

FORUM

Why Do Populations of Southern Pine Beetles (Coleoptera: Scolytidae) Fluctuate?

PETER TURCHIN,¹ PETER L. LORIO, JR.,¹
ANDREW D. TAYLOR,¹ AND RONALD F. BILLINGS²

Environ. Entomol. 20(2): 401-409 (1991)

ABSTRACT It is widely believed that population outbreaks of the southern pine beetle (*Dendroctonus frontalis* Zimm.) are caused by vagaries of climate, such as periods of severe drought. According to this view, *D. frontalis* population dynamics are dominated by density-independent processes. We have statistically analyzed a 30-yr record of *D. frontalis* activity in east Texas and have assessed the relative roles of density-independent and density-dependent factors in beetle population fluctuations. Regressions of the rate of population change on three climatic variables were not significant. By contrast, both time-series and regression analyses provided strong and consistent evidence for delayed density regulation of *D. frontalis* populations. Thus, in contrast to previous analyses, we conclude that *D. frontalis* outbreaks are driven not by stochastic fluctuations of weather, but by some unknown population process acting in a delayed density-dependent manner. This result provides a starting point for a current study that will experimentally test various hypotheses concerning the role of natural enemies in *D. frontalis* cycles.

KEY WORDS Insecta, *Dendroctonus frontalis*, population dynamics, time series

ALTHOUGH POPULATION OUTBREAKS of the southern pine beetle (*Dendroctonus frontalis* Zimm.) cause enormous economic damage, little is known about the factors responsible for fluctuations in the density of *D. frontalis* populations. It is generally held that fluctuations in this beetle are driven by variable climate (Wyman 1924; Craighead 1925; Beal 1927, 1933; St. George 1930; King 1972; Kroll & Reeves 1978; Kalkstein 1981; Michaels 1984). Weather could affect beetles directly, e.g., when extreme winter cold reduces survival (McClelland & Hain 1979). Alternatively, weather could affect beetles indirectly, by reducing host resistance to *D. frontalis* attack. For example, severe water deficits reduce oleoresin exudation pressure in pines (Vité 1961, Lorio & Hodges 1968), and lower the potential amount and duration of resin flow from wounds, thus enhancing attack success of beetles (Lorio & Hodges 1977).

In sum, according to the climate hypothesis, population dynamics of *D. frontalis* are dominated by density-independent processes. An alternative hypothesis is that there is a significant density-dependent component in *D. frontalis* dynamics. For example, beetle numbers might be following some deterministic oscillatory trend caused by population interactions with natural enemies or resources (with stochastic fluctuations superimposed on this trend). To distinguish between these two alternatives, we applied time-series and regression analyses to a record of temporal fluctuations of *D. fron-*

talis numbers in east Texas and analyzed the effects of three climatic variables on the per capita rate of *D. frontalis* population increase.

Materials and Methods

The Data Set. Since 1958 the Texas Forest Service has maintained records of *D. frontalis* spot infestations observed in Texas in aerial surveys (a spot infestation is defined as a group of 10 or more adjacent pines that were killed by beetles). These aerial surveys, which are conducted at 3-6 wk intervals from May to October, cover some 11 million acres in 38 east Texas counties. Only spots of 10 or more trees are recorded, because smaller spots are difficult to identify positively from the air. Recorded spots are separated into size classes: 10-25 trees, 26-50 trees, 51-100 trees, and >100 trees. For more details about aerial detection of *D. frontalis* spots see Billings & Ward (1984). Before 1973, spots were recorded only for southeastern Texas. Thereafter, records of spot infestations were kept for each county. Thus, from 1973 to 1987 we have data on the number of spots detected annually in each east Texas county. Data on spots occurring on National Forest land (600,000 acres) were not included in the data base in most years, so we omitted these spots from the analysis.

We used two indices of *D. frontalis* density. The first was simply the number of spots detected (e.g., Billings & Pase 1979). This was used for the 30-yr record of spots in southeastern Texas (Region 1 of the Forest Survey of East Texas, Lang & Bertelson 1986). For the period 1973-1987, and for the whole of east Texas, we have also estimated the number

¹ USDA-Forest Service, Southern Forest Experiment Station, Pineville, La. 71360.

² Texas Forest Service, Lufkin, Tex. 75901.

of beetle-infested trees in each county in each year by multiplying the number of spot infestations in each size category by the median number of trees in the category and summing the products. This method produces more accurate estimates than the first one, because the average size of spots may fluctuate as beetle populations increase and decline. The number of infested trees was then divided by the area (in acres) occupied by pine and mixed pine-hardwood forest in each county (Earles 1976, Lang & Bertelson 1986) to obtain a relative estimate of *D. frontalis* population density.

Statistical Analysis. The general model that underlies all of our analyses relates *D. frontalis* density in year t , N_t , to density during p previous years and to a density-independent component ϵ_t :

$$N_t = f(N_{t-1}, N_{t-2}, \dots, N_{t-p}, \epsilon_t). \quad (1)$$

The parameter p gives the order of the process; ϵ_t is assumed to be a normally distributed random variable with mean zero and variance σ^2 . Lagged density-dependent effects (N_{t-2}, \dots, N_{t-p}) are expected to arise as a result of interactions among species in the community (Royama 1981, Murdock & Reeve 1987), or as a result of delayed density effects on fecundity of the next generation (Prout & McChesney 1985). Ecologists have long been aware that delayed density dependence can affect population growth and cause periodic population oscillations (Hutchinson 1948, Moran 1953, Berryman 1978, Royama 1981).

