

Scramble competition in the southern pine beetle, *Dendroctonus frontalis*

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Abstract. 1. The nature of intraspecific competition was investigated in the southern pine beetle, *Dendroctonus frontalis*, a highly destructive pest of pine forests in the southern U.S.A. Data were analysed from an observational study of naturally-attacked trees, and from field experiments where attack density was manipulated by adding different numbers of beetles to caged trees.

2. The effect of attack density on gallery construction, oviposition, brood survival, and the overall rate of increase was examined, and a flexible model of intraspecific competition used to classify the type of competition (contest or scramble) at different points in the life cycle.

3. The results of these analyses suggest that contest competition occurs during gallery construction and oviposition, in accord with previous work on *D. frontalis*. Strong scramble competition occurs later on in development, however, and the overall competitive process is better characterized as scramble competition, similar to other bark beetles. Trees with attack densities sufficiently high to produce significant competition are common in the field.

Key words. Bark beetles, intraspecific competition, *Dendroctonus frontalis*.

Introduction

Competition has emerged as an important feature in the ecology of phytophagous insects. Many case studies have demonstrated the importance of intraspecific competition, some recent examples being Hunter & Yeargan (1989), Denno & Roderick (1992), Faeth (1992), Joern & Klucas (1993), Woodson (1994), and Belovsky & Slade (1995), and also interspecific competition, reviewed by Denno *et al.* (1995). Among different groups of phytophagous insects, competition is especially frequent and severe in bark beetles (Coleoptera: Scolytidae), perhaps due to their unique life history. During the initial colonization phase, thousands of adult beetles may attack an individual host tree, which sets the stage for intense competition within the phloem layer of the inner bark. Competition first occurs among the attacking adults, with the parent beetles typically constructing less gallery and laying fewer eggs per beetle at high attack densities (Berryman, 1974; Raffa & Berryman, 1983; Anderbrant *et al.*, 1985; Anderbrant, 1990; Zhang *et al.*, 1992). In these studies, survivorship of the brood

produced by the parent beetles declined as attack densities increased, indicating that competitive effects also occur later in the life cycle. For most bark beetle species, the overall competitive process can be characterized as scramble competition, with fewer individuals emerging per unit area as attack densities increase beyond a certain level (Nicholson, 1954; Hassell, 1975).

The southern pine beetle, *Dendroctonus frontalis* Zimmermann, is a highly destructive pest of pine forests in the southern U.S.A. (Price *et al.*, 1992). This species would appear to be an exception to the pattern of scramble competition in bark beetles. Field and laboratory studies have shown that as attack densities increase, gallery length and the number of eggs laid per attacking adult decrease in an exponential fashion (Coulson *et al.*, 1976b; Coulson, 1979, 1980; Wagner *et al.*, 1981). These processes are believed to generate a constant density of eggs and adult gallery, independent of the number of attacking adults, so that each egg has an equal amount of host resources, regardless of attack density. As a consequence, survival from egg to adult is also thought to be independent of attack density, and the overall process should resemble contest competition. These studies did not examine directly the effect of attack density on brood survival, however, or the beetle's overall rate of increase. In this paper, the nature of these relationships for *D. frontalis* is investigated, and an

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attempt is made to classify the competitive process as contest or scramble at various points in its life cycle. Data are analysed from an observational study of naturally-attacked trees, and from field experiments where attack density was manipulated by adding different numbers of beetles to caged trees. The results indicate that brood survivorship and the rate of increase decline sharply as attack densities increase, and that the overall competitive process in *D. frontalis* is better classified as scramble competition.

Methods

Naturally-attacked trees

Trees were sampled in two large *D. frontalis* infestations in the Indian Mounds Wilderness Area, part of the Sabine National Forest in East Texas. Sampling in the first infestation began in May 1992 and continued until July 1992, with a total of twenty trees sampled. Recently-attacked loblolly (*Pinus taeda* L.) or shortleaf (*Pinus echinata* Mill.) pines 25–35 cm in diameter at breast height (d.b.h.) were located, and as the brood completed development in each tree, 80 × 10 cm rectangular bark samples were taken at heights of 4, 5, 6, and 7 m on the bole or trunk. The direction of the highest sample was chosen at random, and then the lower samples located on alternating sides of the bole. The samples were removed from the tree using a battery-powered saw and chisel. Four emergence traps were then attached to the tree opposite each bark sample, and left in place for 2 months to catch the emerging adult beetles (at this point the parent beetles have already left the tree, so that all beetles trapped were emerging brood). The traps were made from rectangular pieces of plywood, with an 80 × 10 cm opening, and attached to the tree using long wood screws. Foam-rubber strips glued around the opening provided a close fit of the trap to the bark surface. Insects that emerged through the opening entered an enclosure made of polyethylene screening (20 × 20 mesh per cm), and fell into a jar containing antifreeze. The data from the emergence traps were used to estimate the number of progeny emerging per 100 cm². The bark samples were scored to determine the number of attacks, the length of adult gallery constructed, and the number of egg niches (see *Processing of bark samples*). The proportion of the phloem damaged by cerambycid feeding, or discoloured by the bluestain fungus *Ophiostoma minus* (Hedgc.) H. & P. Sydow was also estimated. Both cerambycids and *O. minus* are potential competitors with *D. frontalis* for resources within the tree (Barras, 1970; Coulson *et al.*, 1976a; Bridges, 1985). Sampling in the second infestation proceeded similarly, from June to September 1993, with a total of nineteen trees sampled. The intent of this sampling scheme was to examine the effect of tree-to-tree variation in attack density on *D. frontalis* survival and reproduction. Within each tree, sampling was focused on the midbole population of *D. frontalis*, where most of the attacks occur and attack density is relatively homogeneous (Fargo *et al.*, 1978). Therefore, inferences from these data may be limited to the midbole of 25–35 cm d.b.h. trees.

