

Complex emergence patterns in a bark beetle predator

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- Abstract**
- 1 The emergence pattern of *Thanasimus dubius* (F.) (Coleoptera: Cleridae), a common predator of the southern pine beetle, *Dendroctonus frontalis* Zimmermann (Coleoptera: Scolytidae), was studied under field conditions across different seasons. A simple statistical model was then developed to characterize the emergence data, using the truncated geometric distribution. Data are also presented on the mortality of *T. dubius* eggs at various temperatures and humidities in an effort to explain certain aspects of emergence behaviour.
 - 2 Emergence of *T. dubius* from a given tree usually occurred in several discrete episodes across a two-year period, with most individuals emerging in spring or autumn. Almost no emergence occurred in July and August, which may be an adaptation to avoid high temperature mortality. Emergence patterns appeared similar across seasons, with the time of year serving mainly to shift the pattern through time.
 - 3 Cycles in *D. frontalis* abundance may be the result of delayed density dependence generated by its natural enemy complex. The predator *T. dubius* is likely to be an important component of this delayed density dependence, because of its lengthy development time and apparent impact on *D. frontalis*.

Keywords Bark beetles, *Dendroctonus frontalis*, diapause, predators, *Thanasimus dubius*.

Introduction

The southern pine beetle, *Dendroctonus frontalis* Zimmermann (Coleoptera: Scolytidae), is an economically important pest of pine forests in the southern U.S.A. (Price *et al.* 1992). This native bark beetle is able to attack and kill living trees, typically loblolly (*Pinus taeda* L.) or shortleaf (*Pinus echinata* Mill.) pine, through a process of mass attack coordinated by aggregation pheromones (Payne, 1980). During this process thousands of beetles bore through the outer bark of the tree and begin constructing galleries in the phloem layer. Oleoresin is released by the tree in response to this activity, but the large number of simultaneous attacks usually exhausts this defence. Oviposition and brood development then occur in the girdled (and ultimately dead) tree. Once a tree is fully colonized, the attack process typically shifts to adjacent trees in the stand, the result being a cluster of freshly attacked trees, trees containing brood, and dead and vacated trees (Coulson, 1980). Mass attack and brood development occur more or less continuously throughout the year in the southern

U.S.A., and temperature-driven developmental models indicate that *D. frontalis* can complete about six generations per year (Ungerer *et al.* 1999). Periodic outbreaks are a prominent feature of *D. frontalis* dynamics in the southern part of its range, with the number of infestations varying by three orders of magnitude between endemic and outbreak periods (Turchin *et al.* 1991).

A large community of natural enemies is associated with *D. frontalis*, arriving during mass attack or later on in brood development (Camors & Payne, 1973; Dixon & Payne, 1979b). A number of studies indicate that this community can cause significant mortality of *D. frontalis* brood inside the tree (Moore, 1972; Linit & Stephen, 1983), with the strongest impact occurring in the year following peak *D. frontalis* abundance (Turchin *et al.*, 1999). This delayed density dependence, generated by natural enemies, is a possible explanation for the cyclic nature of *D. frontalis* outbreaks (Turchin *et al.*, 1999; Reeve & Turchin, 2000). Although these studies have not identified which natural enemies are most responsible for the delayed response, the common predator *Thanasimus dubius* (F.) (Coleoptera: Cleridae) is a promising candidate. This predator appears to be a significant source of *D. frontalis* mortality (Thatcher & Pickard, 1966; Tumbow *et al.*, 1978; Reeve, 1997;

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Reeve & Turchin, 2000), and high densities of *T. dubius* are often associated with declining and low level *D. frontalis* populations (Billings, 1988; Reeve, 1997; Turchin *et al.*, 1999), as would be expected if they are agents of delayed density dependence. Adult *T. dubius* arrive almost immediately after mass attack is initiated, attracted by the pheromones of *D. frontalis* (Vité & Williamson, 1970; Dixon & Payne, 1979a). They then prey on the adult *D. frontalis* arriving on the tree and oviposit in crevices in the bark. The larvae feed on the developing *D. frontalis* brood within the phloem, then enter a non-feeding prepupal stage and construct cells in the outer bark, before emerging as adults (Thatcher & Pickard, 1966; Mizell & Nebeker, 1981; Turnbow & Franklin, 1982).