The model (1) is too general to be used in the analysis of the *D. frontalis* temporal records. It is necessary to make the model more concrete by adopting simplifying assumptions. We used two distinct approaches. First, we employed the diagnostic techniques of time-series analysis (Box & Jenkins 1976). Specifically, we estimated the autocorrelation and partial autocorrelation functions (ACF and PACF, respectively). Before the analysis, beetle density in year t was log-transformed, so that $L_t \equiv \log N_t$. The autocorrelation function is estimated by calculating the correlation coefficient between all pairs of $L_{t-\tau}$ and L_t separated by lag τ ($\tau = 1, 2, \dots$ yr). These correlation coefficients are then plotted against the lag τ . If a population undergoes periodic oscillations generated by biotic interactions within the community, then its ACF will also oscillate around zero with each successive peak or trough decreasing in amplitude. In other words, the ACF will behave as a damped sine wave (Nisbet & Gurney 1982).

PACF is an indicator of the number of terms, p , that need to be included in model (1). Although direct influences of past densities on the current population change may be limited to a few lags, indirect influences can persist much longer. Thus, model (1) with $p = 2$ may have a significant autocorrelation at lag 10. Constructing the PACF is analogous to deciding on the number of independent variables to include in a multiple regression (Box & Jenkins 1976). For example, if $p = 2$ (that

is, N_t is directly affected only by population densities during the two previous years), then the PACF will have significant spikes at the first two lags, and will be statistically indistinguishable from zero at higher lags. An application of the time-series analysis to 14 insect data sets can be found in Turchin (1990).

The weakness of the Box-Jenkins approach, when applied to population dynamics, is its implicit assumption that the logarithm of the present population density, $L_t \equiv \log N_t$, is related to the logarithms of past densities in a linear fashion. For example, if there are no delayed effects of the stochastic environmental factors, then L_t is assumed to be generated by an autoregressive process of order p (Box & Jenkins 1976):

$$L_t = a_0 + a_1 L_{t-1} + \dots + a_p L_{t-p} + \epsilon_t. \quad (2)$$

Population dynamics, however, are inherently nonlinear, and a model such as (2) can at best be an approximation of dynamics near an equilibrium (Royama 1981). Thus, inspection of ACF and PACF patterns is useful for detection of multiple lags, but not for modeling population fluctuations, especially if the dynamic behavior of the studied system is deterministically unstable (limit cycles or aperiodic chaos).

Our second approach involved specifying a nonlinear model for N_t and considering a limited number of lags. We used the following model, which is an extension of Ricker's equation (Turchin 1990):

$$N_t = N_{t-1} \exp[r_0 + \alpha_1 N_{t-1} + \alpha_2 N_{t-2} + \epsilon_t]. \quad (3)$$

The parameters r_0 (intrinsic rate of population increase), and α_1 and α_2 (which measure the effects of direct and delayed density-regulation factors, respectively) are readily estimated by regressing the realized per-capita rate of population change $r_t \equiv \log(N_t/N_{t-1})$ on N_{t-1} and N_{t-2} . This procedure assumes that errors are multiplicative and distributed log-normally, which is a standard assumption in statistical analyses of population fluctuations (Royama 1981, Pollard et al. 1987). We employed stepwise regression to determine the significance of the delayed density-dependence term: first regressing r on N_{t-1} and then testing to determine whether adding the term N_{t-2} significantly reduces unexplained variance.

Climatic Effects. A major danger in any analysis of climatic effects is overfitting, that is, regressing a data set with a limited number of degrees of freedom on too many variables (Linhart & Zucchini 1986). Accordingly, before conducting the analysis we selected three weather variables that we thought were the most likely to influence beetle population change:

- (1) Heating degree-days accumulated during December through February. This number was taken from the monthly summaries of east Texas climatological data published by National Oceanic and Atmospheric Administration (NOAA, data obtained from the National Cli-

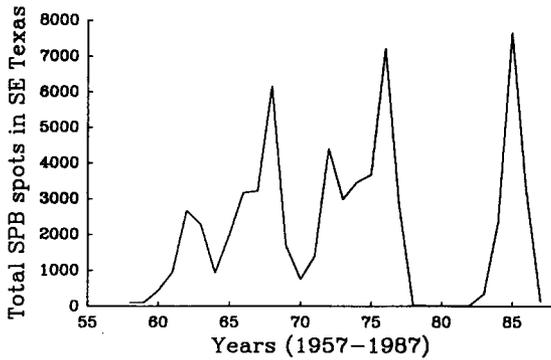


Fig. 1. The total number of spot infestations detected in southeastern Texas, 1958-1987.

matic Data Center, Asheville, N.C.). A heating degree-day is accumulated for each whole degree that the daily mean temperature is below 65°F.

- (2) The number of days above 90°F during the months of June through August, also taken from NOAA monthly summaries. We were unable to use cooling degree-days because NOAA did not begin reporting them until 1980.
- (3) Cumulative annual water balance deficits. NOAA data were used to calculate Thornthwaite monthly potential evapotranspiration for each of the years 1973-1987 (Thornthwaite & Mather 1957). Deficits of monthly rainfall to meet PE were then determined for each month and totaled for each year.

