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Predators of the Southern Pine Beetle

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Abstract

This chapter of the Southern Pine Beetle II reviews the overall influence of predators on southern pine beetle (SPB) population dynamics, as well as recent research on specific predators such as the clerid beetle *Thanasimus dubius*. Several lines of evidence suggest that predators and other natural enemies generate significant SPB mortality that contributes to outbreak collapse, likely operating with a time delay and so causing delayed density-dependence. The predators that seem most likely to significantly impact SPB are *T. dubius*, the dolichopodid fly *Medetera bistriata*, and several woodpecker species. The chemical ecology of both *T. dubius* and *M. bistriata* indicates they are well synchronized with mass attack by SPB. The prolonged development of *T. dubius* under field conditions, however, suggests it is a component of the delayed density-dependence seen in SPB. It is recommended that trees vacated by SPB be left intact during control operations because these often contain immature *T. dubius* 1-2 years after SPB attack, and also provide foraging and nesting opportunities for woodpeckers. Current research is exploring methods for mass-rearing *T. dubius* using an artificial diet, for potential use as a control tactic.

10.1. INTRODUCTION

Predators and other natural enemies are important factors in the population dynamics of many insect pests, and southern pine beetle (*Dendroctonus frontalis* Zimmermann) (SPB) is no exception. In this chapter of the Southern Pine Beetle II, I review evidence of the overall impact of predators on SPB and their potential effects on SPB population dynamics. For several common predators, I also summarize recent research on their life histories, chemical ecology, mortality inflicted on SPB, and dispersal behavior. For the majority of predator species, however, there is little information beyond that provided in a previous review (Berisford 1980).

10.2. IMPACT OF PREDATORS ON SPB

There are several lines of evidence suggesting that natural enemies, including predators, have a role in SPB dynamics and population regulation. One is that time-series analysis suggests that delayed density-dependence is an important factor in SPB population dynamics. In particular, Turchin and others (1991) analyzed a 30-year record of SPB activity in East Texas and found evidence for delayed density-dependence in SPB population growth. More recent analyses incorporating additional data also detected delayed density-dependence (Reeve and Turchin 2002) as well as a temperature effect (Friedenberg and others 2008). Because natural enemies often affect prey populations with a time delay, this provides circumstantial evidence that natural enemies affect SPB dynamics. In addition, a commonly used forecasting method employs a predator/prey ratio to predict SPB population trends, in particular the ratio of the clerid beetle *Thanasimus dubius* (see below) to SPB in trap catches (Billings 1988), further implying a role for natural enemies in SPB dynamics.

More direct evidence for the effect of natural enemies comes from exclusion studies. Linit and Stephen (1983) excluded natural enemies at various times after SPB attack using cages, and found that natural enemies arriving early in the attack (which would typically be predators) caused the greatest amount of mortality. Turchin and others (1999b) compared the survival rates of SPB brood in caged and uncaged trees during the course of an SPB outbreak. They observed a highly significant difference in survival rates 1 year after SPB populations reached peak levels, with brood survival approximately two times higher in the caged vs. exposed trees (Figure 10.1). This pattern suggests that natural enemies could be a component of the delayed density-dependence found in the time-series analyses, but does not identify the type of natural enemy, such as predators or parasitoids, much less the actual species involved. The most likely candidate appears to be *T. dubius*, however, because of its lengthy development time and probably substantial impact on SPB.

