CONSIDERATIONS OF THE RELATION OF VARIOUS ERRORS TO ESTIMATES OF POPULATION CHARACTERISTICS

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Introduction

I HAVE been asked to discuss with you "the effects of sampling errors in estimating population numbers, mortality rates, etc. on the validity and/or reliability of the mathematical models developed thus far for analysis of life-table data." I must confess to some difficulty in deciding how to deal with the assignment, for it gives a lot of room in which to roam. In the end it seemed that the purposes of this workshop would be met best by attempting a simple common-sense discussion of the central, practical question: just what *is* the difference between an estimate and the true value being estimated?

This difference, called *total error*, always exists; and it is upon our knowledge of its components, their properties, and their relative sizes that we base our judgments of both the validity and the reliability of an estimate. Indeed, the whole purpose of sampling theory and methodology is to make possible the appraisal and control of total error. Despite its importance, the question of total error has been avoided or overlooked generally in the development of mathematical models of population phenomena.

Error enters estimates in many varied and often subtle ways. It is almost always the result of many factors operating simultaneously—some known, other conjectural. Total error can seldom be evaluated directly. One must usually rely on assumption, analogy, rigorous application of suitable methods, and sometimes mere guesswork in its appraisal.

To gain some insight into the problem of appraising error, we

will first identify the several kinds of error. Then, we will show how each kind can contribute to total error. And, finally, we will discuss how these contributions, in turn, are related to our judgments of the validity and reliability of estimates.

Some Fundamentals

To begin, I think it is necessary to review some of the definitions and notions that are basic to any discussion of sampling in general and of sampling errors in particular because usage tends to vary with the subject matter to which it is applied.

It must be emphasized, first of all, that any material that is to be sampled consists, at least conceptually, of a well-defined set of objects or events. The set is referred to as the *population* and the objects or events as *individuals*. The group of similar populations that contains the population of interest is called the *universe*.

In the population of interest all individuals have at least one attribute or characteristic of interest, and each individual possesses a particular *true* value of that attribute. In practice, it is convenient to speak of the set of values corresponding to the individuals in a population as *the* population.

Obviously, any set of attribute values or measurements made on a population contains information about the original population of objects or events, but that information is not very useful until it is condensed into a form that is more comprehensible than a simple list of the individual values. The device used to describe a population more succinctly is the *frequency distribution*, which is simply a tabulation of the frequency of occurrence of each value that appears in the population. Such a tabulation can be expected to contain far fewer entries than there are individuals in the population. In trivial cases it is possible to have only a single entry, but in most cases that concern us, the number of entries may be very large so that further condensation of the information is desirable or even necessary.

The most generally satisfactory method is to describe the frequency distribution in terms of its moments. The moments are

simply a series of arithmetic means of successively higher powers of the values in the population, thus

$$m_k = (1/N) \sum_{i=1}^{h} f_i \, y_i^k$$

where

m_k = the kth moment, k being the power.
N = the size of the population.
h = the number of different values (or classes) that appear in the population.
f_i = the ith frequency from the distribution.
y_i = the true value corresponding to the ith frequency.

When the frequency distribution encompasses the whole population, $h = N$ and $f_i = 1$.

The first moment, of course, is simply the well known measure of location. It fixes the position of the population (or of the distribution) within the range of values that are possible for the attribute being studied. If one is dealing with an attribute that is constant over all the individuals in the population[1], then each individual value equals the first moment which then provides a perfect description of the population with respect to the given attribute.

In contrast, if more than one value appears in a population, then the first moment is no longer a perfect description, although it still serves as a measure of location. The description can be improved by including a measure of the dispersion of the individual values, and this is provided by the second moment, which will be discussed in the next section. The first two moments usually give an adequate description of a population if its frequency distribution is reasonably symmetrical. Occasionally, the third and fourth moments will be needed to improve the description of an abnormal distribution, but higher order moments will be of use only rarely.

[1] When all the individuals in a population have the same (constant) true value for an attribute but the value changes from one population to another, the attribute is called a *mathematical variable*. If all individuals in all populations in the universe possess the same value, the attribute is called a *mathematical constant*.

Random Variables and Random Error

Any attribute or measurement for which more than one true value can appear in the population is a *random variable*, and we have just seen that its description requires both the first moment to measure location and the second moment to measure dispersion.

