

# Nonlinearity of a Generic Variance-Mean Equation for Stored-Grain Insect Sampling Data

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**ABSTRACT** Equations predicting the variance for a mean insect density have been widely used to calculate the precision of density estimates. Traditionally, the logarithm of the variance is regressed against the logarithm of the mean giving a linear equation. We fit a single nonlinear variance-mean regression equation to 4 stored-product insect sampling data sets. This generic nonlinear regression equation described the stored-product insect sampling data for 25 additional studies, 3 different sampling methods, and the 6 most commonly encountered species. The asymptotic slope of this generic nonlinear regression equation increased with insect density, and at mean densities of 0.01, 0.1, 1, 10, and 100 insects per sample unit was 1.06, 1.32, 1.64, 2.05, and 2.55, respectively. This density-dependent change in the asymptotic slope explains the differences among studies in the slopes of linear regression equations. We generated a similar regression equation by randomly assigning insects to sampling units to simulate random dispersal of insects in a grain mass. This suggests that the observed insect sampling distributions could be the result of random dispersal, and that the mechanism underlying the regression equation is fairly general. Compared with the predictions of the generic nonlinear regression equation, the linear regression equation overpredicted the 95% CL within the 0.3-3 insects per sample unit density range, and underpredicted them at higher or lower insect densities. This generic nonlinear regression equation can be used to calculate the precision of mean insect density estimates over a 0.025-100 insects per sample unit density range and thus reduce the cost of developing new sampling programs.

**KEY WORDS** sampling statistics, stored product, precision of estimates, variance-mean equation, probe trap, sticky trap

PREDICTIONS OF VARIANCE as a function of the mean insect density or mean trap catch have been widely used in planning sampling programs and evaluating their performance (Pedigo and Buntin 1994). For a wide range of organisms and sampling methods, Taylor (1961, 1984) has demonstrated that the variance-mean relationship is described by the linear equation,

$$\log s^2 = a + b \cdot \log m, \tag{1}$$

where  $s^2$  = variance and  $m$  = mean. On an arithmetic scale, equation 1 can be expressed as

$$s^2 = A \cdot m^b, \tag{2}$$

where  $A$  is the antilogarithm of  $a$  from equation 1. The precision of density estimates ( $C$ ) expressed as a percentage of the mean insect density ( $m$ ) obtained by taking a given number of sample units ( $n$ ) can be calculated using the equation,

$$C = 100 \cdot t \cdot \sqrt{A \cdot m^{b-2} / n} \tag{3}$$

from Hagstrum et al. (1988) where  $t$  is the value of  $t$  distribution with a confidence limit of  $\alpha/2$  and the degrees of freedom for  $t$  equal the degrees of freedom for the equation 1 from which  $A$  and  $b$  are taken. The number of sample units needed for a given level of precision can be calculated using the equation,

$$n = (100/C)^2 \cdot t^2 \cdot A \cdot m^{b-2} \tag{4}$$

from Ruesink and Kogan (1982).

Although taking additional sample units improves the precision of estimates, it also increases the cost. Estimation of precision during the planning stage of a sampling program before a variance-mean regression equation can be fitted to the data is thus important in balancing the precision of estimates against the cost of taking additional sample units. Before beginning a study, preliminary data are collected to calculate a variance-mean regression equation. The amount of data needed to calculate the variance-mean regression equation accurately may make this prohibitively expensive. A generic variance-mean regression equation applicable to a

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Table 1. Parameter values (mean  $\pm$  SE) and  $r^2$  for equation 1 fitted to data sets with broad range of mean densities

ID	n	Intercept	Slope	$r^2$	Reference
1A	473	0.55 $\pm$ 0.013	1.67 $\pm$ 0.018	0.95	Data sets 1J-4J combined
1B	86	0.29 $\pm$ 0.036	1.41 $\pm$ 0.048	0.91	Vela-Coiffier et al. 1997 <sup>a</sup>
1C	765	0.37 $\pm$ 0.012	1.46 $\pm$ 0.017	0.91	Dowdy and McGaughey 1994 <sup>b</sup>
1D	239	0.48 $\pm$ 0.015	1.47 $\pm$ 0.021	0.95	Vela-Coiffier et al. 1997 <sup>b</sup>
1E	162	0.34 $\pm$ 0.022	1.51 $\pm$ 0.037	0.91	Reed et al. 1993 <sup>c</sup>
1F	270	0.41 $\pm$ 0.015	1.52 $\pm$ 0.023	0.94	Flinn and Hagstrum 1994 <sup>d</sup>
1G	186	0.54 $\pm$ 0.020	1.55 $\pm$ 0.029	0.94	Hagstrum 1987 <sup>d</sup>
1J	74	0.48 $\pm$ 0.037	1.57 $\pm$ 0.053	0.92	Lippert and Hagstrum 1987 <sup>e</sup>
1H	250	0.51 $\pm$ 0.023	1.59 $\pm$ 0.024	0.95	Flinn et al. 1996 <sup>f</sup>
1I	93	0.38 $\pm$ 0.041	1.61 $\pm$ 0.052	0.91	Subramanyam et al. <sup>b,g</sup>
2A	74	0.51 $\pm$ 0.047	1.61 $\pm$ 0.053	0.93	Meagher et al. 1986 <sup>c</sup>
2B	79	0.55 $\pm$ 0.039	1.62 $\pm$ 0.047	0.94	Subramanyam et al. 1993 <sup>b,h</sup>
2C	218	0.35 $\pm$ 0.026	1.63 $\pm$ 0.029	0.94	Hagstrum et al. 1994 <sup>b</sup>
2D	70	0.47 $\pm$ 0.035	1.64 $\pm$ 0.049	0.94	Arthur 1994 <sup>b</sup>
2J	175	0.53 $\pm$ 0.017	1.65 $\pm$ 0.024	0.97	Hagstrum <sup>i,j</sup>
2E	107	0.68 $\pm$ 0.026	1.65 $\pm$ 0.032	0.96	Gates 1995 <sup>b</sup>
2F	182	0.50 $\pm$ 0.030	1.66 $\pm$ 0.031	0.94	Vela-Coiffier et al. 1997 <sup>b</sup>
3J	107	0.60 $\pm$ 0.028	1.69 $\pm$ 0.041	0.94	Hagstrum et al. 1985 <sup>d</sup>
2G	275	0.43 $\pm$ 0.021	1.70 $\pm$ 0.029	0.93	Subramanyam and Hagstrum 1995 <sup>h</sup>
4J	117	0.54 $\pm$ 0.030	1.73 $\pm$ 0.038	0.95	Lippert and Hagstrum 1987 <sup>k</sup>
2H	95	0.35 $\pm$ 0.039	1.78 $\pm$ 0.036	0.96	Subramanyam et al. 1994 <sup>b</sup>
2I	1,000	0.35 $\pm$ 0.006	1.73 $\pm$ 0.006	0.99	Random

