and reaching 70 percent in specific areas where *Monochamus* was foraging (Coulson and others 1980a). Dodds and others (2001) experimented with interactions of bark beetle larvae (*I. calligraphus*) and their common associates, *Monochamus carolinensis* (Olivier). They established that *Monochamus* larvae are facultative predators upon the bark beetles, and when encounters occurred, cerambycid larvae usually attacked, killed, and frequently ingested the bark beetles. The importance of competition in SPB population dynamics appears critical, yet not fully understood (chapter 12).

Moore (1972) reported that in *P. taeda* L. parasitoids and predators of the SPB caused an average of 24 percent mortality to developing brood. He also reported that 22 percent of the SPB contained potentially pathogenic bacteria (Moore 1971). Given their potential importance to SPB population dynamics (Sikorowski and others 1979), it is surprising that more research on diseases has not been undertaken.

Models and Analysis of Impact

Simulations were made using SPBMODEL (Stephen and Lih 1985) to predict growth of SPB populations in several infestations that had been monitored and sampled during 1975 and 1978. The model was used to simulate growth of observed populations, and those populations were also surveyed and monitored by counting infested numbers of trees during the periods when growth was occurring. Mortality rates in the model were then conservatively modified to remove the estimated impact caused by parasitoids (one SPB larva for each parasitoid), and predators (two SPB immatures for each predator) to the SPB, and the simulations were again conducted. In all cases the predictions showed that when mortality to the SPB caused by those natural enemies was removed, infestation growth was dramatically increased (Stephen and Lih 1985).

A frequently cited paper by Turchin and others (1991) reports that both time-series and regression analysis of an index of SPB population levels in East Texas (spots greater in number than 10 trees) over time shows population change to be a result of as yet unknown delayed density-dependent process. The authors suggest that natural enemies, particularly predators, may be the causal agent. While their conclusions as to the importance of natural enemies in the cyclic dynamics observed to occur with SPB populations may be correct, their reasoning and methodology raise questions. Two are worth mentioning. First, data used in the analyses are infested spots (as an index of SPB numbers) counted on a yearly basis, and the best fit to their model was a 2-year time delay. Given that the SPB may undergo seven generations per year (Payne 1980), and some natural enemy species even more than that (Jones and Stephen 1994), a time delay of 2 years may encompass about 14 generations of the beetle and perhaps

significantly more generations of its natural enemies. That fact confounds the biological interpretation of their perceived interactions with the SPB and its natural enemies. Second, the Texas Forest Service, private landowners, and at times the USDA Forest Service, did their best to prevent and minimize damage from the SPB during most of those years. The predominant control tactics were salvage and cut-and-leave (Billings and Pase 1979a, Swain and Remion 1981). The impact of these control procedures on survival and population dynamics of the SPB is not known; however, the unknown density-dependent process response, hypothesized by Turchin and others (1991), unfortunately cannot be separated from the density-related suppression efforts of foresters and pest managers.

28.4. BIOLOGICAL CONTROL OF SOUTHERN PINE BEETLE

Attempts at biological control of the SPB have been limited in scope but fall into two basic groups: those that deal with introductions of natural enemies, and those that seek to manipulate or conserve existing natural enemies. The latter efforts to enhance naturally occurring biological control are the more common and may show the most promise for the future. As with many complex systems, a primary concern should be to avoid forest or insect pest management tactics that negatively affect existing natural enemies, thus disrupting a system that may be working better than we realize. Human interventions in forest ecosystems can lead to unexpected disruption of naturally occurring biological control (Luck and Dahlsten 1975), and such results merit wise planning in regard to forest management decisionmaking.

28.4.1. Introduction of Exotic Natural Enemies

The most noteworthy and successful attempts at classical biological control of bark beetles involve the greater European spruce beetle, *Dendroctonus micans* (Kugelann) (Dahlsten and Mills 1999). This bark beetle, native to Eurasia, became a problem in the Massif Central region of France in the 1970s and was later discovered in 1982 in spruce plantations in Wales. In France, *Rhizophagus grandis* was relocated from Soviet Georgia, mass reared, and released. The predators became established and are at least partially successful

in reducing populations of the bark beetle (Dahlsten and Mills 1999, Gregoire and others 1989). *D. micans* was accidentally introduced to Great Britain from continental Europe and became a serious pest of spruce there in the absence of natural enemies. Again, its major predator, *Rhizophagus grandis*, was imported and released, and appears to be limiting populations and minimizing impact of the outbreaks (Fielding and Evans 1997). About 220 of these predatory beetles were introduced into Southern United States for biological control of *D. terebrans* (Miller and others 1987, Moser 1989), but successful colonization was not reported.

