THE DISTRIBUTION OF ADULT ARGENTINE STEM WEEVILS IN CANTERBURY DRYLAND PASTURES

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SUMMARY

On a small scale (0.018 m² cores), the distribution of adult Argentine stem weevils in Canterbury dryland pastures is aggregated but becomes progressively less so as density increases. The distribution obeys the Taylor Power Law, and problems are highlighted in the usual interpretation of this law. The distribution is also adequately described by a negative binomial with k increasing with the mean. The field data on weevil distribution allow identification of the optimum sampling regime using cores, and the use of 'mean crowding' or 'effective density'/mean density relationships provides a link from laboratory pot experiments to densities prevailing in the field.

Keywords: Argentine stem weevil, *Listronotus bonariensis*, distribution, aggregation.

INTRODUCTION

This paper has two aims. The first is to assess the nature of the distribution of adult Argentine stem weevils (*Listronotus bonariensis*) within Canterbury dryland pastures, in particular to determine the existence and extent of any spatial aggregation. Such aggregation could have considerable significance in population regulation, by accentuating the density-dependent oviposition suggested by laboratory experiments (Barker *et al.* 1989). Specifically, it would mean that local densities, hence the effect on oviposition, would be greater than suggested by mean densities prevailing in the field. Quantifying the relationship between local density and mean density in the field would allow direct extrapolation of results from laboratory pot trials to the field. The second aim of the paper is to optimise the sampling regime for population studies of Canterbury weevils, using the 0.018 m² rectangular cores described in Proffitt *et al.* (1993).

METHODS

Adult weevils were sampled fortnightly from November 1990 to May 1994 in a dryland ryegrass pasture (cv Manawa) at Lincoln. On each occasion 20 - 50 cores were taken, located across drill rows as described in Proffitt *et al.* (1993). Given this constraint, the cores were otherwise taken without conscious bias. The data spanned 80 sampling occasions, each of which provided a mean and distribution, and a range of mean weevil densities from 1 (16/12/91) to 436/m² (8/2/93). Relationships were derived using linear regression or regression of log transformed values (to the base 10).

RESULTS

The distribution of weevils obeyed Taylor's Power Law (1961), originally applied by Bliss (1941), namely a linear relationship between log variance (s^2) and log mean (m , Fig. 1a):

$$\begin{aligned}\log s^2 &= 0.16 + 1.16 \log m \\ R^2 &= 0.95, \text{ df } 1, 78, P < 0.001\end{aligned}\tag{1}$$

with the intercept significantly greater than zero (Student's $t = 10.7$, df 78, $P < 0.001$) and the slope significantly greater than 1 ($t = 5.4$, df 78, $P < 0.001$).

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Figure 1: Relationships between a) log variance (s^2) and b) log k for the negative binomial distribution, and log mean weevil density per 0.018 m^2 core (m). The horizontal dashed line in b) corresponds to $k = 8$, below which the distribution is aggregated.

Hence $s^2 = 1.45 m^{1.16}$ (2)

The Taylor Power Law is essentially empirical but has been shown to hold for a variety of distributions, from uniform through random to aggregated. The problem with many data sets is that the nature of this underlying distribution may change, particularly as the mean changes. In this case, however, all the data fitted the negative binomial distribution, though its exponent, k , increased with the mean. For each sampling occasion k was calculated (Southwood 1978) as:

$$k = \frac{m^2}{s^2 - m} \quad (3)$$

High values of k , over about 8 (see for example Southwood 1978), indicate a random distribution approaching Poisson as k tends to infinity, while small values indicate aggregation. Out of the 80 sets of core samples, 54 had k values less than 8. k was related to the mean as shown in Fig. 1b and represented by the following equation (ignoring samples in which k was effectively infinite because the variance was less than the mean):

$$\log k = 0.44 + 0.54 \log m \quad (4)$$

$R^2 = 0.21$; $df \ 1,68$; $P < 0.001$

Hence: $k = 2.75m^{0.54}$ (5)

Thus the negative binomial distribution with a variable k adequately describes the distribution of weevils. However, to explicitly relate mean field densities to densities in small-scale pot experiments or to the likely impact of density-related processes, it is necessary to estimate the densities actually experienced by an average individual weevil given the overall mean and the degree of aggregation. Such a measure is provided by the 'mean colony size' (C) of Tanigoshi *et al.* (1975), where

$$C = \sum X^2 / \sum X \quad (6)$$

with X = number of weevils/core. C is thus the ratio of the mean number of weevils squared per core to the mean number of weevils per core, equivalent to the number of weevils per core averaged over all weevils rather than all cores, or the average number of weevils 'experienced' per weevil. C thus excludes all cores containing no weevils,

which contribute to and lower the overall mean but have no effect on the degree of local crowding actually experienced by the weevils. C is also equal to Lloyd's (1967) 'mean crowding' + 1, and is referred to here as 'effective density' rather than 'mean colony size'.

For the weevil data, C was regressed against the mean density m , giving the following relationship:

$$C = 1.18 + 1.18m$$

$$R^2 = 0.95; \text{df } 1,78; P < 0.001 \quad (7)$$

Converting to numbers/m² (C' and m'), given the core size of 0.018 m²:

$$C' = 66 + 1.18m' \quad (8)$$

showing that the effective density is considerably higher than the mean when the latter is low.