The effect of these variables on the rate of population change, r , was analyzed by linear regressions. Because temperature and, especially, amount of rainfall vary widely over large geographic areas such as east Texas, we selected one county for this analysis, Hardin County. This county was selected because it is located in the center of the area affected by beetle outbreaks, and because the results obtained would be directly comparable with those obtained by Kalkstein (1981), who had also studied beetle fluctuations in Hardin County. The rainfall data was collected at Warren weather station, while temperature data was taken from Town Bluff Dam data (both stations are located in Tyler County, to the north of Hardin County).

Results

Time-Series Analysis. Between 1958 and 1987 the *D. frontalis* population in southeastern Texas went through four cycles (Fig. 1). The time-series analysis provided strong evidence of delayed density-dependent regulation of beetle populations. (Identical results were obtained with both number of spots and number of infested trees as alternative dependent variables, so only results for number of spots are given.) PACF graph (Fig. 2) is the most useful diagnostic tool for determining the order of an autoregressive process (Box & Jenkins 1976).

Table 1. Regression analysis of per-capita rate of increase, r_t , on the climate variables. NS, $P > 0.05$

Variable	df	Mean square	F	R ²
Heating degree-days	1, 12	12.749	2.81 NS	0.19
Days above 90°F	1, 12	2.744	0.51 NS	0.04
Water deficit, cm	1, 12	1.699	0.13 NS	0.02

The theoretical PACF of the first-order autoregressive process is characterized by a single spike at lag 1, and is zero everywhere else (Box & Jenkins 1976). The PACF of the time series, however, has two spikes (at lags 1 and 2) that are significantly different from zero. Such a pattern is consistent with the theoretical PACF of the second-order autoregressive process (Box & Jenkins 1976). Note that PACF at lag 2 is negative. The presence in the model (2) of a negative term containing N_{t-2} implies delayed density regulation. The ACF of the time series (Fig. 2) behaved as a damped sine wave, which suggests that there is an oscillatory deterministic component in beetle population dynamics (Nisbet & Gurney 1982).

Regression Analysis. The conclusion that *D. frontalis* populations in Texas are regulated by a delayed density-dependent mechanism was reinforced by results of the regression analysis. There was a highly significant regression of r_t on N_{t-2} ($F_{1,26} = 31.79$, $P < 0.001$, $R^2 = 0.550$). However, this analysis did not detect any evidence of direct (nonlagged) density dependence ($F_{1,26} = 4.06$, $P > 0.05$, $R^2 = 0.135$). While surprising, the absence of direct density-dependence is not inconsistent with the occurrence of a significant PACF spike at lag 1 (see above), because the regression analysis was performed on the realized per-capita rate of population change r , whereas time-series analysis examined lag correlations between N_t 's. If we accept that r_t is a function of N_{t-2} only, then

$$r_t = r_0 + \alpha_2 N_{t-2}$$

and

$$N_t = N_{t-1} \exp r_t = N_{t-1} \exp[r_0 + \alpha_2 N_{t-2}].$$

In other words, N_t is a function of both N_{t-1} and N_{t-2} , and there should be significant PACF spikes at both lags 1 and 2.

Influence of Climate. Visual comparison of time-series plots reveals no consistent patterns in the association between climate variables and beetle numbers (Fig. 3). Furthermore, regression analysis detected no significant effects of variation in climate on beetle population change (Table 1). Finally, including climatic variables in the analysis in a stepwise fashion after accounting for the effect of N_{t-2} yielded no significant results.

Discussion

Our results contradict the hypothesis that *D. frontalis* population outbreaks in east Texas are

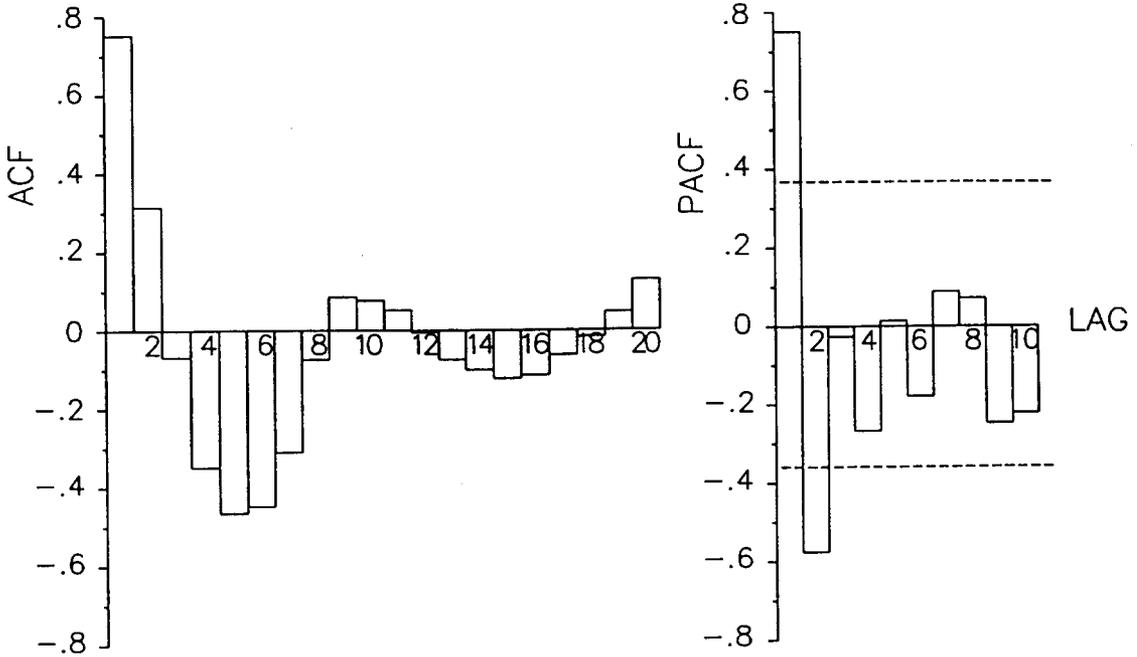


Fig. 2. The estimated autocorrelation and partial autocorrelation functions plotted against the time lag. The dashed lines indicate bounds within which PACF is not different from 0 (at 0.05 confidence level).