The first moment of a random variable, usually called the *arithmetic mean* or simply the *mean*, also serves as a *measure of central tendency*, meaning that it is the value each individual in a population *tends* to possess. The notion here is that the mean is the value each individual *would* possess if it were not for the operation of one or more chance mechanisms in the determination of individual true values. In consequence, a true value of a random variable, Y, is conceived to have two parts: a constant part that is equal to the population mean, $\overline{Y}$; and a variable part, e, which represents the effect of chance on the value of a given individual; thus

$$Y = \overline{Y} + e$$

The population of values of the variable part, e, is the *random error*. Taking the mean of both sides of the definitional identity one gets

$$\overline{Y} = \overline{Y} + \overline{e}$$

so that $\overline{e} = 0$, which simply means that the average deviation from the population mean is zero.

As a measure of dispersion, the second moment of the random variable has the disadvantage that it depends upon the value of the first moment since it is calculated by squaring the individual values of the random variable

$$Y^2 = (\overline{Y} + e)^2 = (\overline{Y})^2 + 2\overline{Y}e + e^2$$

and then taking the mean over the population

$$\overline{Y^2} = (\overline{Y})^2 + 2\overline{Y}e + (\overline{e^2})$$

which, with $e = 0$ always, reduces to

$$\overline{Y^2} = (\overline{Y})^2 + (\overline{e^2})$$

Because the *second moment about the origin*, as it is properly called, is not comparable between similar populations with different means, it is customary to use the *second moment about the*

mean as the standard measure of dispersion; that is the average of

$$(Y - \bar{Y})^2 = e^2$$

This value, called the *population variance*, σ^2, measures the dispersion of individual values around the population mean without regard to sign. Because $\bar{e} = 0$, both the random variable and the random error have the same population variance. In fact, the random error can now be recognized as a kind of standard random variable with mean equal to zero, variance equal to the variance of the corresponding attribute, and frequency distribution equal to the frequency distribution of the attribute translated to the origin.

The concept of a random error is sometimes difficult to accept for people working to uncover casual order in living systems. Whereas the values of a random error are assumed to arise by chance, we tend to believe that the individual true values can be explained entirely by casual relations and without any recourse to random error or the laws of chance. Actually, there should be no conflict between these concepts if one keeps in mind the scope of any given problem in which the concept of random error is used. Then random error is properly regarded as that part of the individual true values *not explained within the context of the problem.*

For example, suppose the subject matter is the body size of a population of insects. The basic problem we have been discussing is the description of a population, in which case the model of an individual true value is, of course

$$Y = \bar{Y} + e_1$$

with the individual value of the random error given as

$$e_1 = Y - \bar{Y}$$

But, the problem might be to describe the relation between body size and age so that the model becomes

$$Y = \bar{Y} + a_1(A - \bar{A}) + e_2$$

so that an individual value of the random error becomes

$$\begin{aligned} e_2 &= Y - \bar{Y} - a_1(A - \bar{A}) \\ &= e_1 - a_1(A - \bar{A}) \end{aligned}$$

This may be smaller than in the previous problem. Again, the

problem might be to describe the relationship between body size and both age and nutritional level with the model

$$Y = \bar{Y} + b_1 (A - \bar{A}) + b_2 (N - \bar{N}) + e_3$$

yielding

$$\begin{aligned} e_3 &= Y - \bar{Y} - b_1 (A - \bar{A}) - b_2 (N - \bar{N}) \\ &= e_1 - b_1 (A - \bar{A}) - b_2 (N - \bar{N}) \end{aligned}$$

This may be a still smaller value for the random error. There is no theoretical limit to the smallness of the random error. If the scope of a problem were expanded indefinitely, it might be possible to decrease the size of the random error indefinitely, but one can always expect to reach a practical limit both in the scope and complexity of a problem that can be handled and in the reduction of random error long before the error is as small as is desired.

Now random error is not the only kind of error with which we must deal. On the one hand, the random error is inherent in the population; it is the variation in true value or measurement of an attribute left unexplained by the model, and we have seen that it is basic in describing the material with respect to that attribute or measurement. On the other hand, there are extraneous errors that detract from that description by distorting it in one way or another. In this category are all the errors that are inherent in the particular set of procedures by which observations are made on a population. These errors are the subject of the next section.

Extraneous Errors

There are two general types of extraneous error. One type, which we will call a *compensating error*, a, is like a random error, except that it arises from different sources and, therefore, has different interpretations. Like the random error, its first moment is zero, but its second moment is not the population variance. The second type of extraneous error we will call a *systematic error*, b, because it is always one-directional. It is, in fact, a nonzero constant, having the same value for each observation. Although we will deal with systematic error here only as an additive constant, it may also be a constant proportion of the true value of an individual. Our generalizations about systematic error will hold for either case.

