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Predation and bark beetle dynamics

Abstract Bark beetle populations may undergo dramatic fluctuations and are often important pests in coniferous forests. Their dynamics are thought to be primarily driven by factors affecting the resistance of the host tree to attack, i.e., bottom-up forces, while natural enemies are usually assigned a minor role in these systems. I present behavioral experiments that suggest that the clerid beetle *Thanasimus dubius* may be an important source of mortality for the bark beetle *Dendroctonus frontalis* during attack of the host tree, and determine the nature of the functional response of *T. dubius* under conditions close to natural. I also examine the numerical response of *T. dubius* to large-scale fluctuations in *D. frontalis* density, and the relationship between bark beetle population trends and predator density, and find that beetle populations tend to decline when predator densities are high. Combined with the effects of clerid larvae on bark beetle broods, these results suggest that top-down forces generated by natural enemies could also be an important component of bark beetle dynamics. The implications of these results for bark beetle dynamics are discussed in relation to the prolonged life-cycle of clerid beetles.

Key words Scolytidae · Cleridae · Predation · Ratio dependence

Introduction

Populations of bark beetles (Coleoptera: Scolytidae) may undergo dramatic fluctuations and are often important pests in coniferous forests. Outbreaks are believed to occur when some factor, such as drought or aging, reduces the ability of the tree to resist beetle attack through its oleoresin system (Rudinsky 1962; Berryman 1972, 1973; Raffa and Berryman 1983; Berryman and Ferrell 1988; Christiansen and Bakke 1988; Raffa 1988), although there is evidence that the relationship between resistance and water stress is not simple (Lorio 1988; Lorio et al. 1990). As their densities increase, beetles are often able to overcome even resistant trees through mass attack, and the population may only collapse when the supply of host trees has been depleted. In contrast, natural enemies are usually assigned a minor role in bark beetle dynamics, at best only accelerating the collapse of the beetle population (Berryman 1973; Berryman and Ferrell 1988; Grégoire 1988). Bark beetle dynamics would appear to be primarily driven by factors affecting the resistance of the host tree to attack, and are thus dominated by bottom-up forces (Hunter and Price 1992; Power 1992).

There is increasing evidence, however, that natural enemies may be important factors in the dynamics of at least some bark beetles. Studies using exclusion cages have shown that the natural enemy complex as a whole can inflict significant mortality on the brood (immature stages) of bark beetles within an infested tree (Linit and Stephen 1983; Miller 1984, 1986; Riley and Goyer 1986, Weslien 1992). Clerid beetles (Coleoptera: Cleridae) in particular appear to be major natural enemies in several systems, preying on both bark beetle adults and their brood. Studies of *Thanasimus formicarius* (L.) have shown that its larvae can generate high levels of brood mortality in *Ips typographus* (L.) (Mills 1985; Weslien and Regnander 1992; Weslien 1994) and *Tomicus piniperda* (L.) (Schroeder and Weslien 1994) in Eurasia, and *Thanasimus dubius* (F.) larvae are thought to be important predators on *Ips grandicollis* (Eichh.) and *Dendroctonus frontalis* Zimm. in North America and Australia (Thatcher and Pickard 1966; Mignot and Anderson 1969; Moore 1972; Linit and Stephen 1983; Lawson and Morgan 1992). There is less quantitative information on the impact of adult clerids on adult bark beetles. Fiske (1908) found numerous fragments of adult *D. frontalis*

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lodged in the bark crevices of trees where adult *T. dubius* were abundant, which suggests a high predation rate. Thatcher and Pickard (1966) released *D. frontalis* and *T. dubius* adults into a room containing a freshly cut pine log and found that predation reduced the number of bark beetles successfully attacking the log by about 50%. In contrast, some studies have reported very low densities of adult clerids (Schmid 1970), or few encounters between predator and prey resulting in predation (Bunt et al. 1980). Studies in simple laboratory arenas provide further indications that adult clerids can potentially consume large numbers of bark beetles, and have also provided detailed information on their behavior (Berryman 1966; Turnbow et al. 1978; Nebeker and Mizell 1980; Turnbow and Franklin 1980; Frazier et al. 1981).

