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Characterizing Flight Aggregation of the Southern Pine Beetle^{1,2}

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ABSTRACT

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Spatial aggregation patterns of flying southern pine beetles, *Dendroctonus frontalis* Zimm., were studied using a systematic grid of sticky flight traps placed in 3 beetle infestations. Five methods of characterizing dispersion were compared: Lloyd's index of patchiness (IP), Morisita's index of dispersion (I_{δ}), the coefficient of dispersion (CD), the slope of Taylor's power function (b), and the slope (β) of Iwao's regression of mean crowding (\bar{m}) on mean density (m).

All indices indicated a high degree of aggregation of flying southern pine beetles within the infestations. The indices varied, however, in their ranking of aggregation for the 3 study sites. IP and I_{δ} gave the same relative results while CD showed a different pattern. The two regression techniques showed no significant differences between slopes for the various study sites.

The \bar{m} -m regression provided more information for interpretation and more potential for evaluating influences of system manipulations. It is recommended, therefore, for characterization of southern pine beetle aggregation within infestations. IP (which serves as the theoretical basis of the regression), is suggested for comparisons between daily aggregation patterns.

The \bar{m} -m regression may be useful for evaluating behavioral chemical effects on aggregation through comparison of daily \bar{m} -m pairs to the 95% prediction limits about the regression line; pairs falling outside these limits represent aggregation patterns significantly different from the norm.

Many bark beetles in the family Scolytidae produce aggregation pheromones which are released when the beetles locate a suitable breeding habitat. In combination with host-produced volatiles, the pheromones cause a

marked degree of aggregation of flying beetles which, in turn, results in mass attack of the host tree. Pheromone systems are known for 16 bark beetle species (Vité and Francke 1976).

The southern pine beetle, *Dendroctonus frontalis*, Zimm., occurs in pine forests throughout the southern and southeastern U.S., Mexico, Guatemala, and Honduras. Aggregation for attack and breeding is in response to a system of volatiles composed of the insect-produced compound frontalin and the host tree-produced

¹ Coleoptera: Scolytidae.

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compound alpha-pinene (Kinzer et al. 1969). Females initiate attack but both sexes subsequently respond to the pheromone system (Renwick and Vité 1969). The density of flying beetles increases with proximity to freshly attacked trees (pheromone sources) (Coster and Gara 1968) and, when population levels are high and the rate of attack is rapid, mass attack by the responding beetles subsequently is concentrated on an adjacent tree (Gara and Coster 1968). Continued attraction results in aggregation on, and colonization of, additional adjacent trees.

The effects of pheromones on dispersion of the southern pine beetle are vital considerations in its population dynamics. During periods of low population levels the primary resource exploited by the beetle is an ephemeral one consisting of weakened and damaged pines. These may quickly pass to a physiological condition unsuitable for colonization and/or brood development. Pheromones emitted by attacking beetles ensure utilization of such temporary habitats. Healthy vigorous trees are attacked when beetle populations are high. Pheromones facilitate such attacks by inducing "en masse" aggregation with the result that vigorous host trees are overcome and rendered suitable for colonization and brood development. Since both sexes arrive at host trees, aggregation also facilitates mating through the increased number of sexual encounters in the aggregation.

Aggregation incorporates a number of behavioral responses to environmental stimuli which, when considered collectively, are indicative of behavior that is characteristic of the species (Taylor 1971). Indices to quantify aggregation were suggested by Taylor to be of value in studying the responses of populations to environmental stresses. Such indices would also appear to be useful in quantifying changes in population dispersion in response to pheromones, including both attractant and inhibitory pheromone systems. This information, in turn, would lend understanding to population dynamics studies and to evaluation of pheromone systems for pest management applications.

Hedden and Gara (1976) applied Morisita's index of dispersion (Morisita 1959) to within-tree distribution of the Douglas-fir beetle, *Dendroctonus pseudotsugae*. Flight aggregation of bark beetles has been quantified for two species of *Ips* in a study by Mason (1970). The beetles exhibited a high degree of flight aggregation and Mason used aggregation indices (the slope of Taylor's power function and Morisita's index) to make inferences about the relative "aggressiveness" of the 2 beetles in colonizing host trees.

This paper reports on a field study to determine dispersion patterns of flying southern pine beetles within infestations, to quantify daily flight aggregation, and to compare flight aggregation under different beetle densities.

