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PHENOLOGY, LIFE HISTORY, AND HABITAT SELECTION OF THE EUROPEAN CORN BORER, *Ostrinia nubilalis*, IN ALBERTA

by

DENNIS ALLAN LEE

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH

IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE

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.....
Supervisor

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Date APRIL 15,1986

Dedication

I dedicate this thesis with much gratitude to my supervisor, Dr. J. R. Spence.

Abstract

Life history traits of colonizing populations of the European corn borer in Alberta were compared to traits of populations in the centre of the species' range. Not only were differences observed in these traits between Alberta populations and those in Iowa, but differences were even observed between two populations of *O. nubilalis* in Alberta. Adaptations were compared in terms of phenology, physiology, and behaviour of both larvae and adults. I concluded that a peripheral population of a colonizing species, such as *O. nubilalis*, adapts to new environments primarily by changes in life history traits.

Although phenology studies indicated that *O. nubilalis* is mainly univoltine in Alberta, populations in the South Saskatchewan River valley pupated and emerged three to six days earlier than those on the plains. In 1983, flight peaks occurred on 8 July in the valley and on 14 July on the plains. Valley borers had a partial second generation (flight peak= 30 August), which plains borers did not have. Mean pupal mass was significantly less for plains populations than valley populations. Transplant experiments demonstrated that these differences reflected both environmental and genetic influences.

Observed differences in phenology were controlled by adaptation of physiological traits. Alberta corn borer developmental thresholds for postdiapause pupation (12.8°C), fourth (15.3°C) and fifth (14.1°C) instars, were higher than

those (10°C) of Iowa borers. Higher temperature thresholds delayed development in Alberta populations, reducing midsummer pupation. Selection for univoltinism was apparently less intense for valley populations, partly because they developed faster than plains populations during some life stages. Also, lower and upper thresholds for the fifth instar were less for valley populations (11.9°C, 30.0°C) than for plains populations (14.0°C, 32.5°C). Valley moths laid significantly more eggs than did plains moths (559 *vs.* 267 eggs/female) over a longer timespan (9.1 *vs.* 5.1 days) at 15°C/29°C. Upper thresholds for both oviposition rate and optimum egg viability were less for plains borers (25°C, 22°C) than for valley borers (27°C, 27°C). Analysis in terms of reproductive cost theory suggests that fecundity and lifespan are plastic phenotypes in the corn borer, that change rapidly in response to differing environments.

Habitat selection by larvae and adults was also adapted to Alberta conditions. Larvae first dispersed to leaves, ligules, sheaths, ears and tassel buds, depending upon whether the feeding site was filled with other larvae, and upon plant growth stage at hatching. This opportunistic behaviour contrasts with that of Iowa borers, which feed mainly at specific sites. Alberta borers only entered the stalk after the second instar, and diet of early- and late-instar larvae differed. 84% of larvae left the original host plant, and inter-plant dispersal was greater along corn

rows than between them. More moths were caught in pheromone traps, and more eggs were found, in centres of Alberta fields than at field borders. Because of the semi-arid climate in Alberta, dense weeds were absent in field borders, so moths did not aggregate there, as they do in Iowa.

Climatic extremes in Alberta were associated with greater larval mortality than were biotic factors. Total larval mortality (64%) was less than in Iowa (90%), which suggests why Alberta corn borer populations have increased since their introduction.

Acknowledgements

This study was supported through operating grants from the Natural Sciences and Engineering Research Council, the Central Research Fund of the University of Alberta, the Government of Alberta's Farming for the Future fund, the Alberta Vegetable Growers and Fresh Vegetable Marketing Boards. The author gratefully acknowledges scholarship support from the Natural Sciences and Engineering Research Council. I thank the Alberta Environmental Centre for the use of light traps, and Alberta Agriculture for providing pheromone traps. I thank H. Netolitzky and R. Sargent for for providing laboratory facilities at Medicine Hat College. I am grateful to R. Byers (Agriculture Canada) for egg masses, to R. Howard for assistance in isolating fungi, and to W. Priusak (Canada Environmental Service) for weather data. Insects were identified by the Biosystematics Research Institute, Ottawa; and fungi were identified by L. Sigler, Mold Herbarium, Edmonton. I am grateful to A. Harper, D.G.R. McLeod, R. Byers, D. Strubble, U. Soehengen, S. Dereniwski and M. Dolinski for discussions concerning the research. I thank my field assistants J. Richard, D. Netolitzky, and M. Rothlander, and my laboratory assistants D. White, N. Berg, E. Strong, and D. Blades. I also thank participating growers K. Biemans, J. Hunter, T. Nishimoto, P. Plesky. T. Moore, K. Franklin, A. Reynar, M. Huber, T. Sunderland and R. Van Wert. J. Scott helped prepare the figures. This thesis was improved by comments from A. Harper and D.G.R. McLeod. Above

all, I thank my supervisor, J.R. Spence, and my wife Debora for their encouragement and support.

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I. Introduction

The European corn borer (ECB) is one of the most serious insect pests of corn. Yield losses for hybrid and sweet corn are about 3% and 8% per borer per stalk, respectively (Martin *et al.* 1976). The ECB also causes serious losses in sorghum, potatoes, peppers and tomatoes. The insect has a wide host range, having been found on more than 200 wild plants (Hodgson 1928).

The original host plant of the ECB in Europe was wild hemp. With the introduction of cultivated corn in Europe, the ECB abandonned hemp in preference for corn (Babcock and Vance 1929). The insect was introduced to North America in 1917, near Boston, as a result of importing broom corn from Hungary and Italy (Wressel 1960). The ECB was reported in Ontario in 1920, and in Manitoba and Saskatchewan in 1949 (Wressel 1953). A small infestation in southeastern Alberta was eradicated in 1956, but a subsequent infestation was not noted until 1980, by which time it had spread beyond control (Lilly and Harper 1982). Since 1980 the corn borer has expanded its range from Medicine Hat to Lethbridge (U. Sohengen, personal communication).

The corn borer's successful colonization of North America is due partly to it's great plasticity with respect to life history traits. Most ECB populations have one generation per year in Canada but populations of the same species may go through up to four generations per year in the southeastern United States (Showers 1981). Host plant

adaptability is an advantage in areas where several generations occur. In North Carolina, first-generation ECB feed on potatoes, while later generations infest corn (Anderson *et al.* 1982).

ECB life history has been studied mainly in the context of finding means to control it. However, because the ECB is a colonizing species with a high degree of phenotypic plasticity in life history traits, it is an ideal subject for testing current ecological theories. Phenotypic plasticity occurs when a given genotype produces several different phenotypes (Parsons 1983). Life history characters examined in this thesis include fecundity, body size, lifespan, diapause, behaviour, developmental rate and temperature thresholds for development. Similar to other phenotypic characters, they are subject to selection pressure and evolution (Taylor 1981, Gill *et al.* 1983, Parsons 1983). Selection favours those individuals appropriately timing their life history with events in the environment (Taylor 1981). Until recently however, life history traits have not been studied in an evolutionary context.

ECB populations in Alberta are situated on the extreme north-west corner of the species' North American range. Because these populations were only recently introduced, this represents an unique opportunity to observe adaptations of ECB life history in new environments. Therefore one goal of this research was to compare life history traits of

Alberta ECB to those of ECB in eastern North America. I expected to observe differences not only in developmental rates and thresholds, but also in habitat selection by larvae and adults. A similar objective, which arose after I observed the phenology of Alberta ECB, was to compare differences in traits between two geographical populations of the ECB in Alberta. Differences were observed not only in the above-mentioned traits, but also in larval behaviour patterns between the two Alberta populations. I have designated these groups as "populations" only, in accordance with Beck and Apple (1961). Thus, both directions of study have provided evidence for microevolution of life history traits in Alberta ECB.

The chapters of this thesis have been arranged to emphasize the general theme that the ECB is capable of adapting life history traits when it colonizes new environments. Chapter II describes and explores the basis of the phenological pattern in the ECB in Alberta. The phenological differences examined between valley and plains populations lay the groundwork for the chapters that follow. Chapters III and IV assess physiological adaptations, for larvae and adults respectively, that are part of the basis for the observed phenology. I expected Alberta ECB to have lower thresholds for development than ECB from the United States, thus enabling Alberta populations to complete development within the short growing season in this area. Chapters V and VI discuss adaptations of the larvae and

adults, respectively, to the Alberta environment. Chapter V describes ECB larval dispersal immediately after hatching, within microhabitats in the corn plant, and between corn plants. In Chapter VI, I test the hypothesis that relative abundance of adults and eggs would be greater in centres of fields than along field borders, because environmental conditions at field borders are incompatible with requirements for survival of adults and eggs. In Chapter VII, factors affecting ECB mortality are categorized, and used to construct a life-table. Part of this chapter deals with the selective factors that maintain the observed behavioural patterns. A further objective was to determine if and why a population increase is occurring. The thesis is summarized, and general conclusions drawn, in Chapter VIII.

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II. PHENOLOGY IN SOUTHERN ALBERTA

A. Introduction

The European corn borer (ECB) has successfully colonized much of eastern and central North America since its introduction to the continent in 1914 (Showers 1981)[1]. A partial explanation for the success of the corn borer is its adaptive plasticity which permits colonizing populations to modify food habits and voltinism to suit local conditions.

More than one generation may occur in areas with an extended growing season. Bivoltine populations of the ECB have been found in Quebec (McLeod *et al.* 1979), south-western Ontario (McLeod 1976) and sometimes in Manitoba and Saskatchewan (Lilly and Harper 1982). Further south, populations of *O. nubilalis* are multivoltine (Showers 1981), often using several agricultural crops as hosts during successive generations (Anderson *et al.* 1982). Voltinism is controlled by the diapause response, which varies in ECB populations (Showers 1981). The initiation and maintenance of diapause is influenced by both intrinsic (genetic strain and sex) and extrinsic (mainly temperature and photoperiod) factors (Tauber and Tauber 1973).

In Alberta, mature fifth instar larvae of ECB overwinter within corn debris. Pupation follows in the spring and moth emergence occurs in early summer. The first

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[1]A version of this chapter has been accepted (pending revision) for publication. Lee, D.A., and Spence, J.R. 1986. *Can. Entomol.*

infestation of the insect in Alberta was eradicated in 1956. A subsequent infestation, first noted in 1980, has now expanded out of control in the corn growing region around Medicine Hat (Lilly and Harper 1982), at the northwestern extreme of the North American range of *O. nubilalis*.

I undertook this study to increase understanding of processes involved in the success of an exemplary colonizing species. In this chapter I aim to describe the phenology of the ECB in Alberta, and to discuss experiments to determine the nature of phenological differences noted between two populations.

B. Materials and Methods

Field Studies of Phenology

Pupation and Emergence

In 1983, diapausing corn borer larvae were dissected from corn stalks periodically throughout May and June. Larvae were collected from two sources (Table II-2, Fig. II-1): a field (site 1) near the city of Medicine Hat in the South Saskatchewan River valley (Valley), and from the plains (site 4) 16 km south of the river (Plains). Individual larvae from each source were placed in separate Petri dishes 9 cm in diameter (3-5 larvae/dish), with moistened filter paper to provide free water required for pupation (Beck 1967). The dishes were held in a screened

cage located on the Medicine Hat College grounds. A continuous temperature recorder (Weathertronics® Hi-Q Hygrothermograph Model 5020) was placed inside the cage. Every one to four days, numbers of larvae pupating and emerging were noted. As a check on accuracy of data from the cage, pupation and emergence (defined as the percentage of empty pupal cases found inside stalks) were also monitored by sampling the field in the river valley.

In 1984 corn borer populations were much higher than in the previous year, and so phenology of plains and valley borers was monitored solely by periodic field sampling. Corn stalk pieces were collected at one to five day intervals and dissected the same day in the laboratory to determine numbers of diapausing larvae, pupae, and empty pupal cases (range=20-136 borers collected/interval/site; median=50, no. samples=23).

Flight Patterns

In 1983 and 1984 emergence data were compared with light trap catches. Flight activity was monitored with standard New Jersey light traps, set up in several locations (Fig. II-1) spanning the elevation gradient between valley (2175 m) and plains (2490 m). In 1983 two valley sites were monitored, and the results are presented as the average of the two traps. Moths were killed upon collection by a dichlorvos strip suspended in the middle of the jar. Traps were checked every one or two days. The second flight was monitored with only one trap in the valley in 1983, and a

trap in both valley and plains in 1984.

Physiological Time Measurement

Degree-day (DD) accumulations were computed by a sine wave approximation method (Gilbert *et al.* 1976). A threshold for development of 12.8°C was used for postdiapause pupation and 11.2°C for postdiapause emergence (see Chapter III), with March 1 as the beginning day.

Reciprocal Transplantation

In March 1984 diapausing larvae were collected from field corn in the Saskatchewan River valley, and on the plains 20 km south (Fig. II-1). Field corn stalks from a single source (Plains) were split, live larvae were inserted (3 to 4 larvae/stalk), and the stalks were then taped back together. Fifty larvae from the valley were placed in stalks in a screen cage on the plains. Stalks containing 50 plains larvae were likewise placed in a screen cage in the valley. As a control, 50 similarly treated plains larvae were placed in a screen cage on the plains, and 50 valley larvae were similarly placed in the valley. In late May 1984 larvae were transferred to Petri dishes with moistened filter paper discs, and then examined daily for pupation. Cumulative percent pupation and wet pupal mass in each of the four cages was recorded.

Continuous temperature recorders (Peadbody-Ryan Instruments, Model J) were set up within one of the screen cages at each site. Minimum and maximum temperatures were

compared between sites from June to August during both 1983 and 1984. Unfortunately temperature data from both sites are not available for March to June for these years. However, in order to compare temperature regimes between valley and plains, temperature data were collected from February to July 1985.

Field Estimates of Postdiapause Growth

Larvae from the plains and valley were dissected from stalks of field corn and weighed live on 5 April, 5 June, 10 June and 15 June 1984 with a Mettler PC440 balance (accuracy=±0.001 g). Additional valley and plains larvae collected June 15 were oven-dried at 60°C for 120 hours, then weighed. Plains and valley pupae collected from the field at the end of June were also weighed.

