

# Extended Development in *Thanasimus dubius* (F.) (Coleoptera: Cleridae), a Predator of the Southern Pine Beetle<sup>1</sup>

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**ABSTRACT** *Thanasimus dubius* (F.) is an important predator of the southern pine beetle, *Dendroctonus frontalis* Zimmermann, a major pest of pine forests in the southern United States. We examined the development of *T. dubius* in the field using emergence traps, and by sampling the bark of trees previously attacked by *D. frontalis*. Over a 2-year period, several distinct episodes of *T. dubius* emergence occurred in trees enclosed by emergence traps, and bark sampling of other trees uncovered many *T. dubius* immatures almost 2 years after attack by *D. frontalis*. These results indicate that *T. dubius* development may be significantly longer and more variable under natural conditions than previously thought, and suggest that some individuals may undergo a diapause.

**KEY WORDS** *Thanasimus dubius*, *Dendroctonus frontalis*, diapause, predator-prey dynamics, biological control

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The southern pine beetle, *Dendroctonus frontalis* Zimmermann (Coleoptera: Scolytidae), is an important pest of pine forests in the southern United States (Price et al. 1992). The insect predator *Thanasimus dubius* (F.) (Coleoptera: Cleridae) is generally regarded as one of the most important natural enemies of *D. frontalis* (Thatcher and Pickard 1966, Moore 1972, Turnbow et al. 1978, Dixon and Payne 1979, Reeve et al. 1995). Both adult and larval *T. dubius* are predators of *D. frontalis*. As the host tree is attacked by adult *D. frontalis*, adult *T. dubius* arrive and prey on the individuals walking on the bark surface. The adult predators also deposit eggs within crevices in the bark, and after hatching the larvae feed on the immature stages of *D. frontalis* developing within the phloem. Late-instar larvae of *T. dubius* excavate cells in the corky outer bark of the tree, where the prepupae and pupae reside before emerging as adults.

Several studies have measured the development time of *T. dubius* under different temperature regimes (Thatcher and Pickard 1966, Mignot and Anderson 1969, Nebeker and Purser 1980, Turnbow and Franklin 1982, Lawson and Morgan 1992). This predator takes substantially longer to complete development than *D. frontalis* or other scolytids (such as *Ips* spp.) on which it

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preys. It completes the egg and larval stages in 49 to 56 days at 21°C (Nebeker and Purser 1980, Lawson and Morgan 1992), about the same time as required by *D. frontalis* to complete its entire life cycle (from egg to adult) and emerge from the host tree. Time spent as prepupae and pupae exceeds the time spent in the egg and larval stages. Data from Nebeker and Purser (1980) suggest a combined prepupal and pupal period of 87.1 days at 21°C, on average across different site and feeding treatments. Lawson and Morgan (1992) report a combined period of  $56.4 \pm 1.0$  days ( $\bar{X} \pm \text{SE}$ ) in their experiments at room temperature (20 to 25°C), but also noted that there was considerable variation among *T. dubius* individuals in their development time. In another experiment, they attempted to induce diapause in *T. dubius* by exposing both larvae and prepupae to low temperatures, but observed no significant effect of these treatments on *T. dubius* development time. They concluded that the prolonged prepupal and pupal period they observed was non-diapausal in nature.

This study was undertaken to demonstrate that *T. dubius* development may be significantly longer and more variable under natural conditions than previously reported, and that some individuals may undergo an extended period of diapause. The study was prompted by preliminary work indicating that *T. dubius* immatures were present in trees a year or more after mass attack by *D. frontalis* (L. M. Roton, unpublished data).