The sampling methods used and differences between data sets in the density range covered and the distribution of means over that range are shown in Figs. 1 and 2. ID, cross references tables and figures.

<sup>a</sup> Grain sample unit size of 0.65 kg and mean is average of 6-9 sample units.

<sup>b</sup> Trapping duration is 7 d and mean is average of 6-122 sample units.

<sup>c</sup> Grain sample unit size of 1 kg and mean is average of 9 sample units.

<sup>d</sup> Grain sample unit size of 0.5 kg and mean is average of 7-36 sample units.

<sup>e</sup> Grain sample unit size of 0.265 kg and mean is average of 10 sample units.

<sup>f</sup> Grain sample unit size of 3 kg and mean is average of 21 sample units.

<sup>g</sup> Unpublished data of Bh.S., D.W.H., and B. Dover for pheromone trap catches of *Rhyzopertha dominica* (F.) on farms, at elevators, near wheat fields and on Konza prairie.

<sup>h</sup> Trapping duration is 14 d and mean is average of 8-20 sample units.

<sup>i</sup> Trapping duration is 3-4 d and mean is average of 18 sample units.

<sup>j</sup> Unpublished probe trap data of D.W.H. collected in the same bins used for Hagstrum et al. 1985. The design was the same except 2 probe traps, one above the other, were used instead of grain trier and 2 checks of traps per week were used instead of 2 trier samples at the same site.

<sup>k</sup> Trapping duration is 2 d and mean is average of 10 sample units.

wide range of situations could reduce the cost of developing new sampling programs.

Several studies have investigated the possibility of developing a generic linear equation to describe the variance-mean relationship (Downing 1979, Hagstrum et al. 1988, Trumble et al. 1989, Jones 1990). These efforts have been hampered by a lack of explanation for the differences among studies in the slopes of the linear equation. Routledge and Swartz (1991) reported that the logarithm of variance-logarithm of mean regression equation was not linear in some cases and that the asymptotic slope increased with insect density. Downing (1979) reported that linear variance-mean regression equations sometimes differed significantly among sampling methods. Downing (1986) found, in comparing 221 invertebrate species, that the variation in the slopes of linear equations within a species was as great as among species. Taylor et al. (1988) discussed some of the limitations of such comparative analyses.

Our objective was to develop a generic variance-mean regression equation for stored-grain insects. We examined whether the slopes of linear variance-mean regression equations vary with the range of insect densities sampled, whether a nonlinear re-

gression equation fit sampling data better than the linear equation, and whether a single nonlinear regression equation fit sampling data for different insect species and sampling devices.

### Materials and Methods

Most of the 29 insect sampling data sets used in this study were selected from published papers (Table 1). Two unpublished and a randomly generated data set also were used. Twenty insect sampling data sets were selected because they best spanned a density range of 0.025-100 insects per sample unit, and each variance-mean pair was based on 6-122 sampling units. The other 9 insect sampling data sets had narrower insect density ranges.

The sampling methods that are most commonly used with stored-grain insects include grain samples, probe traps and sticky traps. Grain samples generally are taken with a grain trier, deep-bin cup or vacuum probe, and probe traps are a type of pitfall trap that can be pushed into the grain to catch insects (Hagstrum et al. 1995). Grain samples weighed from 0.12 to 3 kg. The duration of trapping ranged from 2 to 14 d. Most of the studies were done inside grain bins on farms, but some of the studies

Table 2. Parameter values (mean  $\pm$  SE) and  $r^2$  for equation 1 fitted to data sets with majority (82–100%) of means  $< 1$  (first 6) or means  $\geq 1$  (last 3), and percentage of means falling within 95% prediction interval for generic equation 6

$n^a$	% means within 95% prediction interval	Intercept	Slope	$r^2$	Reference
148/151	99	0.13 $\pm$ 0.029	1.13 $\pm$ 0.039	0.85	Hagstrum et al. 1996 <sup>b</sup>
37/37	100	0.35 $\pm$ 0.045	1.20 $\pm$ 0.039	0.96	Hagstrum et al. 1996 <sup>b</sup>
109/117	98	0.21 $\pm$ 0.027	1.21 $\pm$ 0.035	0.91	Throne and Cline 1989 <sup>c</sup>
114/126	99	0.44 $\pm$ 0.030	1.32 $\pm$ 0.036	0.92	Gates 1995 <sup>d</sup>
161/166	97	0.49 $\pm$ 0.041	1.33 $\pm$ 0.033	0.91	Smith 1985 <sup>e</sup>
26/27	96	0.80 $\pm$ 0.067	1.37 $\pm$ 0.057	0.96	Barker and Smith 1987 <sup>f</sup>
4/64	92	0.48 $\pm$ 0.075	1.78 $\pm$ 0.061	0.93	Barney and Weston 1996 <sup>g</sup>
39/322	89	0.33 $\pm$ 0.025	1.85 $\pm$ 0.023	0.95	Throne and Cline 1991 <sup>c</sup>
27/151	93	0.47 $\pm$ 0.032	1.89 $\pm$ 0.030	0.96	Arthur 1995 <sup>h</sup>

<sup>a</sup>  $n$  gives the number of variance-mean pairs  $\leq 1$  divided by the total.

<sup>b</sup> Grain sample unit size of 0.12 kg.