The earliest attempt at introduction of an exotic bark beetle natural enemy was made in West Virginia by A.D. Hopkins, who collected ‘*Clerus*’ (*Thanasimus formicarius* (L.)) with assistance from the German scientists Eichhoff, Schaufuss, and Strahmeyer (Hopkins 1899). He traveled with his beetles to England to avoid cholera in Germany and France (and to keep his belongings—and insects—from being fumigated on board ship) and brought them home in his luggage. In October 1892 he released 50 adults and about 25 larvae “on and in the bark of a group of dying scrub pines on Mayfield Hill, about 7 miles from Morgantown, this colony being the first examples liberated in America” (Hopkins 1899). The sudden disappearance of the SPB in 1893, however, meant he had no target population for his planned releases in spring of that year, a fact he believed may have contributed to the apparent failure of his releases. In total more than 2,000 *T. formicarius* were released between 1892 and 1894, but none were recovered.

Although not a *Dendroctonus* species, the five-spined engraver beetle, *Ips grandicollis* (Eichhoff), a species native to the Southeastern United States, was discovered in the exotic pine plantations of Australia in 1943, and in the early 1980s became the focus of a biological control program (Waterhouse and Sands 2001). C.W. Berisford and D.L. Dahlsten collected and transported several species of North American hymenopterous parasitoids to Australia, where they were cultured and some subsequently released. The most successful releases were of the species *Roptrocercus xylophagorum* (Ratzeburg), and *Dendrosoter sulcatus* Muesebeck, with the former species becoming established in all States and reducing host populations on average 25 percent and up to 70 percent in some situations (Waterhouse

and Sands 2001). The predators *Thanasimus dubius* (Fabricius) (Coleoptera: Cleridae) and *Temnochila virescens* (Fabricius) (Coleoptera: Trogositidae) also were introduced from the Southeastern United States to Australia. Although *T. dubius* may have been established in the mid-1980s (Berisford and Dahlsten 1989), subsequent evaluations report that neither species is considered established (Waterhouse and Sands 2001). *Ips grandicollis* remains a serious pest of pine plantations in Australia, particularly during periods of severe drought.

28.4.2. Conserving and Enhancing Naturally Occurring Biological Control

Natural enemies are abundant in SPB infestations (Stephen and others 1997) and collectively help in regulating SPB population abundance. It seems clear, however, that they do not always regulate populations below economically acceptable levels, a fact vividly illustrated by numerous large-scale SPB outbreaks in multiple southeastern States in the past 20 years. When massive outbreaks do occur, natural enemies may, however, be critical both in their termination and in maintaining endemic populations, and extending the period between outbreaks. What may be most important in maintaining bark beetle populations is a collective effort to properly manage forest stands (chapter 23) while working to conserve and enhance natural enemy effectiveness.

Suppression Tactics and Conservation

Direct control for suppression of SPB includes four techniques that are approved for use by the Final Environmental Impact Statement for the Suppression of the SPB (USDA Forest Service 1987). These tactics are cut-and-remove, cut-and-leave, cut-and-hand-spray, and pile-and-burn (see chapters 25, 26, and 27). Development time of most natural enemies is either longer than the SPB or they attack the SPB late enough in its life cycle that they will emerge from trees after emergence of the majority of the SPB brood adults. Trees from which SPBs have emerged will still harbor rich natural enemy populations, and therefore their removal, cut-and-spray, or pile-and-burn will needlessly kill natural enemies. The suggestion that bark beetle natural enemies can be conserved through cultural practices is long-standing (Berryman 1967, DeLeon 1935, Moore 1972). Manuals describing SPB control techniques such as cut-and-leave, in which SPB infested trees are felled and left on the ground,

include recommendations for conserving natural enemies by leaving trees from which all SPBs have emerged, thus allowing natural enemies to complete development (Swain and Remion 1981). The fate of natural enemies in cut-and-leave trees is dependent primarily on solar radiation and temperature, and has not been fully explored.

Suppression of the SPB by use of chemical pesticides is limited to a practice known as cut-and-hand-spray (USDA Forest Service 1987). In national forests in Texas, during the period 1990-99, about 5,600 infestations covering 2900 ha (~7,200 acres) required suppression treatments. Of these treatments, cut-and-hand-spray for SPB suppression was used on about 3,000 trees on about 7.6 ha (~19 acres). Use of pesticides for SPB suppression, more prevalent in previous pest management recommendations than in current ones, has been indicted as harmful to its natural enemies and potentially causal in creating chronic bark beetle problems (Williamson and Vité 1971).

