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# Southern Pine Beetle Ecology: Populations within Stands

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## Abstract

Populations of southern pine beetle (SPB) are typically substructured into local aggregations, each with tens of thousands of individual beetles. These aggregations, known as "spots" because of their appearance during aerial surveys, are the basic unit for the monitoring and management of SPB populations in forested regions. They typically have a maximum lifespan of 1 year, being born in the spring when dispersing SPB aggregate at points in the forest. Spots that survive to the following spring produce the dispersing beetles that form a new population of spots. SPB epidemics rise and fall with interannual variation in the number of spots within a region. Many spots, especially those that begin small, die an early death by midsummer. Others may grow throughout the summer and into the winter via a self-propagating progression of tree attacks that is critically structured by semiochemicals. Forces that influence the growth of populations within spots strongly influence the dynamic fluctuations in SPB impacts on regional forests. These forces include pine species composition, habitat edges, age and basal area of pine stands, tree defenses, the predator *Thanasimus dubius*, interactions with phoretic mites and fungi, climate, and movement of beetles into and out of spots.

## 5.1. THE SOUTHERN PINE BEETLE AS A POPULATION OF SPOTS

The demographic structure of southern pine beetle (*Dendroctonus frontalis* Zimmermann) (SPB) populations is hierarchical (Coulson 1979). As with any population, the direction and rate of change in abundance is determined by the birth rate and death rate of individuals. However, for most of the year SPB populations tend to be substructured into local, semiautonomous aggregations that can be recognized from an airplane as "spots" in the forest where trees are dying and the crowns are changing color (Billings and Ward 1984). In the Southeastern United States, where they have been most studied, these spots tend to have an annual life cycle, typically being "born" in the spring when dispersing beetles aggregate to form local infestations and generally surviving no longer than spring of the next year (≈ 3–5 generations) when beetles disperse and new aggregations can be formed. Thus, some essential properties of SPB populations can be characterized in terms of the birth rate and death rate of spots. SPB abundance in a landscape grows when there are more spots in one year than the previous year. Most simply this can be understood as the population of spots producing more dispersing beetles in one spring than was required to initiate them the previous spring. The Southern Pine Beetle Information System of the USDA Forest Service (SPBIS) monitors populations via systematic aerial surveys for spots followed by inspection on the ground. Management decisions (e.g., cut-and-remove suppression tactic vs. monitoring) are typically applied on a spot-by-spot basis within a forest. Hence, there are both theoretical and practical reasons for understanding the demographics of beetle spots. Accordingly, there have been scores of technical scientific papers that address the factors influencing the biology of SPB spots. What determines the number and location of spots that are formed in the spring? What determines the growth of beetle populations within spots and therefore the number of trees that are eventually killed by any particular aggregation if left untreated? Finally, what determines whether any particular spot will sustain beetle reproduction throughout the upcoming year to produce dispersing beetles the following the spring?

## 5.2. HOW BEETLES TURN INTO SPOTS

Local aggregations of beetles, or spots, are usually started during spring when beetles disperse out of last year's spots and employ pheromones to aggregate in mass attacks of host trees at new points within the forest. Spring dispersal flights in the Southeastern United States are thought to peak at about the time as dogwood (*Cornus florida*) flowers (March to April). Not surprisingly, there is a positive relationship between the abundance of dispersing beetles in spring, as measured by pheromone-baited traps, and the number of beetle spots that subsequently appear in the summer (Billings 1988, Billings and Upton 2002). However, the average number of spots formed increases more than linearly with the abundance of dispersing beetles, presumably because aggregation efficacy increases more than linearly with abundance (Martinson 2007). This is an example of positive demographic feedback ("Allee effect" or positive density-dependence; Berryman 2003, Turchin 2003), which is intrinsically destabilizing to population dynamics (promotes outbreaks and crashes), so the effect of disperser abundance on spot formation presumably contributes to forest pestilence from SPB. The location of new spots within forests is partly nonrandom, but also appears to have a large component of stochasticity. In forests with a mix of loblolly and longleaf pine, spots are 3-18 times more likely to form in loblolly pine than in an equal area of longleaf stands, and the frequency of spots/km$^2$ of loblolly forest is disproportionately high in stands that are about 25-35 years of age, and are more frequent in some soil types than others (Friedenberg and others 2007b, Lorio and Sommers 1985, Zarnoch and others 1984). However, it is not presently possible to accurately predict which particular pine stands will develop SPB spots in a particular year, and probably never will be (the stochastic component). It is common for spots to form around a pine tree that has recently been hit by lightning (Coulson and others 1983, 1986; Ku and others 1980b; Rykiel and others 1988). Of 1,904 spots that were systematically ground checked in the Kisatchie National Forest, 51 percent contained a lightning-struck tree near where the spot began (Mason and others 1985). The conventional wisdom is that dispersing SPB initially orient towards volatiles released as a result of the lightning strike, and that the pheromones produced by the firstarriving beetles synergize the attractiveness for additional beetles that produce more aggregation pheromones, fueling a positive feedback that can attract thousands or tens of thousands more beetles over the next days to weeks (Blanche and others 1985, Hodges and Pickard 1971). Lightning strikes can be very numerous in these forests, and it may be largely chance which ones happen to trigger a cascade of attacking SPB (Coulson and others 1999b, Lovelady and others 1991). It is not known what causes the initiation of the many other spots that are not associated with a lightning-struck tree, but it apparently requires very little to trigger the process of spot formation during spring in a forest with abundant SPB. Captures of dispersing SPB during the spring are quite uniform in space at the scale of a National Forest Ranger District and in forests with high SPB abundance.The deployment of even small amounts of SPB pheromone in the spring can trigger the formation of spots that quickly become self-propagating almost anywhere there are pine trees (Friedenberg and others 2007b).

## 5.3. THE EARLY LIFE OF SPB SPOTS

Because spots are nearly impossible to detect until the first-attacked trees die and their crowns turn red, there have been almost no direct observations of SPB biology during the first 6-8 weeks in the life of a spot. Thus our knowledge of the early life of spots is largely based on what can be inferred beginning about 2 months after the spots were initiated. The SPBIS includes records of the number of beetle-infested trees with red or green crowns at the time of ground inspection (Clarke and Billings 2003, Petty 2005). When the aerial surveys are regular and the ground inspections are conducted shortly after aerial detection, the number of red trees recorded in the SPBIS database can be taken as an estimate of the number of trees attacked by the SPB adults that immigrated into the spot as it was forming. From an analysis of about 26,000 such spots from national forests in 11 States of the Southeastern United States, the median initial size of the spots (red trees at time of detection) was 14, with 90 percent of spots falling within the range of 4 to 50 trees (Friedenberg and others 2007a). With attack densities in the mid-bole of about 10 beetles per dm$^2$, a tree that is 60 feet tall with 10-inch diameter represents 2,000-3,000 attacking adults (Coulson 1980), so a typical spot might represent the aggregation of 25,000-50,000 SPB adults, and large spots in stands with large trees must begin with aggregations of > 100,000 SPB.