Materials and Methods

The Study Areas

During spring and summer, 1974, three southern pine beetle infestations in eastern Texas were studied. One was in Trinity Co. and the other 2 in Montgomery Co. The stands were located on flat terrain and consisted primarily of shortleaf pine (*Pinus echinata*) and loblolly

pine (*P. taeda*) with oaks (*Quercus* spp.) and sweetgum (*Liquidambar styraciflua*) as the secondary hardwood overstory components. The understories consisted mainly of flowering dogwood (*Cornus florida*) and American beauty berry (*Callicarpa americana*). The pine stands were well-stocked with characteristics shown in Table 1.

Avg dbh was based on tally of all trees greater than 10 cm dbh subsequently encompassed by each study plot, while basal area was calculated from maps showing the dbh and location of all trees greater than 10 cm dbh.

At the time each study began, all trees that had been successfully attacked and colonized by the southern pine beetle were tallied as to the predominant life stage of the beetles in the trees. These distributions are shown in Table 2.

Flight Sampling Grid

Spatial distribution of aerial populations of southern pine beetle occurs on 2 different scales. The 1st is infestations that include one or more adjacent trees colonized by the beetle. Density of flying beetles is very high within 30–50 m of these infestations but becomes very low beyond this distance (Payne et al. 1978). The infestation is, therefore, a recognizable natural unit within which to sample air-borne beetles. It is also the focus for insect control efforts. The second scale is the distribution of these infestations throughout the forest. This study is concerned only with the former aspect of southern pine beetle distribution.

A centric systematic sample scheme was used in which sticky flight traps were positioned 15 m apart to produce a systematic grid of the traps. Systematic grid samples have been shown to more accurately estimate insect aggregation patterns than do random samples (Hairston et al. 1971) and Watt (1968) suggested that the use of grid systems is the only reasonable approach to the development of dispersal models to describe insect distribution through time and space.

Each trap consisted of 4 wings or vanes supported by a 1.8 m tall wooden standard. Each vane was 30.5×61 cm and placed in the ground so that vane centers were ca. 1.4 m above the ground. The vanes were constructed of fiber glass insect screen (7 mesh/cm) and coated with Stickem Special®. Traps were centrally located in each of thirty 15×15 m quadrats which were arranged in a 5×6 grid system. The grid was oriented so that its long axis was more or less parallel with the anticipated direction of spread of the infestation and so its center was near the most recently mass attacked pine.

Traps were equipped with devices containing an attractant mixture of frontalinal and alpha-pinene (Kinzer et al. 1969, Renwick and Vité 1969). The chemicals were

Table 1.—Characteristics of 3 pine stands infested by southern pine beetle in east Texas.

Infestation	Avg dbh (cm)	Basal area, m ² /ha
No. 1	22.4	20.4
No. 2	26.6	20.4
No. 3	16.3	16.8

Table 2.—Predominant life stages of southern pine beetle in attacked trees within 3 infestations.

Infestation	Eggs & parent adults	Larvae	Pupae	Callow adults	Brood emerged	Total
				No. trees		
No. 1	4	6	3	7	0	20
No. 2	2	6	2	7	1	18
No. 3	8	21	10	19	16	74

placed in small glass vials that, based on gravimetric estimates, evaporated ca. 2 mg of frontalin and ca. 5 mg of alpha-pinene/trap/day. The vials were placed inside of small aluminum film cans in which several small holes had been drilled through the bottom to allow escape of the vapors. One can, containing chemicals, was attached to each trap at mid-vane height. Previous field tests (T. L. Payne and J. E. Coster, unpublished) had indicated that release of the chemicals at these rates would provide a low level of attraction to flying southern pine beetles but was not high enough to induce attack on trees 2.5–3.0 m from the release point. The chemicals in the present study were used, in effect, to increase the area sampled by an individual trap. Frontalin and alpha-pinene quantities in the vials were replenished every 1–2 days as needed.

Southern pine beetles were removed from the traps and counted daily. The infestations were also inspected daily for newly attacked trees and, when such trees were found, their location and date of attack were recorded. The observation period in each infestation was for 20 consecutive days; infestation no. 1 from May 9 to 29; infestation no. 2 from June 17 to July 7; infestation no. 3 from July 26 to Aug. 15.

