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ADULT POPULATION DYNAMICS AND OVIPOSITION OF NORTHERN AND
WESTERN CORN ROOTWORMS IN CONTINUOUS CORNFIELDS UNDER
COMMERCIAL PRODUCTION

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Adult population dynamics and oviposition of northern and western
corn rootworms in continuous cornfields under
commercial production

by

Gary Lee Hein

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TABLE OF CONTENTS

	PAGE
INTRODUCTION	1
Explanation of dissertation format	3
PART 1. AN ABSOLUTE SAMPLING TECHNIQUE FOR CORN ROOTWORM (COLEOPTERA: CHRYSOMELIDAE) ADULT EMERGENCE THAT ADJUSTS TO FIT COMMON ROW SPACINGS	4
Materials and Methods	5
Results and Discussion	8
PART 2. SEX RATIO SAMPLING AND SEX RATIO CHARACTERISTICS OF NORTHERN AND WESTERN CORN ROOTWORM (COLEOPTERA: CHRYSOMELIDAE) POPULATIONS IN CONTINUOUS CORNFIELDS	17
Materials and Methods	19
Results and Discussion	22
PART 3. DESIGN AND COST CONSIDERATIONS IN THE SAMPLING OF NORTHERN AND WESTERN CORN ROOTWORM (COLEOPTERA: CHRYSOMELIDAE) EGGS	34
Materials and Methods	36
Results and Discussion	39
PART 4. SEASONAL OVIPOSITION OF THE NORTHERN AND WESTERN CORN ROOTWORM (COLEOPTERA: CHRYSOMELIDAE) IN CONTINUOUS CORNFIELDS	50
Materials and Methods	51
Results and Discussion	54
PART 5. ADULT NORTHERN AND WESTERN CORN ROOTWORM (COLEOPTERA: CHRYSOMELIDAE) POPULATION DYNAMICS AND PREDICTIONS OF FINAL EGG POPULATIONS IN CONTINUOUS CORNFIELDS	64
Materials and Methods	66
Results and Discussion	70

	PAGE
PART 6. MODEL OF THE BIOTIC POTENTIAL OF WESTERN CORN ROOTWORM (COLEOPTERA: CHRYSOMELIDAE) ADULT POPULATIONS AND ITS USE IN STUDYING POPULATION DYNAMICS	87
Materials and Methods	90
Results and Discussion	94
SUMMARY	106
LITERATURE CITED	110
ACKNOWLEDGEMENTS	115

INTRODUCTION

The northern corn rootworm, Diabrotica barberi Smith and Lawrence, and the western corn rootworm, Diabrotica virgifera virgifera LeConte, have long been recognized as major pests of corn planted in a cropping sequence of corn following corn (continuous corn). These two species have similar univoltine life cycles. The adults of both species oviposit in the soil in late summer and fall, and the eggs overwinter in the soil. Egg hatch occurs the first part of June, depending on accumulated thermal units. As the larvae develop through three larval instars, they feed voraciously upon corn roots resulting in lodging and reduced yield. When larval development is complete, about a month after hatching, pupation occurs within cells in the soil. Adult emergence begins in early to mid-July.

Crop rotation was the only means of control until the development of synthetic insecticides after World War II. Since this time, the growing of continuous corn has become more economically feasible for many farmers in Corn Belt states. Effective control of corn rootworms has been one of the major reasons for this shift in farming practice. A common practice among farmers who raise continuous corn is the use of an insurance treatment of insecticides every year to avoid the possibility of rootworm damage. This practice of prophylactic use of soil insecticides is a major reason that corn ranks second in the U. S. in insecticide usage and first in total area treated (Eichers et al. 1976).

The increased reliance in many crops upon insecticides has, in many instances, led to the development of insect resistance to insecticides, presence of insecticide residues, and the adverse effect of insecticides on nontarget organisms, including man. These adverse effects of insecticide usage have led to an increased interest in pest management where chemical control alternatives are used only when damaging populations are present (National Academy of Sciences 1969). The insect pest management philosophy calls for "reducing the pest status of detrimental insect populations to levels of toleration by modulating the species life system, while producing minimal alterations in the agroecosystem of which the species is a part" (Pedigo 1975). Fundamental to the implementation of the pest management concept is the development of sampling techniques that adequately measure the population and enable damage prediction.

The desire to predict corn rootworm larval damage has led to the development of many sampling methods for all life stages. Currently, the adult stage seems to be the most promising in developing predictive techniques. Studies by Foster (1983) and Hein and Tollefson (1984b) have shown that, while adult sampling estimates are important in predicting subsequent larval damage, these estimates alone do not adequately predict corn rootworm damage. The reason for the lack of predictability is likely the result of factors acting on the rootworm populations during the 9-10 month period between adult sampling and the occurrence of larval damage. The factors affecting rootworm populations during this period are not well-understood. Effective rootworm damage

prediction utilizing adult sampling will rely, in part, upon a complete understanding and quantification of adult population dynamics and ovipositional relationships.

The objective of these studies was to investigate and quantify, where possible, the parameters involved in corn rootworm dynamics and their relationship to oviposition and seasonal egg populations. Investigations in these areas led to the development of sampling techniques for adult rootworm emergence and adult sex ratios. The sizable amount of egg sampling performed led to a re-evaluation of the current knowledge of oviposition and egg sampling. A final area of investigation involved the incorporation of the available literature into a western corn rootworm model of adult populations and oviposition.

Explanation of Dissertation Format

This document contains six manuscripts written for publication in entomological journals. Research for these studies was performed primarily from 1981 through 1984 at Iowa State University on the Corn Soil Insects Research Project by myself. The trap described in Part 1 was originally designed by Drs. Marlin Bergman and Robert Bruss at Iowa State University, with later improvements added by myself. The 1979 data utilized in Part 1 was collected by Dr. Bergman. Co-authorship of Part 1 will be shared with these researchers. Part 5 contains adult and egg sampling data collected by Dr. Rick Foster and myself from 1979-1981. Publication including these data will involve co-authorship with Dr. Foster.

PART 1. AN ABSOLUTE SAMPLING TECHNIQUE FOR CORN ROOTWORM
(COLEOPTERA: CHRYSOMELIDAE) ADULT EMERGENCE THAT
ADJUSTS TO FIT COMMON ROW SPACINGS

Management of the northern and western corn rootworm, Diabrotica barberi Smith and Lawrence (NCR) and D. virgifera virgifera LeConte (WCR), respectively, has largely dealt with the utilization of adult sampling techniques to reach control decisions. Recent studies by Foster (1983) and Hein and Tollefson (1984b) have shown that adult sampling techniques provide inadequate prediction of subsequent larval damage. Few studies on the dynamics of adult rootworm populations have been done, however, and damage predictions may be improved with additional knowledge of adult population dynamics. Research in this area necessitates the development of an absolute sampling technique for corn rootworm adult emergence that can be readily utilized in commercial production fields to study field populations of adult corn rootworms.

A number of sampling techniques have been used to monitor adult rootworm emergence. Short (1970), Musick and Fairchild (1970), and Pruess et al. (1968) have utilized traps that do not sample the entire row width and provide only relative estimates of emerging adults. Branson and Ortman (1967) and Hill and Mayo (1974) used walk-in cages 0.91 m and 1.83 m square, respectively. These traps do provide absolute estimates for a single common row spacing (0.91 m). But, the use of these large traps is labor intensive, and beetle collection within the cage compacts the soil which may influence beetle emergence. Traps

utilized by Ruppel et al. (1978) and Fisher (1980) provide absolute estimates for 0.91 m and 1.02 m row spacings, respectively. The general design of these traps is desirable in that they are relatively portable; however, they are not applicable for use as absolute methods in different row spacings which would necessitate multiple sets of traps. None of these studies on adult emergence traps have cited trap variability or given optimum sampling pattern and estimates of necessary sample sizes.

One objective of this study was to develop and field test a trapping technique that provides an absolute population estimate of adult NCR and WCR corn rootworm emergence. A second objective was to determine the optimum sampling pattern and estimate sample sizes for adult NCR and WCR emergence sampling. Criteria important for this trapping technique include portability, ease of maintenance, minimum environmental disturbance, and capacity to adjust to several common row spacings.

Materials and Methods

The trap developed consisted of a wood frame with a pyramidal screen, approximately 50-cm high, attached to the top of it. The frame was made with two U-shaped halves, each constructed from three pieces of 1x4 wood, cut and assembled as shown in Figure 1. Holes drilled in the side of the frame as shown were used to bolt the two halves together to form a rectangular frame with the inside length equal to the desired row width. Row width adjustments were made from 76.2 cm (30 in) to 101.6 cm (40 in) in 5.1-cm increments.

During early testing the screen covering was made of 18x16 mesh fiberglass screening. This screen proved very susceptible to cricket and grasshopper feeding, with many screens lasting only a single season. To avoid this problem, 18x16 mesh aluminum screening was used to cover the cages. Excessive sewing of the screens was eliminated by cutting the screens from 91.4 cm wide material using the pattern represented in Figure 2. Right angle creases were made along each of the four dotted lines in Figure 2, and the two adjoining edges were brought together to form 2.5 cm interlocking creases. Braided nylon fishing line was used to tightly secure these interlocking flaps (Figure 1). Screens were then attached to the wood frame using wood stripping. Adjustment to the proper row width involved loosening the center area of the screen from the frame, setting the frame to the desired row width, and refastening the screen.

Placement of the trap in the field involved first cutting off the plant approximately 50 cm above the ground. If a ridge was present in the row, furrows were dug across the ridge to enable the trap to lie level. Care was taken to minimize disturbance within the trap area. Loose soil was moved up around the outside of the frame to adequately seal the base.

Beetles emerging within the trap moved upwards and were trapped in a 0.47 l cylindrical paper carton placed over the cornstalk. The container, coated internally with Tack Trap[®], had an X-shaped slit cut in the bottom to facilitate the cornstalk and was held near the apex of the trap by a nail inserted through the cornstalk. Checking the trap

involved lifting the trap, replacing the container, and resealing the base of the trap with loose soil.

Seasonal emergence was monitored in 12 Iowa cornfields (ca. 4-20 ha) in 1979-1983. In 1979, two, six-row strips running the entire length of the field were sampled in each of four fields. These strips were the only areas of the field that were not treated with a soil insecticide to control rootworm larvae. Fields were sampled by dividing each untreated strip in half, forming four quadrats, randomly selecting three sites within each quadrat, and locating two traps near each site (24 traps/field). Three fields each in 1981 (20 traps/field) and 1982 (30 traps/field) and two fields in 1983 (40 traps/field) were sampled utilizing a stratified random sampling plan covering the entire field. All fields in 1981-83 were treated with planting-time insecticides to control rootworm larvae, and all sampling occurred in treated areas. Traps were placed in early-to-mid July and checked weekly through the season. Traps were moved to new sites approximately two weeks after initial placement to minimize possible adverse effects on larval survival from cutting the plant off at the time of trap placement.

Analysis of the 1979 data included the use of nested analysis of variance procedures to determine the variance components for quadrats within fields, sites within fields and quadrats, and traps within fields, quadrats, and sites. These variance estimates (s_i^2) along with sampling cost estimates (c_i) were used to estimate the optimum number of subsamples (n_i) within each stage (i) of the three-stage sampling plan.

The equations were those of Snedecor and Cochran (1967):

$$n_t = \sqrt{c_q s_t^2 / c_t s_q^2} \quad (1)$$

$$n_q = (s_q^2 n_t + s_t^2) / V_{\bar{x}} n_t \quad (2)$$

where q and t represent quadrats and traps within quadrats, respectively. $V_{\bar{x}}$ is the variance of the mean at the desired precision (SE/ \bar{x}) level and is calculated by squaring the product of the mean and the desired precision level. Analysis of variance procedures were used to exclude field-to-field variation for the data from all years and fields to get variance estimates of NCR and WCR adult emergence. Estimated sample sizes can be obtained by using the resulting mean (\bar{x}) and standard deviation (s) in Southwood's (1978) equation:

$$n = (s / E \bar{x})^2. \quad (3)$$

In this formula, E is the desired standard error expressed as a decimal of the mean.

Results and Discussion

The general performance of this trap was very good. Absolute population estimates can be obtained by using the area values in Table 1. The trap was portable enough for use throughout large fields and resulted in population estimates of reasonable accuracy. However, an occasional gravid female was observed in these traps. The presence of gravid females in the traps indicates a sampling error, because traps were checked approximately once per week. The preovipositional period for WCR females is 12-14 days (Branson and Johnson 1973 and Hill 1975). Kuhlman (1970) noted the preoviposition period for the NCR was slightly less than for the WCR. Entrance to the trap via drought cracks is

possible, but this could be minimized by proper sealing of the trap base with loose soil.

The effect of the trap on the microenvironment near the plant base was not quantified. Evaporation of moisture following a rain was observed to be slower within the trap area, indicating possible microenvironmental effects. Fisher (1984) found no effect of cutting the plant on total rootworm emergence, but an acceleration of seasonal emergence was observed from areas of cut plants compared to uncut plants. He attributed this acceleration to increased humidity and temperature within the caged area due to removal of the canopy. After being cut, the remaining stalk remained alive, and the roots appeared sound for a number of weeks. The effect of plant cutting may be reduced by moving the trap to a new location after the first few weeks. This enables sampling from unaffected areas through the time of peak emergence (late July through early August).

Nested variance components for the 1979 NCR and WCR emergence data, along with estimated component costs of sampling, are shown in Table 2. The cost of sampling a quadrat involves only the time to walk from one quadrat to another (1 human-min x 10). The cost of sampling a site involves the time to move from site to site within a quadrat (0.5 human-min x 10). These costs are estimated for the first trap placement of the season, plus nine changes of the cup through the season. The trap costs include the cost of initial placement of the trap (5 human-min), the cost of changing the collection cup through the season (1 human-min x 9), the time to count the nine collection cups from one

site (0.5 human-min x 9), and the cost of making the collection cups (\$.19 each=2.5 human-min at \$4.50/h). If the determination of the sex of the trapped beetles is necessary, the additional cost of cleaning and sexing the beetles must be added (3 human-min x 9). These costs are estimates determined from field-times required to carry out emergence sampling in the field, throughout this study.

These data were utilized to estimate the optimum sampling scheme for adult NCR and WCR emergence using equations 1 and 2. The calculations resulted in the optimum number of sites within quadrats and traps within sites being one. Therefore, the optimum sampling scheme for corn rootworm emergence is a one-stage sampling plan utilizing a large number of quadrats and only one trap per quadrat. The number of quadrats necessary was calculated using all the data collected for this study.

The mean total seasonal emergence of the 12 fields, along with the ranges, are given in Table 3. Variance and mean estimates from these data were used in equation 3 to estimate sample sizes for NCR and WCR seasonal adult emergence sampling. The sample sizes needed to obtain an estimate with a standard error within 10% of the mean for the WCR and NCR are 80 and 222, respectively. If those fields with extremely low NCR populations are excluded, this estimate of the sample size drops dramatically to 126. The correct sample size for this trap may vary with the field population being sampled. These estimates should provide a guideline for the use of this trap to obtain absolute estimates of emerging field populations of corn rootworm adults.

Table 1. Trapping area of adjustable emergence traps at various row spacings

Row Spacings	Trapping Area	
	m ²	ft ²
76.2 cm (30 in)	0.282	3.03
91.4 cm (36 in)	0.342	3.68
96.5 cm (38 in)	0.362	3.90
101.6 cm (40 in)	0.382	4.11

Table 2. Variance components and estimated sampling costs for NCR and WCR adult emergence, 1979

Source of Variation ^a	Degrees of Freedom	Variance Components		Sampling Cost ^b
		----- NCR	WCR	
Fields	3	6.79	31.45	--
Quadrats/F	12	17.16	17.20	10
Sites/F/Q	32	1.34	5.13	5
Traps/F/Q/S	47	7.77	51.30	41(68) ^c

^a F=Fields; Q=Quadrats; S=Sites.

^b Cost in human-min.

^c Estimate in parentheses includes cost of sex determination.

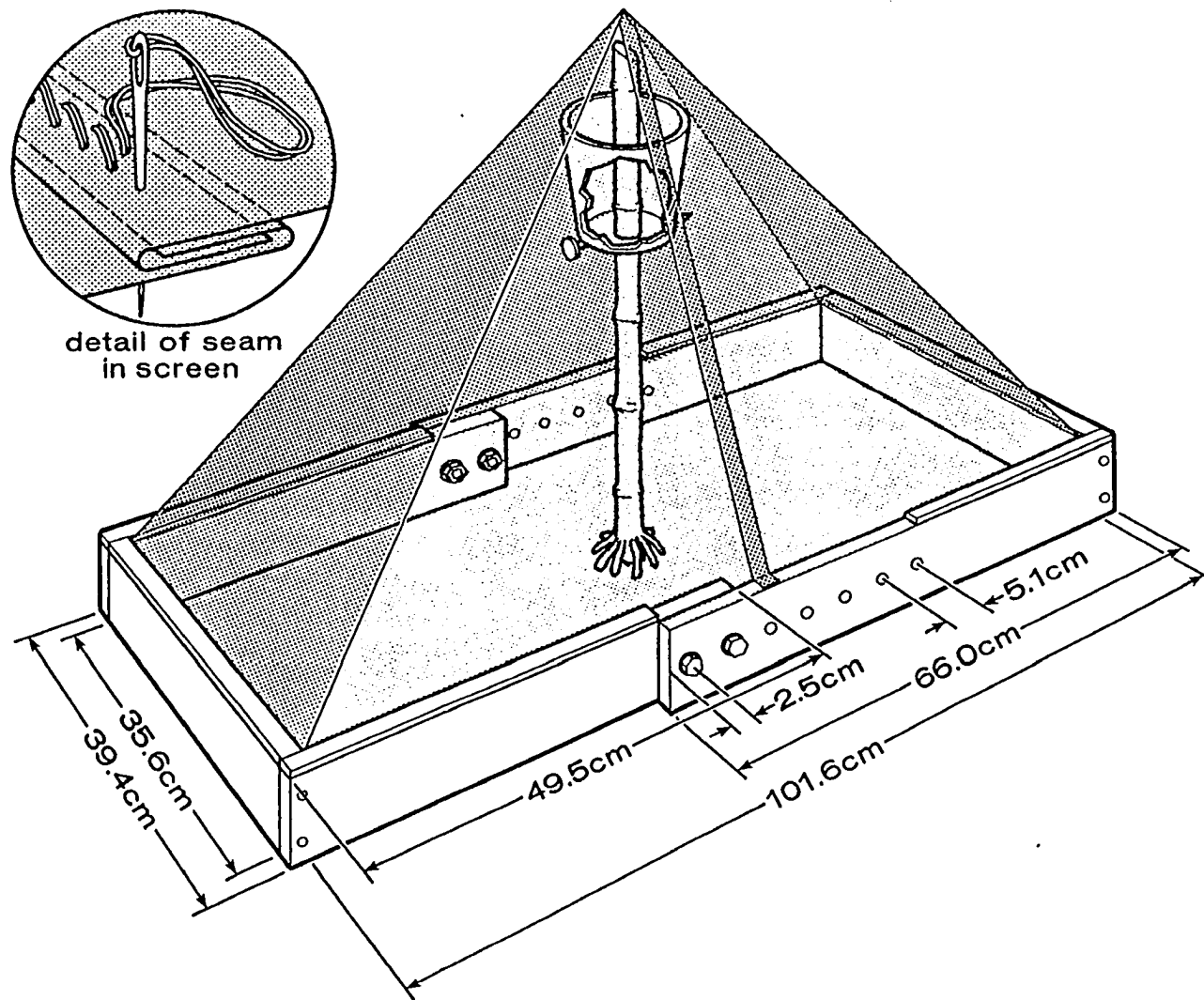
Table 3. Mean seasonal emergence, variability, and estimated sample size for the adjustable emergence trap

Variable	Mean ^a	Range	Standard Deviation	Est. Sample Size	
				E=0.10	E=0.25
NCR+WCR	15.1	4.9-29.3	12.7	71	11
WCR	10.4	2.4-22.6	9.3	80	13
NCR	4.7	0.5-25.4	7.0	222	35
NCR	9.1 ^b	2.5-25.4	10.2	126	20

^a Expressed as beetles per trap; n=12.

^b Fields with means below 2.5 excluded; n=6.

Figure 1. Design, construction, and placement of row-adjustable emergence trap



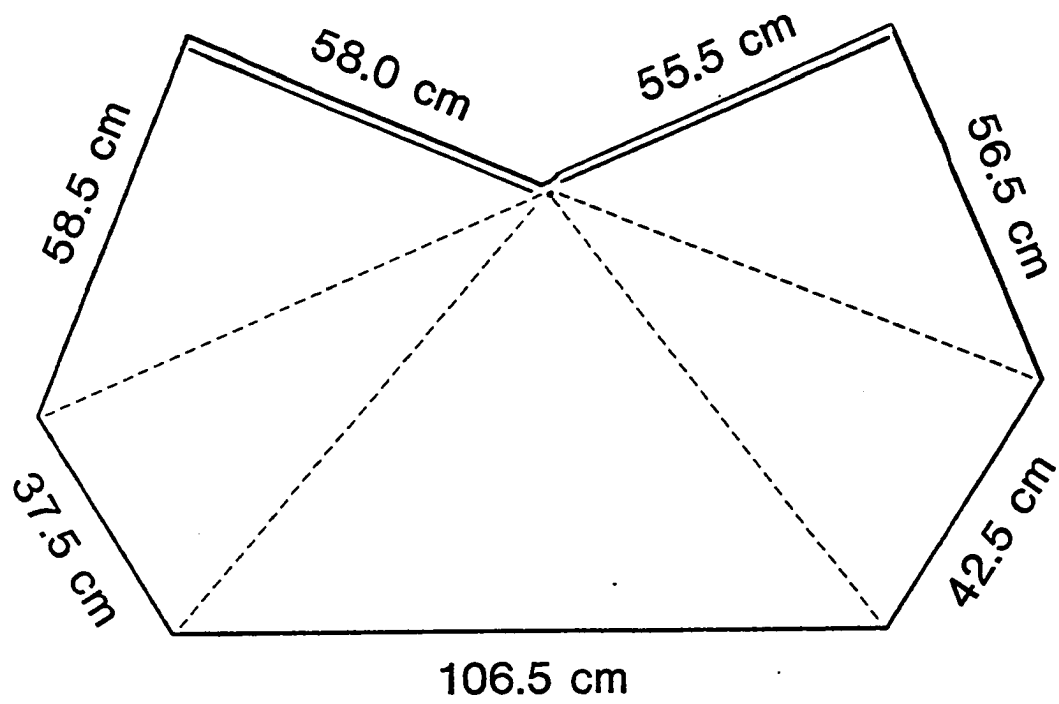


Figure 2. Diagram of screen pattern used for row-adjustable emergence trap

PART 2. SEX RATIO SAMPLING AND SEX RATIO CHARACTERISTICS OF
NORTHERN AND WESTERN CORN ROOTWORM (COLEOPTERA:
CHRYSOMELIDAE) POPULATIONS IN CONTINUOUS CORNFIELDS

The northern and western corn rootworm, Diabrotica barberi Smith and Lawrence (NCR) and D. virgifera virgifera LeConte (WCR), respectively, are univoltine pests of corn grown in a yearly crop rotation of corn following corn (continuous corn). The adults lay eggs in the soil in the summer and fall. The larvae hatch the following year and cause serious damage to corn planted in the same field. Management of these insects has relied upon the use of adult sampling to predict the likelihood of damaging populations the following year. Recent studies by Foster (1983) and Hein and Tollefson (1984b) have shown that, while adult sampling estimates are important in predicting subsequent damage, these estimates alone do not adequately predict rootworm larval damage. This lack of predictability is probably due to factors that affect rootworm populations from the sampled adult stage through the damaging larval stage, 10 months later. This paper deals with one aspect of adult rootworm behavior and population dynamics that may be important in improving damage predictions.