Many spots, especially if they begin small, die an early natural death and therefore fail to contribute dispersing beetles to the population the following spring. Hedden and Billings (1979) reported natural local extinction in 100 percent of SPB spots in East Texas that began with fewer than 10 trees. Analyses of about 26,000 spots in the SPBIS database (encompassing national forests in 11 States over 20 years) indicated that about 35 percent of the smallest spots (4-5 red trees at detection) were already inactive (no new trees under attack) at the time that they were ground checked. Such spots very seldom become active again. In the same database, spots that began with about 25 trees were only inactive in 10 percent of the cases, and spots that began with 50 or more trees were inactive in <5 percent of the cases (Friedenberg and others 2007a). The effect of initial spot size on the probability of spot extinction is another source of destabilizing positive feedback in SPB population dynamics (larger initial population size promotes higher per capita growth rate of the population).

The susceptibility of small spots to extinction is presumably influenced by predation from the specialist predator *Thanasimus dubius* (Reeve 1997) and by the difficulty that small populations of attacking beetles have in overwhelming tree defenses (Berryman and others 1985). However, the strongest force may arise from small populations being more likely to experience a break in the continuity of new attacks. Spot growth is dependent on the successful attack of new trees at the periphery of previously attacked trees. The progeny of the first wave of attacking beetles join in the attack of new trees by detecting pheromone plumes released from those trees by attacking adult beetles that entered the tree within the last 7-10 days (Gara and others 1965, Pureswaran and others 2006). If the wave of attacks that initiated the spot was the product of relatively few beetles, it is more likely that there will be a break in the progression of new attacks; in which case there is no pheromone plume to organize the attack behavior of SPB adults that subsequently emerge, and their searching behavior is more likely to take them out of the immediate area of the spot to an uncertain fate elsewhere (Gara and Coster 1968, Gara and others 1965, Franklin 1970b). In support of this model, experimental removal of trees currently under attack—and therefore removal of the associated pheromone plume—can cause the local extinction of spots via undirected emigration of subsequently emerging SPB (Gara 1967). Further evidence for the generality of this mechanism comes from the observations of researchers and forest health personnel who report that spots that have become inactive—and subsequently remain inactive—frequently contain trees that are still producing thousands of newly developed SPB adults. Models of the progression of age distribution in local SPB populations show that temporal gaps in the abundance of adults are expected under realistic demographic scenarios, especially when the initial spot size is small and/or the waves of attacks that initiated the spot were quite synchronous (Friedenberg and others 2007a). This requirement of SPB spots for an uninterrupted progression of new attacks is the theoretical basis for the suppression tactic known as cut-and-leave (USDA 1987), which is essentially an operational version of the experiments reported by Gara (1967).

## 5.4. SPB SPOTS DURING MID-TO LATE SUMMER

### 5.4.1. Population Structure

If not suppressed (Clarke and Billings 2003), SPB spots that are still active in midsummer (green trees coming under attack) have a relatively high probability of continuing to grow in size during the remainder of the year and surviving to be a source of dispersing beetles the following spring. By this time the beetles that originated the attack in spring are dead, and subsequent growth of the spot reflects the pattern of new trees coming under attack, oviposition by attacking adults within those trees, and the development of new progeny that subsequently emerge as adults and join in further attacks (Coulson 1980; Coulson and others 1989; Feldman and others 1981a, 1981b; Lih and Stephen 1989; Lih and Stephen 1996). Although there may be some immigration of beetles from nearby spots (Cronin and others 1999), local demographics are thought to dominate population dynamics within spots for several more generations until the following spring (Coulson and others 1989; Fargo and others 1982, 1985; Martinson 2007; Thatcher and Pickard 1967; Ungerer and others 1999). The importance of local demographics was evident in studies by Martinson (2007) that revealed temporal waves of dominant cohorts progressing as predicted by physiological models from ovipositing adults to eggs, larvae, pupae, callow adults, and newly emerged adults (Fargo and others 1982; Wagner and others 1981a, 1984a, 1984b). The stage structure of populations within two spots in the Oakmulgee Ranger District tended to converge by late summer on a stable stage structure of approximately 48: 34: 6: 4: 8 for eggs: larvae: pupae: callow adults: and ovipositing adults (with total populations in each of ≈ 50,000 SPB). The population of adults that are attacking trees at any time is a mix of individuals that are attacking their first tree and those that have reemerged from attacks within at least one previous tree (Cooper and Stephen 1978, Coulson and others 1978, Franklin 1970b, Gagne and others 1982, Wagner and others 1981a, 1981b,1982). Based on dissection of the spermathecae, which permitted separation of virgin females attacking their first tree from previously mated females, Martinson (2007) estimated that 47-77 percent (depending on spot and the date) of female adults joining the attack of trees were previously mated, and therefore had previously entered at least one other tree.

### 5.4.2. Spatial Pattern of Spot Growth

By midsummer, the attack of new trees within active SPB spots typically becomes concentrated in one area along the periphery of previously attacked trees and acquires a head that begins to snake slowly through the pine forest (Coster and others 1977a, Franklin 1970b, Payne 1980, St. George and Beal 1929). Figures 5.1-5.3 contain visualizations of actual spot growth in three spots in which SPB landings on trees were monitored at 3-day intervals during mid- to late summer. SPB are remarkable in their ability to aggregate attacks on particular trees (Coster and Johnson 1979b). Landing rates on individual trees frequently exceeded 200 SPB adults · 600 $\text{cm}^{-2}$ · 3 $\text{d}^{-1}$, which on these pulp-sized trees scaled up to ≈ 5000 landing SPB/day. (Note that these values greatly overestimate the number of flying SPB in the population because ≈ 60 percent of landing beetles quickly drop or fly from the tree, presumably to land somewhere else again; Bishir and others 2004) At the same time, most trees further than a few meters distant had zero landing beetles. The next tree to come under attack was almost always immediately adjacent to one or more trees that were already under attack (Gara and Coster 1968, Johnson and Coster 1978). During 48 days of observation, we observed 41 new trees come under attack —an average of 2.5 new trees per 3 days. In almost all cases, initial landings on a tree were quickly followed by mass attack involving tens of thousands of SPB landings over the next 10-14 days, followed soon thereafter by the death of the tree. During this continuing process, SPB adults are recruited into the pool of attacking adults as they emerge from the source tree in which they developed, which is generally within ≈ 50 m of the head of the spot (Pope and others 1980, Schowalter and others 1981b). Examination of a transect running from the head of the spot to the source trees typically reveals a spatial pattern matching the developmental progression, in which the resident SPB tend to be dominated by landing adults, then ovipositing adults and eggs, then young larvae, then late larvae and pupae, and finally callow adults and emerging adults (Coulson and others 1979b, 1980b; Fargo and others 1978). The pattern of spot growth gives little indication of favoring pine trees that are more or less suitable for SPB reproduction. Rather it appears that the next trees to get attacked were just those that happened to be in the wrong place. However, there is evidently some level of discrimination because the progeny of trees that appeared to escape attack have strikingly higher resin flow than the progeny of randomly selected mother trees, implying that the SPB sometimes avoid trees with a genetic tendency for high resin flow (Strom and others 2002).

The patterns of spot growth are structured by plumes of tree volatiles plus SPB pheromones that emanate from trees under active attack (Gara and others 1965, Payne 1980). Our appreciation for the complexity of this chemical and behavioral system has grown from the initial identification of frontalin as an aggregation pheromone (Renwick and Vité 1970), to the description of antiaggregation pheromones that can reduce attack rates on individual trees (Payne and others 1978), to our present recognition that SPB produce at least five different pheromones (Pureswaran and others 2008b), whose effects on SPB behavior depend upon total amounts, relative amounts, chirality, and possibly even relative spatial position (Sullivan and others 2007b). There has been a longstanding interest in the possibility that manipulation of pheromone signals could provide a means for controlling SPB damage by disrupting the normal patterns of tree attacks and spot growth, and some results have been promising, but no semiochemical-based tactics have yet been developed into generally practical operational techniques (Clarke and others 1999, Dickens and others 1992, Gara and others 1965, Payne and Billings 1989, Payne and others 1992, Salom and others 1995, Strom and others 2004, Sullivan and others 2007a, Watterson and others 1982).