<sup>c</sup> Trapping duration is 7 d.

<sup>d</sup> Grain sample unit size of 0.265 kg.

<sup>e</sup> Grain sample unit size of 0.5 kg.

<sup>f</sup> Grain sample unit size of 1,500 ml.

<sup>g</sup> Grain sample unit size of 0.25 kg.

used sticky traps to sample insect populations outside bins. In addition to the previously mentioned methods and locations, data were collected with food-baited traps outside bins, with grain samples from an elevator, and with grain samples from empty bins.

Four insect sampling data sets were combined to increase the number of means at the extremes of the density range, and develop a generic regression equation applicable to a wide range of situations. These data sets were collected with grain samples and probe traps. Lippert and Hagstrum (1987) have shown that the sampling statistics for insect density estimates from grain sample data were similar to those from probe trap data. Each of 20 insect sampling data sets and the combination of 4 insect sampling data sets were fitted to equation 1. Each insect sampling data set was split into 2 parts, one with means  $\leq 1$  and the other with means  $> 1$ . Each part spanned a density range of only 2 orders of magnitude. Equation 1 also was fitted to each part to determine whether the slopes and intercepts of the 2 parts were significantly different from one another.

The logarithm of mean in equation 1 was replaced by  $e^{(c \cdot x)}$  to give the nonlinear equation

$$y = a_0 + b * e^{(c \cdot x)}, \quad (5)$$

where  $x = \log_{10}$  of mean,  $y$  is  $\log_{10}$  of variance, and  $a$ ,  $b$ , and  $c$  were fitted parameters. The parameter  $a$ , equal to the difference between  $a_0$  and  $b$ , was substituted for  $a_0$ , and  $b$  also was subtracted from  $b * e^{(c \cdot x)}$  to give

$$y = a + b * (e^{(c \cdot x)} - 1), \quad (6)$$

so that  $a$  equals the  $\log_{10}$  of the variance when the  $\log_{10}$  of the mean equals 1. Equation 6 was fitted to each of 20 insect sampling data sets and the combination of 4 insect sampling data sets. The parameter  $c$  was fixed at the value for equation 6 derived from the combination of 4 insect sampling data sets, and the new equation,

$$y = a + b * (e^{(0.22 \cdot x)} - 1) \quad (7)$$

also was fitted to each of 20 insect sampling data sets. The fit of equation 6 was compared with that of equation 7 using mean square error. Fixing  $c$  converted the 3-parameter model to a 2-parameter model so that the mean square errors for equation 1 could be directly compared with those for equation 7.

The regression equations, their mean square errors and the 95% CL, the  $t$ -test comparing slopes, and the asymptotic slopes were calculated using commercial statistical analysis software (SAS Institute 1990). This software also was used to plot graphs and randomly assign insects to sampling units using a Poisson distribution. For average densities of 0.2, 0.3, 0.5, 1, 2.5, 5, 10, 20, 50, and 90 insects per sample unit, 2, 3, 5, 10, 25, 50, 100, 200, 500, and 900 insects were assigned randomly to 10 sample units, and the mean and variance were calculated. This procedure simulated random dispersal and was repeated 100 times at each density. The randomly generated data set was analyzed in the same manner as the insect sampling data sets.

## Results

The linear variance-mean regression equations fitted to 20 data sets had slopes of 1.41–1.78 and  $r^2$  values between 0.91 and 0.97 (Table 1). Additional data sets with the majority (82–100%) of means  $\leq 1$  had lower slopes (1.13–1.37) than the data sets in Table 1 (Table 2). When the majority of means were  $> 1$ , the data sets in Table 2 had slopes equal to or higher (1.78–1.89) than those in Table 1. Fitting the means that were  $\leq 1$  and those that were  $> 1$  separately for the insect sampling data sets in Table 1 resulted in slopes of 1.10–1.56 and 1.52–2.17, respectively (Table 3). This indicated that a nonlinear equation might fit the data better than the linear equation.

Table 3. Comparison of slopes and intercepts (mean  $\pm$  SE) of equation 1 fitted to means  $\leq 1$  and means  $> 1$ , and *t*-tests for significant differences in slopes and intercepts

