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OF NORTHERN AND WESTERN CORN ROOTWORM ADULTS
IN IOWA CORNFIELDS.

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Spatial dispersion and population estimation
of northern and western corn rootworm
adults in Iowa cornfields

by

Kevin Lloyd Steffey

A Dissertation Submitted to the
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INTRODUCTION

Justification for Study

Since the first reports of damage to corn roots by larvae of the northern corn rootworm, Diabrotica longicornis (Say), in 1874 (Riley 1880) and the western corn rootworm, D. virgifera LeConte, in 1909 (Gillette 1912), control of these pests has been a major concern of farmers throughout the Midwest. According to Turpin et al. (1972), Iowa corn yield losses caused by larval rootworm feeding have been as high as \$60 million annually. Taylor (1975) showed that the average per-acre returns above corn rootworm control costs in Illinois from 1971-1974 were \$183.49 when soil insecticides were always applied and \$187.85 when a scouting program was used. Wedberg and Black (1978) estimated that during 1977 in Illinois a return of \$29,372,930 over and above treatment costs, based on yield increase from the use of rootworm insecticides, was realized from control of soil insects. The severity of the problem and the economics involved, in conjunction with the continuing practice of planting corn following corn, have influenced many midwestern farmers to make planting-time insecticide applications as insurance against rootworm damage. These prophylactic treatments conflict directly with the first principle of pest detection stated in the National Academy of Sciences Publication (1969): "No control measures should be undertaken against a pest unless it is known that the pest is actually present." Failure to acknowledge this

principle can result in an unnecessary build-up of insecticide residues and the destruction of natural enemies. In addition, the economic implications of insecticide misuse are obvious.

The National Academy of Sciences Committee stated a second principle to be followed once the first principle is acknowledged: "No control measures should be undertaken unless it is known that the pest is present in sufficient numbers to cause economic loss." This principle requires knowledge of the economic threshold of the insect pest. Economic threshold may be defined as the population level of the pest that will cause sufficient damage to make control economically desirable. The development of an economic threshold is imperative for the proper utilization of a pest management program. Turpin (1974) stated that many of the economic thresholds developed for corn insects are "rules of thumb" and are not based on sound research data. Shaw et al. (1975) established a threshold for corn rootworm adults at 1 beetle/plant. They reported that if there were 1 or more beetles/plant, based on 2 plant counts taken during Aug., a soil insecticide should be used the next year if that field were to be planted to corn. Until recently, this "rule of thumb" has been used by most farmers and entomologists in the Midwest. Researchers in Illinois have since lowered the threshold to 0.5 beetle/plant (Illinois Coop. Ext. Service Circ. 899 1978). This threshold, however, is not supported by current research results.

Reliable sampling techniques and population estimates are required before economic thresholds can be established. For this

reason, methods of predicting populations of corn rootworms that would cause economic damage to corn have become major areas of study in recent years. Turpin et al. (1972) developed a corn rootworm damage predictive equation incorporating several edaphic and agronomic factors which affect rootworm populations. Mooney and Turpin (1976) formulated a model for predicting corn rootworm populations throughout a growing season. They concluded, however, that many of the relationships used in the model were hypothetical and that more basic research is necessary to validate the model. Tollefson (1975) examined the possibility of using adult corn rootworm population estimates as predictors of larval damage to corn. He found, through means of an intensive study, that adult corn rootworm population estimates were better predictors of subsequent larval damage than were corn rootworm egg population estimates. Four of the 6 adult-sampling techniques he employed showed promise as predictors of larval damage: (1) 10-plant count, (2) sticky ear of corn, (3) 10-min collection, and (4) 10-ear-tip collection.

To develop an efficient and reliable sampling program for estimating insect populations, the sampling technique must accord the highest accuracy commensurate with the amount of work expended. To optimize the precision and efficiency of a sampling program, it is necessary to gain knowledge of the insect's distribution and the cost of sampling. Therefore, the primary objective of this study was to conduct a sampling program for adult corn rootworms to determine the beetles' dispersion pattern and to examine variance

and cost components of the sampling program. From these data it is intended that a reliable rootworm beetle sampling program will be developed for use by Midwest farmers and insect scouts.

Literature Review

Corn rootworms

The northern corn rootworm was first described by Say (1824) from several specimens obtained in Colorado near the Rocky Mountains. The western corn rootworm was first described by LeConte (1868) from 2 specimens taken on wild gourd near Fort Wallace, Kansas. As previously stated, northern and western corn rootworm larvae were first reported as pests of corn by Riley (1880) and Gillette (1912), respectively. Since these early reports of damage to corn roots, much has been written about the rootworms' biology, ecology, economic importance, and control. An extensive bibliography of both northern and western corn rootworms was published by Luckmann et al. (1974). It covers all literature pertaining to corn rootworms, excluding the southern corn rootworm, from original descriptions through 1973. The bibliography was updated by Irwin in 1977. In addition, Chiang (1973) published a fairly complete review of the bionomics of northern and western corn rootworms. It is not the intent of this section of the literature review to reproduce and expand either the bibliography or review of bionomics. The literature reviewed will consist primarily of the impact of

larval damage, studies of adult behavior, and studies relating to sampling, population estimation, and economic thresholds.

Larval damage and insecticidal control Because both northern and western corn rootworms have only 1 generation/yr and their larvae feed almost exclusively on corn roots, crop rotation has been used as a control measure for many years. As the practice of growing continuous corn on the same land became more popular throughout the Corn Belt, both species of rootworms spread from their original limited distribution in the West until they are now distributed throughout most of the Midwest. With this wide distribution and an increase in continuous corn acreage, corn rootworms became perennial economic pests. As an alternative to crop rotation, soil insecticides applied before planting, at planting, and as cultivation-time treatments were tested for their efficacy in reducing larval rootworm populations and increasing yield. Hill et al. (1948) found that benzene hexachloride applied as both a pre-plant spray and side-dress treatment drastically reduced the number of rootworm larvae. In addition, root damage and lodging were almost eliminated and yield was increased in the treated corn by 15.4-27.4% over untreated corn, although the increase was not statistically significant. Muma et al. (1949) found that benzene hexachloride treatments to corn gave significant increases in yield that correlated with reductions of rootworm numbers and lodging. They pointed out, however, that yield differences were also confounded with differences in soil fertility. Cox and Lilly (1953)

were the first to report insecticide efficacy tests on corn rootworms in Iowa. They found that aldrin, dieldrin, chlordane, heptachlor, and benzene hexachloride, when applied as preplant broadcasts, bands with fertilizer, or sprays at planting, significantly reduced rootworm populations. These treatments also significantly reduced lodging in all experiments and increased yields in some cases. They concluded that chemical control of corn rootworms was both possible and practical.

As a result of the success of these early experiments, corn growers throughout the Midwest began applying chlorinated hydrocarbon insecticides to control rootworms in continuous corn. In many instances these treatments were made by farmers with limited knowledge of population numbers in the field. Widespread application of these insecticides led to the first report of possible resistance in rootworms to the chlorinated hydrocarbons (Weekman 1961). Ball and Weekman (1962) presented convincing evidence that rootworm beetles were developing resistance to aldrin and heptachlor in areas of Nebraska where these chemicals were used extensively. They found no resistance to an organophosphate, diazinon, in beetles tested from the same areas. Organophosphates and another new class of chemicals, carbamates, began to replace chlorinated hydrocarbons as rootworm insecticides. Although these chemicals were short-lived in the environment, they were extremely toxic and very effective in controlling rootworm larvae. Peters (1964, 1965) showed that organophosphate insecticides out-performed chlorinated hydrocarbons

in reducing rootworm damage in several tests conducted in Iowa during 1963 and 1964. As farmers started using the new classes of insecticides, they again relied on these treatments as insurance against rootworm damage. In recent years, an alarming number of farmers' reports of possible phosphate and carbamate insecticide failures have generated research to examine resistance to these chemical classes in rootworms.

Prophylactic or "insurance" applications of soil insecticides to control corn rootworm larvae have been the rule rather than the exception for many years throughout the Corn Belt. Peters (1975) stated that 58.9% of Iowa corn acres grown in 1968 were treated for soil insects. Turpin (1977) found from a survey of 635 Indiana farmers that 93% of corn growers using soil insecticides had applied them as insurance against insect damage. In both states most of the acreage treated was for rootworm control. Apple et al. (1977) reported some advantages in treating for rootworms vs. no treatment. In tests conducted between 1971-1974, researchers in Nebraska and Wisconsin found that rootworms reduced yields 31.7 and 10.7 bu/a, respectively. Missouri researchers reported a 23.8 bu/a loss caused by rootworms in early corn-planting trials. Other researchers conducting the same types of tests in the rest of the Corn Belt states, however, found no significant yield reduction as a result of rootworm damage. Taylor (1975) showed that per-acre returns above corn rootworm control costs averaged \$183.49 when insecticides were always applied; but he added that per-acre returns averaged \$187.85

when a scouting program was used to make treat or no-treat decisions. Scouting or sampling rootworm populations prior to applying insecticides is more sound economically than prophylactic treatments, and growers would benefit from knowledge of rootworm numbers in a cornfield. In light of current pest management philosophy, then, studies concerning corn rootworm sampling are necessary to optimize economic allocations for rootworm control.

Egg sampling and egg population thresholds For several years corn rootworm researchers have been evaluating and comparing sampling techniques to obtain population estimates for use in economic threshold studies and scouting programs. Eggs, larvae, and adults have been sampled by various techniques, but egg and adult sampling have been studied most frequently. Lawson and Weekman (1963) were the first to report a technique utilizing a soil corer for sampling rootworm eggs in cornfields. Gunderson (1964) proposed a uniform egg-sampling technique to be used by all researchers in the Corn Belt states. He summarized the use of a 4-in-diam golf-hole cutter to take five 10-core samples along a diagonal line across the field. He concluded that the average number of eggs/pt (the pt extracted from one 10-core sample) should be multiplied by 1 million to obtain number of eggs/a.

Egg-sampling techniques and methods of washing the soil to retain the eggs were modified and improved for use as a measure of egg density and a method of predicting larval damage. Lawson (1967) sampled 50 Nebraska cornfields and found a relationship between egg

numbers and subsequent larval infestation. Some insecticide applications, based solely on egg numbers, indicated positive effects. Lawson (1968) hypothesized that cornfields with an average of less than 5 eggs/sample need not be treated with a soil insecticide and those with more than 5/sample should be treated. This was the first published threshold for rootworm egg populations.

Pruess et al. (1968) analyzed the dispersion of rootworm eggs in cornfields and found them to be clumped, or aggregated. They stated that an aggregated dispersion pattern may have been the result of females laying eggs in clutches. Chiang (1968) presented a preliminary report of using the frequency index to estimate egg density. He found that the frequency index has a curvilinear relationship with mean density, and he added that density estimates could be determined from the number of samples containing eggs. Gerrard and Chiang (1970) elaborated on this technique and concluded that rootworm egg population densities could be determined without counting every individual sampled. A requirement for this method is a critical threshold density with a fairly high probability of attainment. Much preliminary data, however, would be necessary before a reliable threshold could be developed. Earlier research by Chiang et al. (1969) provided a method for converting numbers of northern corn rootworm eggs obtained by concentrated sampling to absolute density estimates. This, in turn, could aid in the establishment of an absolute threshold density.

Much of the more recent research concerning egg sampling and

egg density thresholds has been conducted by Illinois researchers. Howe and Shaw (1972) compared 3 egg-sampling techniques to determine relative populations in cornfields. They found that systematic random or completely random sampling using composites offered promise as population measures. But they, too, added that density thresholds should be established as a prerequisite. Shaw et al. (1975) established an egg density threshold of 5 million eggs/a. The threshold was determined after an intensive study of cornfields containing 1, 9, 13, and 18 million corn rootworm eggs/a. They suggested that a soil insecticide be applied to those fields containing 5 million or more eggs/a and added that the threshold was conservative.

Adult sampling and adult population thresholds Survey ento-
mologists have recognized the need for a standardized method of counting rootworm beetles in cornfields. Peters and Burkhardt (1961) conducted a survey in Kansas in 1960 to obtain data for a few corn insect pests. Northern and western corn rootworm beetle surveys were conducted during late Aug. and early Sept. Beetle numbers were recorded from four 25-plant counts in each field sampled. Chiang and Flaskerd (1965) compared 2 rootworm beetle-sampling techniques--timed collections and plant counts. They determined that a 10-plant count was less time-consuming than a 10-min collection and had the distinct advantage of approximating beetle numbers that could be converted easily to number of beetles/a. Per-acre density is invaluable for development of thresholds and predictions. Peters (1969) reported that Iowa insect scouts in

1968 sampled rootworm populations by counting beetles on 20 plants in each cornfield. From these counts he found that beetle numbers were significantly correlated with preceding larval numbers and root damage.

Luckmann et al. (1975) suggested sampling rootworm adults in sweet corn fields by cutting off 25-50 ear tips, placing them in plastic bags, freezing the contents to kill the beetles, and counting the beetles in the sample. They also stated that 25-50 plant counts would provide a representative sample of the field. Results from both methods could be converted to per-plant or per-acre densities.

Kaufmann (1966) introduced the idea of using sticky traps to catch rootworm adults. Traps have the advantage of eliminating variability due to sampler differences and reducing variability caused by environmental fluctuations. Tollefson et al. (1975) found that the optimum type of trap for catching beetles was cylindrical (omnidirectional), had a surface area of 946.5 cm^2 , and was painted yellow. Other adult-sampling techniques used by researchers but having no practicality for rootworm scouting programs included a large (3 ft x 3 ft x 6 ft) screen cage placed over several corn plants to collect emerging beetles (Branson and Ortman 1967) and a small emergence cage around an individual corn plant to trap emerging beetles (Musick and Fairchild 1970).

Tollefson (1975) compared 6 egg-sampling methods and 6 adult-sampling techniques as predictors of subsequent larval rootworm damage. He used a step-wise regression analysis procedure to

correlate root damage ratings with population estimates obtained from all 12 sampling techniques. He found that none of the egg-sampling techniques produced significant r^2 's. Four of the adult-sampling methods produced significant r^2 's when root damage was regressed on beetle numbers: (1) 10-plant count, (2) sticky ear of corn, (3) 10-min collection, and (4) 10-ear-tip collection. These 4 methods, then, showed promise as predictors of larval damage. He also found that the optimal time interval for obtaining a population estimate, using adult-sampling techniques that placed little emphasis on the ear of the corn plant, ranged from the second week in Aug. to the end of Aug. Finally, he determined that differences among investigators' experience did not influence the plant count or ear-tip collection at the sample size used, but it significantly affected the timed collection.

Lovett (1975) discussed adult corn rootworm surveys in Wisconsin. The scouting technique involved counting beetles on 25 plants along a systematic path through the cornfield. He found that predictions of the following year's larval population potential based on beetle numbers were generally accurate but lacked the desired precision.