Given the potential influence of natural enemies on *D. frontalis* dynamics, it becomes critical to examine the life cycles of these organisms under field conditions. A natural enemy with a long life cycle relative to *D. frontalis*, for example, would provide a simple explanation for the delayed density dependence in this system. Previous studies of *T. dubius* have examined its development in the laboratory at constant temperatures, where it displays a unimodal distribution of emergence times and a life cycle two or three times as long as *D. frontalis* (Mignot & Anderson, 1969; Nebeker & Purser, 1980; Lawson & Morgan, 1992). However, a preliminary field study found a much more complex pattern of development, including several peaks of emergence, and some individuals emerging nearly 2 years after *D. frontalis* attack (Reeve *et al.*, 1996). In this paper, I examine in more detail the development of *T. dubius* under field conditions. Emergence behaviour is examined for different seasons of the year, because time of year often influences the developmental decisions of insects (Tauber *et al.*, 1986). A simple statistical model of emergence behaviour is then developed using the truncated geometric distribution, and its predictions compared with the actual pattern of emergence. I also present data on the mortality of *T. dubius* eggs at various temperatures and humidities, in an effort to explain certain aspects of emergence behaviour, and review similar studies on egg, larval and adult survival. I then compare the pattern seen for *T. dubius* with other species in this family that attack eruptive bark beetles.

Materials and methods

Sampling the emergence of *T. dubius*

I used two different methods to sample the emergence of *T. dubius* from infested trees: (1) field cages attached to the trees, and (2) rearing boxes containing cut logs. Both techniques were used because it was not clear at the onset of the study which method would prove most effective. (For example, field cages may provide more natural conditions but only function as long as the infested tree remains standing.) The field cages were cylindrical enclosures made of fine polyethylene screening, that encircled a section of the bole from approximately 2–3.5 m in height. To ensure a close fit to the tree, the bark was smoothed at the top and bottom of the cage with a drawknife, a bead of caulk applied to the bark, and the cage pulled tight with a drawstring and sealed with duct tape. The bottom of each cage ended in two collecting funnels leading to jars filled with an ethylene glycol

(antifreeze) solution. The rearing boxes were rectangular wooden enclosures (121 X 56 X 56 cm) with three sides made of screening, and a large collecting funnel at the bottom. The boxes were located in shaded locations adjacent to a laboratory building. Both methods of sampling appeared to yield equivalent results, although the field cages sometimes had to be abandoned when the infested trees were felled by decay and high winds.

I sampled a total of nine beetle infestations from 1994 to 1996 (designated C–K) in the Kisatchie and Sabine National Forests, located in central Louisiana and east Texas. An effort was made to sample infestations in each of the four seasons of the year, because this factor could potentially affect the emergence patterns. The infestations were classified as winter, spring, summer, or autumn infestations by the date of *D. frontalis* emergence from the trees, which was determined by periodic checking of the brood within the trees. It was not possible in most cases to determine the exact date of initial *D. frontalis* attack, because the infestations were often undetected at that point. However, attack probably occurred 2–3 months before *D. frontalis* emergence in winter trees, 1–2 months before in spring trees, and only one month before in summer trees. Within each infestation, trees were examined until a maximum of four trees were found from which *D. frontalis* had recently emerged, ranging from 15 to 40 cm in diameter at breast height. Field cages were then attached to one or two trees in each infestation selected at random. The remaining one or two trees were felled and three 1 m logs removed from each tree and placed in rearing boxes. Both rearing boxes and field cages were checked every 1–2 weeks for emerging *T. dubius* adults, and any larvae that had fallen into the collecting jars. Preliminary data from infestations C–F indicated that no emergence occurred more than 2 years after sampling was begun, so later infestations were sampled no longer than this period. Sampling was also terminated if the tree fell or if no individuals had emerged for a year. Trees with less than 10 emerging *T. dubius* adults were excluded from subsequent analyses. This left a total of eight winter trees in three infestations (C, K and J), four spring trees in two infestations (D and H), and six summer trees in three infestations (E, F, I). The density of *T. dubius* in each tree was estimated by dividing the total number emerged by the surface area trapped. Densities were calculated for only those trees where emergence was judged to be complete, which eliminated a number of caged trees that fell early in the sampling. Data from two trees in infestation C have been published previously (Reeve *et al.*, 1996).

