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Parasitoids of the Southern Pine Beetle

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Abstract

Hymenopterous parasitoids make up a significant portion of the natural enemy complex associated with the southern pine beetle (SPB). Collectively, parasitoids can affect the growth of individual SPB infestations and area populations by reducing the survival rates of developing SPB larval/pupal broods. A substantial body of information on parasitoids has been accumulated, mostly during and after research supported by the Expanded Southern Pine Beetle Research and Applications Program (ESPBRAP) during the 1970s. The parasitoids most closely associated with the SPB have been identified, and a key to larvae of the most abundant species is available. The sequence of arrival of parasitoids at infested pines relative to SPB attack and brood development has been documented. Some chemical cues by which parasitoids locate trees infested with SPB broods that are in susceptible developmental stages have been determined. However, the precise mechanism by which parasitoids locate specific hosts beneath the bark has not been described, although it is thought to involve specific olfactory cues. Factors that affect parasitoid efficacy such as host density and bark thickness have been quantified, and the overall contribution of parasitoids to natural enemy impact has been estimated and incorporated into population growth models.

8.1. INTRODUCTION

The southern pine beetle (*Dendroctonus frontalis* Zimmermann) (SPB) is attacked by a number of parasitoids that directly affect developing SPB broods and reduce numbers of emerging adults. Because the SPB is difficult and expensive to control once infestations develop, there have been a number of studies on SPB parasitoids and other natural control agents that detail life histories, impact, and so forth, and provide information to help assess the potential for integrating this natural control into forest management programs. The development of integrated suppression tactics will require an understanding of the life processes of the beetle and its important associates such as predators, parasitoids, and competitors. Although the existence of SPB parasitoids has been known since the beetle was first studied in the late 1800s, indepth inquiries mostly began during investigations supported by the Expanded Southern Pine Beetle Research and Applications Program (ESPBRAP) during the 1970s (Thatcher and others 1980).

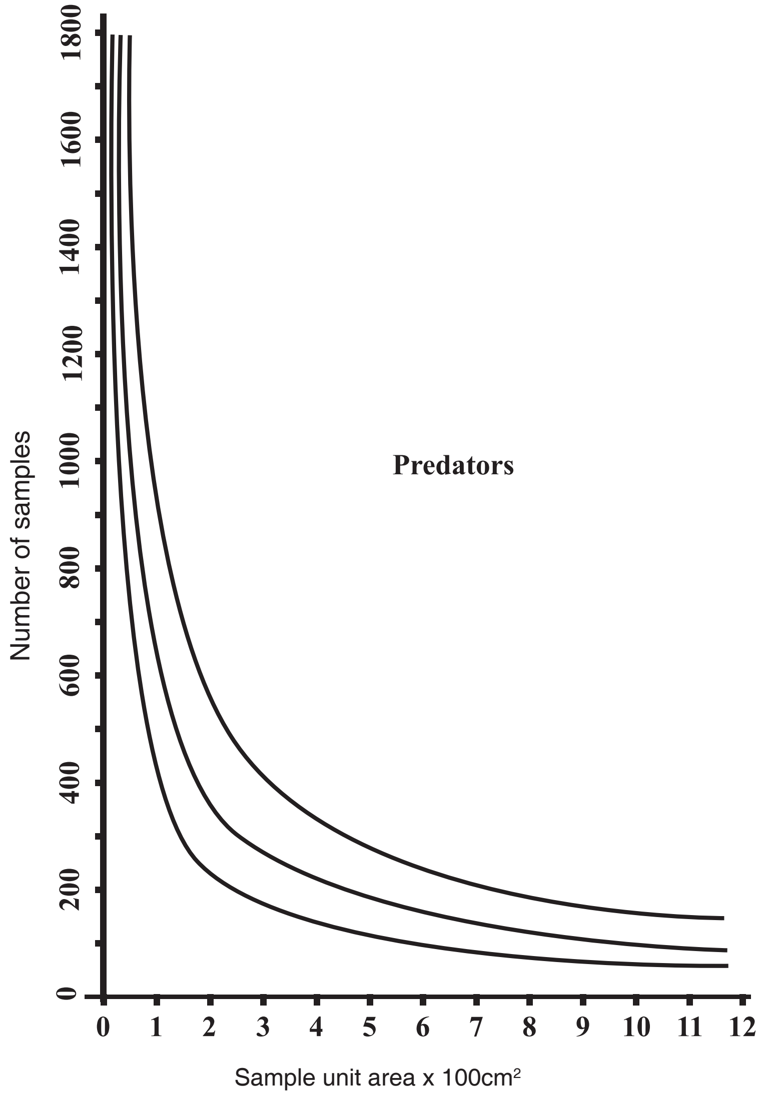

Figure 8.1—Number of samples and size of the sample unit needed to estimate the density of SPB predators. (illustration from Stephen and Taha 1976)

Studies of SPB natural enemies prior to ESPBRAP dealt primarily with compiled lists of SPB associates, usually based on collections of arthropods reared from bolts or bark excised from SPB-infested trees. Most of the attention was focused on insects, mites, and nematodes. The known or suspected roles for associated arthropods and other organisms were usually included (Coulson and others 1972, Dixon and Osgood 1961, Franklin 1969, Moore 1972, Moser and Roton 1971, Overgaard 1968, Thatcher 1960). However, the individual or combined impacts and interactions of these associates were generally unknown. Some studies supported by ESPBRAP were oriented toward determination of the specific roles and impacts of associates, particularly parasitoids and predators. This type of information was considered to be essential for the development of realistic SPB population models that can detect and/or forecast population trends, and to implement appropriate control strategies.

Other insects are among the principal natural enemies of the SPB. Some studies have identified these mortality agents and described their general biologies, plus seasonal, geographic, and within-tree distributions. Other reports concentrate on one or a few species. Dixon and Payne (1979b, 1980), Gargiullo and Berisford (1981) and Hain and McClelland (1979) provided information on SPB associates attracted to infested trees and included data on numbers and their temporal and spatial distributions. An illustrated guide to insect associates of the SPB was developed by Goyer and others (1980). The guide includes color photographs and distinguishing characteristics of each insect. With this manual, individuals with minimal training in entomology can identify common SPB associates, including parasitoids. Stephen and Taha (1976) devised a sampling system for estimating numbers of natural enemies. The system describes a sampling protocol and includes curves for estimating numbers of samples and sample sizes for various statistical confidence levels (Figure 8.1).

