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THE STATISTICAL AND BIOLOGICAL IMPLICATIONS OF SAMPLING UNITS FOR MOUNTAIN PINE BEETLE POPULATIONS IN LODGEPOLE PINE

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INTRODUCTION

The selection of a measurement unit is of basic importance to a population study. The measurement unit's "suitability" depends on the exact kind of information that its use will provide. A measurement unit for mountain pine beetle (*Dendroctonus monticolae* HOPK.) population study must be selected with care, because the kind of information provided by the unit can vary from purely spatial to completely biological. The intent of this paper is to emphasize these differences in kinds of information, through discussion of several measurement alternatives; also, the associated statistics necessary for an insect study or inventory sampling control will be presented. The latter information has been assembled from study plots located within mountain pine beetle infestations on the Caribou, Teton, and Wasatch National Forests of Idaho, Wyoming, and Utah, respectively.

The guiding reason for sampling an insect population should be to gain reliable information on the behavioral, biological, and management aspects of the population. Space sampling provides density estimates, information on reliability of estimates, and spatial patterns of insects. A knowledge of insect life processes within a population unit is essential to an understanding of the insect population ecology.

MEASUREMENTS

The two sample unit sizes taken from standing lodgepole pine (*Pinus contorta* DOUGL.) were: (1) the single gallery—this is the basic "family unit" constructed by the parent beetles with eggs deposited therein; and (2) a 6- by 6-inch square area —the bark was removed and the brood counted.

Data from the 6- by 6-inch sample were recorded in three ways: (1) average brood per 6- by 6- inch sample; (2) average brood per attack per 6-by 6-inch sample; and (3) average brood per inch of gallery per 6- by 6-inch sample. Thus, these three measurements plus the single gallery samples were used for comparison:

1. Average brood per single gallery—SG.
2. Average brood per 6- by 6-inch sample—B(6×6).
3. Average brood per attack per 6- by 6-inch sample—BA(6×6).
4. Average brood per inch of gallery per 6- by 6-inch sample—BI(6×6).

Each measurement unit provides different biological information. Therefore, the kind of information sought by an investigator will determine the unit(s) to be used.

The single gallery: This unit of measurement is used because it can be assumed that the effect of an ecological event on a "family unit" is representative of what would happen in an entire population that experienced a similar event. Use of the single gallery samples of a "family unit" shows the effects of between-gallery and within-gallery crowding.

Single gallery information reflects all of the genetic, physiological, and behavioral characteristics of a *single* female beetle. Behavioral characteristics are especially influenced by the effects of crowding; therefore, crowding, or the effects of attack density, must be recognized as an *added* variable in any biological interpretation of single gallery data. COLE (1962) has shown that increased attack density increases between-brood competition and results in the reduction of egg gallery length. Thus, there is a reduction in total brood per gallery and this causes increased brood mortality.

Averge brood per 6-by 6- inch sample—B(6×6): This measurement unit expresses population survival or total numerical change. Data from this unit mask individual family (or female paarent) differences. This is an all-inclusive measure of within- and between-gallery information including attack density.

Average brood per attack per 6-by 6- inch sample—BA(6×6): The average brood size per attack is determined by: the degree of larval competition between brood galleries; and the effect of attack densities on the egg-laying behavior of the adult female beetle. A greater attack density increases the likelihood of greater brood density. In past studies, when 3 attacks per square foot occurred, the ratio of parent adult to emerging adult was 1:1.9. At 9 attacks the ratio was 1:1.1; and at 18 attacks the ratio was 1:0.3. This brood mortality based on attack density is accounted for in the 6-by 6-inch sample by recording brood density as average brood size per attack. This measurement unit also masks the differences between individual female parents.

Average brood size per inch of gallery per 6- by 6-inch sample—BI (6×6): This measurement unit tends to express larval competition *within* the brood gallery up to the point in time when *between-gallery* competition becomes dominant. As the larvae begin their tunneling close together, within-brood gallery competition is expressed. Mortality occurs, the brood is reduced, and within-brood gallery competition lessens due to greater space per larva. Then as broods from two different galleries begin to encounter one another, the between-gallery competition increases.

It has been observed that egg distribution by sequential inch of gallery might also be used as an infestation trend index (COLE, unpublished). Egg distribution varied from unipeakedcurves to flat-top curves to multipeaked curves, depending upon which infestation and year within span of infestation were being sampled.

METHOD

The comparisons presented in this paper were based on analysis of data covering two generations (1965 and 1966) of the mountain pine beetle on three areas: Caribou, Teton, and Wasatch National Forests. Each generation was sampled three times—fall, spring, and summer. Therefore, this sampling included count of prewinter eggs and immature larvae; postwinter mature larvae; and mature larvae and pupae, respectively. The attack density and gallery length also were measured. Two sample units were taken from each of four trees, within each of three diameter classes (9, 12, and 15 inches d. b. h.)