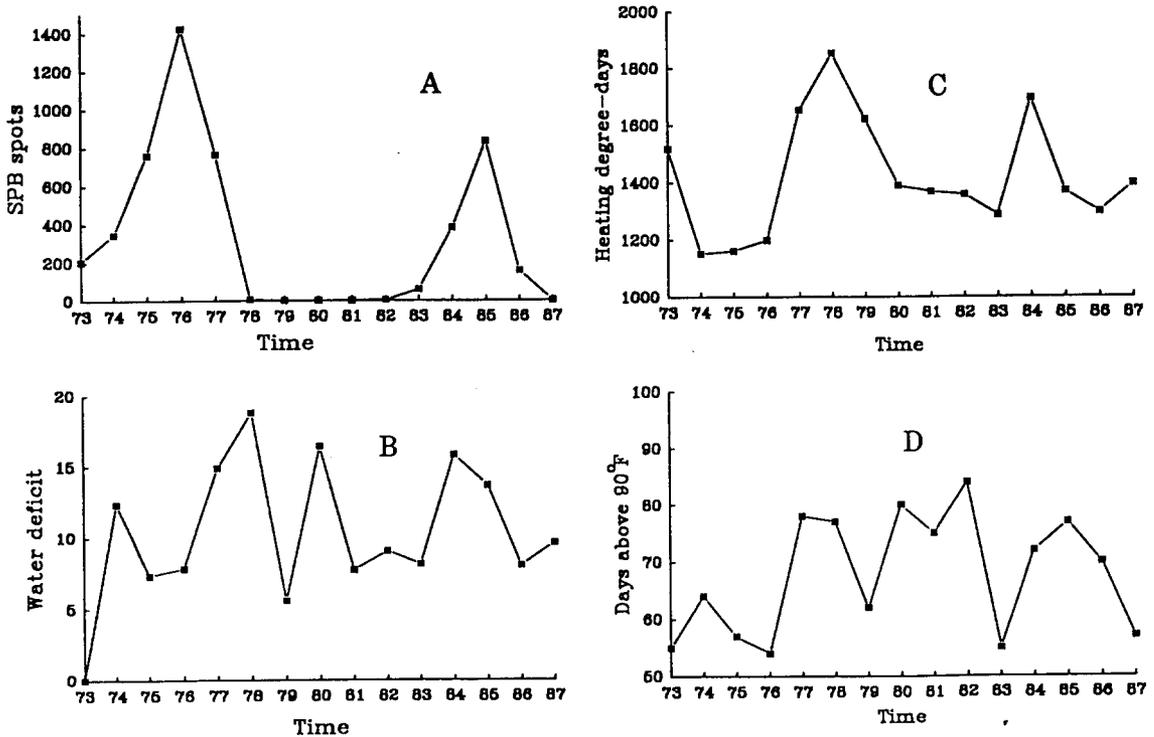


Fig. 3. Time plots of (A) the number of beetle spots in Hardin County, (B) estimated water deficit, in cm, (C) heating degree-days, and (D) the number of days during which maximum temperature exceeded 90°F.

driven by changes in weather. We did not detect any significant effects of climate variables on the rate of population change. Furthermore, both time-series and regression analyses implicated density-dependent factors as principal causes of population oscillations in *D. frontalis*.

There are several reasons why our conclusion is at variance with conclusions of most previous analyses of climate effects on beetle outbreaks. First, overfitting is a major problem with many *D. frontalis*-climate analyses. Records of beetle activity are typically short, and, consequently, degrees of freedom available for regressions are limited. However, the number of climate variables that could influence beetle numbers is large. For example, amount of rainfall could have different effects at different times of the year, and the time lag between a rainfall event and beetle population response is unknown. Thus, using multiple variables in the analyses increases the likelihood of "detecting" a significant correlation by chance alone. King's (1972) comparison of mean monthly rainfalls for epidemic versus nonepidemic years is an example of this problem. Since King made comparisons for each month separately and used 42 localities, the total number of comparisons was $12 \times 42 = 504$ items. At a 0.05 significance level, one would expect $504 \times 0.05 = 25$ apparently significant items if there were no relationship between climate and beetle activity. King (1972) argues that the 32 apparently significant items that he detected are significantly more than the expected 25. Even if this is correct (but see the next paragraph), the fact remains that the majority of apparently significant items are spurious, and we do not know which are spurious and which are not. A similar problem affects the study by Kroll & Reeves (1978), who analyzed a data set consisting of 11 observations by regressing it on 11 independent variables. The danger of spurious correlations can be minimized by severely restricting the set of weather variables before the analysis (a priori). Alternatively, the technique of principal component analysis can be used to reduce the dimensionality of the parameter space (Kalkstein 1981, Michaels 1984).