C. Results

Field Studies of Phenology

Pupation and Emergence

I observed differences in phenology between corn borer populations occurring on the valley and the plains in both 1983 and 1984. The date for 50% pupation for valley borers was 21 June in both 1983 and 1984, while for plains borers it was 25-27 June (Fig. II-2). Dates for 50% emergence were 8-9 July and 13-14 July for valley and plains populations respectively (Fig. II-3). Patterns of pupation and emergence

were similar between years for both valley and plains populations. Although valley populations began pupating 11 days later in 1984 than in the previous year, the pupation rate in 1984 was accelerated so that 90% pupation was achieved earlier. This same pattern occurred for emergence in the valley.

To assess the significance of these phenological differences a X^2 test of independence was performed on the 1984 pupation data, for the four sampling dates on which both populations were sampled. Results (Table II-1) show that differences were significant.

Differences in timing of pupation between valley or plains environments were consistent among fields within either environment. Samples taken in different fields over a three-year period on June 16-20 showed significant differences between valley and plains sites (Table II-2). Differences between environments did not apparently depend on whether sweet or field corn was sampled.

Both pupation (in 1985) and emergence (in 1983 and 1984) were compared between populations in relation to physiological time. 1985 DD data was used to examine spring pupation. 490 DD were recorded at the valley site, from March 1 until June 21, when 50% pupation of valley ECB occurred. Only 331 DD were required for plains borers to achieve median pupation (on June 25). A base threshold of 12.8°C was used for both these computations (see Chapter III). Thus valley ECB required more DD to attain median

pupation than did plains ECB, even though median pupation of valley borers was earlier when measured in calendar time.

When physiological time was used to compare cumulative percent emergence for 1983 and 1984, both plains and valley borers had approximately equivalent distributions (Fig. II-4). A common base threshold of 11.2°C was used (see Chapter III), and DD accumulation began from the calendar date when median pupation occurred. An average 164 DD were accumulated to mean emergence (Fig. II-4), for both populations.

Although both sexes began and completed emergence at the same time in 1983, 27.4% more males than females emerged during the first half of the emergence period (Fig. II-5). Caffrey and Worthley (1927) have also noted changes in the sex ratio of ECB over the progression of the adult flight period. Sex ratio at emergence was nearly equal. For valley borers the ratio was 1.007 (females/males, n=303), while for plains borers it was 0.739 (n=40). A goodness of fit test performed on this data showed that observed frequencies did not vary significantly from the expected equal frequencies (valley: $X^2=0.003$, $df=1$, $P<0.001$; plains: $X^2=0.90$, $df=1$, $P<0.001$).

Flight Patterns

The first flight extended from late June to 5-10 August (Figs. II-6A,B,C). In 1983 peaks of flight activity recorded by light traps coincided with times when median emergence was observed in both environments (Fig. II-6). In 1984 flight peaks occurred on 12 July in the valley, and from 15-21 July at the intermediate site. At this latter site an additional flight peak was observed from 27-30 July. Because dates for 50% emergence were the same in 1984 as they were in 1983, peak flight times did not coincide with days of median emergence in 1984.

The late and bimodal flight pattern in 1984 was correlated with long periods of low nightly temperatures during the emergence period. The spontaneous take-off by an individual insect depends upon a specific temperature threshold (Johnson 1969, pg. 258). Stirrett (1938) correlated temperature at sunset and ECB moth flight. The lowest temperature at which ECB moths flew was 13.3°C (Stirrett 1938). Rather than relating flight of Alberta moths to temperature at sunset, I plotted minimum daily temperature (MDT) against daily trap catches (Fig. II-7) according to the method given by Johnson (1969). Flight was unlikely when MDT fell below 11.5°C (Fig. II-7). Flight was delayed at the valley site because MDT averaged 9.3°C (range=7.5-11.1°C) from 7-12 July. Temperatures at the intermediate site were low from 7-14 July (average temp.=9.2°C; range=5.8-12.8°C). A second period of low

catches occurred at the intermediate site when MDT plunged to an average 9.2°C (range=5.8-13.0°C) from 21-26 July.

In 1983 a second generation flight occurred in the valley from 22 August to 14 September, with the peak flight falling on 28 August (Fig. II-6). The ratio of second generation adults trapped to first generation adults trapped was 1.5, suggesting that the size of the second flight was greater than the first flight. Field counts of pupation conducted at the end of August 1983 showed a midsummer pupation rate of *ca.* 7% (n=28) for valley ECB and 2% (n=156) for plains ECB. In 1984, light trap catches indicated a much smaller second generation than the previous year (Fig. II-6). Field counts showed an equivalent pupation rate of 0.5% for both valley and plains ECB (n=170).

Reciprocal Transplantation

Differences in patterns of cumulative percent pupation were observed between valley and plains controls (Fig. II-8). Valley borers began pupating earlier, and initially at a higher rate than plains borers. Reciprocally transplanted larvae tended to follow the same pattern of pupation as the controls in the environment they were transferred to.

When means of pupation dates were compared, valley controls showed the lowest Julian date (180.6), plains controls had the highest date (183.2), while the transplant samples exhibited intermediate pupation dates (181.6 plains

ECB in valley, 181.9 valley ECB on plains). This pattern is similar to that shown by mean pupal weights (see next paragraph). However, because of the high variance and fairly close sample means, two-way ANOVA revealed no significant effects of either place of origin or transplant environment ($P>0.2$ for both main effects and interaction). When plains and valley controls were compared alone by one-way ANOVA, marginally significant differences were observed ($F=3.69$; $df=1,62$; $P=0.059$).

Both transplant environment and site of origin had significant effects on mean wet pupal mass, but their interaction was not significant (Table II-3B). Valley borers placed in the valley had highest mean pupal weights, and plains borers placed on the plains had lowest weights (Table II-3A). Borers from the two reciprocal transplant experiments had mean pupal weights that were close to each other, and that were intermediate in value between the mean masses of the two controls.

In general, the valley environment receives more heat units than does the plains environment. Mean maximum temperatures at the valley site (mean=22.5±9.67°C) for the months of March to May 1985 were significantly higher ($t=-3.86$, $df=183$, $P=0.0002$) than temperatures on the plains (mean=17.3±8.84°C). Mean minimum temperatures for the months of June through August 1984 were significantly lower ($t=-4.90$, $df=167$, $P=0.0001$) at the plains site (mean=9.7±3.07°C) than at the valley site

(mean=12.3±3.75°C).

Field Estimates of Postdiapause Growth

Both plains and valley larvae increased in wet mass equally by 20% from 5 April to 5 June. Mean larval weights of the two populations were not significantly different on those dates (Table II-4). Just prior to pupation however, mean larval mass of valley borers increased significantly, while mass of plains larvae did not. Between 5-10 June valley larvae increased their wet mass by an additional 11% (t=-2.17, df=99, P=0.032), while the wet mass of plains larvae showed no significant change (t=-0.13, df=97, P=0.90). Samples of pupae taken from the field at the end of June also showed significant weight differences between valley and plains borers (Table II-4).

Dried valley larvae weighed an average 29% more than dried plains larvae (Table II-4). Assuming equal water content of valley and plains borers in April, this result suggests that greater mean mass of valley borers was not due to simply greater water intake, but rather to the accumulation of body material.

D. Discussion

Field Studies of Phenology

Significant differences in phenology between plains and valley populations of ECB that were initially observed in

fields counts and by light trap catches in 1983 were confirmed by a reciprocal transplant experiment in 1984. Differences in pupation and emergence between environments were consistent among fields and corn variety within either environment. Therefore, I argue that these differences are related to differences between valley and plains environments.

1983 was the first year in which a second generation of ECB has been reported for Alberta. The larger size of the second flight compared to the first flight is not unusual. In other areas where two generations occur, the second flight is usually the largest (Oloumi-Sadeghi 1973). The lack of any appreciable second generation in 1984 was undoubtably due to the lateness of the first flight.

The unusual pattern of first flight observed in 1984 probably reflects low nightly temperatures. This is an important parameter to consider when planning control measures for ECB in Alberta. Researchers working in more temperate climates (such as McLeod 1981) have assumed with fair accuracy that light trap catches correspond to emergence. Southeastern Alberta however is a semi-desert environment, where wide temperature fluctuations from high daily temperatures (*ca.* 40°C) to low nightly temperatures (*ca.* 5°C) often occur during the emergence period. Therefore night temperatures during the flight period are commonly below the required minimum for prolonged periods. Since flight peaks in Alberta may differ from emergence peaks,

predicting flight peaks using only DD accumulations may be inaccurate.

Another important component of ECB population dynamics is the migration of moths from heavily infested fields to other fields (Leroux *et al.* 1963). This migration period also differs from the median emergence period, and it is difficult to predict. Therefore individual growers may best protect their crops by monitoring peak flight time in their own fields with pheromone traps.

Reciprocal Transplantation

The purpose of the reciprocal transplant experiment was to assess differences between valley and plains ECB with respect to diapause termination and pupal mass. Differences in mean pupal mass between plains and valley borers were more striking than variation in time to diapause termination. Variation in body mass is a character that has been noted for its plasticity in many species (Smith-Gill 1983). Shapiro (1984) noted that such plasticity of phenotypes or polyphenism is very common among Lepidoptera.

Plasticity is shown by a particular genotype when it's phenotypic expression is altered by environmental influences (Smith-Gill 1983). It is likely that Alberta ECB populations are exhibiting a particular type of plasticity termed "phenotypic modulation", whereby they respond to a variable environment by modulating their phenotypic expression (Smith-Gill 1983).

A variable environment clearly exists in the Medicine Hat area. We have shown that the valley environment receives significantly higher mean temperatures than does the plains environment. In the laboratory, larval body mass of growing ECB increases with increasing temperature (Beck 1983). Diapause in the ECB also depends upon a temperature-specific threshold (Beck 1982). The transplant experiment supports Beck's findings that temperature exerts an influence upon ECB larval mass and diapause termination. Phenotypic modulation of these traits by temperature is probably universal within ectotherms (Smith-Gill 1983).

One question of concern is whether the observed patterns in life history traits have a genetic basis as well, and are therefore subject to natural selection. When plains and valley strains of ECB were grown under constant temperatures, significant differences in pre- and post-diapause larval development were observed (Lee and Spence, in preparation). Results of our transplant experiments also suggest a genetic basis for phenology differences in the ECB. Furthermore, McLeod (1978), Reed *et al*. (1981), and Stengel and Schubert (1982) have demonstrated that diapause traits are heritable in the ECB according to a pattern consistent with that of a male sex-linked system. Therefore I argue that these traits are subject to natural selection in Alberta populations. The actual extent of heritability of larval traits is however unknown, and would need to be estimated by a traditional

half-sib analysis (Falconer 1981). Such tests performed on other species (Berven and Gill 1983) have indicated that environment plays a much larger role than does heredity in the phenotypic variation of body size and metamorphosis.

Berven *et al.* (1979) have presented a model of clinal variation to explain the adaptive significance of natural variation in life history traits. Our work with the ECB supports this model, which depicts a "cline" as a continuous trend in a phenotype over an environmental gradient with several sampling locations. When samples from the two extreme ends of the cline are transplanted to each sampling location (as was done in the transplant experiments), the experimental phenotypes can show no induced variation and thus be entirely genetic, or they can conform exactly to the natural cline, indicating complete environmental induction. A third outcome, that both genetic and environmental influences operate over the cline, was shown by ECB populations over the elevation gradient at Medicine Hat, Alberta populations exhibited "cogradient variation" (Berven *et al.* 1979), in which the transplanted genotypes retained a portion of their original phenotype. It might be argued that phenotypic modulation occurred essentially during pre-diapause development (*i.e.* during larval growth), and therefore results are entirely phenotypic. Undoubtably body mass of growing larvae is temperature dependent (Beck 1983), so some phenotypic modulation of body mass likely occurs between Alberta populations during larval growth. However,

there were no significant differences between populations in larval growth rate during the active feeding stages (see Chapter III). Furthermore, phenotypic modulation during pre-diapause development would not explain why larvae transplanted in spring 1984 showed characteristics intermediate between valley and plains borers during post-diapause development.

Postdiapause Feeding

Both the reciprocal transplant experiment, and spring measurements of wet and dry larval mass clearly demonstrated that valley borers gained more mass on average than did plains borers. The mean increase in wet and dry larval weights of valley borers in the late spring suggests that valley larvae actively fed (June 5-10) during post-diapause development. This implies that there are behavioural as well as physiological differences between the two populations. Normally, all ECB larvae feed briefly in the spring before pupating, to cut an emergence tunnel and hole in the stalk (USDA 1967). However, I do not know of any previous record of increases in mass resulting from spring feeding.

The hypothesis that valley larvae enter a post-diapause feeding period is supported by the fact that valley larvae required ca. 160 more DD to pupate in the spring than did plains larvae, whereas differences in development time between strains from pupation to emergence were not significant.

Further support comes from the observation in spring 1983 that 2.1% (N=328) of all valley borers sampled in the field molted to another instar. Since fourth instar larvae cannot survive the winter (Nordin *et al.* 1984), clearly fifth instar larvae moulted to form a sixth instar. I also observed 16.3% of valley larvae form six instars when reared at constant 17° and 20° under a long-day (pupation-inducing) photoperiod in the laboratory. All of these sixth instar larvae went into diapause (see Chapter III). Although others have also found that ECB can moult during diapause to form six instars (*e.g.* Spencer 1923), they have not suggested that newly formed sixth instar larvae continue to feed in the spring.

Further experimentation is needed to prove that mass gain is actually caused by post-diapause feeding. I did not record the dry weights of larvae in the fall or early spring. Neither did I determine the nutritional value of dried corn stalks. Furthermore, photoperiod can override the temperature response, to prevent spring pupation when daylengths are too short (Mcleod 1963). When I reared diapausing larvae under L:D:: 16:8 (photophase:scotophase) at constant temperatures, valley ECB pupated earlier than plains ECB (see Chapter III), indicating that the delayed pupation observed in field populations of valley ECB did not occur in the laboratory. Thus some environmental cue that was present in the field but not in the laboratory affected the pupation rate of valley ECB.

Life History Strategies

I believe that variation in diapause is a significant part of the life history strategy of ECB which increases fitness in uncertain environments. In Alberta, at the north-western edge of its range, univoltinism is the corn borer's safest strategy. Any second generation larvae would likely be unable to mature before the onset of winter in most years, and would thus die.