### Materials and Methods

The development of *T. dubius* was examined using emergence traps that continuously monitored the emergence of *T. dubius* adults from trees attacked by *D. frontalis*. Two trees attacked by *D. frontalis* were located in an infestation in the Catahoula Ranger District of the Kisatchie National Forest, in central Louisiana. Based upon the phenology of *D. frontalis*, it was estimated that these trees were initially attacked in fall 1992. The two trees were labeled A and B and observed until the emergence of the *D. frontalis* brood was nearly complete, in January 1993. Emergence traps enclosing the bole from a height of 2 to 3.5 m were then attached to each tree. This height range was chosen because there is typically a high frequency of *T. dubius* pupal cells within that area (Mizell and Nebeker 1981). The traps were cylindrical enclosures made of fine polyethylene screening, with two funnels made of galvanized metal screening attached at the bottom. These funnels were crescent-shaped in cross section and large enough to completely surround the bole, and ended in collecting jars filled with an ethylene glycol solution. Over a 2-year period, the jars were collected weekly and the emerging *T. dubius* adults sexed and counted. Sampling was discontinued on Tree B when it fell from high winds late in October 1994; the other tree was sampled through December 1994. These same traps also provided a means of determining when active *T. dubius* larvae were present inside the tree, without dissecting the bark. These larvae frequently leave the phloem and travel over the bark surface (Dix and Franklin 1977), apparently in search of *D. frontalis* entrance and emergence holes. Because of this behavior, the larvae often enter the funnels and are captured in traps of this design (J. D. Reeve, personal observation).

We also sampled for *T. dubius* immatures in a number of trees which had been attacked by *D. frontalis* almost 2 years previously. Two different sites, both dominated by mature loblolly pines, were sampled in September 1993. The first was located within the Catahoula Ranger District in the Kisatchie National Forest. As part of another study at this site, several small *D. frontalis* infestations were generated in December 1991 by "baiting" individual trees with turpentine and frontalin, the *D. frontalis* aggregation pheromone (Payne 1980). This combination of chemicals was highly attractive to *D. frontalis* (Payne et al. 1978) and mass attack of the baited trees occurred rapidly. Although the baited trees were later sampled and removed, a number of surrounding unbaited trees also were attacked by *D. frontalis* at the same time, and these infested trees were not removed and remained standing. We selected 10 of the latter for sampling, omitting those in which *D. frontalis* reproduction appeared to have failed (i.e., trees with few or no emergence holes). Such trees typically contain almost no *T. dubius* immatures (J. D. Reeve, personal observation). The second site was a large natural *D. frontalis* infestation within the Indian Mounds Wilderness Area of the Sabine National Forest in east Texas. In fall 1991, when this infestation was rapidly growing, newly-attacked trees were flagged and numbered at monthly intervals. Using this information, we located 10 trees attacked in October 1991 for sampling, again omitting those in which *D. frontalis* failed to reproduce.

The selected trees were sampled by gently scraping the bark surface with a drawknife, gradually exposing the contents of the *T. dubius* cells (Mizell and Nebeker 1981). We scraped a meter-wide band around each tree, with the center of the band at breast height ( $\approx 1.5$  m). This sampling height was selected because it was unsafe to climb or fell these trees in their advanced state of decay, as well as the fact that the bark only remained at the base of several trees. Recorded were the number of live *T. dubius* prepupae, pupae, and callow adults for each tree, any dead individuals that were found, and the number of empty cells. We also estimated the area of bark sampled (in  $\text{dm}^2$ ) for each tree, assuming a cylindrical shape with diameter equal to the tree's diameter at breast height. The area of bark sampled was used to convert the raw counts of *T. dubius* immatures into surface densities. Regression analysis was used to test for an association between the proportion of cells containing live *T. dubius* in a tree and the log density of all *T. dubius* cells, using SYSTAT statistical software (SYSTAT 1992).

## Results and Discussion

Using emergence traps, several distinct periods of *T. dubius* emergence were observed in the two trees sampled (Fig. 1). The first occurred in spring and early summer of 1993 and corresponds closely with the laboratory results at these temperatures (Nebeker and Purser 1980, Lawson and Morgan 1992). A second emergence episode occurred in fall 1993 in both trees, however, and perhaps a third in spring 1994 for Tree A. A final peak occurred from both trees in fall 1994, approximately 2 years after attack by *D. frontalis*. These results indicate that *T. dubius* development in nature may be significantly longer and more variable than has been observed in the laboratory, and also suggest that some