Aggregation Indices

A number of ways of measuring the degree of aggregation of populations have been proposed. Some of these techniques are discussed by Morisita (1959), Southwood (1966), Iwao (1970), Gérard and Berthet (1971), Stiteler and Patil (1971), and Patil and Stiteler (1974). Five methods for measuring dispersion were chosen for comparison: Morisita's index of dispersion, I_b (Morisita 1959, 1962), Lloyd's index of patchiness, IP (Lloyd 1967), the coefficient of dispersion, CD (Stiteler and Patil 1971), Taylor's power function, b (Taylor 1961, 1971), and the mean crowding (\bar{m}) mean density (m) regression (Iwao 1970, Iwao and Kuno 1971).

These various indices of aggregation, though developed independently and based on different theoretical considerations, are interrelated as follows (Iwao and Kuno 1971):

$$IP = 1 + \frac{CD-1}{m} \sim E(I_b),$$

and, if $\alpha=0$, $IP=\beta$. It also should be noted that

$$CD = am^{b-1},$$

where a and b are the regression coefficients of Taylor's power function.

Results

Characteristics of Trap Catches

The number of additional trees attacked, total number of beetles trapped, mean trap catch, and number of trapping days in each infestation are shown in Table 3. The progression of attack in each infestation was generally to the nearest uninfested tree. In no case did the synthetic frontalin and alpha-pinene alter the natural tree-by-tree progression nor did the chemicals induce attack of trees adjacent to the traps.

Scatter diagrams of trap catches showed that in infestation no. 3 there were 3 days that had unusually high trap catches. Field records for those days revealed that the high catches were due to only 1 or 2 traps that were within 3–6 m of trees that were being mass-attacked. Under these conditions, trap catches reflect not only general flight activity in an infestation but also the landing, circling, and take-off activity that occurs in the vicinity of freshly attacked trees. Therefore, 3 statistical outliers were deleted from infestation no. 3 prior to analysis using Dixon's test for outliers (Dunn and Clark 1974).

The mean trap catches per day were contrasted using the Kruskal-Wallis test. All paired contrasts were significant ($P \leq 0.05$) and flying beetle density in the infestations was ranked as no. 3 > no. 1 > no. 2.

Goodness-of-fit tests were used to compare the flight trap catch to 6 theoretical distributions (Poisson, negative binomial, Fisher's logarithmic series, Neyman's type A, Polya-Aeppli, and Thomas). Trap catch distribution most closely approximated the negative binomial with $\hat{k} = 0.234$ (estimated with 90% efficiency by method 2 of Anscombe 1950). The trap catch distribution for southern pine beetle catch from 0 to 19 is shown in Fig. 1 with the negative binomial distribution overlaid.

Table 3.—Capture of southern pine beetles on traps and number of trees successfully attacked by southern pine beetles in 3 infestations in east Texas. Study period was 20 days for each infestation.

Infestation	No. trees attacked	No. beetles caught	Mean no. beetles/trap/day
No. 1	27	1,570	2.62a
No. 2	7	617	1.03b
No. 3	40	8,821	14.70c
Total	74	11,008	6.12

Means in the same column followed by the same letter are not significantly different ($P > 0.05$).

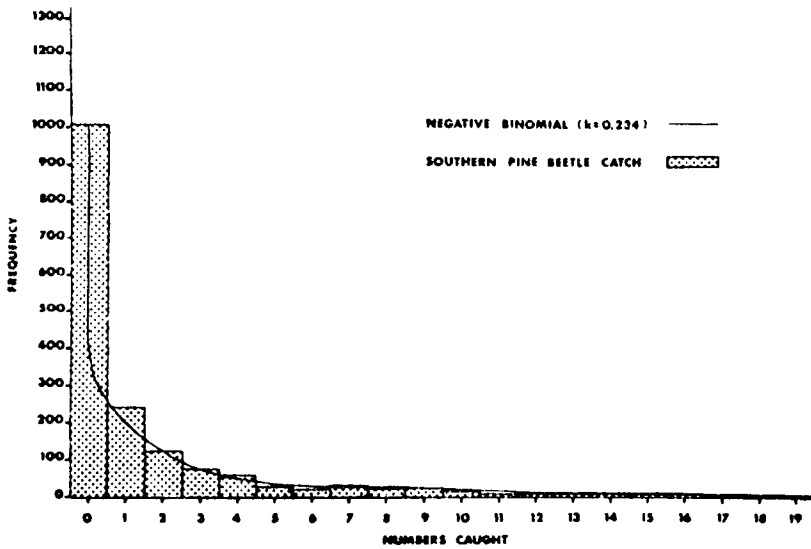


FIG. 1.—Frequency distribution of southern pine beetle trap catches from three infestations ($n=1710$).