Semiochemicals

It is well known that natural enemies of bark beetles respond to host tree and beetle odors as they attempt to locate their prey (Mizell and others 1984, Payne 1989, Raffa 2001). Synthetic chemicals such as frontalin, *trans*-verbenol, *endo*- and *exo*-brevicomin or verbenone attract or repel SPB and may also affect populations of many of their natural enemies (Dixon and Payne 1980, Payne 1989). *Monochamus titillator* (F.), probably the most important SPB competitor, is also attracted to pheromones for the southern pine engravers, *Ips* species (Billings and Cameron 1984). Suppression and prevention programs for bark beetles that have used semiochemicals in trap-out strategies report that, in addition to the target bark beetles, large numbers of predators were also captured (Bedard and Wood 1981).

The effects on natural enemies of stand treatments using the SPB inhibitor, verbenone, were tested for *T. dubius* (Johnson and Coster 1980), and in a well-planned field study for all important SPB natural enemies by Salom and others (1995). Both studies concluded that there was a negligible effect of the verbenone suppression tactic on natural enemies, and that no unusual dispersal of the natural enemies from the treatment areas was detected. However, the fact that natural enemies are intimately tied to the semiochemicals, particularly attractants, associated with bark beetles implies that any

management technique using these compounds should be evaluated carefully to ensure that they are not negatively affecting natural enemies.

28.4.3. Parasitoid Manipulation

Research to more fully understand the biology and role of parasitoids in SPB population dynamics, and to enhance their effectiveness in suppressing SPB population growth, was conducted in a series of experiments in the 1990s by F.M. Stephen and students at the University of Arkansas, in collaboration with L.E. Browne of Entopath, Inc. Their ideas and research efforts are summarized below.

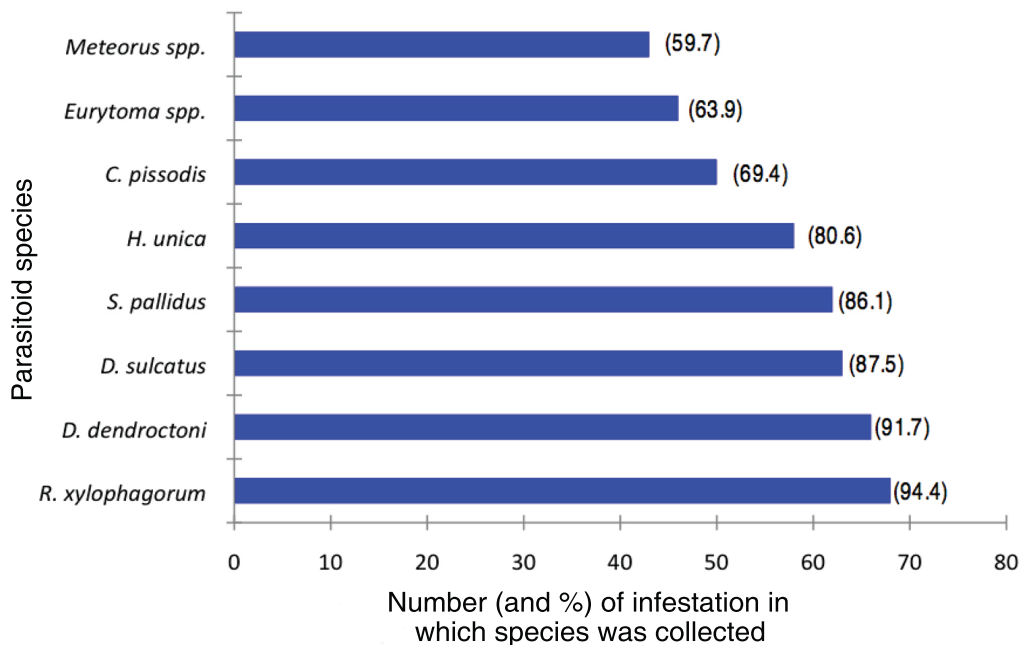
Why SPB Parasitoids Should Be Important

There are several reasons, discussed below, that explain why the SPB parasitoid complex may be unique and more able than enemies of other *Dendroctonus* species to rapidly respond to bark beetle population growth. Berisford (1980), Goyer and Finger (1980), and Moser and others (1971) indicate that there are eight common parasitoids of the SPB. This includes the pteromalids *Roptrocercus xylophagorum* (Ratzeburg), *Heydenia unica* Cook and Davis, and *Dinotiscus dendroctoni* (Ashmead), the eurytomids *Eurytoma* species, and the braconids *Meteorus* species, *Coeloides pissodis* (Ashmead), *Dendrosoter sulcatus* Muesebeck, and *Spathius pallidus* Ashmead. Intensive sampling in a wide variety of infestations between 1975 and 1992 revealed that the parasitoid species named above were present in