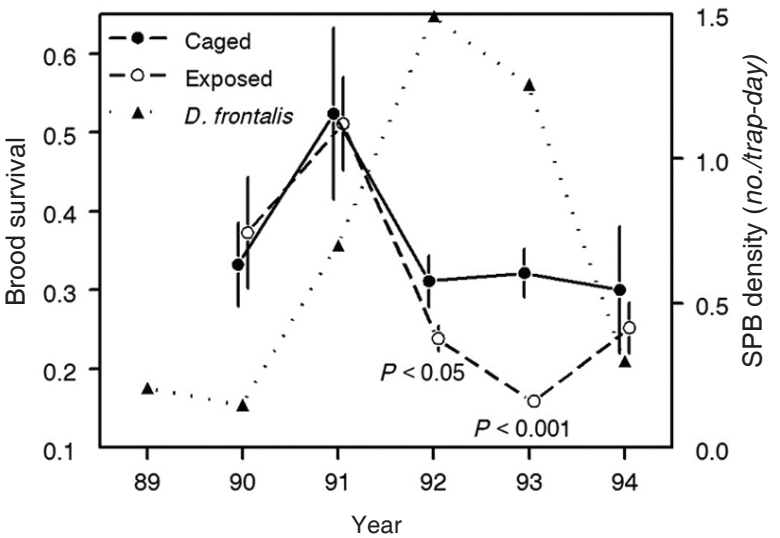

Figure 10.1—Survival of SPB brood (emerging adult density/egg density) for caged vs. exposed trees, during the course of an SPB outbreak. SPB densities were estimated using traps baited with frontalin and turpentine. A two-sample *t*-test was used to compare survival rates in caged vs. exposed trees.

10.3. SPECIFIC PREDATORS

This section summarizes information on the life histories, chemical ecology, dispersal behavior, and impact on SPB of selected predators, where such information is available. Predator species were chosen based on a known response to SPB pheromones, a significant impact on SPB or other bark beetles, and recent attention in the literature. One group excluded by these criteria was histerid beetles; although they appear to be important natural enemies of *Ips* bark beetles (Aukema and others 2004; Aukema and Raffa 2002, 2004), they do not respond to the SPB pheromone frontalin (Aukema and Raffa 2005). Many other predator species are listed for SPB (Berisford 1980, Moser and others 1971, Overgaard 1968), but little new information has been published.

10.3.1. *Thanasimus dubius* (Coleoptera: Cleridae)

Life History

The natural history of *Thanasimus dubius* (Coleoptera: Cleridae) has received the most attention among predators of SPB. Adult *T. dubius* locate trees undergoing mass attack by responding to the semiochemicals emitted by SPB and the host tree (see Chemical Ecology below). Adult *T. dubius* attack and consume the adult SPB (Figure 10.2) arriving on the bark surface during mass attack (Thatcher and Pickard 1966), although they have also been reported on trees where SPB brood adults are emerging (Clarke and Menard 2006). Oviposition occurs in crevices in the bark. The eggs hatch within a few days, and the larvae enter the tree, where they attack the immature stages of SPB within the phloem layer (Thatcher and Pickard 1966). The larvae make use of SPB galleries to move about and can also construct their own tunnels. They have also been observed crawling on the bark surface (Dix and Franklin 1977), presumably traveling between SPB galleries. The larvae reach a nonfeeding prepupal stage (Figure 10.3) at approximately the same time as SPB complete development, and then construct an oval chamber lined with a silvery-white material in the outer bark (Thatcher and Pickard 1966). Most of these chambers are located toward the base of the tree, 2-5 m above ground level (Mizell and Nebeker 1981). The combined prepupal and pupal stage is longer in duration than the egg and larval stages, with most of the time spent in the prepupal stage (Lawson and Morgan 1992, Nebeker and Purser 1980). For example, Lawson and Morgan (1992) reported mean durations of 7.2 ± 0.1 (SE) days for eggs, 41.9 ± 0.6 for larvae, 56.4 ± 1.0 for prepupae and pupae combined, and 50.1 ± 7.1 for adults, when reared at room temperature. However, the length of the prepupal period is extremely variable under field conditions. Reeve (2000) found that there were often several adult emergence periods for an infested tree, with most individuals emerging in spring or fall (Figure 10.4). The maximum adult emergence time observed was approximately 2 years after SPB attack. The pattern of emergence suggests that *T. dubius* has approximately two generations per year in the southern portion of its range, with some individuals taking much longer to complete development (Reeve 2000). Given that SPB has approximately six generations per year (Ungerer and others 1999), this implies a long time delay in the numerical response of *T. dubius* to fluctuations in SPB density, potentially making it a source of the delayed density-dependence found in SPB dynamics. A simple predator-prey model incorporating the life histories of SPB and *T. dubius*, including extended development times and a spring-fall