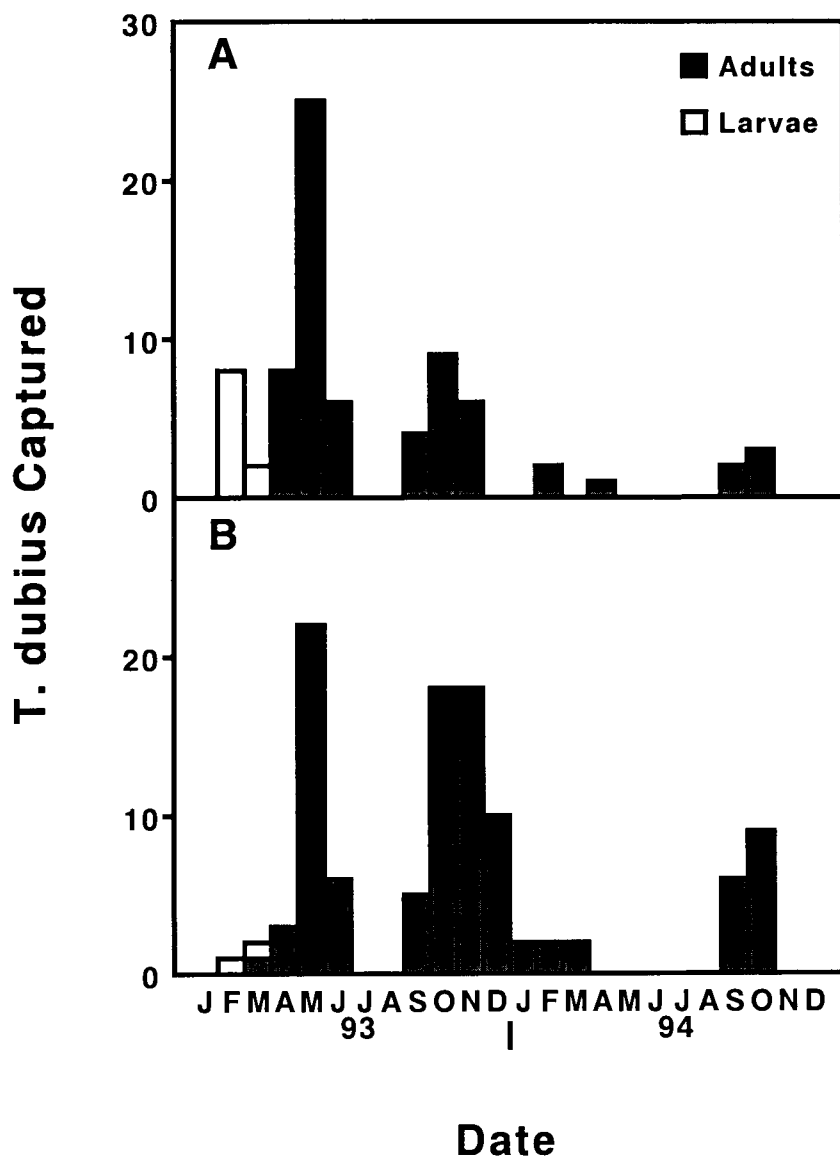


Fig. 1. Numbers of *T. dubius* larvae and adults captured by large emergence traps attached to two trees (A and B) within a *D. frontalis* infestation.

individuals undergo a period of diapause. However, an alternative explanation could be that several different generations develop within the same tree, with later generations consuming some unknown, alternative prey. We feel that a diapause is more likely for two reasons. First, *T. dubius* larvae were only captured near the beginning of observations on these trees. If several generations of *T. dubius* were reproducing within the tree, we would have expected to see an increase in the numbers of larvae before each emergence episode. Second, attempts to feed *T. dubius* larvae on alternative prey that would be common after *D. frontalis* emergence, such as cerambycid and buprestid larvae, have been unsuccessful (Mignot 1966).

A total of 181 and 301 *T. dubius* cells were uncovered through bark sampling at the Catahoula site and Indian Mounds sites, respectively. Averaging across trees, the mean density ( $\pm$  SE) of cells in the bark was  $0.254 \pm 0.068$  per  $\text{dm}^2$  at the Catahoula site, and  $0.315 \pm 0.087$  per  $\text{dm}^2$  at Indian Mounds. These densities were similar to those found in a previous study by Mizell and Nebeker (1981).