8.2. PARASITOIDS VS. PREDATORS AND PARASITES

Parasitoids differ from predators in that parasitoids are more intimately associated with their host. Whereas predators are usually larger than their prey and feed as adults and/or immature stages on several different hosts during their lifetime (a one-meal association), parasitoids are usually only slightly smaller than their hosts and normally develop from egg to adult on a single host, ultimately killing the host (a lifetime association). Parasites, on the other hand, are usually much smaller than their hosts and do not necessarily kill the host in order to survive.

8.3. THE PARASITOID COMPLEX ASSOCIATED WITH SPB

Parasitoids known to attack the SPB are shown in Table 8.1. Some parasitoids are somewhat host-specific in that they attack only one species or a group of closely related species with similar habits. However, only a few host-specific parasitoids are known for the SPB, and most will accept other bark beetle hosts.

The most common SPB parasitoids frequently attack, or will at least accept, other bark beetle or ambrosia beetle species (Bushing 1965, Dixon and Osgood 1961, Thatcher 1960). Many parasitoids of SPB also attack one or more species of *Ips* bark beetles that are often associated with the SPB (Berisford 1974b; Berisford and Dahlsten 1989; Berisford and others 1970, 1971; Kudon and Berisford 1980). Parasitism of more than one bark beetle species is not surprising since one or more *Ips* spp. are often found in trees infested by the SPB.

8.4. IDENTIFICATION OF PARASITOIDS

The more common parasitoids are illustrated in an SPB associates identification guide (Goyer and others 1980). In addition, Finger and Goyer (1978) provided descriptions of the mature larvae of the most common hymenopterous parasitoids of the SPB and included a key for identifying larvae and adults (Table 8.2).

Table 8.1—Confirmed and suspected parasitoids of the southern pine beetle

Hymenoptera	
Braconidae	*Atanycolus comosifrons* Shenefelt
	Atanycolus ulmicola (Vier.)
	Cenocoelius nigrisoma (Rohwer)
	Cenocoelius sp.
	Coeloides pissodis (Ashm.)
	Compyloneurus movoritus (Cress.)
	Dendrosoter sulcatus Mues.
	Doryctes sp.
	Heterospilus sp.
	Meteorus hypophloei Cushman
	Spathius canadensis Ashm.
	Spathius pallidus Ashm.
	Vipio rugator (Say)
Ichneumondiae	*Cremastus* sp.
	sp. (undetermined)
Eupelmidae	*Arachnophaga* sp.
	Eupelmus cyaniceps cyaniceps (Ashm.)
	Lutnes sp.
Torymidae	*Liodontomerus* sp.
	Lochites sp.
	Roptrocerus eccoptogastri (Ratz.)
	Roptrocerus xylophagorum Ratz.
	Roptrocerus sp.
Pteromalidae	*Dinotiscus (=Cecidostiba) dendroctoni* (Ashm.)
	Heydenia unica Cook & Davis
	Rhopalicus pulchripennis (Crawford)
Eurytomidae	*Eurytoma cleri* (Ashm.)
	Eurytoma tomici Ashm.
	Eurytoma sp.
Scelionidae	*Gyron* sp.
	Idris sp.
	Leptoteleia sp.
	Probaryconus heidemanni Ashm.
	Telenonus podisi Ashm.
Bethylidae	*Parasierola* sp.

Table 8.2—Key to the final instar larvae of the major parasitoids of the southern pine beetle (from Finger and Goyer 1978)

1’	Body with some setae but without microspines; head with few if any sclerites; spiracles on segments 2-10.	4
2	Labial sclerite very thick and rounded, often with slight projection on ventral surface and flat on dorsal surface between arms; silk orifice on wide oval sclerite.	*Dendrosoter sulcatus* (figs. 1B, 2B, 3B)
2’	Labial sclerite not as above.	3
3	Thickness of ventral part of labial sclerite about two times as wide as where dorsal arms start; area inside labial sclerite more circular than ovoid; silk orifice forming a straight line (figs. 1A, 2A, 3A) .	*Coeloides pissodis*
3’	Thickness of ventral part of labial sclerite at least three times as thick as where arms start; area inside labial sclerite more ovoid; silk orifice often with slight “V” in middle (figs. 1C, 2C, 3C).	*Spathius pallidus*
4	Head with very long setae; stalk of spiracle with over 20 chambers (figs. 1D, 2E, 3D).	*Heydenia unica*
4’	Head with short setae; stalk of spiracle with less than 20 chambers.	5
5	Stalk of spiracle with less than nine chambers, each decreasing in size from the atrium, forming a continuous funnel-shaped spiracle (figs. 2F, 3E).	*Dinotiscus dendroctoni*
5’	Stalk of spiracle with more than nine chambers, only first three chambers and atrium forming enlarged club-shaped structure (fig. 2G).	*Roptrocerus eccoptogastri*

8.5. PARASITOID ATTACK BEHAVIOR AND HOST LOCATION

Adult parasitoids are attracted to a combination of insect- and tree host-produced odors to locate trees infested with advanced SPB larval brood stages (Camors and Payne 1973).

8.5.1. Parasitoid Responses to SPB-Associated Chemicals

The responses of parasitoids to beetle and/or host chemicals released from SPB-infested trees have received some attention. Camors and Payne (1972) showed that *Heydenia unica* responds to host tree terpenes and a component of the SPB aggregation pheromone. Dixon and Payne (1980) caught four species of SPB parasitoids in traps baited with various combinations of SPB- and tree-produced chemicals, plus pine bolts artificially infested with SPB females. Although no host larvae are present at the time of SPB mass attack, they (Dixon and Payne 1980) suggested that the compounds may serve to concentrate parasitoids in areas where suitable host life stages would soon become available. Kudon and Berisford (1981a) developed an olfactometer to evaluate the response of SPB parasitoids to insect- and tree-produced odors. Olfactometer trials can aid in preliminary screening of chemicals that may attract parasitoids. Final determinations of attractancy must be made in the field, however.