Figure 10.2—Adult *T. dubius* attacking an adult SPB on the bark surface. (photographer unknown)

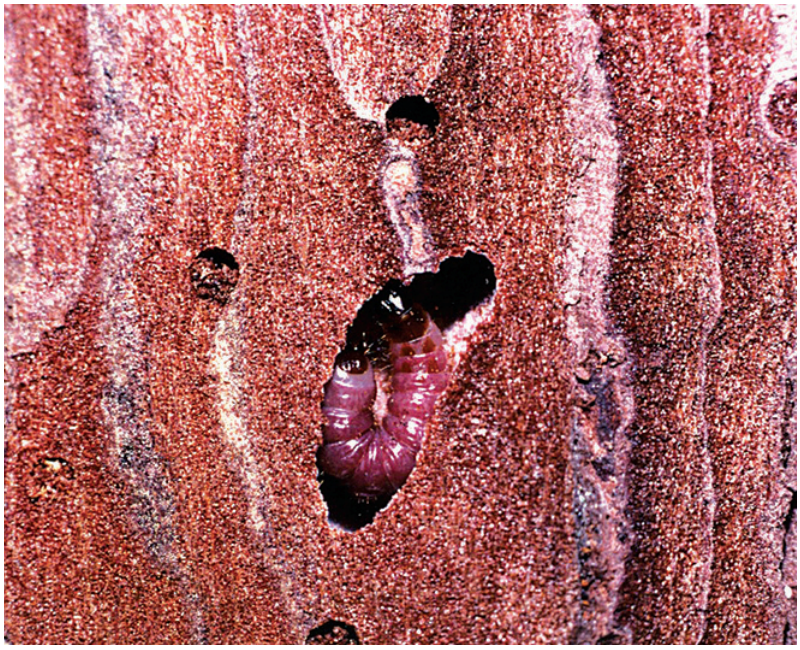

Figure 10.3—Prepupal *T. dubius* larva lying within a cell excavated in the outer bark. (photograph by Erich G. Vallery)

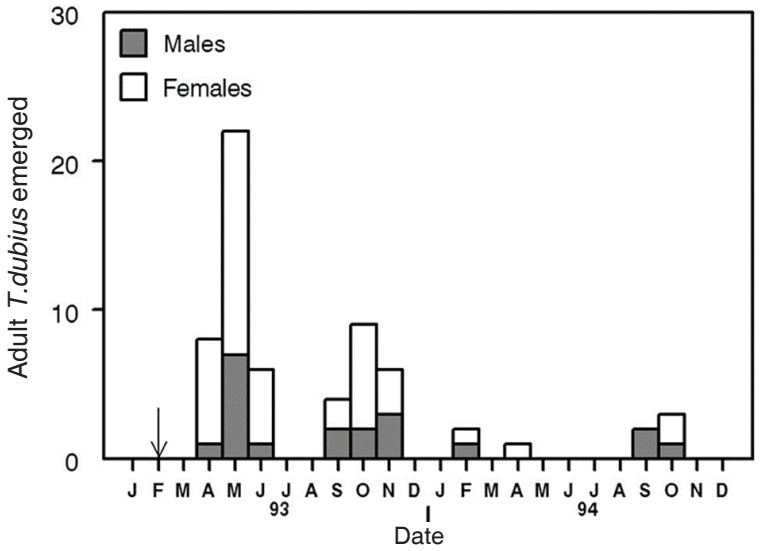

Figure 10.4—Numbers of emerging adult *T. dubius* from a host tree for which SPB emergence was complete in February 1993 (see arrow). The base of the tree was enclosed in a 1.5 m long emergence trap.