Because rootworm adults can be counted before the next year's larval damage and because beetles can be sampled more easily than eggs, insect scouts and farmers rely on beetle numbers as an indication of the subsequent year's rootworm population. This has led many researchers to suggest thresholds which have not always been

based on sound results. These thresholds, however, have been and are useful for making treat or no-treat decisions. Turpin (1974) introduced the idea of a functional zero population threshold for rootworm adults. It is based on the fact that a large percentage of midwestern cornfields have very low or functional zero levels of beetle numbers. Those fields with functional zero populations would not require further sampling or insecticide treatments. Although this concept is based on sound reasoning, it has not yet been utilized by farmers or scouts in the Corn Belt.

Shaw et al. (1975) stated that the threshold level for corn rootworm adults should be 1 beetle/plant and that fields with an average of less than 1/plant need not be treated with a soil insecticide the following year. They suggested counting beetles on 20-25 plants in a field sometime during Aug. Luckmann et al. (1975) used the same threshold (1 beetle/plant) for scouting sweet corn. They suggested sampling 25-50 plants/field and making the counts during early morning or early evening. They stated that insecticide treatment decisions would be based on beetle numbers and planting and harvesting schedules.

Taylor (1975) developed a dynamic threshold which changes with the price of corn and cost of insecticides. He showed that the economic threshold was 1 beetle/plant when the price of corn was \$2.60/bu and 3 beetles/plant when the price of corn was \$1.70/bu. These thresholds are more acceptable along the current guidelines of pest management. More recently, Wedberg and Black (1978) have

lowered the economic threshold of corn rootworm adults to 0.5 beetle/plant. This was done, however, without any explanation for the change.

The recent interest in controlling rootworms by suppressing beetle numbers has led to further development of an economic threshold. The concept involves reducing the number of ovipositing females by means of aerial applications of insecticides to reduce the number of eggs laid in a cornfield. As a result, the next year's larval population would be low. Pruess et al. (1974), using adult emergence cages, determined that an economic threshold of 1 beetle/plant was a conservative estimate which was acceptable for adult control decisions. They also stated that at peak adult emergence, 1.6 beetles/plant was the minimum population that could be associated with damage. More recently it has been suggested that a first spray should be applied when rootworm numbers reach 0.6 beetle/ear zone and 10% of the population consists of gravid females (Puech 1977). A second spray should be applied if the population reaches 0.3 beetle/ear zone in the treated area. These economic thresholds, however, have not been supported by actual results.

Adult corn rootworm behavior Any study concerning adult corn rootworm sampling must be based on knowledge about beetle behavior. From the time northern and western corn rootworms were found to be corn pests, entomologists have examined various aspects of adult behavior including mating, oviposition, flight activity, dispersal or movement, and food preferences. Ball (1957) conducted

one of the earliest studies of western corn rootworm biology. From 3 seasons' data and observations he concluded that beetles first appeared in cornfields in early July and egg-laying began in early Aug. Both mating and egg-laying occurred into early Oct. or until the first killing frost. He also observed that beetles fed on corn leaf surfaces early in the season but moved to silks and tassels after these plant parts appeared. When silks began drying later in the season, the beetles fed on more succulent volunteer corn or the blooms of alfalfa and kochia. Patel (1965) determined that northern corn rootworm adult emergence began in late July in Wisconsin and peaked during the first 2 weeks of Aug. Using cylinder traps and 100-plant counts, Kaufmann (1966) studied several facets of adult northern and western corn rootworm behavior. He confirmed the previously mentioned emergence pattern and found that beetles were more active at night. He observed, however, that more western corn rootworms were found on corn plants during mid-day than at sunrise or sunset. Both species moved at low levels in the cornfields (91% of the westerns and 86% of the northernns below 5 ft), and more beetles moved along the rows rather than across the rows. Cates (1968) reported that male western corn rootworms began emerging before females and that mating was initiated upon female emergence. He noted that peak mating occurred during the morning and evening when beetles were more active. Witkowski et al. (1975) also found that western corn rootworm flight activity peaked during the 2-3 h after sunrise and before sunset. These peaks corresponded with

temperatures ranging between 22.2-27.0°C. Using vertical sticky traps, the researchers confirmed Kaufmann's (1966) results: most beetles flew below 182.88 cm within a cornfield. They added that more females than males were collected between 182.88-304.80 cm.

Cinereski and Chiang (1968) examined pollen grains in the gut contents of northern corn rootworm adults to determine movements of beetles into and out of cornfields. These movements were related to ovarian development in female beetles. They found that beetles fed on Graminae pollen (corn and grassy weeds) within the cornfield and Compositae, Leguminosae, and Cucurbitaceae pollen outside the cornfield. After examining ovarian development, the researchers concluded that during the early part of the season beetles fed mainly in cornfields. When food became more scarce later in the season, beetles made feeding trips into blooming crops surrounding the cornfield. Females with a complement of ripe eggs were attracted to cornfields for oviposition and left the field only for brief feeding excursions. Ludwig and Hill (1975) also studied gut contents of rootworm adults and found varying proportions of corn leaf tissue, corn pollen, corn silks, weed pollen, and fungal spores. Northern corn rootworms fed more often on pollen other than corn than did western corn rootworms. In addition, male beetle gut contents indicated that males were more mobile within cornfields than were females. Shaw et al. (1978) confirmed that rootworm adults fly into surrounding crops from cornfields. They found that both northern and western corn rootworms oviposited in soybeans, although most of

the eggs were found at the bases of volunteer corn plants. Very few rootworm eggs were collected from weed-free, or "clean," soybean fields.

Spatial dispersion and sample size

The literature concerning insect population sampling is extensive and I will summarize the information. Much of the literature deals with specific aspects of sampling, but there are numerous examples of how sampling theory and techniques have been applied to insect pest problems. Among the best examples is Morris' (1955) comprehensive sampling program for the spruce budworm in Canada. He examined all aspects of population sampling theory and techniques including objectives, timing, mechanics, sample universe, sample unit, transformation of data, and optimum sample size. He developed chronological steps for establishing a sampling program, and these steps are still followed by present-day researchers. Southwood (1966), utilizing many insect examples, explained in even greater detail the concepts and techniques of population sampling. Both he and Morris discussed the importance of an effective sampling program for the study of insect pest ecology. Morris (1960), in his review of insect population sampling, further stated that basic data required for a sampling program include the frequency distribution, major sources of variation, and optimum size of the sample unit. This information is a prerequisite for the development of pest management systems which rely on sampling. This section of the literature review, therefore,

will include specific material relating to my study and examples of sampling programs developed for other insect pests.

Spatial dispersion Iwao (1970) listed 2 reasons why the analysis of spatial dispersion is important in animal population ecology:

- (1) "The spatial distribution pattern affects the precision of the estimation of population parameters in sampling surveys, and also the method of analysis of the data."
- (2) "The spatial distribution itself is an important structure of the population."

Sevacherian and Stern (1972) stated that knowledge of an organism's spatial dispersion pattern is a primary requisite to understand better the organism and its ecosystem. A species' spatial pattern is the result of the interaction of complex biological and environmental factors in a given habitat, and it reflects the influence of the factors on the organism's mode of life. As previously stated, this knowledge is essential for the development of prediction equations and pest management programs which rely on sampling. Effective sampling programs and experimental design cannot be devised until the spatial pattern is known.

Much data for spatial dispersion studies have been collected in the form of frequency distributions, i.e., the number of sample units containing 0, 1, 2, 3, . . . n individuals. Wadley (1950) stated that frequency distributions of insect counts are important both biologically and statistically. To describe the actual spatial dispersion, a theoretical mathematical distribution is fit to the

observed frequency distribution. The goodness of fit between these 2 distributions, observed and expected, indicates the spatial pattern of the organisms in nature. Waters (1959) listed the theoretical distributions that are commonly applied to insect counts: Poisson, normal, positive binomial, negative binomial, Neyman type A, logarithmic, and lognormal. These distributions, their theory and use, are explained in detail by Neyman (1939), Fisher et al. (1943), Anscombe (1948), Anscombe (1950), and Iwao (1970). Other mathematical distributions have been described by various authors: Neyman types B and C (Neyman 1939), Thomas' double Poisson (Thomas 1949), Pólya-Aeppli (Anscombe 1950), and Poisson-binomial (McGuire et al. 1957). These theoretical distributions cover the range of the 3 general types of distribution found in animal populations: random, contagious or aggregated, and uniform. Katti (1966) stated that 1 of 5 discrete distributions (negative binomial, Neyman type A, Poisson with zeros, logarithmic with zeros, and Poisson-binomial) would fit a set of discrete data about as well as any distribution. Gates and Ethridge (1972) developed a FORTRAN program to fit 8 of the preceding distributions to a set of observed discrete counts.

Many authors have shown that insect counts often include an excess of zeros and large numbers. This condition indicates a departure from random distribution. In most circumstances, insects seldom are distributed randomly in a natural habitat. This has been well documented in the literature. Most insect species are distributed in a contagious or aggregated pattern in a given habitat.

Several researchers have reported that the negative binomial distribution fits the observed distribution of many insect pest species. Anscombe (1949) demonstrated this with potato aphid egg counts but stated that there were some contradictions to his hypothesis. Bliss and Fisher (1953) fitted the negative binomial distribution to counts of European red mites in apple trees. Their detailed computations revealed a close fit between the observed and expected counts of the negative binomial. Bliss and Owen (1958) found that counts of Colorado potato beetles, wireworms, and leather-jackets conformed well to a negative binomial distribution with a common k (a parameter of the negative binomial). They stated that population means of more than 1 distribution could be compared more easily and directly if a common k were used in the computations. More recently, Sevacherian and Stern (1972) fitted the negative binomial distribution to counts of both nymphal and adult Lygus bugs in cotton fields. They found, however, that their counts were also fit by Thomas' double Poisson, Neyman type A, and Pólya-Aeppli distributions. McGuire et al. (1957) had found that insect counts could be fit by more than 1 distribution. Their counts of European corn borer larvae were fit by the Poisson-binomial and negative binomial, depending on the type of sampling unit used to obtain the counts.

Contagious distributions include both biological and statistical, or artificial, components. The latter reflect the effects of the nature of sampling and size of the sample unit on the final determination of the type of distribution. The truly biological

components of aggregation, listed by Waters (1959), are: (1) responses to physical factors of the environment, (2) responses to the host plant, (3) reproduction behavior, (4) mutual attraction with other individuals of the same species, and (5) interactions with other organisms. These biological components and the statistical components must be separated to determine the actual spatial dispersion of an insect species. Furthermore, the negative binomial distribution can arise in at least 5 different ways (Waters and Henson 1959): (1) heterogeneity in the probability of occurrence, (2) true contagion, (3) compounding of Poisson and logarithmic distributions, (4) birth-death-immigration processes, and (5) inverse binomial sampling. These conditions suggest that care must be taken when drawing conclusions from population counts fit by a theoretical distribution.

Iwao (1970) reported that an observed distribution can be approximated by more than 1 mathematical model and that the method of fitting models may alter the results. He referred to the McGuire et al. (1957) study in which European corn borer larval counts were fit by different mathematical distributions when a complete census was compared with population sampling. Iwao concluded that: (1) the same set of observed counts can be described by more than 1 mathematical model; (2) the distribution of 1 species may vary from time to time so that different mathematical models fit on different occasions; and (3) a particular form of mathematical distribution can be derived from different sets of underlying assumptions.

These drawbacks of fitting theoretical distributions to observed counts suggest that limited information can be obtained by this method. Knowledge of the theoretical distribution, however, is valuable for developing a sequential sampling plan and for use in certain equations for determining optimum sample size.

An easier method of analyzing animal dispersion patterns is to utilize 1 or more dispersion indices. These indices are simple mathematical expressions which include statistical parameters obtained from sampling the population. Furthermore, these indices do not assume any underlying mathematical distribution. The simplest of these indices is the variance/mean (s^2/m) ratio. When $s^2 = m$, a random distribution is indicated. Aggregation, or contagiousness, is indicated when $s^2 > m$; and the dispersion is regular, or uniform, when $s^2 < m$. The s^2/m ratio enables a researcher to form a tentative opinion about an organism's spatial dispersion before he initiates a more extensive sampling program. This information often can be obtained from preliminary sampling data.

One of the first indices introduced was Taylor's power law (Taylor 1961). Taylor examined observed counts of 24 different organisms and found that sample variance is proportional to a fractional power of the mean: $s^2 = am^b$. He stated that a is largely a sampling or computing factor, whereas b is a true index of aggregation. When $b = 1$, random dispersion is indicated; when $b > 1$, aggregated dispersion is indicated. Uniform dispersion is suggested by $b < 1$. Of the 24 sets of counts he used as examples,

23 exhibited b-values greater than 1. Taylor et al. (1978) applied the power law to 156 sets of biological data which included 3,840 samples and 207,055 sample units. Many different taxa, spatial scales, and sampling methods were included in the analyses. Their purpose for the study was to compare Taylor's power law with Iwao's regression (to be discussed), the negative binomial with a common k, and the Poisson distribution. Their conclusions were: (1) the power law is a better measure of dispersion, in a biological sense, than the other 3 measures; (2) the negative binomial with a common k has no consistent biological significance over a range of densities; (3) spatial behavior is density-dependent; and (4) true randomness is biologically rare.

Morisita (1962) proposed the I_{δ} -index as a measure of dispersion of organisms in a population: $I_{\delta} = n(\sum x^2 - \sum x) / ((\sum x)^2 - \sum x)$. Similar to other indices, when $I_{\delta} = 1$, the dispersion described is random; when $I_{\delta} > 1$, the dispersion is aggregated. Uniform dispersion is indicated when $I_{\delta} < 1$. Analyzing another researcher's counts of eggs, larvae, and pupae of the cabbage butterfly, Morisita found that his index was not dependent on population mean density. Morisita (1964) further described the index as a probability ratio (probability of finding 1 individual with another : probability of finding 1 individual alone). The index could then be utilized to determine the degree of nonrandomness. Smith-Gill (1975) developed another index, I_p , which is simply a standardized I_{δ} -index. The standardized index ranges from -1.0 to +1.0 with 95% confidence

limits at +0.5 and -0.5. Random distributions give index values of 0, and aggregated distributions give values greater than 0. All I_g -index values are transformed to common scale so that indices derived from different densities can be compared. Smith-Gill used the I_p -index to compare chromatophore patterns in the leopard frog. She concluded that the results of her analysis were biologically significant.

Green (1966) compared several indices of nonrandomness and developed his own dispersion coefficient, C_x : $C_x = ((s^2/m) - 1) / ((\Sigma x) - 1)$. He stated that this index should be used to analyze positively contagious, or aggregated, distributions. When C_x and $(s^2/m) - 1$ are used to measure positive and negative, or uniform, contagion, respectively, index values range from -1.0 to +1.0. An index value of 0 indicates random distribution. Green further stated that variations in sample number, sample size, density, or total number of individuals/sample would not alter the coefficient value obtained for a population. He provided tests of significance for his proposed index.