Now, we can write a general model for an *observation,* Y′, on an individual in terms of its true value, Y, and its associated errors

$$\begin{aligned} Y' &= Y + a + b \\ &= \overline{Y} + e + a + b \end{aligned}$$

The mean of all observed values over the population, the *observed population mean,* is

$$Y' = \overline{Y} + \bar{e} + \bar{a} + b$$

but under these conditions $\bar{e} = \bar{a} = 0$ and only b is unknown, so

$$\overline{Y'} = \overline{Y} + b$$

As we have seen, the second moment about the mean is based on the deviations of individual values from the mean

$$Y' - \overline{Y'} = e + a$$

and the mean of these deviations squared is the *observed population variance*

$$\begin{aligned} \hat{\sigma}^2 &= (\overline{e + a})^2 \\ &= \bar{e}^2 + 2\,\overline{ea} + \bar{a}^2 \end{aligned}$$

that, under the condition that $\bar{e}^2 = \sigma^2$, becomes

$$\hat{\sigma}^2 = \sigma^2 + 2\,\overline{ea} + \bar{a}^2$$

It can now be seen how the presence of extraneous errors can detract from the description of a population. If systematic error is present, the observed population mean is distorted while the presence of compensating error distorts the observed population variance. The extraneous errors always have these specific effects, regardless of how the errors arise. In this example they could only have arisen as errors of observation or recording because no sampling is involved; but when a sample of observed values is used to estimate the true population mean and variance, the extraneous errors may consist of both these common *measurement errors* and of *sample selection errors.* It is worth noting, then, that poor observational technique has the same effect as poor sampling technique, and vice versa.

Sample-based Estimates of Population Mean and Variance

A *sample* is nothing more than a collection of observed values

taken from the population of interest. Suppose, then, that we designate each individual in the population as a possible sample of size $n = 1$. Now each individual observed value is also the mean value of one of the possible samples. If we were to arrange all the possible sample means into a frequency distribution, we would get what is called the *sampling distribution* of the population. In this special case the sampling distribution and the frequency distribution of the individual observed values are obviously the same.

It comes as no surprise, then, that the arithmetic mean of the sampling distribution is the same as the observed population mean. If each of the possible samples has an equal chance of being selected for observation this result is called the *expected value*, E, of a sample mean which may be written as

$$E\,\bar{y} = \bar{Y} + E\bar{e} + E\bar{a} + b$$

In analogy to the previous section $E\bar{e} = E\bar{a} = 0$, so that

$$E\bar{y} = \bar{Y} + b$$

Now, instead, suppose that we consider the whole population as a single sample of size $n = N$. Then, the sample variance S^2 equals the observed population variance σ^2 from the previous section and, with only one possible sample, the expected value of the sample variance must also equal the observed population variance

$$\begin{aligned} E\,s^2 &= Ee^2 + 2E\,\bar{e}\bar{a} + E\bar{a}^2 \\ &= \sigma^2 + 2E\,\bar{e}\bar{a} + E\bar{a}^2 \end{aligned}$$

The point of these trivial exercises is to show that estimates of both the true population mean and the true population variance can be obtained from sample means and sample variances—at least in the extreme cases considered. It is not so obvious but is nevertheless true that within these limits of sample size:

1. it is always possible to obtain estimates of the true population mean and variance as well as estimates of other population parameters such as regression coefficients; and
2. the estimates are *unbiased* if, in the estimators like those modeled above, the algebraic sum of all terms that arise from extraneous errors can be shown to equal zero.

These conclusions hold—even when the possible samples have unequal probabilities of selection—provided only that:

1. every individual in the population being sampled is contained in one of the possible samples; and
2. every possible sample has a known probability of being selected for observation.

The various forms of random or *probability sampling* are the only sampling designs known to satisfy these conditions theoretically; and even they may fail to do so if not applied very rigorously, or if the estimators are not constructed to correspond properly with the structure of the samples. In general, any failure to satisfy these conditions will create additional extraneous errors of both kinds (systematic and compensating), thus increasing the hazard of bias in the estimates.