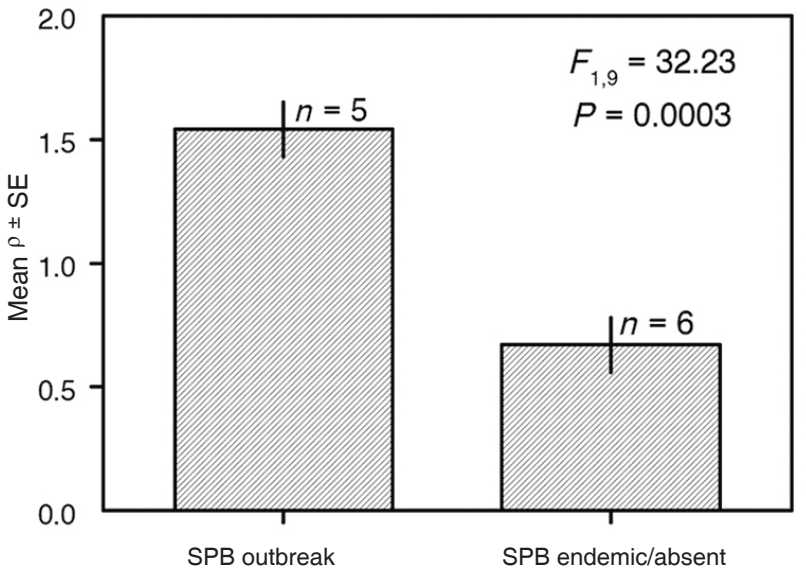

Figure 10.5—Mean values of the preference index ρ (± SE) comparing the response to frontalin vs. ipsdienol and ipsenol, for SPB outbreak sites vs. sites where SPB was endemic or absent. One-way ANOVA was used to test for differences in ρ across the two site types.

pattern of emergence, produced cycles similar in period to those sometimes observed in SPB (Reeve and Turchin 2002).

Chemical Ecology

It has long been recognized that adult *T. dubius* are attracted to trees undergoing mass attack by SPB, arriving shortly after the first attacks are initiated and continuing for several days thereafter in a pattern that matches arrival by SPB (Camors and Payne 1973, Dixon and Payne 1979a). This close synchronization occurs because *T. dubius* is strongly attracted to the SPB pheromone frontalin, with the response synergized by host tree volatiles such as -pinene that are generated by beetle damage (Billings 1985, Dixon and Payne 1980, Payne and others 1984, Vité and Williamson 1970). This predator is also attracted to the pheromones emitted by *Ips* bark beetles, such as ipsdienol and ipsenol, although the response to frontalin generally appears to be stronger (Aukema and Raffa 2005, Billings and Cameron 1984, Erbilgin and Raffa 2001, Haberkern and Raffa 2003, Herms and others 1991, Mizell and others 1984, Raffa 2001, Raffa and Klepzig 1989). Trapping studies have shown this predator is also sensitive to visual cues, with fewer insects trapped in white or yellow traps vs. black traps, similar to the pattern observed for SPB (Strom and Goyer 2001, Strom and others 1999).

This predator also shows a change in its preference for SPB vs. *Ips* pheromones as a function of SPB density, in a pattern that suggests switching in prey preference (Murdoch 1969, Murdoch and Oaten 1975). In particular, *T. dubius* shows a strong response to frontalin vs. ipsdienol and ipsenol at SPB outbreak sites, while the response is more even at sites where SPB are endemic or absent (Billings and Cameron 1984, Reeve and others 2009). This pattern was especially obvious in an analysis that combined the results from four studies that compared trap catches for frontalin vs. ipsdienol and ipsenol (Aukema and Raffa 2005, Billings 1985, Billings and Cameron 1984, Reeve and others 2009). For each site in the four studies, Reeve and others (2009) calculated a preference index of the form