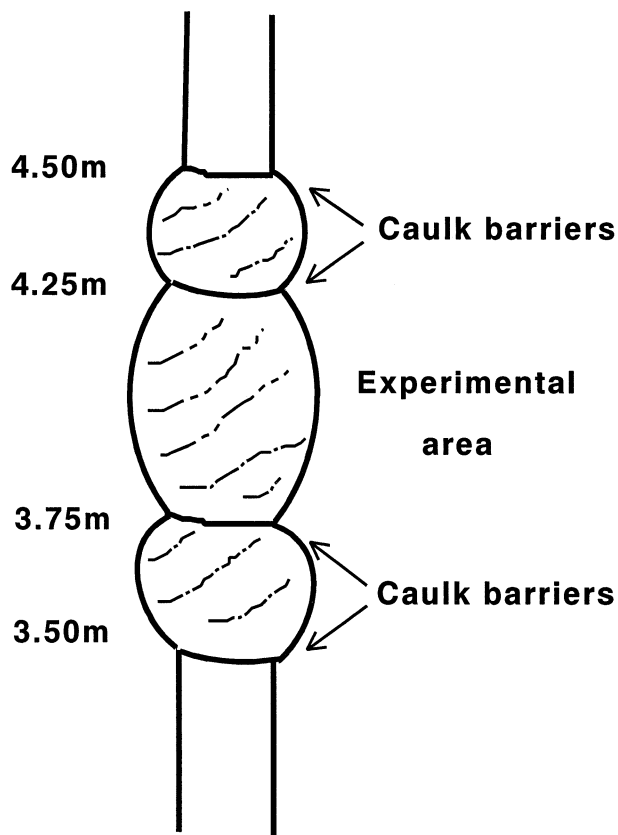


Fig. 1. Tree cages used in the field experiment. Caulk barriers prevented adult *D. frontalis* from entering or leaving the experimental area.

Field experiments

Attack density was manipulated in field experiments by adding different numbers of adult *D. frontalis* to cylindrical cages attached to host trees. These cages were installed and readied for the beetles in several steps. Stands of loblolly pine were located in the Kisatchie National Forest in central Louisiana, and trees selected of approximately the same size (25–35 cm d.b.h.) and separated by at least 100 m. A cylindrical cage of polyethylene screening (20 × 20 mesh per cm) was then installed on each tree. The cage material was drawn in and caulked to the bark at four heights (Fig. 1), forming a 0.5 m experimental area to which the beetles were later added, and buffer zones above and below it where no insects were added. These zones acted as a barrier to the movement of *D. frontalis* and other insects on the bark surface and through the phloem.

The trees were then baited with frontalin (the aggregation pheromone of *D. frontalis*) and steam-distilled turpentine to induce attack. This combination of chemicals is highly attractive to *D. frontalis* (Payne *et al.*, 1978), and attack usually occurred in less than a month. Adult beetles were then added to the experimental area of the cage once attack outside the cage was well under way, and the tree's defences (the oleoresin system) had been overcome by the beetles (Lorio *et al.*, 1990). In the

Table 1. Regression coefficients and ANOVA for total gallery and egg density, and gallery and eggs per attack, for naturally-attacked (NA) and field-experiment (FE) trees. Gallery and eggs per attack were log-transformed before analysis.

Variable	Attack density		Year	
	Coefficient	<i>p</i>	<i>p</i>	<i>R</i> ²
Gallery, NA	11.695	< 0.001	0.072	0.803
Eggs, NA	5.401	< 0.001	< 0.001	0.513
Gallery, FE	11.608	< 0.001	0.001	0.866
Eggs, FE	8.577	0.001	0.001	0.672
Gallery per attack, NA	-0.064	< 0.001	0.255	0.496
Eggs per attack, NA	-0.160	< 0.001	< 0.001	0.906
Gallery per attack, FE	-0.077	< 0.001	0.010	0.605
Eggs per attack, FE	-0.151	< 0.001	0.026	0.533