## 5.4.3. Factors that Influence Population Growth Within Spots

### *Habitat Edges*

SPB spots commonly die when the growing head encounters the edge of a pine stand, or even a fire lane or modest gap within the pine stand. This is presumably because the growth of the spot depends upon there being additional suitable host trees within a few meters of trees that are already under attack, perhaps because new attacks are a consequence of one or a few SPB making a mistake by initiating attacks and beginning to release aggregation pheromones on a tree that is close enough to fall within the pheromone plume of a tree under attack. It has been hypothesized that new attacks are initiated by "pioneer" beetles that have a behavioral predisposition for being the first to attack a tree. However, individual-based natural selection should discourage such behavior because early attacking beetles have low fitness relative to those that join attacks that have already begun, presumably because they typically encounter robust resin flow from healthy trees (Pureswaran and others 2006). Not surprisingly, there does not appear to be any group prescience in the direction of spot growth. That is, local populations do not appear to steer away from upcoming barriers to continued spot growth, such as the edge of a hardwood stand. A simple and perhaps satisfactory model for the orientation of spot growth is that the spot head begins to grow in a compass direction that is effectively random, perhaps influenced by stochastic patterns of air movement within the subcanopy that influence the shape and direction of pheromone plumes (Thistle and others 2004).

### *Basal Area of Host Trees*

There is a strong pattern of SPB spots tending to grow more within stands that have a high basal area of host trees (Belanger 1980; Cameron and Billings 1988; Hedden 1978; Hedden and Lorio 1985; Hicks and others 1981; Ku and others 1980b; Kushmaul and others 1979;

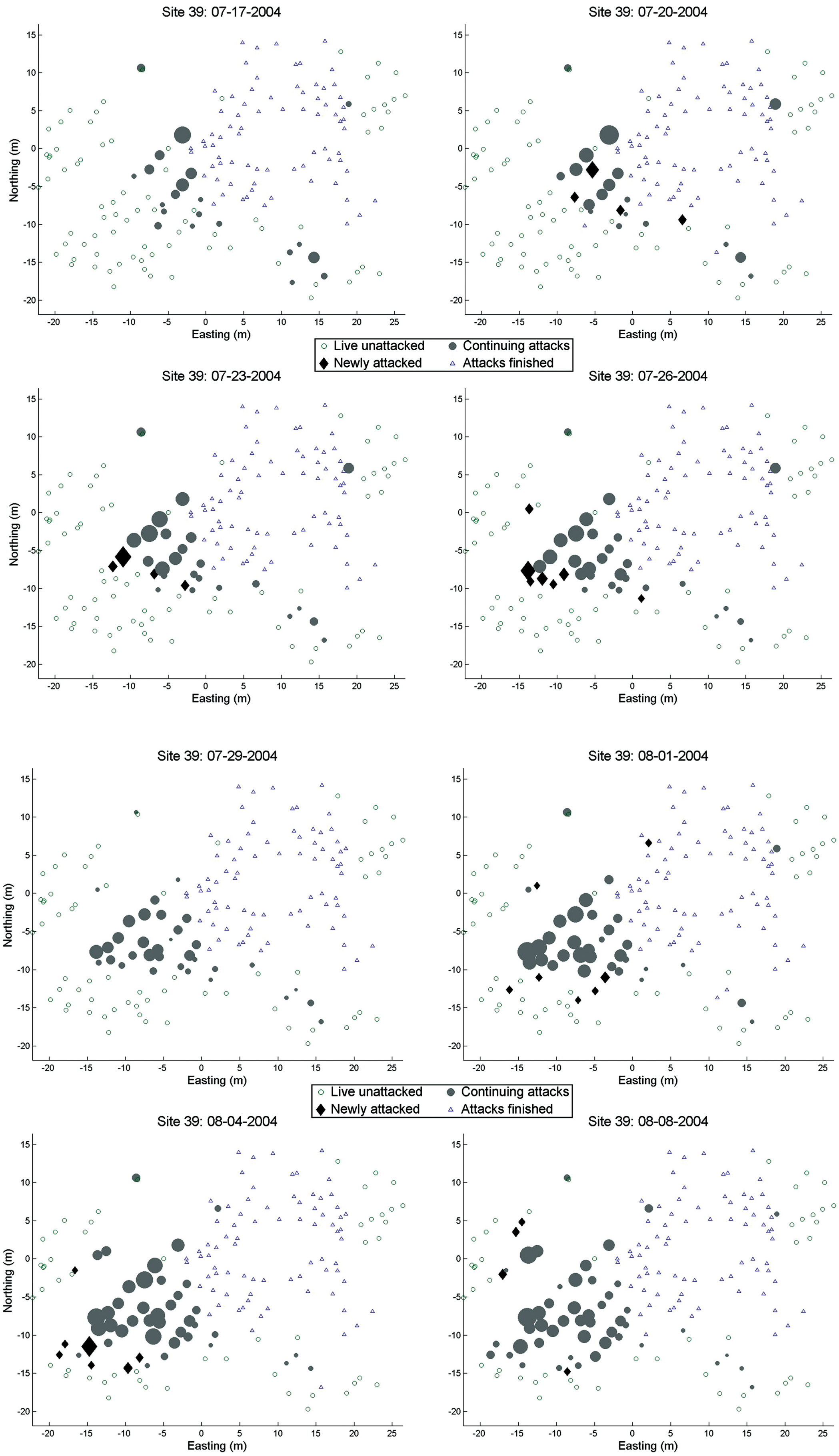


**Figure 5.1**—The progression of tree attacks within a fast-growing infestation (spot) of the southern pine beetle, *Dendroctonus frontalis*. The sizes of symbols for trees under attack are proportional to the number of beetles landing per tree. Data are based upon measurements of tree-specific landing rates by *D. frontalis* in spot #39 (= SPBIS ID) within the Chickasawhay Ranger District, DeSoto National Forest, Mississippi. Each of the 16 panels represents tree-specific landings during the previous 3 days (since the previous panel). Measurements ran continuously from 17 July to 3 September 2004. The infestation was within an even-aged stand of slash pine (*Pinus echinata*) (compartment-stand = 348-23): 22 years old, 13 ha (32 acres), diameter at breast height (± SD) = 19 ± 4 cm (6-9 inches), height = 20 ± 3 m (56-72 feet), percent live crown = 29 ± 10, basal area = 36 ± 7 $m^3$ / ha (125-186 $ft^2$ / acre). The extent of the stand continued beyond the trees that are represented, but there were no other attacks within the stand. (continued on next page)