$$\rho = \log_{10}(\overline{Y}_{FR}) - \log_{10}([\overline{Y}_{IS}+\overline{Y}_{ID}]/2) \quad (1)$$

where $\overline{Y}_{FR}$, $\overline{Y}_{ID}$ and $\overline{Y}_{IS}$ are the mean trap catches for treatments using frontalin, ipsdienol, and ipsenol. This metric is similar in form to the log response ratio used in meta-analysis (Hedges and others 1999). One-way ANOVA was used to compare this index between SPB outbreak sites vs. sites where SPB were either endemic or absent (Figure 10.5). There was a highly significant difference in preference between the two site types, with the preference for frontalin much higher at SPB outbreak sites. This corresponded to a 34.7 to 1 ratio of predators trapped with frontalin vs. ipsdienol and ipsenol at SPB outbreak sites, while the ratio

was only 4.7 to 1 at endemic or absent sites. This switching behavior should enhance the persistence of *T. dubius* populations when SPB are low, because their attraction to alternative prey would be higher under these conditions.

Impact on SPB

Both adult and larval *T. dubius* appear to cause appreciable mortality of SPB. Thatcher and Pickard (1966) first observed that *T. dubius* adults could reduce the number of adult SPB successfully attacking cut green logs in a laboratory setting. Reeve (1997) estimated the density of adult *T. dubius* on pines undergoing mass attack by SPB, then used similar densities in a laboratory study where adult SPB were added to caged green logs. The proportion of SPB successfully entering the logs was significantly reduced by *T. dubius* predation (Figure 10.6), although some SPB always escaped predation and entered the logs. Adult *T. dubius* also appear to have a ratio-dependent functional response (Arditi and Ginzburg 1989), implying that the predation rate depends on the SPB/*T. dubius* ratio rather than on the separate densities of predator and prey.

More results are available for interactions between *T. dubius* and various *Ips* species, because *Ips* are easier to rear and otherwise manipulate using cut logs, whereas SPB often develop poorly under these conditions. A significant impact on *Ips* survival and reproduction was found by Aukema and Raffa (2002, 2004), Mignot (1966), and Mignot and Anderson (1969). However, these studies were not designed to separate the effects of larval vs. adult *T. dubius* on *Ips*. Reeve and Turchin (2002) examined the effect of larval *T. dubius* on the survival and reproduction of *I. grandicollis*, seeding infested logs with different densities of *T. dubius* eggs, chosen using field densities of adult predators and daily oviposition rates. There was a highly significant effect of egg density on the ratio of increase for *I. grandicollis* (Figure 10.7), but the initial density of adult *Ips* also had an effect, presumably because of intraspecific competition.

Dispersal Behavior

Dispersal behavior has been studied in both SPB and *T. dubius*, directly using mark-recapture experiments as well as indirectly with genetic markers. Turchin and Thoeny (1993) fitted a diffusion model to the data from SPB mark-recapture experiments and estimated that the median dispersal distance for SPB was 0.69 km. Cronin and others (2000) estimated that the median dispersal distance for *T. dubius* was approximately 1.25 km, with some individuals moving several times this distance (Table 10.1).

