Measuring mast seeding behavior: relationships among population variation, individual variation and synchrony

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Abstract

Mast seeding, or masting, is the variable and synchronous production of seeds by a population of plants from year to year (Janzen, 1971; Silvertown, 1980). The mechanisms of masting (e.g., Koenig and Knops, 1998) and the adaptive value of masting (Kelly, 1994; Sork, 1993) are of considerable evolutionary interest, both for their own sake and because of the often substantial effects of the pulsed resources produced during a masting event on animal populations (Ostfeld and Keesing, 2000). Two of the most commonly cited benefits of masting include satiation of seed predators (Janzen, 1971; Silvertown, 1980; Kelly and Sullivan, 1997) and increased pollination efficiency (Janzen, 1971; Smith et al., 1990; Kelly et al., 2001).

In general, temporal variation in seed production is expressed as the coefficient of variation (standard deviation/mean, sometimes expressed as a percent) in annual seed production, the idea being that dividing by the mean allows comparison of variation between species that differ in the number of seeds produced per individual as well as comparisons between studies that differ in how seed production was measured (e.g. Silvertown, 1980). The coefficient of variation of the total or mean annual seed crop for the population is denoted $CV_p$. This quantity is often used as an overall measure of variability in seed production; see for example Herrera et al. (1998).

Keywords: Coefficient of variation; Seed production; Spatial correlation; Temporal variation; Time series

1. Introduction

Mast seeding, or masting, is the variable and synchronous production of seeds by a population of plants from year to year (Janzen, 1971; Silvertown, 1980). The mechanisms of masting (e.g., Koenig and Knops, 1998) and the adaptive value of masting (Kelly, 1994; Sork, 1993) are of considerable evolutionary interest, both for their own sake and because of the often substantial effects of the pulsed resources produced during a masting event on animal populations (Ostfeld and Keesing, 2000). Two of the

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Herrera (1998) suggested that $CV_p$ can be divided into two primary components when data exist on seed crops produced by individual plants across years. First is the mean temporal variation of individual plants, denoted $\overline{CV}$, while the second is the synchrony of seed crops among individuals across years. Identifying the contributions to masting is valuable because it allows us to see the extent to which the population variability reflects individual variability and individual synchrony with the population (e.g. DeSteven and Wright, 2002). Species with low synchrony do not qualify as masting species from the perspective of a reproductive strategy regardless of the value of $CV_p$. Thus, synchrony is a key ingredient of masting (Janzen, 1978). In fact, studies of masting that address evolutionary questions should focus on both variability and synchrony among individuals across years rather than population variability alone. Herrera (1998) argues that, without synchrony, the production of large crops by some individuals in a given year should be accompanied by small crops in other individuals such that $CV_p$ will be small relative to $\overline{CV}$, the mean individual level $CV$. Alternatively, if there is a high level of synchrony, $CV_p$ should be similar to $\overline{CV}$. Here we use pairwise Pearson correlation coefficients to measure synchrony primarily because it directly enters into the mathematical relationships resulting from decomposing $CV_p$ data. See Buonaccorsi et al. (2001) for a general review of various methods for quantifying and assessing spatial synchrony.

Reasons for synchrony have been explored elsewhere (e.g., Kelly, 1994; Herrera, 1998; Kelly and Sork, 2002) and here we consider the interrelationships among various metrics used to quantify masting, following initial attempts by Herrera (1998). Specifically, we explore the mathematical relationships among empirical measures of $CV_p$, $\overline{CV}$ and synchrony based on decompositions of data collected over time for many individuals. We show that while individual variability and synchrony contribute to $CV_p$, as suggested by Herrera (1998), there is no simple way to express the exact relationship among the three. In fact, one cannot obtain an expression involving just $CV_p$, $\overline{CV}$ and an overall measure of synchrony. We also show that perfect synchrony does not necessarily imply that $CV_p$ equals $\overline{CV}$, as has been claimed, and characterize the relationship between $CV_p$ and $\overline{CV}$ in the absence of synchrony. Finally, we use our expressions to develop approximate relationships relating $CV_p$ to $\overline{CV}$ and an overall measure of synchrony and demonstrate that this provides an effective fit to 59 mast data sets.