Iwao (1968) introduced a regression method for measuring spatial dispersion in animal populations. He utilized a parameter, mean crowding, proposed by Lloyd (1967): $m^* = m + ((s^2/m) - 1)$. Mean crowding is defined as the mean number of other individuals per individual. Iwao found that when mean crowding was regressed on mean density, there was a direct linear relationship. Regression parameters a , the intercept, and b , the slope, are both

indices of dispersion. He called the a -value an index of basic contagion, an indication that 1 individual would be expected to live with a other individuals in the same quadrat. The b -value represents the density-contagiousness coefficient, the manner in which individuals or groups of individuals distribute themselves in their habitat. When these values were compared with different distributions, random distribution was suggested by $a = 0$ and $b = 1$, and aggregated distributions were indicated by $a \geq 0$ and $b > 1$. Iwao stated that since both indices describe different aspects of dispersion of a species, his regression technique is biologically significant. Iwao and Kuno (1968) used this regression method to develop estimations of sample size and data transformations for analysis of variance. Iwao (1977) utilized a similar index, inter-species mean crowding devised by Lloyd (1967), to examine spatial association between 2 species.

Considering all the available methods for analyzing spatial dispersion in populations, it is not surprising that there are several reviews or critiques concerning their use. In almost all these reviews, several methods are examined, 1 method is preferred above the others, and the rest are criticized in regard to their statistical validity or biological significance. In all these reviews, the use of the negative binomial distribution with a common k , or any other mathematical distribution, to fit observed data is questioned in regard to biological significance. Iwao (1970) summarized the use of several mathematical distributions and dispersion

indices. He concluded that his own regression method was the best way to measure spatial dispersion and that his method solved the problems of selecting sample size and transformations. Iwao and Kuno (1971) merely repeated Iwao's conclusions but elaborated on the use of the regression method to describe density-independent and density-dependent processes in a population. Taylor et al. (1978) stated that the power law was a better, more descriptive measure of spatial dispersion. Both Iwao and Taylor supported their respective indices with numerous specific examples, and both have valid arguments; but each has a stake in his own dispersion index. Patil and Stiteler (1974) reviewed the s^2/m ratio, negative binomial parameter k , Morisita's I_δ -index, Lloyd's mean crowding, and Iwao's regression method. They concluded that many of the dispersion indices were essentially equivalent to the s^2/m ratio.

Myers (1978) employed a simulation model of egg dispersions to test 7 dispersion indices: (1) s^2/m ratio, (2) Green's coefficient (C_x), (3) Morisita's index (I_δ), (4) standardized Morisita's index (I_p), (5) negative binomial k , (6) mean crowding index (\bar{m}^*), and (7) patchiness index (\bar{m}^*/m). She correlated each index with the population mean and a clumping variable which she developed for use in the model. She found that C_x and I_p were independent of population density, and s^2/m was only weakly correlated with density. Variance/mean ratio had the highest correlation with the clumping variable, and \bar{m}^* had the lowest. Based on her results, she concluded that C_x , I_p , and s^2/m were the best methods to use when analyzing

changes in dispersion of an organism with changes in density. One of her concluding statements sums up the usefulness of dispersion indices: "If all measures agree then a strong statement can be made about dispersion." Although she was referring to only 3 indices, the statement holds true for all measures.

Studies concerning spatial patterns of insect pests are well-represented in the literature. The studies include pests of pasture, row crops, truck crops, and forests, and they comprise many geographical locations in the United States and Canada. A review of all these would prove repetitive, so I have selected a few studies which reflect the objectives of many and point out how spatial patterns may vary according to sampling techniques, life stages of the pest, and time. McGuire et al. (1957) measured the spatial dispersion of European corn borer larvae. In 1 of the study areas, all 3,205 plants were dissected and the larvae were counted to obtain a complete census. The researchers sampled 3 other areas by dissecting plants and counting larvae from randomly selected sites. They fit the negative binomial, Neyman type A, and Poisson-binomial distributions to 9 frequency distributions obtained from observed counts. The complete census counts were fit best by the Poisson-binomial, but the random sample counts were fit best by the negative binomial. Both of these distributions indicate aggregation.

Mukerji and Harcourt (1970) utilized 2 mathematical distributions (Poisson and negative binomial) and 2 indices (s^2/m ratio and Taylor's power law) to examine the spatial patterns of immature

stages of the cabbage maggot. Their field plots were divided into 16 subplots, and they counted the different stages on 1-6 randomly selected plants/subplot. The negative binomial provided the best fit in 177 of 190 counts of all life stages sampled. The Poisson fit in only 10 cases. Both indices suggested an aggregated spatial pattern for all stages.

Sevacherian and Stern (1972) conducted an intensive sampling program for Lygus bug nymphs and adults. They fitted 5 distributions (Poisson, Thomas' double Poisson, Neyman type A, Pólya-Aeppli, and negative binomial) to their observed counts and found that the negative binomial provided the best fit. The other contagious distributions provided better fits than did the Poisson, or random, distribution. They also used $(s^2/m)-1$, closely related to the s^2/m ratio, to show that aggregation patterns remained relatively unchanged during the day.

Latheef and Pass (1974) analyzed alfalfa weevil dispersion in alfalfa fields by means of Iwao's regression and Taylor's power law. They randomly sampled for eggs, larvae, and pupae in each of 16 subplots in 3 fields. Both indices indicated aggregation of eggs and larvae at low densities but randomness at high density. The distribution of pupae did not differ from random.

Doane (1977) used 5 different methods to measure the dispersion of 2 wireworm species. The eggs of both species were highly aggregated, but larval dispersion became more random as larval size increased. Adult dispersion was random in 15 of 16 cases when soil

cores were used as the sampling technique; but adult counts obtained from emergence cage samples were fit by contagious distributions.

Christensen et al. (1977) showed that Egyptian alfalfa weevil larvae were basically aggregated, but their dispersion differed among instars. Using Iwao's regression method to measure changes in dispersion over time, the researchers found that the larvae became less aggregated as time progressed.

Sample size Pest management programs today rely on sampling or scouting plans as the means for obtaining information about pest numbers and behavior. This information is used in decision-making processes concerning the need and timing of control measures. An effective sampling plan must provide a reliable estimate of pest population size or density. Among the first questions one must ask, then, is: "How large a sample is needed?"

Optimum sample size has been discussed by many authors in biological literature. The purpose of an optimum sample size is 2-fold: estimate population density with a desired precision and optimize resource allocation. Some information concerning variance of the population is necessary before a sample size can be determined. This can often be accomplished by examination of preliminary sampling data. In addition, limited personnel, time, equipment, or funds will affect the selection of sample size. Morris (1955), in his list of 6 criteria for the sample unit, stated that the sample unit should be of a size that provides a balance between variance and costs.

Methods of determining sample size have been discussed in detail by Oakland (1953), Morris (1955), Cochran (1963), Southwood (1966), and Eberhardt (1978).

Oakland (1953) suggested that questions concerning variability, precision, and accuracy of population estimates should be answered before the problem of sample size can be solved. He proposed the formula, $n = 2t^2V/D^2$, to approximate sample size. In this formula, D represents precision (within a % of the mean), t is the normal deviate corresponding to the level of significance, and V is sample variance, often obtained from an analysis of variance. In addition, he stated that when several factors contribute to total variance, the variance components should be obtained to separate their contributions. He ran an analysis of variance on transformed egg-count data to illustrate this method. Using expected mean squares, he showed what percentage of the total variance each of the components accounted for. He reduced the standard error, thus increasing precision, by increasing the number of samples of the components accounting for the greatest variability.

Morris (1955) discussed in great detail the selection of optimum sample size for the spruce budworm. He examined variance components of tree sampling and found that intertree variance was greater than both intercluster or intratree variance. With this knowledge and an extensive explanation of cost factors, he established a sample size that would give the desired level of precision. Southwood (1966) further stated the necessity of using variance and

cost factors in determination of optimum sample size. He added, however, that since populations are always fluctuating, a rigid determination of optimum sample size should not be stressed. Sample size should be flexible with changing costs and population variation. Southwood listed 4 equations for finding sample size, 1 of which is commonly used: $N = (t_s/D\bar{x})^2$. One of the equations included the parameter k of the negative binomial distribution.

Karandinos (1976) defined optimum sample size as the smallest sample size that would assure the desired reliability of the population estimate. He reviewed several formulae for obtaining optimum sample size and separated these formulae on the basis of definition of reliability. He defined reliability in terms of the coefficient of variability (CV) and in terms of probabilistic statements. He found that when optimum sample size was based on the CV or on a proportion of the mean, sample size decreased as the mean increased. When reliability of the estimate was defined in terms of a fixed positive number, optimum sample size increased as the mean increased. He presented a table of 12 formulae for determining sample size, the different formulae based on 4 underlying parent distributions and 3 definitions of an estimate's reliability.

Eberhardt (1978) stated that selection of sample size depends on the objectives of the study, and he listed and explained 4 broad classes of objectives: (1) population management, (2) population analysis, (3) hypothesis testing, and (4) monitoring populations. Pest management programs are usually developed around the first

objective concerned primarily with population abundance. Eberhardt explained in detail how the objectives affect precision of sample size estimates and discussed sampling methods available for each objective. In his discussion on methods for estimating sample size, he relied heavily on the coefficient of variation (CV) and cited numerous biological examples to support his equations.

The literature contains many examples of determining optimum sample size for crop pest insects. Each involves population surveys or sampling programs which provide the necessary data for estimating variance. Bancroft and Brindley (1958) analyzed European corn borer data from several years' surveys to determine optimum sample size. From the nested design of the surveys, they calculated estimates of variance for the interfield, intersite, and interplant components. Interplant variance contributed significantly to the overall variance. They added a cost factor to determine optimum allocation of resources and suggested that 5 plants at 1 site in each of 147 fields should be dissected to estimate larval corn borer populations in Iowa. Harcourt (1961) used much the same procedure to design a sampling plan for diamondback moths in cabbage. He also found that variation between plant counts constituted the major source of population variation. Other good examples of sampling plans and optimum sample sizes include Stephen and Taha (1976), Ng et al. (1977), Doane (1977), and Sawyer and Haynes (1978). Each of these references provides a somewhat different method of obtaining an optimum sample size for an insect pest.

Capture-recapture

Artificial marking of animals in a population can be utilized to obtain information about a species' movement, migration, mortality, and abundance. One such use of this technique involves the capture, mark, and release of some individuals in a population. The number of recaptured individuals can provide data for an estimation of population size. The reliability of the estimate depends on how a specific capture-recapture experiment is designed and conducted. The data can be analyzed in numerous ways, but there are basic assumptions underlying all methods of capture-recapture analysis:

- (1) Marked animals are not affected by marking, and the marks are durable.
- (2) Marked animals become distributed completely throughout the population.
- (3) All individuals in the population, including marked individuals, are available for capture, i.e., the population is sampled randomly.
- (4) The population is closed. If the population is not closed, birth rates, death rates, immigration, and emigration can be measured or are in balance (birth rate + immigration = death rate + emigration).

These assumptions must be understood before one can interpret correctly the results of the study.

The first assumption can often be met by conducting laboratory studies concerning the effect of marking on a species' behavior and longevity. Marking methods available for insect studies have been discussed in detail by Gangwere et al. (1964) and Southwood (1966). Both listed advantages and disadvantages of several marking methods

and their applications and reported basic criteria for selection of a marking technique. The other 3 assumptions have been examined by many workers. Several techniques for estimating population size from capture-recapture data have been developed as a result of manipulation of these assumptions. MacLeod (1958) reviewed some of the early techniques and used them to analyze his own blow fly data. Southwood (1966) and Cormack (1968) discussed some of the more recent techniques and provided the detailed statistics needed for analysis. Cormack's review is an excellent discussion of the history of capture-recapture methods and the underlying statistical theory and biological assumptions.

The basic principle of capture-recapture studies is simple: the proportion of recaptured individuals (r) to the total number of individuals in the second sample (n) is equal to the proportion of initially marked individuals (a) to the total population (P). From the expression $P/a = n/r$, the absolute population estimate becomes $P = an/r$, often referred to as the Lincoln Index. The principle was developed by 2 men, Petersen in 1896 and Lincoln in 1930, working independently with different organisms (see LeCren 1965). As mentioned previously, however, the principle is valid only when all assumptions are met. If births, deaths, immigration, and emigration are negligible over a short period of time between initial capture and subsequent recapture, the simple Lincoln Index, modified for bias, can be used to estimate population size. If one wishes to measure temporal changes in a population, the study should span a

longer time and the behavior of the population can be represented by a statistical model based on certain assumptions. These models account for changes in the population caused by birth rate, death rate, and migration.

Early models assumed a deterministic death rate, i.e., death rate constant over time. All were merely extensions of the Lincoln Index, but they allowed for mortality and, in some instances, dilution (births and immigration). Jackson (1939) developed 2 techniques for estimating tsetse fly population size. He used what he termed the "positive" method for analyzing data from 1 initial release and a series of recoveries, or recaptures; and he used the "negative" method for a series of releases and 1 recovery. Both methods allowed for dilution and mortality. Dowdeswell et al. (1940), working with Lepidoptera populations, grouped and displayed their observations in a triangular "trellis diagram." Fisher and Ford (1947) further explained this method and provided estimates of survival rate. Survival rate was based on the number of theoretical survivors and was a fixed percentage/day. They also estimated population size but failed to determine the precision of their estimates. Bailey's (1951) triple-catch technique was a combination of Jackson's and Fisher's methods. Bailey used data from 2 releases and 1 recovery to introduce maximum likelihood estimates of population size, birth rate, and death rate. He also showed how to calculate variances for these estimates.

All the previously mentioned techniques were concerned with

serial releases and recoveries of individuals to reduce the significance of large experimental error. All yielded estimates of population size, accessions, and loss rate. Differences among the techniques were caused by the different ways data were grouped and by the methods of calculating the estimates. MacLeod (1958) discussed Jackson's, Fisher's, and Bailey's methods and used each to analyze his own data obtained from serial releases and recoveries of blow flies. He found that all 3 techniques produced biased population estimates because they could not account for zero recaptures. He modified these methods and produced a population estimate and its variance from data pooled over several releases and recoveries. His estimates, however, were also biased, and he suggested the development of a stochastic model for capture-recapture studies.

Since there is natural variability among individuals in a population with respect to birth rate, death rate, and migration, constant expressions for these processes often do not describe population dynamics adequately. Probabilistic, or stochastic, models were developed by several authors to explain capture-recapture results. Leslie (1952) proposed semi-probabilistic models for 3 different combinations of population processes: (1) death rate constant, dilution occurs; (2) death rate changing, no dilution; and (3) death rate changing, dilution occurs. He used maximum likelihood techniques to estimate death rate, population size, and dilution rate and variance for each estimate. Darroch (1959) examined the same 3 combinations and developed a wholly stochastic model for estimating

population size, survival, and number of immigrants. After presenting an extensive deterministic model based on constant survival (Jolly 1963), Jolly (1965) derived a general and simple stochastic model for use in capture-recapture studies. He included the probabilities of an individual being captured, being marked and released again, and leaving the population (death or emigration). Immigration into the population affected only unmarked individuals. He showed calculations of simple estimates of parameters of a population subject to death and immigration. He also provided estimates of variances and covariances of the parameters. He finally demonstrated the applicability of his model and estimates with an example from research conducted on black-kneed capsids in an apple orchard.

