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Spatial Distribution of Flying Southern Pine Beetle (Coleoptera:Scolytidae) and the Predator *Thanasimus dubius* (Coleoptera:Cleridae)[1]

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ABSTRACT

Spatial dispersion patterns of flying southern pine beetles, *Dendroctonus frontalis* Zimm., and the clerid predator *Thanasimus dubius* (F.) were determined within 3 natural infestations of southern pine beetle (SPB) in eastern Texas using grids of sticky traps. There was significant positive association of the 2 insects throughout the trapping grids, although aerial population densities of the clerid were inversely related to aerial densities of SPB.

Aggregation patterns were quantified using the index of patchiness (IP) and the regressions of mean crowding ($\overset{*}{m}$) on mean density (m). Both methods showed a highly clumped pattern for both beetle species. SPB density in the infestations was positively associated with the daily rate of tree attack by the beetles, but the degree of population aggregation in the infestations was inversely related to the daily rate of tree attack. Although densities of the two species did not follow the same trends among the 3 infestations, the degree of aggregation did (i.e., SPB was most highly aggregated in the location where *T. dubius* was most highly aggregated) and Lloyd's index of interspecific patchiness indicated overlapping aggregate distributions.

A kairomonal response mechanism for *T. dubius*, and SPB co-aggregation within infestations is hypothesized.

Aggregation of southern pine beetles (SPB), *Dendroctonus frontalis* Zimm., on host trees is largely the result of olfactory responses of the beetles to attractants generated by the host-selecting female beetles (Vité and Renwick 1968). The pattern of arrival of beetles at trees under mass attack and the vertical distribution of beetles as they arrive at such trees have been described (Coster et al. 1977a, b). Methods for characterizing dispersion patterns of flying SPB within infestations were examined by Coster and Johnson (1979a).

Thanasimus dubius (F.) is a common predator of southern pine beetle (Thatcher and Pickard 1966). Adults of this clerid feed mostly upon adult bark beetles while the larvae feed beneath the bark on immature SPB. Adult *T. dubius* have been observed in large numbers on trees undergoing attack by SPB (Vité et al. 1964) and have been demonstrated to aggregate at these trees in response to frontalin (Vité and Williamson 1970), a component of the SPB aggregation pheromone. Thus, with respect to the clerid, frontalin is a kairomone. The diurnal pattern of response by adult *T. dubius* to attractant sources follows closely that of the bark beetle (Dix and Franklin 1977, Dixon and Payne 1979) and peak numbers of the adult clerids arrive soon after the trees are attacked by SPB.

Most research on scolytid pheromones has centered on behavioral responses of individual insects to discrete sources of natural or artificial pheromones (Borden 1977). Studies on kairomone responses of scolytid predators

have been similarly oriented. The development of suitable techniques for using the behavioral chemicals in pest management requires, in addition, understanding of their effects on orientation of populations of the pest and on major predators and parasites. For SPB, such studies have recently been reported (Johnson and Coster 1978, Coster and Johnson 1979a,b). In this study we report on the concurrent spatial distributions of both SPB and *T. dubius* as observed in active SPB infestations in east Texas. We define the nature of the species association, characterize the dispersion of each species separately, and quantify the degree of overlap in their joint distributions.

Materials and Methods

During the late spring and summer of 1974, 3 SPB infestations in eastern Texas were studied. One was located in Trinity Co., near Apple Springs, TX, and the other 2 were located in Montgomery Co. near Richards, TX. The stands primarily consisted of shortleaf pine (*Pinus echinata* Miller) and loblolly pine (*P. taeda* L.) with oaks and sweetgum as the secondary hardwood overstory component. Pine density of the infested stands, as measured by basal area, ranged from 17–20 m²/ha.

Flying beetles were monitored using sticky wing traps consisting of 4 wings or vanes supported by a 1.8-m wooden standard. Each vane was 30.5×61 cm and constructed of fiberglass insect screen (7 mesh/cm) coated with Stickem Special ® (Payne et al. 1978a). Traps were erected so that the vane centers were 1.4 m above the ground and were equipped with devices that eluted an attractant mixture of frontalin and *alpha*-pinene (Renwick and Vité 1969). These devices released about 2 mg of frontalin and 5 mg of *alpha*-pinene/day/trap. Chemicals were replenished every 1–2 days as needed. In these studies the attractant mixture was used to increase the trapping efficiency of the wing traps. Preliminary field tests had indicated that such low-level releases of attrac-

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tants provided short-range attraction to flying beetles but were unable to induce attack on trees 2.5–3 m from the release point. The release rates were well below those used in other studies on behavioral chemicals (Payne et al. 1978b).