The diapause response, which determines voltinism, is either suppressed or validated during the fifth instar (Mutchmor 1959; Beck and Hanec 1960). This depends upon a 'critical photoperiod' which varies as to ecotype (Beck and Apple 1961; McLeod 1978). In the warmer valley environment, sometimes enough heat units are received for a proportion of first-generation larvae to grow to the final instar before the critical photoperiod arrives. These larvae pupate and form a partial second generation. If this second generation survives, then population growth would obviously be greater than if only a single generation were produced. However, all of the second generation larvae died in 1983 because there were not enough degree-days for them to grow into mature larvae. It would appear that bivoltinism should be selected against in the valley strain.

In another study (see Chapter IV), I have shown that valley females laid significantly more eggs (559) than did plains females (267) when reared at a variable temperature regime of 15°/29°C. Fecundity was significantly correlated

with pupal mass. I believe that because valley females weighed more on average than did plains females, they had greater fat resources to lay more eggs. In a similar study, Gill *et al.* (1983) found that fecundity differences between populations of *Rana sylvatica* were due to differences in female body size.

I speculate that the additional spring feeding by valley larvae affected their subsequent life history in two different ways. Firstly, it postponed development long enough to prevent most valley ECB from pupating in July. Secondly, valley females were, on average, more fecund. Although a portion of the valley population was lost due to second generation deaths, this was more than compensated by the greater fecundity of valley females.

From these results I speculate that behavioural traits (postdiapause feeding), physiological traits (gain in mass) and reproductive traits (increased fecundity) may all be modified when the ECB invades new environments that select for alterations in life history patterns.

Table II-1. Differences in % pupation between valley and plains populations for selected dates. *P* refers to results of X^2 test for independence. Sample size is shown in brackets.

Sampling Date	Environment	% of Pupae	% of Larvae	X^2 *df=1*	*P*
15/6/84	Plains(50)	10.0	90.0	58.51	<0.005
	Valley(45)	28.9	71.1		
18/6/84	Plains(127)	22.0	78.0	118.45	<0.005
	Valley(58)	48.3	51.7		
26/6/84	Plains(54)	59.3	40.7	137.38	<0.005
	Valley(103)	94.2	5.8		
29/6/84	Plains(73)	72.6	27.4	67.06	<0.005
	Valley(40)	95.0	5.0		

Table II-2. Differences in % pupation between valley and plains populations over a 3-year period. Differences between populations were significant at $P=0.001$ (t test for small sample sizes: $df=4$, $t=22.7$). A pooled estimate of the variance was used in the analysis. For location of sites, see Fig. II-1.

Site no.	Location	Corn Type	Date Sampled	Sample Size	% Pupation	Overall Mean ±S.D.
1	Valley	sweet	16/6/83	55	49.1	
2	Valley	field	17/6/84	62	45.2	46.6±1.77
3	Valley	field	17/6/85	11	45.5	
4	Plains	field	20/6/83	56	23.2	
5	Plains	field	18/6/84	127	22.1	22.6±0.46
5	Plains	field	18/6/85	40	22.5	

Table II-3. Analysis of wet mass of ECB pupae observed in transplant experiments.

a. Mean pupal mass for each treatment.

Origin of Stock	Rearing Location	Sample Size	Mean wet mass (mg)	Standard deviation
Valley	Valley	22	112.50	21.858
Plains	Valley	22	99.68	14.519
Valley	Plains	29	95.28	19.705
Plains	Plains	35	85.00	19.787

b. Results of a two-way ANOVA on pupal mass.

Source	*SS*	*df*	*F*	*P*
Origin	3440.028	1	9.258	0.003
Environment	6581.209	1	17.712	0.001
Interaction	41.980	1	0.113	0.737
Residual	38644.066	104		
Total	49168.630	107		

Table II-4. Field measurements of mass of fifth instar larvae and pupae reflecting differences in postdiapause growth between plains and valley populations of ECB. *P* refers to results of *t* tests carried out on samples from plains and valley for each respective date.

Date or stage	Source of insects	Sample size	Mean mass (grams)	Standard deviation	*P*
a. *measurements of wet mass*					
April 5	Plains	22	0.105	0.0222	0.46
	Valley	17	0.096	0.0257	
June 5	Plains	48	0.121	0.0261	0.56
	Valley	40	0.124	0.0251	
June 10	Plains	50	0.121	0.0245	0.01
	Valley	60	0.135	0.0253	
June 15	Plains	42	0.120	0.0201	0.06
	Valley	32	0.131	0.0273	
PUPAE	Plains	64	0.085	0.0224	0.01
	Valley	68	0.100	0.0230	
b. *measurements of dry mass*					
LARVAE	Plains	40	0.035	0.0078	0.001
	Valley	20	0.046	0.0074	

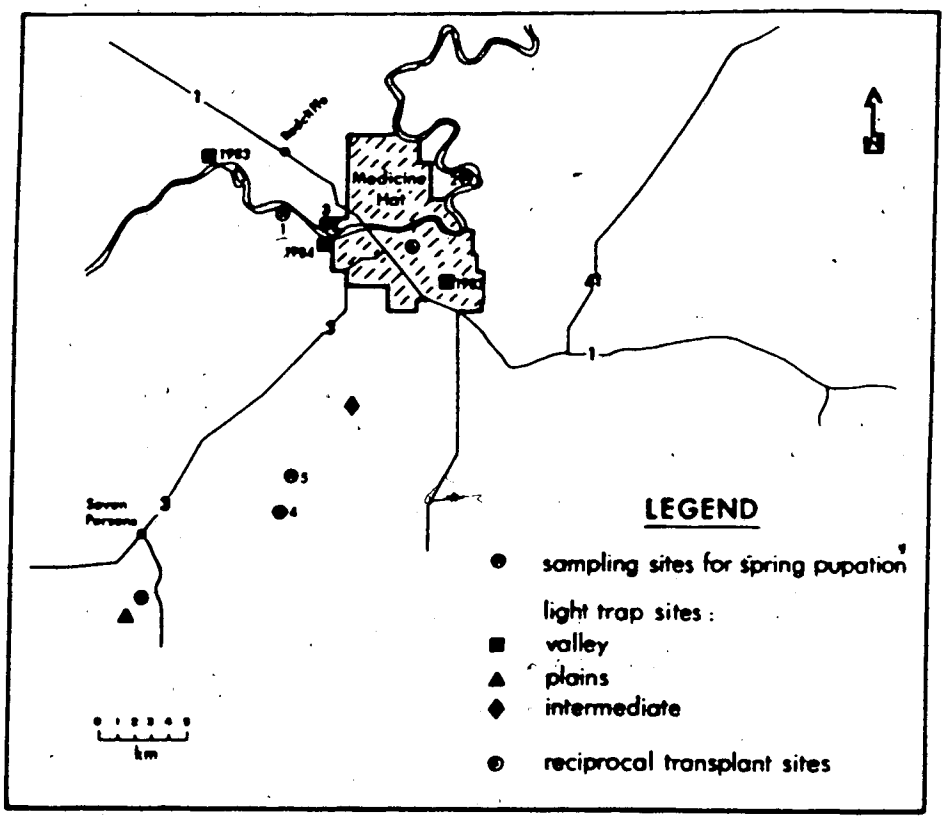

Figure II-1. Map of Medicine Hat and area, with monitoring sites noted.

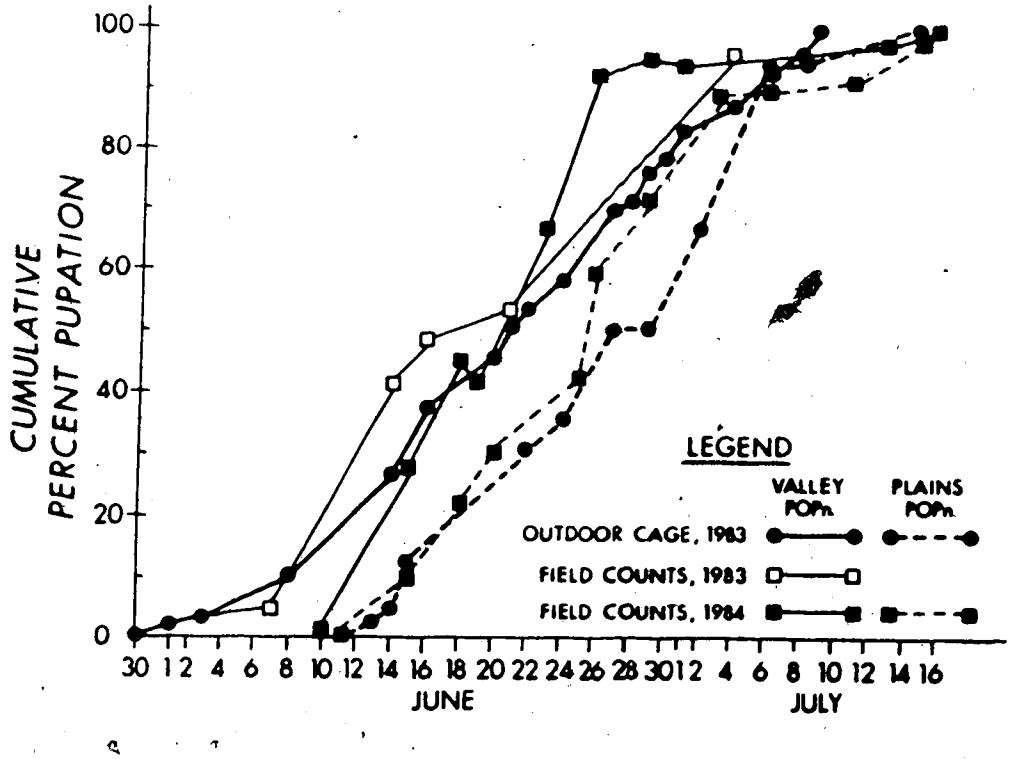

Figure II-2. Seasonal patterns of pupation observed for Alberta populations of ECB in 1983 and 1984.

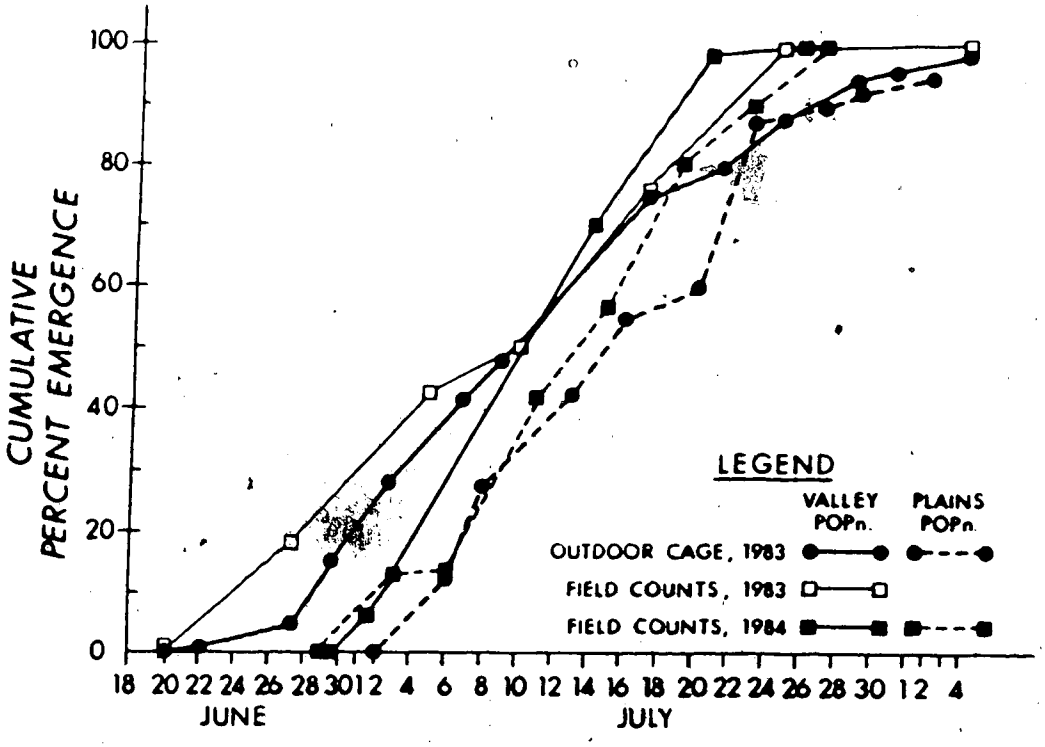

Figure II-3. Seasonal patterns of adult emergence observed for Alberta populations of ECB in 1983 and 1984.

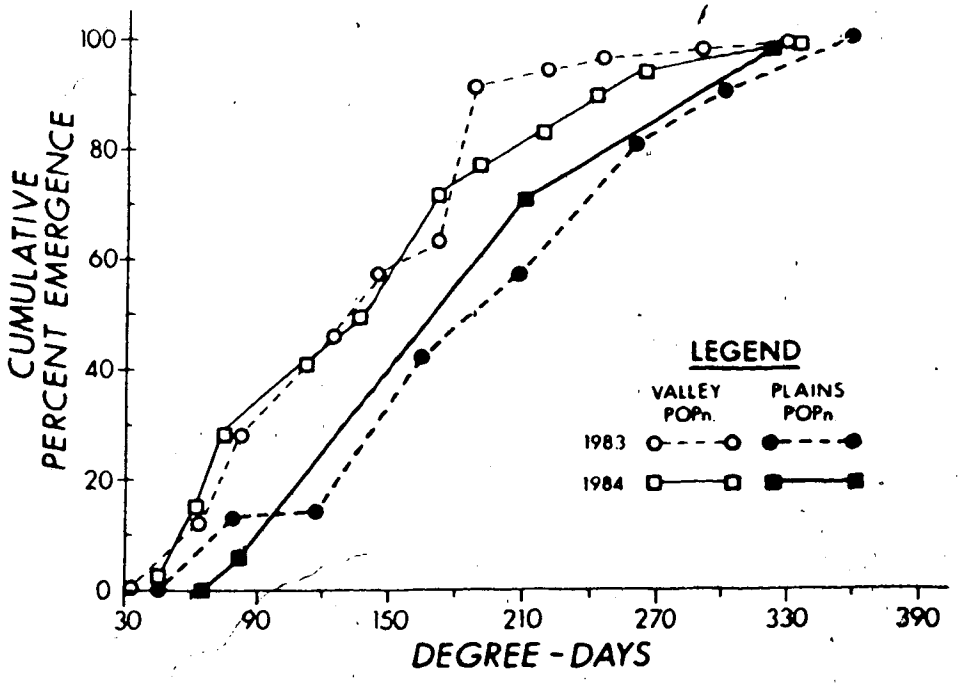

Figure II-4. Patterns of adult emergence in 1983 and 1984 for Alberta populations of ECB, when plotted against a physiological time scale. The base threshold for calculation of DD is 11.2°C. Computation of DD for each curve begins from the day when median pupation was recorded.