Biases in estimates of both the mean and the variance are important components of the total error with which we are concerned. The bias in the estimate of the mean, commonly known as *the bias,* B, is of particular importance as we shall see below. It measures the distance between the true population mean and the mean of the sampling distribution. Another way of viewing this bias is that estimates of the mean are unbiased if, *on the average,* the sample means equal the true population means. This is not to say, of course, that an unbiased estimate from any given sample equals the true population mean, for we know that a sample mean will deviate to a greater or lesser extent from the mean of the sampling distribution.

The second major component of total error is the average deviation of the possible sample means from the sampling distribution. It is called *sampling error,* $\sigma_{\bar{y}}$, and it is well known that the sampling error is a function (depending upon the sampling design) of the sample size and the true population variance. For example, the true (sometimes called "pure") sampling error in simple random sampling is simply

$$\sigma_{\bar{y}} = \sqrt{\sigma^2/n}$$

However, the observed sampling error, $s_{\bar{y}}$, obtained from the estimated population variance, also contains whatever bias enters that estimate by way of the procedures used:

$$s_{\bar{y}} = \sqrt{\frac{\sigma^2 + 2Eea + Ea^2}{n}}$$

The sampling error is the measure of the *precision* of the estimate of the population mean. Its important features are first, that it can be observed readily; and second, that its size can be reduced to any desired level simply by increasing sample size, or by tightening up the set of procedures used, or by both.

Accuracy refers to the magnitude of deviations of sample means from the true population mean resulting from the effects of all errors, including systematic errors. It is the total error, expressed as the square root of the *mean square error*, mse, which can be shown to equal the variance of the estimate $s_{2\bar{y}}$, plus the bias of the estimate, B.

$$\text{mse} = s^2_{\bar{y}} + B^2$$

The bias, although it ordinarily cannot be observed, is an important property of an estimate. Unlike the sampling error, its size can be reduced only by using more rigorous methods of sampling, observation, and estimation. The ratio of bias to standard deviation, B/s, is often used to judge the effects of bias.

When the ratio is less than 0.01, the bias is generally judged to be negligible, whereas a ratio higher than 0.25 is usually judged to be a serious defect.

Bias distorts not only estimates of population means but the judgments or inferences about their precision as well. For example, given a normal sampling distribution, the probability of an error greater than 1.96(s) is 0.05 without bias, but when B/s is 0.6, the probability rises to 0.09, and when B = s, the probability is 0.17—more than three times the probability without bias. Consequently, without adequate controls on the bias, statements about the precision of estimates can often be meaningless.

In summary then, we have described three significantly different types of sampling error; we have seen how bias may enter sample estimates of one or another of the population parameters; and we have seen how bias in an estimate distorts our judgments of the validity of the estimates.

The use of biased estimates in mathematical models can have

serious consequences. If the model is an equation among population parameters and theoretical coefficients, we will find that substitution of biased estimates for the parameters will result in an inequality. If the model is an equation among known parameters and unknown coefficients, we will obtain biased estimates of the coefficients. And, in either case, interpretations of the biological significance of either coefficients or variables by recourse to biased estimates of variances (and covariances) will themselves be biased because the estimates contain variation introduced in the sampling process that can completely obscure the inherent biological variation, which is assumed to be the total content of the estimate in such interpretations.

POPULATION DENSITY AND INSECT BIOLOGY: A REVIEW

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IT WAS A REMARKABLE achievement when Uvarov *(1921)*, from field observations and from examination of a large series of museum specimens, deduced that three species of morphologically and behaviorly distinct locusts, *Locusta migratoria* L., *L. danica* L., and *L. migratorioides* Reiche and Fairmaire, were actually one species, one at the subspecific level. This accomplishment was not wholly an exercise in deductive systematics, but one in applied population dynamics research as well. It is in the latter field that I will limit my remarks today.

The theory of locust phases proposed by Uvarov 46 years ago opened a whole new approach to the explanation of behavioral and biological variation among individual species that is associated with the density of their populations. He explained that the immature, but not the adult, *danica* type, indicative of low density populations, was colored differently from the *migratoria,* or high density type. Striking color differences were shown for the hoppers (immatures) as follows: " . . . it is almost impossible to find any definite type of coloration of the larvae of *danica,* which vary enormously; uniformly green forms are most common, but fawn, grey, brown, and even black ones may be met with together. Quite opposite is the case in *migratoria,* in which each larval stage exhibits quite constant colour characters. Their coloration presents a combination of black and orange-red (or yellow), the earlier stages being almost entirely black, while orange, or yellow, appears first in the third stage . . . ." In regard to adult sexual dimorphism, male *danica* were distinctly smaller than the females, which was not the case with *migratoria.* I deliberately

omit comparisons to *migratorioides,* because of its closeness to *migratoria.*

Ecologically, *danica* showed no marked habitat preference save vast waterless tracts and forests, but *migratoria* required ". . . strictly defined permanent breeding grounds." Is it possible that this statement is noteworthy in terms of endemic and outbreak populations of forest pests?