Studies on the sex ratios of corn rootworm populations have utilized different relative sampling techniques. Short and Hill (1972) utilized a 10-min collection period to sample fields for WCR sex ratios.

They found that in July and early August the sex ratio of WCR was less than 50% female. By mid-August, the sex ratio had become greater than 50% female, with the greatest proportion of females occurring near the end of the third week of August. Godfrey and Turpin (1983) used cylindrical sticky traps placed at ear level to study sex ratios of WCR in first-year and continuous corn. They observed the proportion of females to be much lower than those reported by Short and Hill (1972), approximately 10-15% female at mid-August in continuous corn and 50% by mid-September. First-year cornfields were found to have a higher proportion of females following the first week of August. Proportions determined from collections made by Godfrey and Turpin (1983) in the same fields resulted in estimates 8-40% higher than those determined from sticky traps.

Sex differences in the height of flight of adult corn rootworms were noted by Witkowski et al. (1975), using 3.05 m high sticky traps, and Hein and Tollefson (1984a), using cylindrical sticky traps near ground level and at ear height. These differences indicate that sex ratio estimates may be biased, depending upon the height samples are taken. If height biases do occur, they would be important in determining the accuracy of sex ratio sampling techniques. No work has been done to determine the accuracy of the relative methods used in determining sex ratios of field populations.

The sampling technique chosen to most accurately sample the entire adult population was the yellow, vertical 3.05 m cylindrical sticky trap used by Witkowski et al. (1975). Sex ratios determined from using this

trap should not be biased due to vertical flight differences between the sexes. Tollefson et al. (1975) and Ball (1982) demonstrated the attractiveness of yellow for rootworm adults; however, neither author investigated the possibility of a sex bias toward yellow. The assumption of equal attractiveness of males and females to yellow is supported by Agee et al. (1983), who found, through the use of an electroretinograph, that neither species showed sex-related differences in spectral sensitivity. Proportionate sampling of each sex also involves the assumption that both sexes have equal activity rates within the canopy. VanWoerkom et al. (1980), in laboratory studies, found WCR adult males to be generally more active than females, except at higher temperatures ($>27^{\circ}\text{C}$) where females were more active. Inasmuch as seasonal temperatures are often near or above 27°C , proportionate sampling of each sex is a reasonable assumption. However, the possibility of a slight temperature-dependent activity bias does exist.

The objectives of this study were to test the 3.05-m sticky pole as a NCR and WCR adult sex ratio sampling tool. Because of the intensive labor requirements of this sampling method, subunits were evaluated for their relationship to the overall sex ratio to find the optimum height to obtain accurate sex ratio estimates. Utilizing this method, the height of flight of both sexes and species and the sex ratio differences through the season were determined.

Materials and Methods

Studies were conducted in five, continuous cornfields (ca. 4-20 ha). Fields were located in central (1982, two fields; 1983, one field),

northeast (1982, one field) and southwest (1983, one field) Iowa. All fields were managed using commercial production practices, including rootworm insecticides applied at planting time. During both years, sampling began approximately 13 August and continued through 14 September. In 1982, each field was sampled for three, 7-10 day intervals. Fields were sampled for three or four 3-8 day intervals in 1983, and two additional early August sampling dates were taken in one field in 1983 using a 10-h sampling period.

Plastic PVC pipe, 10.2 cm in diameter and 3.05 m in length was painted Crown Yellow (AZ-3401, Vogel Paint and Wax Co., Inc., Orange City, Iowa), coated with Tack Trap[®], and wrapped in wax paper until deployment in the field. Six and four traps per field were used in 1982 and 1983, respectively. Traps were placed upright over metal fence posts driven into the soil in the corn row and the wax paper removed. Locations for traps were randomly selected from 30 (1982) or 40 (1983) sites per field, systematically established to cover the entire field. Upon removal, the traps were wrapped in plastic and returned to the lab where all beetles were counted and up to 50 beetles removed from each 0.305-m increment of the trap. Beetles were soaked in oleum to dissolve the Tack Trap, their sex determined, and the proportion of females in each 0.305-m increment determined. Total trap catch was determined and the sex ratio estimated for the entire trap and each 0.305-m increment.

An additional study of seasonal adult corn rootworm sex ratios was done in 1978 and 1979 using unbaited, Pherocon[®] AM traps and cylindrical sticky traps. Pherocon AM traps were purchased through Zoecon Corp.

(Pherocon Supply Service, 975 California Ave., Palo Alto, CA) and the cylindrical sticky traps were constructed from 0.94 l paper ice cream cartons, as described by Hein and Tollefson (1984a). Nine and eight traps of each trap type were placed at ear height in each of three (1978) and 15 (1979) fields, respectively. The trapping sites were established systematically to cover the entire field. Sampling began the first week of August and continued at weekly intervals until the first week of September. Total NCR and WCR catch was determined, and up to 25-50 beetles of each species were removed and their sex determined.

All sex ratios were determined separately for each species and expressed as proportion female. Pole-trap and 1978-79 sticky trap sex ratios, based on a total catch of less than 50 and 10 beetles, respectively, of a single species, were excluded from analyses for that species. Paired t-tests were run to determine sex and species differences within height increments of the pole traps. Estimates of sample size (n) were determined using Southwood's (1978) equation:

$$n = (s / E \bar{x})^2. \quad (1)$$

In this equation, E is the predetermined level of precision (SE/\bar{x}). The standard deviation (s) and the mean (\bar{x}) were estimated using nested analysis of variance techniques to estimate within field variation. Correlation and regression techniques were utilized to establish possible relationships among trap sex ratio estimates and between these estimates and Julian date.

Results and Discussion

Population levels in the fields sampled ranged from low to high for both species. Counting adults on entire plants and using plant population to convert to beetle density estimates showed there was a NCR population range of $13.5-257.6 \times 10^3$ adults/ha with a mean for the five fields of 71.0×10^3 adults/ha. The range for the WCR was $35.8-177.4 \times 10^3$ adults/ha with a mean of 88.2×10^3 adults/ha.

Adult flight within corn canopy

Figures 1 and 2 show that both species fly most frequently at intermediate heights within the corn canopy. A comparison between sexes of both species shows a higher percentage of males fly at lower levels, with the flight of WCR males showing a prominent peak height of flight at 0.30-0.61 m. The females of both species show a greater proportion of flight at higher levels. The highest proportion of NCR females caught was at 2.14-2.44 m, and the highest proportion of WCR females caught was at 1.22-1.52 m.

The average height of flight of each sex and species was determined for each 3.05-m trap. The estimated catch for a single sex and species at each height increment was multiplied by the height at the midpoint of that increment. These products were summed for each pole trap and divided by the total catch of the respective sex and species. These calculations resulted in the sex and species heights of flight shown in Table 1. NCR adults fly higher within the canopy than WCR adults, and the females of both species fly higher than males. These data show that the height of sampling would affect the accuracy of NCR and WCR sex

ratio estimates. Correlations between the average increment of flight and Julian date are also shown in Table 1. No seasonal variation in the height of flight was observed for the NCR. For the WCR, however, significant correlations indicate a tendency for lower flight levels for females and higher flight levels for males later in the season.

Sex ratio sampling

The use of the 3.05-m cylindrical sticky trap is assumed to give an unbiased estimate of the population sex ratio. This method gave accurate ($SE < 10\%$ of \bar{x}) estimates of both WCR and NCR sex ratios at both sampling sizes used ($n=6$ and 4).

The labor intensive nature of this sampling technique (5-8 human-h/field/sampling date) make it feasible for use only as a research sampling tool. For this reason, analysis of these data was performed to determine the most appropriate height at which to sample NCR and WCR adult sex ratios. A plot of the sex ratio at each height increment shows differences in the estimates of the sex ratio produced at each height increment (Figure 3). These differences are much more pronounced for the WCR than for the NCR. The WCR sex ratio determined using beetle catch from all height increments was 0.66. This estimate of the sex ratio is very close to the estimate obtained at height increment four (0.92-1.22 m). The NCR sex ratio determined from all height increments was 0.41, which is close to the estimates at height increments one, three, four, six, and seven. Estimates of the sex ratio obtained at these levels should give reasonable estimates of the population sex ratio within the corn canopy.

A further test of the accuracy of the sex ratio estimates obtained at each height increment was done by comparing, for each species, the proportions of the total male and female catch for the entire pole caught at each increment. The increment where equal proportions of the total catch for each sex were caught should produce the most accurate estimate of the sex ratio. Figures 1 and 2 graphically show these comparisons for the NCR and WCR, respectively. Paired t-tests were run to test the equality of the male and female proportions for each species at each height. Equal proportions of male and female WCR were caught only at height increment four (0.92-1.22 m), matching the optimum height of sex ratio estimation in Figure 3. The correlation between WCR sex ratios, determined for each field and sampling date from the entire pole and height increment four, were highly significant ($r=0.91$, $P<0.01$, $n=18$). The proportions of each sex caught for the NCR were equal for height increments one, four, and six. But only the correlations between the NCR sex ratios, determined for each field and sampling date, using the entire pole and height increments four ($r=0.81$) and six ($r=0.85$) were significant ($P<0.01$, $n=15$). The results of these analyses along with the information presented in Figure 3 indicate the optimum height to sample for NCR sex ratio to be height increment four (0.92-1.22 m) and six (1.52-1.83 m). Inasmuch as, both NCR and WCR populations are likely to be sampled at the same time, the best height to sample for sex ratios of adult NCR and WCR populations is from 0.92-1.22 m. This height is at or just below ear height for most corn varieties.

The deployment of sticky traps at ear height was utilized by Hein and Tollefson (1984a) and Godfrey and Turpin (1983). Data collected in 1978 and 1979 using the unbaited Pherocon AM trap and the cylindrical sticky trap, each placed at ear height, show the usefulness of utilizing these traps to sample for adult corn rootworm sex ratios. Correlations between the mean sex ratios obtained using these two trapping methods were highly significant ($P < 0.01$) for both species. But the correlation for the WCR of 0.94 ($n=63$) was much higher than for the NCR ($r=0.56$, $n=39$). Because of this high correlation and excellent sampling efficiency for the WCR (SE within 10% of \bar{x}), either trapping technique should provide an equally good estimate of the field sex ratios. The low correlation between the two methods for the NCR sex ratio is probably due in large part to much larger sample variability (SE within 25-30% of the \bar{x}).

Means and within-field estimates of variation determined from nested analysis of variance techniques were used in equation 1 to estimate sample size. Sample sizes needed to obtain a standard error within 10% of the mean ($E=0.10$) for the NCR were 51 and 75 for the Pherocon AM trap and the cylindrical sticky trap, respectively. Estimates of sample sizes needed to obtain a standard error within 20% of the mean ($E=0.20$) for the NCR were 13 and 19 for the Pherocon AM trap and the cylindrical sticky trap, respectively. Estimates within 10% of the mean for the WCR for both sampling techniques may be obtained by using only six traps.

Seasonal sex ratio patterns

An advantage of having an accurate sex ratio sampling tool is to be able to measure sex ratio changes within field populations. These sex ratio changes would be important in establishing the reproductive potential of adult corn rootworm populations within a field.

Correlations between field sex ratios, estimated using the 3.05-m sticky traps and Julian date, were not significant for either species. But examination of the graph of these data indicated much lower sex ratios for a single field. This field had received severe hail damage in July causing a reduction and premature drying of foliage, producing a very "open" field. As a result, this field was a very atypical cornfield throughout August. Because of the significantly reduced sex ratios in this field, it was thought that a disproportionately large number of females left this field due to some factor resulting from the severe hail damage. The correlation between sex ratio and Julian date were again run without the data from this field. The resulting correlation coefficients were 0.72 (n=13) and 0.73 (n=15) for the NCR and WCR, respectively. Both correlations are significant ($P < 0.01$) and their relationships are shown in Figures 4 and 5.

The relationship between sex ratios and Julian date was established by combining the 1978-79 and the 1982-83 sex ratio data. Significant ($P < 0.01$) regressions of sex ratios on Julian date were obtained for the NCR ($R = 0.27$, $n = 85$) and the WCR ($R = 0.49$, $n = 97$). These relationships along with the regression equations describing them, are shown in Figures 4 and 5. WCR sex ratios continue to increase through August

and do not show the decline in the proportions of females in the field in late August shown by Short and Hill (1972). The data from only the field severely damaged by hail indicate the low female proportions shown by Godfrey and Turpin (1983).

The data revealed a good deal of the variability not accounted for by the linear relationship between sex ratio and Julian date was due to differences between years and fields. To estimate the extent to which this affected the relationship, partial correlation coefficients were determined between sex ratio and Julian date with the effect of years and fields partialled out. The resulting partial correlations for the NCR and WCR were 0.65 (d.f.=62) and 0.90 (d.f.=74), respectively. The lower correlations and partial correlations for the NCR could be due to the larger sampling error involved in sampling the NCR sex ratios in 1978-79. These results show that differences between fields account for 15 and 32% of the overall variability between NCR and WCR sex ratios and Julian date, respectively. The reasons for these differences in sex ratios between continuous cornfields are not known, but the importance of this fact in establishing a complete understanding of NCR and WCR population dynamics indicates a need for further research in this area.

Table 1. Average height of flight of NCR and WCR adults and correlations (r) between height of flight and Julian date

Species-Sex	n	Mean Height (m)	r	P>r
NCR	15	1.42	0.22	0.44
males	15	1.30	0.01	0.98
females	15	1.57	0.18	0.53
WCR	18	1.21	0.13	0.61
males	18	0.89	0.49	0.04
females	18	1.42	-0.52	0.03
(LSD=0.18)				

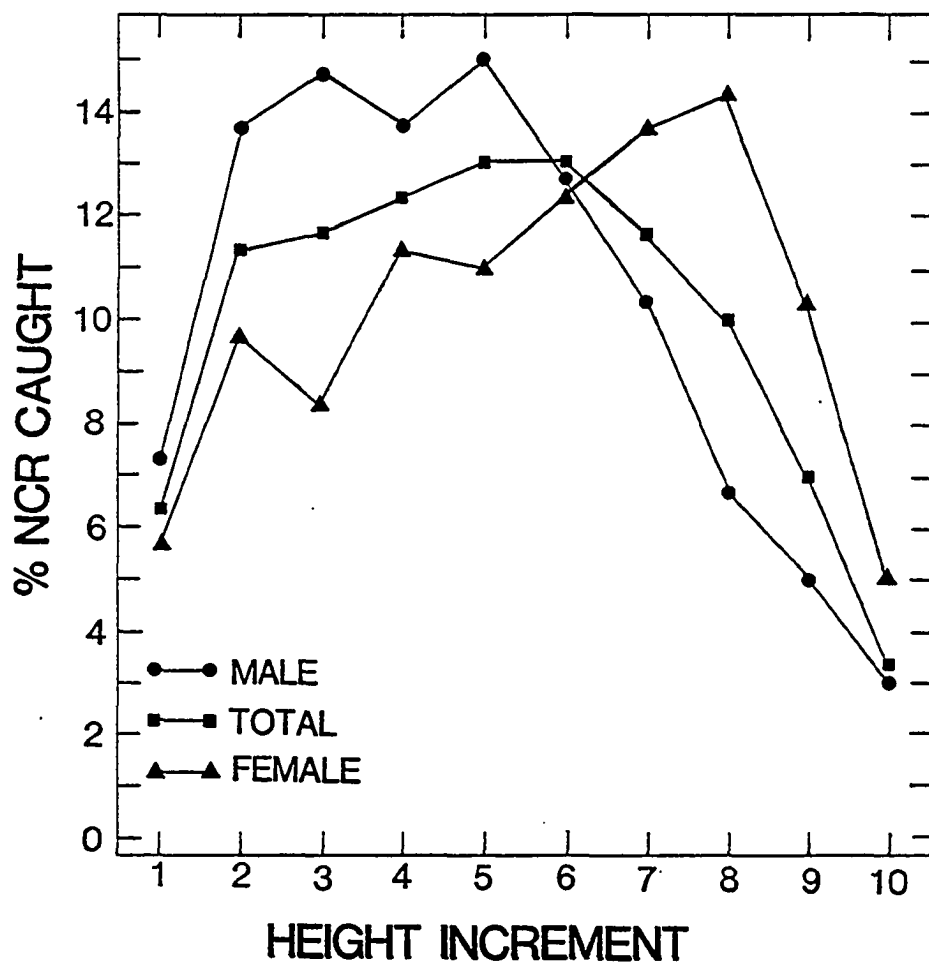


Figure 1. Percentage of NCR males, females, and total adults caught within each 0.305-m increment of the corn canopy using the 3.05-m vertical sticky trap

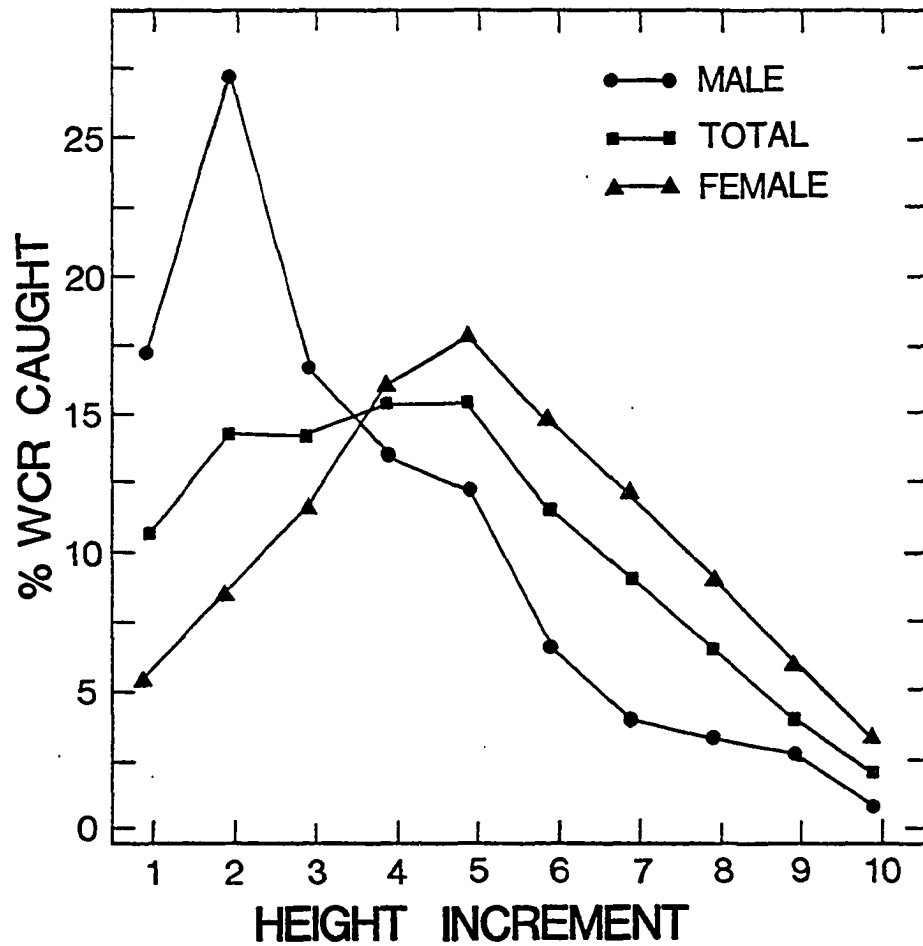


Figure 2. Percentage of WCR males, females, and total adults caught within each 0.305-m increment of the corn canopy using the 3.05-m vertical sticky trap