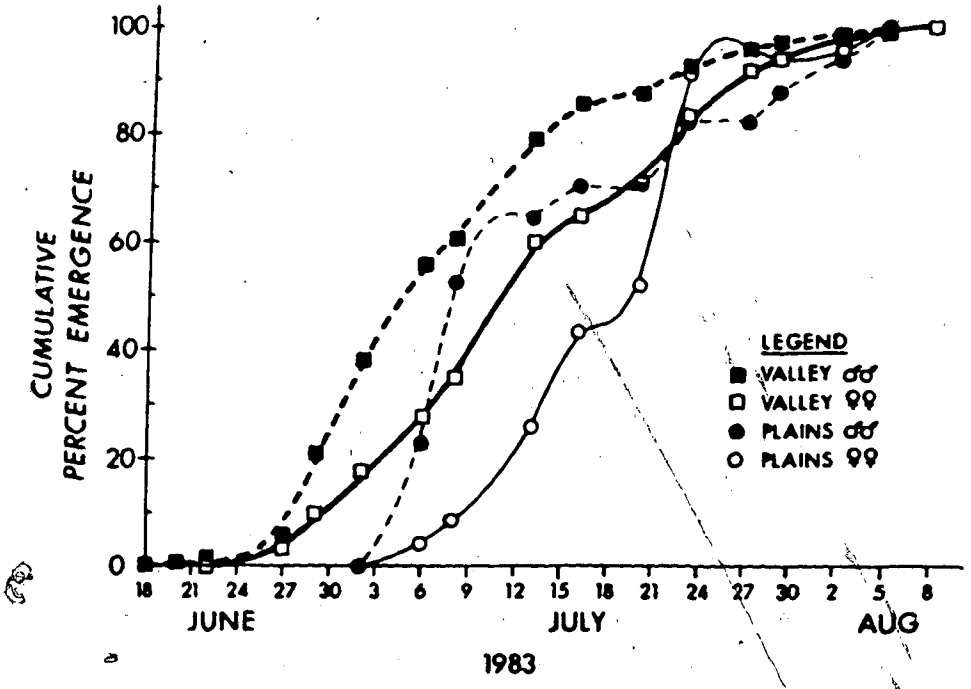

Figure II-5. Patterns of emergence observed for both sexes of ECB in valley and plains environments in 1983.

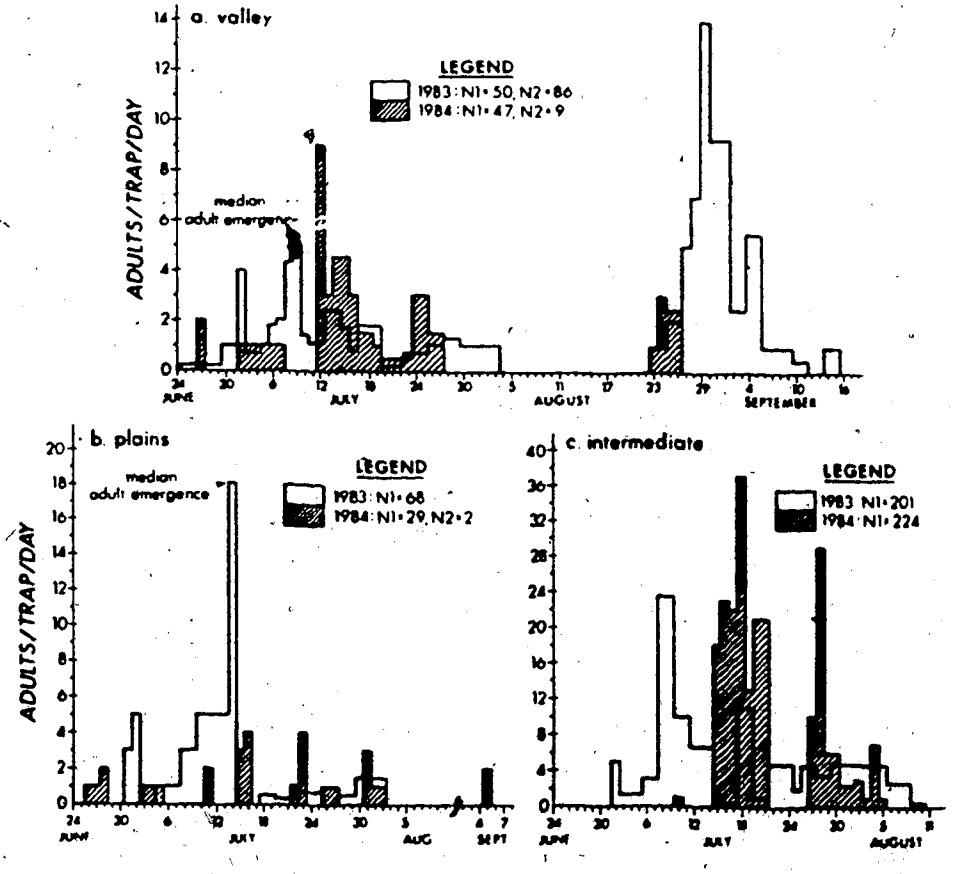

Figure II-6. Seasonal patterns of light trap catches of ECB moths during 1983 and 1984. (a.) valley site, (b.) plains site, (c.) intermediate site.

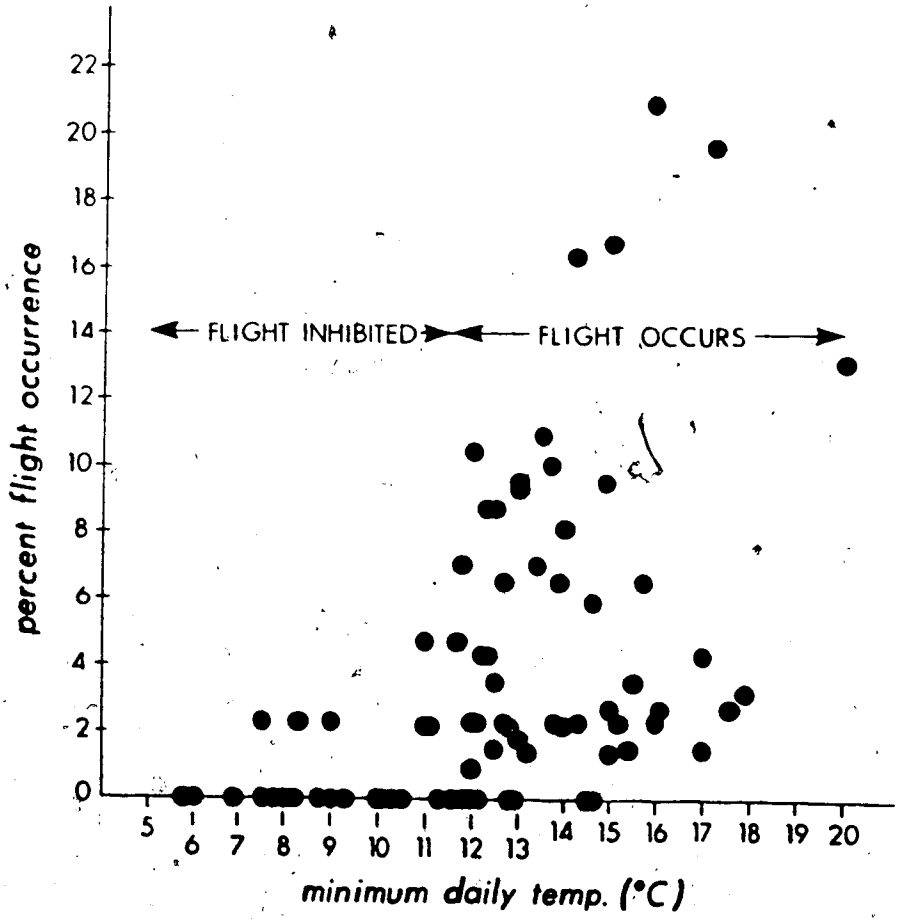

Figure II-7. Apparent temperature threshold for flight take-off of Alberta ECB. Frequency distributions of % of ECB caught/day throughout the season is plotted against Minimum Daily Temperature (MDT). The scatterplot shows a sudden rise as the threshold (11.5°C) is passed. Values are taken from sampling sites at valley and intermediate locations.

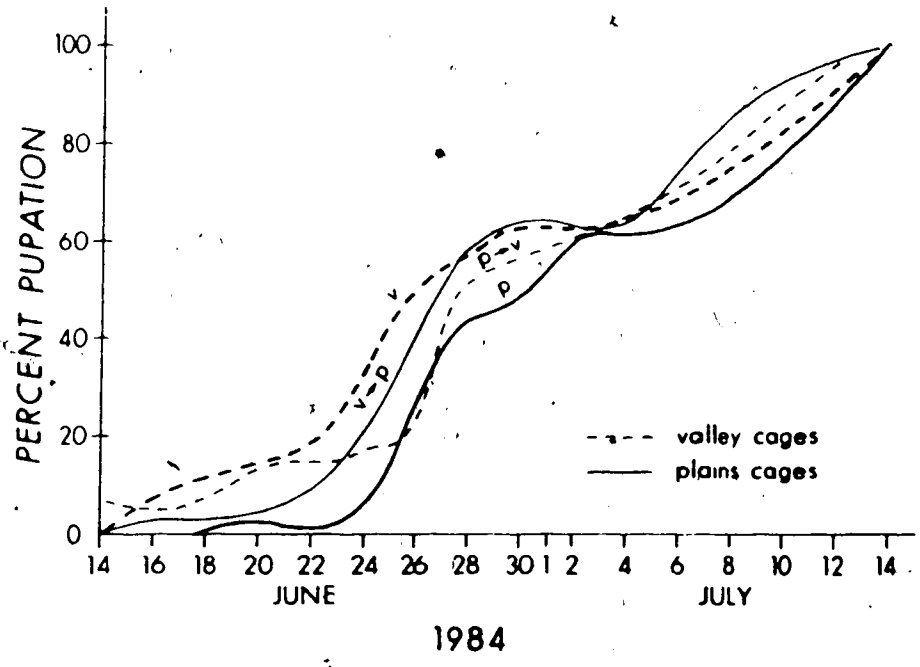

Figure II-8. Patterns of pupation observed during the transplant experiment. v,valley stock reared in the valley; v-p,valley stock reared on the plains; p;plains stock reared on the plains; p-v,plains stock reared in the valley.

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III. DEVELOPMENTAL ADAPTATION IN THE IMMATURE STAGES

A. Introduction

Different populations of the European corn borer (ECB) vary in their rate of development when subjected to equivalent temperature conditions. Arbuthnot (1944) found that under controlled temperatures, larvae of bivoltine populations grew more rapidly than did those of univoltine populations. Beck and Apple (1961) observed differences in degree-days (DD) required to attain pupation among populations sampled from ten different locations in eastern north America, when reared at 26°C in the dark. McLeod (1976, 1978) found that two populations in Ontario differed significantly in the length of time required to terminate diapause. Similar differences in rate of post-diapause development were observed between two populations in Quebec (McLeod *et al.* 1979). Stengel and Schubert (1982) noted differences in larval growth rates between two populations of the ECB in France. All of the above-mentioned authors likewise noted differences in photoperiod sensitivity (*i.e.* diapause induction) between the populations of corn borers they studied.

It is important to consider such regional differences when devising population models based upon physiological time (Gilbert *et al.* 1976). Once the number of DD required to commence a particular insect life stage is known, the Julian date for the occurrence of that life stage can be

predicted by accumulating DD based upon actual field temperatures for any given year. Regional differences in characteristics of growth and development also seem to be subject to natural selection (Taylor 1981). Although rates of ECB development and developmental thresholds have been measured by several authors (Caffrey and Worthley 1927; Matteson and Decker 1965; and Anderson *et al.* 1982a, 1982b, Beck 1983), adaptive explanations for differences noted among populations have not been considered.

In a previous study (see Chapter II), distinct phenological differences were observed between newly established populations of ECB in the S. Saskatchewan River valley, and those on the cooler plains 16 km south. Results suggested that phenological differences had both environmental and genetic components and I hypothesized that there were significant differences in growth characteristics of the two populations. The aim of this study was to determine the developmental thresholds and rates of development for all life stages of the ECB from populations in southern Alberta. Because Alberta populations are at the northwest extreme of the the present North American range of *Ostrinia nubilalis* (50°N, 111°W), I expected them to differ considerably from populations in the United States.

B. Materials and Methods

General Methods

The effect of temperature on egg development, pre-diapause development (*i.e.* growth of larval instars and midsummer pupation), and post-diapause development (*i.e.* termination of diapause and spring emergence) was studied in the laboratory for Alberta populations of the ECB. All experiments were run under a long-day photoperiod (L:D::16:8), and at several constant (±1.0°C) temperatures in Precision (model 818) incubators. Illumination provided by two "cool daylight" fluorescent bulbs averaged *ca.* 8.5 hectolux.

Pre-diapause development was examined at constant temperatures of 17°C, 20°C, 24°C, 30°C, 32.5°C, and 35°C. No variable temperatures were used, because Matteson and Decker (1965), Anderson *et al.* (1982a), and Beck (1983) all found no significant differences in developmental rate of larvae when using either constant or variable temperatures. Studies of post-diapause developmental rate were conducted at constant temperatures of 17°C, 22°C, 26°C, 30°C, 32°C and 35°C. ECB egg development rate was studied at constant temperatures of 17°C, 20°C, 22°C, 25°C, 27°C, 30°C and 32°C.

For studies of egg and post-diapause development, one variable temperature (15°C/29°C; average temperature=22°C) was also used to more closely simulate field conditions. For this regime, a 12:12h::thermophase:cryophase was used, with

the thermophase ocurring during the photophase. The temperature cycles produced by these incubators were of the square-wave type, and temperature transitions were complete within 30 minutes.