most infestations most of the time (Stephen and others 1997) (Figure 28.1).

Developmental times for SPB generations in the warmer parts of the South may be about 1 month in duration (Wagner and others 1984b), resulting in as many as seven to eight generations per year (Thatcher and Pickard 1967). A large proportion of the attacking adult population reemerges shortly after oviposition is completed (Coulson and others 1978), and these reemerging adults, in concert with emerging brood adults, produce a continual allocation of beetles (Coulson and others 1979c) that attack and produce pheromones in adjacent trees (Coster 1970). The continual presence of a pheromone source results in infestations forming as cohesive “spots” that serve to concentrate both the SPB and its natural enemies (Franklin 1970b). In large infestations SPB hosts are abundant and parasitoids do not need to disperse further than adjacent trees to find them. It has also been commonly observed that those parasitoid adults aggregate at SPB-infested trees with susceptible hosts (Camors and Payne 1973, Dixon and Payne 1980, Sullivan and others 1997) and generally parasitize later larval stages (Kudon and Berisford 1980, VanLaerhoven and others 2002). Field and laboratory experiments with five common SPB parasitoid species revealed that at temperatures near 30 °C, the average development time was about 2 weeks, or approximately one-half the time required for their SPB hosts (Jones and Stephen 1994).

Figure 28.1—Constancy of occurrence of eight common parasitoids in SPB infestations. The bars reflect number of times each parasitoid species was collected, by intensive within-tree sampling, from a total of 72 infestations studied between 1975 and 1992. The values in parentheses are percentage of occurrence of those parasitoid species. (adapted from Stephen and others 1997)



Within a large spot that has been growing for several months, the SPB population age structure has beetle immatures in all stages of development that can serve as hosts for parasitoids. It therefore seems probable that over time, in large SPB infestations, parasitoids should have higher population growth rates than their SPB hosts and through numerical response be effective regulators of SPB populations. However, most SPB infestations are fewer than 10 trees and usually decline (Billings 1980b). In these small infestations the host resource is patchy and ephemeral, and parasitoid dispersal to other infestations is critical.

Evidence Parasitoids Are Not Suppressing SPB

Research is extremely limited that provides estimates of parasitoid-caused mortality to SPB populations. Those data that do exist support the conclusion that parasitoids do not cause high amounts of mortality. A large SPB infestation was intensively monitored in 1991 and 1992 by within-tree sampling of infested pines and concurrently counting total numbers of infested and cumulative dead trees on the Indian Mounds Wilderness Area in East Texas. In April 1991, the infestation contained 74 currently infested trees. Rapid growth occurred throughout the summer until by late September 1991, 895 currently infested trees (and nearly 2,600 cumulative dead trees) were counted. Beetle population numbers declined in winter, but infestation growth began again in spring. Population estimates of the SPB in April 1991 showed approximately 2.8 million SPBs present in the infestation, which grew quickly until there were an estimated 33.5 million SPBs present in November. February 1992 estimates indicated about 15.8 million beetles, with fast growth leading to a population of nearly 42 million SPBs by May 1992 (Figure 28.2). The total parasitoid population grew from less than 200,000 in April 1991 to about 1.2 million in November, declined over winter, then grew to about 1.45 million by May 1992. A visual comparison of increase and decrease in parasitoid numbers in relation to the SPB numbers indicates that patterns of change are closely related. Although parasitoid population abundance continually increased throughout spring and summer, average percentage of parasitism was between 6 and 7 percent in both April and September and fluctuated at about those levels in all intervening months, suggesting that although actual numbers of parasitoids increased in relation to changing

Relation of Parasitism to Emerging SPB, Spot 3, Indian Mounds Wilderness, East Texas