Aggregation Indices

Prior to application of statistical analyses the frequency distribution of I_b , IP and CD were tested using the chi-square test for good-of-fit to a normal distribution. The observed values for each index were arrayed into 16 classes in $\frac{1}{2}$ SD units about the mean and compared to expected frequencies of a standard normal distribution. IP and I_b did not deviate significantly ($P > 0.05$) from a normal distribution whereas CD did deviate significantly ($P < 0.001$). The mean \pm SE and number of observations (n) for each index were:

	Mean \pm SE	n
I_b	6.80 \pm 0.40	57
IP	6.61 \pm 0.38	57
CD	19.24 \pm 2.99	57

Values of I_b , IP, and CD relate to unity in the following manner; values greater than 1 occur with aggregated distributions, values equal to 1 with random distributions, and values less than unity indicate uniform (regular) patterns.

All indices show the flying southern pine beetle distribution within infestations to be highly aggregated. I_b was considerably higher than values reported for *Ips avulsus* and *I. grandicollis* by Mason (1970).

Comparisons of I_b and IP between infestations was done using 1-way ANOVA with a priori t -tests to contrast each index between pairs of infestations. Because of its non-normal distribution, CD was contrasted by a series of Kruskal-Wallis tests. The mean \pm SE for each index in each infestation are shown in Table 4.

I_b and IP ranked the 3 infestations in the same order as to degree of aggregation, $2 > 1 = 3$. CD, however, ranked the 3 infestations differently, $3 > 1 = 2$, apparently due to its sensitivity to the higher mean quadrat density in infestation 3. The values of I_b and IP are independent of mean quadrat density (Iwao 1970), whereas

CD is dependent on mean quadrat density, as pointed out by Morisita (1959, 1962).

Regressions

The a and b parameters of Taylor's power function were estimated by regression using the linear model $\ln s^2 = \ln a + b(\ln m)$. The parameters and r^2 values for the three infestations combined were:

n	$\ln a$	$b \pm SE_b$	r^2	SE_{y-x}
57	1.94	1.76 \pm 0.06	0.94	0.46

Parameter b has been proposed as an index of aggregation for a species (Taylor 1961). Random aggregation would assume $b=1$ and the parameter approaches infinity with extreme aggregation.

An analysis of covariance indicated no significant interaction ($P > 0.05$) between infestation and the log of mean catch. Therefore, the combined regression may be used to reflect southern pine beetle aggregation response to environmental conditions as an intrinsic species characteristic, and indicates a highly aggregate population. The b found here indicates a higher degree of aggregation than for the 2 *Ips* species reported by Mason (1970).

Table 4.—Comparison of 3 aggregation indices for 3 southern pine beetle infestations in east Texas. Means are based on $n=20$ for infestation 1 and 2 and $n=17$ for infestation 3.

Infestation	Mean \pm SE		
	I_b	IP	CD
1	6.13 \pm 0.64a	5.97 \pm 0.61a	12.72 \pm 1.96a
2	8.21 \pm 0.65b	7.84 \pm 0.60b	7.76 \pm 0.62a
3	5.94 \pm 0.70a	5.91 \pm 0.69a	40.43 \pm 7.62b

Means in the same column followed by the same letter are not significantly different ($P > 0.05$).

The regression of \bar{m} on m was examined using the linear model, $\bar{m} = \alpha + \beta m$ (Iwao 1970) where α is the intercept on the \bar{m} axis and β is the regression coefficient. The α , β , and r^2 values for the combined infestations were:

n	α	$\beta \pm SE_{\beta}$	r^2	SE_{y-x}
57	2.60	5.11 \pm 0.43	0.72	13.40

Parameter α is termed the index of basic contagion (i.e., the basic population unit, individuals, groups of individuals, etc.) and takes a positive value for colonial populations and a zero value where there is no tendency for individuals to group at low population density or where repulsion between individuals occurs. Dispersion of individuals in relation to density is indicated by β , the density-contagiousness coefficient. It will be less than, equal to, or greater than unity in uniform, random, or aggregated patterns. In other words, α is a measure of "swarm" size and β is a measure of the spatial pattern of the "swarms."

An analysis of covariance indicated no significant interaction between infestations. The combined regression may, therefore, be used to characterize aggregation patterns.