Cormack (1968) stated that the use of deterministic models has been superseded by the more simple and realistic stochastic models of Jolly (1965) and Seber (1965). These latter 2 models are so closely associated that Cormack proposed the term "Jolly-Seber method." He pointed out, however, that estimates and variances of estimates are wholly dependent on the validity of the model. He further suggested the use of a modified Lincoln Index for very short-term (essentially closed populations) studies and the Jolly-Seber model for long-term (temporal changes in population) studies.

Objectives

1. Determine the spatial dispersion pattern for northern and western corn rootworm adults in Iowa cornfields.
2. Examine costs and variance components of 3 adult corn rootworm sampling techniques to determine an optimum sample size for each.
3. Develop a reliable sampling plan, utilizing the best adult-sampling technique, for use by farmers and insect scouts in the Midwest.
4. Obtain an absolute population estimate of adult corn rootworms by means of capture-mark-release-recapture techniques.

PART I. SPATIAL DISPERSION PATTERNS OF NORTHERN
AND WESTERN CORN ROOTWORM ADULTS
IN IOWA CORNFIELDS

Introduction

Larvae of the northern corn rootworm (NCR), Diabrotica longicornis (Say), and western corn rootworm (WCR), D. virgifera LeConte, are perennial pests of continuous corn throughout the Midwest. Both species are univoltine and overwinter as eggs in the soil. Larvae feed on corn roots during June and July. One objective of current corn pest management programs is to predict larval damage before it occurs. Insecticidal control decisions are made on the basis of these predictions. Since rootworm adults can be counted easily in a cornfield during Aug., farmers and insect scouts rely on beetle numbers as an indication of the next year's rootworm population. Several field-scouting methods for rootworm beetles have been suggested (Peters 1969, Lovett 1975, Shaw et al. 1975). A standardized scouting procedure is lacking, however, because there is very little information available about how the beetles' population dynamics affect sampling.

Knowledge of an insect's spatial dispersion is fundamental for the development of a reliable sampling program. This has been the subject of numerous studies of insect pest population ecology (Sevacherian and Stern 1972, Ng et al. 1977, Christensen et al. 1977). One frequently used method of measuring dispersion is to fit a

mathematical distribution to observed counts arranged as a frequency distribution. Iwao (1970) reported, however, that the results of fitting theoretical distributions, such as Poisson and negative binomial, provide limited biological information. He pointed out that 1 set of observed counts can be fit by more than 1 mathematical model and that different models fit as the dispersion of a species varies with time.

Several authors have proposed indices of dispersion intended to describe biological effects separate from statistical factors. The variance/mean ratio is one such index which explains the relationship between population variance (s^2) and mean (m) in terms of underdispersion ($s^2 < m$), randomness ($s^2 = m$), and overdispersion ($s^2 > m$). Many of the indices discussed in the literature are essentially equivalent to the variance/mean ratio (Patil and Stiteler 1974).

Taylor (1961) reported that for many organisms sample variance is proportional to a fractional power of the mean: $s^2 = am^b$. He stated that a is largely a sampling or computing factor, whereas b is a true index of aggregation and is species specific. Uniform, random, and aggregated dispersions are described, respectively, by $b < 1$, $b = 1$, and $b > 1$. Green (1966) developed a dispersion coefficient, C_x , to analyze aggregated, or contagious, distributions and suggested using $(s^2/m)-1$ to analyze uniform distributions when $s^2/m < 1$. C_x -values range from 0, random dispersion, to 1, maximum positive contagion; $(s^2/m)-1$ ranges from -1, maximum

negative contagion, to 0.

Another index frequently used in insect population studies is derived from the regression of mean crowding, \bar{m}^* , on mean density, \bar{m} (Iwao 1968). Mean crowding was defined by Lloyd (1967) as the mean number of individuals found with another individual. The relationship between \bar{m}^* and \bar{m} is expressed as: $\bar{m}^* = a + b\bar{m}$. The intercept, a , is an index of basic contagion, and the slope, b , describes the manner in which individuals or groups of individuals are distributed in the habitat. Random dispersion is described by $a = 0$ and $b = 1$, and aggregated patterns are indicated by $a > 0$ and $b = 1$, or $a \geq 0$ and $b > 1$.

Morisita (1962) proposed the I_δ -index to measure dispersion of individuals in a population. $I_\delta = 1$ when dispersion is random; and $I_\delta > 1$ when dispersion is aggregated. Uniform dispersion is indicated by $I_\delta < 1$. Smith-Gill (1975) proposed an index, I_p , which is simply a standardized I_δ -index. When applied to observed counts, the index ranges from -1.0 to +1.0 with 95% confidence limits at -0.5 and +0.5. I_p -values greater than 0.5 reveal significant aggregation; and I_p -values less than -0.5 show significant uniformity. Random dispersion is indicated by $I_p = 0$.

Myers (1978) tested some of the preceding indices on simulated egg samples with various densities and dispersion patterns. She recommended s^2/\bar{m} , C_x , and I_p for measuring dispersion of dynamic populations because their values were not significantly affected by mean density.

This study was designed to measure the spatial dispersion of NCR and WCR adults. All the aforementioned indices were applied to beetle counts obtained by 3 adult corn rootworm sampling techniques.

Materials and Methods

Field-sampling techniques

Data were collected during Aug., 1976 and 1977, from 59 corn-fields in Iowa. Fields ranged in size from 8.09 to 80.94 ha. NCR and WCR adults were sampled by 3 techniques: 10-plant counts, 10-ear counts, and yellow, cylindrical sticky traps. All 3 methods can be used to predict the next year's larval damage, but plant and ear counts are more reliable (Tollefson 1975). Sticky trap counts, however, are less affected by environmental fluctuations and differences among investigators. Plant and ear counts were selected because they are commonly used to sample rootworm beetles.

The 10-plant count consisted of counting beetles on 10 randomly selected corn plants within a small area. Samplers approached each plant cautiously to avoid disturbing nearby plants. The 10-ear count was a subsample of the 10-plant count. Beetles were counted on the 10 ears, including the silks and ear-leaf sheaths, of plants making up the 10-plant count. Sticky traps were 0.95=1 (1 qt) Sealright[®] ice-cream cartons painted yellow and coated with Tack-Trap[®]. Each trap was placed over a cornstalk chopped off at approx. 30 cm above ground level. Traps remained in a field for 1 wk and then were retrieved and returned to the lab for recording beetle

numbers. Numbers of NCR and WCR were recorded separately for each single-plant and single-ear count and sticky trap.

Each of the 59 fields, 32 in 1976 and 27 in 1977, was divided into quadrants of equal size. Each quadrant was further divided into 4 equal plots. Plot size varied with field size, e.g., an 8.16-ha field contained sixteen 0.51-ha plots and an 80.94-ha field contained sixteen 5.06-ha plots. Four investigators were randomly assigned to the 4 plots in a quadrant so that each investigator sampled in 1 plot/quadrant. Sampling sites were arranged in a systematic pattern in the field, 1 site in the center of each plot. The 3 sampling methods were employed at all 16 sites in each field.

All fields but 1 were sampled between 0600 and 1100 h to reduce the variability in counts caused by changes in beetle activity. Adult rootworms are more active just after sunrise and before sunset, and their behavior is affected by temperature (Witkowski et al. 1975).

Analyses

Count data were analyzed separately by species, year, and sampling method. Ten-plant, single-plant, 10-ear, single-ear, and sticky-trap sample means and variances were calculated for each of the 59 fields. These parameters were based on 16 counts/field for 10-plant, 10-ear, and sticky-trap samples and 160 counts/field for single-plant and single-ear samples. The 6 indices were calculated as follows:

- (1) Variance/mean ratio (s^2/m)--The ratio was tested for

nonrandomness by a χ^2 -test discussed by Southwood (1966): $\chi^2 = (n-1)s^2/m$.

(2) Green's coefficient (C_x)--This index was calculated by solving: $C_x = ((s^2/m) - 1) / (\Sigma x - 1)$, where Σx = total number of beetles sampled. A χ^2 -test of nonrandomness (Green 1966) was applied to C_x to determine significance.

(3) Morisita's index (I_δ)--This index was computed by his equation: $I_\delta = n(\Sigma x^2 - \Sigma x) / ((\Sigma x)^2 - \Sigma x)$, where n = number of quadrats (areas sampled), x = number of beetles in a sample, and Σx = total number of beetles sampled. This index was tested for nonrandomness by an F-test discussed by Southwood (1966): $F = ((\Sigma x - 1) + n - \Sigma x) / n - 1$.

(4) Standardized Morisita's index (I_p)-- I_δ was standardized by solving 1 of 4 equations listed by Smith-Gill (1975). Two significance points were calculated by solving: M_u (uniform index) = $(\chi^2_{.025} - n + \Sigma x) / (\Sigma x - 1)$, and M_c (clumped index) = $(\chi^2_{.975} - n + \Sigma x) / (\Sigma x - 1)$. These significance points were fit into the 4 equations to determine randomness or aggregation.

(5) Taylor's power law ($s^2 = am^b$)--The b-value, or index of contagion, was obtained by converting s^2 and m to logarithms and solving: $\log s^2 = \log a + b \log m$. The b-value was tested for nonrandomness by using a t-test.

(6) Iwao's regression method ($\bar{m}^* = a + bm$)--Lloyd's mean crowding, \bar{m}^* , was calculated by solving: $\bar{m}^* = m(s^2/m - 1)$. Mean crowding was regressed on mean density, m , to determine a and

b , the 2 indices of dispersion. Tests of whether $a = k$ or $b = k$, where $k = 0$ or 1 , were provided by t-tests.

Results

Percentages of sampled cornfields in which NCR and WCR adults were distributed in aggregated patterns are reported in Tables 1 and 2. The 4 dispersion indices were computed for each sampling method in all 59 fields. Each percentage represents the proportion of fields, sampled by a particular technique, in which beetle counts differed significantly ($P < 0.05$) from randomness as measured by the index. Fields with total counts of 0, 1, or 2 beetles were not included in the percentages because index values based on such low numbers are meaningless. Mean beetle numbers for all yr-sample combinations are also included to indicate general population trends over the 2-yr study. Overall means for 1976 and 1977 are based on 32 and 27 field means, respectively.

For all sampling methods and both species, the s^2/m ratio and C_x identified the same fields in which beetles were aggregated. The I_0 and I_p indices for single-plant and single-ear counts of NCR (Table 1) revealed slightly lower percentages of fields with beetle aggregation. The I_0 -index was consistent with s^2/m and C_x for all WCR counts (Table 2), but I_p identified fewer aggregated populations sampled by plant and ear counts.

A noticeable trend in Tables 1 and 2 is that percentages of cornfields with aggregated populations are larger when beetle

Table 1. Percentages of sampled cornfields in which Diabrotica longicornis (NCR) adults were distributed in an aggregated spatial pattern

Year and sample	Mean	Dispersion indices			
		s^2/m	C_x	I_0	I_p
1976 10-plant counts	3.88	46	46	46	43
1976 single-plant counts	0.39	54	54	50	50
1977 10-plant counts	16.06	63	63	63	59
1977 single-plant counts	1.61	59	59	59	59
1976 10-ear counts	2.36	57	57	57	57
1976 single-ear counts	0.24	57	57	52	52
1977 10-ear counts	5.79	52	52	52	52
1977 single-ear counts	0.58	64	64	60	56
1976 sticky traps	10.08	72	72	72	72
1977 sticky traps	49.34	93	93	93	93

Table 2. Percentages of sampled cornfields in which Diabrotica virgifera (WCR) adults were distributed in an aggregated spatial pattern

Year and sample	Mean	Dispersion indices			
		s^2/m	C_x	I_δ	I_p
1976 10-plant counts	26.65	91	91	91	78
1976 single-plant counts	2.66	88	88	88	81
1977 10-plant counts	11.90	85	85	85	70
1977 single-plant counts	1.19	85	85	85	91
1976 10-ear counts	7.62	81	81	81	78
1976 single-ear counts	0.76	69	69	69	69
1977 10-ear counts	2.09	41	41	41	37
1977 single-ear counts	0.21	56	56	56	56
1976 sticky traps	200.61	100	100	100	100
1977 sticky traps	43.77	100	100	100	100

counts, with comparable sample sizes, are larger. This is most obvious when sticky trap counts are compared with plant and ear counts. The trend is also apparent when 1976 and 1977 mean numbers of both species are compared.

Ten-unit samples and single-unit samples did not always identify aggregation in the same fields. In several instances, beetles were aggregated according to indices based on 10-unit samples but were distributed randomly according to indices based on single-unit samples, and vice versa. Identification of aggregated populations, then, depended on the selection of sample unit.

The results of applying Taylor's power law to NCR and WCR counts are presented in Tables 3 and 4. The slope, b , or index of aggregation, characterizes randomness when $b = 1$ and aggregation when $b > 1$. The b -values of NCR (Table 3) and WCR (Table 4) counts ranged from 1.33 to 1.85, and all were significantly greater than 1.0. These values indicate that both species were distributed in aggregated patterns in Iowa cornfields in 1976 and 1977. The r^2 -values show that 90-98% of the variation in NCR counts and 75-94% of the variation in WCR counts was explained by the fitted models. Log variance and log mean for 1976 and 1977 NCR 10-plant counts are plotted in Fig. 1. These 2 examples were selected from all possible examples to illustrate the underlying relationship for both species and all sampling techniques. In both examples, the slope of the line fitted to the sample points is greater than unity ($b = 1$). Both graphs show the trend of aggregation in NCR populations, but

Table 3. Regression coefficients obtained by solving Taylor's power law, $\log s^2 = \log a + b \log m$, for counts of adult northern corn rootworms, Diabrotica longicornis

Year and sample	Intercept (a)	Slope (b)	r^2
1976 10-plant counts	-0.10 n.s. ^a	1.47 ^b	0.95
1976 single-plant counts	-0.01 n.s.	1.33 ^b	0.98
1977 10-plant counts	-0.15 n.s.	1.49 ^b	0.90
1977 single-plant counts	-0.04 n.s.	1.40 ^b	0.98
1976 10-ear counts	-0.06 n.s.	1.39 ^b	0.95
1976 single-ear counts	-0.01 n.s.	1.34 ^b	0.97
1977 10-ear counts	-0.08 n.s.	1.46 ^b	0.96
1977 single-ear counts	-0.01 n.s.	1.54 ^b	0.98
1976 sticky traps	-0.21 n.s.	1.67 ^b	0.94
1977 sticky traps	-0.53 n.s.	1.85 ^b	0.94

^an.s. = not significantly different from 0.0 at $P = 0.10$.

^bSignificantly greater than 1.0 at $P < 0.05$.

Table 4. Regression coefficients obtained by solving Taylor's power law, $\log s^2 = \log a + b \log m$, for counts of adult western corn rootworms, Diabrotica virgifera

Year and sample	Intercept (a)	Slope (b)	r^2
1976 10-plant counts	-0.53 n.s. ^a	1.63 ^b	0.88
1976 single-plant counts	-0.13 n.s.	1.51 ^b	0.92
1977 10-plant counts	-0.34 n.s.	1.65 ^b	0.82
1977 single-plant counts	-0.03 n.s.	1.50 ^b	0.94
1976 10-ear counts	0.03 n.s.	1.35 ^b	0.85
1976 single-ear counts	-0.03 n.s.	1.36 ^b	0.91
1977 10-ear counts	-0.15 n.s.	1.56 ^b	0.89
1977 single-ear counts	-0.02 n.s.	1.51 ^b	0.94
1976 sticky traps	0.68 n.s.	1.64 ^b	0.90
1977 sticky traps	0.36 n.s.	1.66 ^b	0.75

^an.s. = not significantly different from 0.0 at $P = 0.10$.