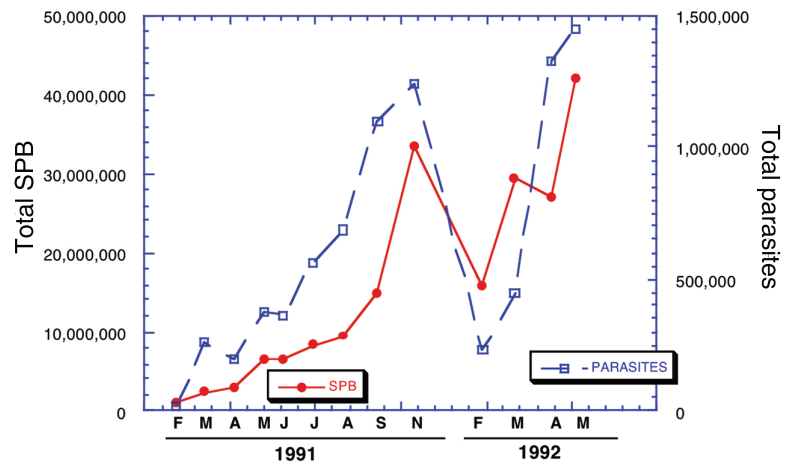


Figure 28.2—Estimated total numbers of adult SPB and adults of its parasitoid complex in a single large SPB infestation sampled intensively from February 1991 to May 1992. Numbers of SPB are shown in red, scaled on the left axis, and total parasitoids are shown in blue, scaled on the right axis. (adapted from Stephen and others 1997)

Relation of Parasitism to Emerging SPB, Spot 3, Indian Mounds Wilderness, East Texas

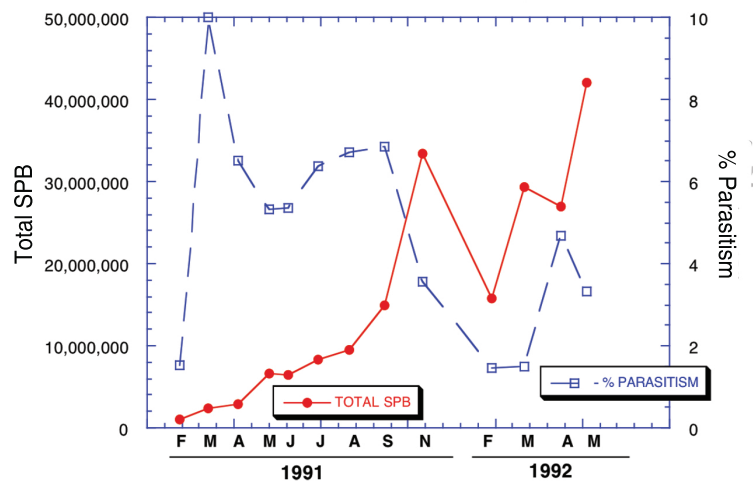


Figure 28.3—Estimated total numbers of adult SPB and percent parasitism from its parasitoid complex in a single large SPB infestation sampled intensively from February 1991 to May 1992. Numbers of SPB are shown in red, scaled on the left axis, and total percent parasitism is shown in blue, scaled on the right axis. (adapted from Stephen and others 1997)

beetle numbers, a numerical response probably did not occur (Figure 28.3).

It appears from the East Texas data that parasitoids inflicted variable but relatively low mortality, and did not exhibit a numerical response to increasing SPB populations. When this conclusion is examined in relation to:

1. superabundance of continuously available

SPB host larvae; 2. parasitoid adults needing only to traverse minimal distances between trees within spots to locate these hosts; 3. observed parasitoid aggregation at trees with suitable host larvae; and 4. Parasitoid immature development rates that are nearly twice as rapid as their hosts, it seems remarkable that over several months of infestation growth a proportionally greater amount of parasitism did not occur. Unfortunately data of this same type were not collected in this area for the next several years as SPB populations remained high in 1993 but collapsed in 1994 (Clarke and Billings 2003).

Hypothesis of Adult Parasitoid Nutrition

From these and additional observations Stephen (1995) proposed a hypothesis that parasitoids are not effective in regulating SPB populations because parasitoid adults, in improperly managed southern pine forests (those which are overstocked, homogeneous in age and species composition, and protected from fire), are limited in reproductive capacity and longevity by lack of suitable nutrition from natural sources. This hypothesis evolved over time as scientific evidence was accumulated in support of the importance of nutrition to parasitoid effectiveness.