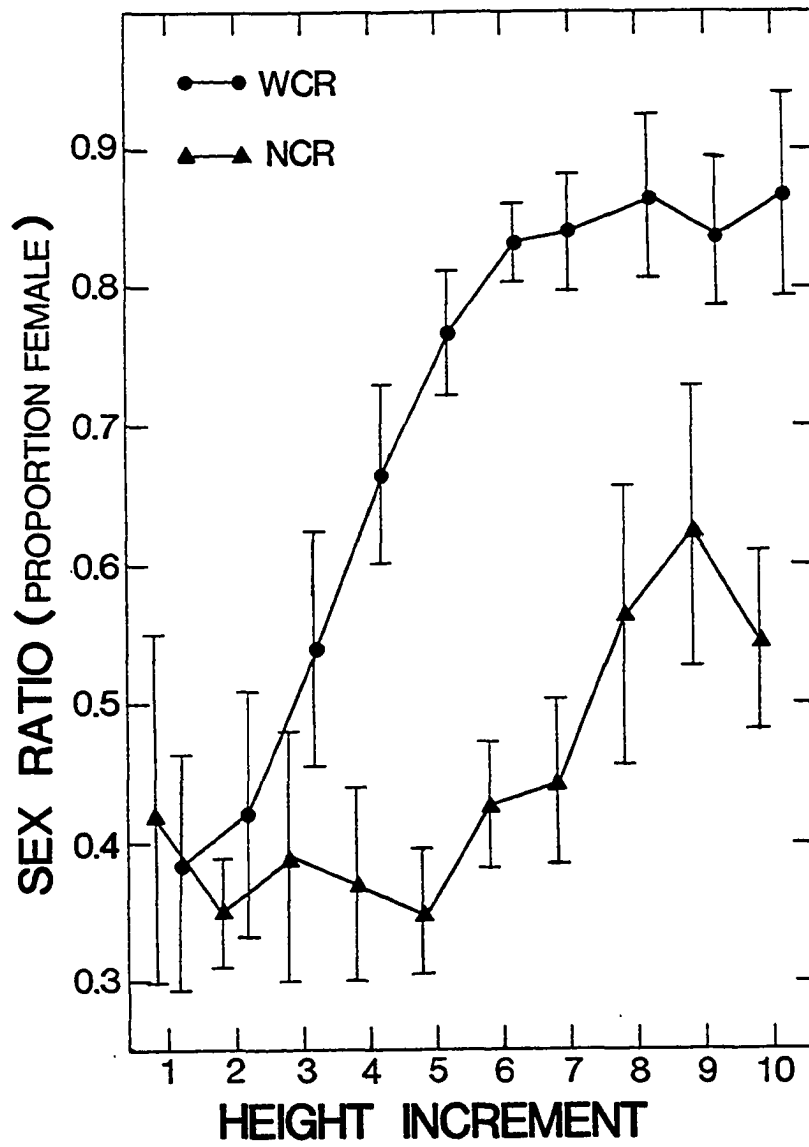


Figure 3. Mean NCR and WCR sex ratios of the catch at each 0.305-m increment of the 3.05-m vertical sticky trap (vertical bars=95% confidence intervals), 1982-83

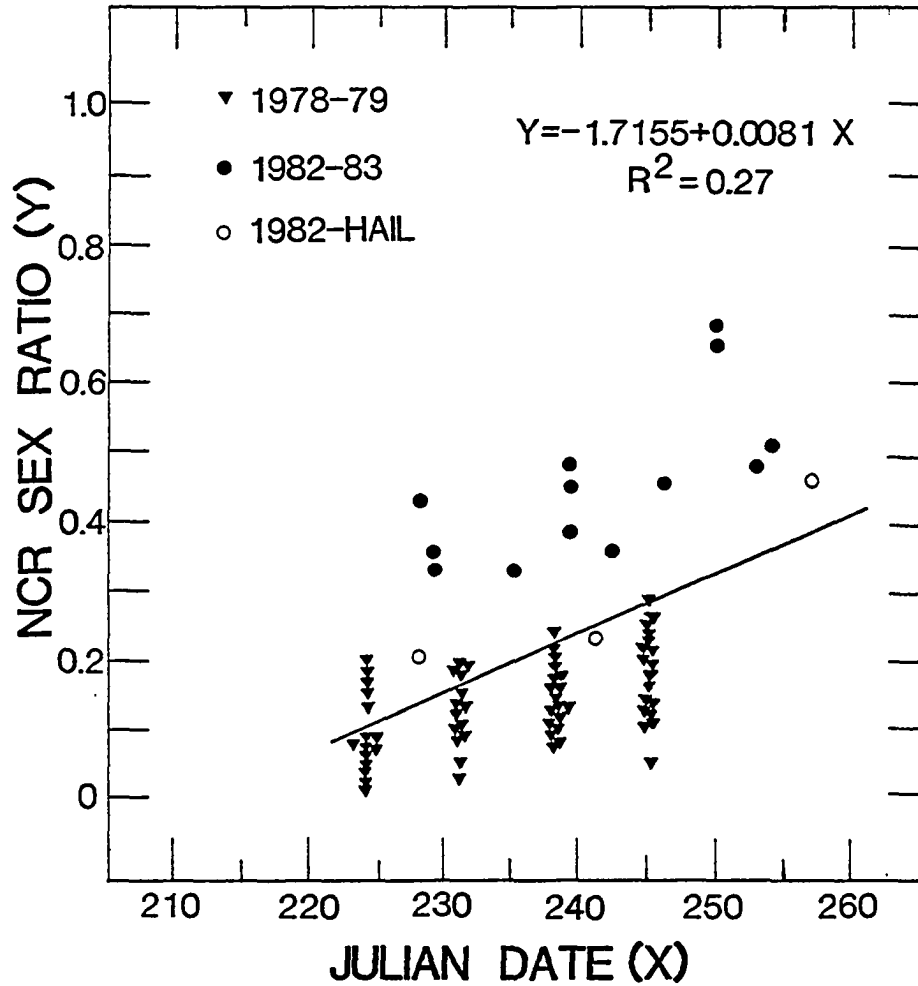


Figure 4. Relationship between NCR field sex ratios, estimated using 3.05-m vertical sticky traps (1982-83 data) and sticky traps at ear height (1978-79 data), and Julian date

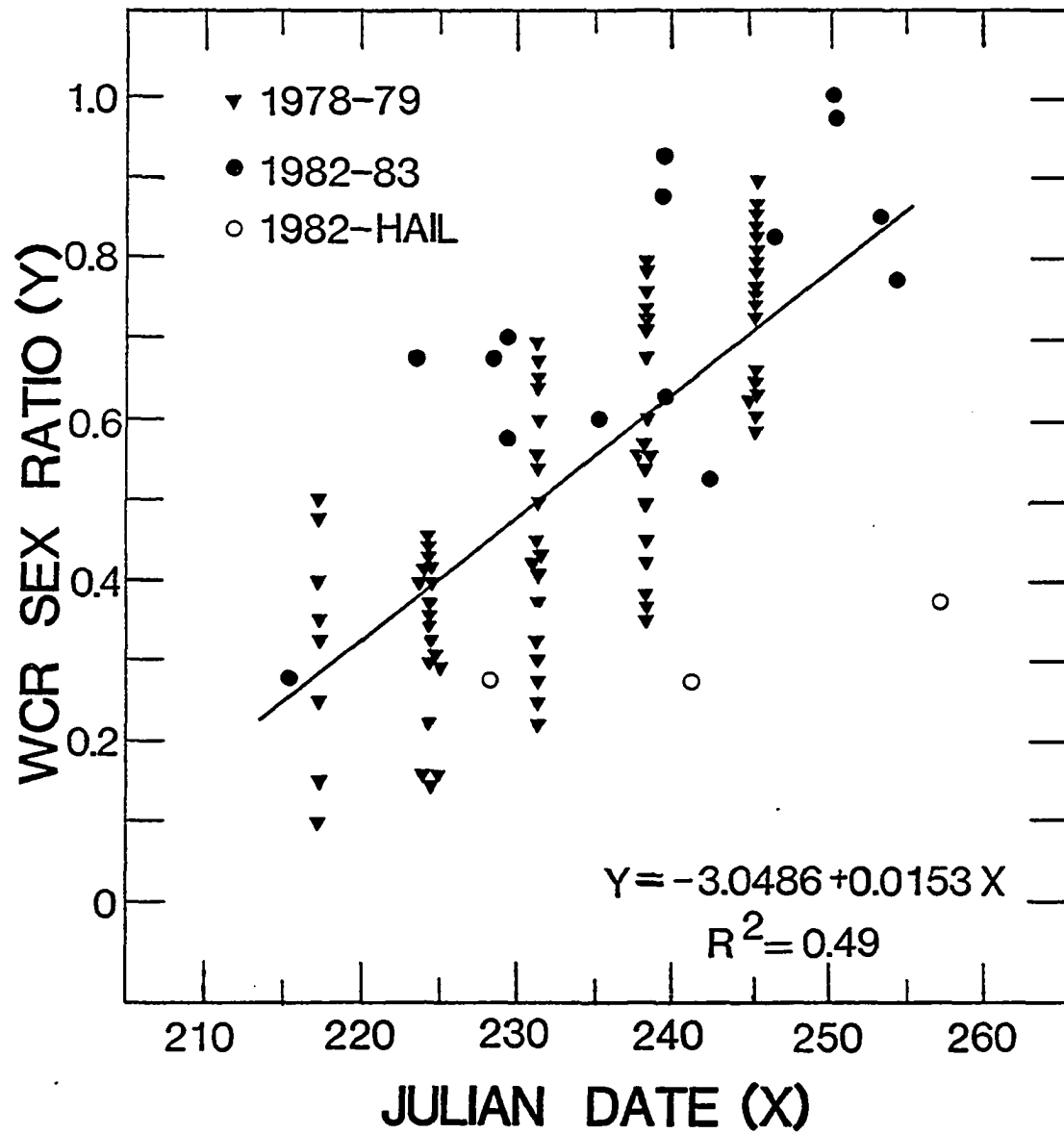


Figure 5. Relationship between WCR field sex ratios, estimated using 3.05-m vertical sticky traps (1982-83 data) and sticky traps at ear height (1978-79 data), and Julian date

PART 3. DESIGN AND COST CONSIDERATIONS IN THE SAMPLING OF NORTHERN
AND WESTERN CORN ROOTWORM (COLEOPTERA: CHRYSOMELIDAE) EGGS

The eggs of the northern and western corn rootworms, Diabrotica barberi Smith and Lawrence (NCR) and D. virgifera virgifera LeConte (WCR), respectively, are laid in the soil, beginning in late July and continuing until the first killing frost. The eggs of both species overwinter in the soil and the larvae hatching from these eggs feed on corn roots, if present. Larval feeding may result in root pruning and potentially severe yield loss.

Corn rootworm egg sampling has been used to try to predict economically damaging populations of corn rootworms (Lawson 1968, Foster et al. 1979, and Apple et al. 1977). These egg sampling methods have been primarily relative sampling methods that sample small areas in relation to the entire width of corn rows (Gunderson 1964, Howe and Shaw 1972, and Foster et al. 1979). The horizontal distribution of the rootworm eggs may influence the accuracy of these sampling methods, being related to the direction and degree of lodging (Sisson and Chiang 1964), tillage practices before and after oviposition (Pruess et al. 1968), and soil moisture levels (Gustin 1979 and Weiss 1983). The degree to which these factors affect oviposition in commercial production fields is difficult to determine. In comparing samples taken at the plant base and samples taken between the corn rows in a number of fields, Foster et al. (1979) concluded that the field-to-field

variability in the proportion of NCR eggs found at the plant base was great enough to necessitate samples from both areas to obtain accurate egg estimates. To overcome this problem they developed an absolute sampling method where a metal frame was driven into the ground and all the soil within the frame to a depth of 10.2 cm and a width equal to the row width was removed. The soil was then mixed and subsamples were taken.

A second important consideration in corn rootworm egg sampling is the proper depth to sample. A number of studies on the vertical distribution of NCR and WCR eggs have been reported. Foster et al. (1979) reported that 95% of the NCR eggs found in the upper 20 cm were present in the upper 10 cm. For this reason, they concluded that a depth of 10 cm was appropriate for NCR sampling. Patel and Apple (1967) and Weiss (1983) found a slightly lower percentage of NCR eggs near the surface (ca. 90% in top 10 cm). Ball (1957) found 80% of the WCR eggs were laid in the top 15.2 cm, and Weiss (1983), in furrow-irrigated corn, found 79% of the WCR eggs were laid in the top 10 cm. Factors found to affect vertical distribution include soil cracking (Foster et al. 1979), tillage (Pruess et al. 1968), and soil moisture (Gustin 1979 and Weiss 1983). The results of these studies are difficult to interpret because of problems with shallow depth of sampling, small or unknown sample sizes, small plot-areas sampled, and/or only one or a few fields sampled. The variability in the depth of NCR and WCR oviposition in normal production fields has not been examined. This understanding

is essential to determine the proper depth necessary to sample to obtain estimates of NCR and WCR eggs.

Using Taylor's power law (Taylor 1961), Foster et al. (1979) determined the spatial distribution of NCR eggs to be aggregated. They also investigated the variability of the different NCR egg sampling methods. Studies on the NCR and WCR have often treated the two species as a single species. To more appropriately conduct egg sampling procedures for these two species, comparisons of the species involving aggregation and sampling variability must be made.

The objective of this study was to compare the variability and cost considerations for sampling NCR and WCR egg populations and propose an optimum sampling design. Variability in the vertical and horizontal distribution of NCR and WCR eggs in commercial production cornfields was determined. A comparison of the mean-variance relationships of NCR and WCR egg sampling using an absolute sampling technique (frame method) was made. Sampling variability and cost estimates were used to determine an optimum egg sampling design.

Materials and Methods

In 1981, three commercial production cornfields, located in Story Co. (central), Fayette Co. (northeast), and Cass Co. (southwest), Iowa, were sampled for NCR and WCR eggs. Different egg population levels were insured by placing out rectangular adult exclusion cages (37.5 cm x 1 row width, see Part 1) to prevent further oviposition at a site. Sites were randomly located within each of 20 blocks, spaced uniformly to cover each field entirely. One trap was placed near each site on four

separate dates beginning approximately 1 August at 7-10 day intervals. Following the first frost, cage sites were marked and cages removed. After harvest, samples were taken within each cage site, plus one additional site, using a 10.2-cm diameter golf-cup cutter to a depth of 20.3 cm. Four cores, one 20-45 cm on each side of the row and two near the base of the plants, were taken at each site and divided into 10.2 cm depth increments. Each sample was thoroughly mixed and a 0.47 l subsample taken (eight/site).

Three fields in 1982 (Story Co.,2; Fayette Co.,1) and one field in each of Story Co. and Cass Co. in 1983 were sampled using the frame method described by Foster et al. (1979). Different egg population levels were obtained by sampling each field on four dates, 7-10 days apart, beginning the first week of August. The fourth date for the Fayette Co. field was not obtained due to extremely wet conditions. Additional sampling was done in each field after harvest.

In 1982 and 1983, 30 and 40 quadrats, respectively, were established in each field systematically to cover the entire field. On each sampling date, a site within each of 24-30 (1982) or 32-40 (1983) quadrats was sampled. Sampling consisted of taking two subsamples (0.47 l) from the soil removed from within the frame to a depth of 10.2 cm. Within the same frame area, two additional subsamples were taken from soil removed from a depth of 10.2 cm to 20.3 cm. All subsamples were returned to the laboratory, washed, and the eggs separated from the soil using the procedures described by Shaw et al. (1976). All eggs were counted and identified to species as described by

Atyeo et al. (1964).

Soil analyses were performed on soil samples taken at each site on each sampling date. Samples were obtained by collecting five, 1.7 cm cores (1981) or one 0.47 l subsample from the top sample of the frame (1982-83). Soil moisture for these samples was determined by using wet and oven-dried weights to determine the percent moisture. Soil texture analysis was performed for each quadrat in each field on a composite of the soil samples (1981) or on the soil obtained from the final sample of the season (1982-83). The percent sand, silt, and clay was determined for each quadrat. Five or eight quadrats, representing different soil conditions (i.e., texture, slope, drainage) were picked in each field and organic matter analyses run by the Iowa State Soil Testing Laboratory.

Comparisons for vertical and horizontal distribution of eggs were accomplished using paired t-tests, to test the significance from zero of the difference between the two quantities of interest. Vertical and horizontal distribution variables were also correlated with soil texture, soil moisture, and organic matter content of the soil.

Mean-variance relationships were investigated using the techniques of Taylor (1961). Variances utilized in these analyses represent differences between quadrats within fields. Comparisons of these relationships between species was done using analysis of variance techniques to test for differences in slope. Nested analysis of variance techniques were used to determine variance components for the frame sampling technique. These variance components (s_i^2) along with sampling cost estimates (c_i) were used to estimate the optimum number of

subsamples (n_i) within each stage (i) of the two-stage sampling plan using Snedecor and Cochran's (1967) equations:

$$n_s = \sqrt{c_q s_s^2 / c_s s_q^2} \quad (1)$$

$$n_q = (s_q^2 n_s + s_s^2) / V_{\bar{x}} n_s \quad (2)$$

In these equations, s and q represent samples and quadrats, respectively, and $V_{\bar{x}}$ is the desired variance of the mean obtained from the mean of the data and the desired precision level.

Results and Discussion

The horizontal distribution of NCR and WCR eggs found in the three cornfields sampled in 1981 is shown in Table 1. Paired t-tests of plant-base and between-row samples taken at the same site showed that the NCR lays significantly ($n=299$, $P<0.01$) more eggs at the plant base than between the rows. However, the WCR lays significantly ($n=299$, $P<0.01$) more eggs between the rows than at the plant base. Even with these high levels of significance, the proportion of eggs found at the plant base varies greatly from field to field, with a range of 55-82% for the NCR and 14-50% for the WCR. The variability in the NCR percentages from field to field supports the findings of Foster et al. (1979) who stated that NCR egg sampling should include both plant-base and between-row samples. These data also show considerable field-to-field variability for WCR horizontal egg distribution. Because of this variability, sampling methods for both species that rely on assumptions concerning horizontal egg distributions or that do not adequately sample the entire inter-row width may produce erroneous estimates.

Correlations between the proportion of NCR and WCR eggs found within the row at a given site and soil moisture, soil texture, and organic matter were determined. The relationship between the proportion of WCR eggs in the row and percent clay (range=18-45%) was significant ($r=-0.33$, $n=56$, $P<0.01$), indicating that an increased clay content in the soil may result in more eggs being laid between the rows. Increased clay content would result in increased soil cracking which is more prevalent between the rows. All other relationships with soil texture and organic matter were not significant. These data indicate that the horizontal distribution of rootworm eggs is a complicated relationship of a number of factors. Sampling techniques that sample the entire inter-row width are least likely to be affected by these factors.

The comparison of the number of eggs found in samples taken to depths of 10.2 cm and from 10.2 to 20.3 cm is shown in Table 2. The percentages of the eggs in the top 20.3 cm found in the upper 10.2 cm varied from 50.5-88.7% for the NCR and 34.9-84.2% for the WCR. Previous reports on NCR vertical distribution (Patel and Apple 1967 and Foster et al. 1979) have not indicated this variability. The depth of WCR egg placement found in this study (only 66% in the top 10.2 cm) is greater than has previously been reported by Lawson (1964) and Weiss (1983); however, these studies were done in furrow-irrigated corn.

The factors that may affect the depth of egg placement were investigated by correlating the percentage of the eggs in the top 20.3 cm found in the top 10.2 cm with the mean seasonal soil moisture

(range=13-22%), mean soil texture, and the mean percent organic matter (range=2.2-6.0%) for each field. A significant negative relationship ($r=-0.75$, $n=8$, $P=0.03$) was found between the percentage of the NCR eggs found in the top 10.2 cm and the mean percent clay (range=23-37%). This correlation is likely the result of more extensive soil cracking in soil with high clay content. A correlation coefficient of 0.69 ($n=8$, $P=0.06$) was found between the percentage of WCR eggs found in the top 10.2 cm and the mean percent soil moisture.

The vertical distribution of rootworm eggs is quite variable from field to field, depending on climatic and edaphic factors. The depth of egg sampling may affect the population estimates obtained. Results from this study indicate that sampling for the NCR should be done to a 20.3 cm depth. The tendency for WCR to oviposit deeper than NCR indicates that WCR females may oviposit as deep as drought cracks will allow. It is unlikely, considering the sample variability involved, that sampling below 20.3 cm will increase population estimates significantly. Under severe drought conditions, sampling to a depth of 30 cm or more may be necessary for WCR sampling, but this is only practical for the motorized trencher method (Ruesink and Shaw 1983).

The mean-variance relationships for the NCR and WCR were investigated using Taylor's (1961) power law, which assumes a linear relationship when log variance was regressed on log mean. These linear relationships were significant ($n=24$, $P<0.01$) with R^2 s of 0.91 and 0.95 for the NCR and WCR, respectively. The analysis of variance was used to

determine if the slopes of these relationships differed between species. This analysis of variance had fields, the linear effect of log variance on log mean, species, and linear effect by species interactions as sources of variation. The remaining variance was considered to be the error used to test the significance of these effects. This analysis resulted in significant ($P < 0.01$) species differences and a significant ($P < 0.01$) overall linear effect. The interaction of these two effects was not significant, indicating no differences in the slopes of the mean-variance relationships between the species. Therefore, the indices of aggregation for these two species are not significantly different. The data for the NCR and WCR were combined and the mean-variance relationship recalculated (Figure 1). The index of aggregation for the combined data was 1.49, indicating an aggregated population. This value is close to the 1.46 obtained by Foster et al. (1979) using a number of egg sampling techniques for the NCR.

Knowing that the mean-variance relationships for these species are not significantly different the NCR-WCR pooled data can be used to calculate variance components and optimum sampling schemes for the frame sampling method. Table 3 gives the variance components for the stages of sampling using the frame sampling method in 1982-83. Nearly half (47%) of the variability in sampling low populations was caused by sample-to-sample variability. This is three times the variability between quadrats. The variability in sampling the higher populations involves equal proportions for quadrats and samples.

The costs of sampling shown in Table 3 are estimates obtained from

averaging the time required to carry out a number of sampling duties under good sampling conditions in the field or the laboratory. The cost involved in sampling a quadrat includes the time required to walk to that quadrat from the field edge or another quadrat (2 human-min), drive the frame into the ground and dig the soil from within the frame (6 human-min), and sift and mix the soil (4 human-min). The cost of each sample includes the time to bag and tag the sample in the field (0.5 human-min), wash and separate the eggs from the soil (6 human-min), and count the eggs in the sample and determine their species. Time to count the eggs will depend upon whether high (6 human-min) or low (4 human-min) egg populations are present.

The sampling costs, along with the variance components (Table 3) were used in equations 1 and 2 to calculate the optimum sampling scheme for corn rootworm eggs. The results of these calculations are shown in Table 4. The sampling scheme developed involved sampling to a depth of 20.3 cm without dividing the sample into depths. This assumes that the variance between samples within depths equals the variance between samples if the depths are mixed. Mixing of the samples would tend to dilute the number of eggs within the sample, resulting in reduced variation. Thus, the variance estimates for these analyses may be slightly overestimated. Using the estimates of total cost, the optimum number of samples per frame for the low and high population levels were two and one, respectively. A large number of quadrats per field was necessary to obtain the desired accuracy.