^bSignificantly greater than 1.0 at $P < 0.05$.

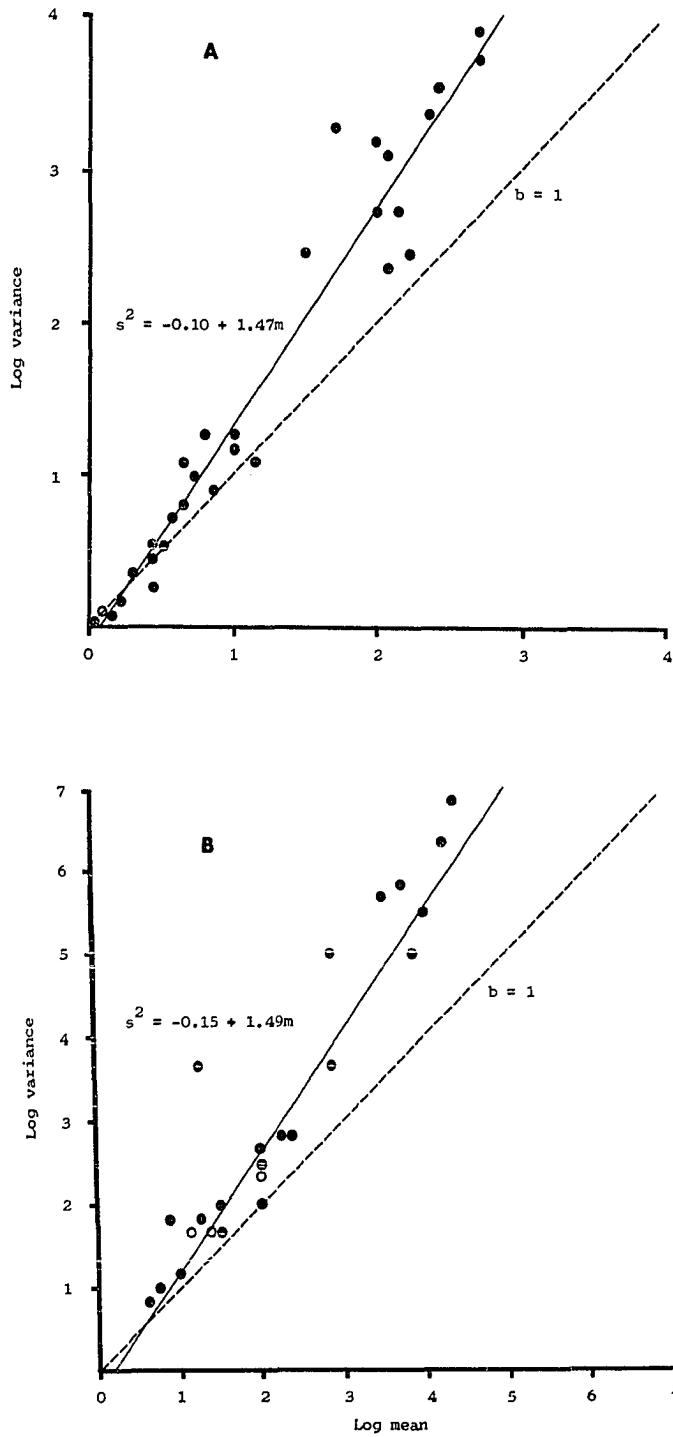


Figure 1. Relationship of log variance and log mean for *Diabrotica longicornis* counts. A. 1976 10-plant counts. B. 1977 10-plant counts

they also suggest that populations tend toward randomness as mean density decreases. This application of Taylor's power law corroborates the results of dispersion index calculations.

The regression of mean crowding on mean density produces 2 indices of dispersion: the intercept, a , and the slope, b . The basic unit of a population is the single individual when $a = 0$ and a group of individuals when $a > 0$. The b -value describes how the basic units are distributed in a habitat: random ($b = 1$) or aggregated ($b > 1$). Coefficients, or indices of dispersion, obtained from regressing mean crowding on mean density of NCR and WCR counts are reported in Tables 5 and 6. The a -values for NCR samples ranged from -0.89 to 1.26, and the b -values ranged from 1.09 to 1.63. The a -values for WCR samples ranged from -5.17 to 28.52, and the b -values ranged from 1.07 to 1.70. None of the NCR or WCR samples were characterized by a combination of $a = 0$ and $b = 1$. So the combination of regression coefficients for all sampling techniques represented aggregated dispersion.

The a -values for most of the NCR counts are not significantly different from 0. This suggests that individual beetles were the basic unit for those populations. Aggregation of individuals is indicated by $b > 1$. When $a > 0$, as in 1977 single-plant and single-ear counts, groups of beetles/plant or ear were the basic unit of the population. These groups were also distributed in aggregated patterns ($b > 1$). The b -values of all WCR counts are significantly greater than 1, and most of the a -values are not

Table 5. Regression coefficients obtained by solving Iwao's regression, $\bar{m} = a + bm$, for counts of adult northern corn rootworms, Diabrotica longicornis

Year and sample	Intercept (a)	Slope (b)	r^2
1976 10-plant counts	0.27 n.s. ^a	1.19 ^b	0.96
1976 single-plant counts	0.10 n.s.	1.40 ^b	0.83
1977 10-plant counts	1.26 n.s.	1.09 ^b	0.98
1977 single-plant counts	0.28 ^c	1.18 ^b	0.98
1976 10-ear counts	0.08 n.s.	1.22 ^b	0.96
1976 single-ear counts	0.05 n.s.	1.63 ^b	0.77
1977 10-ear counts	0.55 n.s.	1.12 ^b	0.98
1977 single-ear counts	0.24 ^c	1.48 ^b	0.91
1976 sticky traps	0.79 n.s.	1.26 ^b	0.96
1977 sticky traps	-0.89 n.s.	1.38 ^b	0.97

^an.s. = not significantly different from 0.0 at $P = 0.10$.

^bSignificantly greater than 1.0 at $P < 0.05$.

^cSignificantly greater than 0.0 at $P < 0.05$.

Table 6. Regression coefficients obtained by solving Iwao's regression, $\hat{m} = a + bm$, for counts of adult western corn rootworms, Diabrotica virgifera

Year and sample	Intercept (a)	Slope (b)	r^2
1976 10-plant counts	1.41 n.s. ^a	1.10 ^b	0.97
1976 single-plant counts	0.26 n.s.	1.26 ^b	0.90
1977 10-plant counts	-0.07 n.s.	1.32 ^b	0.94
1977 single-plant counts	0.41 ^c	1.32 ^b	0.88
1976 10-ear counts	0.93 ^c	1.07 ^b	0.95
1976 single-ear counts	0.10 n.s.	1.29 ^b	0.76
1977 10-ear counts	0.45 n.s.	1.21 ^b	0.90
1977 single-ear counts	0.21 ^c	1.70 ^b	0.63
1976 sticky traps	28.52 ^b	1.15 ^b	0.96
1977 sticky traps	-5.17 n.s.	1.66 ^b	0.86

^an.s. = not significantly different from 0.0 at $P = 0.05$.

^bSignificantly greater than 1.0 at $P \leq 0.05$.

^cSignificantly greater than 0.0 at $P < 0.05$.

significantly different from 0. This again implies aggregated dispersion of individual beetles. The a -values of 1977 single-plant and single-ear counts and 1976 sticky trap counts also suggest that groups of beetles were the basic units of populations sampled by those methods. The r^2 -values show that 77-98% of the variation of NCR counts and 63-97% of the variation in WCR counts was explained by the fitted models. The results of Iwao's regression method agree with the analyses of dispersion by all other methods.

Fig. 2 shows the relationship between mean crowding and mean density of 1976 WCR sticky trap and 10-ear counts. Again, these are 2 examples representing the trend for both species and all sampling techniques. The line fitted to the observed sticky trap counts is clearly greater than unity and suggests aggregation. Although no WCR populations sampled by this technique were described by random dispersion, sample points approach unity as mean density decreases. The 10-ear-count example shows that the slope of the fitted line differs slightly from unity. The a -value is significantly greater than 0, so another type of aggregation is suggested.

Correlations of dispersion indices and mean density of NCR and WCR counts are presented in Tables 7 and 8. The s^2/m ratio was significantly correlated with mean density for all but 1 yr-sample combinations. C_x and I_0 were not significantly correlated with mean density in most instances; but I_p was correlated with mean density in all but 5 instances.

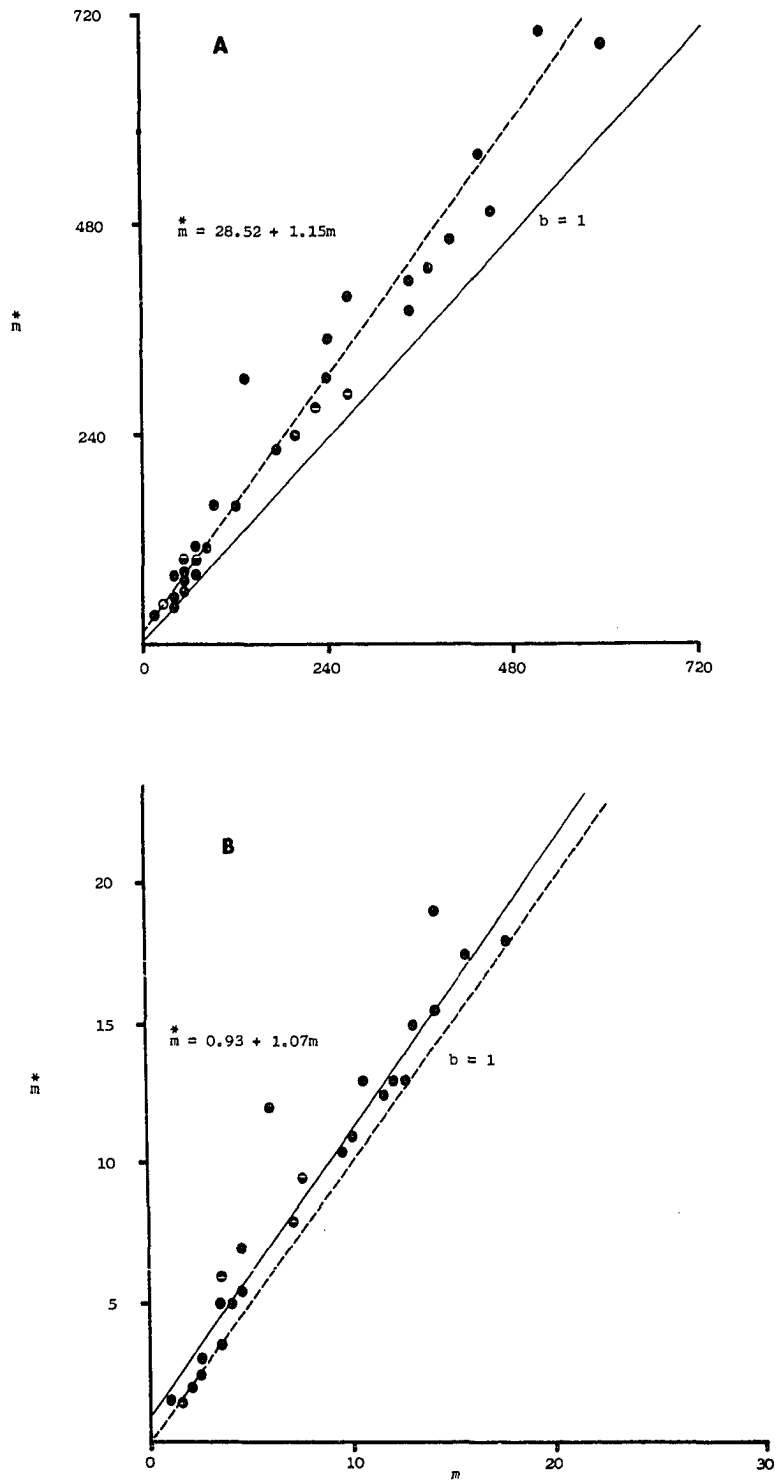


Figure 2. Relationship of mean crowding (m^*) and mean density (m) for *Diabrotica virgifera* counts. A. 1976 sticky traps. B. 1976 10-ear counts

Table 7. Correlation (r) of mean density and dispersion indices of Diabrotica longi-cornis adults sampled by plant counts, ear counts, and sticky traps

Year and sample	Dispersion indices			
	s^2/m	C_x	I_δ	I_p
1976 10-plant counts	0.63 ^a	0.27 n.s.	0.19 n.s.	0.64 ^a
1976 single-plant counts	0.51 ^a	-0.10 n.s.	-0.07 n.s.	0.69 ^a
1977 10-plant counts	0.81 ^a	-0.28 n.s.	-0.28 n.s.	0.39 ^a
1977 single-plant counts	0.72 ^a	-0.35 n.s.	-0.35 n.s.	0.39 ^a
1976 10-ear counts	0.69 ^a	0.18 n.s.	0.33 n.s.	0.58 ^a
1976 single-ear counts	0.56 ^a	-0.06 n.s.	-0.02 n.s.	0.63 ^a
1977 10-ear counts	0.60 ^a	-0.13 n.s.	-0.09 n.s.	0.52 ^a
1977 single-ear counts	0.70 ^a	-0.15 n.s.	-0.13 n.s.	0.48 ^a
1976 sticky traps	0.70 ^a	-0.12 n.s.	-0.12 n.s.	0.41 ^a
1977 sticky traps	0.84 ^a	-0.16 n.s.	-0.16 n.s.	0.19 n.s.

^aSignificant at $P < 0.05$.

Table 8. Correlation (r) of mean density and dispersion indices of Diabrotica virgifera adults sampled by plant counts, ear counts, and sticky traps

Year and sample	Dispersion indices			
	s^2/m	C_x	I_δ	I_p
1976 10-plant counts	0.63 ^a	-0.01 n.s.	-0.01 n.s.	0.43 ^a
1976 single-plant counts	0.54 ^a	-0.17 n.s.	-0.17 n.s.	0.42 ^a
1977 10-plant counts	0.69 ^a	-0.12 n.s.	-0.12 n.s.	0.31 n.s.
1977 single-plant counts	0.54 ^a	-0.23 n.s.	-0.23 n.s.	0.27 n.s.
1976 10-ear counts	0.27 n.s.	-0.40 ^a	-0.40 ^a	0.44 ^a
1976 single-ear counts	0.37 ^a	-0.36 ^a	-0.36 ^a	0.28 n.s.
1977 10-ear counts	0.45 ^a	-0.12 n.s.	-0.10 n.s.	0.39 ^a
1977 single-ear counts	0.70 ^a	-0.15 n.s.	-0.13 n.s.	0.48 ^a
1976 sticky traps	0.70 ^a	-0.12 n.s.	-0.12 n.s.	0.41 ^a
1977 sticky traps	0.84 ^a	-0.16 n.s.	-0.16 n.s.	0.19 n.s.