ID	Mean $\leq 1$			Mean $> 1$			<i>t</i> -test <sup>a</sup> values for	
	n	Slope	Intercept	n	Slope	Intercept	slope	intercept
1A	275	1.36 $\pm$ 0.031	0.38 $\pm$ 0.021	198	1.98 $\pm$ 0.048	0.34 $\pm$ 0.038	189.28	21.22
1B	66	1.33 $\pm$ 0.061	0.24 $\pm$ 0.048	20	1.83 $\pm$ 0.254	0.08 $\pm$ 0.146	7.33	6.77
1C	678	1.24 $\pm$ 0.021	0.22 $\pm$ 0.015	87	2.17 $\pm$ 0.091	0.14 $\pm$ 0.050	105.82	30.83
1D	176	1.30 $\pm$ 0.035	0.36 $\pm$ 0.027	63	1.92 $\pm$ 0.081	0.30 $\pm$ 0.045	79.63	21.79
1E	105	1.32 $\pm$ 0.064	0.26 $\pm$ 0.037	57	1.91 $\pm$ 0.138	0.11 $\pm$ 0.086	25.50	17.11
1F	156	1.48 $\pm$ 0.041	0.39 $\pm$ 0.026	114	1.62 $\pm$ 0.079	0.34 $\pm$ 0.055	17.80	13.78
1G	134	1.43 $\pm$ 0.042	0.44 $\pm$ 0.033	52	1.52 $\pm$ 0.187	0.58 $\pm$ 0.092	2.37	14.24
1J	51	1.49 $\pm$ 0.078	0.44 $\pm$ 0.055	23	1.95 $\pm$ 0.237	0.23 $\pm$ 0.163	7.45	7.06
1H	94	1.56 $\pm$ 0.051	0.52 $\pm$ 0.053	156	1.77 $\pm$ 0.068	0.34 $\pm$ 0.062	29.07	27.05
1I	47	1.44 $\pm$ 0.063	0.46 $\pm$ 0.047	46	1.81 $\pm$ 0.129	0.41 $\pm$ 0.115	17.61	3.43
2A	15	1.10 $\pm$ 0.224	0.45 $\pm$ 0.103	59	1.78 $\pm$ 0.077	0.34 $\pm$ 0.075	12.10	6.71
2B	40	1.44 $\pm$ 0.063	0.46 $\pm$ 0.047	39	1.81 $\pm$ 0.129	0.41 $\pm$ 0.115	17.61	3.43
2C	74	1.28 $\pm$ 0.075	0.23 $\pm$ 0.045	144	1.83 $\pm$ 0.058	0.15 $\pm$ 0.060	61.19	14.22
2D	29	1.47 $\pm$ 0.120	0.37 $\pm$ 0.069	41	1.65 $\pm$ 0.119	0.47 $\pm$ 0.093	6.30	7.46
2J	97	1.36 $\pm$ 0.042	0.38 $\pm$ 0.029	78	2.05 $\pm$ 0.056	0.26 $\pm$ 0.043	140.41	43.49
2E	76	1.31 $\pm$ 0.047	0.42 $\pm$ 0.041	31	2.12 $\pm$ 0.071	0.42 $\pm$ 0.054	111.72	0
2F	52	1.52 $\pm$ 0.087	0.47 $\pm$ 0.054	130	1.79 $\pm$ 0.065	0.35 $\pm$ 0.069	22.72	16.15
3J	68	1.29 $\pm$ 0.059	0.35 $\pm$ 0.039	39	1.90 $\pm$ 0.115	0.55 $\pm$ 0.081	36.33	24.62
2G	147	1.34 $\pm$ 0.051	0.25 $\pm$ 0.032	128	1.93 $\pm$ 0.074	0.27 $\pm$ 0.061	73.05	4.64
4J	59	1.39 $\pm$ 0.086	0.38 $\pm$ 0.056	58	2.00 $\pm$ 0.084	0.30 $\pm$ 0.079	42.55	8.53
2H	50	1.44 $\pm$ 0.107	0.05 $\pm$ 0.095	45	1.81 $\pm$ 0.103	0.33 $\pm$ 0.132	16.95	10.43
2I	400	1.35 $\pm$ 0.032	0.24 $\pm$ 0.015	600	1.93 $\pm$ 0.006	0.09 $\pm$ 0.008	548.11	487.89

ID, cross references tables and figures.

<sup>a</sup> A *t*-test was used to test for significant differences in slopes and intercepts. All of the *t*-tests values were significant at  $p = 0.01$  except for the 2E intercept value of 0.

A nonlinear variance-mean regression equation generally fit stored grain insect sampling data better than a linear equation. Fitting a single generic nonlinear equation to data sets 1J-4J resulted in a 20.1% improvement in the mean square error (Table 4, 1A) compared with linear equation (Table 1, 1A). The generic nonlinear regression line, the 95% prediction interval, and the data sets 1J-4J are plotted in Fig. 1 A. The nonlinear equation fit 13 of 20 data sets

with a 7.2-48.2% improvement in the mean square errors compared with linear equation (Table 4). For 4 of the data sets, the improvement in mean square errors was only 0.5-3.3% and for 3 of the data sets, the linear equation fit better (-1.1 to -8.9%). These variations in the improvement of the fit were probably the result of differences among the data sets in the ranges of the insect densities sampled and the distributions of the mean densities over those

Table 4. Parameter values (mean  $\pm$  SE) for equation 7 fitted to data sets in Table 1

ID	n	% means within 95% prediction interval	a	b	MSE	% improvement in MSE compared with equation 1
1A	473	95	0.45 $\pm$ 0.015	7.46 $\pm$ 0.72	0.0638	20.1
1B	86	93	0.23 $\pm$ 0.033	6.74 $\pm$ 0.21	0.0642	11.2
1C	765	97	0.34 $\pm$ 0.010	7.09 $\pm$ 0.07	0.0371	18.3
1D	239	100	0.42 $\pm$ 0.013	7.18 $\pm$ 0.09	0.0343	18.3
1E	162	91	0.28 $\pm$ 0.021	6.88 $\pm$ 0.16	0.0681	7.2
1F	270	93	0.33 $\pm$ 0.015	6.79 $\pm$ 0.10	0.0638	9.6
1G	186	95	0.48 $\pm$ 0.020	7.48 $\pm$ 0.14	0.0543	0.7
1J	74	91	0.40 $\pm$ 0.035	7.25 $\pm$ 0.23	0.0820	8.5
1H	250	83	0.35 $\pm$ 0.023	7.23 $\pm$ 0.11	0.1293	-1.9
1I	93	80	0.28 $\pm$ 0.043	8.06 $\pm$ 0.28	0.1714	-8.9
2A	74	89	0.51 $\pm$ 0.042	6.40 $\pm$ 0.19	0.0806	20.5
2B	79	86	0.44 $\pm$ 0.039	7.09 $\pm$ 0.20	0.1164	3.3
2C	218	83	0.27 $\pm$ 0.025	6.78 $\pm$ 0.11	0.1018	15.0
2D	70	93	0.40 $\pm$ 0.035	7.11 $\pm$ 0.22	0.0792	-1.1
2J	175	99	0.44 $\pm$ 0.014	7.47 $\pm$ 0.08	0.0323	39.5
2E	107	100	0.57 $\pm$ 0.018	7.72 $\pm$ 0.11	0.0310	48.2
2F	182	92	0.42 $\pm$ 0.031	6.91 $\pm$ 0.13	0.1142	0.5
3J	107	92	0.51 $\pm$ 0.025	7.78 $\pm$ 0.17	0.0647	19.2
2G	275	90	0.34 $\pm$ 0.019	7.39 $\pm$ 0.12	0.1027	13.0
4J	117	95	0.43 $\pm$ 0.029	7.38 $\pm$ 0.15	0.0936	12.4
2H	95	82	0.14 $\pm$ 0.041	7.50 $\pm$ 0.16	0.1527	2.2
2I	1,000	100	0.27 $\pm$ 0.005	6.95 $\pm$ 0.02	0.0159	40.7

Mean squared error (MSE), percentage improvement in MSE, and percentage of means falling within 95% prediction interval for generic equation 7. All of  $r^2$  were within  $\pm 0.01-0.02$  of those in Table 1. ID, cross references tables and figures.