Distribution of emergence times

Preliminary analysis of the data suggested that emergence occurs in several distinct episodes for a given tree, with most occurring in either spring or autumn. The number emerging per episode also typically decreased through time. A tree might therefore have a large emergence peak in the spring of the first year of sampling, a smaller one that autumn, and smaller yet peaks in the spring and autumn of the second year of sampling. This pattern suggests that the emergence data follow a geometric distribution, with a probability s that emergence occurs in each successive spring or autumn. To test this hypothesis, I first converted the data into a form suitable for fitting the distribution. For each tree,

I divided the year into 6-month intervals encompassing spring and autumn, i.e. January-June and July-December, then summed the number emerging in each interval. This yielded a maximum of four numbers for each tree, as sampling was continued for no more than 2 years. I then fitted the truncated geometric distribution to the data, for which the probability of emerging in the x th interval is given by the equation

$$P[X = x] = \frac{s(1-s)^{x-1}}{\sum_{j=1}^m s(1-s)^{j-1}} \quad x = 1, 2, \dots, m, \quad (1)$$

where m is the maximum number of intervals sampled (Mood *et al.*, 1974). The truncated geometric was used because sampling was truncated either by design or naturally when the tree fell. The parameters gives an indication of the overall shape of the distribution, with values near one indicating that most individuals emerge in one episode, whereas small values imply emergence was distributed over several. Maximum likelihood estimates of s were obtained using the module MAXLIK in the GAUSS language (Aptech Systems Inc., 1992). For eight of the trees there were sufficient data for a χ^2 goodness-of-fit test to the truncated geometric distribution. One-way ANOVA was used to examine the effect of season on the value of s using SYSTAT 9 (SPSS Inc., 1999). In addition, the frequency of male and female *T. dubius* in the first emergence interval vs. all later ones was compared using Fisher's exact test.

Survivorship of *T. dubius* eggs under different environmental regimens

A growth chamber was used to examine the effects of temperature and humidity on the survival of *T. dubius* eggs. The eggs were obtained from the third and fourth generation of a laboratory culture of *T. dubius*, initiated from approximately 30 wild individuals collected in the Kisatchie National Forest. This culture was maintained using an artificial diet (J. D. Reeve, M. G. Rojas, and J. A. Morales, unpublished data) for *T. dubius* larvae, whereas the adult beetles were fed adult *Callosobruchus maculatus* (F.) (Coleoptera: Bruchidae) (Nebeker *et al.*, 1980). Eggs were collected from the culture three times per week, and the most recently laid eggs (which were translucent in appearance) separated for use in the experiment. Batches of about 200 eggs were then reared at one of six different temperatures (15, 20, 25, 30, 35 and 37.5 °C), with the sequence of the temperature treatments chosen at random. The batch was subdivided into three roughly equal groups and distributed among dessicators where the relative humidity was maintained at 55% or 76% using saturated salt solutions (Ca(NO₃)₂ or NaCl), or near 100% with water alone (Peterson, 1964). The experiment thus had a total of 18 treatments, six temperatures crossed with three humidities. The eggs were observed daily and the number of hatched larvae recorded. The number of dead eggs was then calculated as the initial number of eggs minus the number of hatched larvae.

I used logistic regression to examine the effect of temperature and humidity on egg mortality (Hosmer & Lemeshow, 1989). Preliminary analyses showed that temperature had a very strong

effect on egg mortality above 30 °C, but it was relatively constant below this temperature. To incorporate this effect in the regression, a transformed temperature variable was constructed that was equal to $(T - 30)^4$ above 30 °C, where T is temperature, and equal to zero below 30 °C. This term provided the best fit to the data compared with lower or higher powers in the transformation. There were some cells with zero counts in the data set, because total mortality occurred at 37.5 °C. To deal with this problem, a small constant, 1×10^{-6} , was added to the counts for all cells. The value of the constant was determined in a sensitivity analysis, in which progressively smaller constants were used until the parameter estimates and goodness-of-fit statistics became stable (Agresti, 1990). The analyses were run using the logistic regression procedure in SYSTAT (SPSS Inc., 1999).