To continue: nowhere are *migratoria* eggs laid in Russia except on little, sandy, grassy islands surrounded by hundreds of square miles of dense growth of reed, *Phragmites communis* Trin. When populations attain a certain level, the hoppers form groups, group meets group to form larger groups, and their previous relatively aimless movement becomes more directional. Temperatures around 15° C. activate the hoppers. They do not move at night, but the warm rays of the morning sun make them active again and they feed. As the temperature rises the insects become still more active and they move to the ground. By so doing, they disturb other hoppers, which increases the movement of the swarm. The movement soon becomes directional, and the swarm marches. As temperatures decrease in the evening to about 15° C., the marching ceases and the hoppers climb up plants and feed, becoming comatose as the temperature drops further. This tendency of the hoppers to repeat the movements of other ones and come together has been investigated and termed "social aggregation" by Ellis *(1953).*

Mass flight of the swarm occurs when air sacs develop in the adults, and they continue to fly, maintaining their gregarious habit. They stop flying and feed when their air sacs shrink and their fat reserves are depleted. Little was known in the early days about the breeding grounds after emigration. In a footnote to his pioneer work, Uvarov *(1921)* stated a legitimate common complaint of entomologists that pests are only studied in outbreaks, and that important clues to their dynamics would come from attention during years of minimum population.

It remained for Faure *(1932)* to test Uvarov's conclusions experimentally. His noteworthy work was a result of his insight and methodology, strong financial backing, and a good supporting staff. In the end, he confidently removed the props from Uvarov's

detractors and added considerable experimental detail to the principal thesis. This is not to say that the works of Uvarov and Faure were without error, but that they made original advances in entomology with uncanny success. Now light was admitted to a room dark since at least biblical times, and between 1932 and 1939 the list of publications on this subject grew rapidly.

Within the last decade insect physiologists have carried out fruitful research on the causes of behavioral differences noted among endemic and swarming locusts. In an arena used for a behavioral study, Ellis *(1956)* showed differences in social aggregation in two species of locusts. Newly hatched desert locusts, *Schistocerca gregaria* (Forsk.), required only 1 day to attain maximum social aggregation, whereas new African migratory locusts, *Locusta migratoria migratorioides*, settled at random until they were 2 or 3 days old. With this species, maximum social aggregation required 3 or more days. Later, Ellis *(1959a)* demonstrated that, as Uvarov suggested, crowding reinforces the instinct to crowd and the important stimulus is contact—not necessarily contact with one another, but even other species of insects and moving fine wires. She concluded that social aggregation is acquired by learning because hatchlings and solitaries did not show this behavior. She also found that the offspring of crowded parents tend to be darker and march more vigorously than those from isolated parents *(Ellis 1959b)*. This is an interesting observation in the light of recent experimental work with RNA, memory, and behavior.

Delving deeper, Ellis and Carlisle *(1961)* observed that the prothoracic gland of *L. m. migratorioides* and *S. gregaria* is shaped differently and is much larger in solitary than in gregarious forms. The corpus allatum was also slightly larger among solitaries, whereas the corpus cardiacum showed no differences. They extirpated a portion of the prothoracic gland from solitaries of *S. gregaria* which resulted in similar coloration to aggregated forms. The controls underwent a blank operation and color change did not occur.

Later, Carlisle and Ellis *(1963)* injected fresh prothoracic gland extracts from the same or another species of locust into gregarious

locusts, and found that this treatment caused a significant decline in marching activity. Boiled homogenate caused the same results.

Nolte *(1964)* presented data to show that chiasma frequency was greater in newly hatched brown desert locusts, *Locustana pardalina* (Walker), from black gregarious parents than were offspring from parents in the solitary color phase. He speculated that this may be important to locusts migrating into a region quite different ecologically from the one they left.