In this paper, I present behavioral experiments that manipulate the densities of adult *D. frontalis* and *T. dubius* on caged pine logs ("bolts") in an effort to estimate the mortality inflicted by adult *T. dubius* under conditions close to natural, and investigate its functional response. While it would be desirable to estimate predation rates in the field, this is impractical because overlapping bark scales conceal the insects much of the time, making it difficult to determine their densities. Much of the evidence of predation, detached *D. frontalis* body parts, would also be lost under field conditions. I examine also the numerical response of *T. dubius* to large-scale fluctuations in *D. frontalis* density, and the relationship between bark beetle population trends and predator density, using data from a long-term survey that spans the most recent outbreak in central Louisiana. The results indicate that *T. dubius* may be an important source of bark beetle mortality during attack of the host tree, and that *D. frontalis* populations tend to decline when predator densities are high. The implications of these results for the population dynamics of *D. frontalis* are discussed in relation to the prolonged life-cycle of *T. dubius*.

Materials and methods

Natural history

In common with a number of other bark beetles, *D. frontalis* can mass attack and kill living trees. Favored hosts in the southern United States are loblolly pine, *Pinus taeda* L., and shortleaf pine, *P. echinata* Mill. (Payne 1980). The mass attack process is initiated by adult females, which bore into the tree and release pheromones that attract large numbers of other beetles, overwhelming the defenses (the oleoresin system) of the host tree (Payne 1980). Adult *T. dubius* arrive shortly after mass attack has been initiated, attracted by the pheromones emitted by *D. frontalis* and volatiles from the damaged host tree (Vité and Williamson 1970; Dixon and Payne 1979a,b, 1980). These predators catch and consume the adult bark beetles arriving on the tree (Thatcher and Pickard 1966), but once the beetles have bored into the tree they are invulnerable to predation. Mating and oviposition by *T. dubius* occurs on the bark surface, and after hatching the larvae enter the phloem were they feed on the brood of *D. frontalis* within the tree (Thatcher and Pickard 1966).

Estimation of adult predator densities

As a precursor to laboratory studies of *T. dubius* and *D. frontalis* behavior (see below), I estimated the density of adult predators on trees undergoing mass attack by *D. frontalis*. Trees currently under attack were first located within *D. frontalis* infestations, and traps were then attached to the bark surface to sample the resident population of adult *T. dubius*. The traps were cylindrical enclosures made of fine polyethylene screening, 1.5 m in length, with two collecting funnels at the bottom. They were attached near the center of the vertical distribution of *D. frontalis* attacks, at a height of 4 m on the bole (Fargo et al. 1978). To prevent any insects from escaping the sample area, the bottom of the trap was attached first, and the screening of the trap was then raised quickly up the bole and sealed. The traps were left in place for 1 week, an interval sufficient for the majority of *T. dubius* present to fall into the collecting funnels (J.D. Reeve, unpublished data). A total of 21 trees (loblolly or shortleaf pines) in eight infestations were sampled across a 2-year period, with a maximum of three trees sampled per infestation. The density of *T. dubius* was expressed as number/dm^2 of bole surface, calculated by dividing the total predators caught by the surface area enclosed by the trap.

Laboratory studies of predation by *T. dubius*

I used the fact that *D. frontalis* will readily attack fresh pine bolts in the laboratory (Thatcher and Pickard 1966) to estimate predation rates by *T. dubius* under conditions resembling those in the field, but where densities can be controlled and the fate of the prey readily determined. I used bolts cut from mature loblolly pines (80 cm long and 20 cm in diameter) as arenas for these studies, with 50 cm of the bolt enclosed by a spherical screen cage 60 cm in diameter. The cage was attached at the top and bottom using duct tape, after smoothing the bark at the attachment points to obtain a close fit. Four different predator densities were used in the experiments (0, 10, 20, and 40 adult *T. dubius*) and crossed with three prey densities (100, 200, and 400 adult *D. frontalis*), yielding a total of 12 treatment combinations. The predator treatments were chosen to represent a range of predator densities similar to that observed in the field, from 0 to 1.25 predators/dm^2 (see Results). Equal proportions of males and females were used in the predator treatments. The prey densities were selected to create a range of attack densities representative of a 1-day period (the experimental time interval) in nature, given what is known about overall attack densities and the duration of mass attack (Fargo et al. 1978; Dixon and Payne 1979a; Coulson 1980). The experiments were conducted in an environmental chamber set at a constant 23°C and illuminated with fluorescent light from 0700 to 1900 hours. The overall experiment was divided into three temporal blocks, each 2 months long; within each temporal block, every treatment combination was replicated once, with the order randomly determined.