Larvae were reared on artificial diet (BioServ Inc., Frenchtown, N.J.). To prevent bacterial and fungal infection, rearing containers were soaked in bleach before use, and instruments and benchtops were rinsed with disinfectant (Hinks and Byers 1974).

Egg Development

ECB egg masses were collected from at least 10 female and 10 male moths placed in clear acrylic cylinders (30 cm high by 8 cm in diam.). Insides of the cylinders were lined with wax paper, and the open ends were covered with screening held secure by rubber bands. To maximize fecundity, drinking water was provided (*cf.* Kira *et al.* 1969) by placing each cylinder on top of a Petri dish bottom containing a 10% sugar solution, with a cotton wick extending from the solution into the cylinder. A relative humidity (RH) of *ca.* 95% was maintained by placing the cylinders inside a sealed plastic bag.

Egg masses freshly laid over a 4-hour period were cut from the wax paper inserts. Most eggs are laid in the dark (Barber 1925), and therefore eggs were removed under red light 4 hours after the start of the scotophase and 4 hours later, at the start of the photophase. Red light invisable

to the moths (Webster and Carde 1982) was obtained by using a Kodak red filter #92, which screened out all wavelengths below 620 nm.

Eggs cut out from the inserts were placed in Petri dishes (diam. 9 cm) with 5-10 egg masses per dish. Petri dish lids had a fine mesh screening to permit air exchange. Petri dishes were separated by spacers, and stacked inside a one litre dessicator that contained a saturated salt (KH_2PO_4) solution to maintain RH at *ca.* 96% (Winston and Bates 1960).

Individual eggs were monitored daily for hatching. Eggs were counted in the blackhead stage. Larvae hatching in each Petri dish were also counted. To prevent larvae from escaping, petroleum jelly was applied to the upper edge of the Petri dish. After all larvae had hatched, numbers of infertile eggs, dead blackhead eggs and cannibalized eggs were counted.

Pre-diapause Larval and Pupal Development

Within 12 hours of hatching, larvae were transferred into transparent 7-dram vials containing a 1/2-cm of medium, poured over a 2-cm wide strip of plastic. The plastic strip provided an interface with the medium, where the larvae began to feed. Guthrie *et al.* (1971) achieved the same effect by scratching the surface of the medium. To prevent larval escape and permit rapid temperature equilibration, the top of each vial was covered with fine-mesh nylon

screening, held by an elastic band.

Vials were placed upside down on a screen platform above a water-filled dish. This apparatus was placed inside a translucent 2-litre container (height 10 cm; diam. 26 cm), covered with a glass plate. The space between the plate and the container lip permitted adequate air entry while maintaining a high RH (*ca.* 95%) inside the vials.

The medium was changed every 2-4 days because larval feeding declined once it became "stale". I suspected that gut bacteria were the main cause of medium deterioration. Although Guthrie *et al.* (1971) added aureomycin to the medium to control bacteria, I felt this chemical might affect developmental time, so I did not use it. As well, preliminary trials showed that even with aureomycin added the medium became stale after 4-5 days.

Larvae were monitored twice daily (0900h and 1700h). Fifth instar larvae were monitored for two distinct phases. At the beginning of this instar, larvae actively feed and grow. Afterwards, they prepare physiologically for pupation during a quiescent "prepupal phase". This phase begins when larvae cease feeding, start to wander and spin a hibernaculum (Beck 1982). We recorded the prepupal phase separately to watch for possible differences in development rate between valley and plains ECB.

At 17°C the percentage of larvae entering diapause was noted for both populations. I had previously observed that at lower temperatures some slower developing larvae

completed six instars instead of five, and the number of such larvae were noted at 17°C and 20°C.

Post-diapause Development

Diapause was induced in larvae by rearing under short days (L:D::12:12) at 30°C (*e.g.* McLeod 1978). Larvae used for diapause induction came from stock colonies maintained at L:D::16:8 and 30°C. Larvae which had not pupated after *ca.* 30 days were assumed to be in diapause, and were transferred to individual storage chambers made by gluing light diffuser strip (with 2-cm by 2-cm cells) onto a clear acrylic sheet. Polyester fabric was wrapped tightly around containers to inhibit larvae from moving out of the cells. Storage containers were stacked between spacers inside a plastic bag. A dish of water inside the sealed bag provided a RH of *ca.* 70% (*cf.* Davis 1983) necessary for survival. Larvae were held in a controlled-temperature chamber at 4°C for at least 90 days to ensure completion of diapause (Beck 1967).

After completion of diapause, larvae were placed individually into 7-dram vials containing strips of moistened felt and blotting paper. The felt was remoistened every two days to provide larvae with the free water essential for post-diapause development (Beck 1967). Vials were covered with screening, and placed in containers as in the pre-diapause experiment. Insects were checked daily for pupation and adult emergence.

Data Analysis

Reciprocals of the developmental times at various constant temperatures express the proportion of development completed per day at each temperature. These developmental rate values were regressed on temperature (T) for each developmental stage for both plains and valley populations.

The X-intercepts resulting from extrapolations of the development curves are the lower developmental thresholds (t_o) at which measurable growth ceases (Gilbert *et al.* 1976). Standard errors of t_o temperatures were calculated according to Campbell *et al.* (1974). The upper developmental threshold (Tm) is the temperature at and above which the rate of development begins to decrease (Zalom *et al.* 1983). Both types of growth thresholds were compared among stages and between the two Alberta populations, as well as between Alberta and United States populations. The number of DD above the t_o, required for completion of development (K), was determined by taking the reciprocal of the slope of the linear regression line (Campbell *et al.* 1974). These were compared to data gathered in field phenology studies (see Chapter II).

Valley and plains ECB were compared for differences in development rate during each life stage. Covariance analysis was used to compare regression lines of development rate plotted against temperature. For a few stages, values for the highest and lowest temperatures were not included because they did not fit the straight line through the other

points. These rejected values reflected the approach of either *Tm* or t_o.

C. Results

Development Rate

Egg Development

When rate of egg development was regressed on temperature, differences were observed between regression lines for valley and plains populations (Table III-1). For egg development I found both significant differences in slope and adjusted mean development rate (Table III-2), with eggs from valley populations (rate=0.1924) developing faster than those from plains populations (rate=0.1907). Because the intersection of the two regression lines occurred at *ca.* 14°C (Fig. III-1), I conclude that valley ECB eggs developed faster over all temperatures above 14°C. The regression equations, the r^2, and *K* values for egg development (and for all other developmental stages) are listed in Table III-1. Regression explained 40-90% (median=76%) of the variance in these data sets, indicating reasonable fits to the linear model. Mean development times with standard errors, development rates, sample sizes and survivorship at each temperature are given in Appendix 1 for egg development (and for all other developmental stages).

Pre-diapause Development

Differences in development rate for the first four larval instars were not significant (P=0.24) between the two Alberta populations, so the data were pooled for analysis. For the first, second and third instars, and for pre-diapause pupation, there was a linear relationship between development rate and temperature, from 17°C to the *Tm* (Figs. III-2 and III-4). For the fourth and fifth instars however, the velocity line curved between 17°C and 20°C, indicating the approach of t_o (Figs. III-3 and III-4).

Differences in pre-diapause development rate between Alberta ECB populations occurred only during the prepupal phase of the fifth instar. Plains borers took 13% longer to complete development in this stage than did valley borers. The adjusted mean for prepupal development rate was significantly less for plains ECB (0.437) than for valley ECB (0.523, Table III-2). Slopes of the regression lines were the same for the two populations (Table III-2), indicating that valley ECB developed faster during the prepupal phase over all temperatures.

During the interval from the start of the fifth instar until the beginning of the prepupal period (*i.e.* the active feeding phase), there were no significant differences (Regression for equal means: F=0.32, df=282, P=0.73) in development rate between populations. When both phases of the fifth instar were combined and the complete fifth instar examined for development rate, significant differences

between populations were found again. While the slopes of the regression lines for the two populations were equal (Table III-2), the adjusted mean for fifth instar development rate for plains ECB (0.139) was significantly less than that for valley ECB (0.159, Table III-2). Thus valley ECB developed faster than plains ECB during the complete fifth instar over the entire temperature range.

When the two populations were compared during pre-diapause pupation, valley ECB developed only marginally faster than plains ECB (Regression for equal means: F=3.34, df=284, P=0.07), and thus data were pooled.

Postdiapause Development

Rate of development for spring pupation was linearly related to temperature between 17°C and 30°C (Fig. III-5). Significant differences in adjusted means of the regression lines were found between valley (mean=0.041) and plains (mean=0.036) populations (Table III-2). Slopes of the two regression lines were equal (Table III-2).

Development from the end of spring pupation until emergence was analyzed separately. Rate of emergence was equal for both valley and plains populations (regression for equal means: df=436; F=0.091; P=0.76). Regression (Table III-1) was linear between 17°C and 32°C (Fig. III-5). The emergence rate was then examined separately as to sex. The adjusted mean for regression of emergence rate was significantly less for male moths (0.094) than it was for females (0.100, Table III-2). Slopes of the regression lines

were equal (Table III-2).

Constant vs. Variable Temperatures

No significant differences were observed in ECB post-diapause or egg development when reared at a constant 22°C or when reared at a variable temperature regime of 15/29°C (mean temp.=22°C). However, insects at the constant regime showed higher variability in development rate. Mean development rate for post-diapause pupation was similar (t=-0.58, df=115, P=0.56) at 22°C (0.032±0.0178) to that at 15/29°C (0.031±0.0255). However, coefficients of variation (CV) for the two temperatures were 55.8 and 8.4 respectively. The higher CV at constant temperatures is probably because ECB in the field are exposed to variable temperatures, not constant temperatures. For post-diapause emergence, development rates were 0.022±0.0099 for 22°C, and 0.022±0.0047 for 15/29°C (t=-.11, df=114, P=0.92). CV's were 44.0 and 21.2 respectively. Similarly for egg development, the CV was larger at 22°C (11.1) than at 15/29°C (6.8). Development rates for the two temperatures were nearly equal (0.172 and 0.170 respectively for valley populations).

Temperature Thresholds

Lower Temperature Thresholds

The t_o for Alberta ECB were compared with thresholds for populations from the United States (Table III-3). Unfortunately development thresholds could not be compared statistically between Alberta and United States populations, because previous studies did not present measures of variance. The two ECB populations in Alberta were also compared. Where there were no significant differences in the threshold temperatures between plains and valley populations, a single pooled estimate is presented.

For the egg stage, plains borers had a lower t_o (9.5°C) than did valley borers (10.8°C, Table III-3). Differences were significant at $P=0.005$ (Weighted ANOVA: $X^2=83.2$, $df=1$). Both Alberta populations had much lower egg t_o than did United States ECB populations (14.1-14.8°C).

A weighted ANOVA test demonstrated significant differences in the base thresholds of the five larval instars ($X^2=95.5$, $df=4$, $P=0.005$) of Alberta ECB. The t_o of the second instar (10.2°C, Table III-3) was less than that of the first instar (11.5°C). This was similar to Illinois ECB (Table III-3). The fourth and fifth (plains) instars of Alberta ECB had much higher t_o than the three previous instars. This trend was not observed in United States ECB populations (Table III-3). In fact, the fourth instar had the highest t_o (15.3°C) of all instars for Alberta ECB,

while it had the lowest t_o (6.7°C) for Wisconsin ECB (Table III-3). The t_o for the combined larval stages of Alberta ECB (13.2°C; calculated by linear regression) was much higher than that reported for United States ECB (9.8 to 11.1°C, Table III-3). The t_o of Alberta ECB for prediapause pupation (12.2°C) was similar to the thresholds (12.5 to 13.0°C) reported for United States ECB (Table III-3).

For Alberta ECB, significant differences were found between the t_o's of valley and plains populations (Weighted ANOVA: X^2=3.99, df=1, P=0.05) during the fifth instar. Marginally significant differences were observed between the t_o's of the two separate phases of the fifth instar (Weighted ANOVA: X^2=3.55, df=1, P=0.06). During the interval from the beginning of the fifth instar to the prepupal period, the t_o was higher (15.6°C) than it was during the prepupal period (Table III-3).

Although a higher development threshold was observed in Alberta ECB for post-diapause pupation (12.8°C) than for the interval from pupation to spring emergence (11.2°C, Table III-3), differences were only marginally significant (Weighted ANOVA: X^2=3.35, df=1, P=0.07).

Upper Temperature Thresholds

As with United States ECB (Matteson and Decker 1965), the *Tm* for Alberta ECB occured at 32.5°C for most stages. However, a higher threshold of 35°C was recorded for the first and third instars (Fig. III-2) of Alberta populations. During the fourth and fifth instars, the *Tm* for the valley

population was lower (30°C) than that for the plains population (32.5°C) of Alberta ECB (see Appendix 1). A *Tm* of only 30°C was also observed for both Alberta populations during post-diapause pupation. For the egg stage, the *Tm* for Alberta ECB (32°C) was greater than that recorded by Matteson and Decker (1965, 27°C) or Caffrey and Worthley (1927, 30.8°C).

Survivorship

Under most temperature regimes survivorship to the next stage ranged from 90-100% (see Appendix 1). First instar larvae experienced higher mortalities at 17°C and 20°C (75% survived). At 35°C postdiapause larvae (19%), prediapause pupae (77%) and postdiapause pupae (40%) showed poor survival. At 32°C only 69% of postdiapause pupae survived.

Survivorship of eggs was monitored at 22°C and 32°C. 4.5±6.30% of eggs at 22°C were infertile, 7.2±9.65% died during the blackhead stage, and 1.6±1.77% died from cannibalism (N=28 samples, 10,513 eggs). At 32°C, 4.9±3.55% of all eggs were infertile, 7.6±8.68% died as blackhead eggs and 3.0±3.56% were cannibalized (N=9 samples, 2,285 eggs).

Diapause Differences Between Populations

16.3% of valley larvae reared at 17°C and 20°C molted five times to form a sixth instar. All of these larvae went into diapause, but failed to pupate when transferred to 30°C for 30 days. All plains larvae molted four times to form the normal five instars.

Sixth-instar larvae were excluded from the general data analysis, and their developmental times calculated separately (Table III-4). When compared with fifth-instar valley larvae (Table III-4), sixth instar larvae took significantly longer to complete development during the second, third, and fourth instars.