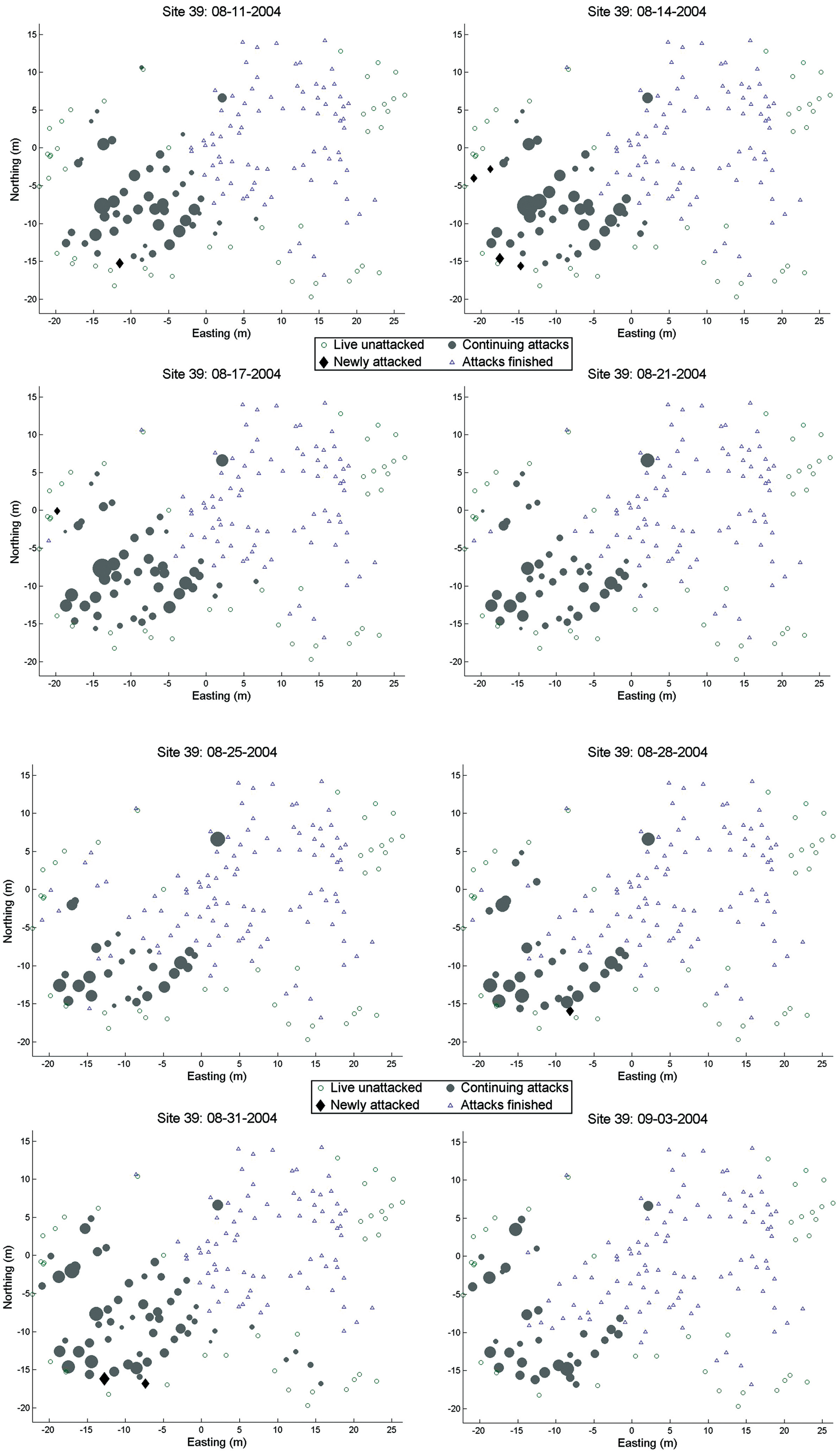


**Figure 5.1 (continued)—** The progression of tree attacks within a fast-growing infestation (spot) of the southern pine beetle, *Dendroctonus frontalis*. The sizes of symbols for trees under attack are proportional to the number of beetles landing per tree. Data are based upon measurements of tree-specific landing rates by *D. frontalis* in spot #39 (= SPBIS ID) within the Chickasawhay Ranger District, DeSoto National Forest, Mississippi. Each of the 16 panels represents tree-specific landings during the previous 3 days (since the previous panel). Measurements ran continuously from 17 July to 3 September 2004. The infestation was within an even-aged stand of slash pine (*Pinus echinata*) (compartment-stand = 348-23): 22 years old, 13 ha (32 acres), diameter at breast height (± SD) = 19 ± 4 cm (6-9 inches), height = 20 ± 3 m (56-72 feet), percent live crown = 29 ± 10, basal area = 36 ± 7 $m^3$ / ha (125-186 $ft^2$ / acre). The extent of the stand continued beyond the trees that are represented, but there were no other attacks within the stand.