Adult *T. dubius* were collected for the experiments using baited multiple-funnel traps (see description below) and were stored in a refrigerator for no longer than 2 weeks. Adult *D. frontalis* were reared from naturally infested bark or logs, and were collected daily and immediately used in the experiments. The predators were starved for 1 day at room temperature (approximately 23°C) before the experiment to standardize their hunger levels, and then added to the arena. Adult *D. frontalis* were then added and allowed to interact with the predators for a period of 1 day. All experiments were initiated between 1200 and 1500 hours, near the peak time of *D. frontalis* arrival on trees in the field (Dixon and Payne 1979a). At the end of the experiment, the bolt was dissected to determine the number of beetles that had bored through the outer bark and entered the bolt, and the detached elytra in the cage were counted. The number of detached elytra was used to estimate the number of adult *D. frontalis* eaten during the experiment (the elytra are typically not consumed by *T. dubius*; see Frazier et al. 1981). Two detached elytra were assumed to represent one consumed beetle. Also recorded were the numbers of live or dead adult *D. frontalis* remaining outside the bolt at the end of the

experiment. Only a small fraction of beetles fell into these two categories.

Analysis of covariance was used to test for effects of predator and prey density, and block, on the proportion of *D. frontalis* attacking the bolt. An arcsine-square root transformation was applied to the proportions to help normalize their distribution. A more detailed analysis using a functional response model was used to examine treatment and block effects on the proportion of beetles eaten (see below).

Determination of the functional response

To help quantify the functional response of *T. dubius*, I fitted a simple but flexible model of predator behavior to data on the proportion of *D. frontalis* eaten. The model is based on the type II functional response equation, modified to include an interference relationship among the predators (Royama 1971; Rogers 1972; Arditi and Akçakaya 1990; Arditi and Saïah 1992). This interference relationship could arise in a number of ways, including non-random search by the predators, prey refugia, and hostile encounters among predators, i.e., direct interference (Hassell 1978; Arditi and Ginzburg 1989). In the model the attack rate (a) of the predator is defined by the equation $a = \alpha p^{-m}$, where α is a constant, p is predator density, and m sets the intensity of interference ($m > 0$ implies that interference occurs). Let n be the initial number of prey in the experiment, n_a the number of prey eaten, and x_a the proportion of prey eaten ($x_a = n_a/n$). Then x_a is defined implicitly by the equation

$$x_a = 1 - \exp(-\alpha p^{1-m} t + \alpha p^{-m} t_h x_a n), \qquad (1)$$

where t_h is the handling time of the prey, and t is the length of time predator and prey interact (Arditi and Akçakaya 1990; Arditi and Saïah 1992). Note that Eq. 1 must be solved numerically for the value of x_a. An important feature of this model is that when $m = 1$, the proportion eaten is determined only by the ratio n/p rather than by n and p separately, and the functional response of the predator becomes ratio dependent (Arditi and Ginzburg 1989; Arditi and Akçakaya 1990; Arditi and Saïah 1992; Berryman 1992). The model can thus describe situations ranging from no interference among predators ($m = 0$) to strong interference and ratio dependence ($m = 1$).

Preliminary analyses revealed differences between the first and the other two blocks in the overall predation rate, suggesting attack rates might differ between these two groups. To incorporate this potential effect in the model, I altered Eq. 1 by replacing α with the expression $\alpha + d_\alpha \cdot i$, where i is a dummy variable that encodes the block ($i = 1$ for the first block, $i = 0$ for the second and third blocks), and d_α measures the block effect (Draper and Smith 1981; Juliano and Williams 1987). The model was then fitted to the data using the SAS non-linear regression procedure NLIN (SAS 1985), using a program adapted from one developed by Arditi and Akçakaya (1990). This model yielded a much higher R^2 value than a model with no block effects. The 95% confidence interval generated by SAS for d_α was used to test for differences in α among blocks; if this interval does not include zero, there is a significant difference at the $P = 0.05$ level.