Often seasonal field time is in short supply, and it is difficult to account for this in these calculations. The above calculations were also carried out using costs including only field time (Table 4). The results of these calculations indicate that a much greater number of samples per quadrat should be taken to optimize field time, but this is done at a great cost of total time involved, which increases about 70%. Therefore, increasing the number of subsamples as Ruesink and Shaw (1983) suggest for the trench sampling method may decrease variability but also greatly increase overall sampling costs. The most cost effective way to reduce egg sampling variability is to take fewer samples from a larger number of quadrats within a field. This may not always be practical; therefore, sampling strategies can be planned based on available field time using the information in Table 4.

The corn rootworm egg sampling considerations presented in this paper, along with previous literature, provide a relatively complete picture of corn rootworm egg sampling. Sampling information discussed in this paper should be sufficient to enable the use of the frame (Foster et al. 1979) and the motorized trencher (Ruesink and Shaw 1983) techniques to obtain accurate absolute NCR and WCR egg population estimates.

Table 1. Total NCR and WCR eggs found in samples^a taken at the plant base and between rows and the percentage of these eggs found at the plant base (3 fields), 1981

Field	NCR		WCR	
	Total Eggs	% Plant Base	Total Eggs	% Plant Base
Story Co.	459	54.9	1196	13.5
Fayette Co.	4776	82.3	991	50.4
Cass Co.	365	71.2	6717	18.1
Total	5600	79.3	8904	21.1

^a Total of four samples taken at each of 20 locations on five sampling dates in each field.

Table 2. Number and percent of NCR and WCR eggs laid in the top 20.3 cm of soil found in the top 10.2 cm of soil, 1981-83

Field	NCR		WCR	
	Total Eggs	% in Top 10.2 cm	Total Eggs	% in Top 10.2 cm
1981				
Story Co.	438	67.6	1184	39.1
Fayette Co.	4763	87.4	989	66.3
Cass Co.	358	81.6	6313	84.2
1982				
Story Co. #1	706	77.6	1828	60.4
Story Co. #2	240	81.2	987	52.9
Fayette Co.	1421	88.7	204	61.8
1983				
Story Co.	384	50.5	888	34.9
Cass Co.	764	64.8	1947	49.5
Total	9074	82.0	14440	66.0

Table 3. Variance components and costs for the stages used for corn rootworm sampling with the frame sampling method, 1982-83

Source of ^a Variation	Mean<2.5 eggs/sample				Mean>2.5 eggs/sample			
	d.f.	s	%	cost ^b	d.f.	s	%	cost ^b
F-S	8	0.359	9.4	--	14	3.830	10.2	--
Q/F-S	271	0.586	15.3	12	446	9.718	26.0	12
D/Q/F-S	280	1.091	28.4	--	460	13.290	35.5	--
S/D/S/F-S	555	1.798	46.9	10.5	898	10.595	28.3	12.5

^a F-S=field and sampling dates, Q=quadrats, D=depths, S=samples.

^b Cost expressed in human-min.

Table 4. Optimum sampling schemes and costs for corn rootworm egg sampling using the frame method

Sampling Constraints ^a	Desired Precision	Optimum Sampling Scheme		Field Costs	Total Costs
	(SE/ \bar{x})	quadrats/ field	samples/ quadrats	(h)	(h)
Total Cost Minimized					
Mean<2.5 ^b	0.10	199	2	43	109
	0.25	32	2	7	18
Mean>2.5 ^c	0.10	85	1	18	35
	0.25	14	1	3	6
Field Cost Minimized					
Mean<2.5	0.10	106	9	29	188
	0.25	17	9	5	30
Mean>2.5	0.10	50	5	12	62
	0.25	8	5	2	10

^a Expressed as eggs/0.47 l sample.^b Mean of all fields and sampling periods equals 0.86.^c Mean of all fields and sampling periods equals 4.88.

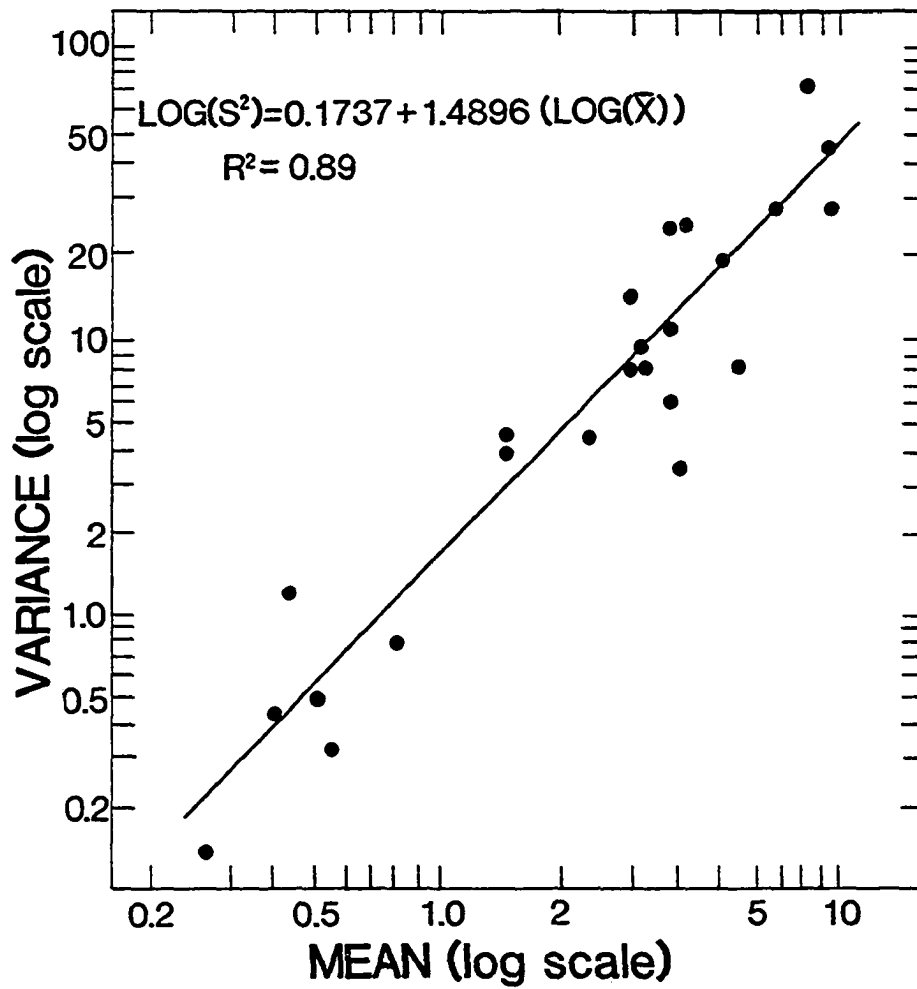


Figure 1. Relationship between the log (base 10) of the variance and the mean for corn rootworm (NCR+WCR) egg sampling using the frame method, 1982-83

PART 4. SEASONAL OVIPOSITION OF THE NORTHERN AND WESTERN CORN
ROOTWORM (COLEOPTERA: CHRYSOMELIDAE) IN CONTINUOUS
CORNFIELDS

The northern and western corn rootworms, Diabrotica barberi Smith and Lawrence and D. virgifera virgifera LeConte, respectively, are univoltine pests of corn planted in a corn-following-corn rotation (continuous corn). The adults of both species oviposit in the soil in late summer. These eggs hatch the following June, and the larvae feed on the roots of corn planted in the same field. Management of this insect has relied primarily upon the prophylactic use of a soil insecticide treatment to diminish the potential for significant rootworm larval damage. Attempts at utilizing pest management strategies, through the use of adult sampling techniques to predict the potential for larval damage, have had limited success (Foster 1983 and Hein and Tollefson 1984b). One explanation for this lack of success is, in part, the inability to predict fall egg populations using adult sampling techniques. A better understanding of corn rootworm seasonal oviposition patterns may help improve these predicting abilities.

The seasonal oviposition patterns of adult corn rootworms have been studied under both laboratory and field conditions. Laboratory studies on individual field collected WCR females by Branson and Johnson (1973) show that, following a 14-day preovipositional period, oviposition begins at a high level, peaks after 10-15 days, and then slowly

declines. Using field collected WCR mating pairs under laboratory conditions, Hill (1975) found that 24% of the total oviposition had occurred by 25 August, 57% by 10 September, and 90% by 10 October. Field studies by Short and Hill (1972) indicate earlier WCR oviposition than previously stated. They found that in fields in eastern Nebraska 29% of the eggs were laid by 20 August and 75% were laid by 5 September. Studying both species, Kuhlman (1970) noted a more rapid ovarian development and earlier oviposition for the NCR.

Small numbers of samples and unknown sampling precision makes the data from these studies of little use in developing quantitative relationships for these species with regard to seasonal oviposition in the field. The objective of this study was to sample rootworm egg populations under a number of environmental conditions through the ovipositional period and quantify the NCR and WCR seasonal oviposition pattern in continuous cornfields.

Materials and Methods

Eight different commercial production cornfields were sampled during 1981 (3), 1982 (3), and 1983 (2) for NCR and WCR eggs. In 1981 one field in each of Story Co. (central), Fayette Co. (northeast), and Cass Co., (southwest) Iowa was sampled by placing out rectangular cages (see Part 1), covering 37.5 cm of row and extending from the center of one row to the center of another, to prevent further oviposition at a site. Sites were randomly located within each of 20 blocks, spaced uniformly throughout the entire field. One cage was placed at each site

in each field at approximately 10-day intervals beginning near 1 August and continuing through 1 September. Following the first frost, cage sites were marked and cages removed. Post-harvest samples were taken at each cage site, plus one additional uncaged site. Sampling at each site consisted of four cores taken to a depth of 20.3 cm using a 10.2-cm diameter golf-cup cutter. One core was taken 20-45 cm on each side of the row and two cores were taken near the plant base. Each core was divided into increments 10.2 cm deep, thoroughly mixed, and a 0.47 l subsample taken. This procedure resulted in eight samples being taken from each site.

Sampling was done in Story Co. (2 fields) and Fayette Co., (1 field) Iowa in 1982 and one field in Story Co. and Cass Co., Iowa in 1983. In both years sampling began the first week of August and continued at 7-10 day intervals until the first week of September. The 1982 Fayette Co. field was not sampled between 19 August and the final sampling date due to extremely wet field conditions. The 1983 Story Co. field was not sampled after 8 September because tillage of the field occurred before the final samples could be taken, and the effect of tillage on sampling was unknown. Oviposition was assumed negligible in this field following 8 September, because low NCR (0.03 adults/plant) and WCR (0.25 adults/plant) adult populations were observed at this time.

In 1982 and 1983, 30 and 40 quadrats, respectively, were established systematically to cover each entire field. On each sampling date, a site within each quadrat was chosen at random and sampled.

Occasional quadrats were omitted due to labor constraints when sampling, resulting in 24 or 30 quadrats being sampled in 1982 and 32, 36, or 40 quadrats being sampled in 1983. To obtain better precision, sampling in 1982-83 involved the use of the frame method described by Foster et al. (1979). The frame method involved driving a 10.2 cm (width) x 101.6 cm (length) x 10.2 cm (depth) metal frame into the ground perpendicular to the corn row and removing all the soil within the frame area to a depth of 10.2 cm and a width equal to the row width of the corn. An additional sample of soil within the same frame area was taken to a depth of 20.3 cm. Each sample was sifted, mixed, and two 0.47 l subsamples were taken. Subsamples were returned to the laboratory, washed, and the eggs separated from the soil using the procedures described by Shaw et al. (1976). All eggs were counted and separated to species as described by Atyeo et al. (1964).

Seasonal oviposition patterns for each species were determined by expressing the mean egg population for each field on each sampling date as a percentage of the final egg population. Data from the final dates (100%) were not included in these analysis, as it was not known when 100% oviposition was reached. As a result of the sampling error involved, some egg population estimates were greater than the final egg population. These estimates were expressed as 100% cumulative oviposition for these analyses. These cumulative oviposition data were regressed on different variables to determine a predictive equation of cumulative oviposition. Linear regression techniques were used to test for differences between the NCR and WCR. Independent variables used in

the regressions with cumulative oviposition were Julian date, accumulated air heat units (15°C base) from March 1, accumulated soil heat units (11°C base) from March 1, and accumulated air heat units (15°C base) from July 15. Log (base 10) and probit transformations of the cumulative oviposition data were also used as dependent variables in attempts to improve these relationships. All temperature data were obtained from National Oceanic and Atmospheric Administration climatological records from the reporting station nearest each field.

Results and Discussion

The mean final egg populations for all fields sampled are shown in Table 1. Precision (SE/\bar{x}) for the egg sampling technique used in 1981 averaged 0.27 for the NCR and 0.32 for the WCR. Sampling precisions for the frame method used in 1982-83 were calculated for low (<2.5 eggs/0.47 l) and high (>2.5 eggs/0.47 l) egg populations using all fields and sampling dates. Nested analysis of variance was used to remove variance between fields and sampling dates and to obtain estimates of quadrat, depth, and sample variances for the 1982-83 data. Standard error estimates were then obtained using these variances. Low populations of both species were estimated with a precision of 0.26 (NCR, $n=21$; WCR, $n=15$), and high populations of the NCR and WCR were estimated with precisions of 0.14 ($n=3$) and 0.19 ($n=9$), respectively.

Table 2 shows the regression equations and the coefficients of determination (R^2) for the relationships between cumulative oviposition for both species, separate and combined, and Julian date, accumulated air heat units, and accumulated soil heat units. Air heat units

accumulated from July 15 and probit and log transformations of cumulative oviposition produced regressions similar to but not better than those in Table 2.

All regression equations account for a significant ($P < 0.01$) amount of the variability. As soil temperatures are not readily available in many areas, the best regression equation for cumulative NCR oviposition was based on air heat units. The data and regression line for this relationship are shown in Figure 1. The best equations for WCR and total corn rootworm cumulative oviposition were based on Julian date. These relationships are shown in Figures 2 and 3, respectively.

Examination of these data led to questions about the extent of field-to-field variability in seasonal oviposition. These questions were examined by comparing correlation coefficients and partial correlation coefficients for the relationships between seasonal oviposition and Julian date (WCR) or accumulated heat units (NCR). With differences between fields removed (partialled out) the correlation for this relationship for the NCR increases from 0.74 to 0.89. This accounts for approximately 24% of the variability in the data shown in Figure 1. A similar comparison between the seasonal oviposition of the WCR and Julian date accounts for approximately 10% of the variability as the partial correlation coefficient was 0.85 as compared to the correlation coefficient of 0.79. The reasons for this amount of variability between fields are unknown. Possible explanations could

involve differences in larval development rates, nutrition, or adult population dynamics.

Comparisons between the cumulative seasonal oviposition of the two species were made using their relationships with Julian date. Analysis of variance was used to test for species differences in seasonal oviposition. The overall linear effect of Julian date, the effect of differences between species, and their interactions were determined. Field-to-field differences were also accounted for and the remainder was considered to be the error term. The test for the common slope, the linear effect of Julian date, was found to be highly significant ($P < 0.01$). The differences between the linear effect of Julian date for species was not significant, demonstrating equal slopes for both species. The effect of species, which measures the differences between the species means, was not significant ($P = 0.10$). The results of this analysis indicate that no differences between species in time of oviposition or oviposition rate could be detected from these data.

Utilizing these regression equations to estimate seasonal oviposition events results in the estimates presented in Table 3. It should be noted that, as with all regression equations, those values near the mean of the values used to determine the equation will provide the most reliable estimates, and those values further from the mean will provide the least accurate estimates. By 1 August, oviposition has begun at low levels (<10%). Oviposition is approximately 50% complete by 19 August and 90% complete by 6 September. These data show oviposition

progressing at a much faster rate than observed by Hill (1975) or Short and Hill (1972).

These estimates are for "typical" continuous cornfields in Iowa. Adult populations in typical cornfields in early September have been observed to be rather low, and thus oviposition should be near completion. This may not be the case in first-year cornfields (Godfrey and Turpin 1983) or in late-planted cornfields (Hill and Mayo 1974) and the estimates in Table 3 may not apply in these situations.

Differences in geographical location would also have an effect on the accuracy of these equations, particularly those involving Julian date. Utilization of these relationships in areas other than Iowa should rely on accumulated air heat units. These relationships will be useful in predicting corn rootworm seasonal oviposition and may be helpful in determining the proper timing of adult control tactics and/or adult sampling strategies.

Table 1. Final egg populations for the eight fields sampled to determine seasonal NCR and WCR oviposition

Field	Final Egg Population (x10 ⁶ eggs / ha)	
	NCR	WCR
1981		
Cass Co.	2.0	65.6
Story Co.	2.1	19.4
Fayette Co.	22.9	13.1
1982		
Story Co. #1	9.3	26.3
Story Co. #2	4.4	13.2
Fayette Co.	35.1	5.7
1983		
Story Co.	4.0	11.7
Cass Co.	8.2	15.8

Table 2. Regression equations and coefficients of determination (R^2) for relationships between cumulative corn rootworm seasonal oviposition and Julian date and seasonal heat units

Regression Equation	R^2 ^a
Cumulative % = -343.63 + 1.718 (Julian date)	0.42*
NCR	
Oviposition = -114.11 + 0.218 (Air heat units)	0.55*
= -75.99 + 0.105 (Soil heat units)	0.56*
Cumulative % = -458.51 + 2.183 (Julian date)	0.62*
WCR	
Oviposition = -135.34 + 0.235 (Air heat units)	0.59*
= -64.09 + 0.089 (Soil heat units)	0.36*
Cumulative % = -469.96 + 2.251 (Julian date)	0.76*
Combined	
Oviposition = -131.48 + 0.236 (Air heat units)	0.68*
= -53.51 + 0.083 (Soil heat units)	0.37*

^a_n=31.

*Significant at $P < 0.01$.

Table 3. Estimates of Julian dates and seasonal air heat units for cumulative oviposition events for corn rootworms (NCR+WCR)

Cumulative Oviposition Event	Julian Date	Accumulated Air Heat Units ^a
10%	213 (1 Aug.)	599
20%	218 (6 Aug.)	642
50%	231 (19 Aug.)	769
80%	244 (1 Sept.)	896
90%	249 (6 Sept.)	938
95%	251 (8 Sept.)	960

^a Accumulated from 1 March using 15°C base.

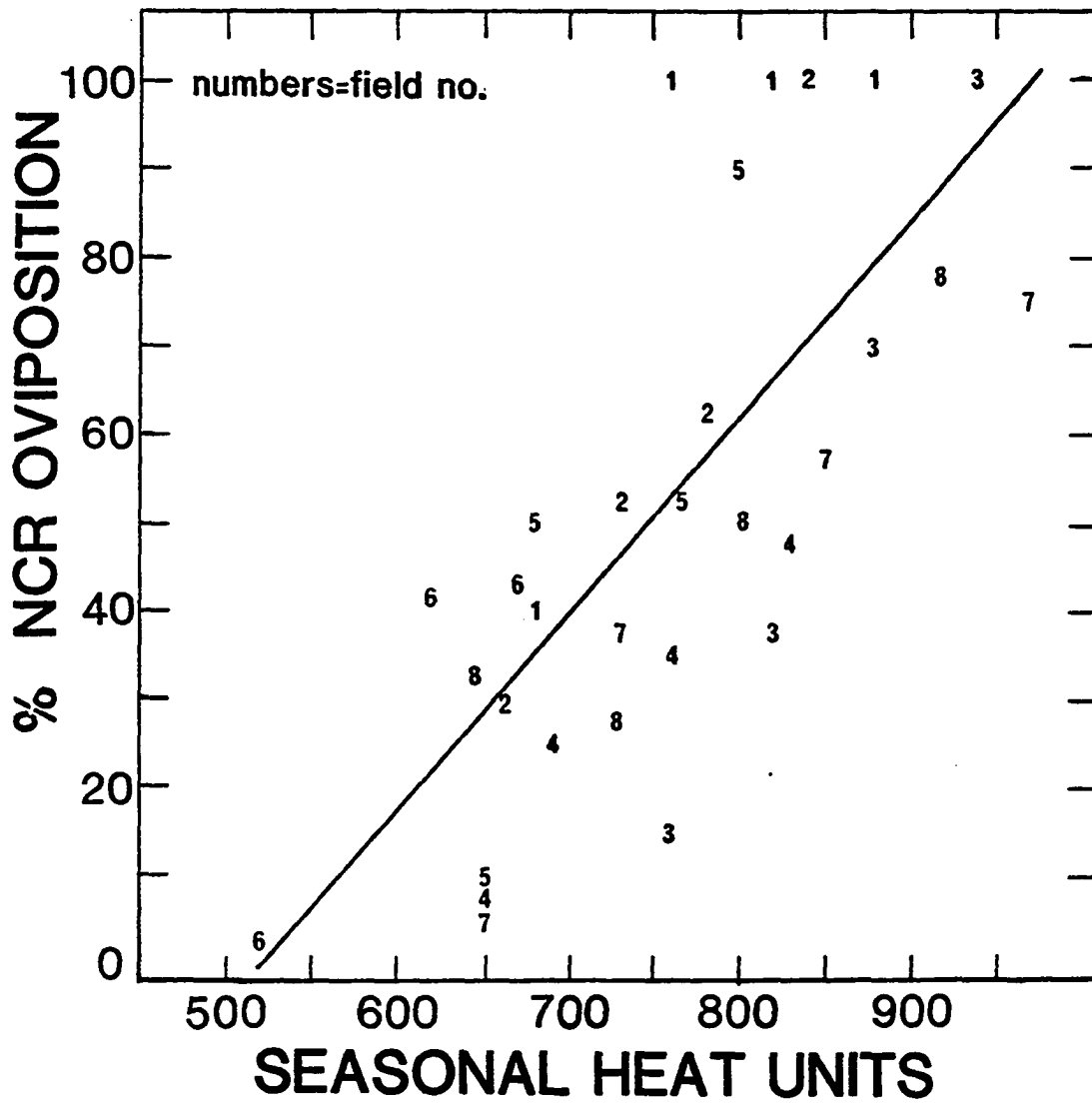


Figure 1. Relationship between percent cumulative NCR seasonal oviposition and air heat units (15°C base) accumulated from 1 March (1981-83 data)