Our objective here is to resolve some issues concerning the exact numerical relationship among population variability, individual variability and synchrony based on data. There are other approaches that can be taken to provide additional insight, but are beyond the scope of this paper. One approach, under study, is to formulate a stochastic model which captures dynamics for individual plants, spatial correlation among plants and additional within plant variability, and then examine the relationships among theoretical measures of population $CV$, individual $CV$s and synchrony under these models. A second approach is to explore the data empirically (e.g., carrying out various regression analyses) without relying on underlying theoretical models, in order to identify emergent patterns. Extensive investigations of this sort, using different models than the ones presented here, are carried out by Koenig et al. (2003).

2. General relationships among CVs and synchrony

This section examines the mathematical relationship between $CV_p$, individual variation, and synchrony for a set of data with $n$ plants and $T$ years, where $x_{it}$ is the seed count for plant $i$ in year $t$. The mean, standard deviation and $CV$ for plant $i$ are denoted by $\bar{x}_i$, $s_i$ and $CV_i$ respectively. The mean individual $CV$ is $\overline{CV} = \frac{1}{n} \sum_i CV_i$. It will also be useful to define the coefficient of variation for plant $i$ relative to the overall mean $\bar{x}$; that is

$$CV_i = \frac{s_i}{\bar{x}_i}$$

The standard deviation of yearly means is denoted by $s_p$ and the population coefficient of variation by $CV_p = s_p/\bar{x}$. The $CV_p$ is the same if yearly totals, rather than means, are used since $s_p$ and $\bar{x}$ will both change by the same scaling constant.

There are two natural decompositions associated with the data, which are described in detail in Appendix A. The first leads to

$$CV_p^2 = \frac{\sum_i s_i^2}{n \bar{x}^2} - \frac{SSI}{n \bar{x}^2 (T-1)}$$

$$= \frac{\sum_i CV_{in}^2}{n} - \frac{SSI}{n \bar{x}^2 (T-1)}$$

$$= \frac{\sum_i \bar{x}_i^2 CV_i^2}{n \bar{x}^2} - \frac{SSI}{n \bar{x}^2 (T-1)}$$

(1)

where $SSI$ is the sum of squares due to the interaction of plants and years and is related to synchrony, in that $SSI = 0$ under one concept of perfect synchrony (described in more detail later).
The second decomposition leads to

\[ CV_p^2 = \frac{\sum_i s_i^2}{n^2 \bar{x}^2} + \frac{\sum_i \sum_{k \neq i} r_{ik} s_i s_k}{n^2 \bar{x}^2} \]

\[ = \frac{\sum_i CV_{im}^2}{n^2 \bar{x}^2} + \frac{\sum_i \sum_{k \neq i} r_{ik} s_i s_k}{n^2 \bar{x}^2} \]

\[ = \frac{\sum_i \bar{x}_i^2 CV_i^2}{n^2 \bar{x}^2} + \frac{\sum_i \sum_{k \neq i} r_{ik} s_i s_k}{n^2 \bar{x}^2} \]

(2)

where \( r_{ik} \) is the Pearson correlation between counts for plants \( i \) and \( k \) and \( s_{ik} \) is the covariance between plants \( i \) and \( k \). Correlation has been widely used to measure synchrony and one summary measure of synchrony over the \( n \) individuals is the mean correlation \( \bar{r} = \sum_i \sum_{k \neq i} r_{ik}/(n(n-1)/2) \) over all pairs of plants.

Unfortunately, as seen from Eqs. (1) and (2), the relationship between \( CV_p, CV \), and synchrony is not simple, even when the latter is measured as the mean Pearson correlation coefficient. One reason for this stems from the use of individual \( CV \)'s, each defined relative to the mean of the individual plants, rather than individual \( CV \)'s defined relative to the overall population mean (\( CV_{im} \)).