Survey of *D. frontalis* and *T. dubius* densities

A long-term survey of the densities of adult *D. frontalis* and *T. dubius* was conducted in the Kisatchie National Forest (central Louisiana, USA) using baited multiple-funnel traps (Lindgren 1983). Beginning in 1989 and continuing through 1996, three traps were deployed in a transect across each of four Ranger Districts in the Kisatchie, each trap separated by a distance of at least 1.6 km (1 mile). From 1993 through 1996, an additional six traps were deployed in one of the districts. The traps were baited with two 0.5 ml vials of frontalin, the aggregation pheromone of *D. frontalis*, and a 120-ml bottle of turpentine (released by a wick). This com-

bination of chemicals is highly attractive to both *D. frontalis* and *T. dubius* (Vité and Williamson 1970; Payne et al. 1978; Dixon and Payne 1980). The traps were monitored weekly, and the chemicals replaced before depletion occurred.

The densities of *D. frontalis* and *T. dubius* were estimated for each year and district by dividing the number of *D. frontalis* and *T. dubius* caught by a measure of sampling effort, the number of days each trap was deployed summed over all traps within each district (i.e., the total number of trap-days). Because most *D. frontalis* and *T. dubius* individuals were caught in the interval from January to June each year, I used only these months of trapping data in the density calculations for each year. Data from traps where the bait had initiated a mass attack on trees in their immediate vicinity were omitted, because this can greatly elevate the number of insects caught in the trap and therefore bias estimates of density.

Results

Densities of adult *T. dubius*

The density of *T. dubius* varied considerably across the 21 trees and eight infestations and had a highly skewed distribution (Fig. 1). The mean density of adult *T. dubius* was 0.715 ± 0.148 dm^{-2}. These results suggested the range of predator densities used in the laboratory experiments, 0–1.25 *T. dubius* dm^{-2}, was representative of field densities.

Predation by *T. dubius* on *D. frontalis*

Predation by adult *T. dubius* substantially reduced the proportion of adult beetles successfully attacking the bolts in the laboratory experiments (Fig. 2). As the predator density increased from 0 to 40 adults per bolt, the proportion of beetles entering the bolt declined significantly, from about 60% to 20% ($F = 43.1$, $df = 1$, 30, $P < 0.001$). *D. frontalis* density also had a small but significant effect on the proportion entering the bolt, with a somewhat higher fraction successfully attacking it at high versus low densities ($F = 6.6$, $df = 1,30$, $P = 0.015$). There was also a significant block effect in the experiment ($F = 11.3$, df = 2,30, $P < 0.001$), presumably because different blocks used predator, prey, and bolts collected at different times and locations.
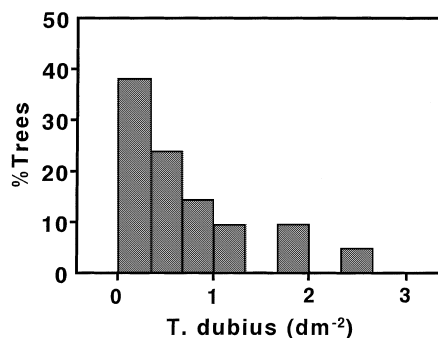

Fig. 1 Surface densities of adult *Thanasimus dubius* captured on 21 pines undergoing attack by *Dendroctonus frontalis*

Table 1 Parameter estimates, asymptotic confidence intervals (*c.i.*), mean-square (*MS*) residuals, and R^2 values for Eq. 1, and a purely ratio-dependent model obtained by fixing $m = 1$ (see text for further explanation)

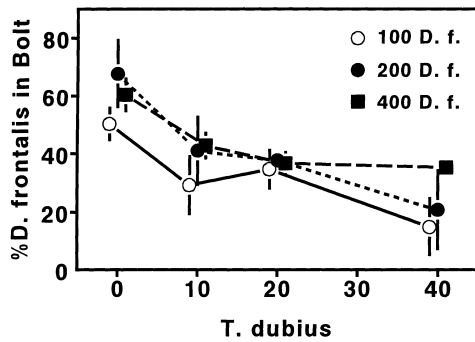| Parameter	Eq. 1	Ratio-dependent model
α (95% *c.i.*)	1.05 day^{-1} (−0.61, 2.71)	1.04 day^{-1} (0.72, 1.36)
d_α (95% *c.i.*)	−0.51 day^{-1} (−1.39, 0.37)	−0.50 day^{-1} (−0.82, −0.19)
t_h (95% *c.i.*)	0.12 days (0.07, 0.18)	0.12 days (0.08, 0.17)
m (95% *c.i.*)	1.00 (0.58, 1.43)	–
MS residual	0.00632	0.00605
R^2	0.73	0.73