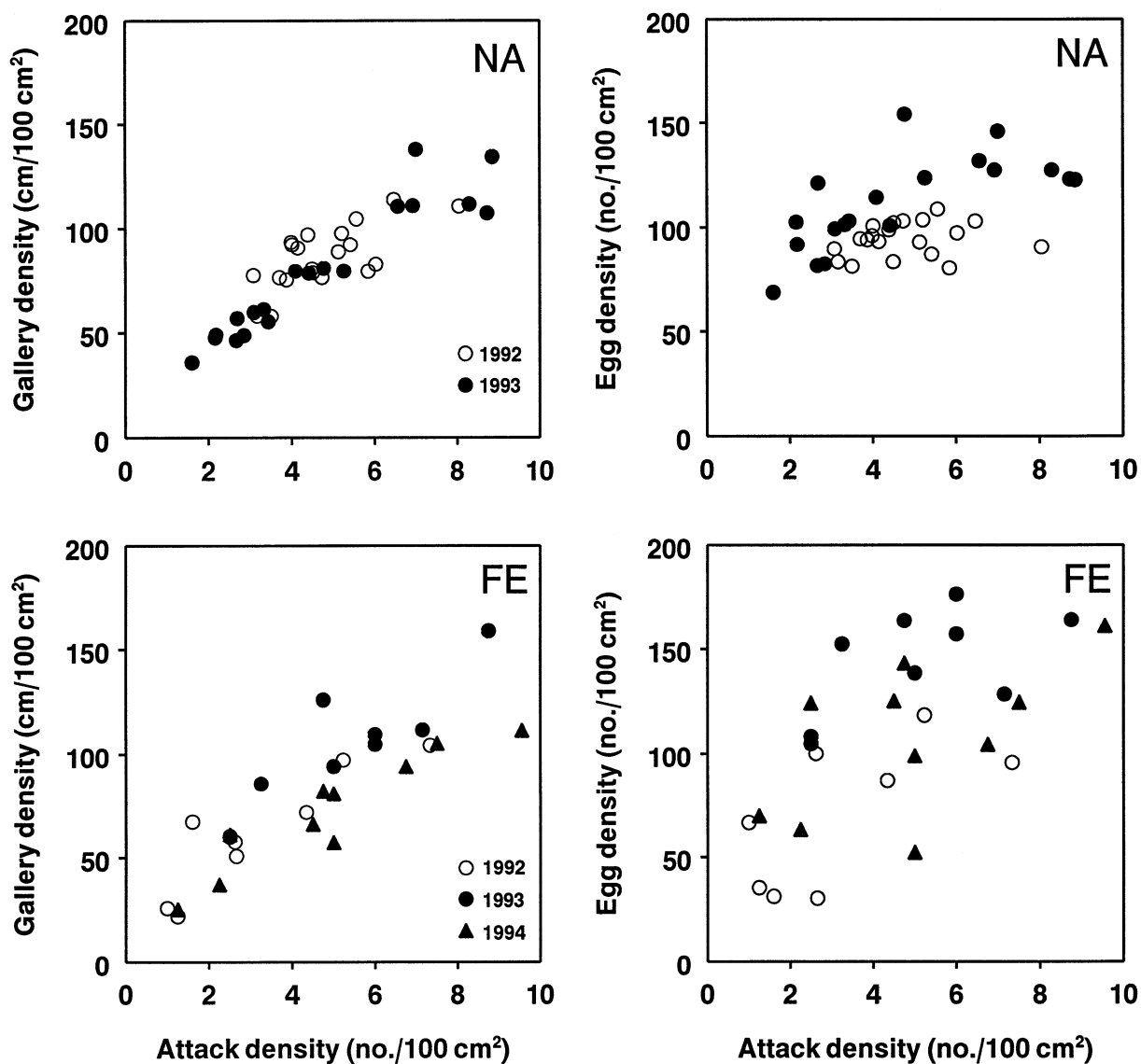


Fig. 2. Total gallery length and egg density vs. attack density, for naturally-attacked (NA) and field-experiment (FE) trees. Data from different years (replicates) of the studies are denoted with different symbols.