Traps were placed on 15-m centers extending out from the center of the infestation in 4 directions using a 5×6 grid system. The long axis of the grid was oriented more or less parallel with the anticipated direction of spread of the infestation and so that its center was near the most recently mass-attacked pine. Where necessary, trap position was altered so that no trap would be closer than 3 m to a pine tree. Thirty traps were placed in each infestation. SPB and *T. dubius* were removed from the traps each day and sexed; the presence of the transverse pronotal ridge identified females in SPB (Osgood and Clark 1963) and the configuration of the last abdominal sternite separated the sexes in *T. dubius* (Struble and Capelan 1941). Beetle response was monitored for 20 consecutive days in each infestation; from May 9 – 29 at Apple Springs, from June 17 – July 7 at Richards I and from July 26 – Aug. 15 in Richards II.

The association between trap catches of SPB and *T. dubius* was examined using a 2×2 contingency table arrayed for the presence or absence of each species on each trap. The association tests were done for all traps over all days (30 traps × 20 days × 3 infestations = 1800 observations) and separately for each infestation (30 traps × 20 days = 600 observations/infestation). The observed values were compared to expected values by a chi-square test.

Dispersion patterns of the separate species within the infestations were analyzed using 2 methods: the Index of Patchiness (IP) (Lloyd 1967); and the regression of mean crowding ($\overset{*}{m}$) on mean density (m) (Iwao 1970, Iwao and Kuno 1971). The regression is of the form $\overset{*}{m} = \alpha + \beta m$ where α is the intercept on $\overset{*}{m}$ axis and β the regression coefficient. The parameters were estimated using covariance analysis (ANCOVA) through multiple regression which permits an estimate of the factor x covariate interaction (see Nie et al. 1975 for a discussion of this technique). In our analysis, individual spots were the factor and mean trap density the covariate. The factor x covariate interaction term would therefore detect changes in aggregation behavior between spots (i.e., changes in β).

The α value is a measure of the basic population unit for the species, while β measures the dispersion of these units such that $\beta > 1.0$ indicates an aggregate distribution, $\beta = 1.0$ indicates a random distribution and $\beta < 1.0$ indicates a uniform distribution. If sampling occurs within the smallest aggregation unit (i.e., $\alpha = 0$), the individual is the basic unit of population dispersion and $\beta \simeq$ IP. For flying SPB, the basic population unit is the individual; therefore, Coster and Johnson (1979a) have suggested using IP as a measure of daily SPB aggregation and the $\overset{*}{m}$ - m regression for characterizing SPB aggregation over a series of trapping days.

Quantification of the joint distribution of SPB and *T. dubius* used Lloyd's (1967) measure of interspecific patchiness, IP_{XY}, as recommended by Hurlbert (1978)

for measurement of distributional overlap:

$$IP_{XY} = \frac{\sum\limits_{i=1}^{n} X_i Y_i}{\sum\limits_{i=1}^{n} X_i \sum\limits_{i=1}^{n} Y_i}$$

where X_i is the catch of species X on trap i, Y_i is the catch of species Y on trap i and n is the total number of traps. The value of IP_{XY} will be 0 when there is no co-occurrence of species X and Y within quadrats (traps); 1.0 when both species are uniformly or randomly distributed over the quadrats; and greater than 1.0 when the distributions of both species are aggregated and tend to coincide.

Prior to analysis, the daily trap catch data were screened for statistical outliers using Dixon's test (Dunn and Clark 1974). Total trap catch data from 3 days in Richards I and 3 days in Richards II showed extremely high catches due to natural mass-attack of trees near 1 or 2 of the traps. Since SPB attack behavior includes repeated landing/flight episodes (Bunt 1979) presumably separated by flight in the vicinity of the tree, the probability of being caught on a trap in the immediate vicinity of a newly attacked tree is increased, which results in a false measure of population aggregation; therefore these 6 days were deleted from subsequent analyses. Species association tests, since they depend only on presence or absence of the species and not absolute numbers present, were performed on the complete data set. Statistical tests were judged to be significant at the 0.05 probability level unless otherwise noted.