Fig. 2 Proportion ($\pm$SE) of adult *D. frontalis* (*D. f.*) successfully entering the bolt in the laboratory experiments as a function of *D. frontalis* and *T. dubius* density
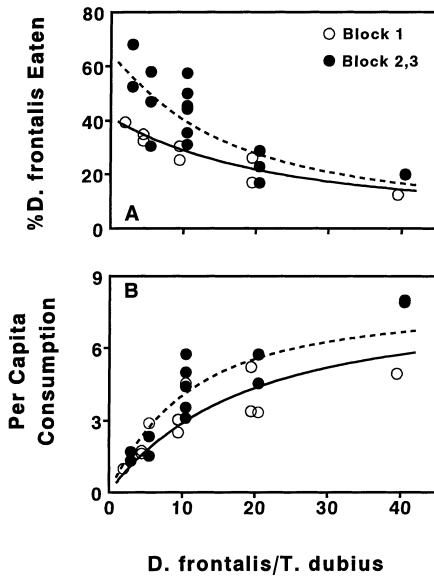

Fig. 3 Fitted curves for the ratio-dependent model, and data from the laboratory experiments, as a function of the *D. frontalis*/*T. dubius* ratio. Separate curves are drawn for different blocks in the experiment, with the *solid line* indicating the curve for the first block, the *dashed line* for the other two blocks. **A** Proportion of adult beetles eaten by *T. dubius*. **B** Per capita consumption of beetles by *T. dubius*
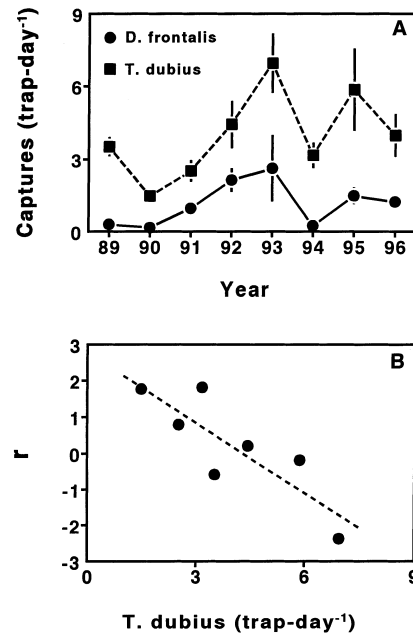

Fig. 4 Results of a long-term survey of *D. frontalis* and *T. dubius* densities within the Kisatchie National Forest, La., USA. **A** Mean number ($\pm$SE) of *D. frontalis* and *T. dubius* caught per trap-day of sampling, averaged across four ranger districts, for the period 1989–1996. **B** The population growth rate of *D. frontalis*, *r*, versus the density of *T. dubius* ($y = 2.78 − 0.65x$, $R^2 = 0.71$, $P = 0.017$)

Eq. 1 provided a good fit to the data on the proportion of adult *D. frontalis* eaten by *T. dubius* (Table 1). The analysis showed potential differences in the parameter α between the first and the other two blocks, although the effect was not significant (the 95% confidence interval for d_α overlapped 0). The value of m

obtained suggests that the attack rate of *T. dubius* depends strongly on predator density, and we can reject outright a model with no interference, because the 95% confidence interval for m does not include 0. To test whether a purely ratio-dependent model might be appropriate, I fixed $m = 1$ in Eq. 1 and fitted the model again, once more using a dummy variable to allow for differences in α among blocks. This ratio-dependent model fit the data as well as the full model, and in this case the effect of block on α was significant (Table 1). Figure 3 shows the experimental data and the fitted curves generated by this model, for the proportion of *D. frontalis* eaten and also per capita prey consumption, as a function of the *D. frontalis*/*T. dubius* ratio. The proportion eaten was highest at low *D. frontalis*/*T. dubius* ratios, where a substantial fraction of the beetles were consumed (up to 60%), and declined as this ratio increased, apparently from handling time constraints or satiation. Per capita consumption increased from about one beetle at low *D. frontalis*/*T. dubius* ratios to a maximum of six beetles at high values (Fig. 3B).