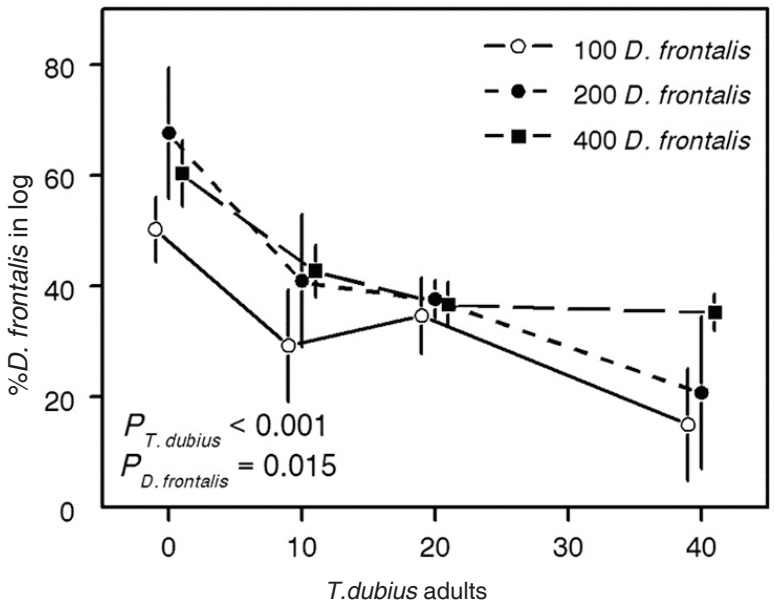

Figure 10.6—Effect of predation by adult *T. dubius* on the percent of adult SPB successfully attacking a green log, as a function of predator and SPB density. *P*-values indicate the effect of predator and SPB densities on the percent attacking, tested by fitting general linear models. (from Reeve 1997, Reeve and Turchin 2002)

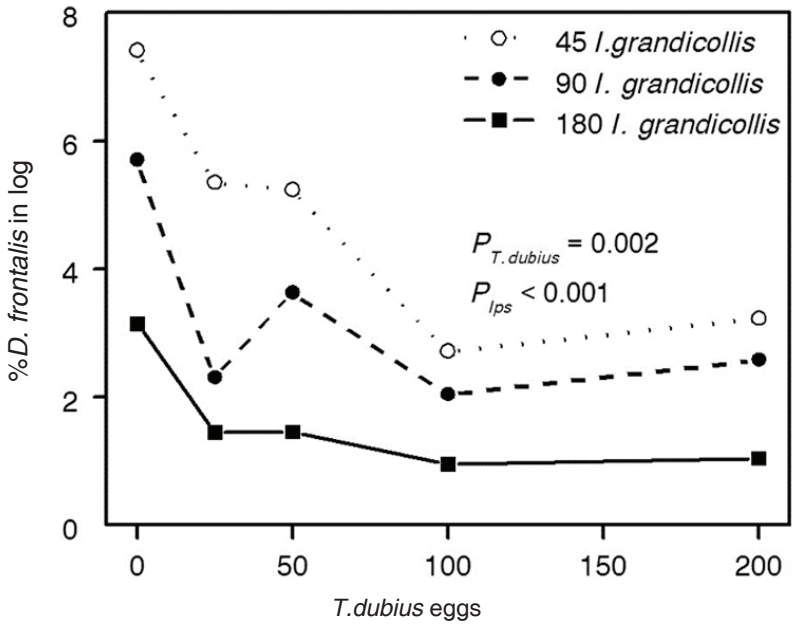

Figure 10.7—Effect of predation by larval *T. dubius* on the ratio of increase for *I. grandicollis* as a function of the density of predator eggs and initial densities of adult *I. grandicollis*. *P*-values indicate the effect of predator and *I. grandicollis* densities on the ratio of increase (emerging adults/attacking adults) for *I. grandicollis*, tested by fitting general linear models. (from Reeve and Turchin 2002)

Table 10.1 — Estimated dispersal quantiles (radius of a circle in km enclosing a given proportion of dispersers) with 95 percent confidence intervals for *T. dubius* and SPB (from Cronin and others 2000)

Dispersal quantiles	*T. dubius*	SPB
50%	1.24 (0.74, 4.48)	0.69 (0.45, 0.92)
75%	2.02 (1.30, 6.73)	0.99 (0.65, 1.34)
95%	5.10 (3.56, 15.89)	2.27 (1.48, 3.05)

Thus, *T. dubius* can apparently disperse farther than SPB, likely enabling it to track changes in SPB abundance in space. Less is known about the effects of habitat fragmentation and isolation on dispersal behavior. Ryall and Fahrig (2005) showed that densities of *I. pini* were higher in isolated red pine patches than nonisolated ones, while *T. dubius* densities were unaffected, leading to a significantly lower predator-to-prey ratio in isolated patches. This suggests little or no effect of isolation for *T. dubius*, at least at the spatial scale of the patches used in this study.