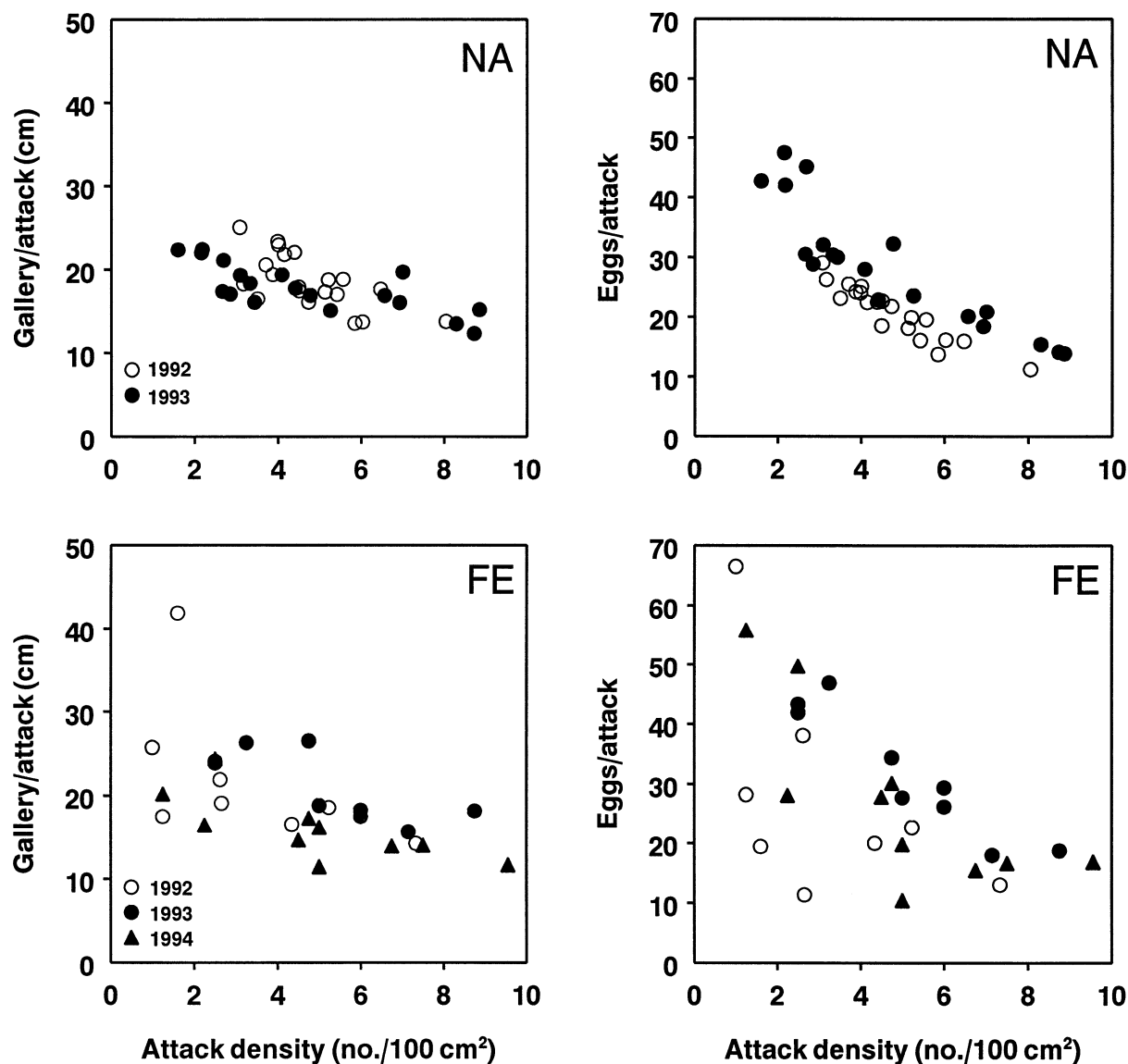


Fig. 3. Gallery and eggs per attack vs. attack density, for naturally-attached (NA) and field-experiment (FE) trees.

first replicate of the experiment, carried out in May–July 1992, eight trees were stocked with different densities of unsexed adult *D. frontalis* (100, 200, 500, 750, 1000, 1250, 1500, and 2000 adults per cage). The insects for the experiment were obtained by placing bark or bolts (short logs) from infested pines in rearing boxes in the laboratory. The emerging adults were collected daily and used immediately to stock the cages, or at most refrigerated overnight. A somewhat different protocol was used in two other replicates of the experiment, one carried out in May–June 1993 and another in June–November 1994 (this particular replicate took longer because beetle populations were low, but it was still completed during the yearly interval of active brood development). Before the beetles were added to the cage, the trees were girdled just above and below the experimental area and the cage material drawn into the girdle and sealed with latex caulk. This procedure confined the beetles

better to the experimental area, and should have had little impact on population processes inside the cage, as wild beetles had already girdled the trees extensively. Five density treatments were applied to the trees in 1993 (250, 500, 1000, 1500, and 2000 adults per cage), and a further low-density treatment added in 1994 (125 adults per cage), with each treatment replicated on two trees in each year. One of the treatments produced an unnaturally high attack density on one tree in 1993, and for this reason it was dropped from later analyses. Two trees in 1994 could not be used because their emergence data were lost.

As the brood in the cages completed development, the trees were felled and the experimental area of the bole removed and returned to the laboratory. Four bark samples (10 × 10 cm) were then removed from this bolt using a portable electric saw and chisel. The surface area of each bolt was estimated, and

Table 2. Parameter estimates and asymptotic 95% confidence intervals for the Maynard Smith & Slatkin model, fitted to gallery per attack and eggs per attack data from naturally-attacked (NA) and field-experiment (FE) trees. Parameter estimates for c_{92} and c_{93} describe year effects obtained using dummy variables.

Variable	Parameter	Estimate	95% c.i.	R^2
Gallery per attack, NA	λ	27.596	− 3.954, 59.146	0.500
	a	0.114	− 0.188, 0.417	
	b	0.828	− 0.868, 2.525	
	c_{92}	0.059	− 0.036, 0.154	
Eggs per attack, NA	λ	54.075	31.864, 76.286	0.906
	a	0.226	0.087, 0.366	
	b	1.501	0.854, 2.147	
	c_{92}	− 0.238	− 0.321, − 0.155	
Gallery per attack, FE	λ	25.639	3.984, 47.293	0.615
	a	0.133	− 0.105, 0.371	
	b	0.914	− 0.587, 2.415	
	c_{92}	0.149	− 0.050, 0.348	
	c_{93}	0.301	0.117, 0.485	
Eggs per attack, FE	Unable to estimate parameters (see text)			

Table 3. Regression coefficients and ANOVA for brood survival and the ratio of increase, for naturally-attacked (NA) and field-experiment (FE) trees. Brood survival and the ratio of increase were log-transformed before analysis.

Variable	Attack density		Blue-stain		Cerambycid damage		Year	R^2
	Coefficient	p	Coefficient	p	Coefficient	p	p	
Brood survival, NA	– 0.419	< 0.001	– 1.669	0.039	– 2.965	0.072	0.015	0.662
Ratio of increase, NA	– 0.582	< 0.001	– 1.999	0.015	– 2.889	0.079	0.097	0.760
Brood survival, FE	– 0.221	0.009	– 0.858	0.513	–	–	0.522	0.353
Ratio of increase, FE	– 0.383	< 0.001	– 2.387	0.064	–	–	0.364	0.602

it was placed in a rearing can to catch the emerging adult beetles. The bark samples were scored to determine the number of attacks, the amount of adult gallery constructed, the number of egg niches, and the proportion of the phloem stained by *O. minus* (see next section). The number of adult beetles emerging from the bolt and its surface area were used to estimate the density of emerging insects. Cerambycid feeding damage was minor or absent in the samples, because these insects were excluded by the cage.