Results

Infestation Development and Insect Numbers

At the time trapping began in the Apple Springs infestation, 20 trees were infested with SPB. Richards I had only 17 infested trees while Richards II contained 58 attacked trees. In all 3 infestations the majority of the trees contained callow adults, pupae and larvae. During the 20-day trapping period 27 trees were successfully attacked at Apple Springs, 7 trees at Richards I, and 40 were successfully attacked at Richards II. In no case did the small amounts of synthetic pheromones appear to induce attack on adjacent trees.

The number of SPB and *T. dubius* caught are shown in Table 1. Mann-Whitney tests were used to contrast all pairs of means since the distributions of both SPB trap catch and trees attacked per day were non-normal. SPB trap catches were all significantly different from one another and flying beetle density in the infestations was ranked as Richards II > Richards I > Apple Springs. *T. dubius* numbers did not differ between Apple Springs and Richards I. Both Apple Springs and Richards I, however, had significantly greater *T. dubius* density than Richards II. The rate of attack of new trees was less in Richards I than in the other two infestations.

The overall sex ratio of SPB was 1:0.83 (male:female) and of *T. dubius* was 1:0.82. Both ratios differed significantly from unity (χ^2 test) and are similar to those reported by Coster et al. (1977a,b) and Dixon and Payne

Table 1.—Numbers of SPB and *T. dubius* caught on sticky traps and the average number of trees attacked per day (NTA) in 3 infestations.

Infestation	Trapping days	NTA[a]	SPB		T. dubius	
			Total no.	Mean no./trap/ day[a]	Total no.	Mean no./trap/ day[a]
Apple Springs	20	1.35 a	1,570	2.62 a	465	0.78 a
Richards I	17	0.35 b	532	1.05 b	395	0.78 a
Richards II	17	2.06 a	4,058	7.96 c	149	0.29 b

[a] Means in a column followed by the same letter are not significantly different ($P \leqslant 0.05$).

(1979) for in-flight populations of the 2 beetles in east Texas.

The ratio *T. dubius*:SPB varied widely between the 3 infestations; it was 1:3.4 at Apple Springs, 1:1.3 at Richards I, and 1:27.2 at Richards II. The ratios between the two species varied significantly among infestations (χ^2 test). It was lowest in the smallest infestations (Apple Springs, Richards I) and highest in the large infestations (Richards II). Variations in the ratio may be due to the general lack of synchrony between life cycles of the 2 species (Thatcher and Pickard 1966) and seasonal differences in numbers of clerids (Stein and Coster 1977).

Trap Catch Distributions

The observed trap catch distribution of SPB was compared to 6 distributions, including the negative binomial, and found to differ significantly from all (Coster and Johnson 1979a). The closest fit, however, was to a negative binomial with $\hat{k} = 0.23$ ($\bar{x} = 2.49$, $s^2 = 23.64$). The *T. dubius* trap catch distribution did not differ from a negative binomial with $\hat{k} = 0.32$ ($\bar{x} = 0.60$, $s^2 = 1.71$). The small values of $\hat{k}$ indicate both species have aggregated dispersion patterns.

Species Association

All species association tests were significant indicating dependence of the 2 species. The strength of the association between flying SPB and *T. dubius* was measured with Cole's coefficient of association C_1, and found to be +0.302. A C value of +1.0 indicates maximum possible co-occurrence of the species (both species always occur together), while a C value of −1.0 indicates complete lack of association (both species never occur together), and a C value of 0 occurs when the species are distributed independently. The calculated value for these data indicate that out of all the possible combinations of occurrence of the 1800 trap observations for the 2 species, 30.2% of the traps had either both species present or both species absent, i.e., co-oc-

currence occurred on 30.2% of the traps in the infestations.

Aggregation Indices

IP was calculated for both species in each infestation for each day. Prior to application of statistical analyses, the frequency distributions of IP values were tested using Kolmogorov-Smirnov tests for goodness-of-fit to a normal distribution over all infestations (n = 54 days). The distribution of IP values for SPB was normally distributed whereas the distribution of *T. dubius* values differed significantly from normality.

IP values are shown in Table 2. The value of IP takes a value > 1 with an aggregated pattern, < 1 with a uniform pattern and equal to unity with a random pattern (Lloyd 1967). Highly aggregated patterns are indicated for both species in all infestations. IP values were contrasted using Mann-Whitney tests.