The second difficulty arises because the values of the dependent variable (number of beetle spots) are not statistically independent. As our time-series analysis showed, successive numbers of beetle spots in Texas are strongly positively correlated. Thus, one of the basic assumptions of the analysis of variance is violated (Sokal and Rohlf 1981), and consequently *F* values reported by Kroll & Reeves (1978) and Kalkstein (1981), whose studies are also based on the Texas data set, are incorrect. The problem of serial correlations can be avoided by analyzing not spot numbers, but the residuals from fitting the time series with a second-order autoregressive process, or—even better—model (3).

Finally, most previous analyses have ignored biological features of *D. frontalis* population processes. This could lead to unrealistic predictions

about the future course of a beetle epidemic. In one study, a model based on regression results predicted the following numbers of beetle spots in Hardin County in 1979: 0 spots for June, 1,254 spots for July, and 0 spots for August (Kalkstein 1981). The peak number of spots observed in Hardin County at the height of the most recent outbreak (in 1985) was 836, and it took three years for beetle populations to build up to this level (beginning with three spots in 1982). Clearly, a predictive model of *D. frontalis* activity must take beetle population dynamics into account.

It is probably not surprising, given the pitfalls associated with quantifying weather influences on changes in insect numbers, that different authors came to opposite conclusions about the effects of climate on beetle populations. For example, King (1972) concluded that higher than usual rainfall during the months of January and February was associated with beetle epidemics during the following summer. Kroll & Reeves (1978), however, concluded that high rainfall during the previous fall and spring decreased beetle activity, while winter rainfall had no effect. Kalkstein (1981) found that moisture surpluses during November through January and May through June contributed to beetle outbreaks, while moisture surpluses during February and March reduced the probability of an outbreak. The inconsistency between factors identified as causing outbreaks by previous authors has been noted by Gagne et al. (1980), whose results indicated no relationship between moisture conditions and brood survival. They found that during January and February of 1972, rainfall was 4 cm below average, while during the same period of 1974, rainfall was 6.4 cm above average. However, brood survival was virtually the same in these two years, 17 and 16%, respectively. Thus, the conclusion that these conflicting results of previous weather analyses resulted from use of too many weather variables, and the associated spurious significance, seems almost inescapable to us.

It is revealing that a recent study, which avoided the pitfalls listed above, found that fluctuations in weather exerted only a weak influence on change in beetle numbers. Michaels (1984) analyzed effects of weather on *D. frontalis* outbreak patterns in Atlantic coastal and piedmont regions. His final regression equation included 7 independent variables, but explained only 25% of variance in *r* (the per capita rate of change). This result is typical; climate commonly accounts for <30% of variation in insect population numbers (Martinat 1987). By contrast, a single variable, N_{t-2} , explained 55% of the variance in *r* in our analysis of Texas spot numbers.

To determine the temporal pattern of population dynamics predicted by model (3), we have simulated a 60-yr period of beetle fluctuations using first the deterministic model only (Fig. 4A), and then the deterministic model with stochastic variation (Fig. 4B). These simulations indicate that fac-

tors acting in a delayed density-dependent manner can produce periodic oscillations similar to those observed in spot numbers. The deterministic pattern of *D. frontalis* oscillations is quasiperiodic; that is, *D. frontalis* numbers cycle with a period that is an irrational number, so that the solution never repeats itself exactly (at least, the computer solution never repeated itself during 100,000 iterations).

Directions for Future Research. A large gap in our understanding of *D. frontalis* dynamics concerns the identity of the biological interactions responsible for delayed density-dependent regulation and lag-induced population cycles revealed by the analyses in this paper. Time-series analysis cannot answer this question, relying as it does on observational rather than experimental data. The finding of delayed density dependence does, however, suggest various hypotheses regarding possible mechanisms. Two of us (P.T. and A.T.) currently are testing the hypothesis that delayed regulation arises from an interaction with natural enemy populations. According to this hypothesis, beetle outbreaks occur when the mortality caused by predators and parasites decreases, or outbreaks collapse due to an increase in this mortality, or both. Our approach consists of measuring the impact of natural enemies on the within-tree rate of *D. frontalis* increase at periodic intervals (twice a year) throughout a complete outbreak cycle. This impact of natural enemies is measured by using cages to exclude all beetle associates from a portion of a tree, and then comparing the ratio of beetle increase within the exclusion cages to that outside the cages. The pattern of variation in natural enemy impact, in relation to the phase of *D. frontalis* outbreak cycle, will allow us to determine the dynamical role of enemies in this cycle, as illustrated in Fig. 5. The crucial question—essentially that of traditional key-factor analyses—is to what extent changes in enemy-induced mortality are correlated with changes in beetle rates of population change, r , (Fig. 5B). At one extreme, beetle outbreak dynamics might be entirely due to interactions with natural enemies. In this case (Fig. 5C), the ratio of increase inside the cages (protected from enemies) is constant throughout an outbreak, with both the increase in r , triggering an outbreak, and the decline in r , causing outbreak collapse reflecting changes in the action of natural enemies. At the other extreme, we may find that the impact of enemies does not change through the outbreak cycle (Fig. 5D). This would indicate that outbreaks are driven by some factor which affects beetles inside as well as outside cages, such as disease or host resistance. Intermediate situations also are possible: enemies may suppress outbreaks but not trigger them (Fig. 5E), or vice versa (Fig. 5F).