Nolte *(1963)* postulated that a pheromone triggers color change in several species of locusts. A biochemistry student attempted to bring about the light colors of *S. gregaria* solitary hoppers by isolating them but the succeeding instars were mostly black. Poor ventilation in the laboratory during the winter was suspected as a contributing factor, and tests were designed to learn if pheromones were involved. Three species of locusts were studied, *S. gregaria, L. m. migratorioides,* and *L. pardalina.* At the conclusion of the tests, Nolte offered that the grouping of hoppers permits the accumulation of pheromone in the air around the group and that this stimulates the melanization process. He also suggested that the pheromone collects in the eggs of gregarious locusts which results in dark hatchlings, compared to light ones from solitaries. Incidentally, Faure *(1932)* imagined such a substance existed and called it "locustine."

Norris *(1964)* showed that crowding accelerates maturation in *Schistocerca* and inhibits it in *Locusta.* She also demonstrated that the presence of mature males accelerates maturation, and that groups of immature males dampen maturation. Pheromones in the mature males appear responsible for speeding up development. In *Schistocerca,* the pheromone stimulated ovarial development and readiness to copulate in the females.

Although the drama surrounding biological effects of population density opened with Uvarov's deductive conclusions, the plot thickened with some fairly recent contributions by Faure *(1943).* His were the earliest published results of studies of color changes associated with various population densities of Lepidoptera. Working with the lesser armyworm, *Laphygma exigua* (Hübner), Faure learned that when the larvae were reared in isolation they were

light in color, but when reared in groups the larvae turned dark. This discovery is similar to his findings concerning the locusts. Unlike the paurometabolous locusts, the holometabolous armyworm has no carryover of this effect. That is, hatchling locusts tend to resemble their parents in color phase, but armyworm larvae do not. Crowded armyworm larvae were more active than those reared in isolation. Faure felt that dense populations of armyworms required more time to develop, but he had no proof of this.

It wasn't until the decade of the 1950's that emphasis was directed toward the ecological implications of color variation-crowding relationships of Lepidoptera. In 1950, a brief note appeared in NATURE, telling of color variation in *Plusia gamma* L., and promising publication of much more significance later *(Williams and Long 1950)*. Subsequently, Long *(1953)* published a portion of his doctoral thesis which was concerned with the effects of population density on lepidopterous larvae. His studies emphasized color, the number of instars, pupal weight, larval and pupal developmental rates, and mortality at different densities. The principal conclusions from these studies were that larval darkening was directly related to population density, solitary larvae were somewhat heavier than those from groups, crowding increased development rate (many crowded larvae underwent fewer instars than those in isolation), and lower pupal weight and lower larval mortality were encountered in groups. The higher mortality went along with the increased number of instars among many larvae reared in isolation. The grave mistake of not keeping data separate by sex casts a shadow over the interpretation of much of the foregoing.

Utida *(1954)* found that the density of young larvae of the cowpea weevil, *Callosobruchus quadrimaculatus* (F.), has a strong influence on the physiology, morphology, and behavior of its adults. Larval density regimes resulted in the production of only parthenogenetic females which were found to have low egg deposition, flight capability, light weight, and long life. This is in contrast to a nonflying bisexual phase where the females were heavy and deposited many eggs. As a result of additional study, he concluded that the flying phase represents a field-type weevil

and the nonflying phase is adapted to storage conditions *(Utida 1956)*. I do not feel that it is important to this discussion to go further afield in the area of stored products insects, because they present special cases in their closed environments.

The crowding of certain Lepidoptera may effect changes in fecundity as indicated by oviposition plus retained eggs or simply oviposition. Unfortunately, in the literature one term is used synonymously with the other. Thus it was stated that the fecundity (oviposition) of *Plusia gamma* L. was increased by crowding, whereas it decreased in *Pieris brassicae (Zaher and Long 1959)*. It is debatable whether oviposition alone is a reliable basis for studying this relationship when dealing with reared insects. The only way of knowing this would be to collect freshly spent females in the field and determine the number of remaining eggs and oocytes. Insects may be sensitive to rearing environments and die before they have fulfilled the reproductive potential that might be attained in the field. This is true with the elm spanworm, where spent females in the field are normally almost void of eggs, but laboratory moths rarely oviposit completely—if at all in some cases.

An important discovery was that eggs from solitary rearings were significantly heavier on the average for both *P. gamma* and *P. brassicae*. In the light of work by Campbell *(1962)* and Wellington *(1965)*, the influence of egg weight on the subsequent generation should not be overlooked. These investigations also point up the need to continue studies of this nature through several generations, rather than to stop after demonstrating significant differences in egg populations.