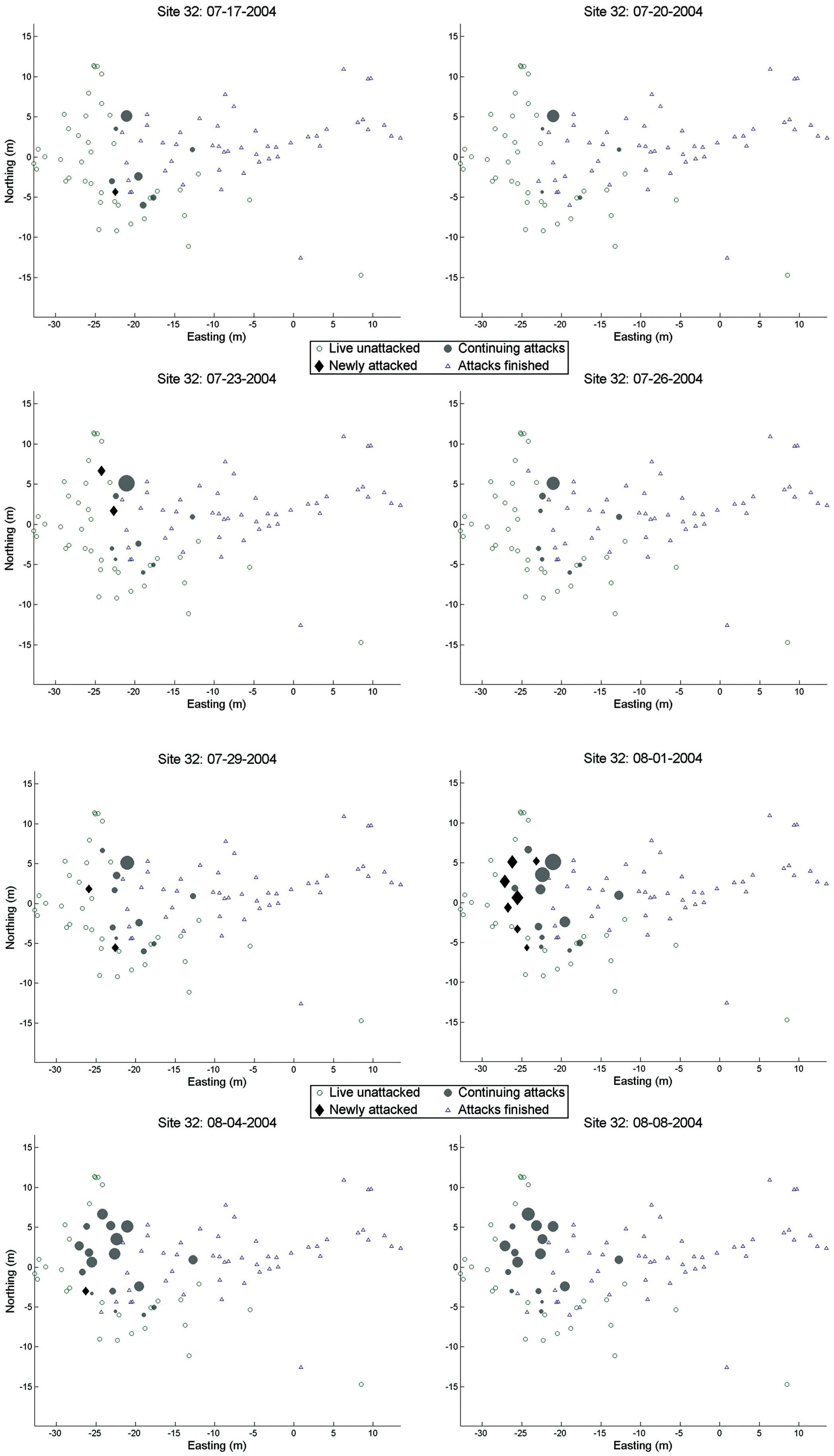
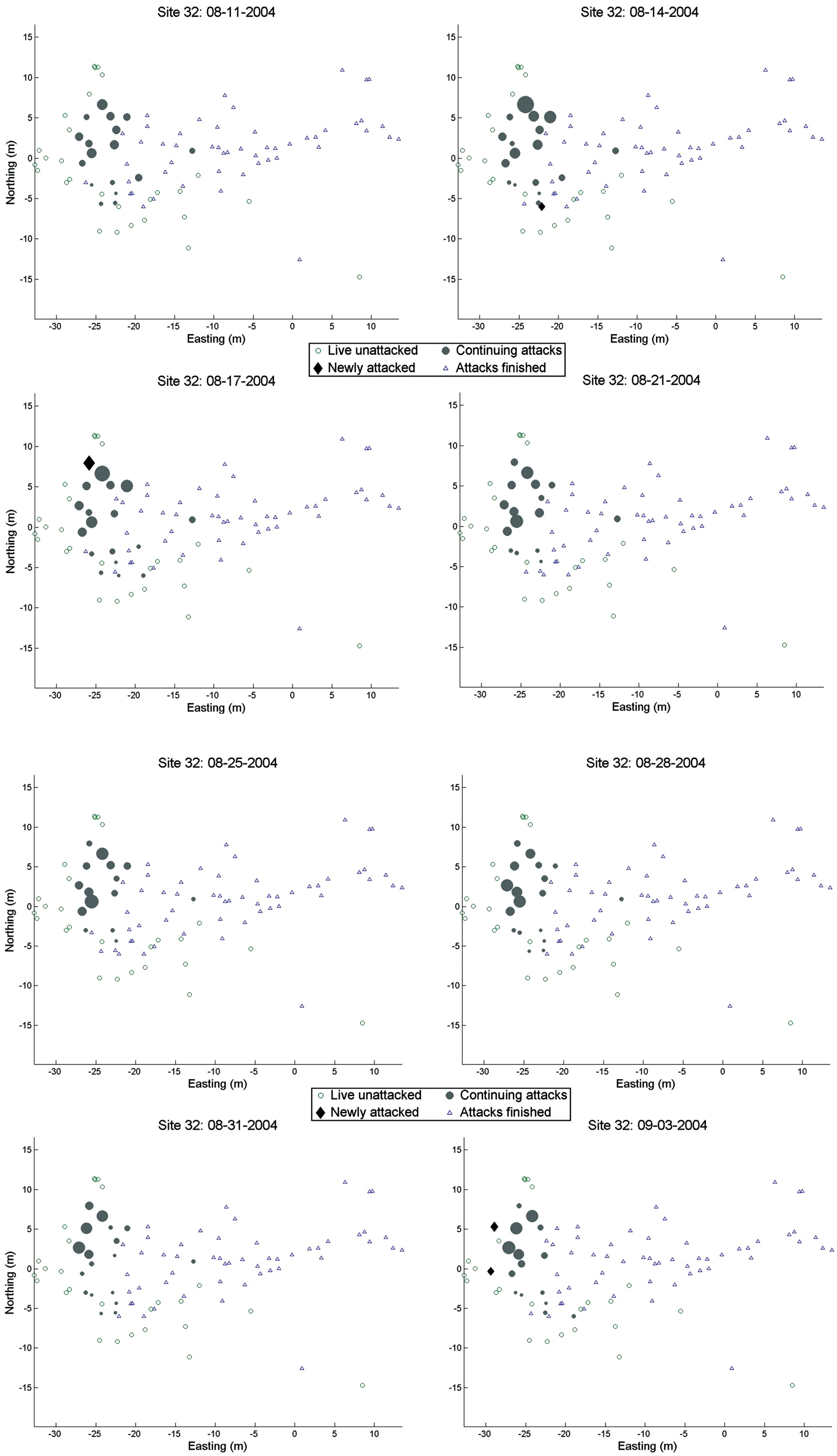


**Figure 5.2** — The progression of tree attacks within a moderately fast-growing infestation (spot) of the southern pine beetle, *Dendroctonus frontalis*. The sizes of symbols for trees under attack are proportional to the number of beetles landing per tree. Data are based upon measurements of tree-specific landing rates by *D. frontalis* in spot #32 (= SPBIS ID) within the Chickasawhay Ranger District, DeSoto National Forest, Mississippi. Each of the 16 panels represents tree-specific landings during the previous 3 days (since the previous panel). Measurements ran continuously from 17 July to 3 September 2004. The infestation was within an even-aged stand of slash pine (*Pinus echinata*) (compartment-stand = 434-9): 21 years old, 20 ha (49 acres), diameter at breast height (± SD) = 18 ± 4 cm (5-9 inches), height = 19 ± 1 m (57-67 feet), percent live crown = 22 ± 11, basal area = 36 ± 7 $m^3$ / ha (124–186 $ft^2$ / acre). The extent of the stand continued beyond the trees that are represented, but there were no other attacks within this area of the stand. (continued on next page)


Site 32: 08-11-2004

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Site 32: 08-17-2004

Site 32: 08-21-2004

Site 32: 08-25-2004

Site 32: 08-28-2004

Site 32: 08-31-2004

Site 32: 09-03-2004

**Figure 5.2 (continued)—** The progression of tree attacks within a moderately fast-growing infestation (spot) of the southern pine beetle, *Dendroctonus frontalis*. The sizes of symbols for trees under attack are proportional to the number of beetles landing per tree. Data are based upon measurements of tree-specific landing rates by *D. frontalis* in spot #32 (= SPBIS ID) within the Chickasawhay Ranger District, DeSoto National Forest, Mississippi. Each of the 16 panels represents tree-specific landings during the previous 3 days (since the previous panel). Measurements ran continuously from 17 July to 3 September 2004. The infestation was within an even-aged stand of slash pine (*Pinus echinata*) (compartment-stand = 434-9): 21 years old, 20 ha (49 acres), diameter at breast height (± SD) = 18 ± 4 cm (5-9 inches), height = 19 ± 1 m (57-67 feet), percent live crown = 22 ± 11, basal area = 36 ± 7 m$^3$ / ha (124–186 ft$^2$ / acre). The extent of the stand continued beyond the trees that are represented, but there were no other attacks within this area of the stand.