Results

Typical emergence patterns are shown in Fig. 1, for trees where sampling was initiated in the winter, spring, or summer, just after *D. frontalis* emergence. Nearly all trees had at least two and some as many as four different emergence episodes, centred around spring and autumn, with some individuals emerging during the second year of sampling. The first emergence episode was in general the largest. Only a few individuals emerged in the summer months of July and August, and emergence in summer trees (Fig. 1C) was apparently delayed until autumn. Male and female emergence appeared to be equally distributed over time. Small numbers of *T. dubius* larvae were often trapped at the beginning of sampling, usually preceding but sometimes overlapping the first emergence episode, but were never trapped after this time.

Estimates of s and other statistics are given in Table 1. All but one tree had a value of s less than one, while the mean development time was greater than one. Both results reflect the fact that emergence occurred in two or more episodes per tree. The value of s provided a useful overall characterization of the emergence pattern, with smaller values of s indicating a greater fraction of individuals undergoing delayed development. However, the truncated geometric distribution failed to fit the data (the χ^2 goodness-of-fit test was significant) in four of eight possible cases (Table 1). This result probably indicates a more complex pattern of development (at least in some trees) than can be described by this simple distribution. One-way ANOVA revealed a marginally significant effect of season on s ($F_{2,15} = 4.308$, $P = 0.033$), with the smallest values of s occurring in winter trees ($\bar{s} = 0.528 \pm 0.113$), followed by spring ($\bar{s} = 0.667 \pm 0.033$) and then summer ($\bar{s} = 0.890 \pm 0.040$). Averaging across all trees, the mean density of emerging adults was 0.279 ± 0.053 per 100 cm². Sex ratio did not differ significantly between the first emergence episode vs. later episodes (Table 1).

Egg mortality was strongly influenced by temperature above 30 °C but was relatively constant below this temperature (Fig. 2A). The mortality rate was approximately 20% at or below 30 °C, increasing to 50% at 35 °C and 100% at 37.5 °C. The temperature term in the logistic regression analysis was highly significant, whereas the humidity terms were non-significant (Table 2).