In other work, Zaher and Moussa *(1962)* showed that females from high density larval populations of the cutworm, *Agrotis ypsilon* Rott., produced fewer eggs, and that the total duration of the larval and pupal stages was increased by rearing them in groups. Similar results were observed from what appears to be self-regulating populations of a psyllid which infests eucalyptus foliage in Australia *(Clark 1963)*. When the adults of *Cardiaspina albitextura* Taylor are crowded, they lay only one-fifth to one-third the number of eggs deposited by uncrowded females. At both high and low population densities, the mean number of eggs laid

per female on fresh foliage was twice the number oviposited on foliage previously occupied by adults of the same generation. Because high quality foliage is required by the psyllids, Clark believes that it is the limiting factor which causes violent population changes common to this insect. He concluded that high population densities of nymphs resulted in much unfavorable foliage for oviposition and the adults responded with declining egg deposition. Therefore, the loss of foliage quality dampens the psyllid population by reducing the number of oviposition sites and the amount of food available for the oncoming generation.

Coming to more familiar ground, Ghent *(1960)* showed experimentally that larval aggregations were necessary for survival of the jack pine sawfly, *Neodiprion pratti banksianae* Rohwer. Similar results have been indicated for field populations of Swaine's jack pine sawfly, *Neodiprion swainei* Middleton *(Lyons 1962)*. This is so despite heavier egg parasitism among large egg colonies than among small egg colonies *(Lyons 1962)*. Low egg populations per colony were found to have correspondingly low survival. Lyons *(1962)* suggested that low survival among eggs in small clusters might be due to an "internal factor" involving the female, and that it has nothing to do with the size of the egg clusters themselves. Quite possibly he was dealing with the maternal factors that affect progeny, as related by Wellington *(1965)*.

Later on, additional investigations were conducted to determine the elements which preclude the success of feeding by isolated sawfly larvae *(Henson 1965)*. He published the results of laboratory studies on the European pine sawfly, *Neodriprion sertifer* (Geoffroy), which indicated that isolated larvae have a low tolerance for withstanding even a slight variation from optimal conditions of food, temperature, and humidity. In the case of either group or individual rearing, brief storage of the eggs was important for eclosion and survival of early-instar larvae. Prolonged storage caused depletion of nutritional reserves.

Henson made a curious finding when he reared some isolated sawfly larvae for 4 days and then grouped them on fresh food. All these larvae died within 2 days, whereas a control reared as a group from the start survived. A test was established to learn

the population density which would have survival benefit to the sawfly, and it was learned that eight young larvae was optimum. Apparently, group feeding permits more effective feeding and allows the sawfly larvae to live, despite rearing conditions of low ambient humidities and partly desiccated food. During preliminary olfactometer studies, the presence of a feeding larva was more attractive to other larvae than whole or mashed foliage or mashed insects.

Henson concluded that in predicting population changes from generation to generation, not only would overwintering eggs have to be considered, but also the period over which they were deposited. Thus, if weather protracted the oviposition period, small scattered larval colonies with low environmental resistance might result.

The phenomenon of population density and its effects on individual or groups of Lepidoptera has received considerable attention in Japan. Hirata, at Hirosaki University, and Iwao, at Kyoto University, have conducted very interesting investigations into the mechanisms and results of variations in population density of several lepidopterous insects. Hirata's principal efforts are directed to population density studies of the cabbage armyworm, *Mamestra (Barathra) brassicae* (L.). The latest information I have shows his list of publications began with part one of a series in 1954 and ended with part eight in 1963. Naturally enough, the first paper concerned color and population density phenomena *(Hirata 1954)*. At high densities, 80 percent of the larvae became typically dark, and the remaining 20 percent kept their lighter colors. As population density increased, pupal weight decreased and the larval stage was shortened. By shortening time in the larval stage, more cabbageworms went into pupal diapause. In a later paper he reported no conspicuous effect of larval density on pupal diapause *(Hirata 1960)*. Hirata *(1963)* also observed that neither developmental velocity nor mortality was so strongly affected in crowded cultures of the cabbage armyworm as it was among solitary larvae. This is similar to the case of the armyworm, *Leucania separata* Walker, reported by Iwao *(1962)*. This noctuid had better survival on poor host material and resisted