Within each infestation, *T. dubius* was less aggregated than SPB, but the pattern of mean IP between infestations was the same for both species (Richards I > Richards II, Apple Springs). Aggregation of both species was inversely related to both NTA and SPB density, but unrelated to clerid density (Tables 1 and 2). SPB was most highly aggregated in Richards I; this area also had the lowest SPB density (Table 1). The greater degree of aggregation in this low density area supports the prediction of Knipling and McGuire (1966) that pheromones will be relatively more effective in aggregating low density populations than high density populations. *T. dubius* also had the highest aggregation in Richards I, but relative density of the clerid in this infestation was high (Table 1). These results suggest that a predator such as *T. dubius*, utilizing a kairomone response to locate prey, may also become more aggregated when the prey's pheromone level is low.

Aggregation in Apple Springs and Richards II did not differ significantly for either species (Table 2), even though mean densities of both beetles differed between the areas (Table 1). The increased dispersion in these 2

Table 2.—Index of Patchiness (IP ± SE) and Interspecific Patchiness (IP$_{xy}$ ± SE) for SPB and *T. dubius* caught on sticky traps in 3 infestations.

Infestation	Trapping days	IP[a]		IP$_{xy}$[a]
		SPB	T. dubius	
Apple Springs	20	5.97±0.61 a	3.50±0.82 a	2.64±0.32 a
Richards I	17	7.89±0.62 b	5.23±1.10 b	3.42±0.66 ab
Richards II	17	5.91±0.69 a	2.33±0.55 a	3.52±0.41 b
Combined	54	—	—	3.10±0.28

[a] Means in a column followed by the same letter are not significantly different ($P < 0.05$).

areas is thought to result from the higher rate of attack on trees (Table 1) which, in turn, produced more pheromone sources. Extension of the pheromone odor plume would stimulate both beetle landing and general flight activity to occur over a larger area (Coster and Gara 1968).

The $\overset{*}{m}$ - m regression was performed for each infestation and for the three infestations combined (Table 3). An ANCOVA (Table 4) showed no significant factor x covariate (infestation x m) interactions for either species (i.e., slopes of the separate regressions were homogenous). A significant covariate (m) effect was found for both species, while only $T.$ $dubius$ showed a significant infestation effect. This allows the use of a combined regression of $\overset{*}{m}$ on m to characterize SPB aggregation (Table 3):

$$\text{SPB}\overset{*}{m} = 2.69 + 5.10\ m \quad (\text{r}^2 = 0.73),$$

while the significant spot effect suggests caution in the use of a combined regression to characterize aggregation of $T.$ $dubius$. Moreover, the low r^2 values for the $T.$ $dubius$ regressions suggest that clerid aggregation is less dependent on clerid density than is the case for SPB. Apparently, its degree of aggregation is determined not only by population density but also by intrinsic site factors.

Standard error of the estimates, SE$_{\hat{y}}$, were used to construct 95% CI about α for the combined regressions, and we found no significant difference from 0 for either $T.$ $dubius$ or SPB. An $\alpha = 0$ implies that the basic aggregation unit of SPB and $T.$ $dubius$ is the individual insect (Iwao and Kuno 1971) and that, in the absence of pheromones, both species are randomly distributed. An α value >0, on the other hand, would be evidence of "swarming" and the flying insects would occur in discrete clumps, even though the clumps or swarms, themselves may be randomly distributed.

As with IP, the β values (Table 3) indicate a higher degree of aggregation for SPB than for $T.$ $dubius$ and a highly aggregated pattern for both species. The pattern of β over the individual infestation regressions for SPB is similar to that found for the mean IP values (Table 2), although no significant differences between β's were found in the ANCOVA. For β's in the $T.$ $dubius$ regressions, however, there is no similarity in pattern with the mean IP values (Table 2), further suggesting that the $\overset{*}{m}$ - m relationship alone is insufficient to account for observed clerid aggregation.

Table 4.—ANCOVA results for SPB and $T.$ $dubius$ daily $\overset{*}{m}$ in 3 infestations.

Source	df	F-Values	
		SPB	T. dubius
Regression	5	25.88*	8.42*
Covariate:			
Mean (M)	1	27.71*	8.34*
Factor:			
Infestation (I)	2	1.74	9.99*
Interaction:			
m × I	2	0.08	0.41
Residual	48		
Total	53		

* $P \leq 0.005$

Distributional Overlap

Lloyd's index of interspecific patchiness, IP$_{XY}$, was calculated for each day of trap catch and mean values for each infestation compared using Mann-Whitney tests (Table 2). All mean IP$_{XY}$ values indicated aggregate distributions which tended to overlap. Over all infestations, the probability of an SPB/$T.$ $dubius$ encounter (i.e. simultaneous occurrence on a trap) was 3.10 X greater than would be expected if they were randomly distributed over the quadrats[5].