Processing of bark samples

The bark samples taken from naturally-attacked and experimental trees were scored in a similar way. For each bark sample, the amount of cerambycid damage was first determined by overlaying a piece of clear mylar marked with dots in a 1×1 cm grid, and counting the number of dots overlying damaged areas. The undamaged portions of each sample were then scored for blue-stain, adult gallery, egg niches, and beetle attacks (damaged areas could not be scored). The same grid was used to determine the area of blue-stain, i.e. dark blue or black areas of phloem discoloured by *O. minus*. The length of gallery produced by the parent

beetles was then measured with a metric map reader, and egg niches counted and used to estimate the number of eggs laid (Clarke *et al.*, 1979; Wagner *et al.*, 1981). Finally, the number of attacks was determined by dissecting the bark samples (Stephen & Taha, 1976; Linit & Stephen, 1978). Loose bark was shaved from the back of the sample, and a probe was used to explore any holes observed. Holes were judged to be beetle attacks if they held a mixture of oleoresin and frass, were slanted relative to the bark surface, and emerged into the beginning of a gallery. Attacks were then classified as unsuccessful or successful, with unsuccessful attacks having gallery filled with oleoresin, whereas successful attacks had some clear gallery and evidence of oviposition.

Statistical procedures

For the naturally-attacked trees sampled at Indian Mounds, the attack density for each bark sample was calculated by dividing the number of successful attacks by the area of undamaged sample, in units of 100 cm^2 . Gallery and egg density were calculated in a similar way. Attack density, gallery density, and egg density were then averaged across the four bark samples in each tree to obtain a single value,

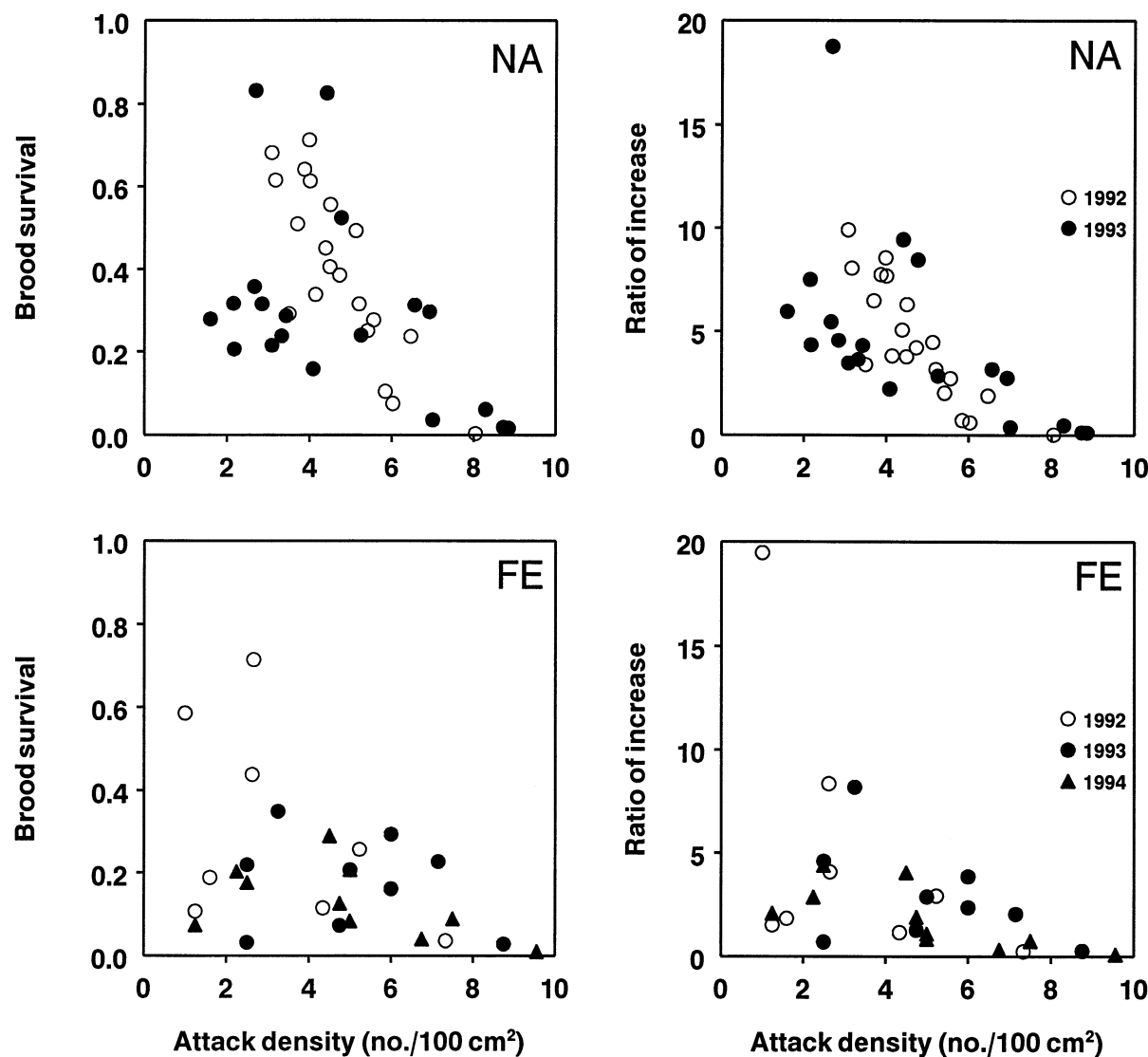


Fig. 4. Brood survival and ratio of increase vs. attack density, for naturally-attached (NA) and field-experiment (FE) trees.

as were the emergence trap data for the tree. These quantities were then used to calculate the length of gallery and number of eggs per attack, the survival rate from egg to emerging adult (brood survival), and the ratio of increase of the beetle population. The ratio of increase is defined as $R = B/2A$, where B is the density of emerging adults and A is attack density (Thatcher & Pickard, 1964). It is equivalent to the beetle's finite rate of increase, with the formula incorporating the 1:1 sex ratio found in *D. frontalis* (Osgood & Clark, 1963). A similar procedure was used to obtain an estimate of attack density and other variables for each bolt in the field experiments, by averaging the four bark samples taken from the bolts.