Differences in the percentage of normal fifth-instar larvae entering diapause were observed between populations. At 17°C, 67.9% of plains larvae entered diapause (N=81), while only 11.7% of valley larvae went into diapause (N=60). Differences were not observed between populations at higher temperatures.

D. Discussion

Degree-days and Development

Surprisingly few studies have been conducted to determine the growth thresholds for different populations of the ECB, despite the well-known variability of this species with respect to development rate. Published versions of previous studies do not report data for all life stages of

the ECB. Following Jarvis and Brindley (1965), most researchers have assumed that a lower growth threshold of 10°C is adequate for prediction purposes for all populations and for all life stages of the ECB. This assumption is clearly erroneous for Alberta populations.

A reason for using DD is to provide better predictions than are possible by relying upon calendar dates. Because DD are cumulative, small differences in t_o can result in very large differences in the number of DD calculated for a given life stage. We have shown not only that Alberta ECB generally have a higher t_o than do other ECB populations for most life stages, but also that the thresholds for the different life stages of Alberta ECB differ significantly from each other.

The value of K for post-diapause pupation of plains ECB, as calculated from laboratory studies (307 DD), was comparable to that calculated from field data (331 DD, t=12.8°C, see Chapter II). That the latter value was slightly larger than the former may be due to a slight delay in pupation in the field because of inadequate rainfall. Free water is essential for termination of diapause (Beck 1967).

The value of K for post-diapause pupation of valley ECB, as calculated in this study (272 DD), was much less than that calculated from field data (490 DD, see Chapter II). This inconsistency may result in part because valley larvae seemed to enter a post-diapause feeding period in the

field (see Chapter II), which delayed pupation.

Post-diapause growth characteristics are strongly influenced by diapause intensity (McLeod 1978). Because a greater proportion of plains borers entered diapause at 17°C than did valley ECB, I suggest that the two populations may have different critical temperature thresholds for diapause induction (*e.g.* Beck 1982,1983). This threshold must be between 17°C and 30°C, because when reared at 30°C under a diapause-inducing photoperiod (12:12::L:D), the same proportion of valley larvae entered diapause (86.1%, n=230 larvae) as did plains larvae (86.7%, n=211).

The formation of six instars by some ECB larvae is not unusual. A variable number of instars has been reported for many insects, and can result from several different causes (Goettel and Philogene 1979). Possibly for a proportion of Alberta valley ECB, the combined effect of low temperatures with a growth-inducing photoperiod caused some larve to moult an extra time.

Evolutionary Significance of Development Rate in ECB

The relationship between the rate of development and temperature can be divided into three ranges (Campbell *et al.* 1974). Within the middle range there is a straight-line relationship between development rate and temperature. On either side of this middle range, excessively low or high temperatures destroy this linearity. However, development at low temperatures is usually negligible. Also, field

conditions lie almost exclusively in the middle range. Therefore the threshold temperature t_o (extrapolated from the development rate curve) and the developmental time K are fairly accurate parameters for use in predictive models for many species (Campbell *et al.* 1974).

Recently much effort has been expended in devising non-linear models for insect development (*e.g.* Wagner *et al.* 1984). Use of non-linear models in warm climates undoubtably offers better prediction than do straight-line models. This is mainly because insects frequently experience temperatures higher than the Tm, so development rate slows down. In Alberta however, only a negligible amount of development time occurs at temperatures higher than Tm. Also, because the correlation coefficients for most of our data were high, it is unlikely that a non-linear model would significantly improve the "fit" of the data. Furthermore, Gilbert *et al.* (1976) have pointed out that the extra accuracy gained from using non-linear models is rarely important when models are applied to field situations.

Insect development rate therefore can be modelled by the following equation given by Taylor (1981):

$$R(t) = rm \exp\{-1/2 \, [(T-Tm)/T\alpha]^2 \} \; ;$$

where: $R(t)$ is the instantaneous development rate (*i.e.* proportion of development completed/day) at a given temperature, T; rm is the maximum development rate; Tm is the temperature at which rm is attained; and $T\alpha$ is the rate

at which $R(t)$ falls away from rm (*i.e.* the slope of the regression line). $T\alpha$ is dependent upon t_o, the lower temperature threshold. Taylor (1981) proposed that the parameters measuring physiological time (specifically: rm, Tm, $T\alpha$ and t_o) are life history traits that can vary through natural selection. These types of life history traits have not been studied well in an adaptive evolutionary context. Our results show that plains and valley populations of ECB in Alberta exhibited different developmental life history strategies from each other, and from other ECB populations in general.

Because second generation larvae have a low probability of maturing before the onset of winter in Alberta, selection for univoltinism should be intense. Temperature-dependent larval growth is linked to the suppression of diapause, because if larvae enter the fifth instar before a critical photoperiod occurs, then larvae will pupate (Mutchmor 1959; Beck and Hanec 1960). The critical photoperiod for Alberta ECB, 15.0-15.5 hours of daylight, occurs from 20-30 July (unpublished data). A higher t_o for spring pupation (12.8°C) delays development of Alberta ECB so that the chance of midsummer pupation is reduced. An additional advantage of a high t_o is the lessened risk of late spring frosts killing borers that have broken diapause. That females emerged slightly earlier in the spring than males has also been reported for other insect species (Baker and Miller 1978).

The t_o for the fourth and fifth (plains) instars were significantly higher for Alberta ECB than for ECB examined in the United States. As well, the lower point of the straight velocity line was much higher (20°C) for these instars in Alberta ECB than it was (15.6°C) for those of United States ECB (Matteson and Decker 1965). Again, the higher t_o delays development and ensures that most Alberta ECB will enter diapause.

Survival of Alberta ECB eggs is increased by having a lower t_o (*ca.* 10°C) than other ECB. Because eggs are exposed, they can be more susceptible than other stages to destruction by adverse climate and natural enemies. A lower t_o reduces development time in the egg stage, which is particularly important because of lower mean temperatures in Alberta than ECB would encounter elsewhere. Since I can thus expect ECB populations which inhabit cooler environments to have a lower t_o for egg development, it is not surprising that ECB on the cooler plains had a lower t_o than those ECB in the warmer valley environment.

The proportion of larval life spent in the fifth instar also varys among ECB populations. While Illinois larvae spent 40.6% of their larval lives in the fifth instar (Matteson and Decker 1965), the figure was 38.0% for Alberta plains ECB and only 36.3% for valley ECB. These differences are likely because the prepupal period appears to be highly susceptible to natural selection. Besides having a significantly shorter prepupal period and lower t_o, valley

borers also had a lower *Tm* during the fourth and fifth instars (30°C) than did plains borers (32.5°C). If *Tm* is lower, then more of the temperature regime that the insect experiences falls under portions of the *R(t)* curve that are near to *Tm*, and so development proceeds more rapidly (Taylor 1981). Since the fifth instar is one of the longest life stages, a lower *Tm* for this stage further reduced development time for valley ECB.

The above discussion suggests that selection for univoltinism is not as intense within valley populations as it is within plains ECB. The effect of faster development of valley ECB during the fifth instar is that a larger proportion of larvae mature before the arrival of the critical photoperiod, and thus will pupate. This explains why I observed a larger partial second generation in valley populations in 1983 than I saw for plains ECB (see Chapter II). The marginally faster development during pre-diapause pupation of valley ECB also reduces development time for the second generation. These data support the hypothesis that phenological differences between populations were due at least in part to differences in growth characteristics.

My observations of Alberta populations of the ECB can be compared with those described for other species. Geographical populations of European cherry fruit flies (Baker and Miller 1978) and several aphid species (Campbell *et al.* 1974) that inhabited warmer areas generally required more DD to complete development (*i.e.*, *K*) than did those in

cooler areas. In contrast, I found that populations in the warmer valley environment needed less DD to complete development than did those on the cooler plains.

It has been shown that pea aphid (Campbell *et al.* (1974), lacewing (Tauber and Tauber 1978), and mosquito (Trimble and Lund 1983) populations inhabiting warmer climates have a higher t_o than do those living in cooler climates. This resembles the trend I observed with ECB eggs, but is an opposite trend to that which I found with ECB larvae. Campbell *et al.* (1974) also summarized data showing that the t_o for *P. rapae* decreases with successive larval instars. Spence *et al.* (1980) showed a similar trend for the egg and first four larval stages of several partially bivoltine *Gerris* species. In contrast, the general trend for Alberta ECB is that of higher t_o values with successive larval instars. Clearly, trends in variation of t_o depend upon the the life history strategy employed by a particular insect species. I believe that Alberta ECB larvae demonstrate trends opposite to the examples cited because of selection for univoltinism.

It is significant that distinct divergences in physiological time parameters have developed between plains and valley populations of the ECB within a very short time period (*ca.* five years). Natural selection for developmental characters has been observed to occur in other species within short time spans (Stearns 1983). My data for the ECB support Taylor's contention (1981) that physiological time

parameters are real, definable characteristics of organisms, and are sensitive to adaptation and microeveolution.

Table III-1. Regression equations with r^2 values and K (±S.E.), for the developmental stages of Alberta ECB

Stage	Origin	Equation	r^2	K±S.E
Egg	P	Y= -0.12660+0.013308T	.80	75.1±0.53
Egg	V	Y= -0.15833+0.014694T	.87	68.1±0.21
1st Instar	C	Y= -0.26334+0.022813T	.90	43.8±0.61
2nd Instar	C	Y= -0.24134+0.023680T	.82	42.2±0.85
3rd Instar	C	Y= -0.32119+0.026941T	.84	37.1±0.77
4th Instar	C	Y= -0.49234+0.032148T	.79	31.1±1.02
5th Instar	P	Y= -0.17286+0.012311T	.72	81.2±4.38
5th Instar	V	Y= -0.14015+0.011816T	.86	84.6±3.01
Fifth Instar (Feeding Stage)	C	Y= -0.37238+0.023898T	.57	41.8±2.18
Prepupal Stage	P	Y= -0.49287+0.037137T	.40	26.9±1.56
Prepupal Stage	V	Y= -0.65433+0.046632T	.63	21.4±1.51
Combined Larval Stages	P	Y= -0.05589+0.004239T	.90	227.6±6.23
Combined Larval Stages	V	Y= -0.05920+0.004459T	.90	224.3±9.08
Prediapause Pupation	C	Y= -0.09995+0.008186T	.85	122.2±3.50
Postdiapause Pupation	P	Y= -0.04162+0.003263T	.44	307±23.8
Postdiapause Pupation	V	Y= -0.04719+0.003682T	.57	272±19.3
Emergence	P	Y= -0.02591+0.002120T	.63	472±26.8
Emergence	V	Y= -0.03284+0.002564T	.71	390±21.7
Postdiapause Pupation to Emergence	M	Y= -0.08188+0.007326T	.62	136.5±7.82
Postdia. Pupation to Emergence	F	Y= -0.08859+0.007855T	.76	127.3±6.49

1 P=plains population; V=valley population; C=combined; M=males; F=females

2 Y= rate of development at temperature T

Table III-2. Covariance analyses. (A) Between plains and valley populations of Alberta ECB for various life stages.

Life Stage	Regression of Equal Adjusted Means	*df*	*MS*	*F*	*P*
Egg	regression:	2	0.0872	114.21	0.0001
	eq. means:	1	0.0112	14.47	0.0001
	eq. slopes:	1	0.1631	213.82	0.0001
	error:	21653	0.0008		
Pre-pupal Per-iod	regression:	2	0.2292	3.70	0.026
	eq. means:	1	0.3525	5.68	0.018
	eq. slopes:	1	0.1059	1.71	0.19
	error:	232	0.0619		
Fifth Instar	regression:	2	0.0195	10.04	0.0001
	eq. means:	1	0.0191	19.81	0.0001
	eq. slopes:	1	0.0003	0.32	0.57
	error:	258	0.0010		
Post-dia-pause Pupation	regression:	2	0.0012	4.12	0.017
	eq. means:	1	0.0019	6.48	0.0113
	eq. slopes:	1	0.0005	1.76	0.19
	error:	359	0.0003		

(B) Comparison between male and female spring emergence.

Pupa-tion to Emergence	regression:	2	0.0020	3.28	0.039
	eq. means:	1	0.0034	5.56	0.019
	eq. slopes:	1	0.0006	1.00	0.32
	error:	380	0.0006		

Table III-3. Straight line developmental thresholds ±S.D. for various ECB populations.

Stage	Mas-sachu setts[1]	Illin-ois[2]	Wiscon-sin[3]	Alberta[4]
1. Egg	14.83	14.06	-	P: 9.51±0.128 V: 10.78±0.055
2. 1st Instar	-	12.1	9.5	11.54±0.343
3. 2nd Instar	-	11.3	11.7	10.19±0.391
4. 3rd Instar	-	12.2	11.7	11.92±0.046
5. 4th Instar	-	10.5	6.7	15.32±0.414
6. 5th Instar	-	10.8	-	P: 14.04±0.877 V: 11.86±0.639
7. 5th Instar to prepupal period		-	-	15.58±0.637
8. Prepupal period		-	-	13.26±1.058
9. All larval stages	9.8	11.1	10.9	13.25±0.478
10. Pupae	13.0	12.5	-	12.21±0.577
11. Postdiapause pupation	-	-	-	12.79±0.707
12. Postdiapause pupation to emergence	-	-	-	11.15±0.541

[1]Caffrey & Worthley 1927

[2]Matteson & Decker 1965 (values obtained by linear regression of data given)

[3]Beck 1983

[4]Lee, Chapter 3

Table III-4. Development of sixth-instar larvae over the first five instars. A *t*-test is used to compare differences in the length of time to complete each instar, between sixth-instar larvae and normal fifth-instar valley larvae.