Another avenue for future investigation is suggested by one feature of the data that the model (3) did not capture: increased amplitude of beetle oscillations with time (Fig. 1). Although the mean

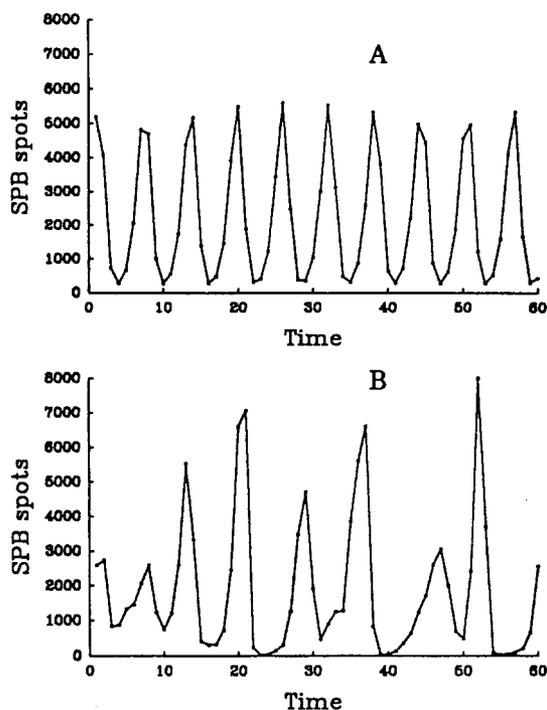


Fig. 4. Time plots of *D. frontalis* oscillations predicted by the model (3): (A) without stochastic component, and (B) with stochastic component, $\sigma = 0.4$. The parameters of the model (3) were estimated by regression (estimate \pm SE): $r_0 = 1.25 \pm 0.31$, and $\alpha_2 = -0.0006 \pm 0.0001$. α_1 was assumed equal to 0.

number of beetle spots was approximately constant from 1958 to 1987, the peaks of each successive outbreak increased, while the troughs between outbreaks decreased. The analysis of Turchin & Taylor (1991) with a generalized version of the model (3) suggested that the *D. frontalis* dynamical system may be moving farther away from equilibrium as time increases. Turchin & Taylor (1991) fitted their model to the first and the second half of the time series separately and found, respectively, diverging oscillations and chaos. One possible explanation of this pattern is a shift from immature understocked stands to mature overstocked stands that occurred in east Texas during the last several decades (Hedden 1978). For example, between 1955 and 1975 the area occupied by commercial forest (industry, national forests, and private holdings) has decreased by 6%. At the same time, the total volume of softwood sawtimber increased by 85% (Hedden 1978). This change represents an almost 2-fold increase in density of resources available to beetles. Thus, progressively more extreme oscillations of beetle numbers could be a result of the enrichment of their resource base (Rosenzweig 1971). An experimental test of this hypothesis is clearly needed.

Although our results indicated that a periodic oscillation in *D. frontalis* was caused by density-dependent population factors, and that three cli-