Numerical response of *T. dubius*

The different districts involved in the long-term survey showed similar temporal patterns of *D. frontalis* and *T. dubius* abundance, and so I averaged the trap catches across the four districts to yield a mean value for each year of the survey (Fig. 4A). The data clearly show a numerical response by the predator to changes in prey density. As *D. frontalis* populations changed from endemic levels in 1989–1990 to a mild outbreak in 1993, followed by a collapse in 1994 and a small increase in 1995, trap catches of *T. dubius* paralleled these changes in prey density (Fig. 4A). The overall pattern suggests that *T. dubius* may help regulate *D. frontalis* populations, and indeed there is an inverse relationship between the growth rate of *D. frontalis* from year to year and predator density (Fig. 4B). In particular, the density of *T. dubius* at time $t-1$ has a significant negative effect on the population growth rate of *D. frontalis*, defined as $r_t = \ln(n_t/n_{t-1})$, where n_t is the density of *D. frontalis* at time t.

Discussion

The results of this study indicate that adult *T. dubius* could be an important source of beetle mortality during mass attack of the host tree. Adult predators were often abundant on the bark in nature, and in laboratory experiments using densities typical of the field, generated substantial mortality and a significant reduction in the proportion of beetles successfully entering the bolt. It seems likely that under field conditions, predation by adult *T. dubius* would slow the attack process and, because it diminishes the overall pool of adult beetles, would also reduce the total number of trees infested. This predator also showed a marked numerical response to increases in *D. frontalis* density, and the population growth rate of *D. frontalis* was inversely related to predator density. Although this finding is only a correlation, it does suggest that *T. dubius* may help suppress outbreaks of this pest, and could explain why *D. frontalis* activity can often be predicted from the relative proportions of *D. frontalis* and *T. dubius* caught in pheromone traps (Billings 1988). For example, the number of infestations tends to decrease when *T. dubius* comprises a large proportion of the catch in pheromone surveys (Billings 1988), and this may reflect its ability to suppress *D. frontalis* populations.

The natural enemy complexes of different bark beetle species are often quite similar, with clerid beetles usually being common predators (Dahlsten 1982; Mills 1983; Moeck and Safranyik 1984). Predation by adult clerids could therefore be an important source of mortality in systems besides *D. frontalis* and *T. dubius*, but might be easily overlooked because it is cryptic and difficult to estimate. Combined with the effects of clerid larvae on the brood, it may be that the top-down forces generated

by clerids (and other natural enemies) are an important general component of bark beetle dynamics, in addition to the role of host tree resistance.

The functional response of *T. dubius* is well described by a simple ratio-dependent model, as has been found for many predators and parasitoids (Arditi and Akçakaya 1990). Several different mechanisms have been proposed to generate ratio dependence, including direct interference among the predators, non-random predator foraging, and refuges for the prey (Arditi and Ginzburg 1989). Because antagonistic interactions appear to be rare among adult *T. dubius* (J.D. Reeve, personal observation) it seems unlikely that direct interference is the source of ratio dependence in this predator. A more likely explanation is the existence of a prey refuge in the system; once the adult beetles bore into the host tree they are safe from attack by *T. dubius*. This innate heterogeneity in the distribution of predator and prey could generate what is known as "pseudo-interference" in the predator (Free et al. 1977; Hassell 1978), causing the attack rate to decline at high predator densities, and may explain why ratio dependence occurs in *T. dubius*.

One consequence of a ratio-dependent functional response is that it can exert a stabilizing effect on predator-prey dynamics, with an efficient ratio-dependent predator capable of generating both a low and stable prey equilibrium (Arditi and Berryman 1991; Berryman 1992). However, the prolonged life-cycle of *T. dubius* might counter this stabilizing effect. Laboratory rearing studies have shown that the life-cycle may take from 4 to 6 months, about three times as long as *D. frontalis* (Nebeker and Purser 1980; Lawson and Morgan 1992). In addition, a significant fraction of *T. dubius* individuals appear to undergo an extended period of development under field conditions, up to 2 years in duration (Reeve et al. 1996). This asynchrony between predator and prey development could in theory have a highly destabilizing effect on predator-prey dynamics (Nunney 1985; Murdoch et al. 1987; Godfray and Hassell 1989), and so might contribute to the large oscillations observed in *D. frontalis* abundance (Turchin et al. 1991). Thus, even though *T. dubius* may help to suppress *D. frontalis* outbreaks, it is possible that its long and perhaps destabilizing life-cycle contributes to their formation as well. It may ultimately be necessary to construct a detailed model of the system, including ratio dependence and developmental time delays, and as-yet-unexamined processes like predation by larval *T. dubius*, to determine whether this predator has a net stabilizing or destabilizing effect on *D. frontalis* dynamics.

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