In the regression, α does not deviate significantly from 0 (95% CI = $-2.12 \leq \alpha \leq 7.32$), implying that the basic population unit is the individual. That is, α means that "an individual will live together with α other individuals in the same quadrat when mean density becomes infinitesimally small" (Iwao and Kuno 1971). When $\alpha=0$, $IP > 1$ indicates a negative binomial distribution with $\beta = 1 + \frac{1}{k}$, but when $\alpha > 0$, the underlying distribution

may be any of several contagious distributions (Iwao and Kuno 1971). Moreover, they state that, if $\alpha \neq 0$, single indices of aggregation (such as IP or I_b) are inappropriate and misleading. An $\alpha > 0$ would indicate failure to sample within the smallest aggregation unit—a violation of the assumption necessary for use of IP or I_b .

The 2nd aspect of spatial distribution dealt with by the \bar{m} - m regression is the nature of the dispersion patterns of the basic units, i.e., individuals in relation to changes in mean density. The regression coefficient, $\beta = 5.11$, indicates an aggregated dispersion pattern. Moreover, since $\alpha=0$, β should be roughly equivalent to IP, and $\beta > 0$ indicates a negative binomial distribution with $k = \frac{1}{\beta - 1} = 0.254$. These values for β from the regression approximate the mean IP (6.61) found in prior analyses of the data. The calculated value (\hat{k}) for the negative binomial distribution is 0.234.

Discussion and Conclusions

Comparisons of Methods

The 5 methods of quantifying dispersion patterns examined in this study describe different aspects of the spatial distribution of southern pine beetles. The regression coefficients b and β provide measures of aggregation that, over a range of environmental conditions, are intrinsic to a species and that quantify changes in disper-

sion with density. The indices I_b , IP, and CD, on the other hand, provide measures of aggregation that, under a specific set of environmental conditions, describe the dispersion of a population.

The aggregation indices are primarily of value for within-species comparisons between differing sets of environmental conditions. The comparisons may concern temporal displacement, spatial displacement, treatment effects, etc. I_b or IP may be used to compare species subjected to the same environmental conditions (e.g., Mason 1970, used I_b to compare *I. avulsus* and *I. grandicollis* dispersion in 3 study sites), but results are applicable only for the studied conditions. CD should not be used for such interspecific comparisons since it is sensitive to mean density which will usually differ between species. Moreover, use of CD for within-species studies should be restricted to conditions where population density remains relatively constant, thus making it unsuitable for use in the present study.

The indices I_b and IP, however, are independent of mean density and give an equivalent measure of aggregation. They also change systematically with changing quadrat size (Morisita 1959, Lloyd 1967), allowing estimation of mean aggregation area relative to quadrat size and individual distribution within aggregation areas.

The regression methods, on the other hand, are appropriate for (1) comparing dispersion patterns between species and (2) detecting significant deviations in aggregation from the species characteristic norm in response to abnormal levels of an environmental factor. Regressions may be particularly useful with southern pine beetle in comparing dispersion patterns of the pest and certain of its insect enemies that exhibit a kairomone response to the beetle's aggregation pheromone.

Although Taylor's power function provides a better fit to the data presented here than does Iwao's \bar{m} - m regression, Iwao's approach provides information concerning the basic population unit ($\alpha=0$) and the nature of the underlying distribution (negative binomial; $k \sim 0.25$). Moreover, Iwao and Kuno (1971) discuss a variety of ways in which the mean crowding regression may be used to examine dynamic population processes through their effect on dispersion patterns, and it is felt that Iwao's β represents the more useful approach to measuring aggregation.

Uses in Evaluating Population Manipulation Practices

Pheromones are the primary agent regulating aggregation of flying southern pine beetles. In synthetic form, they have been proposed as means to manipulate insect behavior for purposes of population regulation. Experimental applications of attractants (Vité et al. 1976) and inhibitors (Payne et al. 1977) have been carried out. Two general strategies for use of such behavioral chemicals may be envisioned: (1) increase dispersion of the population so that higher numbers of beetles are taken by various mortality agents and so that insufficient numbers of insects are available to successfully attack trees; (2) increase aggregation at selected sites such as traps, unsuitable hosts, or into forest tracts predestinated for removal of trees subsequent to colonization by beetles. In either case, one measure of the efficacy of the strategy is the change in dispersion patterns of a population.