Lorio 1980a, 1980b; Lorio and others 1982; Mason and others 1985; Nebeker and others 1985). Several possible explanations have been proposed. The time-honored explanation is that trees growing in relatively high density (overstocked) have smaller crowns that produce less photosynthates for oleoresin synthesis, and are therefore less well defended against beetles (Brown and others 1987, Lombardero and others 2000b, Matson and others 1987). This hypothesis is weakened by the observation that spot growth is lower even in mixed stands of pine and nonhost hardwoods where total basal area is still high (presumably limiting crown size and defensive capabilities just as it would if it was a pure pine stand; Schowalter and Turchin 1993, Zhang and Zeide 1999). An alternative hypothesis is that beetle aggregation efficiency declines as the distance between host trees increases (Turchin and others 1999a). A weakness of this model is that the distance among tree stems declines as stands mature (similar basal area but fewer larger stems per hectare), and yet mature stands can also support high spot growth if the basal area of host trees is high. A third hypothesis is that spots grow faster in overstocked stands because the relatively dense closed canopy, limits air movement below the canopy, which results in greater integrity of the pheromone plumes and makes it easier for beetles to locate and join attacks in progress. The effect of canopy structure on plume integrity has been experimentally validated (Thistle and others 2004), and is probably of considerable importance, but this model, like the tree defense model, still fails to explain why mixed pine-hardwood stands with closed canopies are less suitable than pure pine stands for spot growth. Further research is required to understand why high densities of host trees promote spot growth. This is especially important because forestry management tactics that limit stand susceptibility to spot growth are arguably the best long-term solution for mitigating undesirable impacts of SPB (Belanger and others 1993, Nowak and others 2008).

## Stand Age

At least for loblolly pine, spot growth appears to be related to stand age. During a large epidemic in the Bankhead National Forest of northern Alabama, the extent of infestations within infested stands was highest in loblolly pine stands that were 20-40 years of age and declined in older stands (Ylioja and others 2005). This could be because interstem distances increase in older stands, because canopy closure (and therefore the integrity of pheromone plumes) is less in mature stands, because larger trees require more SPB to overwhelm defenses, or perhaps just because older stands are a selected subset that have survived previous epidemics partly because they were initially more resistant for any reason. Notably, the pattern of reduced susceptibility in older pine stands runs counter to the common generalization in forest entomology that trees and stands become increasingly susceptible to pests with increasing age (Edmonds and others 2000).

## Tree Defenses

There is high intraspecific variation among trees in their constitutive resin flow, and the amount of resin has demonstrable effects on the reproductive success of SPB (Blanche and others 1983, Nebeker and others 1992, Tisdale and others 2003a). In trees with relatively high resin flow, attacking adult beetles spend more time moiling in the resin and less time excavating galleries and laying eggs, leading to markedly lower per capita reproductive success (Reeve and others 1995). Thus stands where the trees have low average resin flow must permit greater spot growth, with other things being equal. However, this probably does not explain very much of the variation in spot growth across a forest because average constitutive resin flow does not vary greatly among stands across a ranger district—rather most of the variation is among trees within stands, even at the relatively fine scale of a beetle spot (Martinson and others 2007). It is probable that there is more variation among stands in the inducible capacity for resin flow because this is more strongly related to crown size and tree physiological status (Knebel and others 2008, Lombardero and others 2000b, Tisdale and others 2003b), but consequences for the growth of SPB spots is not well known. It is probable that pronounced seasonal and interannual variation in resin flow influences tendencies for growth in the population of spots across a forested landscape (Lorio 1986, Lorio and others 1990, Wilkens and others 1997).

## The Predator Thanasimus dubius

The predator *Thanasimus dubius* is of well demonstrated general importance in the population dynamics of SPB (Frazier and others 1981, Reeve 1997, Reeve and others 1980, Thatcher and Pickard 1966, Turchin and others 1991). The abundance of *T. dubius* tends to be quite uniform across the scale of a

National Forest Ranger District (Cronin and others 2000, Friedenberg and others 2007b), so it is not obvious that variation in predation by *T. dubius* would produce important variation in the growth of spots within a forest in any given year. There is conspicuous variation in the abundance of *T. dubius* among years and among forests separated by at least a few hundred kilometers (Billings and Upton 2002, Martinson 2007), so this coarser variation is likely to make some forests in some years more or less likely to support high spot growth. Indeed, the ratio of *T. dubius* to SPB that are captured during spring dispersal is recognized as a predictor of regional risk for high growth of SPB populations (Billings and Upton 2002). Some of the interannual variation in abundance of *T. dubius* is explained by abundance of SPB the previous year (Reeve and Turchin 2002, Turchin and others 1999b). Within a summer, the abundance of *T. dubius* relative to SPB tends to decline quite markedly; e.g., Martinson (2007) reported that the predator: prey ratio from captures on sticky traps within spots declined from about 0.19 to 0.02 from early July to late July. Presumably, the effect of predators is greatest in the early summer. Friedenberg and others (2007a) estimated that relatively modest changes in predation rate during the early life of a spot could affect the probability of the spot dying by midsummer from a break in the continuity of attacks. Any features of trees or stands that influence predation by *T. dubius* could have important effects on the growth of SPB spots.

## Interactions with Mites and Fungi

Community interactions involving mites and fungi are of surprisingly high importance in the population dynamics of SPB (Hofstetter and others 2006a, Lombardero and others 2003). SPB larvae depend upon the presence of one of two species of mutalistic (mycangial) fungi for their nutrition: *Entomocorticium* sp A and *Ceratocystiopsis ranaculosus* (Ayres and others 2000, Klepzig and others 2001a). Their relative abundance within SPB populations varies over space and time (Hofstetter and others 2006b). *Entomocorticium* seems to be a generally superior associate from the perspective of SPB (Coppedge and others 1995), and spots with a higher proportion of beetles carrying *Entomocorticium* appear to have higher reproductive success (Bridges 1983). Another common fungus, *Ophiostoma minus*, easily outcompetes the mycangial fungi (Klepzig and Wilkens 1997), and its abundance is highly variable from year to year and forest to forest, largely due to variation in the abundance of *Tarsonemus* mites that transport, propagate, and feed upon *O. minus* (Hofstetter and others 2006a, Lombardero and others 2000c). Spots in which the abundance of *Tarsonemus* mites is high tend to have low growth because of the resultant proliferation of *O. minus* within host trees. When the percentage of phloem occupied by blue stain (signaling the presence of *O. minus*) exceeds about 34 percent, spots tend to go extinct during the summer and fail to contribute SPB to dispersal flights the following spring (Hofstetter and others 2006b). Monitoring, and perhaps even manipulation, of *Tarsonemus* mites and *O. minus* has potential for predicting and managing SPB spot growth.