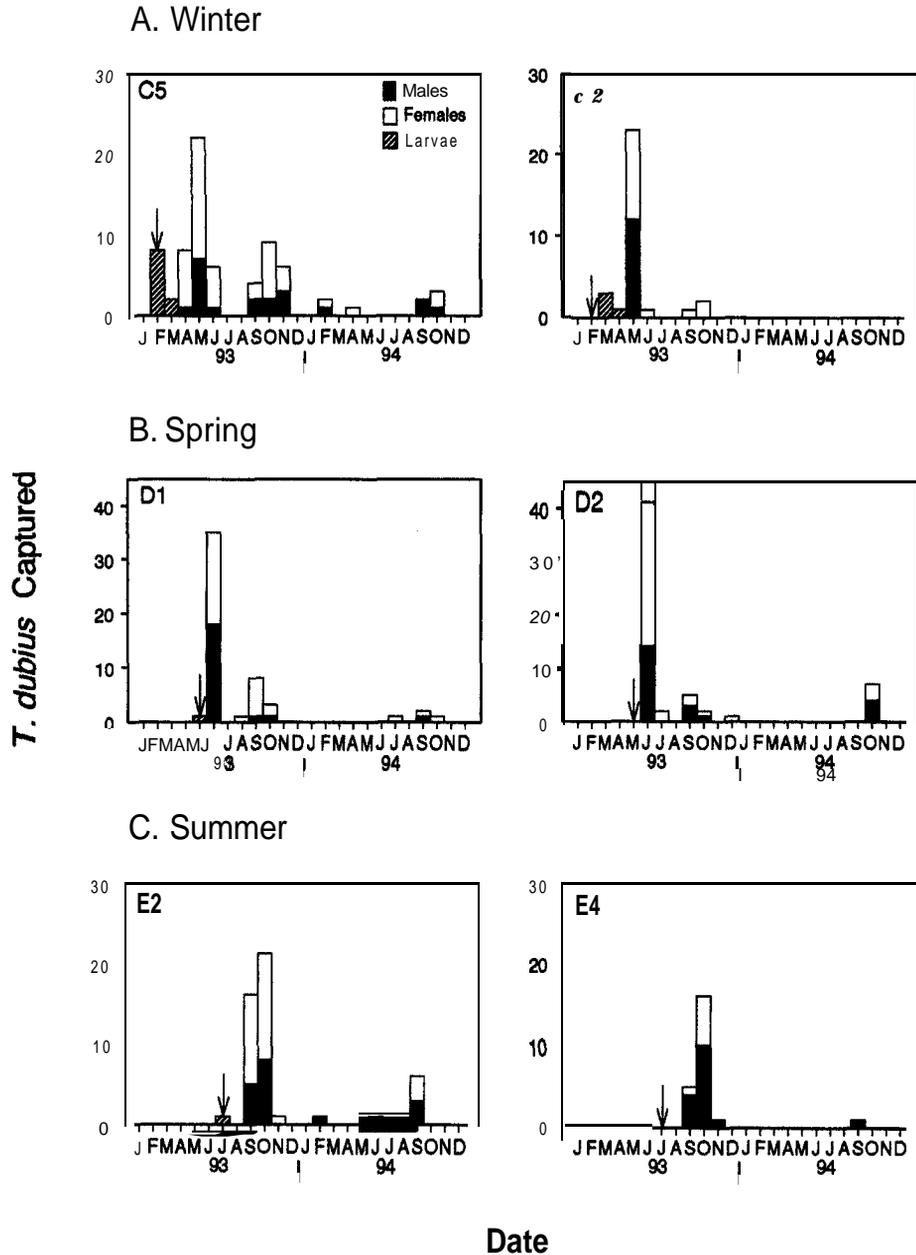


Figure 1 Examples of *T. dubius* emergence for trees where sampling was initiated in the winter (A), spring (B), or summer (C). An arrow indicates the first sampling date. Trees are identified in the upper right-hand corner of each graph using the same designations as Table 1.

Discussion

Emergence behaviour for *T. dubius* was complex and heterogeneous. Emergence generally occurred in several different episodes distributed across a 2-year period, with the bulk of the emergence in spring and autumn. The first emergence episode for a given tree roughly coincides with the development time found in laboratory studies at constant temperatures (Nebeker & Purser, 1980; Lawson & Morgan, 1992). For those emerging after the first peak there are two likely explanations: (1) some individuals undergo a period of diapause (Tauber *et al.*, 1986),

probably as prepupae in their cells in the outer bark, or (2) some larvae take considerably longer to develop, perhaps due to a shortage of prey inside the tree. The second explanation seems less probable given the pattern observed for *T. dubius* larvae (Fig. 1). These larvae are highly active and often travel on the bark surface (Dix & Franklin, 1977) and if present would have been trapped by either sampling method. The fact that they were only captured before the first episode suggests that a period of diapause is the most likely explanation for these emergence patterns. However, some variability in larval development times could help explain why certain individuals underwent diapause

Table1 Maximum likelihood estimates of s and χ^2 goodness-of-fit tests for the truncated geometric distribution. Also shown are the total number (n) and density of *T. dubius* emerged (number per 100 cm² of surface area). The mean development time was calculated as the mean number of 6-month intervals taken to emerge. Fisher's exact test is used to compare the frequency of male and female *T. dubius* in the first emergence interval vs. all later ones combined.

Season	Tree	Cage/Cut	n	Intervals sampled*	s	χ^2	d.f.	P	Mean devel. time	Number per 100 cm ²	Fisher's exact test	
Winter	C1	Cut	43	4	0.935				1.070	0.219	ns	
	c2	Cut	27	4	0.900		-		1.111	0.277	ns	
	c5	Cage	63	4	0.557	3.976	2	ns	1.635	0.495	ns	
	C6	Cage	102	4	0.314	26.810	2	< 0.001	2.039	0.772	ns	
	K1	cut	68	4	0.637	8.005	2	< 0.025	1.500	0.315	ns	
	K2	Cage	22	2	0†				1.772		ns	
	K3	Cage	29	4	0.257	22.464	2	< 0.001	2.138	0.269	ns	
	J1	Cage	17	4	0.619	0.263	1	ns	1.529	0.110	ns	
	Spring	D1	cut	51	4	0.661	0.278	1	ns	1.451	0.277	0.035
		D2	Cage	58	4	0.616	1.732	1	ns	1.534	0.325	ns
H1		Cage	11	2	0.625				1.273		ns	
H2		Cage	10	4	0.762				1.300	0.048	ns	
Summer	E1	Cage	20	2	0.947		-		1.050		ns	
	E2	cut	46	4	0.759	9.934	1	< 0.005	1.304	0.275	ns	
	E3	Cage	11	2	0.778		-	-	1.182		ns	
	E4	cut	23	4	0.920				1.087	0.165	ns	
	F4	Cage	16	2	0.933				1.063		ns	
		Cage	13	3	1‡				1.000	0.077		

* Total number of 6-month intervals sampled.