A substantial fraction of the cells sampled in our study contained live *T. dubius* immatures (Fig. 2). At the Catahoula site,  $31.8 \pm 7.6\%$  of the cells contained live *T. dubius* on average across the 10 trees, while at the Indian Mounds site  $38.2 \pm 6.7\%$  of the cells contained live *T. dubius* ( $\bar{X} \pm \text{SE}$ ). The most commonly encountered live stages were pupae, followed by prepupae and callow adults; relatively few dead individuals were observed (Fig. 2). An explanation for these results is that a fraction of *T. dubius* individuals undergo a period of diapause, particularly because data from the emergence traps suggest multiple episodes of *T. dubius* reproduction are unlikely (Fig. 1). Given that these trees were attacked in the fall of 1991, it is possible that some individuals remained within the trees nearly 2 years after attack by *D. frontalis*, about 15 months after they would have been predicted to emerge (in spring and early summer of 1992). Our data also suggest that extended development in *T. dubius* may be a relatively common phenomenon, having occurred at three different locations and in trees attacked by *D. frontalis* in both 1991 and 1992. A prolonged period of development has also been recorded in another species of clerid beetle, *Enoclerus zonatus* (Klug) (Powell 1975).

The proportion of cells containing live *T. dubius* increased significantly as the total density of *T. dubius* cells in the tree increased (Fig. 3). One possible explanation for this result is that extended development is somehow density dependent in *T. dubius*, perhaps because a higher fraction enter a diapause at high densities. An alternative hypothesis is that the incidence of diapause and the survival of *T. dubius* immatures prior to forming the pupal cell are related, perhaps because both are determined by the density of prey (*D. frontalis* brood) within the tree. These two possibilities cannot be distinguished using our data. Tauber et al. (1986) and Danks (1987) review examples of other insects in which crowding and the quantity of food can affect the incidence of diapause.

In an environment where there is considerable temporal variation in the probability of successful reproduction, selection can favor a strategy in which a significant fraction of the population delays its development (Hanski 1988). There are several potential sources of temporal variation in the reproductive success of *T. dubius*. An obvious one is the regular oscillations that occur in the

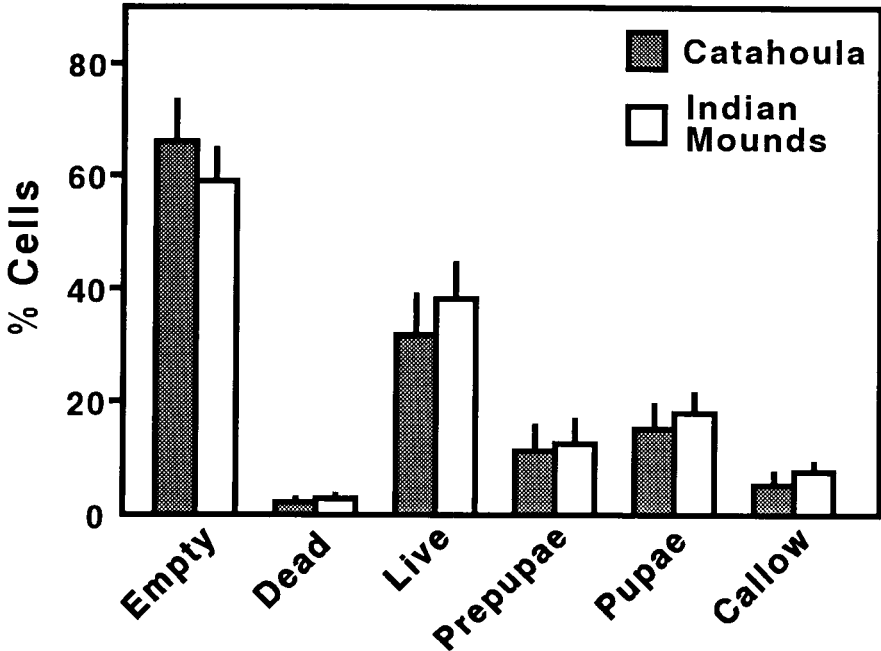


Fig. 2. Mean proportion ( $\pm$  SE) of *T. dubius* cells that were empty, had dead or live individuals of all stages, or had live prepupae, pupae, or callow adults. Each mean was based on the 10 trees within each study site.

density of *D. frontalis*. A time-series analysis of *D. frontalis* abundance in east Texas showed four episodes of outbreak and collapse over a 30-year period (Turchin et al. 1991). On a shorter time scale, seasonal factors like temperature may also affect the ability of *T. dubius* to reproduce. Adult *T. dubius* lay few eggs at temperatures above 25°C and might experience difficulties in reproducing during the summer months (Turnbow and Franklin 1980). It may be adaptive to avoid emerging during this period, thus explaining why no individuals were collected in July and August (Fig. 1).