## Climate

Climate—temperature in particular—has strong affects on most aspects of SPB biology. Development rates, oviposition rates, re-emergence rates, and probably the location of host trees by flying adults generally increase from approximately zero at 5°-10 °C, to a maximum at 27°-32 °C, and decline at higher temperatures (Wagner and others 1981a, 1984a). As a result, the rate at which growing spots enlarge (as in Figure 5.1) follows about the same pattern with temperature. Longevity tends to decrease across temperatures (Wagner and others 1984b), so the rate at which collapsing spots become inactive goes faster with increasing temperatures. The temperature-dependence of spot growth has been modeled by Coulson and others (1989), Feldman and others (1981a), and Lih and Stephen (1989). The temperature-dependence of generation time and cohort structure (eggs: larvae: pupae: adults) has been modeled by Friedenberg and others (2007a), who hypothesized that regional and interannual variation in temperature, through its effects on cohort structure, can influence the probability of spots dying because of an interruption in the continuity of pheromone plumes that structure attack behavior. Extreme temperatures can produce mortality of SPB that increases the probability of spot death prior to producing dispersing adults the following spring and reduces the number of dispersing adults that are produced by surviving spots. When the minimum winter temperature drops below about -14 °C (the approximate lower lethal temperature for SPB), populations tend to decline (Tran and others 2007). Effects of extreme summer temperatures are less studied, but there is evidence that temperatures can

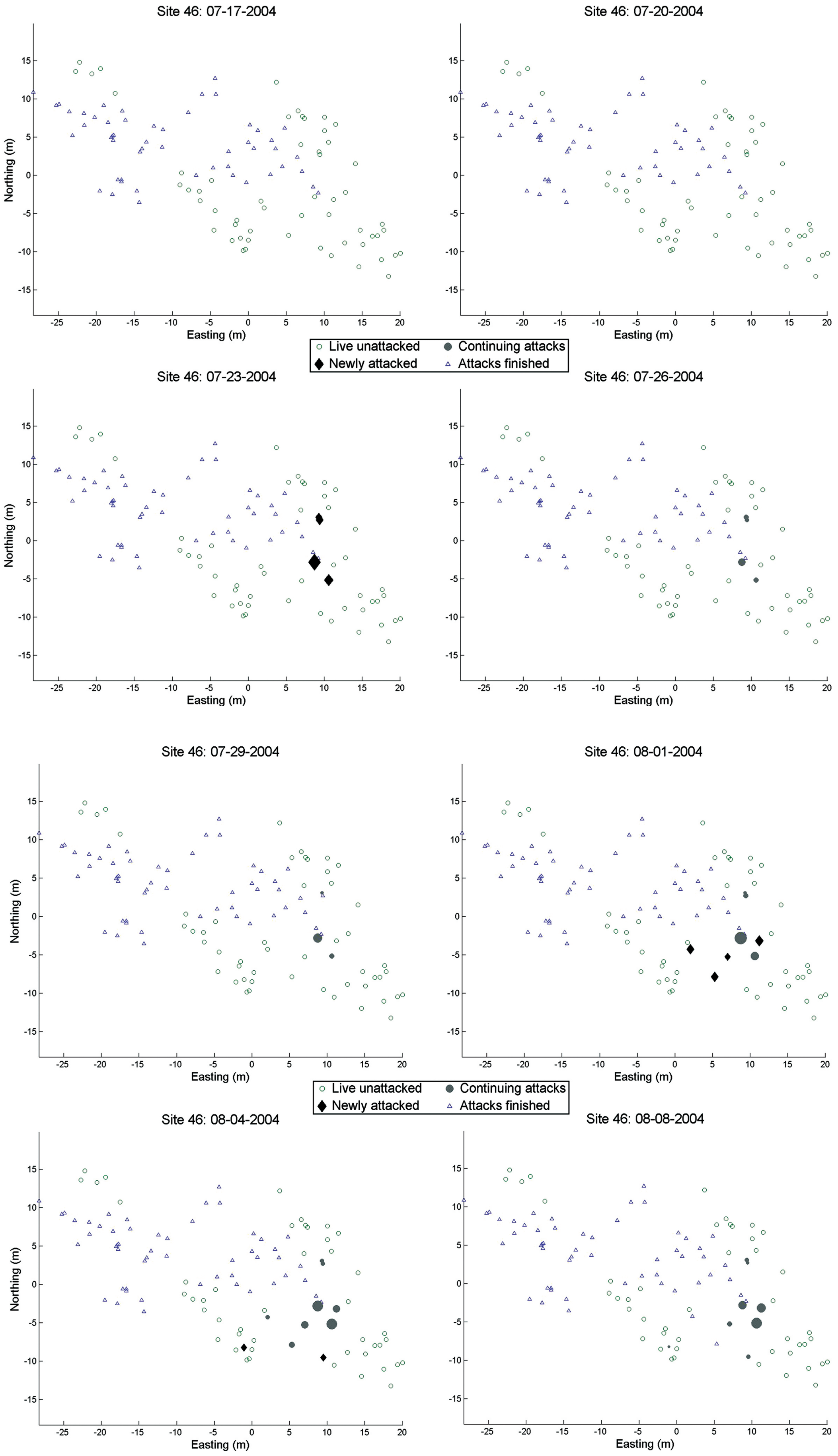

**Figure 5.3** —The progression of tree attacks within a slow-growing infestation (spot) of the southern pine beetle, *Dendroctonus frontalis*. The sizes of symbols for trees under attack are proportional to the number of beetles landing per tree. Data are based upon measurements of tree-specific landing rates by *D. frontalis* in spot #46 (= SPBIS ID) within the Chickasawhay Ranger District, DeSoto National Forest, Mississippi. Each of the 16 panels represents tree-specific landings during the previous 3 days (since the previous panel). Measurements ran continuously from 17 July to 3 September 2004. The infestation was within an even-aged stand of slash pine (*Pinus echinata*) (compartment-stand = 389-18): 24 years old, diameter at breast height (± SD) = 17 ± 5 cm (5-9 inches), height = 19 ± 3 m (53-72 feet), percent live crown = 29 ± 11, basal area = 32 ± 14 $m^3$ / ha (81–191 $ft^2$ / acre). The extent of the stand continued beyond the trees that are represented, but there were no other attacks within the stand. (continued on next page)