‡ $s = 0$ because more individuals emerged in the second than the first interval

† $s = 1$ because all individuals emerged in the first interval.

while others developed immediately, even within the same tree. As environmental cues indicate the approach of summer and poor conditions for reproduction (see below), slower developing larvae may be more likely to enter diapause and wait for better opportunities (Cohen, 1970; Tauber *et al.*, 1986; Bradford & Roff, 1993).

Emergence patterns appeared more similar than different across the seasons, with season mainly serving to shift the pattern through time. There was some indication that delayed emergence was more common in winter and spring vs. summer trees, because s differed significantly across seasons, but every season showed delayed emergence. A more prominent feature of the data was the absence of emergence in July and August (see Fig. 1). This behaviour may have evolved to avoid exposure to high summer temperatures and hence increased mortality. Maximum daily temperatures in July and August fall frequently into a range sufficient to cause high egg mortality (Fig. 2B). Similar results were found by Mignot & Anderson (1969), who demonstrated that egg, larval and adult mortality increased at high temperatures. By contrast, (Tumbow & Franklin, 1980) observed little or no egg mortality at temperatures at or below 35 °C, but did find that oviposition rates were sharply reduced at high temperatures. The combined effect of temperature on mortality and oviposition rates would probably generate strong selective pressure for diapause during the summer months. Conversely, under field conditions the overall mortality rate of prepupae in their bark cells is very low (Reeve *et al.*, 1996). In this study, prepupae were exposed to the full seasonal range of temperatures across a 2-year period, and it seems plausible that they are more resistant to temperature extremes than the egg stage.

The geographical distribution of *T. dubius* is very broad, apparently extending from Wisconsin (Schenk & Benjamin, 1969) south to Texas and Louisiana (Thatcher & Pickard, 1966). Across this range of climates one would expect to see a cline in the number of generations per year and the pattern of diapause, as seen in many other insects (Istock, 1981; Showers, 1981; Tauber *et al.*, 1986). In Louisiana and Texas, *T. dubius* could potentially have two generations per year, but with a significant proportion of the population having one generation per year or even one generation every 2 years. It is likely that in more northern populations this mixture would shift toward generation times of one and 2 years. Two other clerid species also display various mixtures of generation times. *Thanasimus Zeconeti* (Wolcott) is a predator of the western pine beetle, *Dendroctonus brevicornis* Le Conte, in western North America. This predator can complete two generations per year (while its prey completes three), but 5–20% of the population take a year to complete development (Person, 1940; Berryman, 1970). In northern Europe, *Thanasimus formicarius* (L.) primarily has one generation every 2 years, but a small fraction of the population is univoltine (Schroeder, 1999).

Why does such a complex pattern of emergence occur in *T. dubius*, in which some individuals develop immediately whereas others apparently undergo a lengthy diapause? This behaviour could have evolved as a risk-spreading strategy in response to temporal variation in reproductive success. In this scenario, each female produces both diapause and non-diapause offspring, with diapausers being favoured in more variable environments (Cohen, 1966; Ellner, 1985; Ellner, 1987; Hanski, 1988; Hopper, 1999). There is likely to be substantial variation of this type for *T. dubius* because the number of *D. frontalis*