A significant difference was found between IP$_{XY}$ values for Apple Springs and Richards II, but the pattern exhibited by IP$_{XY}$ was different than that shown by IP over the infestations (Table 2).

Discussion

The results suggest interesting relationships between population densities, aggregation tendencies, and attack of host trees for the 2 beetle species. Not unexpectedly, there was a general positive association between mean SPB density and number of trees attacked per day (NTA). Mean values for the 2 variables rank in the same sequence for the 3 infestations. The degree of SPB aggregation as measured by both IP and β, was inversely associated with NTA; aggregation was greatest in the infestation where the fewest pheromone sources (newly attacked trees) occurred. This relationship between number of naturally occurring pheromone sources and dispersion pattern of SPB has also been described by Johnson and Coster (1978). Ranking of population densities of $T.$ $dubius$ in the three locations was totally different than for SPB; where SPB density was highest (Richards II) $T.$

[5] It should be noted that SPB and $T.$ $dubius$ do not interact in the air, but on and under the bark surface of host trees. Distributional overlap would be most meaningful when measured on the bark surface.

Table 3.—Parameters for regression of mean crowding on mean density for SPB and $T.$ $dubius$ in 3 infestations.

	Trapping days	α		β ± SE		r²		SE$_{\hat{y}}$	
		SPB	T. dubius	SPB	T. dubius	SPB	T. dubius	SPB	T. dubius
Combined	54	2.69	0.57	5.10±0.44	2.53±0.48	0.72	0.35	13.76	1.62
Apple Springs	20	3.04	0.47	4.17±0.29	2.12±0.56	0.92	0.44	3.14	1.34
Richards I	17	1.92	2.25	5.57±0.85	1.57±1.53	0.74	0.07	1.66	2.18
Richards II	17	8.43	−0.08	4.72±1.25	3.30±0.76	0.49	0.56	24.85	0.73

dubius was lowest, and vice versa. Degree of aggregation of SPB and *T. dubius*, however, followed the same relative trends from one infestation to another. The mechanism of co-aggregation between the species is hypothesized as follows.

When the density of flying SPB within an infestation is high, the daily rate of attack of trees is increased. Consequently, on any given day there are more active pheromone sources within the infestation than when attack rate, and SPB density, are low. Simultaneous occurrence of multiple pheromone sources within an infestation causes flying SPB distribution to be more dispersed than in an infestation where only 1 or 2 attractive trees occur (Tables 1 and 2) (Johnson and Coster 1978). Because of the kairomone response of *T. dubius* to SPB pheromone, the clerid's aggregation pattern tracks that of SPB. Thus, the causal pathway for co-distribution of the 2 beetles within an infestation is: SPB density →→NTA→→SPB distribution →→*T. dubius* distribution. *T. dubius* density in an infestation, while ultimately dependent to some extent on SPB density, is also dependent on general availability in the vicinity of the SPB Jinfestation, and the age of the infestation. That is, in a young infestation, *T. dubius* density is dependent on immigration, while lack of synchrony in brood development may result in high *T. dubius* emergence during periods of low SPB emergence.

The relationship is further supported by the $\overset{*}{m}$ - m regressions. For SPB, a reasonably good model ($r^2 = 0.73$) was characteristic for the species over all 3 locations. For the clerid, the combined model (all sites) accounts for much less of the variation in aggregation ($r^2 = 0.35$), indicating that aggregation was not as strongly a species characteristic and must be considered on an infestation-by-infestation basis. Its aggregation is also conditioned, in large part, by environmental attributes such as degree of aggregation of the prey.

Kairomone response of certain insect enemies of scolytids is well documented (Borden 1977) and occurs for *T. dubius* in response to SPB aggregation pheromones (Vité and Williamson 1970). This study further demonstrates that parameters such as IP and the intercept and slope coefficients of the $\overset{*}{m}$ - m regression are useful in quantifying SPB aggregation (Coster and Johnson 1979a) and that they also are valuable in comparing aggregation of 2 species that respond to a common stimulus. Quantification of aggregation is also useful for understanding insect population dynamics since aggregation incorporates a number of behavioral responses to environmental stimuli that, when considered collectively, is an index of behavior that is characteristic of a species (Taylor 1971). Simultaneous monitoring of changes in aggregation of a pest and its important insect enemies in response to behavioral chemicals would be useful in assessing survey and control strategies utilizing such behavioral chemicals.

Acknowledgment

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