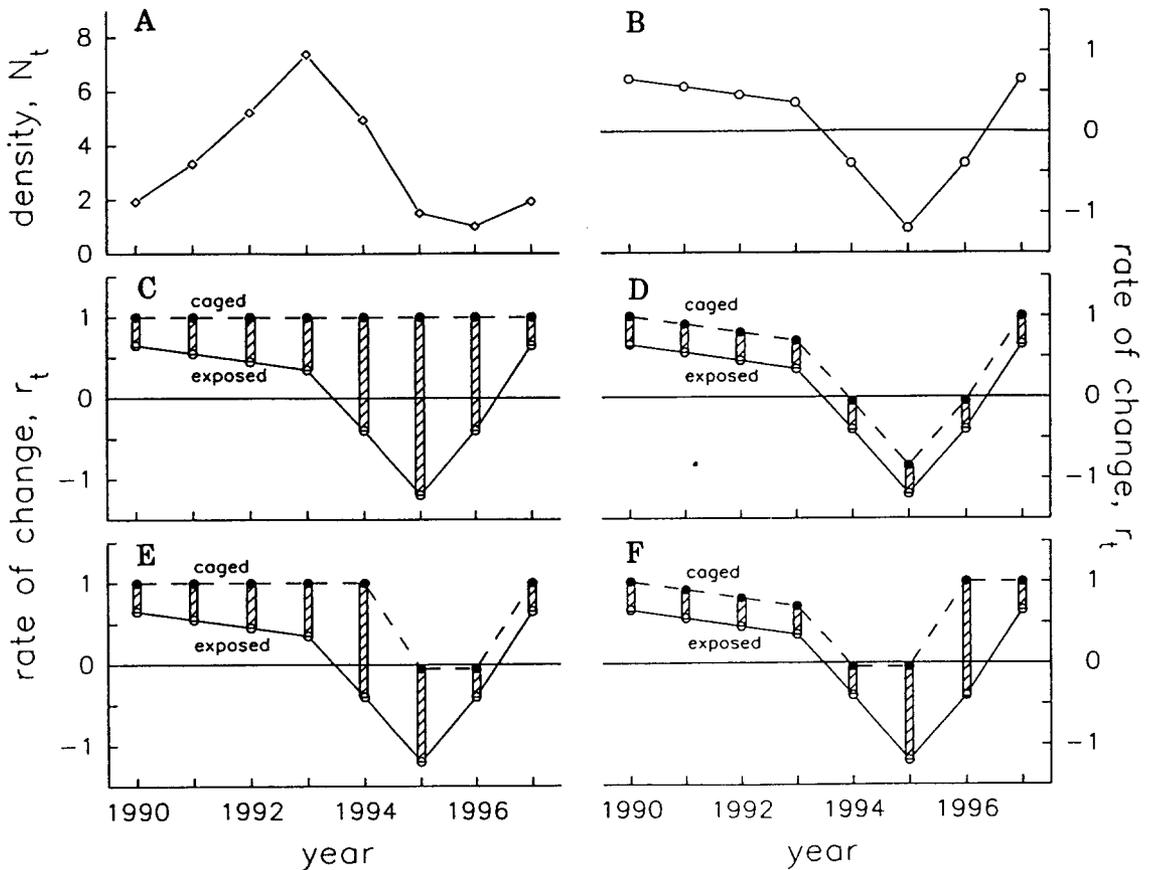


Fig. 5. Conceptual model for determining the role of natural enemies in *D. frontalis* cycles. (A) A hypothetical 7-yr cycle of beetle population density, N_t , modeled loosely on trends in spot numbers in east Texas from 1957 to 1987. (B) The cycle in the realized per capita rate of population change, $r_t = \log(N_t/N_{t-1})$, calculated from the population cycle in (A) (r for 1997 assumes that the cycle will repeat itself). It is important to note that the peaks and troughs of r_t (1990 and 1995, respectively) precede those for N_t (1993 and 1996, respectively). (C)–(D) Comparisons between r_t for caged beetles and for beetles exposed to natural enemies, for each of four dynamical hypotheses. The difference between the two r values measures the impact of natural enemies. It is assumed that the changes in overall rate of population change in (B) are entirely due to changes in within-tree ratios of increase. (C) A pure predator-prey cycle: r_t within cages is constant, so that all changes in r_t outside the cages are attributable to natural enemies. (D) The null hypothesis: some factor affecting beetles inside as well as outside cages is responsible for the cycle, while the impact of enemies remains constant (trends inside and outside cages are parallel). (E) Enemies suppress outbreaks, but do not trigger them. r_t outside cages begins to decrease in 1990 while r_t inside cages remains high. Some unknown other factor then leads to further decline in r_t , both inside and outside cages, even after the impact of enemies returns to low levels in 1996. The next outbreak then is caused by a change in this other factor, from 1996 to 1997, without any change in enemy impact. (F) Enemies trigger outbreaks, but do not suppress them. This is the opposite of (E). The decline in r_t from 1990 to 1994, which causes collapse of the outbreak, occurs both inside and outside cages: there is no change in enemy impact. The impact of enemies eventually does increase (perhaps due to a delayed numerical response by predators), so that r_t outside cages remains negative in 1995 and 1996 despite a reduced effect of the unknown factor which suppressed the outbreak. The next outbreak then is caused by a reduction in the impact of enemies.

matic variables chosen a priori were incapable of explaining this oscillation, we do not wish to imply that climate has no effect on beetle population dynamics. Weather could advance or delay the onset of a beetle outbreak, as well as affect the outbreak amplitude. For the reasons stated earlier, however, we do not think that statistical analyses of observational data will be successful in establishing the effects of various climatic components on beetle

dynamics. We advocate an approach that will experimentally test a set of clearly stated hypotheses. An additional reason for an experimental approach is that the relationship between some weather variables, such as rainfall, and the susceptibility of pine hosts to beetle attack may be quite complex. Moderately limited water supply reduces the use of carbon in growth processes, while freeing carbon for synthesis of pine oleoresins (Lorio & Hodges

1985, Lorio 1986). Thus, although extreme water stress will be detrimental to the defensive ability of pines against bark beetles, moderate water stress may enhance host defenses due to increased oleoresin synthesis. Currently one of us (P.L., in collaboration with J. Dunn) is conducting an experimental study to test this hypothesis. This study will compare two groups of experimental trees: pines in which moderate water stress was induced by sheltering their root systems from rainfall, and pines under near-optimal water conditions (for which rainfall is supplemented by irrigation if necessary). Defensive ability of pines in each treatment will be assessed by inducing beetle attack, and measuring the ratio of unsuccessful to successful attacks and the number of beetles killed per unit area of bark. We hope that a research program combining such experimental studies with population analysis techniques developed in this paper will give us a more complete picture of interrelations between the abiotic and biotic factors affecting *D. frontalis* population change.

Acknowledgment

We thank A. Berryman, T. Royama, and H. A. Pase III for discussions and criticisms. L. Mitchell provided invaluable assistance with preparing data for analysis.