^aSignificant at $P < 0.05$.

Discussion

Beetle populations in all 59 fields were sampled by 3 techniques: 10-plant counts, 10-ear counts, and sticky traps; and 10-plant and 10-ear counts were subsequently partitioned into single-unit components. So all populations were actually measured by 5 methods. Significant aggregation was identified by all 6 methods of dispersion analysis in 80% of WCR counts and 62% of NCR counts. These results reveal that in most of the populations sampled in 1976 and 1977, NCR and WCR adults were distributed in aggregated patterns. They also suggest that for 20% of the WCR counts and 38% of the NCR counts, beetle dispersion did not differ significantly from randomness. A number of these instances were the direct result of encountering very few beetles in a sampled cornfield. Taylor et al. (1978) suggested that spatial dispersion of a species may be indistinguishable from randomness when mean density is so low that the whole sample contains only a few individuals and they do not have an opportunity to interact. I also found, however, that some samples with larger beetle counts did not differ significantly from random. This indicates that beetles in some of the sampled populations were distributed randomly. In contrast, some samples with small counts were identified as significantly aggregated. This occurred when all or most of the beetles in a field were counted at 1 or 2 sites. This again points out that little faith can be placed on a statement of aggregation for small counts at the sample size used.

Identification of spatial dispersion can be affected directly by method of sampling and sample size. Because sticky traps were left in a cornfield for 1 wk, they usually captured many rootworm adults. As a direct result of the large numbers and large sample variances inherent with sticky trap samples, beetles in 100% of the WCR populations and 81% of the NCR populations sampled were distributed in aggregated patterns. Plant and ear counts revealed different percentages of aggregated populations. Because the ear counts were a subsample of the plant counts, plant counts were always equal to or greater than ear counts. NCR adults were more often found around the corn ear rather than elsewhere on the corn plant, so plant and ear counts were equal in many fields. Percentages of fields in which NCR were aggregated were similar for plant and ear counts. WCR beetles, however, were commonly found anywhere on the plant, so plant counts were often greater than ear counts. Percentages of fields with aggregation were greater for WCR plant counts than ear counts.

Plant-to-plant beetle aggregation in a cornfield occasionally was obscured when the 10 plants were combined as 1 count and compared with other 10-plant counts. On the other hand, aggregated spatial dispersion for 10-plant counts sometimes became random when counts were separated into single-plant units. Since the corn plant is the basic unit of habitat for rootworm adults, it seems more realistic to consider aggregation or randomness on a per-plant or per-ear basis. Seventy-five percent of WCR single-unit counts and

62% of NCR single-unit counts were identified as aggregated dispersions.

Aggregation in animal populations is the result of complex interactions between a species and its environment. Not enough is known about rootworm beetle behavior and environmental factors affecting that behavior to make a strong statement about the reasons for beetle aggregation. WCR females produce a sex pheromone which attracts WCR and NCR males, but no other pheromones have been identified. Although a cornfield is a fairly uniform habitat, variability in soil texture, plant attractiveness, and other factors within a field may produce "pockets" of attractiveness for beetle feeding, mating, or oviposition. Data gathered for the objectives of this study, however, are insufficient for suggesting the underlying mechanism of WCR and NCR aggregation.

Finally, the selection of a dispersion index for population studies deserves discussion. Myers (1978) stated that the ideal dispersion index should have no correlation with mean density. She recommended s^2/m , C_x , and I_p for use when analyzing actual changes in dispersion with changes in mean density because their values were not significantly affected by simulated egg count densities. I ran similar correlations for my data and found s^2/m was highly correlated with mean density and I_p was highly correlated with mean density on several occasions. C_x and I_δ usually were not correlated with mean density, and the 2 indices were also highly correlated ($r > .90$) with each other. All 4 indices, however, were

very consistent in identifying aggregation, regardless of mean density. Taylor et al. (1978) stated that s^2/m ratio changes systematically and disproportionately with population density. They further concluded that spatial behavior is density-dependent in most species. Examination of Figs. 1 and 2 reveals this same tendency in both NCR and WCR populations. In addition, 82% of all counts not departing significantly from random were from relatively small beetle populations with small mean densities (≤ 0.5 beetle/plant or ear). My results, then, suggest that spatial dispersion of NCR and WCR adults tends to be density-dependent. Although C_x and I_ϕ values are not correlated with mean density, they both identified randomness in populations with small mean densities. Both C_x and I_ϕ contain expressions of s^2 and m , so their consistency with s^2/m is not surprising.

The results of my study suggest that for determination of aggregation in a population, any of the analyses discussed can be used with consistent results. Tests of randomness for all methods provide the measures of significance desired for the study. The I_p -index identified more instances of random beetle dispersion, so it may be a more conservative test of significant aggregation. The use of an index which is not correlated with density would be preferable only if dispersion is density-independent. Otherwise, the change from randomness to aggregation, or vice versa, as density changes would be revealed by any of the aforementioned indices and their corresponding tests of significance.

PART II. A SAMPLING PLAN FOR POPULATION ESTIMATION
OF NORTHERN AND WESTERN CORN ROOTWORM
ADULTS IN IOWA CORNFIELDS

Introduction

Sampling pre-larval stages of the northern corn rootworm (NCR), Diabrotica longicornis (Say), and western corn rootworm (WCR), D. virgifera LeConte, has been the usual method of predicting potential damaging populations in a cornfield. Corn insect investigators have commonly relied on rootworm egg counts from soil samples to locate research plots. Farmers and insect scouts, on the other hand, use the previous year's beetle counts to make rootworm control decisions for the current year's corn crop. Beetle sampling requires less time and equipment than egg sampling, and beetle numbers have been significantly correlated with larval numbers and root damage (Peters 1969). Tollefson (1975) found 4 adult corn rootworm sampling techniques to be better predictors of subsequent larval damage than egg-sampling techniques. Of these 4, 10-plant counts and 10-ear-tip collections are common practices today. Several authors have suggested the use of plant counts as estimates of NCR and WCR populations and have proposed plans for taking the samples in a field (Chiang and Flaskerd 1965, Luckmann et al. 1975, Shaw et al. 1975, Lovett 1975). But no plan has yet been standardized for use in a pest management program.

Optimum sample size is a necessary requisite for estimating

population density with a desired precision and optimizing resource allocation. Amount of available personnel, time, funds, and equipment will affect the selection of sample size; but variability in insect numbers in a habitat will play a large role in allocating sampling resources and establishing precision of the estimate.

Significant variance components of sampling procedures have been determined for a number of insect pests (Morris 1955, Bancroft and Brindley 1958, Harcourt 1961, Ng et al. 1977). These same authors discussed cost factors in conjunction with sample size measurement.

I report here a 2-yr NCR and WCR adult-sampling study conducted in 59 Iowa cornfields. My objectives were to compare the costs and variance components of 3 beetle-sampling techniques and to determine which method provides the most precise density estimate for the least cost. This information was used to propose a standard sampling plan for use by Midwest farmers and insect scouts.

Materials and Methods

Field-sampling techniques

Data obtained for this study were the same as those for the spatial dispersion study (Part I). Experimental design and methods of sampling NCR and WCR adults are explained in Part I. All field information from the dispersion study applies equally to this study. In addition, the amount of time required to take a sample and record beetle numbers was registered for all 3 sampling techniques. Man-h expended for each sampling method depended on the relative beetle

density in a field. These man-h were averaged over 3 population levels (small, medium, and large) to obtain the mean time necessary to complete a sampling procedure.

Analyses

NCR and WCR counts were combined because the data of interest were total number of beetles/sampling technique. Variance components for all 3 sampling techniques were calculated by a nested analysis of variance procedure. Sources of variation were fields, quadrants/fields, sites/quadrants, and plants/sites. Fields were classified into separate categories in 2 ways: 3 categories based on field size--small (≤ 20.24 ha), medium (20.24-40.47 ha), and large (> 40.47 ha); and 2 categories based on relative beetle density--small (avg < 1 beetle/plant) and large (avg > 1 beetle/plant) populations. These categories were first analyzed separately to determine if field size or relative density affected the sources of variation.

Optimum allocation of sampling resources was determined for the 3 sampling techniques by employing equations from Snedecor and Cochran (1967). Plant and ear counts involved 3-stage sampling (quadrants, sites, and plants or ears), and sticky traps involved 2-stage sampling (quadrants, and sites = traps). For the 3-stage samples, the optimum number of plants or ears/site was found by solving:

n_p (or n_e) = $\sqrt{c_s s_p^2 / c_p s_s^2}$, where c_s = man-h required to move to another site, c_p (or c_e) = man-h required to take a 1-plant (or 1-ear) sample, and s_s^2 and s_p^2 (or s_e^2) are the variance components for

sites and plants (or ears), respectively. The product of variance (V) and cost (C) was minimized by inserting optimum n_p (or n_e) and c_p (or c_e) into: $VC = (s_s^2 c_s + s_p^2 c_p) + n_p s_s^2 c_p + (s_p^2 c_s / n_p)$. The variance of a field mean for 3-stage sampling was found by solving: $V(\bar{y}...) = s_q^2 / n_q + s_s^2 / n_q n_s + s_p^2 / n_q n_s n_p$, where s_q^2 and n_q represent the variance component for quadrants and number of quadrants sampled, respectively, and s_e^2 and n_e can be substituted for s_p^2 and n_p . Different combinations of n_q , n_s , and n_p were used in the equation to obtain several variance estimates. The variance for each combination of n_q , n_s , and n_p was used to determine precision: % precision = $(2 \sqrt{V(\bar{y}...)}/\bar{y}...) \times 100$ for 95% C.I. Overall cost for a 3-stage sampling plan was found by solving: $\text{Cost} = c_q n_q + c_s n_q n_s + c_p n_q n_s n_p$.

The equations were simplified for sticky trap (2-stage sampling) allocation. $V(\bar{y}..) = s_q^2 / n_q + s_s^2 / n_q n_s$, where subscripts q and s represent quadrants and sites, respectively. Overall cost was found by solving: $\text{Cost} = s_q^2 / n_q + s_s^2 / n_q n_s$. Precision of a sticky trap-sampling plan was determined in the same manner as for plant- and ear-sampling plans.

Results

The analyses of variance of beetle counts for fields separated into categories indicated that field size and relative beetle density had no significant effect on values of the different variance components within fields. The variance component for field-to-field variation, however, was considerably different for the 2 categories

based on density. This was expected since the range of densities for small populations was only 0 to 1. Mean densities of the large populations ranged from 1 to 8, so the variation between fields was greater. But this did not alter the relationship among components for quadrants, sites, and sample units within fields in the 2 categories. For this reason, and to take advantage of estimates of variance from 2 seasons' data, all analyses reported herein are based on beetle counts pooled over 59 fields.

Analyses of variance for plant, ear, and sticky trap counts are presented in Tables 9-11. The variance components and the percentage of total variance accounted for by each component are listed. Differences among plant counts and differences among ear counts accounted for the largest percentage of variability in their respective analyses. The percentage of variability accounted for by differences between quadrants was very small for both plant and ear counts. Site-to-site variation was greater for plant counts than for ear counts. The large percentage of variability accounted for by differences among fields was expected because of the large variation in beetle numbers from field to field.

The percentage of variability accounted for by differences among trap counts (Table 11) was much larger than the percentage of variability accounted for by differences between quadrants. Field-to-field variation, however, was greater than trap-to-trap variation because of the very large variation in beetle densities in different fields.

Table 9. Analysis of variance^a for plant counts of adult corn rootworms^b. Mean number of rootworm beetles/plant = 2.934

Source of variation	d.f.	Expected M.S.	Variance component	Percentage
Fields	58	$\sigma_P^2 + 10\sigma_S^2 + 40\sigma_Q^2 + 160\sigma_F^2$	4.353	38.83
Quadrants/fields	177	$\sigma_P^2 + 10\sigma_S^2 + 40\sigma_Q^2$	0.114	1.02
Sites/quadrants/fields	708	$\sigma_P^2 + 10\sigma_S^2$	2.070	18.47
Plants/sites/quadrants/fields	8496	σ_P^2	4.672	41.68

^aPooled over 59 fields and 2 years.

^bNCR and WCR counts combined.

Table 10. Analysis of variance^a for ear counts of adult corn rootworms^b. Mean number of rootworm beetles/ear = 0.902

Source of variation	d.f.	Expected M.S.	Variance component	Percentage
Fields	58	$\sigma_E^2 + 10\sigma_S^2 + 40\sigma_Q^2 + 160\sigma_F^2$	0.562	25.42
Quadrants/fields	177	$\sigma_E^2 + 10\sigma_S^2 + 40\sigma_Q^2$	0.018	0.83
Sites/quadrants/fields	708	$\sigma_E^2 + 10\sigma_S^2$	0.121	5.48
Bars/sites/quadrants/fields	8496	σ_E^2	1.510	68.27

^aPooled over 59 fields and 2 years.

^bNCR and WCR counts combined.

Table 11. Analysis of variance^a for sticky trap counts of adult corn rootworms^b. Mean number of rootworm beetles/trap = 161.80

Source of variation	d.f.	Expected M.S.	Variance component	Percentage
Fields	58	$\sigma_T^2 + 4\sigma_Q^2 + 16\sigma_F^2$	18764.80	60.63
Quadrants/fields	177	$\sigma_T^2 + 4\sigma_Q^2$	571.86	1.85
Traps/quadrants/fields	708	σ_T^2	11613.80	37.52

^aPooled over 59 fields and 2 years.

^bNCR and WCR counts combined.

Various allocations of plant, ear, and sticky trap sample units and their respective precisions and costs (man-h) are presented in Tables 12-14. The optimum number of plants/site, determined from $n_p = \sqrt{c_s s_p^2 / c_p s_s^2}$, was 2. The optimum number of ears/site was 5. These optima were the numbers which minimized the product VC. Included in the tables are sampling plans incorporating the optimum number of sample units, the sampling plan used for this study, and some sampling plans which have been suggested for scouting rootworm beetles. Estimates of variance are also included, and their calculation requires some explanation. Although quadrant-to-quadrant variation was small for all 3 sampling techniques, it contributed enough to the estimate of $V(\bar{y} \dots)$ that the desired precision could not be attained unless the number of quadrants equaled 4. Since insect scouts usually walk the entire cornfield when sampling (E. S. Raun, Pest Management Consultants, Inc., personal communication), all quadrants would be included in the sample plan. The variance component for 4 quadrants (s_q^2/n_q , where $n_q = 4$), therefore, was included in each estimate of a field variance. Each sampling plan is presented with the assumption that all quadrants in a cornfield are sampled and the sample sites are arranged along a systematic path.

The cost (man-h) for each sampling plan was calculated separately for 16.19-ha (40 a) and 64.75-ha (160 a) fields. The man-h required to walk from site to site increases with increasing field size.