Table 1. Estimated means and standard deviations by diameter class, by observation, and by measurement unit (years pooled).

Diameter class (inches)	Observation	Measurement unit	Sample size (n)	Estimated standard deviations: Among units within trees (s_w)	Among units (s_u)	Among unit totals (s_y)	Mean ($\bar{y}$)
9	Fall	S. G.	36	20.5	9.8	2.5	19.0
		B(6×6)	46	27.1	20.6	5.9	55.4
		BA(6×6)	46	15.4	5.5	4.4	20.2
		BI(6×6)	46	2.5	1.3	0.2	2.8
	Spring	S. G.	48	13.7	4.1	2.1	9.4
		B(6×6)	46	18.9	17.9	4.7	19.0
		BA(6×6)	46	11.1	7.2	2.2	6.1
		BI(6×6)	46	1.2	0.6	0.1	1.0
	Summer	S. G.	48	8.9	3.7	1.0	3.5
		B(6×6)	48	11.7	4.4	1.4	11.0
		BA(6×6)	48	4.5	1.7	0.5	3.3
		BI(6×6)	48	1.0	0.6	0.1	0.6
12	Fall	S. G.	36	16.6	9.5	1.6	21.9
		B(6×6)	40	64.1	39.5	4.9	67.8
		BA(6×6)	40	15.9	8.5	3.2	21.6
		BI(6×6)	44	2.4	1.3	0.2	2.9
	Spring	S. G.	40	7.1	1.8	1.0	7.3
		B(6×6)	40	14.9	5.8	2.7	17.3
		BA(6×6)	40	7.6	4.2	0.8	5.0
		BI(6×6)	40	0.9	0.5	0.1	0.7
	Summer	S. G.	40	8.6	3.5	1.1	2.5
		B(6×6)	40	8.9	3.3	1.2	12.4
		BA(6×6)	40	3.4	0.8	0.6	3.7
		BI(6×6)	40	0.8	0.4	0.1	0.4
15	Fall	S. G.	36	13.8	5.3	1.9	9.5
		B(6×6)	36	41.3	12.3	5.2	35.1
		BA(6×6)	36	13.5	7.1	1.4	8.3
		BI(6×6)	38	1.7	1.0	0.1	0.7
	Spring	S. G.	36	13.8	5.3	1.9	9.5
		B(6×6)	36	23.5	14.3	5.2	35.1
		BA(6×6)	36	10.9	4.9	1.4	8.3
		BI(6×6)	38	1.1	0.6	0.1	0.7
	Summer	S. G.	36	3.4	2.4	0.8	3.7
		B(6×6)	36	6.2	8.8	2.3	20.8
		BA(6×6)	36	2.8	2.3	0.7	5.1
		BI(6×6)	38	1.0	0.5	0.1	0.6

Results

In the case of two-stage sampling, the entire tree should be the primary sampling unit; but to make measurement a practical possibility, insect broods in a 1-foot-wide strip of bark around the sample tree (at d. b. h.) were used as the primary sampling unit. The brood within the 1-foot strip were considered as indicators of insect population within the whole tree. The average count for the 1-foot strip was estimated either from two 6-inch square subsamples drawn at random from the array of subsamples on the strip (Carlson and Cole, 1965) or from single galleries selected from the strip. The results of brood sampling are shown in Table 1.

Sample trees, themselves, were numerous and widely distributed over the area infested by the mountain pine beetle. The average count for all trees observed within any category *cannot* be taken as an unbiased estimate for any specific infestation. However, the data means and the associated variance statistics *do* provide potentially useful sampling control information as described. These statistics are also of interest in that trends of means over d. b. h. and season are meaningful.

The overall estimate of the unweighted mean is defined as follows:

$$\bar{\bar{y}}=\frac{\sum_{i=1}^{n}\sum_{j=1}^{m} Y_{ij}}{nm}$$

where: Y_{ij}=the count for the jth subsample on the ith strip; n=the number of strips or trees included in the sample; and m=the number of subsamples per strip for which counts were obtained. An estimate of the primary sampling unit (tree) mean is:

$$\bar{y}_i=\frac{\sum_{j=1}^{m} Y_{ij}}{m}$$

The variance of the mean can be separated into between- and within-unit variances as developed by Cochran (1963):

$$v(\bar{\bar{y}})=\frac{s_u^2}{n}+\frac{s_w^2}{nm} \quad \text{(For the infinite tree population case)}$$

where $s_u^2=\frac{s_b^2-s_w^2}{m}$, $s_b^2=\frac{m\sum_i(\bar{y}_i-\bar{\bar{y}})^2}{n-1}$, and $s_w^2=\frac{\sum_i\sum_j(y_{ij}-\bar{y}_i)^2}{n(m-1)}$

The effects of limited alternative (n) and (m) unit sampling allocations on $v(\bar{\bar{y}})$ can be determined. Holding the allowable errors (E) at 15 percent of the sample means from Table 1, m at specified levels 1, 2, 3, 4, and the confidence level at 68 percent, n can be computed (Table 2) for the error and confidence levels specified as follows:

$$E^2=\frac{s_u^2}{n}+\frac{s_w^2}{nm}$$

where $E^2=[SE(\bar{Y})]^2$ and $n=\frac{\frac{s_w^2}{m}+s_u^2}{E^2}$.