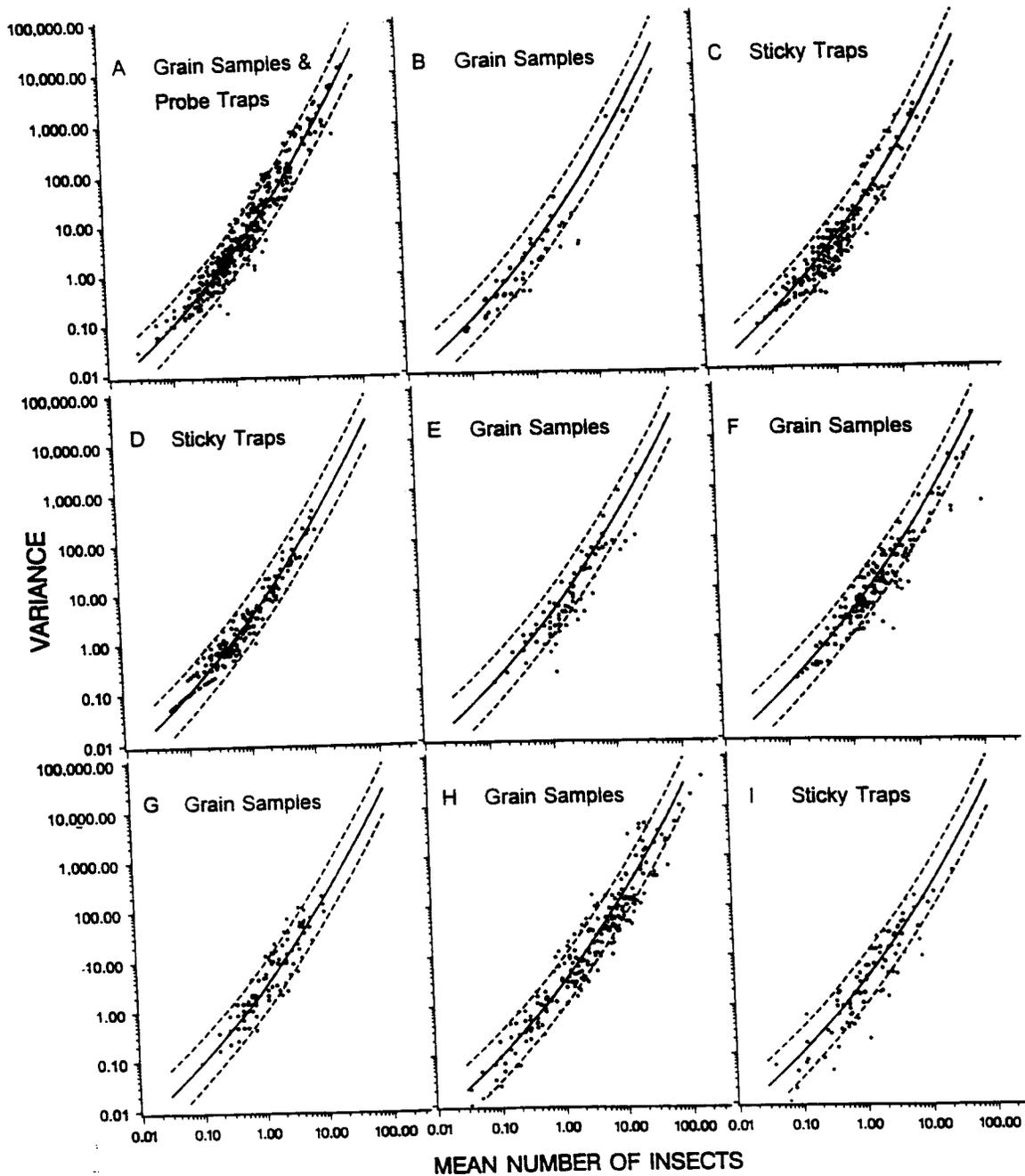


Fig. 1. (A) Plots of generic nonlinear variance-mean regression line (equation 7, solid line), 95% prediction interval (dashed line), and data sets 1J-4J in Table 1 (dots). (B-I) Plots of 8 additional data sets (1B-1I in Table 1) along with the regression line and the 95% prediction interval for generic. Different data sets were collected by grain sampling, probe traps and sticky traps.

ranges. With the generic nonlinear variance-mean regression equation, the slope changed with insect density. Asymptotic slope,  $0.22 * b * e^{(0.22 * \log \text{mean})}$ , at the mean densities of 0.01, 0.1, 1, 10, and 100 insects per sample unit was 1.06, 1.32, 1.64, 2.05, and 2.55, respectively.

Equation 7 with parameter  $c$  fixed at 0.22 described 20 insect sampling data sets nearly as well as equation 6 in which the parameter  $c$  was estimated. In fitting equation 6 to the 20 insect sampling data sets, the parameter  $c$  was highly correlated with the parameter  $b$  ( $r^2 = 0.99$ ). Fixing  $c$  fixed the curvature,