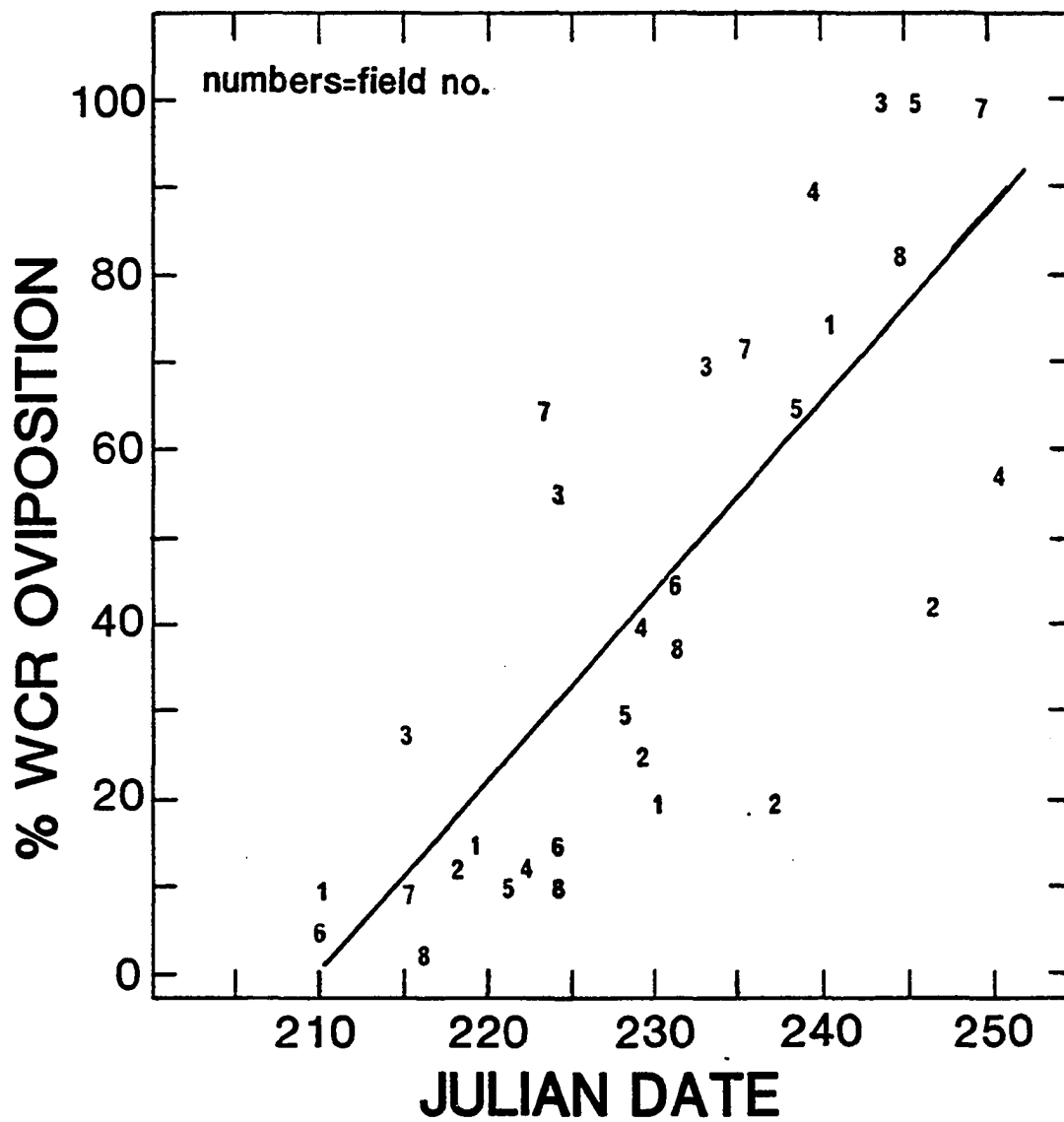


Figure 2. Relationship between percent cumulative WCR seasonal oviposition and Julian date, 1981-83

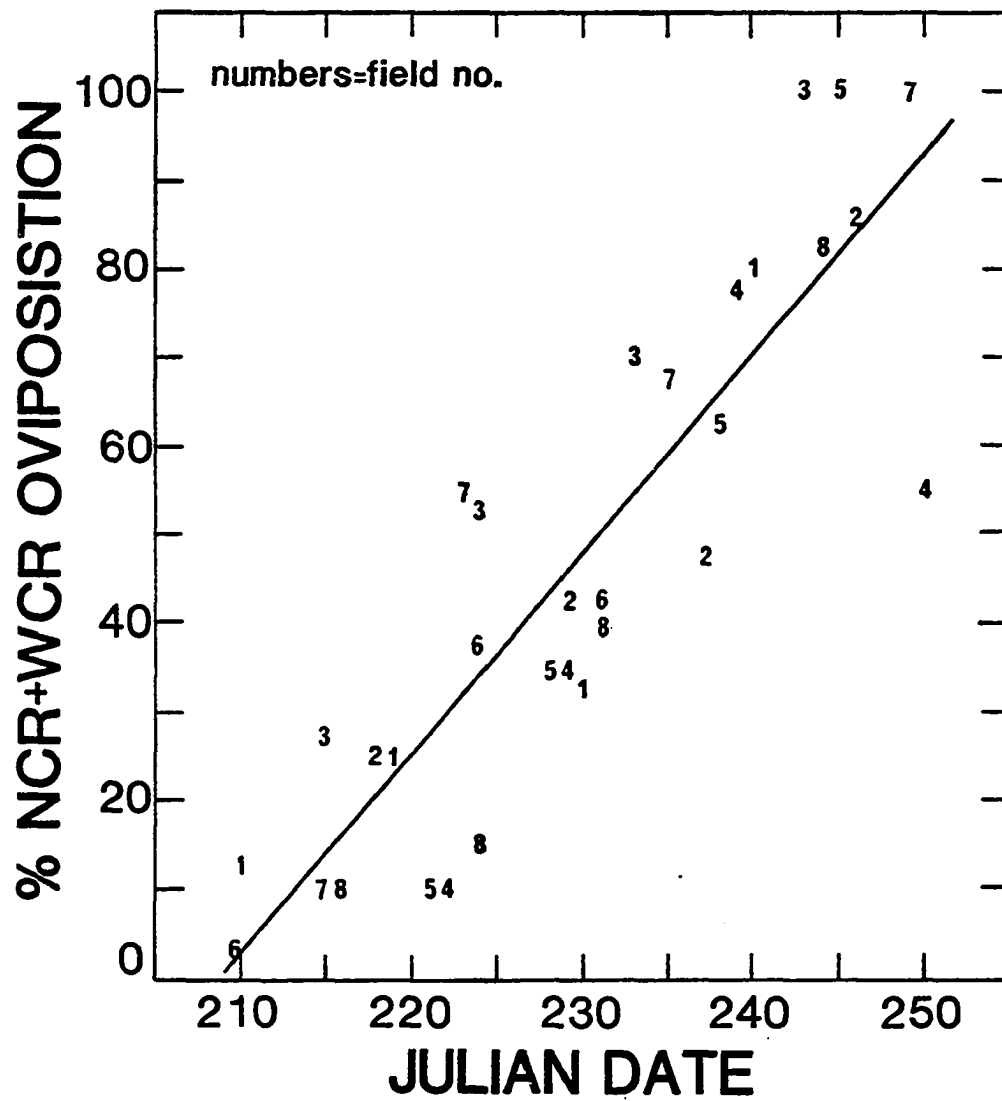


Figure 3. Relationship between percent cumulative corn rootworm (NCR+WCR) seasonal oviposition and Julian date, 1981-83

PART 5. ADULT NORTHERN AND WESTERN CORN ROOTWORM (COLEOPTERA:
CHRYSOMELIDAE) POPULATION DYNAMICS AND PREDICTIONS OF
FINAL EGG POPULATIONS IN CONTINUOUS CORNFIELDS

There have been few field studies on the population dynamics of either the northern or western corn rootworms, Diabrotica barberi Smith and Lawrence (NCR) and D. virgifera virgifera LeConte (WCR), respectively. Musick et al. (1980) sampled the seasonal emergence of both species from a variety of corn planting dates. They determined that late May and early June planting results in later and less synchronous emergence, with WCR adults emerging 1-2 weeks earlier than NCR adults. Pruess et al. (1968) found a delay of emergence in reduced tillage plots when compared to conventional tillage. This difference was likely due to cooler environmental temperatures in the reduced tillage plots. Difficulty in predicting cumulative emergence using calendar date or heat unit accumulations led Ruppel et al. (1978) to suggest the use of the number of days since the first field sighting of adults.

Godfrey and Turpin (1983) compared adult rootworm populations between corn grown in a cropping sequence of corn following corn (continuous corn) and corn following a non-corn crop (first-year corn). They noted higher densities in continuous cornfields during early August, but first-year cornfields had higher populations later in August. Pruess et al. (1974) studied adult populations in relation to the application of insecticides to suppress adult populations and subsequent oviposition.

Estimates of WCR longevity in the lab (ca. 65-95 days) indicate potential survival well beyond favorable environmental conditions (i.e., first frost) in the field (Hill 1975 and Branson and Johnson 1973). Estimates of NCR longevity by Kuhlman (1970) are considerably shorter (ca. 28 days) and may be due to the difficulty of maintaining NCR adults in the lab. Important factors that complicate field estimates of NCR or WCR mortality are immigration and emigration. NCR and WCR adults are very active insects and capable of interfield movement (VanWoerkom et al. 1983, Godfrey and Turpin 1983, and Cinereski and Chiang 1968). It is thought that this movement is due to the beetles search for food and/or oviposition sites. Determination of the extent of immigration or emigration has not been done. But it has been observed that beetles will move in large numbers from mature fields into cornfields that are silking and pollinating (Hill and Mayo 1974). Observations by Godfrey and Turpin (1983) indicate that the majority of WCR adults moving from field to field are females.

The objectives of this study were to investigate and quantify adult NCR and WCR field population parameters and the relationship between adult populations and oviposition. The parameters studied were adult emergence, adult longevity in the field, and factors affecting population change (i.e., population density, weather). Attempts were made to establish and quantify the relationship between NCR and WCR adult populations and final season egg populations within commercial continuous cornfields.

Materials and Methods

Eight continuous cornfields were sampled from 1981-1983 for NCR and WCR adult emergence, adult population densities, and final egg populations. These fields were located in Story Co. (1981, 2 in 1982, 1983), Cass Co. (1981, 1983), and Fayette Co., Iowa (1981, 1982). All fields (ca. 4-16 ha) were maintained using standard commercial production practices, including the application of a planting-time rootworm soil insecticide. Each entire field was divided into 20 (1981), 30 (1982), or 40 (1983) quadrats for sampling purposes.

Adult emergence was sampled using emergence traps that sampled an specific area of each field, yielding absolute population estimates (see Part 1). In 1982-83, one trap was randomly located within each quadrat of each field sampled. Traps were placed in early July, and all emerging adults were caught in a collection cup which was changed weekly. These adults were counted and their sex determined. After two weeks, all traps were moved to new locations within the quadrat to minimize the effects upon emergence (Fisher 1984) of truncating the plant for trap placement.

Adult population estimates were obtained by counting all NCR and WCR adults on an entire corn plant and the surrounding soil surface (plant count). Five, two-plant counts were taken within each quadrat in 1981 and 1982, and three, two-plant counts were taken within each quadrat in 1983. Sampling efficiencies estimated by Steffey et al. (1982) indicated two-plant counts to be the most efficient and that this level of sampling should provide estimates having a standard error within

10% of the mean. Plant population estimates were obtained for each field to enable the conversion of adult population estimates (adults/plant) to a per area basis (adults/ha).

Egg population estimates were obtained in 1981 by utilizing a 10-cm diameter golf-cup cutter to obtain soil samples. One site within each quadrat was sampled by taking four sets of cores to a depth of 20 cm. Two cores were taken between the corn rows and two were taken near the plant base. Each core was divided into 10-cm deep intervals and one 0.47-l sample taken. Conversion of these data to a per area basis was made. The product of the average number of eggs/0.47 l for the plant-base samples and the volume of soil in one hectare to a depth of 20 cm in a 20 cm strip centered on the corn row and the product of the average number of eggs/0.47 l for the between-row samples and the remaining volume of soil per hectare not accounted for by the plant-base calculation were determined. These products were added to give the average number of eggs per hectare.

Egg populations in 1982 and 1983 were estimated using the frame sampling method described by Foster et al. (1979). With this method, a 101.6 cm (length) x 10 cm (width) x 10 cm (depth) metal frame was driven into the ground perpendicular to the corn row. All the soil within the frame to a length equal to the corn row-width was removed, mixed thoroughly, and two, 0.47-l subsamples removed. This sampling procedure was repeated in the same frame area to sample soil from 10 cm to 20 cm in depth. This method was employed at one randomly selected site within each quadrat in each field. Conversion of population estimates to a per

hectare basis followed the procedures described by Foster et al. (1979). Egg samples were returned to the lab, and the eggs were separated from the soil utilizing the procedures of Shaw et al. (1976). All eggs in each sample were counted and their species determined according to Atyeo et al. (1964).

An additional study of adult NCR and WCR populations and oviposition was done in 1979-81. Over these three years, 65 fields were sampled for NCR and WCR adults in Story Co., Cass Co., and Fayette Co., Iowa beginning in late July and continuing at approximately 7-10 day intervals. Twenty-six, two-plant adult counts were taken in 1979-80. Population estimates in 1981 were obtained utilizing the sequential sampling plan presented by Foster et al. (1982). All population estimates were converted to a per hectare basis utilizing estimates of plant populations obtained for each field. Egg populations in 35 of these fields were estimated using a 10-cm diameter, golf-cup cutter to obtain 10 cores from areas between the rows and 10 cores within the row near the plant base. Each of these composite samples was sifted, mixed, and a subsample removed. This procedure was repeated 16 times in each field for a total of 32 samples/field. All samples were handled as previously described. Conversion of these data to an egg per hectare basis was done as previously described.

Seasonal adult emergence for each species was expressed as the accumulated emergence for each sampling date as a proportion of the total seasonal emergence. These values were correlated with air heat units (15°C base) accumulated from March 1, soil heat units (11°C

base) accumulated from March 1, and Julian date. Log (base 10) and probit (inverse normal distribution function) transformations of cumulative emergence were also correlated with air and soil heat units and Julian date. Linear regression techniques were used to describe the relationship between the two variables showing the highest correlation, and analysis of variance was used to determine differences in emergence patterns between sexes and species. A paired t-test for each field was used to test for sex differences in total emergence.

One population parameter used to estimate adult longevity in the field and oviposition was the estimated accumulated area under the population curve. This area was estimated using a modification of the rectangular area summation method. This method involved multiplying each adult population estimate by one-half the number of days between the previous sampling date and the next sampling date. The area estimates for the first and final sampling dates were determined by multiplying the population estimate by half the number of days until the next sampling date (first date) or since the last sampling date (final date). The area before the first sampling date was estimated by determining the area of a triangle with the height equal to the population estimate for the first sampling date and the base equal to the number of days between first emergence (considered to be Julian date 190) and the first sampling date. Similar estimation for the final season area was used, with the triangle height equal to the final population estimate and the base equal to the number of days between the final sampling date and the date of the first frost. All area estimates

were added for a seasonal total area in adult-days. Because of the use of the triangle area estimation at the beginning and end of the population curve, it was assumed probable that this method provided an overestimation of the actual area. Remaining analyses utilized correlation techniques to determine possible relationships between variables and regression techniques to develop predictive equations. All weather data used in these studies were obtained from the National Oceanic and Atmospheric Administration reporting station nearest each location.

Results and Discussion

Total seasonal emergence for the five fields sampled in 1982-83 ranged from 23,000-742,000 adults/ha for the NCR and 114,000-464,000 adults/ha for the WCR. Sampling precision (SE/\bar{x}) for these fields averaged 0.23 for the NCR and 0.19 for the WCR. Maximum adult populations in the eight fields sampled in 1981-83 ranged from 8,000-258,000 adults/ha for the NCR and 36,000-232,000 adults/ha for the WCR. Adult sampling precision for these fields was calculated to be better than 0.10, except for those sampling dates and fields with low populations ($\bar{x} < 15,000$ adults/ha). Adult sampling precision for the 1979-81 study was approximately 0.15, according to Steffey et al. (1982). Calculated precision for egg population estimates averaged 0.28 (1981) and 0.18 (1982-83). Egg sampling precision for the 1979-81 study was considered to be better than 0.25, according to Foster et al. (1979).

Adult emergence

Cumulative adult emergence by species and sex was found to be significantly correlated ($P < 0.01$) with air heat units, soil heat units, and Julian date. These correlations ranged from 0.77 to 0.94. These variables were utilized as the independent variables of regressions, with cumulative adult emergence and log- (base 10) and probit-transformed cumulative adult emergence. The best equations produced from these analyses for all dependent variables were the regressions of probit transformed cumulative emergence on Julian date (Table 1). Discrepancies in n are due to undefined values for zero and one in probit transformation. Equations were obtained that describe 94 and 96% of the variability in the WCR female and total emergence, respectively. Highly significant, but smaller R^2 's were obtained for NCR emergence. The relationships between NCR and WCR cumulative emergence and Julian date are shown in Figures 1 and 2, respectively.

The analysis of variance was used to determine if the slopes or intercepts of these relationships differed between species and sexes within species. These analyses had fields, the linear effect of cumulative emergence (probit) on Julian date, species or sex, and the linear by species or sex interaction as sources of variation. The remaining variance was considered the error used to test the significance of these effects. The linear effect of species or sex of either species on Julian date was not significant, indicating no slope (emergence rate) differences could be detected between species or sexes of either species. Inasmuch as no slope differences were found,

species or sex differences would indicate earlier or later emergence. This analysis showed that WCR emerge significantly ($P=0.05$) earlier than NCR, and male WCR emerge significantly ($P<0.01$) earlier than WCR females. Differences in NCR male and female emergence could not be detected; however, this may be a result of the lower NCR populations and higher variability involved in NCR sampling (see Part 1).

Examination of the number of males and females of each species emerging indicated a deviation from the expected 1:1 sex ratio. The proportion of females of the total NCR adults emerging averaged 0.67 (range=0.47-0.80). The female proportion of the total emergence for the WCR averaged 0.73 (range=0.62-0.79). Paired t-tests for each species were used to test for differences between the number of males and females caught within each field. These analysis showed that significantly ($P<0.01$) more WCR females emerged in all fields sampled. Significantly ($P<0.01$) more NCR females emerged in three of the five fields, with the remaining two fields having equal numbers of males and females. The reasons for these unbalanced sex ratios is not known, but differences this large could have a significant impact on the biotic potential of a population.

Adult longevity in continuous cornfields

To obtain estimates of NCR and WCR adult longevity, it was assumed that emigration was equal to or exceeded immigration in the continuous cornfields studied. This assumption was thought to be valid because the fields involved (1982-83 data) were of similar or greater maturity as those cornfields surrounding them. Therefore, they would not be more

attractive to adult corn rootworms than the surrounding areas. WCR emigration above the level of immigration was considered to be mortality, with regard to the individual field studied. Therefore, the only addition to the population was adult emergence and the only losses from the population resulted from adult "mortality".

The average NCR and WCR adult longevity in a field was calculated from field samples obtained in 1982 and 1983 by dividing the average total seasonal emergence into the estimated cumulative area under the population curve in beetle-days (Table 2). This provided an estimate of the average number of days a beetle was present in the field. WCR estimates ranging from 10.0-12.4 days are much smaller than the 65-95 days reported by Hill (1975) and Branson and Johnson (1973) from lab studies. Estimates for the NCR are slightly longer (11.0-15.9 days). These estimates must be considered quite variable when considering the error involved in the area estimation and emergence sampling. However, these values are surprising in that, with a preovipositional period of 14 days (Branson and Johnson 1973), very few eggs would be laid in these fields. But, large egg populations did result in these fields. Underestimation of adult longevity in the field using these data may occur for two reasons. First, a larger proportion of relatively young adults may be dying or leaving the field, resulting in a greater average longevity for the remaining adults. Secondly, an underestimation of the absolute population, via plant counts, would lead to an underestimation in the area under the curve. Inasmuch as, the seasonal emergence estimates are absolute, a decrease in the area under

the curve would lead to underestimates of average longevity.

Utilizing the seasonal emergence and adult population estimates to calculate the proportion of emerged adults being counted on the plants on each sampling date, the relationship of adult "survivorship" to Julian date is obtained (Figures 3 and 4). Examination of Figures 3 and 4 reveal that on a number of occasions early in the season the number of adults counted on the plants was close to the number of adults of the respective species that had emerged to that date ("survival"=1). This is evidence that the absolute population was not greatly underestimated by the plant counts during the early part of the season.

Regression analysis showed the linear effect of Julian date to be significant ($P<0.05$) for both species, with the quadratic effect adding significantly ($P<0.05$) to the model for only the WCR. The presence of the significant quadratic term for the WCR indicates a more rapid decrease in "survival" for the WCR early in the season. This may be the result of early migration of a portion of the population to another area and/or some mortality factor within the rapidly emerging population. "Mortality" is very extensive for both species. Only a third of the total WCR that have emerged by 15 August remain in that field. Fifty-four percent of the total NCR emerged remain within the field by 15 August. At this time, 62% of the WCR adults and 42% of the NCR adults have emerged according to the previously stated emergence equations, and 37% of the seasonal oviposition has taken place (see Part 4). Because newly emerging adults will go through a preovipositional period, only about 20% of the emerged population of each species will be ovipositing

in these fields between 15 August and 1 September. According to estimates obtained in Part 4, approximately 40% of the oviposition will occur during this time. Therefore, the extent of this early "survival" of both species is of great importance in determining final egg populations. Further studies to determine the factors involved in these "survival" rates are needed.