Our results have certain implications for the dynamics of the *T. dubius*-*D. frontalis* interaction. In a time-series analysis of *D. frontalis* activity, Turchin et al. (1991) found that *D. frontalis* populations were apparently regulated by delayed density dependence, through the action of some unknown (as yet) agent operating with a 1-year time lag. The protracted development of *T. dubius* makes it a viable candidate for generating this delayed density dependence. In addition, theoretical studies suggest that a long development time in the predator, relative to the prey, has a strong destabilizing effect on predator-prey dynamics (Nunney 1985, Murdoch et al 1987, Godfray and Hassell 1989). It is

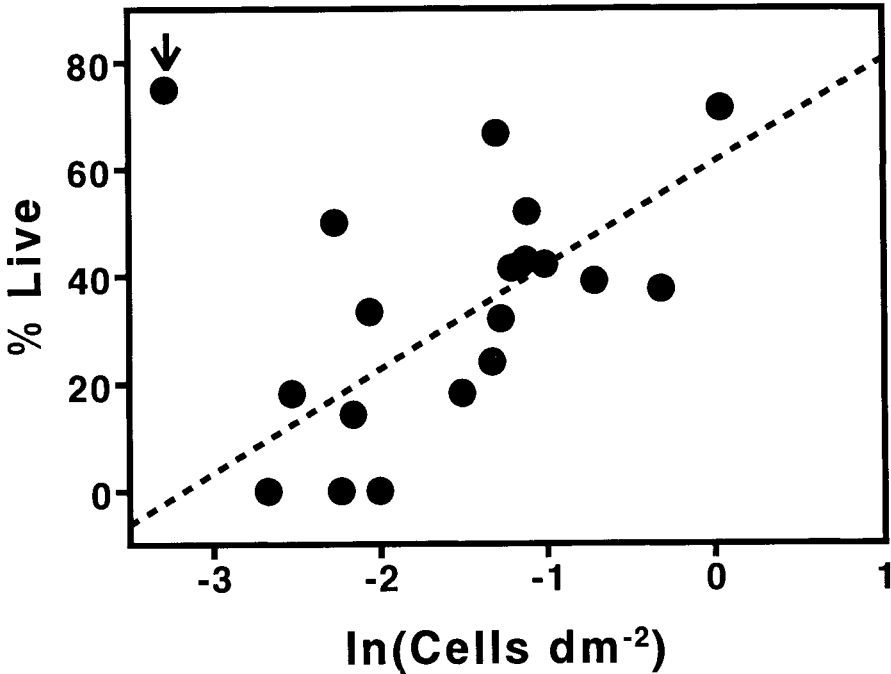


Fig. 3. Relationship between the proportion of *T. dubius* cells containing live individuals and the log density of cells, for data from both sites combined ( $y = 0.61 + 0.19x$ ,  $R^2 = 0.47$ ,  $df = 17$ ,  $P = 0.001$ ). A single point at low density (denoted by an arrow) appeared to be an outlier, and was omitted from the analysis.

conceivable that the extended development of *T. dubius* could have a destabilizing effect on *T. dubius*-*D. frontalis* dynamics, exacerbating the pronounced oscillations that occur in this system (Turchin et al. 1991).

Control operations for *D. frontalis* could be improved by modifications that consider the long life cycle of *T. dubius*. The most commonly advocated technique, "cut-and remove," removes all trees infested with *D. frontalis* and a buffer area of uninfested trees (Billings 1980, Swain and Remion 1983, USDA Forest Service 1987). It is also recommended that trees vacated by *D. frontalis* be left standing because their removal would have no effect on infestation growth, and permits the natural enemies of *D. frontalis* to complete their development and emerge. Our results provide further support for this recommendation because *T. dubius* immatures were often found in trees a year or more after *D. frontalis* attack. Many control operations, however, remove these vacated trees because of their potential salvage value. While this may provide some short-term economic benefits, removal of vacated trees could ultimately be detrimental to the biological

control of *D. frontalis* because it reduces the overall population of natural enemies, making it more likely new *D. frontalis* infestations will occur. When circumstances permit, it would be prudent to leave some proportion of these vacated trees intact to conserve *T. dubius* and other natural enemies.

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