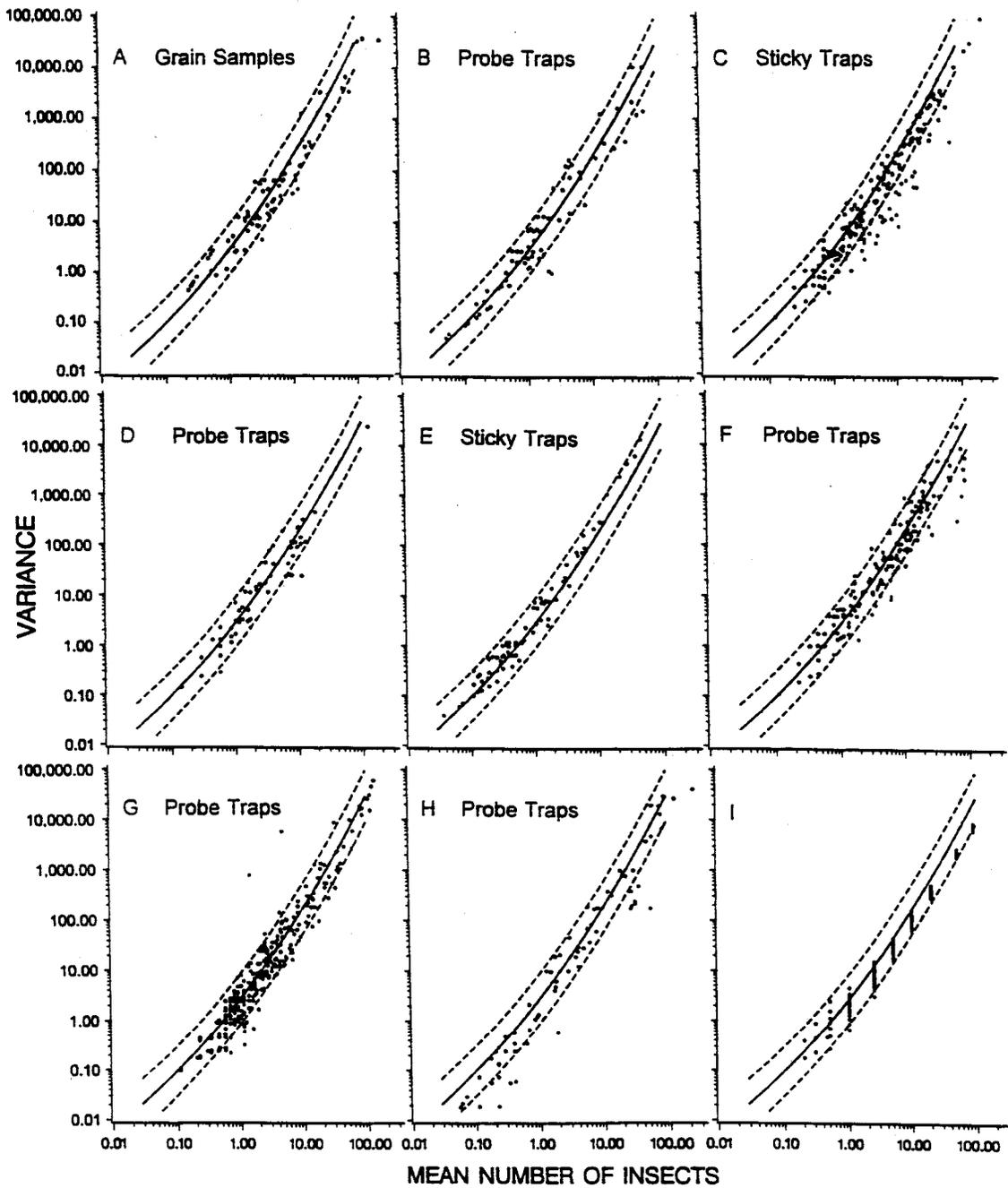


Fig. 2. (A-H) Plots of 8 data sets (2A-2H in Table 1) and (I) a randomly generated data set (2I) along with the regression line and the 95% prediction interval for generic from Fig. 1A. Different data sets were collected by grain sampling, probe traps, and sticky traps.

greatly reduced the standard error of  $b$ , and converted a 3 parameter equation to a 2 parameter equation. For 14 studies, the mean square errors for equation 7 were only 0.21-8.71% larger than those for equation 6. For the remainder of studies, the mean square errors for equation 7 were 0.25-1.34% smaller than those for

equation 6. The curvatures of the regression lines for equation 7 were slightly greater than those for equation 6.

A generic nonlinear variance-mean regression equation fit the insect sampling data for 25 studies, 3 different sampling methods, and the 6 most com-

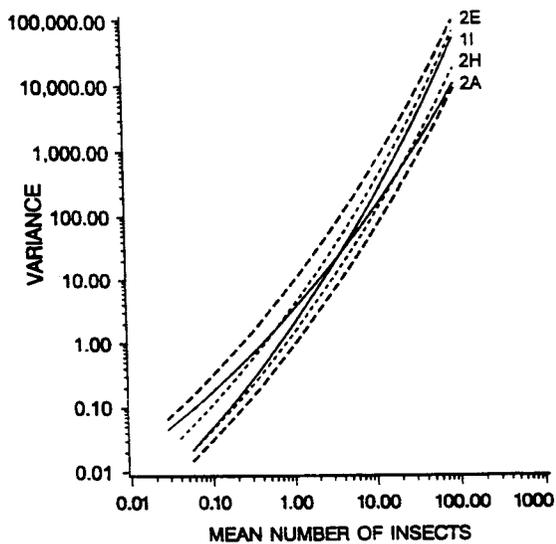


Fig. 3. Plots of 4 nonlinear regression lines (2 solid and 2 short-dash lines) for equations with most extreme parameter values (Table 4) along with the 95% prediction interval for the generic equation from Fig. 1A (long-dash lines).

monly encountered insect species. Data sets 1B-I and 2A-H collected with 3 different sampling methods are plotted along with the generic regression line and its 95% prediction interval in Fig. 1 B-I and Fig. 2 A-H, respectively. Most of the means (82–100%) fell within the 95% prediction interval for the generic equation (Table 4). The regression lines also fell within the 95% prediction interval for the generic equation (Fig. 3). Also, for the 9 data sets with narrow mean density ranges (Table 2), 89–100% of the data fell within the 95% prediction interval for the generic equation. Randomly assigning insects to 10 sampling units also resulted in data and a regression line that all fell within the 95% prediction interval for the generic equation (Fig. 2 I; Table 4, 2I). For 5 of the most commonly encountered insect species, 90–96% of the data fell within the 95% prediction interval for the generic equation (Fig. 4 A, B, D, E, F). For *Oryzaephilus surinamensis* (L.) (Fig. 4 C), 85% of the data fell within the 95% prediction interval. Other insect species represented only 27% of the 3,691 means for the 20 insect sampling data sets.