Sullivan and others (1997) identified chemicals from loblolly pines infested with SPB larvae, including many of the chemicals involved in parasitoid attraction. They subsequently showed that different species of parasitoids are attracted to different SPB developmental stages or different combinations of chemicals (Figure 8.2) (Sullivan and others 2003). The precise mechanism by which female parasitoids locate and attack hosts beneath the bark is still unknown. Some experimental evidence from studies of other bark beetles suggests that they may orient to physical cues such as sound (Ryan and Rudinsky 1962) or heat (Richerson and Borden 1972). However, a considerable body of evidence shows that SPB parasitoids and many species that attack other bark beetles use olfactory cues that are closely associated with developing broods of larvae (Birgersson and others 1992; Pettersson 2001a, 2001b; Pettersson and others 2000, 2001; Sullivan and others 1997, 2000). Female parasitoids generally oviposit through the bark onto 3rd or 4th instar SPB larvae and occasionally, onto pupae (Berisford and Dahlsten 1989). Most parasitoids apparently sting their hosts to immobilize and preserve them before depositing eggs. One of the most common SPB parasitoids, *Roptrocerus xylophagorum* Ratzeburg (Hymenoptera: Torymidae), enters egg galleries through beetle entrance or ventilation holes and oviposits onto nearby beetle larvae through the sides of the egg galleries. Another parasitoid, *Heydenia unica* Cook and Davis (Hymenoptera: Pteromalidae), arrives at SPB or *Ips*-infested trees during the beetle's attack stage, possibly to mate, since no late instar larvae would be available for oviposition at that time (Camors and Payne 1972, Dixon and Payne 1979). Most of the parasitoids associated with the SPB arrive at infested trees when large numbers of acceptable hosts are available (Berisford and Franklin 1969, Camors and Payne 1973, Dixon and Payne 1979b). Figure 8.2 shows arrival patterns of some common parasitoids relative to SPB brood development.

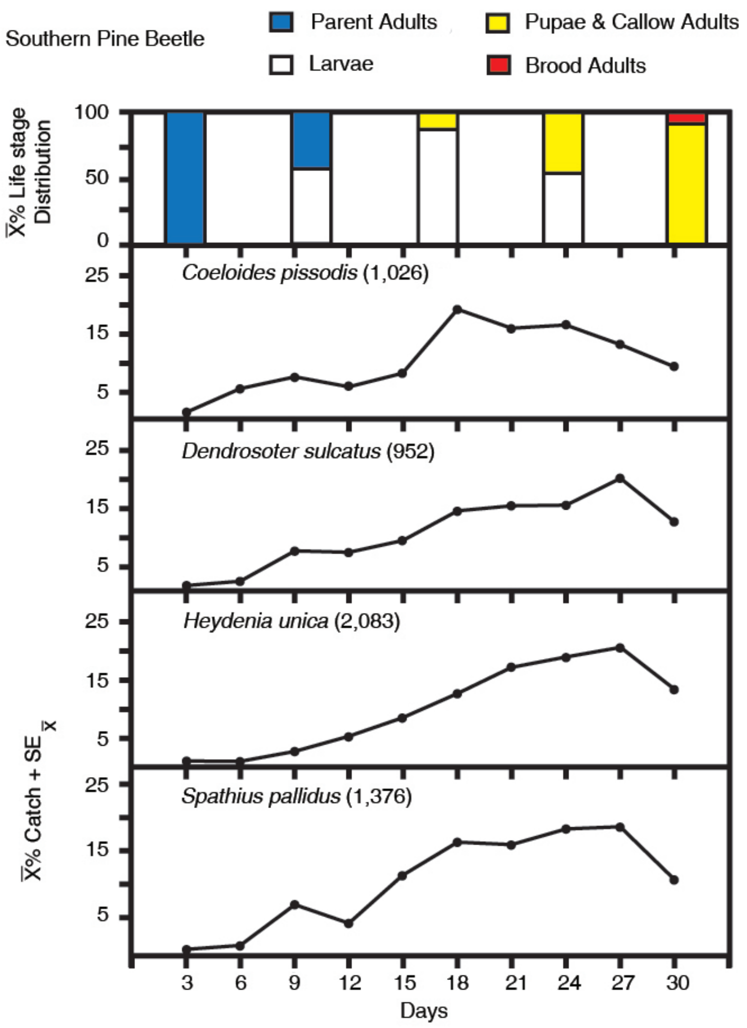

Figure 8.2—Sequence of arrivals of the SPB parasitoids: *Coeloides pissodis*, *Dendrosoter sulcatus, Heydenia unica*, and *Spathius pallidus*, in relation to SPB brood development. Numbers trapped are shown in parentheses. (illustration from Dixon and Payne 1979b)

8.6. FACTORS INFLUENCING PARASITOID IMPACT

Parasitoids in SPB-infested trees may be strongly influenced by bark beetle host brood density and bark thickness (Goyer and Finger 1980, Gargiullo and Berisford 1981). Regressions of numbers of parasitoids against SPB brood density for different bark thickness categories show the relative effect of each factor on different parasitoid species. Figure 8.3 shows regressions calculated for two common SPB braconid parasitoids, *Spathius pallidus* Ashmead and *Coeloides pissodis* Ashmead, both of which oviposit through the bark.

Parasitism by the most common hymenopterous parasitoids—*Heydenia unica* Cook and Davis (Pteromalidae), *Cecidostiba dendroctoni* Ashmead (Pteromalidae), *Dendrosoter sulcatus* Musebeck (Braconidae), *Coeloides pissodis* (Ashmead) (Braconidae), *Eurytoma* spp. (Eurytomidae), *Rhopalicus* spp. (Pteromalidae), and *Spathius pallidus* Ashmead (Braconidae)—increases as tree host bark becomes thinner (Gargiullo and Berisford 1981). *Roptrocerus xylophagorum* (Ratzeburg) (Torymidae) is strongly affected by bark thickness even though it enters SPB egg galleries to locate hosts. Most of the parasitoid species reach maximum parasitism rates at intermediate host densities (Figure 8.3), with the exception of *Eurytoma* spp. However, *Spathius pallidus* is apparently unaffected by host density, and *R. xylophagorum* becomes increasingly abundant as host density increases and bark thickness decreases. *R. xylophagorum* is the only parasitoid that shows a significant interaction with both bark thickness and SPB brood density (Gargiullo and Berisford 1981).