Finally, the number of cores required for a given level of precision (= ratio of standard error to mean) can be estimated directly from the data, without invoking the variance/mean relationship or any underlying distribution (eg. Barker and Addison 1988, 1989). Given that the standard error = $s/\sqrt{n}$ where n is the number of cores, then if the required ratio of standard error to the mean = D :

$$n = s^2/m^2 D^2 \quad (9)$$

n was estimated using this formula for each sampling occasion and was related empirically to the mean (m) using linear regression. For $D = 0.2$:

$$\log n = 1.56 - 0.84 \log m$$

$$R^2 = 0.91; \text{df } 1,78; P < 0.001 \quad (10)$$

Hence: $n = 36m^{-0.84} \quad (11)$

(Fig. 2a). To estimate the number of cores required for other levels of precision (D), n in equation 11 and Fig. 2a is multiplied by $(0.04/D^2)$.

Figure 2: a) Fitted relationship between the number of cores required to obtain a standard error/mean ratio of 0.2, and the mean density per core. b) Two examples of relationships between variance (s^2) and mean number of weevils per core (m), which contravene the $b > 1$ criterion for aggregation: $s = 0.25m^2$, $b > 1$, not aggregated at low density; 1 - - - - - $s = 2m^{0.5}$, $b < 1$, aggregated at low density.

DISCUSSION AND CONCLUSIONS

The parameter b of the Taylor Power Law relating variance (s^2) to mean (m):

$$s^2 = am^b \quad (12)$$

has been described as an index of aggregation, with values significantly greater than 1 denoting aggregation as opposed to randomness in a distribution of insects (Taylor 1961; Southwood 1978; Barker and Addison 1988, 1989).

The more fundamental criterion for aggregation $s^2 > m$ ($s^2 = m$ representing the random Poisson distribution), suggests that the parameter a is at least as important as b in determining the existence of aggregation. Specifically, a better interpretation of the power law parameters a and b (or more usefully, $\log a$ and b , the intercept and slope respectively of the log variance/log mean regression) is given in Table 1.

TABLE 1: The existence or otherwise of aggregation, given different values of $\log a$ and b in the Taylor Power Law: log variance = log a + b log mean.

		b	
		< 1	> 1
$\log a$	< 0	No	Maybe ¹
	0	No	Yes
	> 0	Yes ²	Yes

¹ aggregation may exist at high densities depending on the values of a and b

² aggregation confirmed at low densities.

Student's t tests can be used to assess the regression parameters' departure from 0 and 1, and, as the Table shows, the criterion $b > 1$ is not sufficient to determine aggregation; rather it indicates a concave-up variance/mean relationship which must cross the variance = mean line at some density, but there is no guarantee that this density lies within realistic limits. A hypothetical example of such a relationship is $s^2 = 0.25m^2$, shown in Fig. 2b. This has $b > 1$ but denotes a distribution changing from near uniform through random at $m = 4$ to aggregated for $m > 4$. Neither is $b > 1$ a necessary criterion for aggregation; if $\log a$ is significantly greater than zero then aggregation exists at low densities irrespective of the value of b . Again, Fig. 2b shows a hypothetical example, $s^2 = 2m^{0.5}$, with $b < 1$ but an aggregated distribution below $m = 4$. In fact, $\log a > 0$ is a sufficient criterion for aggregation, at least at some density within realistic limits.

For the Canterbury weevil data, $\log a$ is significantly greater than zero and b is significantly greater than 1, confirming aggregation over the range of densities measured. The relationship between the negative binomial k and the mean also indicates aggregation, decreasing in extent as density rises (Fig. 1b). Using the criterion of $k = 8$, equation 2 suggests that weevils are aggregated at densities below $7.2/\text{core} = 400/\text{m}^2$.

Barker and Addison (1989) show that adult weevils in Waikato pastures are also slightly aggregated, using similar-sized sampling units. However, the aggregation was less than in Canterbury, since $\log a$ in the Taylor Power Law was close to zero (0.02) and b was significantly greater than 1 only at $P = 0.05$.

In terms of sampling, the distribution of weevils in Canterbury (Fig. 2a) suggests that to obtain a standard error/mean ratio of 0.2 or less requires 64 cores at a mean density of 0.5/core (28/m²), reducing to 36 at 1/core (56/m²) and 20 at 2/core (112/m²). These are slightly higher than the number suggested for Waikato samples (Barker and Addison 1989).

Finally, the effective density/mean density relationship from the core data allows extrapolation of results from pot experiments to the field. Thus, Barker *et al.* (1989)

recorded density-dependent oviposition in pots of turf with surface area 0.0256 m² holding 2, 4, 8 or 32 weevils. A direct conversion to weevils/m² gives densities per pot of 78, 156, 313 and 1250/m² respectively for the four treatments. However, if these are interpreted as local or effective densities, then from equation 3 the corresponding overall mean densities in the field would be 10, 76, 209 and 1003/m² respectively. In the experiment, total eggs laid per female declined over the full density range, reducing by about half as the density increased from 2 weevils/pot to 4/pot. In the field, therefore, one would expect fecundity to reduce by a half as density increases from 10/m² to 76/m².

In conclusion, adult weevils in Canterbury dryland pastures are aggregated on a small scale (0.018 m² cores), becoming less so as density rises and approaching randomness at 400/m². The distribution obeys the Taylor Power Law and is adequately described by a negative binomial with k increasing with the mean. The field data on weevil distribution have allowed identification of the optimum sampling regime for Canterbury weevils using cores, and have provided a link from laboratory pot experiments to field densities.

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