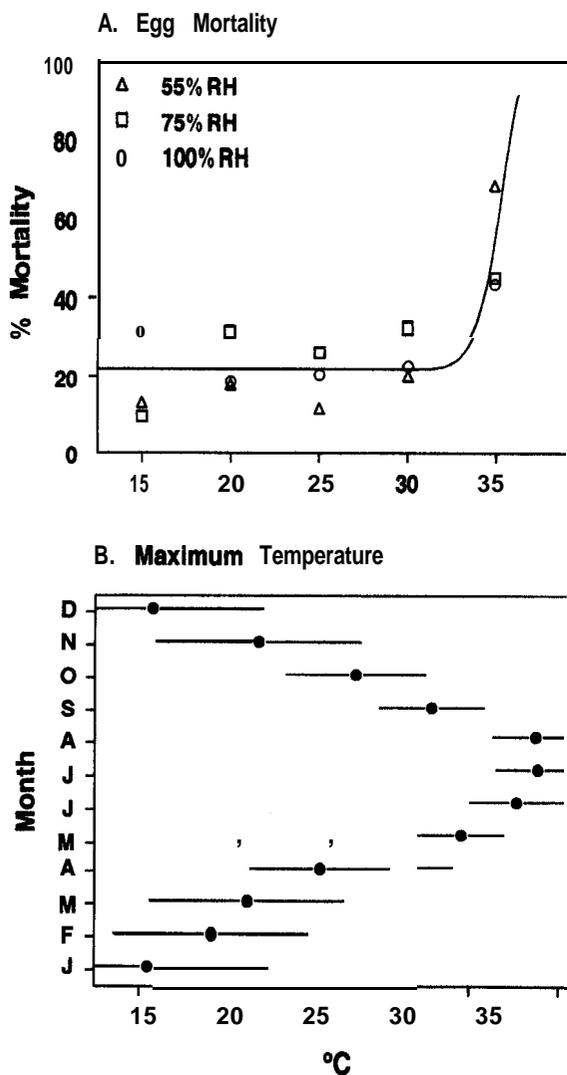


Figure 2 (A) Percent mortality of *T. dubius* eggs at various temperatures and humidities. The fitted curve for the logistic regression model is also shown, averaged across the three humidity treatments. (B) Mean maximum temperatures for the 15th of each month (\pm SD) from 1930–1993 weather records for Alexandria, Louisiana (National Climatic Data Center, 1995).

infestations (and hence prey availability) fluctuates greatly during the outbreak cycle (Turchin *et al.*, 1991). Alternatively, it may be that the pattern observed for *T. dubius* is a genetic polymorphism in which different genotypes either develop immediately or undergo diapause. The polymorphism would be maintained by a shifting pattern of selection in which the optimal strategy changes from year to year, or by gene flow between populations with different strategies (Hairston & Dillon, 1990; Bradford & Roff, 1993). Studies of diapause behaviour at the individual level, including the heritability of diapause, would be necessary to resolve this question (Bradford & Roff, 1993; Hopper, 1999).

Given the results presented here, it seems likely that *T. dubius* is a component of the delayed response seen in the natural enemy community (Turchin *et al.*, 1999). This predator could at best complete two generations per year, whereas *D. frontalis* has the potential for six generations (Ungerer *et al.*, 1999), and the occurrence of a diapause in some individuals would add further delays to its numerical response. A simple predator-prey model that incorporates these features, including spring and autumn episodes of emergence and periods of diapause, generates delayed density dependence and cycles similar in period and amplitude to those known for *D. frontalis* (Reeve & Turchin, 2000). A possible complicating factor in this system is the existence of alternative prey for *T. dubius*, in particular three species of *Ips* (*I. avulsus*, *I. calligraphus* and *I. grandicollis*) that attack southern pines (Hopping, 1964, 1965). Unlike *D. frontalis*, which can become exceedingly rare between outbreaks, trapping data suggest *Ips* may always be available as prey (J. D. Reeve, unpublished data). *Ips* are probably not the preferred prey for *T. dubius*, because they appear much more attracted to *D. frontalis* than *Ips* pheromones (Billings & Cameron, 1984; Billings, 1985). However, these alternative prey may provide a resource base for *T. dubius* when *D. frontalis* are scarce, and so set a lower limit to predator density. Alternative prey also raise the intriguing possibility of switching behaviour (Murdoch, 1975), with *T. dubius* changing its preference for the different prey species in response to fluctuations in *D. frontalis* abundance (Billings & Cameron, 1984; Mizell *et al.*, 1984). Studies by the author and collaborators are further evaluating these factors and their effects on *D. frontalis* dynamics.

Table 2 Logistic regression analysis of the effect of temperature and humidity on egg mortality. Humidity was treated as a categorical and temperature as a continuous variable in the analysis. The overall model was highly significant as compared to a model including only a constant ($\chi^2 = 466.3$, d.f. = 3, $P < 10^{-15}$).

Variable	Estimate	Odds Ratio	SE	t-ratio	P
Constant	-1.3049		0.0739	-17.664	$< 10^{-15}$
Humidity					
55%	-0.0826	0.9207	0.0941	-0.878	0.380
75%	0.0476	1.0487	0.0912	0.521	0.602
Transformed temperature*	0.0023	1.0023	0.0002	10.349	$< 10^{-15}$

* See formula in Materials and Methods.

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