References Cited

- Beal, J. A. 1927. Weather as a factor in southern pine beetle control. *J. For.* 25: 741-742.
1933. Temperature extremes as a factory in the ecology of the southern pine beetle. *J. For.* 31: 328-336.
- Berryman, A. A. 1978. Population cycles of the Douglas-fir tussock moth (Lepidoptera: Lymantriidae): the time-delay hypothesis. *Can. Entomol.* 110: 513-518.
- Billings, R. F. & H. A. Pase. 1979. Spot proliferation patterns as a measure of the area-wide effectiveness of southern pine beetle control tactics. *USDA Forest Service Tech. Bull.* 1613: pp. 86-97. *In* J. E. Coster & J. L. Searcy [eds.] *Evaluating control tactics for the southern pine beetle.*
- Billings, R. F. & J. D. Ward. 1984. How to conduct a southern pine beetle aerial detection survey. *Texas Forest Service Circular* 267.
- Box, G.E.P. & G. M. Jenkins. 1976. *Time series analysis: forecasting and control.* Holden Day, Oakland, Calif.
- Craighead, F. C. 1925. Bark beetle epidemics and rainfall deficiency. *J. Econ. Entomol.* 18: 557-586.
- Earles, J. M. 1976. Forest statistics for East Texas pineywood counties. *USDA-Forest Service Resource Bulletin* SO-60.
- Gagne, J. A., R. N. Coulson, J. N. Foltz, T. L. Wagner & L. J. Edson. 1980. Attack and survival of *Dendroctonus frontalis* in relation to weather during three years in east Texas. *Environ. Entomol.* 9: 222-229.
- Hedden, R. L. 1978. The need for intensive forest management to reduce southern pine beetle activity in east Texas. *So. J. Appl. For.* 2: 19-22.
- Hutchinson, G. E. 1948. Circular causal systems in ecology. *Ann. N.Y. Acad. Sci.* 50: 221-246.
- Kalkstein, L. S. 1981. An improved technique to evaluate climate-southern pine beetle relationships. *For. Sci.* 27: 579-589.
- King, E. W. 1972. Rainfall and epidemics of the southern pine beetle. *Environ. Entomol.* 1: 279-285.
- Kroll, J. C. & H. C. Reeves. 1978. A simple model for predicting annual numbers of southern pine beetle infestations in east Texas. *So. J. Appl. For.* 2: 62-64.
- Lang, L. L. & D. F. Bertelson. 1986. Forest statistics for east Texas countries—1986. *USDA-FS, Southern Forest Experiment Station Resource Bull.* SO-118.
- Linhart, H. & W. Zucchini. 1986. *Model selection.* Wiley, New York.
- Lorio, P. L. 1986. Growth-differentiation balance: a basis for understanding southern pine beetle-tree interactions. *For. Ecol. Mgt.* 14: 259-273.
- Lorio, P. L. & J. D. Hodges. 1968. Oleoresin exudation pressure and relative water content of inner bark as indicators of moisture stress in loblolly pines. *For. Sci.* 14: 392-398.
1977. Tree water status affects induced southern pine beetle attack and brood production. *USDA Forest Service Research Paper* SO-135.
1985. Theories of interactions among bark beetles, associated microorganisms, and host trees, pp. 485-492. *In* E. Shoulders [ed.] *Proceedings of the third biennial southern silvicultural research conference, Atlanta, Ga.* *USDA-Forest Service Technical Report* SO-54.
- Martinat, P. J. 1987. The role of climatic variation and weather in forest insect outbreaks, pp. 241-262. *In* P. Barboda & J. C. Schultz [eds.] *Insect outbreaks.* Academic, San Diego.
- McClelland, W. T. & F. P. Hain. 1979. Survival of declining *Dendroctonus frontalis* populations during a severe and nonsevere winter. *Environ. Entomol.* 8: 231-235.
- Michaels, P. J. 1984. Climate and the southern pine beetle in Atlantic coastal and piedmont regions. *For. Sci.* 30: 143-156.
- Moran, P.A.P. 1953. The statistical analysis of the Canadian Lynx cycle. *Aust. J. Zool.* 1: 163-173.
- Murdoch, W. W. & J. D. Reeve. 1987. Aggregation of parasitoids and the detection of density dependence in field populations. *Oikos* 50: 137-141.
- Nisbet, R. M. & W.S.C. Gurney. 1982. *Modelling fluctuating populations.* Wiley, Chichester.
- Pollard, E., K. H. Lakhani & P. Rothery. 1987. The detection of density-dependence from a series of annual censuses. *Ecology* 68: 2046-2055.
- Prout, T. & F. McChesney. 1985. Competition among immatures affects their adult fertility: population dynamics. *Am. Nat.* 126: 521-558.
- Rosenzweig, M. L. 1971. Paradox of enrichment: destabilization of exploitation ecosystems in ecological time. *Science* 171: 385-387.
- Royama, T. 1981. Fundamental concepts and methodology for the analysis of animal population dynamics, with particular reference to univoltine species. *Ecol. Monogr.* 51: 473-493.
- Sokal, R. R. & F. J. Rohlf. 1981. *Biometry.* Freeman, New York.
- St. George, R. A. 1930. Drought-affected and injured trees attractive to bark beetles. *J. Econ. Entomol.* 23: 825-828.
- Thornthwaite, C. W. & J. R. Mather. 1957. pp. 311. *Instructions and tables for computing potential evapotranspiration and the water balance.* Vol. X. Number 3. Drexel Institute of Technology, Labora-

- tory of Climatology, Publications in Climatology, Centerton, N.J.
- Turchin, P.** 1990. Rarity of density dependence or population regulation with lags? *Nature* 344: 660-663.
- Turchin, P. & A. Taylor.** *In press.* Complex dynamics in ecological time series. *Ecology*.
- Vité, J. P.** 1961. The influence of water supply on oleoresin exudation pressure and resistance to bark beetle attack in *Pinus ponderosa*. *Contrib. Boyce Thompson Inst.* 21: 37-66.
- Wyman, L.** 1924. Bark beetle epidemics and rainfall deficiency. *U.S. Forest Service Bull.* 8: 2-3.

Received for publication 5 June 1990; accepted 2 November 1990.