8.7. PARASITOID POPULATION FLUCTUATION

Hain and McClelland (1979) reported quantitative and qualitative differences in

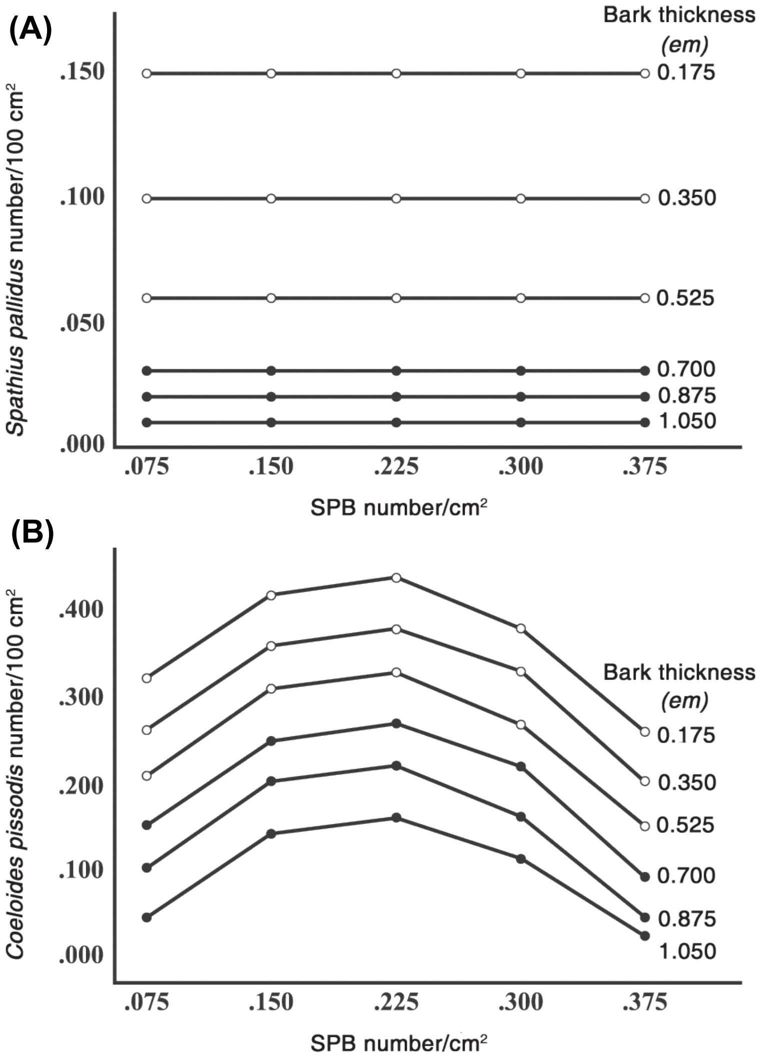

Figure 8.3—Numbers of the parasitoids (A) *Spathius pallidus* Ashmead and (B) *Coeloides pissodis* Ashmead relative to SPB host density and bark thickness. (illustration from Gargiullo and Berisford 1981)

natural enemy populations at three locations in North Carolina (Figure 8.4). A similar study in Louisiana found that natural enemy population differences were generally correlated with SPB brood adult densities (Goyer and Finger 1980). In Louisiana, highest numbers of parasitoids occurred during April to June, with a second peak in August. Lowest parasitoid populations were found in the fall and winter, when SPB populations were also low (Figure 8.5). Similar seasonal patterns were observed in Texas (Stein and Coster 1977).

Many of the parasitoids that attack SPB also attack other bark beetles, as noted previously. In fact, the parasitoid complexes associated with *Ips avulsus* Eichoff, *I. grandicollis* Eichoff, *I. calligraphus* (Germar), *I. pini* Say, and the eastern juniper bark beetle *Phloeosinus dentatus* (Say) share with the SPB three of the most common species—*Roptrocerus xylophagorum (= eccoptogastri), Heydenia unica,* and *Coeloides pissodis* (Berisford 1974b, 1974a; Berisford and Franklin 1971; Berisford and others 1970, 1971).

It has been assumed in the past that SPB parasitoids that are not host-specific would prefer the SPB even if other hosts were available, and that other bark beetles (e.g., *Ips* spp.) would serve as reservoir hosts when SPB populations were low or absent. However, Berisford (1974b) found that when both SPB and *Ips* spp. were available, parasitism did not readily shift from one species to the other, regardless of the relative abundance. This suggests that some degree of host preference may occur, at least temporarily, among parasitoids that are not considered to be host-specific. Kudon and Berisford (1980) found that when adult parasitoids were reared from SPB-infested logs and provided with simultaneous choices of logs containing late-instar larvae of SPB or *Ips* and SPB or Eastern juniper beetle (*P. dentatus*), a high percentage of the parasitoids selected logs with SPB (Figures 8.6A and B). Conversely, when parasitoids were reared from *Ips* or *P. dentatus*, they showed a preference for those species over the SPB (i. e., the hosts on which they developed as larvae) (Figures 8.6C and D). The preferences were accentuated when parasitoids could simultaneously select both beetle hosts (e.g., SPB vs. *P. dentatus*) and tree hosts (pine vs. cedar) instead of beetle hosts only (e.g., SPB vs. *Ips*) with both species infesting loblolly pine. Thus, it appears that the parasitoids, although not host-specific, may be at least temporarily entrained to initially select the host on which they were reared. This phenomenon appears to be a manifestation of Hopkins (1916) Host-Selection Principle. However, Hopkins' principle applies to phytophagous insects, and no references were made to predators or parasitoids.

8.8. IDENTIFICATION OF PREVIOUS HOSTS OF PARASITOIDS

Since several SPB parasitoids are known to attack other bark beetles, knowledge of the identity of previous hosts of parasitoids or predators that respond to SPB-infested trees would help to determine if other bark beetles are acting as alternate, competing, and/or reservoir hosts. Miller and others (1979) and Miller (1979) utilized immunodiffusion and immunoelectrophoresis techniques to produce antisera that were specific for the SPB and some of its bark beetle associates (e.g., *Ips* spp. and black turpentine beetle). These techniques were used to help determine the prey of SPB predators such as the clerid beetle *Thanasimus dubius* and may provide a means to estimate the number of prey consumed. Kudon and Berisford (1981b) found that the fatty acid composition of parasitoids reared from SPB and some if its common associates closely matched the fatty acid composition of their beetle host(s). Therefore, the host origin of a single parasitoid could be determined, provided that the host's lipid profile has already been established. Figures 8.7A and B shows the similarity between the lipid profile of the SPB and a parasitoid, *Heydenia unica*, reared on SPB. Figures 8.7C and D shows lipid profiles for *I. calligraphus* and *H. unica* that had been reared on *I. calligraphus*. The technique of comparing lipid profiles could also help to determine predator hosts, particularly if they feed on a single prey species. When *Thanasimus dubius* was fed either on SPB or the cowpea weevil (*Callosobruchus maculatus* [Fabricius]), the lipid profile of *T. dubius* reared on SPB matched the host profile well, but although the profile of clerids that fed on the weevil (an unnatural host) differs from that of clerids that fed on the SPB, it did not match the weevil profile. This technique, however, appears to need some refinement. The host-induced preferences of parasitoids may be a factor affecting the overall impact of the parasitoid complex on SPB populations. Although relatively high populations of *Ips* spp. usually present in logging slash, damaged trees, lightning strikes, and so forth, can support substantial parasitoid populations, *Ips* may not be a particularly good reservoir for SPB parasitoids in regard to biological control of the SPB, partially due to induced host preferences. On the other hand, the parasitoids are apparently able to attack other hosts if the preferred host is not readily available, and high *Ips* populations may maintain parasitoids for eventual attacks on SPB.