General linear models were used to test for attack density and year (or site) effects on the length of gallery constructed and egg density, for both naturally-attached and field-

experiment trees. Attack density was treated as a continuous, and year as a categorical, variable in these analyses. General linear models were also employed in a preliminary analysis that tested for density dependence in gallery per attack, eggs per attack, brood survival, and the ratio of increase. Each of these rates was log-transformed, then regressed on attack density, with year as a categorical variable. For brood survival and the ratio of increase, the models also included terms for the proportion of blue-stained phloem, and for naturally-attached trees the proportion of phloem damaged by cerambycids (cerambycids were excluded in the experimental trees). Tree species was not included in these models because preliminary analyses suggested that it had little effect on any variable.

The competitive process was then classified at different points in the life cycle of *D. frontalis* using methods adapted

Table 4. Parameter estimates and asymptotic 95% confidence intervals for the Maynard Smith & Slatkin model, fitted to brood survival and ratio of increase data from naturally-attacked (NA) and field-experiment (FE) trees. Parameter estimates for c_{92} and c_{93} describe year effects obtained using dummy variables, $c_{\text{bluestain}}$ and c_{damage} , the effects of blue-stain or cerambycid damage.

Variable	Parameter	Estimate	95% c.i.	R^2
Brood survival, NA	λ	0.724	0.452, 0.995	0.822
	a	0.165	0.147, 0.184	
	b	9.094	5.794, 12.294	
	$c_{\text{bluestain}}$	-2.105	-3.281, -0.929	
	c_{damage}	-1.794	-4.216, 0.629	
	c_{92}	0.220	-0.173, 0.612	
Ratio of increase, NA	λ	13.148	8.347, 17.949	0.881
	a	0.180	0.162, 0.197	
	b	9.303	6.756, 11.851	
	$c_{\text{bluestain}}$	-2.439	-3.578, -1.301	
	c_{damage}	-1.787	-4.133, 0.558	
	c_{92}	-0.086	-0.473, 0.301	
Brood survival, FE	λ	0.159	0.054, 0.264	0.514
	a	0.143	0.111, 0.175	
	b	8.184	0.726, 15.643	
	$c_{\text{bluestain}}$	-0.668	-3.107, 1.770	
	c_{92}	0.513	-0.269, 1.295	
	c_{93}	0.230	-0.516, 0.977	
Ratio of increase, FE	λ	3.738	0.841, 6.636	0.671
	a	0.193	0.136, 0.251	
	b	5.306	2.256, 8.355	
	$c_{\text{bluestain}}$	-2.568	-4.974, -0.161	
	c_{92}	0.372	-0.418, 1.162	
	c_{93}	0.481	-0.260, 1.221	

from Bellows (1981, 1982). These methods are based on a simple but highly flexible model of intraspecific competition first proposed by Maynard Smith & Slatkin (1973). If N_t is the density of insects at time t , and N_{t+1} the density at time $t + 1$, then N_{t+1} is given by the equation:

$$N_{t+1} = \lambda N_t / [1 + (aN_t)^b] \quad (1)$$

where λ is the rate of increase in the absence of competition, a is a scaling parameter, and b describes the intensity of the competitive process ($b = 0$ implies no competition, $b \approx 1$ contest competition, and $b \gg 1$ scramble competition). Nonlinear regression is then used to fit eqn 1 to the data and so obtain estimates of λ , a , and b (Bellows, 1981, 1982). When applied to the data for *D. frontalis*, however, the residuals showed signs of heteroscedasticity, with the variance increasing in proportion to the mean. This problem was overcome by using the transformed model:

$$\ln(N_{t+1} / N_t) = \ln \lambda - \ln [1 + (aN_t)^b] \quad (2)$$

In this form, the model describes how initial density affects the per capita rate of population growth, rather than the final density as in eqn 1. Equation 2 was first used to classify the competitive process during gallery construction, by fitting the equation:

$$\ln(G/A) = \ln \lambda - \ln[1 + (aA)^b] \quad (3)$$

where A is attack density and G/A is gallery per attack. Dummy variables were also incorporated in the regression equation to allow for differences among years in the rate of gallery formation (Draper & Smith, 1981). A similar model was used to classify the competitive process during oviposition, and was obtained by substituting eggs per attack (E/A) for G/A in eqn 3. Models for brood survival and the ratio of increase were derived by substituting brood survival (B/E) or the ratio of increase ($R = B/2A$) for G/A in this same equation. In the case of brood survival, the parameter λ represents the proportion surviving in the absence of competition. These models also included linear terms for the proportion of blue-stained phloem, and for naturally-attacked trees the proportion of phloem damaged by cerambycids. For example, the full equation used for brood survival in naturally-attacked trees was:

$$\ln(B/E) = \ln \lambda - \ln[1 + (aA)^b] + c_{\text{bluestain}} X + c_{\text{damage}} Y + c_{92} Z \quad (4)$$

where X and Y are the proportion of blue-stained and damaged phloem, and Z is a dummy variable equal to one for 1992 and zero for 1993 data. All models were fitted using a nonlinear regression routine in SYSTAT 7.0 (SPSS Inc., 1996).