Natural sources of food for adult parasitoids could be in the form of flower nectar or honeydew secreted by forest Homoptera. Laboratory studies demonstrated that parasitoid adults would take flower nectar if it were readily available (Drumtra and Stephen 1999). Flowering plants are rare in intensively managed pine forests, and in field studies artificially placed flowers within SPB infestations were not visited (Drumtra and Stephen 1999). VanLaerhoven and others (2005) reported that SPB parasitoid adults will feed on artificial food applied to the bole of host pines. Those parasitoid adults also move considerably away from potential host larvae, located in subcortical tissues of infested pines, and forage in the forest understory and in the canopies of pines and hardwoods. Foraging in locations where their hosts do exist suggests these locations may provide a source of adult nutrition, and indeed a significant amount of honeydew is produced, especially by hardwoods, in those locations (VanLaerhoven and others 2005, VanLaerhoven and Stephen 2008). It is also possible that foraging in tree canopies may provide a corridor for parasitoid movement and dispersal within SPB infestations.

Testing the Hypothesis

Parasitoids of SPBs employ a reproductive strategy, termed “synovigenic,” in which adult females have large, nutrient-rich eggs that are few in number but can be resorbed by the adult if hosts are not available (Figure 28.4). If adults do find nutrition they can produce more eggs and they live longer (Mathews and Stephen 1997, VanLaerhoven and others 2002). In the mid-1990s Lloyd E. Browne (Entopath Inc. Easton, PA) developed a nutritionally complete, environmentally safe, artificial food for SPB parasitoids that he named Eliminate®. In laboratory trials, Mathews and Stephen (1997) tested more than 2,800 individual SPB parasitoids of seven species, reared from field-collected SPB infested logs, by exposing them to water only or water plus the Eliminate® diet (Figure 28.5). All seven species fed on the diet and all had significantly greater longevity when they consumed artificial diet (Mathews and Stephen 1997). Further experiments also showed that under more extreme laboratory conditions designed to more closely mimic hot summer field conditions, particularly in high temperature-low humidity situations, parasitoid adults only lived a very short time, but that with nutrients and moisture their longevity was significantly improved (Mathews and Stephen 1999).

To further explore manipulation of parasitoid effectiveness by augmenting adult nutrition, plastic paint balls each were filled with 2.1 g Eliminate® to which blue dye was added as a means to visually identify diet on trees and in guts of parasitoids. Field experiments were conducted in which food balls were shot from compressed air rifles onto the boles and into the crowns of SPB-infested trees (Stephen and Browne 2000). Parasitoids searching for hosts or ovipositing on SPB-infested tree boles (Figure 28.6) were subsequently collected using modified Dustbuster® vacuums (Figure 28.7), and dissected to determine if they had Eliminate® and dye in their guts (Figure 28.8). Adults from all eight species of parasitoids (Figure 28.1) fed on Eliminate® in field trials (Stephen and Browne 2000). Application of food via compressed air rifles and food balls was too labor-intensive and slow for operational suppression, thus prompting aerial spray trials of Eliminate® from helicopters into the pine canopy of an SPB infestation. Following aerial application 514 parasitoid adults were collected on boles of infested trees and dissected. Nearly 75 percent showed evidence of feeding on

Eliminate® (Stephen and Browne 2000) (Table 28.2). Stephen and Browne (2000) proposed that aerial application of Eliminate® could be a direct control for SPB by enhancing longevity, fecundity, and effectiveness of SPB parasitoids. Subsequent field experiments to validate this idea were hampered by epidemic SPB population levels, coupled with unpredictable movement of adult SPB among infestations, plus lack of funding for aerial Eliminate® treatments and simultaneous area-wide monitoring of the SPB and their natural enemies in multiple infestations across the landscape.

28.4.4. Predators and Competitors

The clerid beetle, *Thanasimus dubius* (F.), has captured the attention of forest entomologists since the time of A.D. Hopkins (Hopkins 1893, 1899). Its response to the SPB aggregation pheromone (Dixon and Payne 1979a, Thatcher and Pickard 1966), coupled with its abundance and highly visible habits as a predator of SPB adults on the bark of newly infested trees and larval predation of SPB immatures, has made it a prime candidate for study and possible manipulation (chapter 10). Reeve suggests that *T. dubius* may, under field conditions, slow the attack process of the SPB and help regulate SPB populations, as he noted an inverse relationship between year-to-year growth rate of the SPB and *T. dubius* populations (Reeve 1997). Miller and others (1987) suggest that predators, specifically the North American clerid *Thanasimus undatulus* Say and the palearctic predator of *D. micans*, *Rhizophagus grandis*, may be suitable for colonization and manipulation as they respond to aggregation pheromones of the SPB.