It is only exactly true that population variation = individual variation + synchrony, if we think of population variation as \( CV_p^2 \), measure individual variation with \( \sum_i CV_{im}^2/n^2 \) and measure synchrony with either \( \sum_i \sum_{k \neq i} r_{ik} s_i s_k/n^2 \bar{x}^2 \) or \(-SSI/n\bar{x}^2(T-1)\).

2.1. Perfect synchrony

One, but not the only, definition of perfect synchrony is that plots of counts over time for different individuals are piecewise parallel (see Figs. 1 and 2). Mathematically, this means there are constants \( c_2, \ldots, c_T \) such that \( x_0 = x_{i,t-1} + c_t \) for each \( i \) and for \( 2 \leq t \leq T \). This means that seed production in all plants changes by the same amount in moving from one year to the next. The interaction term \( SSI \) is related to synchrony in that when the data are piecewise parallel, then \( SSI = 0 \), as noted by Herrera (1998). This does not imply however that \( CV_p \) will equal \( CV \). With piecewise parallelism, the standard deviation in counts over years is the same for each plant and is equal to \( s_p \), the standard deviation in mean counts over years. This leads to

\[ CV_p - CV = s_p \left[ 1 - \frac{\sum_i(1/\bar{x}_i)}{n} \right] \leq 0. \]

The inequality at the end results from the fact that the harmonic mean is less than or equal to the arithmetic mean (Casella and Berger, 1990, p. 183). Hence, \( CV_p \) is not equal to \( CV \) and the difference can be made large or small depending on several factors (see below). If the individual \( CV \)'s are defined relative to the overall mean, however, then it is true with perfect synchrony of this type, that \( CV_p = \sum CV_{im}/n \).

Figs. 1 and 2 illustrate further how factors other than synchrony influence the difference between \( CV_p \) and \( CV \) in masting data. Under conditions of perfect synchrony.
as just defined, with the among-year standard deviation fixed, the difference between \( CV_p \) and \( CV \) will increase with the standard deviation in mast production across individual plants (which reflects the term in brackets in Eq. (3)) as portrayed in Fig. 1. In other words, the larger the discrepancy in crop size between good producers and poor producers, the larger the difference between \( CV_p \) and \( CV \): For Fig. 2, we continue to maintain perfect synchrony, keep the variation among plants and \( CV_p \) constant, while allowing the overall mean and among-year variation to change. Again the \( CV_p \) remains constant while \( CV \) decreases as the yearly mean increases. These two figures illustrate that the difference between \( CV_p \) and \( CV \) cannot be interpreted as being just due to synchrony, since there is perfect synchrony throughout.

Perfect synchrony in the sense of piecewise parallelism will imply a mean pairwise correlation coefficient of \( r = 1.0 \). The converse is not true, however; that is \( r = 1.0 \) can occur even without piecewise parallelism.

Another type of perfect synchrony is to have constant relative change; that is \( x_{i,t} = c_t x_{i,t-1} \), where as before this is for each \( i \) and \( 2 \leq t \leq T \). This is equivalent to piecewise parallelism on the \( \log(x) \) scale. In this case it can be shown (see Appendix B) that all the pairwise correlations, and hence the mean correlation, equal 1.0, when calculated in terms of either \( x \) or \( \log(x) \). Further, in terms of the \( x \) values, \( CV_p = \bar{CV} \), yet \( SSI \neq 0 \). Meanwhile, for the \( \log(x) \) values, there is piecewise parallelism, that is \( SSI = 0 \) and \( r = 1.0 \), but \( CV_p \neq \bar{CV} \) (although \( CV_p = \sum CV_{im}/n \)). These results point out further the difficulty with trying to characterize what “perfect synchrony” implies about the relationship between \( CV_p \) and \( \bar{CV} \).