Table 12. Allocation of sample units for desired precision of plant counts for adult corn rootworms

No. sites (n_s)	No. plant/site (n_p)	Variance ^a	Precision ^b	Cost (man-h)	
				16.19 ha ^c	64.75 ha ^d
220	2	0.0485	15	6.75	8.91
77	2	0.0861	20	2.34	3.10
27	2	0.1917	30	0.83	1.09
14	2	0.3432	40	0.43	0.57
9	2	0.5181	50	0.28	0.36
16 ^e	10 ^e	0.1960	30	1.83	1.99
80	2	0.0850	20	2.45	3.24
8	10	0.3599	41	0.92	1.00
40	2	0.1415	26	1.23	1.62
20	4	0.1961	30	1.03	1.23
10	10	0.2936	37	1.15	1.24
20	5	0.1844	29	1.24	1.44

^aVariance (V) of field mean ($\bar{y}...$) = $s_q^2/n_q + s_s^2/n_q n_s + s_p^2/n_q n_s n_p$.

^b% precision = $(2\sqrt{V(\bar{y}...)/\bar{y}...}) \times 100$ for 95% C.I., where $\bar{y}... = 2.934$.

^cCost = $c_s n_s + c_p n_s n_p$, where $c_s = 0.58$ man-min, $c_p = 0.63$ man-min.

^dCost = $c_s n_s + c_p n_s n_p$, where $c_s = 1.17$ man-min, $c_p = 0.63$ man-min.

^eSampling plan used for this study.

Table 13. Allocation of sample units for desired precision of ear counts for adult corn rootworms

No. sites (n_s)	No. ears/site (n_e)	Variance ^a	Precision ^b	Cost (man-h)	
				16.19 ha ^c	64.75 ha ^d
115	5	0.0082	20	3.51	4.64
31	5	0.0186	30	0.95	1.25
15	5	0.0327	40	0.46	0.60
9	5	0.0515	50	0.27	0.36
16 ^e	10 ^e	0.0227	33	0.82	0.98
32	5	0.0183	30	0.98	1.29
5 ^f	10 ^f	0.0626	55	0.26	--
20 ^f	10 ^f	0.0190	31	--	1.22

^aVariance (V) of a field mean ($\bar{y}_{...}$) = $s_q^2/n_q + s_s^2/n_q n_s + s_e^2/n_q n_s n_e$.

^b% precision = $(2 \sqrt{V(\bar{y}_{...})}/\bar{y}_{...}) \times 100$ for 95% C.I., where $\bar{y}_{...} = 0.902$.

^cCost = $c_s n_s + c_e n_s n_e$, where $c_s = 0.58$ man-min, $c_e = 0.25$ man-min.

^dCost = $c_s n_s + c_e n_s n_e$, where $c_s = 1.17$ man-min, $c_e = 0.25$ man-min.

^eSampling plan used for this study.

^fSampling plan proposed by Union Carbide Corp. scientists for scouting different-size fields for rootworm adults.

Table 14. Allocation of sample units for desired precision of sticky trap counts for adult corn rootworms

No. sites (n_s)	Variance ^a	Precision ^b	Cost (man-h)	
			16.19 ha ^c	64.75 ha ^d
98	261.47	20	13.90	15.83
26	589.65	30	3.69	4.20
13	1036.33	40	1.84	2.10
8	1594.69	49	1.13	1.29
16 ^e	904.56	37	2.27	2.58

^aVariance (V) of a field mean ($\bar{y}_{..}$) = $s_q^2/n_q + s_s^2/n_q n_s$.

^b% precision = $(2 \sqrt{V(\bar{y}_{..})}/\bar{y}_{..}) \times 100$ for 95% C.I., where $\bar{y}_{..} = 161.8$.

^cCost = $c_s n_s$, where $c_s = 8.51$ (includes time needed to place trap in field, time to walk between sites initially and for return trip, time needed to count beetles, and cost of trap).

^dCost = $c_s n_s$, where $c_s = 9.69$ (includes time needed to place trap in field, time to walk between sites initially and for return trip, time needed to count beetles, and cost of trap).

^eSampling plan used for this study.

The cost component for quadrants was removed from the overall cost equation. When a systematic sampling plan is employed over an entire field, the man-h required to walk from 1 quadrant to another are the same as those required to walk from the last site in 1 quadrant to the first site in the next quadrant. So the man-h required to walk to another quadrant are included in the site-to-site component.

The average within-field times required to complete plant and ear counts were as follows: plant count--0.63 man-min; ear count--0.25 man-min; walk to another site in a 16.19-ha field--0.58 man-min; walk to another site in a 64.75-ha field--1.17 man-min. The within-field time required to complete a sticky trap count included placing the trap in the field (1.5 man-min), walking from site to site (same as for plant and ear counts), retrieving the traps (0.58 and 1.17 man-min for 16.19- and 64.75-ha fields, respectively), counting the beetles on the trap (3.75 man-min), and the initial cost of the trap (\$0.14/trap converted to 2.1 man-min based on an average scout salary of \$4.00/h).

Discussion

The results of the analyses revealed that plant-to-plant, ear-to-ear, and trap-to-trap variations were the largest variance components on a within-field basis. This indicates that a large number of plant, ear, and trap counts are required to obtain precise estimates of beetle density in a field. The allocation of these sample units is also governed by site-to-site and quadrant-to-quadrant

variation. Two plants/site and 5 ears/site are optimum for plant and ear counts, whereas 1 trap/site is optimum since trap = site. I recommend a systematic sampling plan, e.g., the systematic arrangement proposed by Lovett (1975), which involves sampling in each quadrant. Although the selection of sample sites is not completely random, a systematic plan is more practical and ensures that the entire field is sampled. The optimum number of plants and ears/site may decrease as field size decreases below 16.19 ha (distance between sites is less) and increase as field size increases above 64.75 ha (distance between sites is greater). The cost factor will also change as distance between sites changes.

A comparison of precisions and costs for the 3 sampling techniques reveals that plant counts provide the most precise estimate of rootworm beetle populations for the least cost. As an example, the man-h expended for 20% precision are 2.34, 3.51, and 13.90 for plant, ear, and sticky trap counts, respectively (Tables 12-14). On a within-field basis, variability among ear counts and among trap counts were both greater than variability among plant counts. This accounts for the larger sample sizes for ear counts and sticky traps. The large number of man-h required to sample beetles with sticky traps was explained in the preceding section. Based on the results of this study, I recommend plant counts as the most reliable and practical method of sampling adult corn rootworm populations.

The analyses of beetle counts in fields categorized into groups based on field size indicate that the sampling plan should not be

altered for different field sizes. To obtain equivalent precision in fields of different sizes, the same sampling plan should be used. Only the distance between sites will change according to field size. This will change the overall cost, but the same precision will be maintained.

When cost is fixed, a sampling plan may have to be altered to accommodate available time and resources. Although the precision may be reduced when a different sampling plan is used, the money saved by minimizing costs may be a more important factor in the overall sampling program. Allocation of sampling resources can be manipulated until the desired combination of cost and precision is achieved.

All recommendations for sampling rootworm beetles in cornfields are based on 2 seasons' data from Iowa fields. The estimates of variance could be improved with additional data from other years and states. But these samples from 59 fields and 2 years represent a wide variety of biological and environmental conditions and are adequate for measuring variation in beetle numbers. Southwood (1966) stated clearly that too much stress should not be placed on exact determinations of sample size since population density and variance are always changing. I propose a basic outline for sampling adult corn rootworms, but optimum number of units and overall sample size may vary with changing costs and population densities. The usefulness of a standard sampling plan will become even more important when reliable economic thresholds are established.

PART III. ESTIMATING ABSOLUTE POPULATIONS OF NORTHERN
AND WESTERN CORN ROOTWORM ADULTS BY A
CAPTURE-RECAPTURE TECHNIQUE

Introduction

One means of measuring absolute population of mobile insects is to capture, mark, and release a known number of individuals in the population. An effort is then made to recapture some of the initially marked individuals. The number of recaptures provides data for the estimation of population size and may provide additional information about dispersal in the habitat. The proportion of recaptures (r) to total numbers in the second sample (n) is equal to the proportion of initially marked individuals (a) to the total population (P). This can be expressed as $P = an/r$ and is commonly referred to as the Lincoln Index. One of the assumptions underlying this principle, however, is that the population being studied is closed, or birth rates, death rates, immigration, and emigration are measurable or are in balance. Pest insect populations are seldom closed, so dynamic processes must be allowed for in an estimation of population size. Cormack (1968) discussed in detail how several authors accounted for these processes in their estimates. Earlier deterministic models (Jackson 1939, Bailey 1951, Leslie 1952, Jolly 1963) have been superseded by simpler and more realistic stochastic models (Seber 1965, Jolly 1965) for estimating population parameters. These models are useful for examining temporal changes

in a population when a capture-recapture study spans a longer period of time. Short-term studies often can be analyzed with the simple Lincoln Index modified for inherent bias (Cormack 1968).

Measuring absolute populations of northern corn rootworm (NCR), Diabrotica longicornis (Say), and western corn rootworm (WCR), D. virgifera LeConte, adults in cornfields has been attempted by counting the number of beetles/unit habitat. Beetles/plant in a cornfield can be converted to beetles/ha simply by multiplying by plants/ha. This method, of course, does not account for beetles not resting on plants at the time of sampling. So plant counts tend to underestimate populations of adult rootworms in cornfields. Absolute population measures are important for any study concerned with insect pest mortality, natality, and dispersal.

This study was designed to examine the effectiveness of capture-recapture techniques in corn rootworm research. The main objectives were to estimate absolute population of NCR and WCR adults and to study intrafield movement in an Iowa cornfield. A precise absolute population estimate would aid in calibrating current beetle-sampling techniques.

Materials and Methods

Laboratory test

The effect of artificially marking adult corn rootworms with enamel paint was tested in the laboratory. NCR and WCR adults were not available for the test, so adult southern corn rootworms from a

laboratory colony were used. Forty beetles were placed in each of 8 small (30.5 cm^3) screen cages. Four of the cages contained beetles which had been sprayed with Day-Glo[®] fluorescent paint, and the other 4 cages held unmarked beetles. The numbers of dead beetles/cage were recorded daily for 1 mo. The mean numbers of marked and unmarked beetles surviving after 1 mo were 33.5 and 31.5, respectively. A t-test revealed no significant difference between the 2 means. Marked beetles were observed flying as readily as unmarked beetles. So it seemed that the marking technique did not markedly affect adult southern corn rootworm longevity or behavior. In addition, 1-mo-old marked beetles still appeared fluorescent under UV light.

Screenhouse trial

A preliminary mark-release-recapture trial was conducted in a 70-m^2 screenhouse. Four rows of corn were planted the length of the screenhouse. One thousand NCR and WCR adults, numbers of each species not known, were sprayed with fluorescent paint and released in the center of the screenhouse. An equal number of unmarked rootworms was released at the same time. Twenty sticky traps (see Part I) were placed systematically throughout the screenhouse and were left in place for 1 wk. At the end of the wk the traps were removed, and marked and unmarked beetles were counted. A total of 131 marked beetles were recovered on 19 of the 20 traps. So this technique proved to be feasible for use in a field trial.

Field technique

The study was conducted in a 15.78-ha, first-year cornfield 0.3 km NW of Ames, Iowa. Preliminary counts indicated an average population

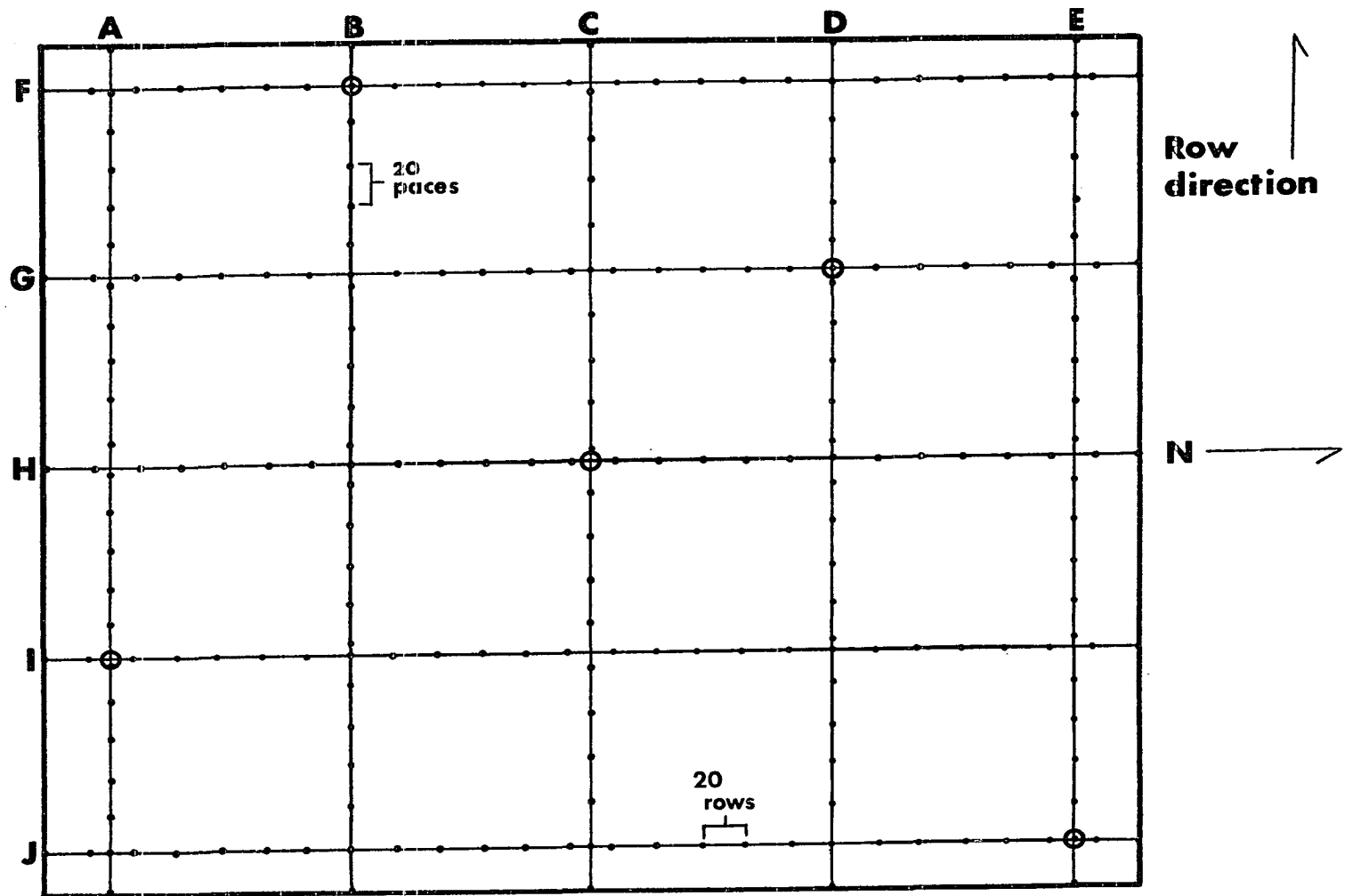
of 4-5 beetles, mostly NCR, per plant. On 13 Aug., 1978, 5 cylindrical holding cages were placed at 5 sites in the field (Fig. 3). The cages were separated in the field in a manner that would allow the released beetles to become completely mixed in the population. The cages were each 152.40 cm tall and 30.48 cm in diam and constructed from 18 x 16-mesh aluminum screen. The top of each cage was covered with a plywood lid fastened to the screen, and an aluminum funnel was fit into a hole in the lid.