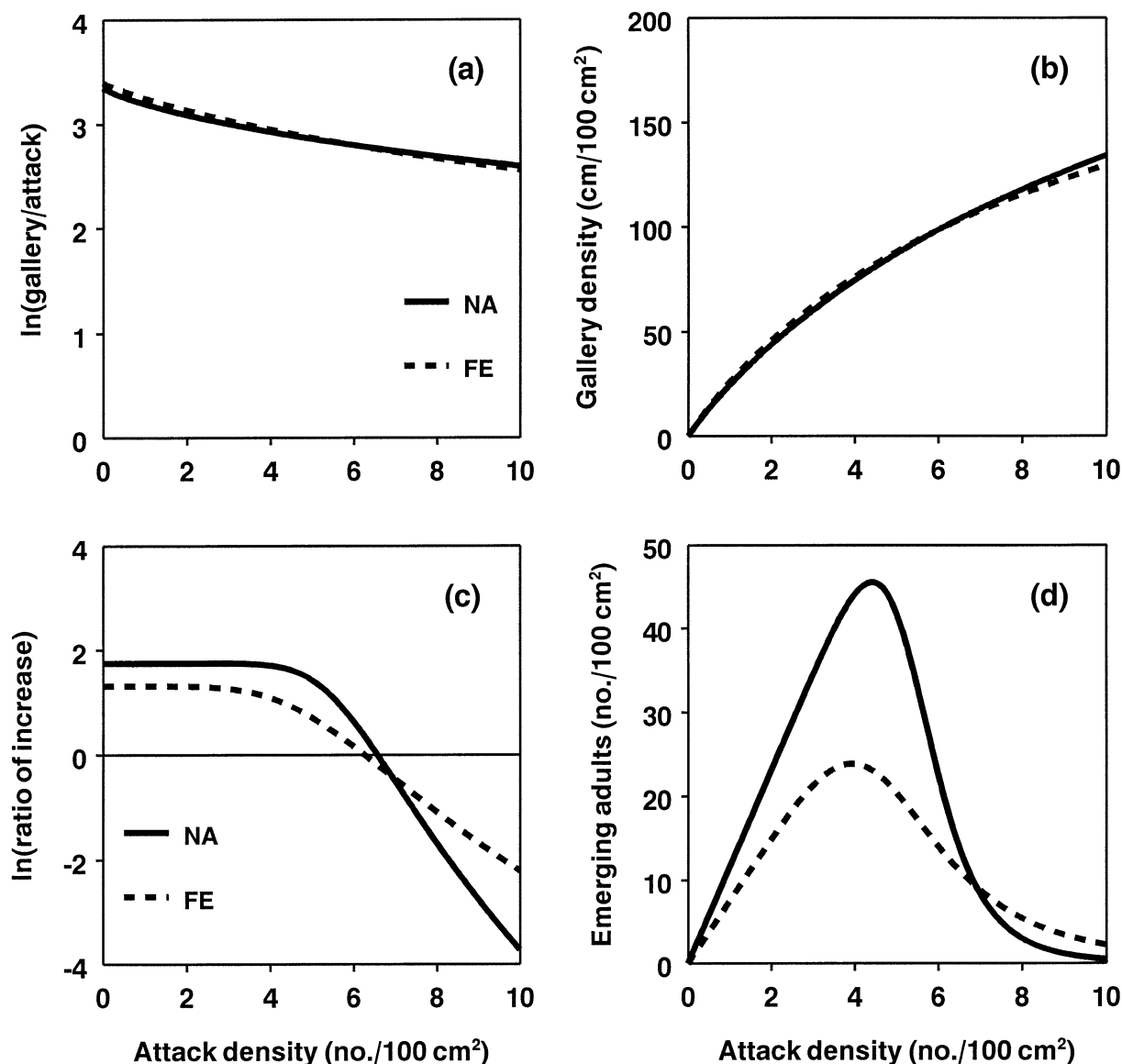


Fig. 5. Curves generated by the Maynard Smith & Slatkin (1973) model using the parameter values in Tables 2 and 4, for naturally-attacked (NA) and field-experiment (FE) trees. (a) Log gallery per attack, (b) gallery density, (c) log ratio of increase, and (d) emerging adult density, vs. attack density. A single curve was generated for each study by averaging effects across years to yield a single value, and by using the average values of blue-stain and cerambycid damage in the model.

Results

Gallery and egg production vs. attack density

Total gallery length and egg density increased significantly with attack density for both naturally-attacked and experimental trees (Table 1, Fig. 2), accompanied by a significant year effect in most cases. Gallery per attack and eggs per attack decreased significantly as attack density increased, indicating density dependence, and significant year effects were again observed (Table 1, Fig. 3). The values of

b found for gallery per attack and eggs per attack ($b \approx 1$) indicate that the interaction at this point can be characterized as contest competition (Table 2). It was not possible to estimate the model's parameters in one case, however, because the nonlinear regression routine failed to converge on a solution.