starvation more in crowded rearings than it did in isolated rearings. Iwao *(1962)* investigated the reactions of nine species of Lepidoptera: *Parnara guttata* Bremer and Grey, a member of the family Hespelidae, and eight noctuids, *Leucania separata* Walker, *L. loreyi* Dopunchel, *L. placida* Butler, *Prodenia litura* F., *Trachea atriplicis* L., *Naranga aenescens* Moore, *Lithocodia stygia* Butler, and *Maliattha signifera* Walker. He concentrated his studies on *Leucania separata, L. loreyi,* and *Naranga aenescens* and reported on the other species in a preliminary way. All the species showed a decline of pupal weight as crowding increased. However, this was the only attribute common to all the test insects. As a result of his work, Iwao divided his insects into two categories. One, where he believed crowding lowered the metabolic activity, which increased mortality, prolonged development, and reduced fecundity. Into this class he put: *Parnara guttata, Naranga aenescens, Maliattha signifera, Leucania placida,* and possibly *L. loreyi.* The second group was categorized by increased metabolism when crowded, which accelerated development, voraciousness, and often darkened coloration. In this class were *Leucania separata, Prodenia litura,* and *Trachea atriplicis.* The first group of species live in a more solitary manner than the second group, which commonly occurs in outbreak numbers. The individual responses of the second group may give it better survival advantage under the stress of outbreak conditions. Members of the species *Leucania loreyi* and *L. placida* do not occur in outbreak, and they maintain themselves at lower population levels that do not fluctuate greatly. When crowded, they do not darken, and both larval and pupal periods are protracted.

Fecundity was affected variously with the different insect species. Significant differences were not apparent for the mean fecundity of *L. separata* or *L. loreyi* reared in isolation or in groups. Adults from isolated larval rearings of *N. aenescens* were significantly more fecund than adults from group-reared larvae. Pupal diapause also increased with population density in *N. aenescens.* In fact, under conditions that otherwise prevent diapause, this insect would diapause when reared in pairs.

Iwao *(1963)* showed that late-instar larvae of *L. separata* re-

cage—and fed ample fresh food daily. The mean time required for completing the hatch to adult stages was significantly greater for group-reared specimens of both sexes. Male pupal weight did not vary at the densities tested, but females from isolated rearings were significantly heavier than those in groups. Among females there was a direct correlation between pupal weight and fecundity (oviposition + retained eggs), and it followed that spanworms reared singly had significantly more eggs, on the average, than group-reared spanworms. Egg production is easily studied with the spanworm because freshly emerged females contain their full complement of developed eggs, and usually only a few undeveloped eggs. Conclusions reached in the laboratory have yet to be field tested. The payoff is in the field where the vagaries of weather, biological regulators, and host reactions enter the real test arena.

Following a 7-year study of the reaction of the pine looper, *Bupalus piniarius* L., to various field densities, Klomp *(1958)* concluded that the decrease in fecundity at high population levels did not regulate the pine looper population. At least this is the result of that study in that time and place. On the other hand, Tanner *(1966)* concluded that for herbivorous insects and some vertebrates, " . . . a population's growth rate is a decreasing function of population density, and that this will result in regulation of its numbers."

I have recounted some of the research carried out on the effects of population density on insect biology. It seems to me that much of this work is contributed only in bits and pieces. Many studies lack fecundity statistics, and there is little replication or continuity. Actually, a number of generations should be used—6 to 8 perhaps, based upon the number usually involved in the expression of resistance to insecticides. In some cases, developmental statistics are not identified by sex, so it is evident that this was not taken into account. Despite the failure to answer some important questions, the results point out that with many "outbreak-type" insect species, population density should be considered as an element of a population model. The work thus far has been the concern primarily of entomologists in the field of ecology. To gain penetrating un-

derstanding of the processes of biological change due to population density, physiologists and biochemists should be engaged in this endeavor.

Field study of population density and its effect on insect biology has been lacking in all but a few important cases. Understandably, this is very difficult research to conduct under field conditions. I believe the effort should be made, however, especially after an understanding of the phenomenon has been obtained in the laboratory.

With insect species such as the elm spanworm, which I have been studying lately, the opportunity to investigate its ecology in the field might come infrequently. Therefore, it's even more important to get observations and quantitative data into print so that future investigators will be aware of them. For example, the recent elm spanworm outbreak in the Southern Appalachians eroded after 2 or 3 years in a particular locale, while it prospered on new sites. The movement of the outbreak followed prevailing winds, but most certainly local populations were not completely removed from areas where they had developed to outbreak proportions.

In our present state of affairs, we have more questions than answers. Certainly, if we hope to construct meaningful population models our research will have to be strengthened by the inclusion of other disciplines, and we should develop a carefully structured team approach. Only in this way can we gain a true understanding of the forest ecosystem, our most important renewable natural resource, and develop ecologically sound ways of controlling the destructive insects that threaten it.

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