At this point, we do not understand the mechanism that determines how parasitoids switch from one host to another. If we assume that temporary host-induced preferences will create a lag in acceptance of nonpreferred hosts,

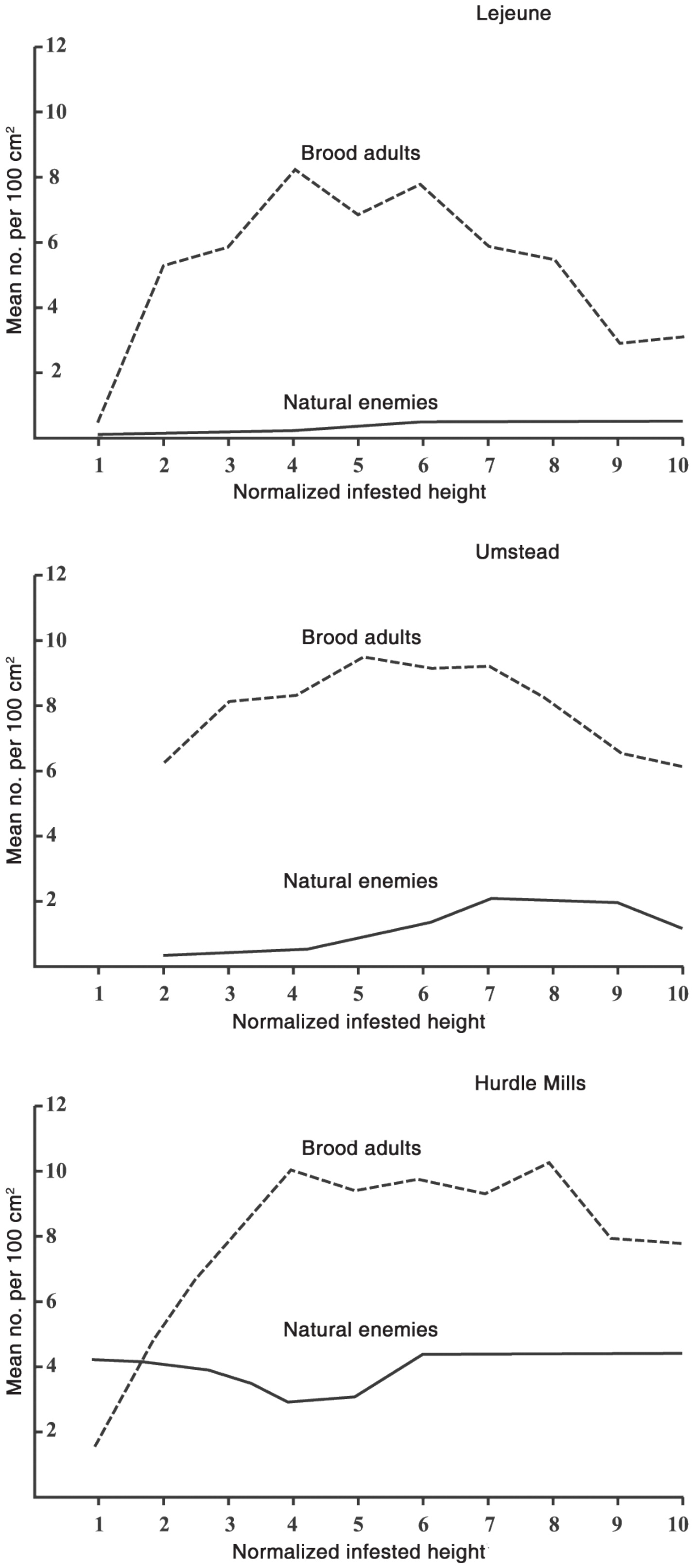

Figure 8.4—Numbers of natural enemies, including parasitoids, relative to numbers of SPB brood adults at three locations in North Carolina. (illustration from Hain and McClelland 1979)

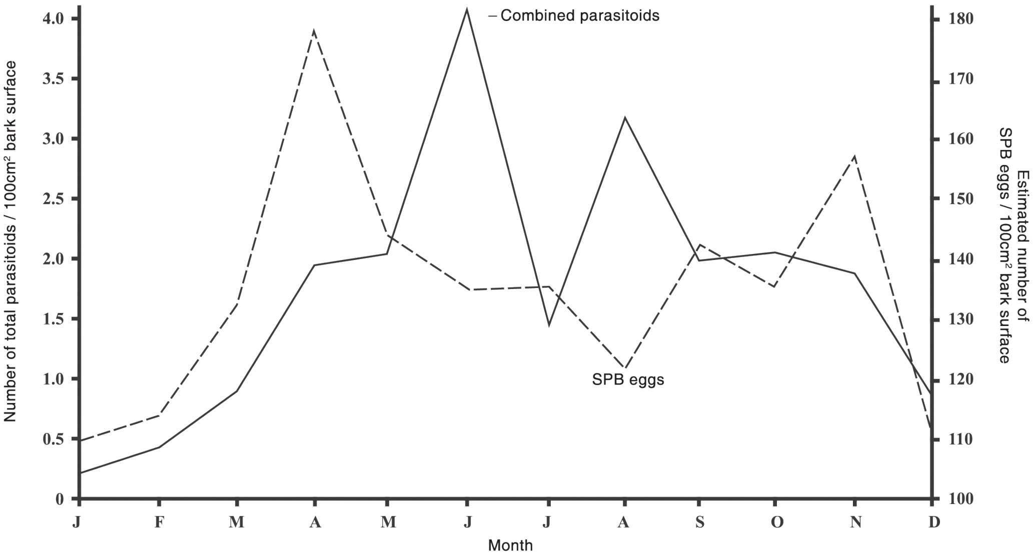

Figure 8.5—Seasonal abundance of parasitoids relative to numbers of SPB eggs in SPB-infested trees in Louisiana. (illustration from Goyer and Finger 1980)