As in the linear equation, the parameters  $a$  and  $b$  in the nonlinear generic equation were retained as the intercept and slope, respectively. The parameter  $a$  is the  $\log_{10}$  of variance when the  $\log_{10}$  of the mean equals 1 and is thus the height of the curve above the x-axis. In Fig. 3, the regression line for 2E had an  $a$  of 0.57 and was above that for 2H with an  $a$  of 0.14. The parameter  $b$  determines the slope of the curve. In Fig. 3, the regression line for 1I had a  $b$  of 8.06 and was sloped more than that for 2A with a  $b$  of 6.40.

The 95% CL predicted for insect density estimates made with 10, 30, and 100 sample units are given in Table 5. Compared with the predictions of the generic nonlinear equation, the linear equation over predicted the 95% CL within the 0.3–3 insects per sample unit density range, and under predicted them at higher or lower insect densities.

### Discussion

The results of several previous studies suggested that it should be possible to find a generic equation. Downing (1979) found that the variance-mean relationship was similar enough for 1,500 benthos sampling data sets that the same transformation could be used to stabilize the variance. Grouping the data by taxa, the type of sediment sampled, and the type of sampling device used, he found that the linear equations fitted to these groups were generally not significantly different from an overall regression equation. Hagstrum et al. (1988) found that sampling data for a variety of stages and species of stored-product insects, sampling devices, locations in the marketing system, and types of grain could be described by a single linear variance-mean regression equation with narrow 95% CL. Lippert and Hagstrum (1987) found that the sampling statistics for insect density estimates from grain sample data were similar to those from probe trap data, and Subramanyam et al. (1993) found that sampling statistics were similar for different types of probe traps. Trumble et al. (1989) found that, in some cases, the slopes ( $b$ ) of linear variance-mean regression equation were not significantly different among locations and years, but they were cautious about pooling data into a generic regression equation because the stop lines for fixed-precision sampling plans changed with  $b$ . However, they did acknowledge that sometimes the same linear variance-mean regression equation had worked in different years and cropping systems by saying, "In fact, it is surprising that pest management programs utilizing fixed-precision level estimation plans have proven useful for many years in many different cropping systems."

Jones (1990) developed 2 generic linear variance-mean regression equations. One was developed by pooling 22 estimates of the parameters from different studies in the literature for several species of the genus *Tetranychus* on several crops. A 2nd was developed for species in the genus *Panonychus*. We found that the asymptotic slope of our generic equation increased from 1.06 at a density of 0.01 insects per sample unit to 2.55 at a density of 100. Therefore, the difference between the slopes (1.49 versus 1.32) of the 2 generic regression equations fitted by Jones (1990) may be the result of differences in the density ranges spanned and the distributions of means over those ranges. The distribution of means over the density range can be as important as the density range spanned when the least squares method is used to fit the linear variance-mean regression