Instar	Temperature (°C)	Mean Development Time (days)	Standard Deviation	Mean Development Rate (1/days)	Sample Size (N)	*t-TEST* *t*	*d.f.*	*P*
First	17	8.83	1.512	0.1163	8	-0.35	71	0.73
	20	5.58	0.779	0.1823	16	-0.89	84	0.38
Second	17	10.13	1.246	0.1002	8	-7.65	70	0.001
	20	5.58	0.430	0.1801	16	-9.30	84	0.001
Third	17	20.42	4.713	0.0513	8	-19.6	67	0.001
	20	18.22	4.181	0.0576	13	-11.2	79	0.001
Fourth	17	12.25	1.488	0.0827	8	-8.81	66	0.001
	20	12.46	4.132	0.0890	11	-6.45	76	0.001
Fifth	17	19.10	4.063	0.0548	7	-1.44	58	0.158
	20	15.36	4.273	0.0699	11	-2.80	20	0.011

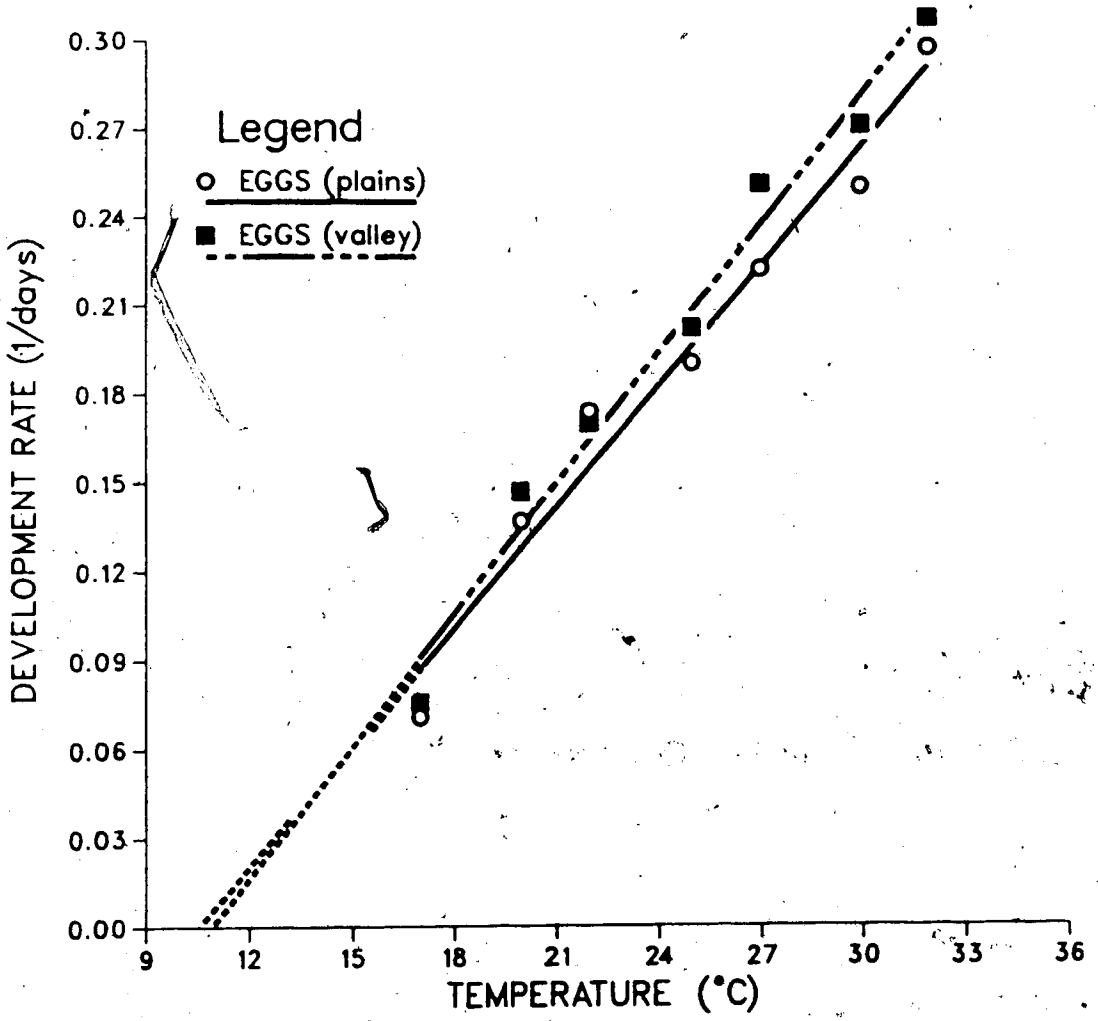

Figure III-1. Regression of percent development/day against constant temperature, for egg development of plains and valley populations of Alberta ECB. Interpolated values are represented by dashed lines. Refer to Table III-1 for regression equations.

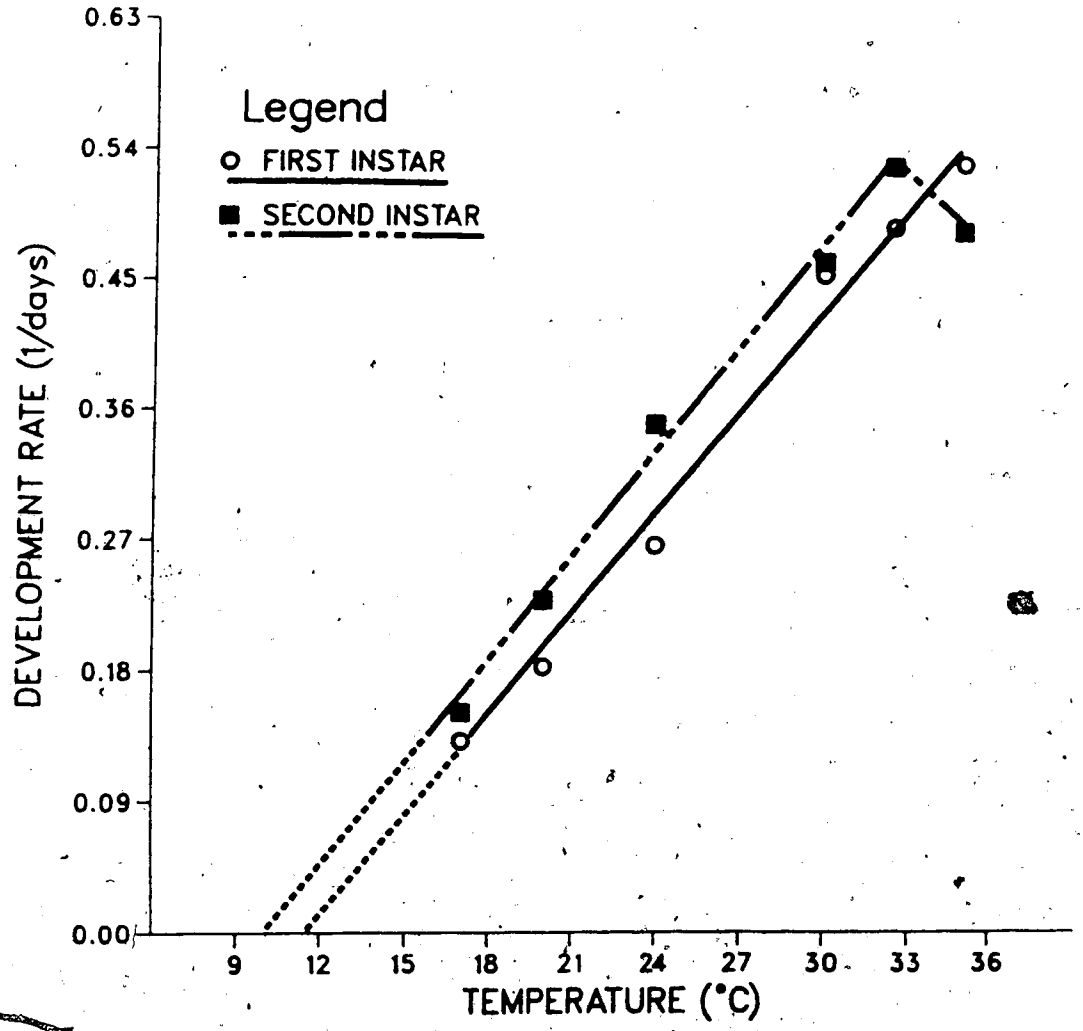

Figure III-2: Rate of development (% development/day) for first, and second instars of Alberta ECB. Interpolated values are represented by dashed lines. Refer to Table III-1 for regression equations.

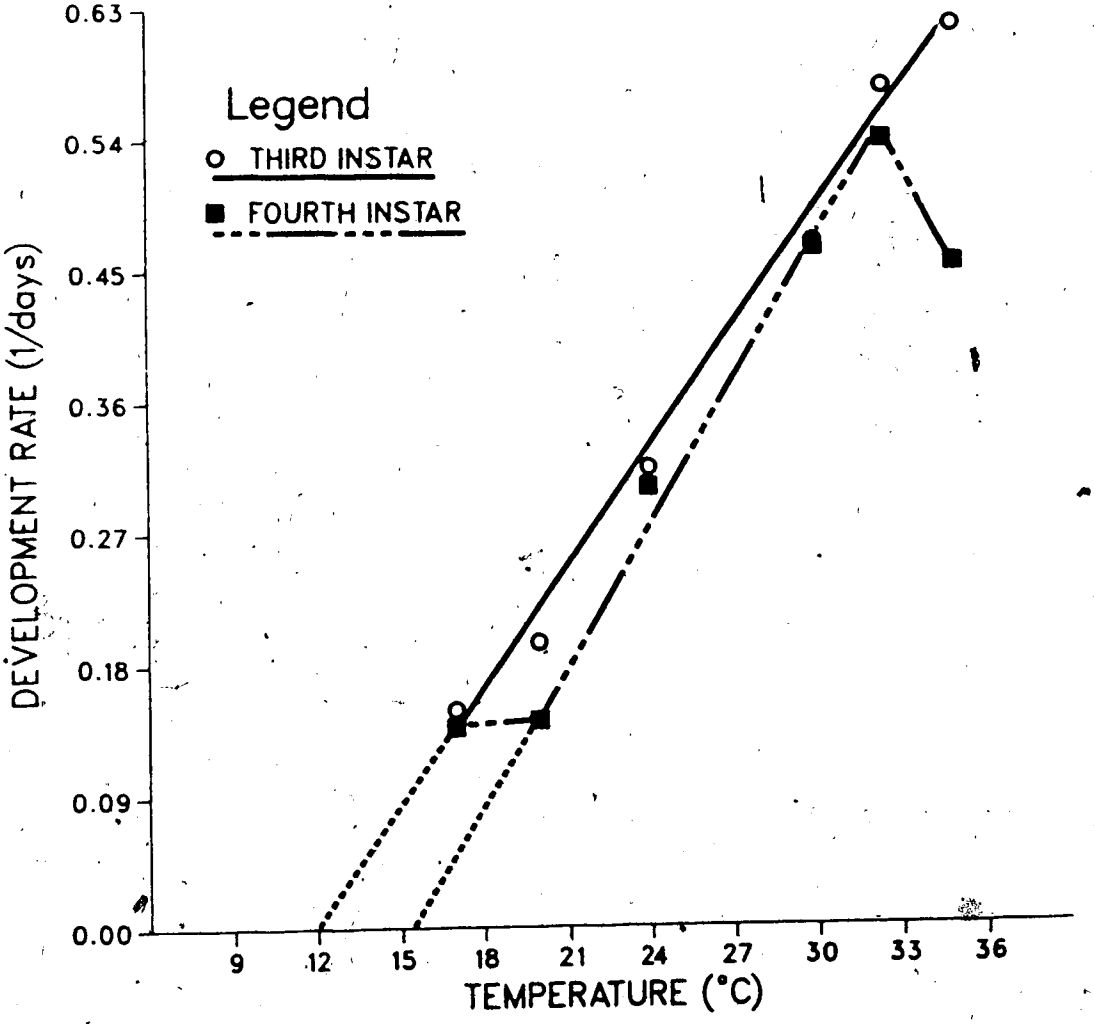

Figure III-3. Rate of development (% development/day) for third and fourth instars of Alberta ECB. Interpolated values are represented by dashed lines. Refer to Table III-1 for regression equations.

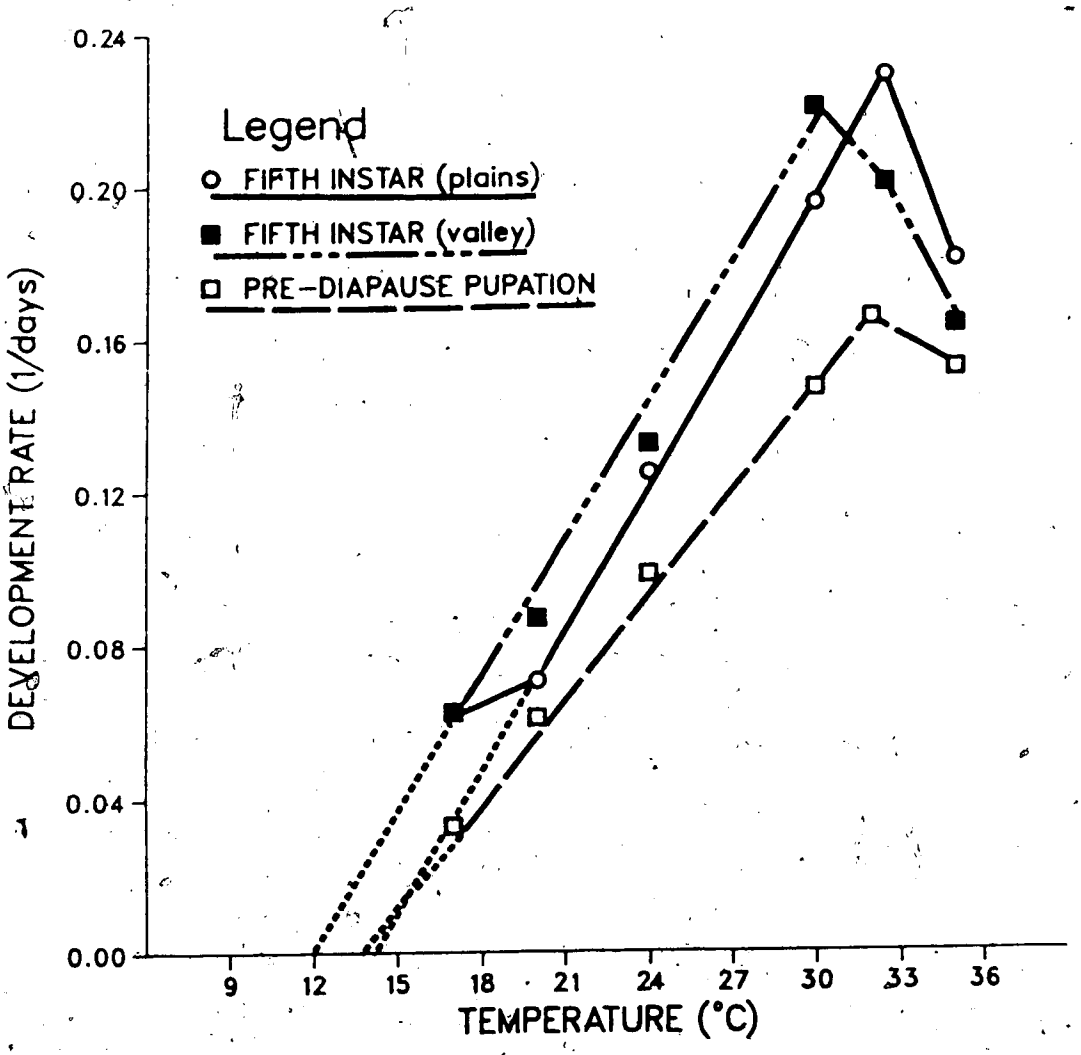

Figure III-4. Rate of development for the fifth instar of both valley and plains ECB; and for pre-diapause pupation of Alberta ECB. Interpolated values are represented by dashed lines. Refer to Table III-1 for regression equations.