Factors affecting adult populations

The data collected in the 1979-81 study were used to study possible relationships between population change and weather. A number of weather factors were correlated with the adult NCR and WCR population change that had occurred prior to each sampling date. This population change was calculated by expressing each population estimate as a percentage of the peak population and obtaining differences between sampling dates. Average weekly weather factors tested were air heat units (15°C base and 29°C base), evaporation, precipitation, wind, and maximum and minimum air temperature. These weather factors were averaged over the one, two, and three weeks prior to each sampling date, and correlations with population change over the previous one, two, and three weeks were determined.

A few weather factors, including temperature and wind, were significantly ($P < 0.05$) correlated with percent population change. However, none of these factors produced consistently significant correlations across consecutive sampling dates. Therefore, none of these factors could be shown to have a major effect on population change.

Another factor analyzed that did produce consistently significant ($P < 0.01$) correlations with percent population change was the peak NCR and WCR adult population. The correlations between the percent population change from early August through early September averaged 0.39 for the NCR ($n=51$) and 0.49 for the WCR ($n=51$). These results indicate the possibility of some density dependent factor affecting the population, but it is difficult to determine from these data how important this may be in the dynamics of field populations.

Population density and oviposition

The 1981-83 relationship between the egg-population estimates and the maximum adult population estimates (adults/ha) for the NCR and WCR are shown in Figure 5. The NCR relationship appears to be lacking the extreme variability present in the WCR relationship. Linear regression for the NCR data resulted in the equation ($R^2=0.95$, $n=8$, $P < 0.01$):

$$10^6 \text{ NCR Eggs/ha} = 3.15 + 0.13 (10^3 \text{ peak NCR adults/ha}). \quad (1)$$

A similar relationship was found between NCR egg populations and the estimated area under the population curve ($R^2=0.95$, $n=8$, $P < 0.01$):

$$10^6 \text{ NCR Eggs/ha} = 3.18 + 0.0041 (10^3 \text{ NCR adult-days/ha}). \quad (2)$$

The WCR relationship is much more variable, and linear regression resulted in the equation ($R^2=0.51$, $n=8$, $P < 0.05$):

$$10^6 \text{ WCR Eggs/ha} = -3.69 + 0.22 (10^3 \text{ peak WCR adults/ha}). \quad (3)$$

Analysis of the WCR data, excluding the single extreme data point, resulted in a much smaller, non-significant R^2 (0.17). Therefore, this relationship is considered tentative. The relationship between WCR egg populations and the area under the population curve was significant

($R^2=0.60$, $n=8$, $P<0.05$):

$$10^6 \text{ WCR Eggs/ha} = -2.42 + 0.0057 (10^3 \text{ WCR adult-days/ha}). \quad (4)$$

But, this relationship also was tentative due to the inordinate influence of the one extreme data point.

The 1979-81 data were utilized to compare against the adult-egg relationship for 1981-83. This was only done for the NCR as the 10-cm sampling depth was considered too shallow to obtain accurate egg population estimates for the WCR. A plot of the NCR egg population estimates versus the peak NCR adult population is shown in Figure 6. The regression line for the predictive equation (1) is shown for comparison. The egg populations in a number of fields are overestimated by the predictive equation. This may result in part from an underestimation of the egg populations in 1979-81 due to shallow sampling (see Part 3). However, the egg populations in two fields were greatly overestimated in fields with very high adult populations.

It is evident from these data that there is a large amount of variability in NCR and WCR adult population dynamics and oviposition, particularly in fields with high populations. Possible reasons for this could be intraspecific and/or interspecific competition among corn rootworm adults and larvae, nutritional differences between field populations, or environmental differences. These studies are only a first step in the understanding of corn rootworm adult population dynamics. Significant early season adult "mortality" has been shown, indicating the importance of later (late August) population levels. The reasons for this "mortality" are not known, but this study indicates a

possible relationship between peak population density and population change. Further studies are needed to delineate and quantify the effects of factors important in adult corn rootworm population dynamics and oviposition.

Table 1. Regression equations and coefficients of determination (R^2) for relationships between cumulative proportion NCR and WCR emergence (probit) and Julian date

Probit of Proportion Cumulative Emergence	=	Equation	n	R^2
NCR	=	$-18.9011 + 0.0851(\text{Julian date})$	22	0.78**
Female NCR	=	$-19.4790 + 0.0868(\text{Julian date})$	21	0.85**
Male NCR	=	$-16.9352 + 0.0783(\text{Julian date})$	16	0.55**
WCR	=	$-17.0837 + 0.0780(\text{Julian date})$	29	0.96**
Female WCR	=	$-19.3141 + 0.0867(\text{Julian date})$	29	0.94**
Male WCR	=	$-17.5640 + 0.0837(\text{Julian date})$	23	0.87**

** Significant at $P < 0.01$.

Table 2. NCR and WCR adult population parameters and estimated average adult "longevity", 1982-83 data

Field	Total Seasonal Emergence (x10 ³ adults/ha)		Cumulative Area Under ₃ Population (x10 ³ adult- days/ha)		Average Adult "Longevity" (days)	
	NCR	WCR	NCR	WCR	NCR	WCR
1982						
Story Co. #1	150.4	319.7	1877.6	3192.5	12.5	10.0
Story Co. #2	30.6	166.6	485.6	1847.8	15.9	11.1
Fayette	741.9	114.3	8291.2	1349.3	11.2	11.87
1983						
Story Co.	23.1	229.1	303.1	2852.5	13.1	13.1
Cass Co.	39.3	464.4	432.1	4995.6	11.0	10.8

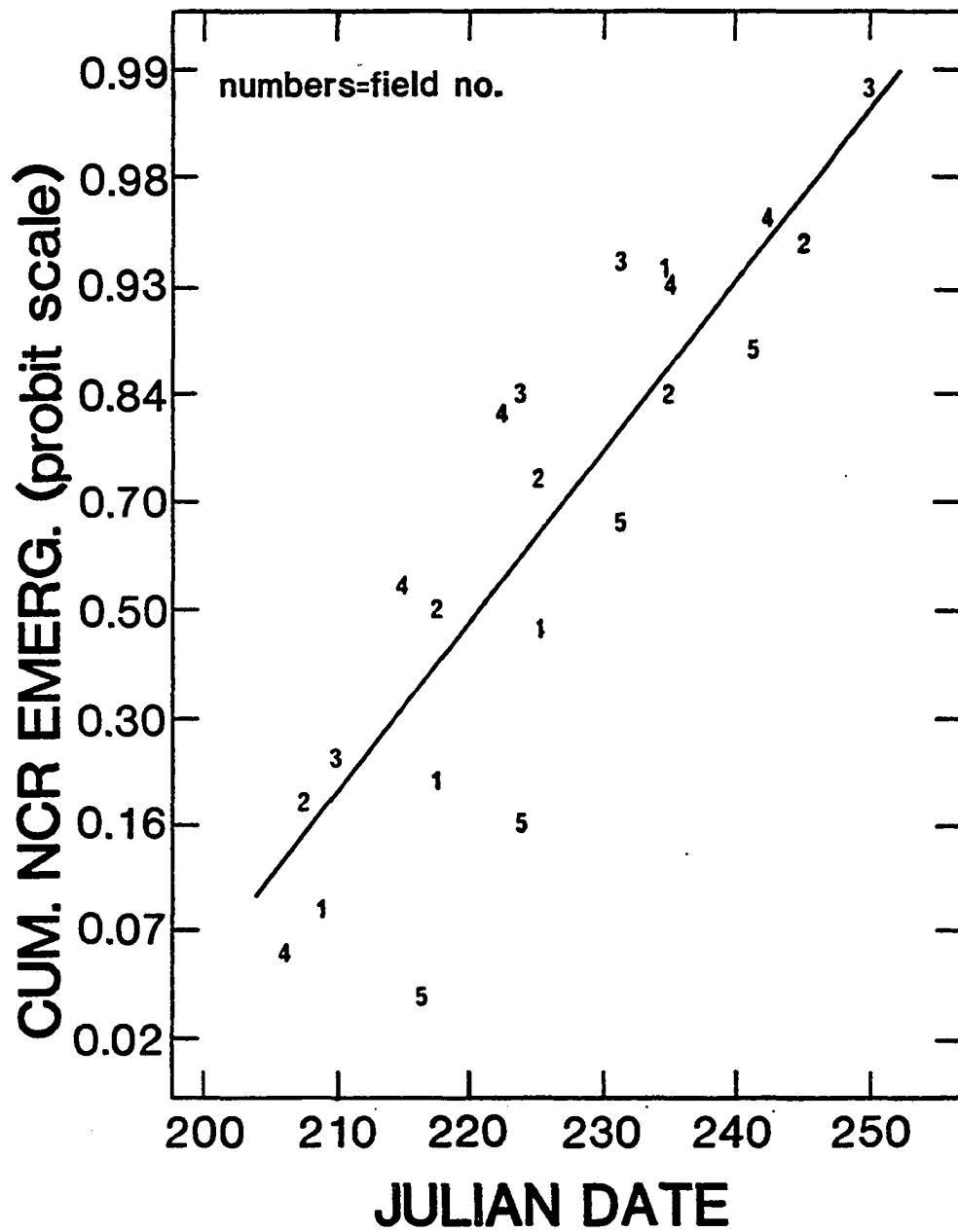


Figure 1. Relationship between the probit transformation of the cumulative proportion NCR adult seasonal emergence and Julian date, 1982-83

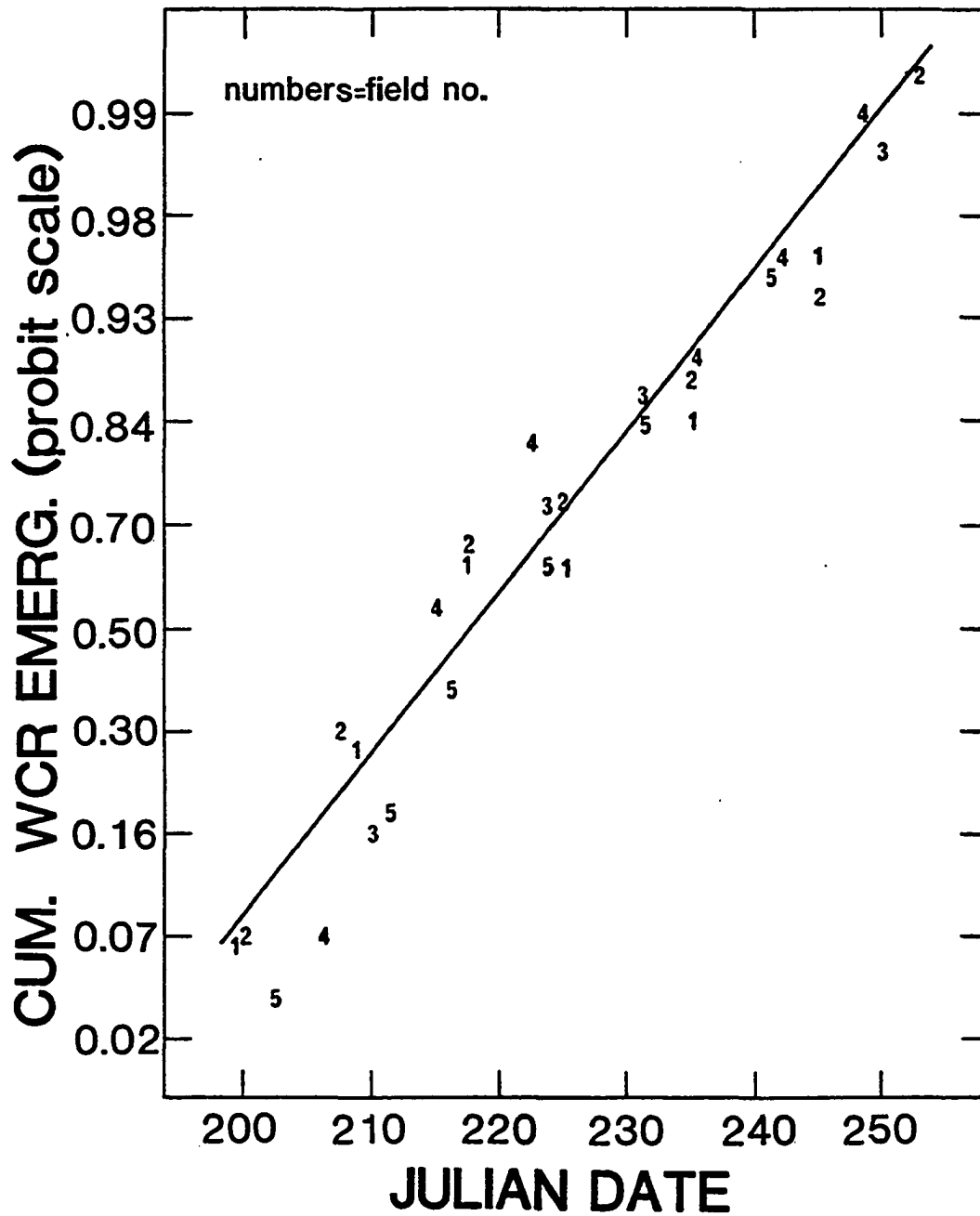


Figure 2. Relationship between the probit transformation of the cumulative proportion WCR adult seasonal emergence and Julian date, 1982-83

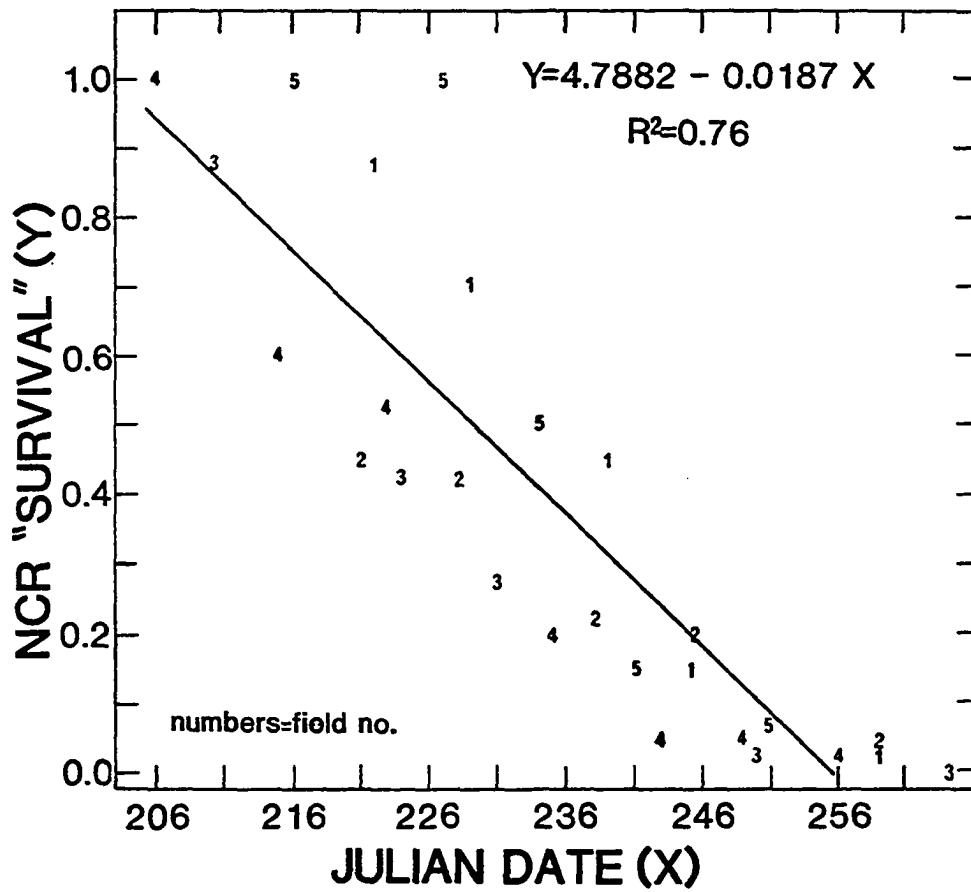


Figure 3. Relationship between the estimated NCR adult "survival" and Julian date, 1982-83

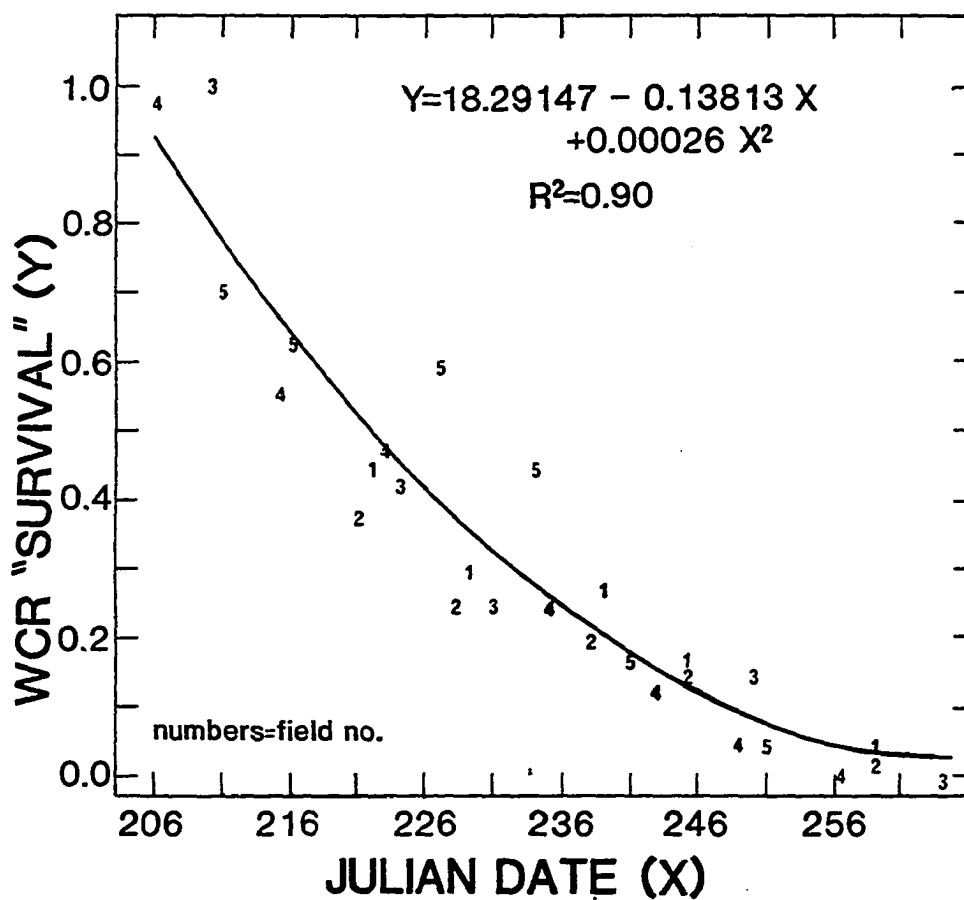


Figure 4. Relationship between the estimated WCR adult "survival" and Julian date, 1982-83

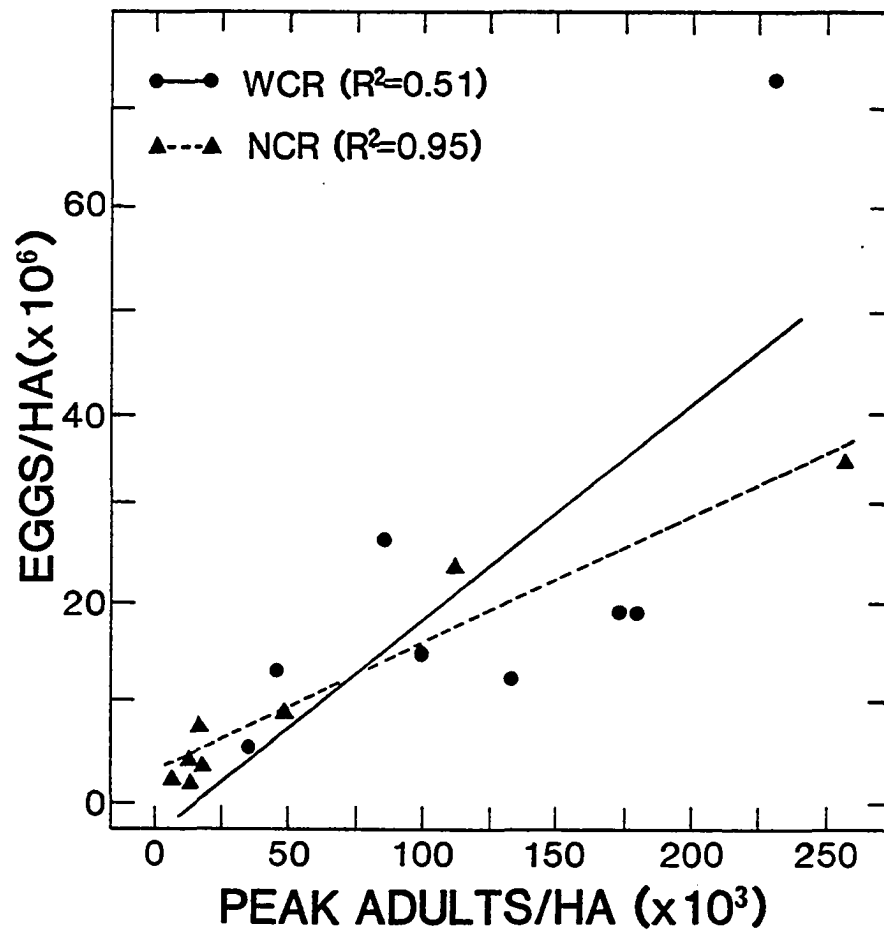


Figure 5. Relationship between final season NCR and WCR egg populations and peak dult NCR and WCR populations, 1982-83

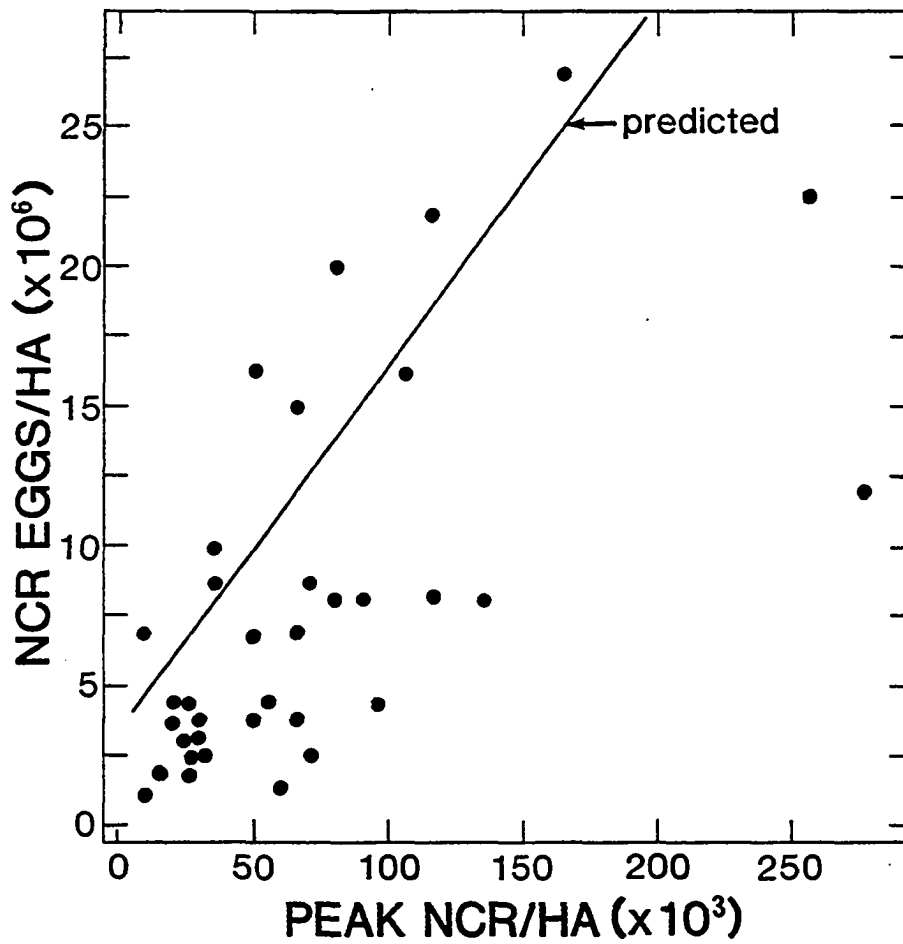


Figure 6. Relationship between seasonal NCR egg populations and NCR adult populations (1979-81 data); predicted values from regression for 1981-83 data

PART 6. MODEL OF THE BIOTIC POTENTIAL OF WESTERN CORN ROOTWORM
(COLEOPTERA: CHRYSOMELIDAE) ADULT POPULATIONS AND ITS
USE IN STUDYING POPULATION DYNAMICS

The western corn rootworm, Diabrotica virgifera virgifera LeConte (WCR), is an economically damaging pest of corn grown in a cropping sequence of corn following corn (continuous corn). The damaging stages of the WCR are the three larval stages that feed on corn roots during June and early July. Larval development is temperature dependent, and the lower threshold has been shown to be 11.1°C (Wilde 1971) or 11.7°C (Kuhlman et al. 1970). The optimum developmental temperature is thought to be between 22.2°C and 29.4°C (Chiang 1973). Bergman and Turpin (1984) found the development and thus, the seasonal appearance of corn rootworm larvae was delayed with late May and early June planting dates.