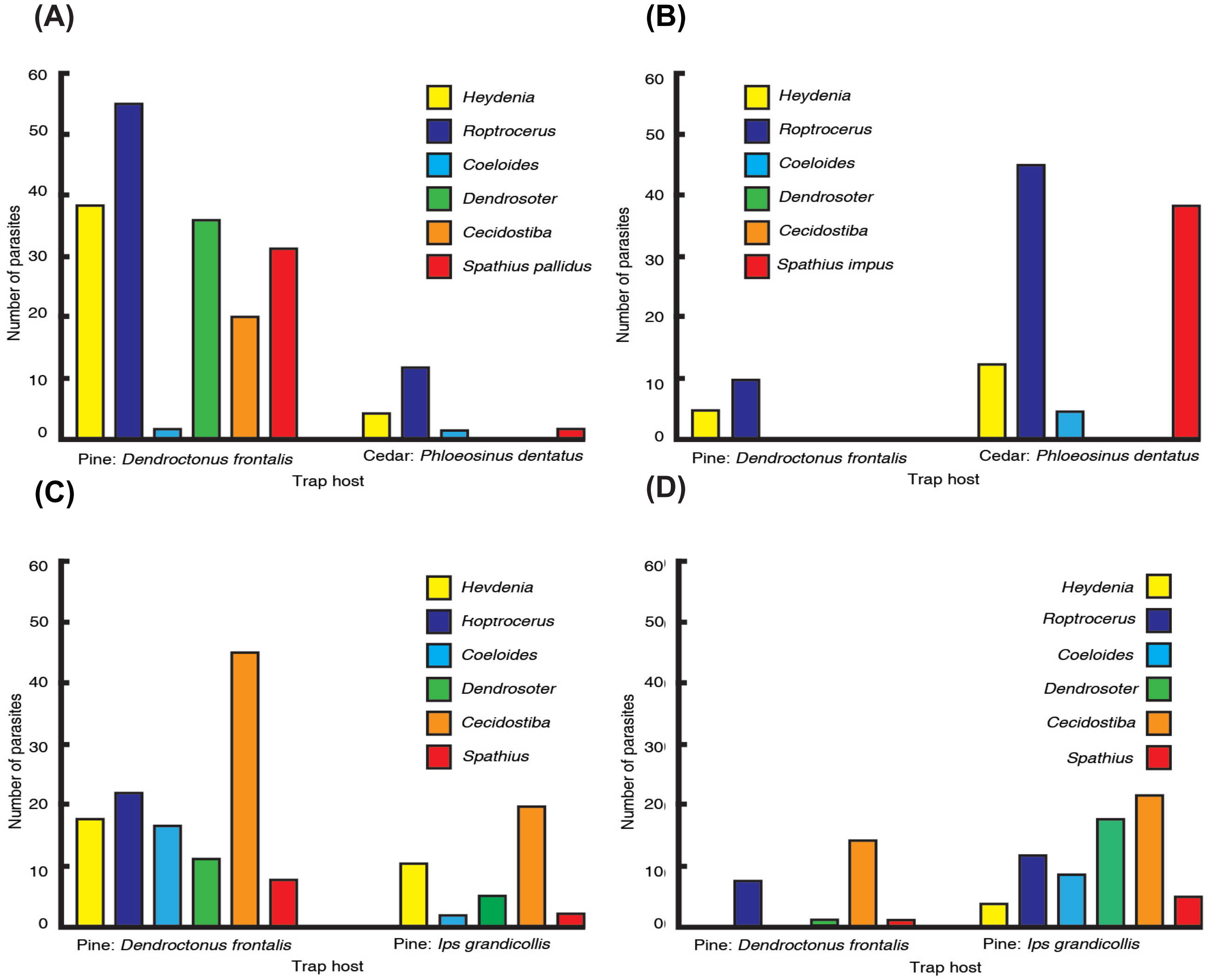

Figure 8.6—Parasitoids reared from (A) SPB and (B) *Phloeosinus dentatus* presented with simultaneous choices of logs infested with SPB or *Phloeosinus dentatus*. Parasitoids reared from (C) SPB and (D) *Ips grandicollis* presented with simultaneous choices of logs infested with SPB or *Ips grandicollis*. (illustration from Kudon and Berisford 1981b)

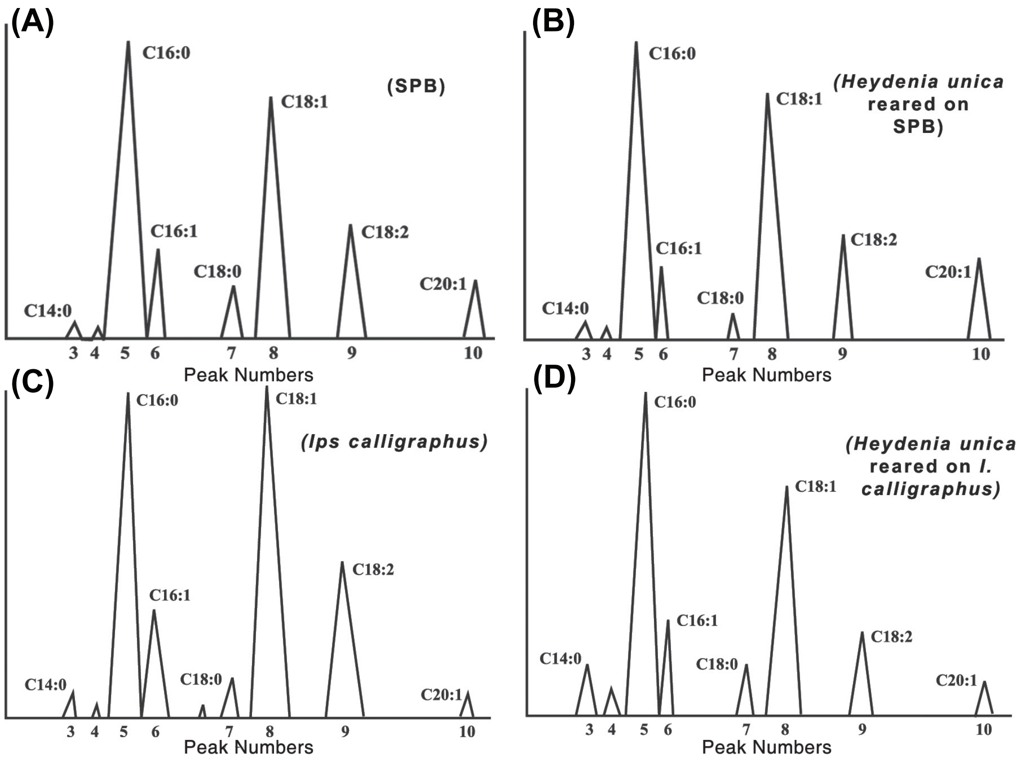

Figure 8.7—Lipid profile of (A) SPB and (B) a parasitoid, *Heydenia unica*, that had been reared on SPB. Lipid profile of (C) *Ips calligraphus* and (D) the same *Heydenia unica* that had been reared on *I. calligraphus*. (illustration from Kudon and Berisford 1980)