Brood survival and ratio of increase vs. attack density

Brood survival and the ratio of increase declined significantly as attack densities increased, indicating that

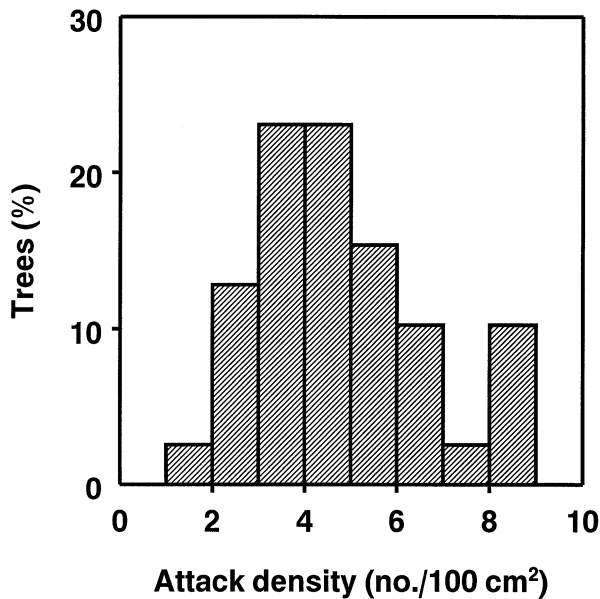


Fig. 6. Frequency distribution of attack density for naturally-attacked trees.

density dependence also occurs at these stages in the life cycle (Table 3, Fig. 4). Blue-stain had a significant negative effect on brood survival and the ratio of increase for naturally-attacked trees, but cerambycid damage did not (Table 3). Year effects were only significant for brood survival in naturally-attacked trees. The values of b obtained for brood survival and the ratio of increase indicate that strong scramble competition occurs during brood development (Table 4). In three out of four cases, the 95% confidence interval for b did not include 1, indicating a competitive interaction significantly stronger than contest competition (Table 4).

Discussion

The results can be summarized graphically by plotting eqns 1 and 2 at different points in the life cycle of *D. frontalis*, using the parameter estimates in Tables 2 and 4. Early in the life cycle, during adult gallery formation, the rate of gallery construction decreases logarithmically and total gallery density increases asymptotically with attack density (Fig. 5a,b). This pattern is diagnostic of contest competition, and the results agree qualitatively with previous work on *D. frontalis* (Coulson *et al.*, 1976b; Coulson, 1979, 1980; Wagner *et al.*, 1981). However, the competitive process appears quite different at the end of the life cycle. Here the population growth rate (the log of the ratio of increase) declines sharply as attack densities increase above five per 100 cm², indicating scramble competition, and emerging adult density follows a hump-shaped curve (Fig. 5c,d). This pattern occurs because brood survival rates decrease sharply at high attack densities, presumably because fewer resources are available for the developing larvae. Because the ratio of

increase spans the complete life cycle, from attacking parent beetles to brood adults, this suggests that the overall competitive process in *D. frontalis* is best characterized as scramble competition, as has been found in other bark beetles (McMullen & Atkins, 1961; Berryman, 1974; Sasakawa & Katayama, 1975; Raffa & Berryman, 1983; Anderbrant *et al.*, 1985; Furuta, 1989; Anderbrant, 1990; Zhang *et al.*, 1992; Lawson *et al.*, 1995).

Tree-killing bark beetles like *D. frontalis* have evolved a complex system of pheromone signals that concentrates them on individual trees during mass attack, to overcome host tree resistance, and once these are colonized switches the attack to adjacent trees (Payne, 1980; Alcock, 1982; Raffa & Berryman, 1983; Byers, 1989; Raffa *et al.*, 1993; Smith *et al.*, 1993). Does this system usually regulate attack density below levels where intraspecific competition becomes important, or is competition a common occurrence for *D. frontalis*? This question can be addressed using data from the naturally-attacked trees to derive a frequency distribution of attack density (Fig. 6). If six attacks per 100 cm² is chosen as the threshold where competitive effects become important (see Fig. 5c,d), it appears that beetles in 23% of the trees experienced significant intraspecific competition. Other studies involving *D. frontalis* have reported similar or broader distributions of attack densities (Fargo *et al.*, 1978; Lih & Stephen, 1996), so strong competitive effects should be a frequent occurrence.

Several factors in addition to attack density had significant effects on *D. frontalis* reproduction. Year effects were significant in many of the analyses, suggesting that rates of gallery construction and oviposition can differ among years (or sites and infestations). Lih & Stephen (1996) have also reported significant site and seasonal effects on *D. frontalis* reproduction. High levels of blue-stain significantly reduced brood survival and the ratio of increase in some instances, providing further evidence of its negative impact on *D. frontalis* (Barras, 1970; Bridges, 1985).

How would intraspecific competition within the tree affect the dynamics of *D. frontalis* at the population level, particularly during outbreaks? In some systems, attack densities have been observed to increase during the course of an outbreak, generating increased competition that is thought to hasten the collapse of the beetle population (Berryman, 1973; Cole *et al.*, 1976; Amman, 1984; Berryman & Ferrell, 1988; Furuta, 1989). Data from a recently completed study suggest that this pattern may hold to some extent for *D. frontalis* (P. Turchin, A. D. Taylor and J. D. Reeve, unpublished). In this study, trees were baited to induce *D. frontalis* attack twice a year from 1990 to 1994, an interval spanning a mild outbreak in central Louisiana. Attack densities at the peak of the outbreak were approximately double that before the outbreak, but quickly returned to low levels as the beetle population subsided. This suggests that intraspecific competition could be a source of immediate density dependence in the beetle's population dynamics. Competition is probably not the most important force in the dynamics of this system, however, because beetle populations exhibit regular oscillations that appear

to be driven by delayed density dependence (Turchin *et al.*, 1991).

Acknowledgements

We thank J. Fryar and J. Simpson for their invaluable field assistance, O. Anderbrant, S. Clarke, J. Hayes, M. Hunter, K. Raffa, and R. Wilkens for many helpful comments on the manuscript, S. Zarnoch for statistical review, and the Kisatchie and Sabine National Forests for providing study sites and access to beetle infestations.

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Accepted 25 February 1998