When corn rootworm larvae are mature they pupate in the soil and adults emerge throughout July and August. Thermal requirements for WCR adult emergence have not been delineated. Ruppel et al. (1978) have argued that first emergence could not be predicted accurately using thermal requirements. Delayed and less synchronous WCR emergence from corn planted in late May and early June has been reported by Musick et al. (1980) and Bergman and Turpin (1984). Bergman and Turpin (1984) used Julian dates rather than thermal unit accumulations for predicting adult emergence dates.

Oviposition in the soil by the females begins two to three weeks after emergence. The length of this preovipositional period is not clearly established by the literature. Short and Hill (1972) estimated it to be approximately 20-23 days, while Kuhlman (1970) determined it to be 23-32 days. Shorter estimates have been made by Hill (1975), 12.2 days, and Branson and Johnson (1973), 14.3 days.

Oviposition by field collected beetles in the lab has been shown to begin at a moderate rate, increase to a peak at approximately 10-15 days, and slowly decline (Hill 1975 and Branson and Johnson 1973). Estimates of field oviposition reported in the literature (Short and Hill 1972 and Pruess et al. 1974) are of little value because of extremely small or unknown sample size. Fecundity has also been measured in the lab by Branson and Johnson (1973) and Short and Hill (1972). Both established fecundity throughout the the lifespan of the female and found the number of eggs laid per female to be approximately 1100. Fecundity within field populations has not been established.

Many researchers have investigated the relationship between oviposition and temperature. Ball (1957), Kuhlman (1970), and Mihm and Chiang (1974) have indicated a lower limit for oviposition of 10°C. These researchers have also indicated an optimum range of oviposition between 15.6°C and 21.1°C. Cates (1968) demonstrated an increasing oviposition rate up to 30°C.

The effects of a number of other factors upon oviposition have been investigated including soil pH (Kuhlman 1970), photoperiod (Cates 1968 and Kuhlman 1970), soil type (Howe and Kuhlman 1968), soil moisture

(Gustin 1979, Kuhlman 1970, and Kirk 1979), and population levels (Gustin 1979 and Cates 1968). Results from these experiments have indicated either no effect or wide ranges of tolerance for oviposition.

Lab estimates of WCR longevity have ranged from 65 days (Short and Hill 1972) to 95 days (Branson and Johnson 1973). These studies indicate that WCR adults can potentially survive until environmental conditions are no longer favorable (i.e., first frost). There have been no studies to estimate the factors involved, nor the extent of field mortality of WCR adults. An important factor that complicates field estimates of mortality is immigration and emigration. The WCR is a very active insect and capable of interfield movement (VanWoerkom et al. 1983 and Godfrey and Turpin 1983). It is thought that this movement is due to the beetles search for food and/or oviposition sites. Determination of the extent of immigration or emigration has not been done. It has been observed, however, that beetles will move in large numbers from mature fields into corn fields that are silking and pollinating (Hill and Mayo 1974). Observations by Godfrey and Turpin (1983) indicate that the majority of beetles moving from field to field are females.

The objective of this study was to integrate the available historical data on WCR development, adult emergence, adult longevity, fecundity, and oviposition into an adult population and oviposition model to express its biotic potential. The model was used to study the population dynamics and oviposition of observed populations in continuous cornfields and determine the effects of different mortality

factors upon the population.

Materials and Methods

Formulation of the model

The system modeled included a single field. Utilizing this constraint results in a more uniform system, considering agronomic variables, and a more manageable system, considering population parameters. To handle the inconsistencies and gaps in the published data, certain assumptions had to be made. It was assumed that adult WCR immigration was less than adult WCR emigration. It was thought that this was a valid assumption if the field involved was of similar maturity as those cornfields surrounding it, because it would not be more attractive and would lose beetles to the surrounding agroecosystem. This assumption may not be acceptable for first-year cornfields (Godfrey and Turpin 1983) or late planted or delayed maturity cornfields (Hill and Mayo 1974), because adults present and those that arrive by random movement would tend to stay due to greater attractiveness of the later maturing fields. WCR emigration above the level of immigration was considered to be "mortality" with regard to the field modeled. Considering these assumptions, the only addition to the population was adult emergence and the only losses from the population resulted from adult "mortality". Because of the lack of knowledge on "mortality" (including emigration), "mortality" was set equal to zero and the maximum oviposition potential determined.

Initialization of the model involved the input of the number of female and total adult WCR emerging through the season. These adult populations were partitioned into cohorts of females and total adults emerging on each day (M). Inasmuch as no published literature quantifies the seasonal emergence pattern of the WCR, the 1979 and 1981 data from Part 1 were used to obtain regression equations for seasonal emergence. Using multiple regression techniques, a highly significant ($P < 0.01$) relationship between the probit transformation of the proportion cumulative emergence and Julian date (JD) and soil heat units (SHU) was obtained for female ($R^2 = 0.90$, $n = 37$) and total adult ($R^2 = 0.86$, $n = 38$) emergence:

$$\text{FEMALE}(M) = -13.83097 + 5.63106E-2 * JD + 1.38783E-3 * SHU \quad (1)$$

$$\text{ADULT}(M) = 112.63899 + 5.28266E-2 * JD + 1.18216E-3 * SHU \quad (2)$$

Soil heating units were accumulated from March 1 using Allen's (1976) modified sine wave method (11°C base, 30°C maximum).

On each simulation day, beginning when ADULT(M) was greater than -2.3 (probit of 1% emergence), the cumulative proportions of adults and females emerging were determined by using equations 1 and 2. The cumulative emergence from the previous day was subtracted from the cumulative emergence for each day to determine the proportion of total and female emergence that day. These values were then multiplied by the seasonal total for adults and females to determine the number of beetles emerging each day. On each day following emergence, air heating degree-days (11°C minimum, 30°C maximum) were accumulated for each emerged female cohort. These heat unit summations were utilized to

determine the preovipositional period of each female cohort.

Data on the WCR preovipositional period by Branson and Johnson (1973) were used to determine the preovipositional period. These data were used because they represent the maximum reproductive potential and provide temperature data to estimate heat unit requirements. It was assumed that the preoviposition period was determined by ovarian development and that this was temperature related with thresholds of 11° C and 30°C. The mean preoviposition period was determined to be 172 heat units, and when the accumulated heat units after emergence for each female cohort reached 172, the entire cohort began ovipositing.

Oviposition rates have been shown to be related to beetle age (Branson and Johnson 1973 and Hill 1975). The data from these studies were combined to obtain a single linear regression equation describing the relationship between oviposition rate in eggs/female/day (EFD) and age in days following first oviposition (AGE):

$$\text{EFD} = 19.9647 - 0.1792 * \text{AGE} \quad (3).$$

Thermal units were not used in this regression because temperature data were not provided by Hill (1975). This equation produced a significant ($P < 0.01$, $n = 32$) R^2 of 0.88 for the combined data. Oviposition rates calculated for each cohort using the appropriate AGE in equation 3 were multiplied by the number in that cohort. These values were then summed to obtain daily and seasonal accumulated egg populations.

Collection of observed data

In 1982-83, five continuous cornfields were sampled through the season for adult emergence, adult populations, and egg populations to compare against the results obtained from the model. In 1982, two fields were sampled in Story Co., Iowa and one field was sampled in Fayette Co., Iowa. One field in Story Co. and one field in Cass Co., Iowa were sampled in 1983. All fields (ca. 4-20 ha) were commercial production fields grown under standard production practices, including the use of planting-time rootworm insecticides. Each entire field was divided into 30 (1982) or 40 (1983) quadrats/field for sampling purposes.

Adult emergence was sampled using emergence traps that provided absolute estimates of the emerging population (see Part 1). One trap was randomly located within each quadrat of each field sampled. Traps were placed in early July and collection cups containing emerged adults were replaced weekly. All adults in the cups were counted and their sex determined. After two weeks all traps were moved to new locations within the quadrat to minimize the possible effects upon emergence of truncating the plant for trap placement (Fisher 1984).

Adult population estimates were obtained by counting all WCR adults on entire corn plants and the surrounding soil surface (plant counts). Five, two-plant counts were taken within each quadrat in 1982 and three, two-plant counts were taken within each quadrat in 1983. Sampling efficiencies estimated by Steffey et al. (1982) indicated two-plant counts to be the most efficient and that these levels of sampling should

provide estimates with a standard error within 10% of the mean. Plant population estimates were obtained for each field to enable the conversion of adult population estimates (adults/plant) to a per area basis (adults/ha).

Egg populations were estimated using the frame sampling method described by Foster et al. (1979). With this method, a 101.6 cm (length) x 10 cm (width) x 10 cm (depth) metal frame was driven into the ground perpendicular to the corn row. All the soil within the frame area to a depth of 10 cm and a length equal to the corn row width was removed, mixed thoroughly, and two 0.47 l subsamples removed. This sampling procedure was repeated in the same area to sample the soil from 10 cm to 20 cm in depth. The sampling method was employed at one randomly selected site within each quadrat of each field on each sampling date. Sampling began in each field the first week of August and continued at 7-10 day intervals for four sampling dates. Final season egg populations were also estimated using these techniques. Conversion of population estimates to a per hectare basis followed the procedures described by Foster et al. (1979). All egg samples were returned to the lab, and the eggs were separated from the soil utilizing the procedures of Shaw et al. (1976). All eggs in each sample were counted and WCR eggs separated according to Atyeo et al. (1964).

Results and Discussion

The model developed attempts to express the potential oviposition of different levels of emerging populations. The approximation of this model to the actual population biotic potential would be difficult to

determine. Considering the published literature, Branson and Johnson (1973) and Hill (1975) present preoviposition, fecundity, and oviposition rate data that seem to represent the biological limits of this insect. Because of this, one can assume that these data are at least approaching the biotic potential of the WCR.

The partitioning of the population into emerging cohorts is of primary importance in determining the accuracy of the model. To test the accuracy of the model in predicting emergence, the predicted total and female cumulative emergence was correlated with the observed total and female cumulative emergence data, respectively, for the 1982-83 data. The correlations between observed and predicted values for both total and female emergence ($r=0.98$) were highly significant ($P<0.01$, $n=34$). A plot of the data for female emergence in Figure 1 demonstrates good agreement between predicted and observed values. As a result of this agreement, the model can be assumed to provide a reasonable estimate of WCR adult emergence and the reproductive potential of the WCR.

Comparison of the observed adult and egg population estimates predicted by the model reveal large discrepancies (Figures 2-6). From these comparisons, the importance of "mortality", including emigration, in determining adult WCR populations and subsequent oviposition can be seen. The observed peak adult populations were approximately 30-40% below the total emergence, and the observed egg populations were approximately one-sixth the predicted population. The adult "mortality" factors acting on the population are great enough to cause the

population to decline while emergence is still occurring. The model also demonstrates that the maximum potential oviposition rate for WCR populations occurs after Julian date 220, agreeing with the field oviposition dates presented in Part 4.

By imposing different "mortality" rates upon the emerging populations, characteristics of these population "mortality" factors can be obtained. A constant "mortality" rate was determined that would approximate the observed populations for these fields. This "mortality" factor was 3.5% of each emerged cohort per day and was imposed on the modeled population. The results of these simulations are shown in Figures 2-6. Predicted egg populations in two of the five fields (Figures 5 and 6) were close to those observed, and the remaining egg estimates were far below those observed. Inasmuch as the maximum oviposition rate is used in the model, underestimates of the observed egg populations by the model should not occur and overestimates of the observed values would result from inadequate rates of "mortality". In this case, the underestimated egg populations may be the result of an age structure within the modeled population that is too young, leading to a greater proportion of time being spent by the female population in the preovipositional period. This would result in an underestimate of the egg population.

A progressive "mortality" rate was also developed that would result in the predicted adult populations approximating the observed values. This "mortality" rate was 1.25% on day 1 of the simulation and increased 1.25% on each succeeding day. The "mortality" rates were imposed each

day upon the total and female population in each emerged cohort, regardless of previous "mortality". This "mortality" results in a greater proportion of older adults surviving longer, leading to an older age structure for the populations simulated. The use of this "mortality" factor led to good estimates of the observed egg populations in three of the five fields (Figures 2, 3, and 4). The remaining two estimates overestimated the observed egg populations. Because so few factors are included in the model, overestimation is not surprising. Any factor that would cause a reduction in fecundity or oviposition in the field would result in the model overestimating the population. As a result of these simulations, it seems likely that WCR "mortality" acts in a progressive manner. This idea would be a reasonable result of the less ideal nutritional availability in the field for those adults emerging after the completion of silking and pollination in late July and early August.

Utilizing the progressive "mortality" rate in simulations should give a reasonable estimate of how oviposition is affected by insecticide applications for adult control to reduce oviposition. A series of simulations were run where 95% mortality was imposed upon the population for two weeks to simulate the effect of an insecticide application. The total adult emerging population was 607,200 adults/hectare with 440,000 females/hectare. The sex ratio of the emerging adults was the average of the ratio from the 1982-83 data. The simulations were run using weather data from two years (1982 and 1983). Non-sprayed populations resulted in 206,400 and 214,500 beetles/hectare for the two

years, respectively. The results of these simulations are shown in Table 1. The highest percentage reduction in seasonal egg populations was obtained in both years for applications occurring in early August. These simulations indicate that insecticide sprays to reduce adult populations and subsequent oviposition may be quite effective.

Current recommendations for the use of adult control techniques to reduce subsequent oviposition call for the application of insecticides when adult populations reach one beetle/plant (ca. 50-60,000 beetles/ha) and 10% of the female population being gravid. The model shows sufficient mortality when insecticide applications are applied in early August even though the adult populations at that time are 2.5-3.0 beetles/plant and 20-30% of the females are ovipositing. These results demonstrate that the current recommendations may be conservative. This may be necessary in practice when dealing with the variability of the WCR field populations; however, improvements in economics and effectiveness of adult control procedures may be gained by eliminating the less effective insecticide treatments occurring before August 1.

This model shows some utility in the study of the general characteristics of the factors involved in WCR population dynamics. However, WCR populations show a great deal of variability from field to field that is not accounted for in this model. When further research has identified and quantified these factors, their incorporation into the model of the biotic potential of the WCR would greatly improve its predictive capabilities.

Table 1. Predicted pre-spray and final egg populations and percent reduction of potential egg population for model simulations of adult control insecticide applications on WCR populations of 607,200 adults emerging/ha

Mortality	1982 Simulation			1983 Simulation		
	Imposed	Pre-spray Eggs ^a	Final Eggs ^a % Red.	Pre-spray Eggs ^a	Final Eggs ^a % Red.	
7/17-7/31		0.02	15.91 41	0.001	22.53 54	
7/24-8/7		0.36	7.58 81	0.41	12.11 75	
7/31-8/14		1.75	4.13 89	1.70	5.82 88	
8/7-8/21		4.11	4.46 89	4.97	5.72 88	
8/14-8/28		8.66	8.66 78	11.01	11.01 78	
8/21-9/4		15.02	15.02 62	19.53	19.53 60	

^a Egg populations expressed in million eggs/ha.

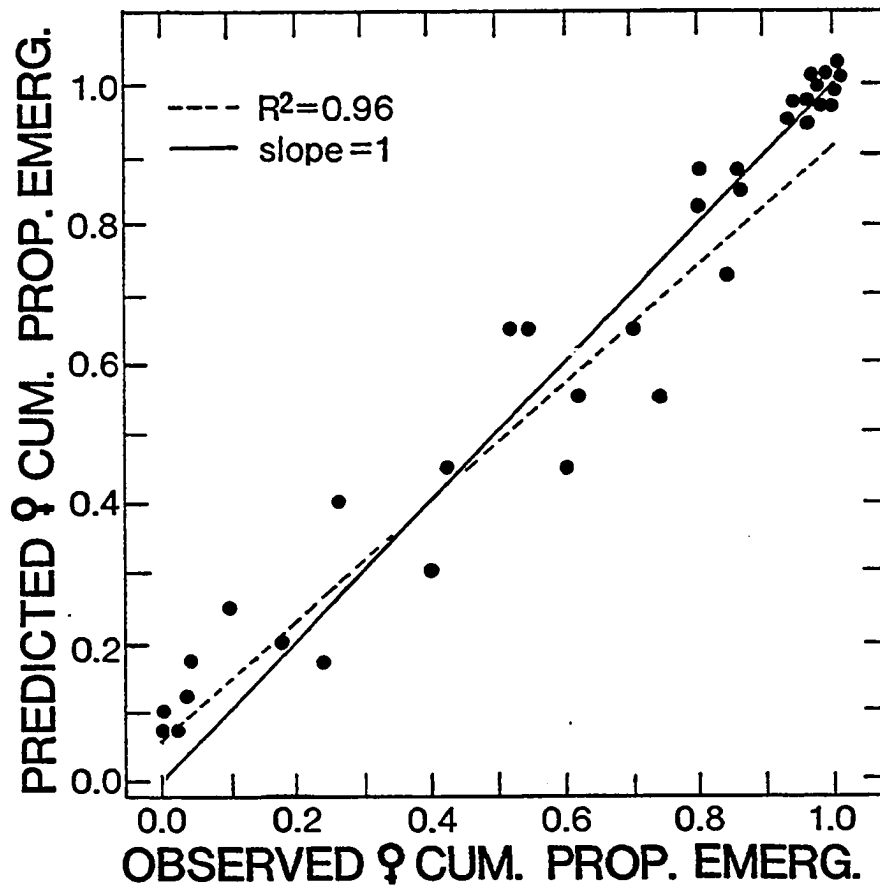


Figure 1. Comparison of predicted and observed values for cumulative proportion female WCR emergence