then potential SPB parasitism by parasitoids from *Ips* spp. might be reduced for at least one generation. A conceptual model of potential parasitoid-host interactions among SPB, *Ips*, and their common parasitoid complex has been proposed (Berisford 1980). The model assumes a relatively stable *Ips* population vs. fluctuating SPB populations and describes theoretical shifts of parasitoids among the beetle hosts as each host becomes more or less abundant relative to the other over time. During SPB epidemics, *Ips* populations will also increase since *Ips* spp. frequently attack SPB-infested trees. The relative populations, however, still fit the hypothesis of the model; i.e., that the relatively scarce host loses parasitoids to the relatively abundant one regardless of absolute populations (Figure 8.8).

The SPB and most of its associated bark beetle competitors produce aggregation pheromones (Birch 1978), or they cause the release of attractive host compounds during initial attacks. Some bark beetles may use pheromones as species isolation mechanisms (Lanier and Wood 1975, Wood 1970). Birch and Wood (1975) and Byers and Wood (1981) demonstrated that two closely associated bark beetles may utilize reciprocal inhibition to avoid competing for the same food. These species may colonize the same tree but occupy different parts due to inhibition of attacks by beetles that arrive after the species that makes the initial successful attacks. Predators of the SPB, particularly clerid beetles, respond to aggregation pheromones where adults feed on arriving SPB adults and females subsequently oviposit on the trees. Other natural enemies, including parasitoids, may use SPB aggregation or sex pheromones as kairomones to locate potential hosts. Birch and others (1980) determined the response of different beetles to logs infested with various combinations of SPB, *I. avulsus*, *I. grandicollis*, and *I. calligraphus*. The first beetles to arrive were generally SPB if SPB females were present in experimental logs. Southern pine beetles did not respond, however, to logs infested with any *Ips* species. Response by *I. avulsus* and *I. grandicollis* was enhanced when SPB plus males of either of the *Ips* spp. were present. The response of *I. avulsus* to its own attractant was also enhanced by the presence of *I. grandicollis*. This phenomenon was also reported by Hedden and others (1976). *Ips calligraphus* was inhibited by *I. avulsus*. Conversely, *I. avulsus* response was enhanced by the presence of *I. calligraphus*. Reciprocal inhibition occurred between the SPB and *I. grandicollis*. The olfactory interactions during attack on new host material resulted in rapid colonization of trees with minimal competition among different bark beetle species.

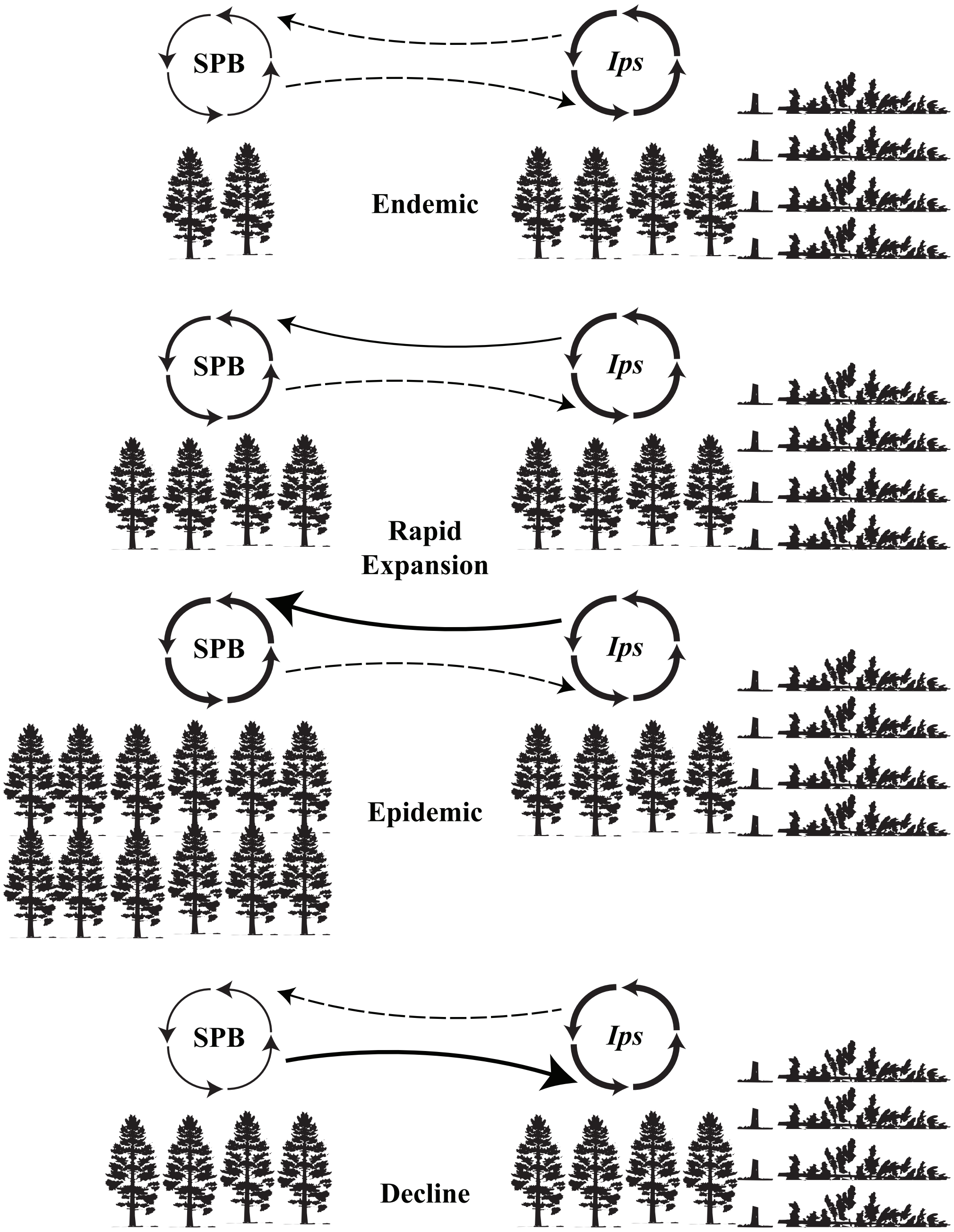

Figure 8.8—Theoretical model of parasitoid shifts from relatively scarce hosts to more abundant hosts (*Ips* spp. and SPB) during the buildup of SPB from endemic to epidemic levels and the subsequent decline to endemic populations. (illustration from Berisford 1980)