### 2.2. No synchrony

In the case of no synchrony, which we take here to be that all pairwise correlations are equal to 0, then from Eq. (2),

\[
CV^2 = \frac{\sum_i x_i^2 CV_i^2}{n^2 \bar{x}^2} = \frac{\sum_i x_i^2}{n^2 \bar{x}^2}.
\]

This relationship shows explicitly how even in the absence of synchrony, a change in individual variances can lead to an increase in \( CV_p \). It also shows that other things being equal, \( CV_p \) will decrease as the number of individuals in the study increases. This effect of sample size makes sense intuitively because unless the plants are perfectly synchronized, adding more plants will increase the chance that high producers will cancel out low producers in their effect on total crop size. This effect is important because plant level data sets are rare and many of those available have low numbers of individuals (e.g., half of the 16 data sets in Herrera (1998) had less than 30 plants).

### 2.3. Some approximate relationships

In terms of correlation, Eq. (2) shows that, other things being equal, an increase in correlation between plants will lead to an increase in \( CV_p \), but this result...
involves the individual pairwise correlations rather than an overall measure of synchrony for the population. As this expression shows, there is nothing exact that can be stated about the relationship between \( CV_p \), \( CV \) and \( \bar{r} \) = the average pairwise correlation between distinct pairs of plants. We can make, however, make use of Eq. (2) to try and develop some approximate relationships.

Define

\[
A = \sum_i CV^2_{im}/n
\]

to be the average of the squared individual CVs when defined relative to the overall mean. Writing \( s_i = X A^{1/2} + e_i \), where \( e_i = (s_i - X A^{1/2}) = s_i - (\sum_i s_i^2/n)^{1/2} \), then \( CV^2_p = A + Q \) (exactly) where

\[
Z = A \left( \frac{1}{n} + \frac{(n-1)\bar{r}^2}{2n} \right)
\]

and \( Q = \sum_i \sum_{k \neq i} r_{ik} [X A^{1/2} (e_i + e_k) + e_i e_k]/n^2 \bar{s}^2 \).

Using a linear Taylor series expansion about \( Q = 0 \) yields

\[
CV_p \approx Z^{1/2} + E, \tag{5}
\]

where \( E = Q/(2Z^{1/2}) \). Given the definition of \( e_i \), the quantity \( Q \), and hence the remainder \( E \), will be largely influenced by the “variability” in the individual plant standard deviations. Notice that if all the \( s_i \) are the same then each \( e_i \), and hence \( Q \), equals 0. Eq. (5) provides some insight into how \( CV_p \) depends on the mean correlation, the within plant variances, the number of plants and the average within plant variability (relative to the overall productivity). In particular, it shows that with a fixed \( n \) and amount of within plant variation, then \( CV^2_p \) increases approximately linearly in synchrony.

The mean of the individual CVs, is widely used in summarizing individual variability (see Herrera, 1998), but does not arise naturally from the decompositions. One can make use of it by treating \( A^{1/2} \) as approximately \( CV \). There are a couple of ways to motivate this approximation; one by using just the first terms of a Taylor series expansion of the \( CV^2_{im} \) around \( CV \) and another by considering the inequality \((\sum_i (a_i^2)^{1/2})^2 \geq n^{-1} \sum_i |a_i| \) (see Casella and Berger, 1990, p. 181) and treating the inequality as an approximation. Using this ad hoc approximation yields

\[
CV_p \approx CV \left[ \frac{1}{n} + \frac{(n-1)\bar{r}^2}{2n} \right]^{1/2} + E. \tag{6}
\]

3. Data fitting

The effectiveness of the above simple, but approximate, expressions, are examined by seeing how well they fit to 59 masting data sets involving 24 species of plants. These data, which are described in detail in Koenig et al. (2003), involve a wide range of values for the number of individuals and the number of time points. Fig. 3 shows a three-dimensional plot of \( CV_p \) versus \( \bar{r} \) and \( CV \) for these data. We examine two fits to the data. The first fit, based on Eq. (5), is

\[
CV_p \approx A^{1/2} \left[ \frac{1}{n} + \frac{(n-1)\bar{r}^2}{2n} \right]^{1/2} + 0.1349,
\]

where the 0.1349 is the value of \( E \) in Eq. (5) which minimized the sum of squared residuals. This fit explained 94.2 percent of the total variation in observed \( CV_p \), with a plot of fitted \( CV_p \) versus observed \( CV_p \) given in Fig. 4a.