Percent of larval survival (Table 3) was rather consistent in all measurement units, regardless of point in time. The less consistency and generally higher survival within the 15-inch diameter class are probably attributable to the increased attack density and the greater food quantity (phloem depth).

The encouraging aspect of these survival rates is their general similarity. Thus, one could use a single unit, or combined measurement units, to estimate survival, particularly for life table studies, and be reasonably assured of maintaining coherency between these life stages. The information desired by the sampler, and time of year, will determine the selection of a measurement unit.

Table 2. Allocations of sampling effort without consideration of differential sampling cost (cost=time) and the secondary sampling unit (m) is predetermined.

	Observation											
	Fall				Spring				Summer			
If $m=$	1	2	3	4	1	2	3	4	1	2	3	4
Then n by diameter class and measurement unit would be:												
9 in. S.G.	47	28	22	18	102	55	40	32	337	193	145	122
B(6×6)	17	11	9	9	83	62	54	51	57	32	24	20
B(6×6)	22	12	9	7	209	136	111	99	94	52	38	32
BI(6×6)	45	27	21	18	80	48	37	32	169	106	85	74
12 in. S.G.	34	21	17	15	45	24	17	13	613	350	262	219
B(6×6)	55	35	28	25	38	21	16	13	26	15	11	9
BA(6×6)	31	19	15	13	135	83	66	57	39	20	14	11
BI(6×6)	39	24	20	17	95	60	47	41	222	133	104	89
15 in. S.G.	107	61	45	37	61	32	23	18	56	38	32	28
B(6×6)	67	36	26	21	27	17	14	12	12	0	9	9
BA(6×6)	150	91	72	62	92	53	41	34	23	16	14	13
BI(6×6)	353	222	178	156	142	87	69	60	154	93	72	62

Table 3. Percent of larval survival as estimated by measurement unit.

Diameter class	Measure-ment unit	Percent of larval survival from: Fall to spring	Spring to summer	Fall to summer	Avg. attack density/diameter class
9 in.	S. G.	49.58	36.90	18.30	3.04
	B(6×6)	34.28	58.16	19.94	
	BA(6×6)	30.11	54.37	16.37	
	BI(6×6)	35.13	62.24	21.86	
12 in.	S. G.	33.12	33.75	11.18	3.37
	B(6×6)	25.54	71.81	18.34	
	BA(6×6)	23.19	74.05	17.18	
	BI(6×6)	24.91	60.56	15.09	
15 in.	S. G.	46.57	38.38	17.87	4.04
	B(6×6)	46.10	59.22	27.30	
	BA(6×6)	74.98	61.10	45.81	
	BI(6×6)	31.86	81.94	26.11	

Summary

Populations of the mountain pine beetle in lodgepole pine were measured using two sample sizes: a single gallery—this is the basic family unit constructed by the parent beetles; and a 6- by 6-inch square area—the bark was removed and the brood counted. Data from the 6- by 6-inch sample were recorded in three ways. Each measurement unit provided different biological information and required different statistical considerations. The single gallery sample provided the most representative data of the entire population, but required additional biological measurement of attack density. The 6- by 6-inch sample brood data taken on an attack density basis provided the most statistically reliable information and encompassed the pertinent biological information. Percent survival, as could be used in elementary life tables, was rather consistent in all measurement units, regardless of point in time of sampling.

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Lodgepole 松を害するキクイムシの1種 *Dendroctonus monticolae* の個体群調査のための抽出単位について

Walter E. Cole

抽出単位の異なる2種類の調査法を用いて *Dendroctonus monticolae* の個体数推定を行ない，それぞれの有効性を比較した。1つは1匹の親世代虫に由来する一連の孔道全体 (gallery) を，今1つは樹皮に設定した 15cm 四方の quadrat をそれぞれ抽出単位とするもので，後者の場合は記録のしかたをさらに3通りにわけてデータを取った。個体群の生物学的特性の反映という点からいうと gallery 単位の抽出が最もよいが，この場合は全体の個体数を推定するためには親世代虫の密度 (attack density) を別に推定しなければならない。統計学的な信頼度が最も高く，生物学的情報量の点でも適当と考えられたのは，quadrat 法の内データを attack density あたりの形で扱ったものであった。なお，生命表作製のための生存率の算出には上記のどの方法を用いても大差ない結果が得られた。

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