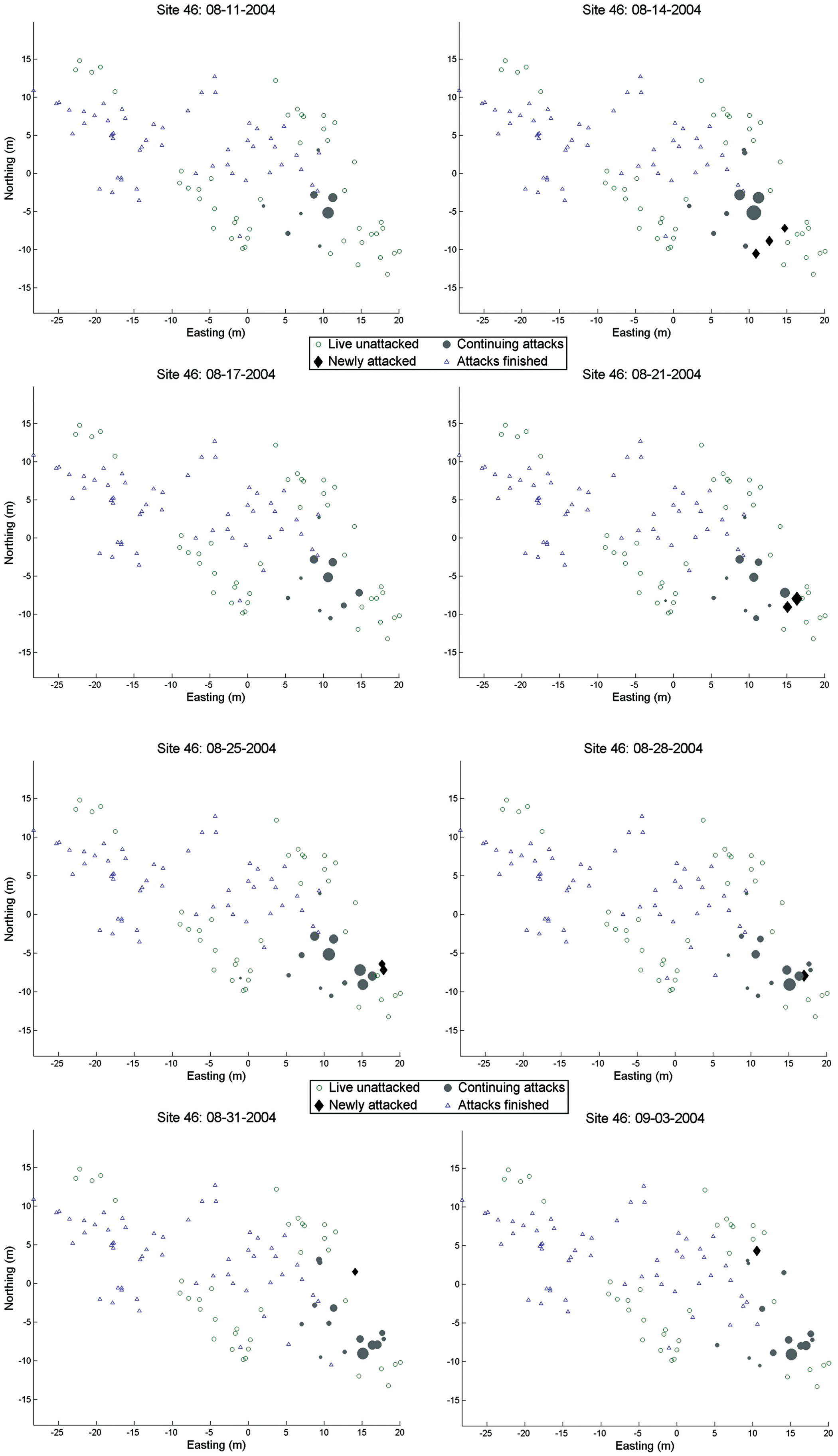

**Figure 5.3 (continued)—** The progression of tree attacks within a slow-growing infestation (spot) of the southern pine beetle, *Dendroctonus frontalis*. The sizes of symbols for trees under attack are proportional to the number of beetles landing per tree. Data are based upon measurements of tree-specific landing rates by *D. frontalis* in spot #46 (= SPBIS ID) within the Chickasawhay Ranger District, DeSoto National Forest, Mississippi. Each of the 16 panels represents tree-specific landings during the previous 3 days (since the previous panel). Measurements ran continuously from 17 July to 3 September 2004. The infestation was within an even-aged stand of slash pine (*Pinus echinata*) (compartment-stand = 389-18): 24 years old, diameter at breast height (± SD) = 17 ± 5 cm (5-9 inches), height = 19 ± 3 m (53-72 feet), percent live crown = 29 ± 11, basal area = 32 ± 14 $m^3$ / ha (81–191 $ft^2$ / acre). The extent of the stand continued beyond the trees that are represented, but there were no other attacks within the stand.

sometimes get warm enough to kill beetles (Beal 1933, Wagner and others 1984b), and that spots have a greater tendency to collapse when temperatures exceed about 32 °C (Friedenberg and others 2008). There may also be important but less conspicuous effects of temperature on SPB populations via effects on species interactions within the community (Hofstetter and others 2006b, 2007; Lombardero and others 2003).

### *Other Community Interactions*

Some other community interactions may also be of importance in influencing the growth of SPB spots. Competition with other species of bark beetles may be important in the early stages of spot formation (Bryant and others 2006; Flamm and others 1987b, 1989, 1993), and competition (and incidental predation) from cerambycid beetles, especially *Monochamus* spp., could influence SPB populations under at least some circumstances (Clarke and Billings 2000). Some parasitic hymenoptera prey on SPB (Moore 1972), but seem to be restricted to relatively low abundance under most circumstances (VanLaerhoven and Stephen 2008).

### *Immigration and Emigration*

Although the population dynamics of spots from midsummer onward appear to be chiefly determined by patterns of SPB birth rates and death rates within the spot, immigration into spots might be important under some circumstances. SPB are capable of flying a kilometer or more (Turchin and Thoeny 1993). Some SPB that were marked with florescent powder within one spot have been later detected in nearby spots (Cronin and others 1999). It appears that many spots that go inactive during the summer (e.g., due to a break in the continuity of attacks and lack of a local pheromone plume) continue to produce SPB that disperse into the forest (Gara 1967). The demographic impact of these beetles on other spots is frequently assumed to be small (indeed the suppression tactic of cut-and-leave assumes this to be true; USDA 1987), but this remains a debatable point (Cronin and others 1999, Fitzgerald and others 1994). For untreated spots that remain active, there has been little consideration of how emigration might influence the growth of spots from which SPB are departing. New evidence suggests that emigration might be more important than generally recognized as a factor in spot growth. Martinson (2007) estimated high population growth for two spots based upon conventional measures of per capita reproductive success within trees, but independent measurements indicated that population sizes were actually stable or declining over the same time period. One explanation is that half or more of adult beetles emerging from the trees where they developed failed to locate the pheromone plume at the spot head and wandered out of the spot. If emigration can be this high, it would only require modest variation in emigration rates among spots to have a large impact on spot growth. Further studies would be useful.

## 5.5. SPB SPOTS FROM WINTER TO THE END

While SPB spots have been studied quite intensively during the summer months, less is known about their winter biology. There is no diapause or endogenously enforced seasonal cessation of activity in SPB (Payne 1980). In the Southeastern United States all life stages can be found at all times of year (Beal 1933; Thatcher and Pickard 1964, 1967), indicating that the same processes are occurring as during the summer (emergence, flight, attacks, oviposition, larval development, and pupation). But the processes go slower. Biophysical measurements indicate that SPB generation time is about 50 days at 25 °C, 100 days at 17 °C, and 200 days at 12.5 °C (Friedenberg and others 2007a, Wagner and others 1984a). At the same time, resin flow from attacked trees is slower (Lorio and Sommers 1986), growth rates of fungal and mite associates are slower (Hofstetter and others 2007, Lombardero and others 2000c), and development rate of the predator *Thanasimus dubius* is slower (Nebeker and Purser 1980). Presumably because of natural selection for sustaining activity during the winter months, SPB are physiologically capable of flight at unusually low temperatures for a bark beetle (≈ 7 °C; Moser and Thompson 1986). Besides going generally slower, the process rates for different life stages of SPB are affected differently. As a result, the relative frequency of the various life stages change during the winter. In western North Carolina and East Texas, studies indicate a preponderance of larvae by late winter (Beal 1933, Thatcher 1967). In New Jersey, at the extreme northern edge of SPB distribution in the United States, Tran and others (2007) observed 99 percent of the population to be prepupae in February. When the stage structure of the population becomes concentrated as larvae, it becomes increasingly likely that there will be a cessation of adult activity and a break in the continuity of pheromone plumes that would be required to organize the attacks of the dominant cohort when they complete development and emerge as adults in early spring (Friedenberg and others 2007a). This provides a parsimonious explanation for the characteristic dispersal of adults away from their natal spots in spring, which generally terminates the life of spots that were born the previous spring and survived into the winter. Hedden and Billings (1977) found relatively high lipid content in SPB adults emerging in spring, which they interpreted as an adaptation for supporting the energetic requirements of spring dispersal flights (but see Coppedge and others 1994). Forest Health personnel in New Jersey report that some individual SPB spots have remained active for multiple years, so there may be regional variation in the tendencies of SPB to disperse in the spring.