NCR and WCR adults were collected by exposing ear tips and counting the beetles as they fell into the funnel of a collection bottle. The number of beetles was recorded each time a bottle was emptied into a cage. More than 10,000 beetles were collected for each cage, but an approx. value of 10,000 was used to account for escapes from and deaths in the cage.

Beetles were sprayed with fluorescent paint, thinned with turpentine, by means of a compressed air sprayer powered by a gasoline motor. Each group of caged beetles was sprayed with a different paint color (yellow, blue, red, pink, or orange). Paint was sprayed directly through the screen for approx. 5 min to ensure that all beetles were marked. After the paint had dried thoroughly, the cage was lifted off the ground to allow the beetles to move away from the area. Very few beetles died as a result of the spraying procedure. Many were observed cleaning their antennae and legs, but almost all were capable of flight soon after release. An examination of the area 2-3 h after release revealed few dead beetles. The entire process (capture-mark-release) was completed at 1 cage

Figure 3. Field diagram for grid pattern of sticky trap sites used in 1978 capture-recapture study, Ames, Iowa. Capital letters (A-J) identify trap lines

.



○ holding cage
 • sticky trap

before beginning the process at another cage. Two groups of beetles were captured, marked, and released on both 14 and 16 Aug; the last group was captured, marked, and released on 17 Aug. All releases were made during the afternoon because rootworm beetles are less active during that time period (Witkowski et al. 1975) and are less likely to disperse unnaturally after being handled.

On 18 Aug., the day after the last cage of beetles had been released, 241 sticky traps were placed in the field in a grid-like pattern (Fig. 3). Traps along each trap line were placed alternately at ground level and ear level. Traps on the E-W trap lines (A-E) were placed 20 paces apart, and traps on the N-S trap lines (F-J) were placed 20 rows apart. This first set of traps remained in place for 2 days and then was picked up and returned to the laboratory. A second set of 241 traps was placed in the same pattern on 20 Aug. and removed 3 days later. A final set of traps was placed on 23 Aug. and removed 5 days later (28 Aug.). Each trap was placed under UV light to check for marked beetles. Number and color of the painted beetles were recorded. The numbers of unmarked NCR and WCR were also recorded.

Natality was monitored by 10 emergence cages placed randomly in the field on 18 Aug. They were removed on 28 Aug. and examined for emerged beetles. One 3-m² window trap (Southwood 1966) was placed on each of the 4 sides of the cornfield to measure relative beetle movement into and out of the field. No results were obtained from these traps because heavy winds knocked them over. Ten randomly located 10-plant and 10-ear counts (see Part I) were taken on

3 different dates--18, 23, and 28 Aug. These counts were compared with results of the capture-recapture study.

Results

Total numbers of captured NCR and WCR adults, marked and unmarked, are reported for each of the 3 trapping intervals and the overall trapping period (Table 15). Population size estimates, calculated from total beetle numbers, are included in the table. Separate estimates of NCR and WCR populations could not be made because the numbers of each species marked and released were not known.

The Jolly-Seber method of estimating population size from capture-recapture data was not used because it requires multiple-recapture data over a longer time period. Although some assumptions which underlie capture-recapture analysis were not met or were improperly measured for this study, the simple Lincoln Index was calculated because of the short duration of the study. For the equation $P = an/r$, the n - and r -values were obtained from Table 15 and the a -value was 50,000 for previously mentioned reasons. The population size estimates in Table 15 are valid only if immigration + births equaled emigration + deaths for the 10-day trapping period. This assumption sometimes can be made for short-term studies.

Comparisons of population size estimates determined by 10-plant counts and the Lincoln Index are presented in Table 16. The Lincoln Index estimates are much larger than the plant-count estimates for

Table 15. Numbers of unmarked and marked adult corn rootworms captured on sticky traps from 18 to 28 Aug., 1978, in a 15.78-ha cornfield near Ames, Iowa

Trapping interval	Total no. NCR in 2nd sample (n)	Total no. marked NCR in 2nd sample (r)	Total no. WCR in 2nd sample (n)	Total no. marked WCR in 2nd sample (r)	Population size estimation by Lincoln Index ($P = an/r$) ^a
18-20 Aug.	13,824	20	2,484	4	33,975,000
20-23 Aug.	16,703	16	3,626	5	48,402,381
23-28 Aug.	13,348	17	5,407	8	37,510,000
18-28 Aug. (overall)	43,875	53	11,517	17	39,565,714

^aValues of (n) and (r) are the sum of NCR + WCR.

Table 16. Comparisons of population size estimates determined by beetles/plant and the Lincoln Index

Trapping interval	Avg no. beetles/plant ^a	Population size estimated by no. beetles/plant ^b	Population size estimated by Lincoln Index
18-20 Aug.	1.64 (18 Aug.) ^c	1,534,740	33,975,000
20-23 Aug.	1.23 (23 Aug.) ^c	1,151,055	48,402,381
23-28 Aug.	0.69 (28 Aug.) ^c	645,714	37,510,000

^aAvg from ten 10-plant counts/trapping interval.

^bBeetles/plant x 59,304 plants/ha x 15.78 ha.

^cDate 10-plant counts were taken.

all trapping periods. Plant counts show a steady decrease in beetle numbers from 18 Aug. to 28 Aug. Lincoln Index estimates, however, reveal a large increase in beetle numbers between 20 and 23 Aug. followed by a decrease between 23 and 28 Aug. Numbers of each species captured on sticky traps (Table 15) show that NCR numbers follow the same pattern of increase followed by a decrease, whereas WCR numbers increased during each trapping interval.

No beetles were collected from the 10 emergence traps left in the field for 10 days. This was expected since the field was a first-yr cornfield following soybeans planted the previous yr, 1977. No beetles were collected from the 4 window traps because high winds and heavy rains knocked them over before their contents could be examined.

Little information was obtained on intrafield dispersal by the recapture of marked beetles. Of the 70 marked beetles recaptured, 34 beetles were recaptured at trap sites only a short distance from the release site. Several marked beetles were recaptured a relatively far distance from their original release site, but their movement revealed no underlying pattern. Total beetle numbers captured on sticky traps, however, suggested a gross pattern of beetle movement in the field. The cornfield was bordered by a gravel road on the south, soybeans on the west, cut oats on the north, and corn on the east. For the first trapping interval, total beetle numbers were largest at the south side of the field. Over the next 2 trapping intervals, beetle numbers were largest

toward the northern and eastern sides of the field. This general trend indicated an overall increase in beetle numbers in the northern and eastern portions of the field during the 10-day study.

Discussion

The results of this study indicate that capture-recapture techniques show some promise for future research of NCR and WCR adult population estimation and beetle movement. It is also apparent, however, that some problems typical of capture-recapture studies may alter or bias the results. I was unable to measure beetle deaths, emigration, and immigration, and the number of emergence traps used to determine "births" was probably too small for a desirable precision. The Jolly-Seber model is useful for estimating these dynamic processes, but the study was not designed for multiple-recapture analysis. Although the study was short-term, gross changes in beetle numbers revealed that the population was not closed and the dynamic processes were not in balance. For this reason, the Lincoln Index population size estimates are biased.

The increase in NCR numbers from 20 to 23 Aug. and the increase in WCR numbers from 20 to 28 Aug. suggest that beetle immigration from surrounding fields was greater than loss from the population (emigration + deaths). In addition, numbers of recaptures were not significantly different among trapping intervals. These factors affect the Lincoln Index estimates because n , the total numbers captured in the second sample, would increase and r , the number of

recaptures, would remain relatively constant. If this was the case, population size was overestimated. Another bias results from the fact that many beetles were recaptured near their original release sites. This violates the assumption of complete mixing of the population. Finally, the actual number of beetles released was approximated, and this, too, would bias the end result.

A comparison of Lincoln Index estimates and plant-count estimates (Table 16) indicates that population size is underestimated by counts of beetles/plant. This was a hypothesis before the study was initiated; but the large discrepancy between the 2 types of estimates is probably not realistic for several reasons. Results of Part II reveal that a sample size of 100 plants is too small for the precision desired in population ecology research. A larger sample size and more frequent samplings may have provided a better estimate of average beetles/plant. Secondly, the plant counts were taken at 3 specific times, whereas sticky traps sampled the population over 2-5-day intervals. As a result, average beetles/plant did not reveal the dynamic processes, especially immigration, occurring in the population. The random locations of the plant counts also did not adequately sample the northern and eastern portions of the field where increases in beetle numbers were noted for the last 2 trapping intervals. Finally, the probable overestimation of population size by the Lincoln Index, discussed previously, increases the gap between the 2 types of estimates. Plant counts will underestimate rootworm adult numbers, but the underestimation is probably

less drastic than indicated by this study.

For a study of this type, the recovery of any marked beetles is encouraging. The capture-mark-release process was effective and, with modification, is feasible as a technique to be considered for further study. Reliable measures of population gain (immigration + births) and loss (emigration + deaths) would improve the results obtained from such a study. With a more comparable sample size, plant counts could be calibrated with the capture-recapture results. If the experiment is designed properly, stochastic models that allow for dynamic processes in the population are available. Once absolute population estimates are obtained for adult corn rootworms by these techniques, comparisons can be made with larval populations and damage in the same fields the next year. Improvements might be realized in establishing economic thresholds and in predicting larval damage by counting beetles.

SUMMARY AND CONCLUSIONS

Because corn rootworms are perennial pests of corn and can cause severe economic losses, they have been the focal point for many corn insect control programs. For many years they have been controlled with planting-time insecticide applications, and the insecticides used are usually effective and easy to apply. Over the past 20 years, however, problems concerning insecticide overuse, misuse, and resistance have occurred. These factors, in conjunction with rising costs and increasing social awareness, have encouraged the development of corn insect pest management programs. Reliable economic thresholds and estimation of population size are necessary inputs into such programs. Research involved with these factors for corn rootworms has lagged behind some other areas of investigation. This study was designed to obtain information concerning spatial dispersion and population estimation of adult NCR and WCR. Data from the spatial dispersion study would provide some insight into how beetles arrange themselves in a homogeneous habitat and how their numbers vary in that habitat. Variation in numbers leads directly to the determination of sampling precision. Sampling precision and costs, then, are the major elements in the optimum allocation of sampling resources. The ultimate objective for this study, therefore, was to propose a standard rootworm beetle sampling plan which could be utilized by farmers and insect scouts to obtain reliable estimates of beetle populations. These estimates might

then be used to determine more reliable economic thresholds.

Three adult-sampling techniques were employed in 59 Iowa cornfields, ranging in size from 8.09 to 80.94 ha, during Aug., 1976 and 1977. All fields were divided into 4 equal quadrants, and the quadrants were subdivided into 4 equal plots. Each sampling technique was employed at the center of each of the 16 plots. The 3 sampling methods were: 10-plant count, 10-ear count, and sticky traps. The 10-plant and 10-ear counts were also partitioned into single-plant and single-ear components.

Counts of NCR and WCR adults obtained by these sampling methods were analyzed by 6 dispersion indices: (1) s^2/m ratio, (2) Green's coefficient (C_x), (3) Morisita's index (I_δ), (4) standardized Morisita's index (I_p), (5) Taylor's power law, and (6) Iwao's regression method. These indices and their respective tests of significance were used to identify the type of dispersion (uniform, random, or aggregated) displayed by rootworm beetles. All indices generally were consistent in identifying the same dispersion pattern for beetles in a cornfield. The interpretation of spatial dispersion was affected by sample unit, sampling technique, and relative beetle density.

Both NCR and WCR adults revealed a definite trend toward aggregation. Sixty-two percent of NCR and 75% of WCR populations sampled revealed aggregated dispersion. Of the 38% of NCR and 25% of WCR populations which did not differ significantly from random dispersion, most had very small mean densities. Some of the sampled

populations with relatively larger mean densities, however, also did not differ significantly from randomness. The fact that most populations with small mean densities do not differ significantly from randomness is supported by Taylor et al. (1978) who stated that true random dispersion is rare in animal populations and spatial behavior is density-dependent. Spatial dispersion in NCR and WCR adults appears to be density-dependent, but there are also obvious exceptions. The mechanisms of spatial behavior in rootworm beetles were not determined from this study.

Correlations of mean density and dispersion indices revealed that s^2/m and I_p were highly correlated with mean density. C_x and I_0 were usually not significantly correlated with mean density. Since the indices were consistent in identifying the same dispersion patterns, however, it appeared that correlation with mean density did not affect the analysis of aggregation or randomness. It was proposed that any of the indices and their respective tests of significance could be used to identify an organism's spatial dispersion.

Plant counts, ear counts, and sticky trap counts were analyzed with a nested analysis of variance procedure. Sources of variation in these analyses were fields, quadrants/fields, sites/quadrants, and plants or ears/sites. Examination of the variance components on a within-field basis revealed that plant-to-plant, ear-to-ear, and trap-to-trap variation accounted for the greatest percentage of total variability in their respective analyses. This indicated

that a large sample of plants, ears, or traps would be required for a very precise estimate of beetle density in a cornfield. Site-to-site and quadrant-to-quadrant variation were large enough to contribute significantly to the variance of a field mean.

Different allocations of sampling resources were selected for each sampling technique. The optimum allocations were 2 plants/site, 5 ears/site, and 1 trap/site. These optima were found by solving an equation which included both variance and cost components. The precision and overall cost (man-h) of each suggested sampling plan were determined. A comparison of plant, ear, and trap counts and their respective precision and cost showed that plant counts provided the most precise estimate of rootworm populations for the least cost. A systematic sampling plan in which all quadrants are sampled by plant counts was proposed as the most practical and least costly adult corn rootworm sampling technique.

A capture-mark-release-recapture technique was employed in a 15.78-ha cornfield near Ames, Iowa, during 18-28 Aug., 1978. The objective was to measure absolute population size of adult corn rootworms in the field. Approx. 50,000 beetles were captured, held in 5 cages distributed across the field, sprayed with fluorescent paint, and released on the same date of capture. Two hundred forty-one sticky traps were placed in a grid pattern across the field on each of 3 dates. All traps were examined for marked beetles under UV light, and numbers of both marked and unmarked beetles were recorded. An attempt was made to measure natality and migration into

and out of the field, and 10 randomly selected 10-plant counts were made on 3 dates as a population estimate comparison.

The simple Lincoln Index was used as a measure of absolute population and it was compared with 10-plant count estimates converted to absolute by multiplying average number of beetles/plant x plants/ha. The Lincoln Index estimates for the 3 trapping dates and for the overall study were much larger than the plant count estimates. It was concluded that plant counts underestimate rootworm beetle populations. It was also concluded, however, that some assumptions underlying capture-recapture techniques were violated in this study and that the Lincoln Index estimates were biased toward overestimation. The capture-recapture technique indicated possibilities for future use in studying rootworm beetle populations.

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