8.9. IMPACT OF PARASITOIDS ON SPB BROODS

Mortality of SPB broods caused by parasitoids and predators has been determined by excluding them from SPB-infested trees during specific periods of SPB brood development (Linit and Stephen 1983). More than half of the natural enemies, mostly predators, arrived during the first week of SPB development. Since predators are presumed to consume more than one host, highest SPB mortality probably occurs due to their activities. Total mortality caused by parasitoids and predators during SPB brood development was estimated to be about 15 percent. However, parasitism of *Ips grandicollis* in Australia by *Roptrocerus xylophagorum* averaged 17 percent (Berisford and Dahlsten 1989), suggesting that individual species of parasitoids may be capable of parasitism rates higher than observed where they are in competition with other parasitoids and predators. Obviously, any evaluations of SPB population dynamics should consider the role and impact of parasitoids and predators.

Stephen and others (1989) developed SPB population dynamics models that allow testing of the role of natural enemies in the regulation of SPB populations. These models make it possible to simulate the impact of natural enemies on SPB population growth as affected by factors such as host tree species and season of the year. Figures 8.9A and B shows a simulation of SPB population growth in loblolly and shortleaf pine stands. The growth rate of SPB populations in the absence of natural enemies is rapid with either tree host, but substantially higher in shortleaf pine, which normally has thinner bark than loblolly pine. This suggests that parasitoids are likely to contribute more to SPB mortality on shortleaf pine since they are known to be more effective on trees with thin bark (Gargiullo and Berisford 1981). Simulations of SPB spot growth, starting at different times of the year, show that natural enemies are particularly important in regulating SPB spot growth in early summer (June). Natural enemies appear to be less effective in late summer and early fall, when simulated spot growth trends were similar with or without natural enemies.

8.10. ROLE OF PARASITOIDS IN SPB MANAGEMENT

Although natural enemies are presumed to regulate SPB populations at endemic levels, it is obvious that they cannot prevent periodic outbreaks in areas with large concentrations of highly susceptible trees, particularly overstocked plantations. Parasitoids may be less effective in dense pine plantations due to a lack of plant diversity, particularly flowering plants that provide nectar and pollen as energy sources for foraging adults (Stephen and others 1997). It may be possible to increase parasitoid impact on developing SPB broods by providing a nectar substitute (Stephen and Browne 2000). There is good experimental evidence that supplemental food can increase parasitoid adult longevity and egg production (Mathews and Stephen 1997). Future SPB management plans will likely acknowledge the contribution of hymenopterous parasitoids to SPB population regulation and attempt to conserve or perhaps augment this source of natural control.

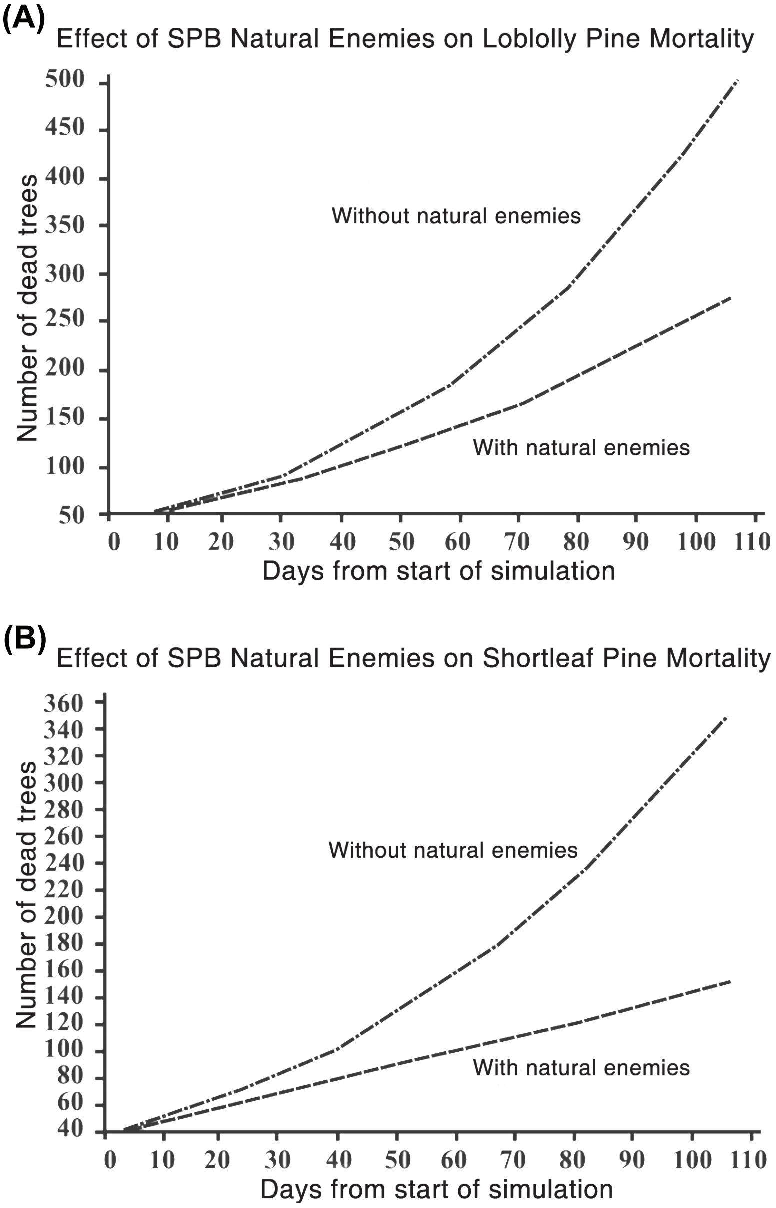

Figure 8.9—Predicted effect of SPB natural enemies on (A) loblolly and (B) shortleaf pine mortality. (redrawn from Berisford 1980)