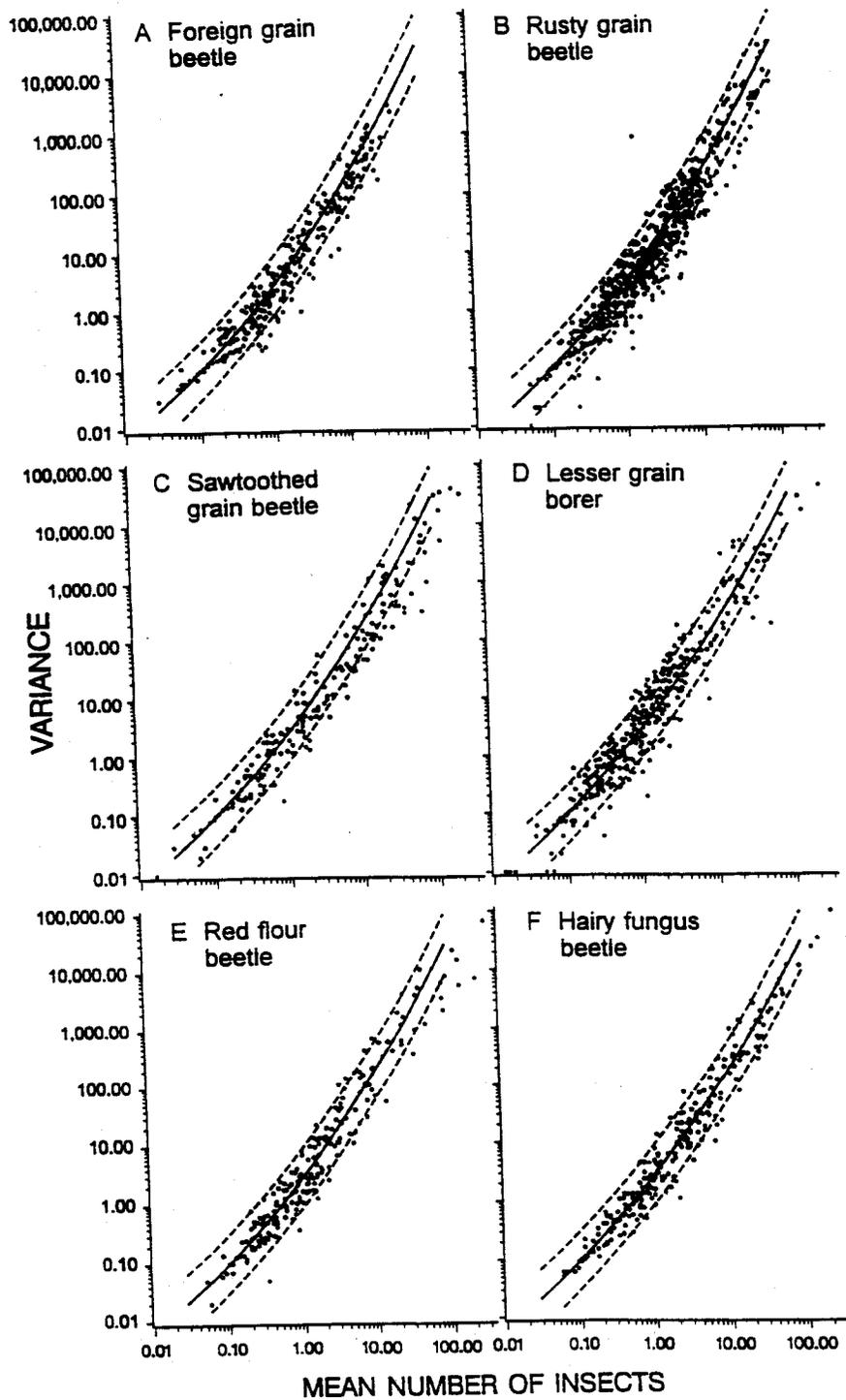


Fig. 4 (A-F) Plots of data for 6 most common species along with regression line and the 95% prediction interval for generic from Fig. 1A. The 6 species are (A) *Ahasverus advena* (Waltl) (Coleoptera: Silvanidae), (B) *Cryptolestes ferrugineus* (Stephens) (Coleoptera: Cucujidae), (C) *Oryzaephilus surinamensis* (L.) (Coleoptera: Silvanidae), (D) *Rhyzopertha dominica* (F.) (Coleoptera: Bostrichidae), (E) *Tribolium castaneum* (Herbst) (Coleoptera: Tenebrionidae), (F) *Typhaea stercorea* (L.) (Coleoptera: Mycetophagidae). Data represent a pooling of 20 insect sampling data sets from Table 1.

Table 5. The 95% CL of estimates as a function of number of sample units

Mean insect density	No. sampling units examined					
	10		30		100	
	Linear	Nonlinear	Linear	Nonlinear	Linear	Nonlinear
0.01	0.025	0.051	0.014	0.029	0.008	0.016
0.03	0.062	0.093	0.036	0.054	0.020	0.029
0.1	0.171	0.195	0.099	0.113	0.054	0.062
0.3	0.427	0.415	0.247	0.240	0.135	0.131
1.0	1.170	1.040	0.674	0.601	0.369	0.329
3.0	2.920	2.650	1.690	1.530	0.924	0.838
10.0	7.980	8.300	4.610	4.790	2.520	2.620
30.0	20.000	26.500	11.500	15.300	6.320	8.380
100.0	54.600	109.000	31.500	63.200	17.300	34.600

Confidence limits were calculated using linear equation 1 for data set 1A or generic nonlinear equation 6. The 95% CL of estimate =  $1.96 \cdot \sqrt{\text{variance}/n}$  based on equation from Snedecor and Cochran (1968).

equation because large means have more influence than small means. A single nonlinear equation might fit the data for both *Tetranychus* and *Panonychus*. Jones (1990) achieved acceptable precision using these generic linear equations in fixed-precision and binomial sampling plans. He concluded that a generic regression equation would save time, energy, and money; would speed technology transfer from better studied crops to minor crops; and would allow researchers to concentrate on studying pest biology rather than statistics.

The nonlinear equation fit sampling data better than the linear equation, because of the disproportionate increase in variance as mean insect density increased (Hagstrum et al. 1985, 1988). Increases in the percentages of sample units with insects have a dominant influence on the variance-mean regression equation at low densities, and the variance increases more slowly than at higher densities. At higher densities, the increases in the number of insects per sample unit are more influential and the variance increases more rapidly than at lower densities. The logarithm of variance-logarithm of mean regression equation is nonlinear as a result of the gradual transition from the dominance of the percentage of sample units with insects to a dominance of the number of insects per sample unit.

A variance-mean regression equation similar to our generic equation was generated by randomly assigning insects to sampling units. This indicated that the observed insect sampling distributions could be the result of random dispersal. The mechanism underlying the generic equation may be fairly general, and our generic regression equation may be useful in other sampling situations. Downing (1986) found that the slopes of the linear equations were similar among species and studies, and suggested that "Either there is a high degree of convergence in the evolution of species behaviour or stochastic, mathematic or demographic factors are operating similarly on many different species." Insect sampling distributions and variance-mean regression equations resulting from random dispersal could be produced by either of these mechanisms. Random

dispersal is perhaps the simplest explanation for the similarity.

Southwood (1966) considered the slope ( $b$ ) of the linear variance-mean regression equation to be a species-specific index of aggregation. However, Downing (1986) found that  $b$  varied as much within as among species. Sawyer (1989) has shown that  $b$  also increased with sample unit size. Routledge and Swartz (1991) found that, in some cases, the logarithm of variance-logarithm of mean regression equation was not linear and that the asymptotic slope increased with insect density. These changes in slope with species, quadrat size, and insect density may limit the usefulness of slope as an aggregation index. Thus, differences in pre- and posttreatment slopes of the logarithm of variance-logarithm of mean regression equation for insecticide efficacy tests (Trumble 1985, Taylor 1987) may not indicate decreased aggregation. Because of the nonlinearity of the logarithm of variance-logarithm of mean regression equation, lower densities after an insecticide application can result in lower slopes.

The simplest nonlinear regression equation, the quadratic used by Routledge and Swartz (1991), fit sampling data only over a narrow range of densities of <2 orders of magnitude. The nonlinear generic equation developed in the current study had the advantage of fitting sampling data over a broad range of densities as indicated by a high  $r^2$  and a low mean square error. It also retained  $a$  as the intercept and  $b$  as the slope as in the linear equation and reduced a 3- to a 2-parameter equation.

A nonlinear generic variance-mean equation applicable to many different situations could be fit to sampling data, because much of the variation in the slopes of the linear equations among studies is the result of differences in the range of insect densities sampled. In the current study, a generic equation for stored-grain insects fit the insect sampling data for 25 other studies, 3 different sampling methods and the 6 most commonly encountered species. Further studies are needed to determine the extent to which our generic nonlinear equation is useful in situations

other than stored grain. The generic nonlinear equation can be used to calculate the precision of mean insect density estimates over a 0.025–100 insects per sample unit density range and thus can reduce the cost of developing sampling programs. Also, it may provide a single regression equation useful in insecticide efficacy testing for both pre- and post-treatment data.

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