Studies using genetic markers indicate both predator and prey are capable of considerable long-range dispersal, with *T. dubius* again showing higher dispersal rates than SPB. Schrey and others (2005) used a mitochondrial DNA marker to examine the population genetic structure of *T. dubius* throughout the Eastern United States. There was significant structuring between northern and southern populations, roughly corresponding to portions of its range with and without SPB. No structure was detected among southern populations, suggesting considerable gene flow occurs among predator populations within the range of SPB. Schrey and others (2008) examined the genetic structure of SPB within a single State (Mississippi) using microsatellite markers, and found that on this scale SPB populations were quite homogeneous. Previous work using isozymes showed significant structure among sites in different states, however, implying that gene flow is reduced at larger scales (Anderson and others 1979, Namkoong and others 1979, Roberds and others 1987). The overall pattern for SPB suggests gene flow among forests within States, but reduced flow at higher spatial levels, whereas *T. dubius* populations could be mixing even at these higher levels.

10.3.2. *Medetera bistriata* (Diptera: Dolichopodidae)

Life History

Adult *M. bistriata* (Figure 10.8) arrive on the host tree shortly after the initiation of SPB attack (Dixon and Payne 1979b). The adults of *M. dendrobaena* have been reported to feed on collembolans and thrips on the bark surface as well as *Drosophila melanogaster* in the laboratory (Nicolai 1995), and one would expect *M. bistriata* to forage on insects of similar size, but not adult SPB. Oviposition

Figure 10.8—*Medetera* spp. adult. (photograph by Gerald J. Lenhard, www.forestryimages.org).

likely occurs close to SPB attack holes to facilitate entry by the larvae, similar to the behavior observed in *M. aldrichii* (Fitzgerald and Nagel 1972). The larvae (Figure 10.9) then attack the immature stages of SPB, likely paralyzing them with a venom delivered using their tentorial rods (Aukema and Raffa 2004, Nagel and Fitzgerald 1975). Pupation occurs on the bark surface in *M. dendrobaena* (Nicolai 1995), and *M. bistriata* is probably similar.

Chemical Ecology

It has been shown that adult *M. bistriata* are attracted to logs infested with SPB and *Ips*, as well as pheromone components including frontalin and host volatiles (Dixon and Payne 1980, Goyer and others 2004, Williamson 1971). Goyer and others (2004) found that the number of *M. bistriata* attracted to *Ips*-infested logs was affected by log color (fewer were trapped on white vs. black or natural color logs), suggesting visual cues are also important in prey location. Newly hatched larvae *M. aldrichii* are attracted to α-pinene, a behavior that presumably helps them locate attack holes (Fitzgerald and Nagel 1972).

Impact on SPB

No studies were found that directly examined the impact of *M. bistriata* on SPB, but findings from other systems give indications it could be significant. Aukema and Raffa (2004) observed an effect of larval predator density on the number of dead *I. pini* immatures in laboratory studies using bark sandwiches. Nicolai (1995) observed up to 45 percent mortality in the larvae of *Pityogenes chalcographus* (a European bark beetle species) generated by *M. dendrobaena* using infested logs. Based on prey consumption rates for larval *M. dendrobaena*, Dippel and others (1997) projected similar mortality values for *P. chalcographus*.