The second fit, based on Eq. (6), is

\[
CV_p \approx CV \left[ \frac{1}{n} + \frac{(n-1)\bar{r}^2}{2n} \right]^{1/2} + 0.2554,
\]
where again the constant was chosen based on least squares. This fit explained 83.2 percent of the variation in observed $CV_p$ (Fig. 4b).

The quality of these fits, suggest that Eqs. (5) and (6) (and especially the former) provide a useful tool for understanding the contributions of synchrony and individual variation to $CV_p$.

4. Discussion

Herrera (1998) has argued that, while population $CV$ may provide a useful index of mast seeding, it is an inadequate measure for dissecting out the ecological and evolutionary cause of mast seeding in plants. The approach he suggested was to decompose the population-level temporal variation into two components; within-plant variability and among-plant synchrony. In this paper, we have shown that the population temporal variation, as measured by the coefficient of variation, is a complicated function of a combination of factors, predominantly affected by within-plant variability and synchrony, but also including the number of plants and the overall mean productivity. While it is true that population $CV$ is related in some manner to mean individual $CV$ and an overall measure of synchrony, we have shown that there is no simple expression for this relationship. The expressions given also lead to the conclusion that:

1. Perfect synchrony (in the sense of piecewise parallel profiles over time), does not imply that population $CV$ is equal to mean individual $CV$, as is demonstrated in Eq. (3), unless the individual $CV$s are defined relative to the overall mean rather than using the individual means. Related to the latter point, it is the $CV$s defined relative to the overall mean that enter into the decompositions in a natural way. On the other hand, if the profiles over time are piecewise parallel over time in terms of log(seed count) (meaning all plants have the same relative change in seed counts in a year) then population $CV$ does equal mean individual $CV$, when calculated on the seed values themselves.

2. The population $CV_p$ may be large even when there is no synchrony among plants, (Eq. (4)), especially when the number of sample plants is low or the mean productivity is low.
(3) With a fixed amount of within-plant variability, \( CV_p \) increases as the amount of synchrony increases, with the rate of increase generally depending on the number of individuals, the amount of within plant variability, and the overall mean.

(4) While no simple relationships resulted, Eqs. (5) and (6) provide some simple and useful approximations which account for 83–95 percent of the variation in \( CV_p \) in 59 real data sets.

Nothing in this analysis suggests that \( CV_p \) is not a useful measure of variation in population-level seed output (cf. Herrera, 1998). The \( CV_p \) is clearly affected by mean \( CV_i \) and inter-plant synchrony (as also shown empirically by Herrera). However, there are also influences of sample size in terms of number of plants sampled, and productivity per plant.

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Appendix A. Justification of Eqs. (1) and (2)

Eq. (1) results from the use of analysis of variance decompositions (Neter et al., 1996). Using the standard notation for means over indices, write \( \bar{x}_i = \sum_j x_{ij} / T \) for the mean for plant \( i \), \( \bar{x}_j = \sum_i x_{ij} / n \) for the mean for year \( j \), and \( \bar{x}_. \) for the grand mean. For notational convenience, the main text uses simply \( \bar{x}_i \) and \( \bar{x}_j \) for \( \bar{x}_i \) and \( \bar{x}_j \) respectively. Define \( SS_{\text{tot}} = \sum_i \sum_j (x_{ij} - \bar{x}_i)^2 \) (total sum of squares), \( SS_T = T \sum_i (\bar{x}_i - \bar{x}_.)^2 \) (among plant sum of squares), \( SS_W = \sum_i \sum_j (x_{ij} - \bar{x}_j)^2 \) (within plant sum of squares), \( SS_Y = n \sum_i (\bar{x}_j - \bar{x}_.)^2 \) (among year sum of squares) and \( SS_I = \sum_i \sum_j (x_{ij} - \bar{x}_i - \bar{x}_j + \bar{x}_.)^2 \) (sum of squares due to interaction between plant and year).