Massive outbreaks of the SPB in East Texas slowed and collapsed in 1994, and analysis of causes suggested that available host trees were still abundant, and the collapse was probably a function of predation, plus competition from pine engravers (*Ips* species) and long-horned wood borers (*Monochamus* species) (Clarke and Billings 2003). Although their assessment as to the cause of the collapse was speculative, other scientists who have observed the rapid decline of bark beetle infestations in the South have also alluded to the importance of competition from *Monochamus* species in particular (Dodds and others 2001, Hain and Alya 1985). The roles and impact of predation (chapter 10) and competition (chapter 12) deserve additional study and must be more clearly defined in order to adequately understand SPB population dynamics.

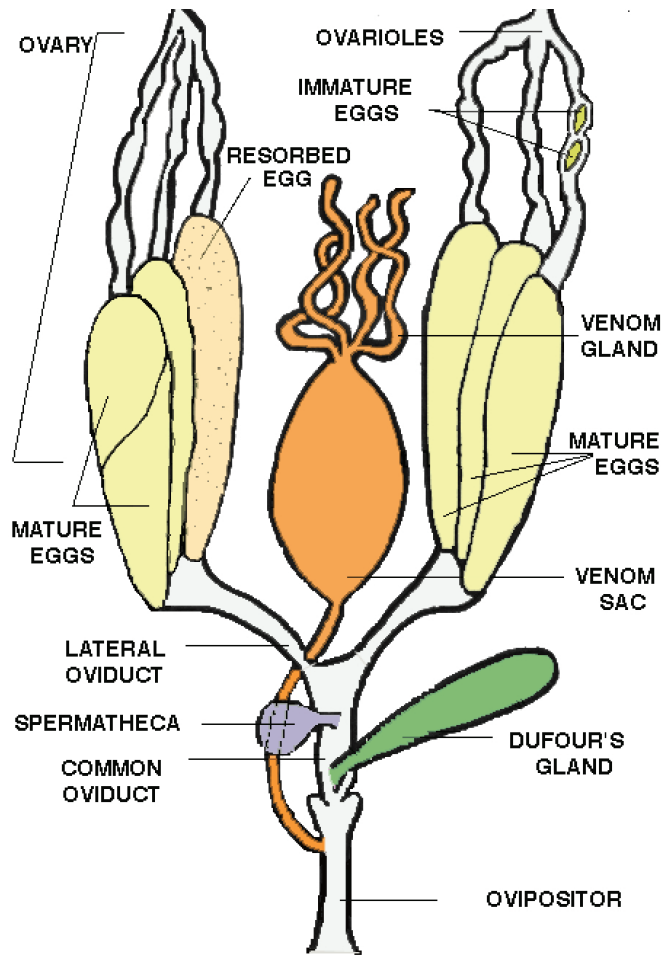


Figure 28.4—Stylized rendering of the reproductive system of an adult female synovigenic parasitoid, showing ovaries containing immature, and mature, large nutrient-rich eggs, plus a partially resorbed egg. (adapted from Gauld and Bolton 1988. *The Hymenoptera*. Oxford University Press)



Figure 28.5—*Roptrocercus xylophagorum* adults in the laboratory feeding on a drop of blue-dyed Eliminate®



Figure 28.6—*Coeloides pissodis* adult ovipositing on surface of pine bark



Figure 28.7—Dustbuster® cordless vacuum, modified for parasitoid collection

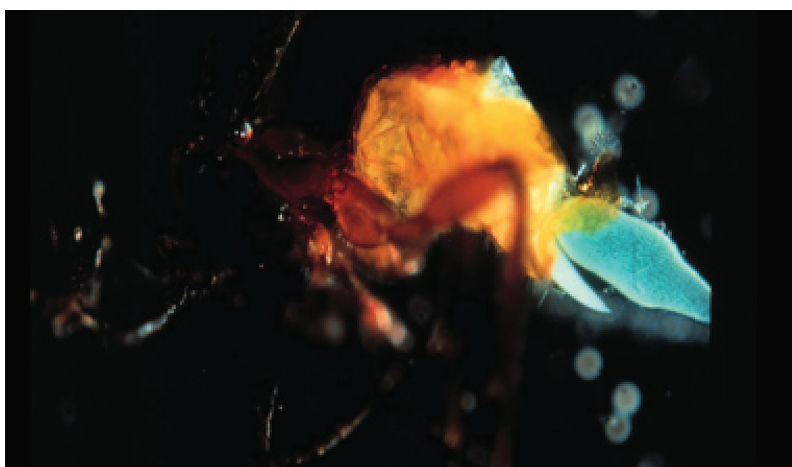


Figure 28.8—*Coeloides pissodis* adult, dissected to show blue-colored mid-gut resulting from feeding on Eliminate®