10.3.3. Woodpeckers (*Picidae* spp.)

Impact on SPB

A few studies have considered the impact of woodpeckers on SPB brood within infested trees (Figure 10.10). Kroll and Fleet (1979) found that woodpecker foraging had a significant impact on the densities of SPB pupae and adults at mid-bole (but apparently not the upper and lower bole), in a comparison of infested trees with and without woodpecker exclusion cages. The species commonly associated with SPB infestations are the downy, hairy, and pileated woodpeckers (*Picoides pubescens*, *P. villosus*, and *Dryocopus pileatus*, respectively) (Kroll and Fleet 1979, Kroll and others 1980). These species also showed elevated densities in an infested vs. uninfested stand, a pattern that has been observed in other woodpecker-bark beetle systems (Fayt and others 2005, Morrissey and others 2008). This increase in density may represent a short-term aggregative response to increases in prey density, but Kroll and others (1980) also observed an increase in overall

Figure 10.9—*Medetera* spp. larva. (photograph by Gerald J. Lenhard, www.forestryimages.org)

Figure 10.10—Evidence of woodpecker feeding on SPB brood. When attacking SPB, woodpeckers first flake off the loose outer bark and then cut grooves into the cork-like inner bark to extract late-stage SPB brood. (photograph by Terry Price, www.forestryimages.org)

woodpecker densities with the number of SPB infestations over a 10-year period, possibly indicating a true numerical response to changes in SPB density. Given these results, it seems likely that woodpeckers exert some effect on SPB dynamics, but the overall magnitude of the effect and whether it generates density-dependence in SPB growth remains unknown. Fayt and others (2005) hypothesized that woodpeckers associated with bark beetles attacking spruce in North America likely exert their greatest effect in locations where outbreaks are just beginning, before their response becomes saturated by high beetle populations, and this scenario also seems plausible for SPB.

Although this review has focused on predator-prey relationships, there is one woodpecker species for which the relationship is more ambiguous: the endangered red-cockaded woodpecker (*P. borealis*). Attacks by SPB are a major source of cavity tree mortality (Conner and others 1991, 2001b; Conner and Rudolph 1995), although SPB brood are also a food source for red-cockaded woodpecker (Schaefer and others 2004).

10.4. CONSERVATION AND BIOLOGICAL CONTROL

Given the apparent impact of predators and other natural enemies on SPB, it seems logical that control methods for SPB should attempt to minimize their impact on natural enemy populations. It is commonly recommended that cut-and-remove or salvage operations leave trees vacated by SPB in place, to spare the natural enemies remaining behind (Mizell and Nebeker 1981, Swain and Remion 1981, Thatcher and Pickard 1966). This is especially the case for *T. dubius* because some individuals remain in the tree years after initial colonization by SPB. Such trees also provide foraging and nesting opportunities for woodpeckers (Kroll and others 1980).

In addition to conservation, it may eventually be possible to use laboratory-reared predators to augment natural populations within an infestation, as a control method (augmentative biological control). An artificial diet for rearing *T. dubius* larvae has been developed with this purpose in mind (Reeve and others 2003). It is also possible to feed adult *T. dubius* using cowpea weevils, *Callosobruchus maculatus* (Mizell and others 1982, Nebeker and others 1980), meaning that no bark beetles are required to complete the life cycle. This predator has been successfully reared for many generations in the laboratory, producing adults of similar quality (size and fecundity) to wild adults that also retain their preference for natural prey (Reeve and others 2003). Current research is focused on extending the time between predator feedings by adding a preservative to the artificial diet (A. Costa and J. D. Reeve, unpublished data). However, the overall rearing process remains time consuming and thus expensive because the cannibalistic larvae must be separately confined and fed. Another unsolved problem concerns the method of deployment in SPB infestations. Is it better to release adults within an infestation, even though they could easily disperse from the release point, or place eggs or larvae on infested trees? Laboratory studies indicate that eggs and larvae placed on the bark surface will enter infested logs and attack the developing brood (Reeve and Turchin 2002), but this method has not been tested under field conditions. At present, our rearing methods can provide sufficient predators for research purposes but will require significant improvements to make augmentative biological control of SPB feasible.