The standard decomposition for the one-way analysis of variance with plants as groups, yields \( SS_{\text{tot}} = SS_T + SS_W \), while the standard decomposition for a two way analysis of variance with one observation per cell yields \( SS_{\text{tot}} = SS_Y + SS_T + SS_I \). Equating these two, \( SS_T + SS_Y + SS_I = SS_T + SS_W \) and so \( SS_Y = SS_W - SS_I \). Using the earlier defined \( s^2_p \) and \( s^2_i \), we have \( s^2_p = SS_Y / (n(T-1)) \) and \( SS_W = (T-1) \sum_i s^2_i \). Hence \( s^2_p = (SS_W - SS_I) / n(T-1) = \sum_j s^2_j / n - SS_I / (n(T-1)) \). Dividing both sides by \( \bar{x}_j^2 \) leads to Eq. (1).

Eq. (2) results from first expressing \( \sum_i \sum_k \sum_j (x_{ij} - \bar{x}_i)(x_{kj} - \bar{x}_k) \) in two ways; as

\[
\sum_i \sum_j (x_{ij} - \bar{x}_i) \sum_k (x_{kj} - \bar{x}_k) = n^2 \sum_j (\bar{x}_j - \bar{x}_.)^2
\]

and as

\[
\sum_i \sum_j (x_{ij} - \bar{x}_i)^2 + \sum_i \sum_{k \neq i} \sum_j (x_{ij} - \bar{x}_i)(x_{kj} - \bar{x}_k) = (T-1) \left[ \sum_i s^2_i + \sum_i \sum_{k \neq i} s_{ik} \right] .
\]

Equating the two,

\[
n^2 \sum_j (\bar{x}_j - \bar{x}_.)^2 = (T-1) \left[ \sum_i s^2_i + \sum_i \sum_{k \neq i} s_{ik} \right] .
\]

Dividing both sides by \( n^2(T-1) \bar{x}_j^2 \) yields Eq. (2).

Appendix B

Suppose \( x_{ij} = c_i x_{it-1} \), for each \( i \) and \( 2 \leq t \leq T \). Defining \( c_1 = 1 \), then from successive multiplications \( x_{ij} = q_i x_{it-1} \) where \( q_i = \prod_{t=1}^T c_j \), with \( \prod \) denoting product. Denote the mean and variance of \( x_{it} \), and denote by \( \bar{q} \) and \( s^2_q \) respectively. Now \( \bar{x}_t = \sum_{i=1}^T x_{it} / T = \bar{q} \bar{x}_1 \) and \( x_{it} - \bar{x}_t = (q_i - \bar{q}) x_{it} \), which implies that \( s^2_t = \sum_{i=1}^T (x_{it} - \bar{x}_t)^2 / (T-1) = x_{it}^2 s^2_q \) and hence for every \( i \), \( CV_t = x_{it} / \bar{x}_t = s_q / \bar{q} \). The mean in year \( t \) is \( \bar{x}_t = \sum_i x_{it} / n = q_t \bar{x}_1 \), where \( \bar{x}_t \) is the mean in year \( 1 \). Hence \( \bar{x}_t \), the grand mean, equals \( q_t \bar{x}_1 \), \( s^2_p = \bar{x}_1^2 s^2_q \) and so \( CV_p = s_q / \bar{q} = CV_t \), since each individual \( CV_t \) equals \( s_q / \bar{q} \).

The correlation between series \( i \) and series \( j \) is

\[
\rho_{ij} = \frac{\sum (x_{it} - \bar{x}_t)(x_{jt} - \bar{x}_j) / (T-1)}{s_{ij} s_{kj} / \sqrt{(s^2_t s^2_q)(s^2_j s^2_q)}} = 1.
\]

References