28.4.5. Natural Enemies Share a Host Resource

A long-noted and important observation associated with SPB infestations is that a complex of bark beetles is commonly present in the same infested trees (Berisford 1980, Dixon and Payne 1979b, Paine and others 1981). This complex of bark beetles is attacked by many of the same natural enemies, and this is true in general for bark beetles throughout North America. Wasps in the braconid genus *Coeloides*, for example, parasitize six species of *Dendroctonus*, three species of *Scolytus*, and seven *Ips* species in North America (Stephen and others 1993). Long-legged flies, *Medetera* (a bark beetle predator), are reported to attack six *Dendroctonus*, two *Scolytus*, and five *Ips* species. Similar patterns of host utilization occur with many predators and parasitoids, and better information on host prey selection and rearing records would further confirm this fact. This information is important because as populations of the SPB shift in abundance, their natural enemies still can locate *Ips* species or even other bark beetle or weevil genera in their habitat that will serve as suitable hosts and maintain a natural enemy complex in the forest. Research conducted by Kudon and Berisford (1980) confirmed that the most common hymenopterous parasitoids of the SPB also are found parasitizing *Ips* engraver beetles, and even the eastern juniper bark beetle, *Phloeosinus dentatus* (Say). They suggest that when SPB populations are low and *Ips* bark beetle populations are high, *Ips* could serve as reservoir hosts for these parasitoid species, and during SPB epidemics *Ips* bark beetles may compete as alternate hosts for SPB parasitoids. Although SPB parasitoids are not host-specific, they do prefer to oviposit on the host bark beetle species and host tree species from which they emerged (Berisford 1974b, Kudon and Berisford 1980). A model describing possible host choice and patterns of resource use during shifting levels of SPB and *Ips* abundance in forest stands has been proposed and is illustrated by Berisford, chapter 8.

28.5. RESEARCH NEEDS

Considerable research has been done that strongly implies parasitism, predation, and competition are important causes of mortality to the SPB throughout all life stages and may alter the trajectory of population growth within infestations and on a wider scale across

landscapes. Field-based studies during all phases of bark beetle population cycles, from endemic to epidemic, coupled with laboratory experiments and systems modeling are still needed to confirm the roles and impact of naturally occurring biological control in SPB population dynamics.

A further need is for area-wide assessment of SPB populations. Sampling of bark beetles and their natural enemy populations has been accomplished in individual infestations (Stephen and Taha 1976), but during epidemic SPB infestations field experience suggests that movement of adult beetles among infestations occurs (F.M. Stephen and L.E. Browne unpublished data), and that the only way to adequately assess manipulation of natural enemies is to evaluate total populations of the SPB over a wide area. If, for example, parasitoids are important in killing a significant number of beetles in a single infestation but immigration of SPB adults from nearby infestations occurs, it may swamp the effects of manipulation. The costs of field-based sampling programs are high and the efforts involved great, but this type of field assessment must be supported if we are to understand these interactions sufficiently to take full advantage of this naturally occurring biological control.

Long-term studies of bark beetle population dynamics are needed, and bark beetle natural enemies and associates should be included

Table 28.2—Results of parasitoid foraging tests with Eliminate®. Aerial application, by helicopter, of 8 L. Eliminate® on day zero to foliage of tree crowns in Alabama SPB infestation. Parasitoids collected on bark surface of SPB-infested trees containing late-stage immatures on the day of treatment and for 4 subsequent days. Dissections were made to confirm Eliminate® feeding.

Day of treatment	SPB attacks/dm ²	SPB eggs/dm ²
0	48	0
1	161	75
2	157	76
3	143	78
4	82	61

in these long-term efforts. There are too few examples of individual research efforts that address population dynamics of bark beetles and associates during endemic/epidemic population levels and the transition phases between them. Research relating seasonal phenology of both beetles and their natural enemies should be coupled with tracking infestations through low-level, endemic phases, and on to increasing and epidemic outbreaks and subsequent decline. Studies which target natural enemy biology, behavior, and density must not be conducted in isolation, but rather be related clearly to population dynamics of the bark beetles upon which they are dependent.