Iwao's regression of \bar{m} on m appears to be the best procedure for characterizing southern pine beetle aggregation over a wide range of environmental conditions. However, when restricted to a single day's observation, the estimate of β reduced to IP. We, therefore, recommend the use of IP for characterizing southern pine beetle flight aggregation where direct comparisons between daily aggregation patterns are desired (e.g., interspecific comparisons under comparable environmental conditions and intraspecific comparisons between substantially different environmental conditions). Although IP and I_b are roughly equivalent, IP is more suitable since it is the theoretical basis of Iwao's regression.

Analysis of a series of quadrat data, obtained from centric systematic samples, proceeds as follows. Mean crowding and mean density are computed for each sample period. Using either linear regression or analysis of covariance techniques, a regression of \bar{m} on m is obtained and the α is tested for significant deviation from 0.

Using the information obtained about α and β , the underlying statistical distribution of the dispersion pattern may be characterized (Iwao and Kuno 1971). The value of α indicates certain characteristics of the species aggregation behavior since it implies that an individual of the species will share the quadrat with α other individuals under low population density. If $\alpha=0$, then IP values may be used to compare within-species population dispersion for specified conditions. Techniques for comparing data distributed as a negative binomial are provided by Lloyd (1967).

Construction of 95% prediction limits about estimated \bar{m} values (Sokal and Rohlf 1969) allows easy comparison of specific dispersion patterns to the expected norm

for the species. The \bar{m} - m regression line with 95% confidence limits and 95% prediction limits for southern pine beetle obtained from the present study is shown in Fig. 2. If an observed IP value falls within the confidence limits for its predicted value, it does not deviate significantly ($P \leq 0.05$) from the norm. An assumption is that the treatment does not alter the index of basic contagion (α) of the flying beetle population. This is acceptable since pheromones are not known to be released from flying southern pine beetles and a treatment should not alter perception of the beetles by one another. Comparison of an experimentally induced dispersion pattern to an expected characteristic pattern would be useful for detecting treatment effects where appropriate experimental controls are impractical or impossible.

The existence of synthetic behavioral chemicals for many insects, including southern pine beetle, has led to proposals for their incorporation into pest management schemes. Assessment of the efficacy of such chemicals is difficult, however, and is usually done using various estimates of changes in population density. Since many insect pheromones, especially the aggregation pheromones of Scolytidae, appear to exert major influences on dispersion patterns of the insect, it is suggested that use of experimental and statistical methods to quantify changes in aggregation in response to experimentally induced levels of behavioral chemicals provides an ecologically sound way to assess chemical application strategies.

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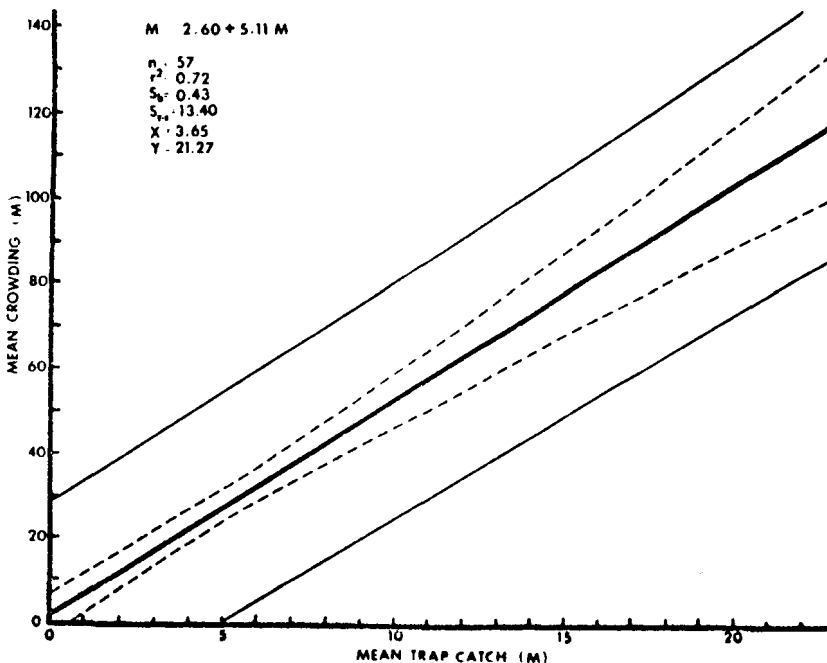


FIG. 2.—Regression of mean crowding on mean SPB catch, including 95% confidence limits (---) and 95% prediction limits (—).

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