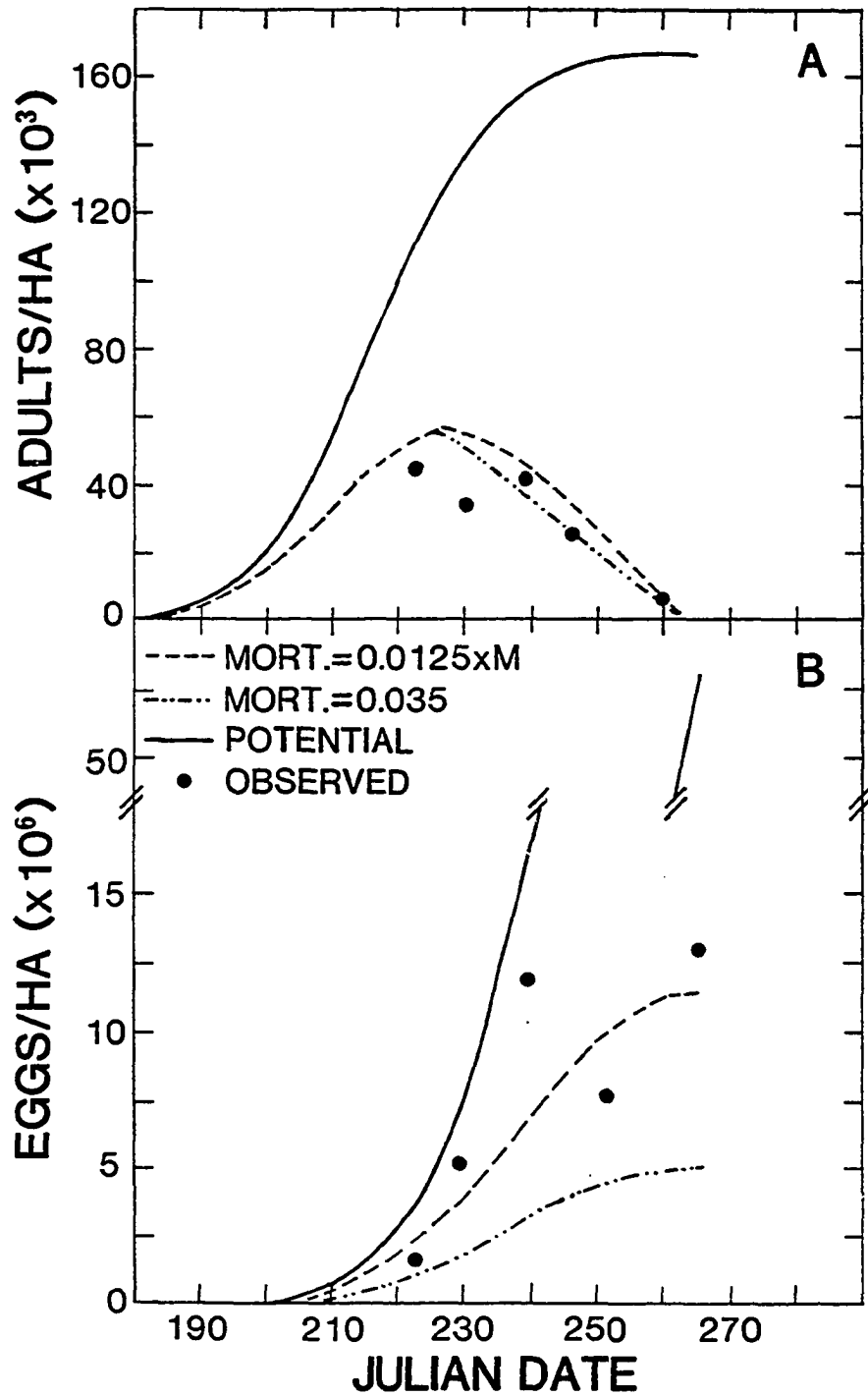


Figure 2. Observed estimates and values predicted by WCR oviposition model for adult and egg populations through the season, (emerging population=128,600 adults/ha, 77% female) Story Co. (Field #2), IA 1982

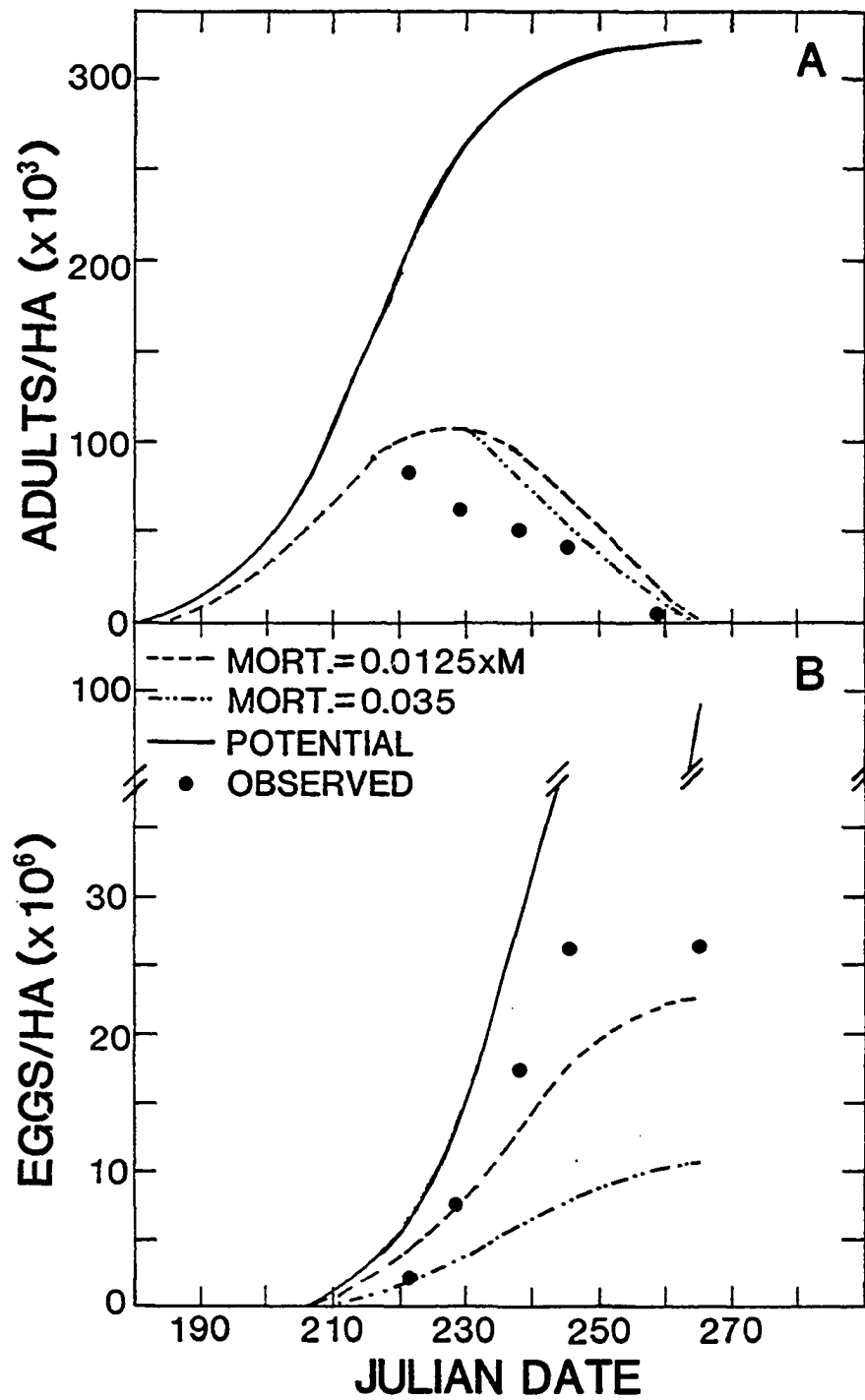


Figure 3. Observed estimates and values predicted by WCR oviposition model for adult and egg populations through the season, (emerging population=252,200 adults/ha, 79% female) Story Co. (Field #1), IA 1982

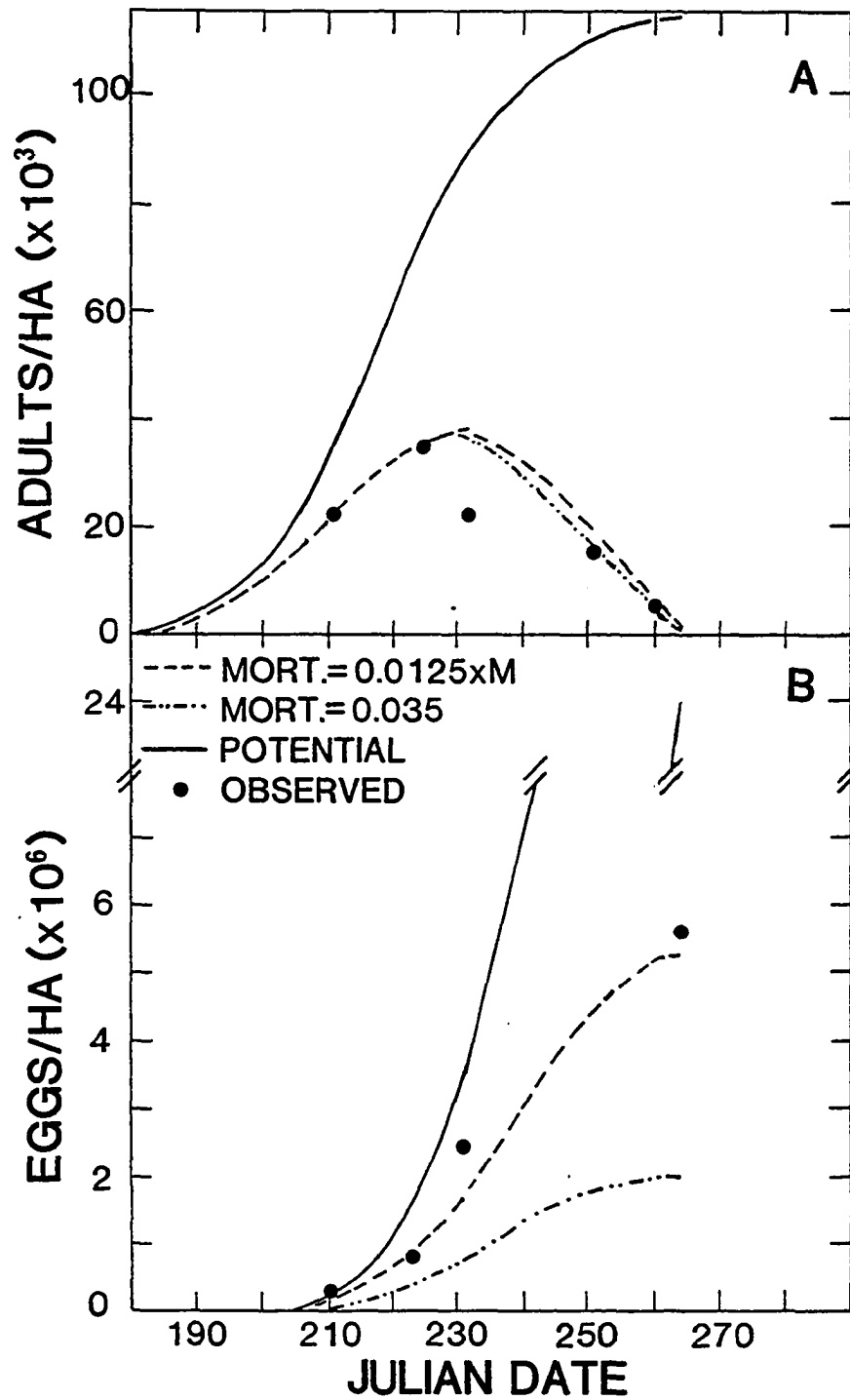


Figure 4. Observed estimates and values predicted by WCR oviposition model for adult (A) and egg (B) populations through the season, (emerging population=114,300 adults/ha, 62% female) Fayette Co., IA 1982

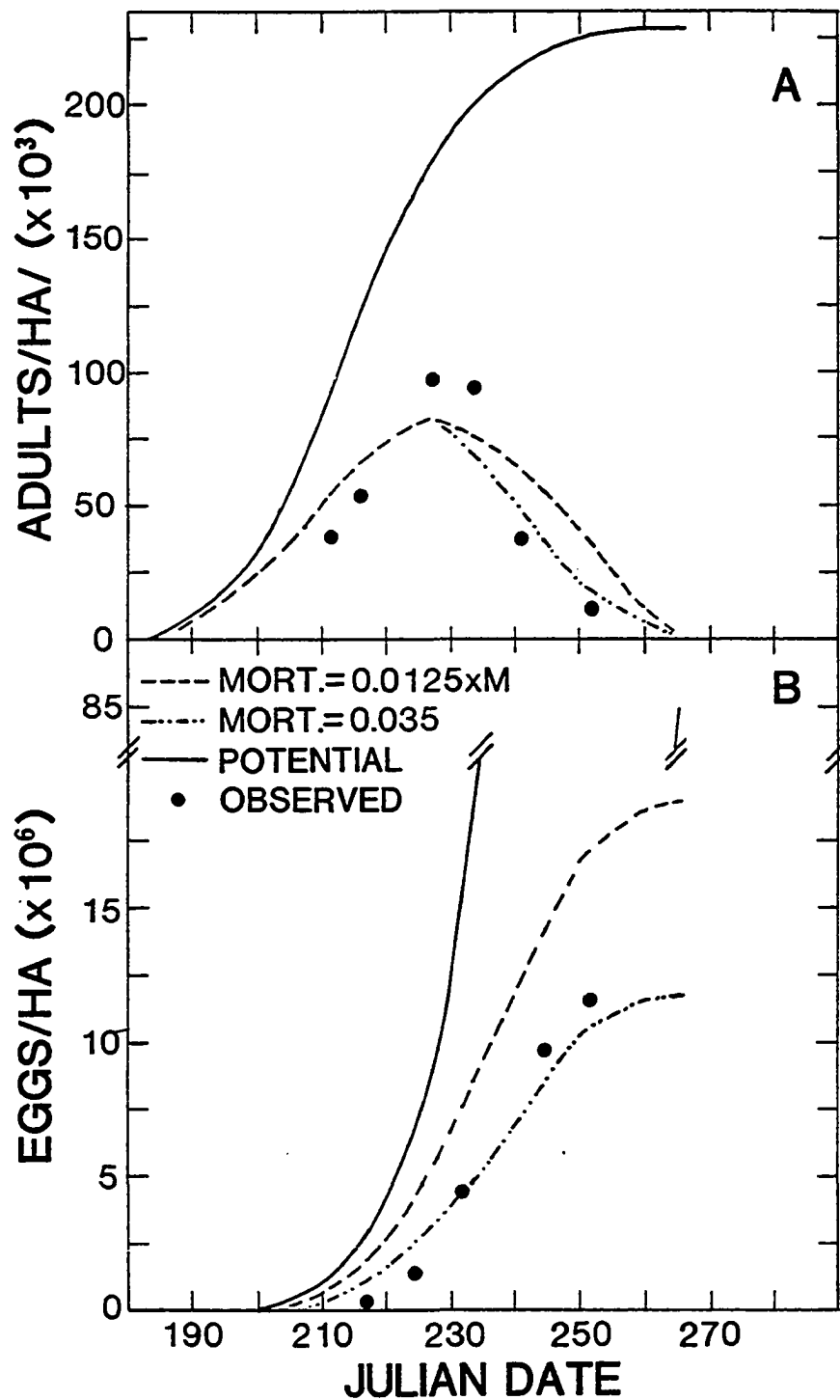


Figure 5. Observed estimates and values predicted by WCR oviposition model for adult (A) and egg (B) populations through the season, (emerging population=229,100 adults/ha, 74% female) Story Co., IA 1983

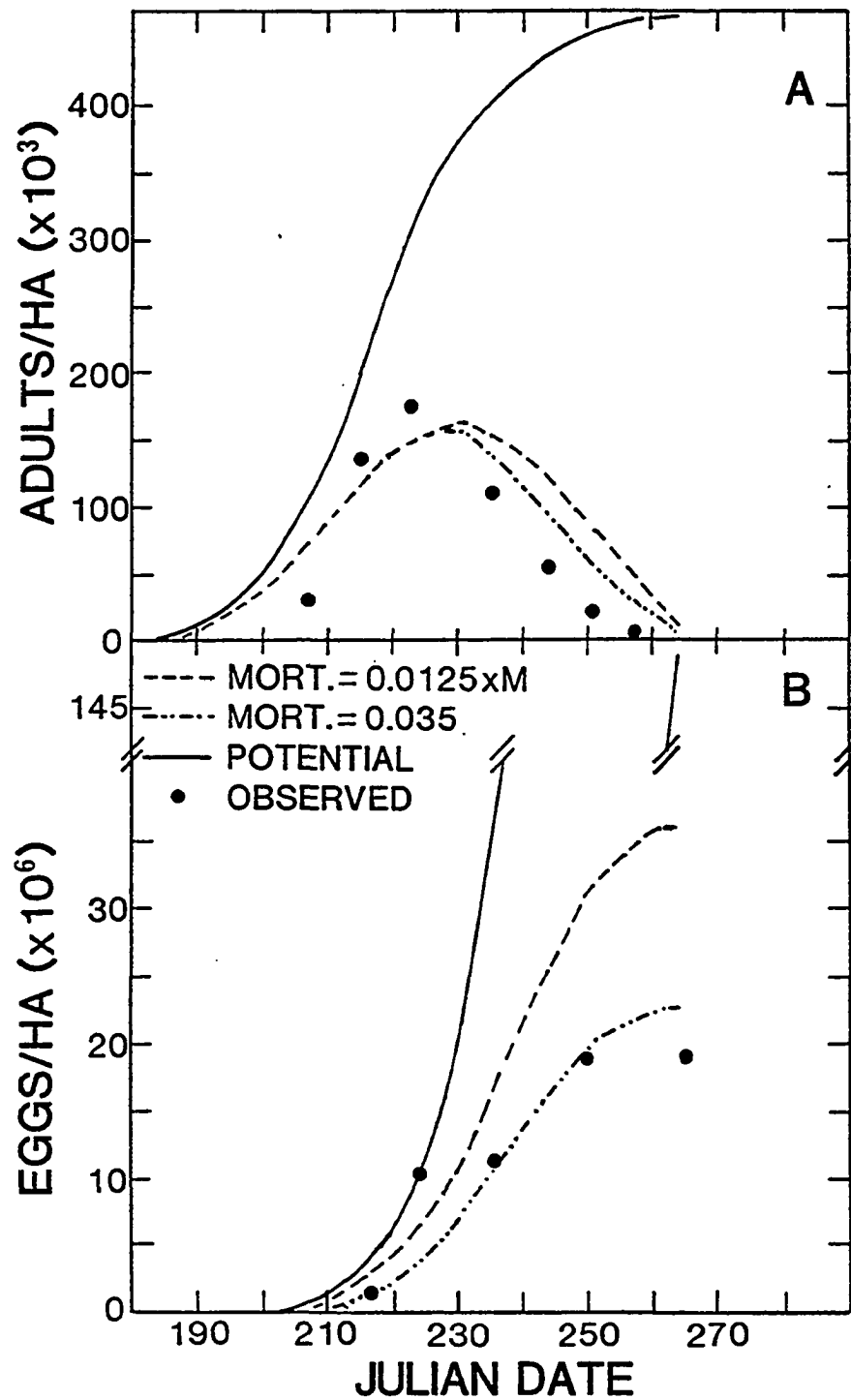


Figure 6. Observed estimates and values predicted by WCR oviposition model for adult (A) and egg (B) populations through the season, (emerging population=464,400 adults/ha, 72% female) Cass Co., IA 1983

SUMMARY

The objective of these studies was to investigate and quantify the parameters involved in corn rootworm adult population dynamics and oviposition. Little previous research had been done in these areas, and early work indicated a need for an absolute adult emergence sampling tool and an accurate method to determine the sex ratios of field populations of adult corn rootworms. The extensive amount of egg sampling data gathered led to the re-examination of current and past practices in corn rootworm egg sampling. Adult population dynamics was studied by attempting to quantify adult emergence, adult "survival", and oviposition and attempting to determine the major factors affecting adult population dynamics.

An absolute sampling technique for NCR and WCR adult emergence was developed and utilized in 12 fields from 1979-83. The optimum sampling scheme for the emergence of NCR and WCR field populations was found to involve sampling at a single site within each of a large number of quadrats located throughout the field. Sampling cost and size estimates were calculated for the NCR and WCR.

"Absolute" sex ratio estimates within continuous cornfields were obtained using a 3.05 m vertical sticky trap. This method was found to be an accurate sex ratio sampling tool; however, sampling with it was very labor intensive. Data collected using this trapping technique showed a relationship between sex ratios and the height of sampling. Vertical flight distributions for both species and sexes were

determined. The optimum height to sample for NCR and WCR sex ratios was determined to be 0.92-1.22 m. Regression equations describing seasonal sex ratio changes for the NCR and WCR were obtained. Analyses performed on these data indicated a significant portion of the variability in seasonal sex ratios not accounted for by Julian date was due to field and/or year differences. Further research in this area is needed to determine the reasons for these sex ratio differences.

Cost and design considerations of NCR and WCR egg sampling were examined using sampling data collected in a number of commercial continuous cornfields. Significant variability was found in the horizontal and vertical distributions of NCR and WCR eggs. Previous literature does not indicate the extent of this variability for either species. Therefore, sampling for NCR and WCR eggs should utilize a sampling method that samples the entire row-width, and samples should be taken to a depth of at least 20 cm. Deeper sampling may be necessary when drought cracks enable deeper oviposition.

Sampling characteristics of the frame sampling method were examined. The mean-variance relationship was not found to differ significantly for the NCR and WCR. The index of aggregation (1.49) calculated from the pooled data (NCR+WCR) indicate aggregated egg populations. Sampling cost analyses show the most efficient method to reduce sampling variability for NCR and WCR egg sampling is to take one or two samples per frame and a large number of frames within a field. Sample size estimates for different sampling strategies are given.

Seasonal oviposition was measured in eight continuous cornfields in

1981-83. These data indicated earlier seasonal ovipositional patterns than previous literature suggests. No differences were detected between NCR and WCR seasonal oviposition. By 19 August or 761 seasonal accumulated air heat units, 50% of the oviposition had occurred. Ninety percent of the seasonal oviposition had occurred by 6 September.

Adult populations were also monitored in the eight continuous cornfields sampled in 1981-83. Regression equations describing the relationship between cumulative seasonal emergence (probit transformation) and Julian date and air and soil heat units were determined for both species. Estimates of adult "survival" indicate rapid early season "mortality" (including emigration) for WCR populations. A rapid decline in adult "survival" was also seen for the NCR. Knowledge about the "survival" of the adults would be of great importance in determining the oviposition potential of field populations. Results from this study indicate no major relationship between weather factors and population change, but significant correlations were determined between peak populations and the percentage population change. Use of a model of the biotic potential of the WCR to study population dynamics indicate that adult "mortality" may more strongly affect the later emerging beetles. Little is known about the factors affecting corn rootworm populations and considerable research needs to be done in this area.

The relationship between adult population and subsequent oviposition was found to be significant for the NCR and WCR. But, this relationship for the WCR was considered tentative due to one extreme

data point. A better understanding of NCR and WCR adult population dynamics will be necessary to improve these relationships.

This study has resulted in the development and/or enhancement of corn rootworm adult emergence, adult sex ratio, and egg sampling techniques. Quantification of seasonal emergence, adult "survival", and seasonal oviposition will provide understanding of the basic characteristics of adult NCR and WCR population dynamics. The relationship between adult populations and subsequent egg populations, particularly for the WCR, is not well-understood. Further research needs to be undertaken to determine the factors that affect adult "survival" (including migration), field fecundity, and oviposition before egg population prediction will be completely successful.

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