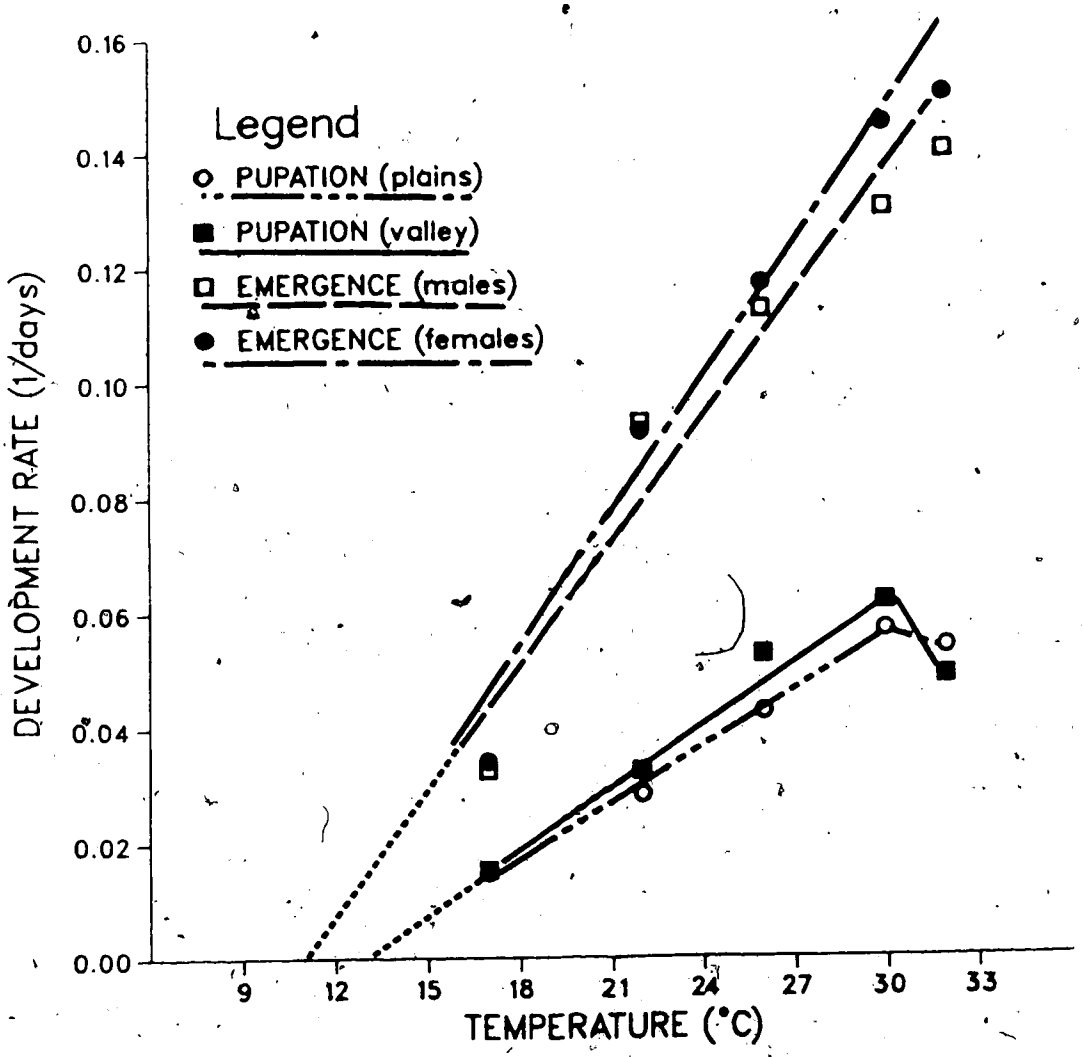

Figure III-5. Rate of development for post-diapause pupation of plains and valley ECB. Regression of % development/day from pupation to emergence is separately plotted for males and females. Interpolated values are represented by dashed lines. For regression equations see Table III-1.

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IV. REPRODUCTIVE PATTERNS

A. Introduction

Reproductive variables are life history characteristics that are subject to natural selection (Stearns 1976, Snell and King 1977). Organisms can respond to gradients in the environment by phenotypic adaptation of reproductive variables (Gill *et al.* 1983). In many insects for example pupal mass is inversely proportional to the temperature under which the larva develops (Jones *et al.* 1982). Mean body mass, which is a good predictor of potential fecundity (Gilbert 1984), varies for populations exposed to different natural environments (Gill *et al.* 1983).

In a previous study (see Chapter II), I reported distinct differences in phenology and larval growth characteristics between European corn borers (ECB) established in the S. Saskatchewan River valley, and those on the cooler plains 16 km south. These differences evolved within several years, since the ECB only became established in Alberta in 1980 (Lilly and Harper 1982). I hypothesized that variation in larval and pupal mass would be correlated with differences in fecundity and longevity between the two populations. In this study I show that the generally heavier valley ECB females lay more eggs over a longer period of time than do plains females, and I offer an explanation for the evolution of these differences in terms of reproductive cost theory (Snell and King 1976, Bell 1980).

The concept of reproductive cost is fundamental to life history theory (Snell and King 1977, Bell 1980), and has been demonstrated experimentally for fish species (Schaffer and Elson 1975, Leggett and Carscadden 1978) and rotifers (Snell and King 1977). This theory, which states that resources directed towards reproduction reduce those available for growth and maintenance, has received little experimental support from work on insect species. In the present study I examine this trade-off between reproduction and future survival in the ECB, a semelparous (*i.e.* "big-bang" reproduction) species.

Many studies of reproductive patterns in insects have focused on management of pest populations (*eg.* Greenfield and Karandinos 1976, Bari and Lange 1980, Mason and Mack 1984). Such studies quantify lengths of the reproductive (REP), pre-reproductive (PRE), and post-reproductive (POST) periods, at different temperatures. The present study is the first attempt to obtain this data for populations of the ECB. Previous studies (Caffrey and Worthley 1928, Huber *et al.* 1928) have only measured the lengths of these periods in outdoor insectaries. This study also compares the effect of fluctuating temperatures *vs.* constant temperatures upon ECB reproduction and survival.

The present study however goes beyond a simple description of changes in ECB reproductive characteristics with temperature. Other proximate objectives were to study the adaptation of reproductive variables in ECB populations,

to examine how reproductive strategies differ between the sexes, and to relate observed reproductive patterns to reproductive cost theory.

B. Materials and Methods

Experimental Procedure

Adult ECB lifespan and reproductive variables were examined by monitoring moths at constant (±1.0°C) temperatues of 20°C, 22°C, 25°C, 27°C, and 32°C, in Precision (model 818) incubators. Incubators were illuminated by two "cool daylight" fluorescent bulbs (intensity= ca. 8.5 hectolux), and maintained under a long-day photoperiod (L:D::16:8).

Because Sparks (1963) stated that a cycling temperature is necessary to ensure adequate mating, a variable temperature regime of 15°C/29°C (average temperature=22°C) was used to compare results with those obtained from adults exposed to a constant 22°C. An additional cycling temperature of 10°C/24°C (average temperature=17°C) was used to determine if egg-laying would decline when the temperature during half the lifetime of ECB adults was below the lower development threshold (see end of section for explanation of this threshold). In each case the amplitude of the temperature fluctuation was 14°C, which was representative of field temperatures during mating season. For the fluctuating regimes, a 12:12h::thermophase:cryophase

was used, with the thermophase occurring during the photophase. The temperature cycles produced by these incubators were of the square-wave type, and temperature transitions were complete within 30 minutes.

Moths from both valley and plains populations were tested at each constant temperature. Because of personnel and time constraints, only a small sample size (from 4-14 females, Table IV-3) could be used for each population at each temperature. To compare populations, larger sample sizes were used at a variable temperature of 15°C/29°C. Only valley borers were used at the 10°C/24°C regime.

Adults used in the experiments were obtained from diapausing larvae dissected from stalks in spring 1984. Field samples rather than laboratory stocks were used so that results obtained might better represent the reproductive potential of adults in the field. Larvae and pupae were placed in Petri dishes (5 ECB/dish) with moistened cotton, and shipped in several batches from the field sites (near Medicine Hat) to the laboratory in Edmonton. Upon arrival they were weighed, then placed individually in 7 dram vials containing moistened blotter paper, and were monitored daily for emergence.

Newly emerged females were individually placed with two male moths in separate oviposition chambers. Chambers were inverted one liter opaque plastic containers (height 13 cm, diameter 6 cm) with airtight lids (Fig. IV-1). A constant relative humidity (RH) of ca. 96% was maintained by use of a

saturated salt (KH_2PO_4) solution (Winston and Bates 1960). A felt wick (*cf*. Kira 1969) was used to transmit a 10% sugar solution from a small dish (diameter=4cm) to the moths. The wick was fitted through a slot in the wire mesh insert, so that when the container bottom was inverted over and onto its lid, then the wick became dipped into the solution (Fig. IV-1).

Oviposition chambers were checked daily for egg masses, which were deposited on wax paper that lined the containers. Egg masses were cut out from wax papers, after moths had been transferred to a new container. Eggs were placed in Petri dishes (diameter=9cm) with 5 to 10 egg masses per dish. Each Petri dish was labelled as to date and the female which the eggs came from. Petri dishes were stacked inside one-liter dessicators having a RH of 96%. Air exchange was facilitated by placing spacers between dishes, and by 3-cm diameter holes cut in Petri dish lids, which were covered with fine mesh.

Fecundity for each female was determined by counting individual eggs in the blackhead stage. Larvae hatching in each Petri dish were also counted. To prevent the escape of larvae, petroleum jelly was applied to the upper edge of the Petri dish. Infertile and dead eggs were counted after all larvae had hatched.

For every female the wet pupal mass, time of emergence, date of first reproduction, date of last reproduction, and date of death was recorded. Dates of emergence and death

were also recorded for males. To ensure adequate mating, the two males from each oviposition chamber were rotated among the females. Thus, each female was exposed to many different males, and the possibility of impotency affecting the results was eliminated. Each male was colour-coded with a dot of Testor's® enamel on the thorax, so that male longevity could be monitored. To decrease moth activity and prevent their escape during transfer operations, moths were cooled in their chambers at 4°C for five minutes. Transfer operations were also conducted inside a 1m X 1m acrylic enclosure, so that moths could easily be retrieved if escapes occurred.

Data Collected

Information was collected for each temperature regime to determine the total number of eggs produced/female in her life (fecundity); the mean number of eggs produced/day of reproductive life (oviposition rate); the distribution of egg-laying over time; the percentage of total eggs produced on the first day of maturity and on the last day of life; the lengths of PRE, REP, and POST; and the lifespan of both males and females.

Both mating and oviposition occur during the scotophase (Barber 1925). For calculation purposes the reproductive period included all nights in which egg-masses were laid, while the prereproductive period was measured as the number of nights from emergence up to the start of the reproductive

period. Reproductive output was measured only in terms of fertile eggs. Infertile eggs, and those females which laid only infertile eggs were not included in counts.

Growth Thresholds

Lower developmental thresholds (t_o) for each stage were established by linear regression of reciprocals of development time on temperature (T) and solving the resulting equations for the X-intercept (Gilbert *et al.* 1976). The number of DD above the t_o, required for completion of development (K), was determined by taking the reciprocal of the slope of the linear regression line (Campbell *et al.* 1974). Standard errors of t_o temperatures were calculated according to Campbell *et al.* (1974). The upper developmental threshold (Tm) is the temperature at and above which the rate of development begins to decrease (Zalom *et al.* 1983) was also determined. Both types of growth thresholds were compared among stages and between the two Alberta populations by weighted analysis of variance.

C. Results

Differences Between Populations

No significant differences were found at 15°/29°C between plains and valley populations with respect to male and female longevity, PRE and POST (Table IV-1). Consequently population samples for these variables were

pooled for further analysis.

Significant differences were found however between the two stocks with respect to REP and fecundity (Table IV-1). On average valley females laid about twice as many eggs as did plains females, and valley females laid eggs over a longer time span (Table IV-1).

For some of the variables examined, population variances were significantly different between ECB stocks (Table IV-1). Variance in valley populations was much greater than in plains ECB for female lifespan, PRE, REP, and for fecundity. For these variables, a Mann-Whitney *U*-Test was used to compare differences between populations (Table IV-1). Mean developmental times with standard errors, and developmental rates for all reproductive variables are given in see Appendix 2.

Differences Between Temperature Regimes

Longevity of ECB under a cycling temperature regime of 15°/29°(mean temp.= 22°C) was significantly greater than at a constant 22°C (Table IV-2) for both males (26% greater) and females (46% greater). Females lived slightly longer than males.

No significant differences between the two temperature regimes were observed for any other reproductive variable. Inequality of variances led to the use of non-parametric tests for some variables (Table IV-2). For all variables related to lifespan (*i.e.* PRE, REP, and POST), mean duration

of the period was slightly greater at variable temperatures than at constant temperatures (Table IV-2), suggesting that significant differences in overall longevity were not concentrated in any particular phase. Only plains borers were used to compare differences between temperature regimes for the variables REP and fecundity, because these variables differed between plains and valley stocks (see below), and sample size was insufficient to support separate analysis for valley moths.

Development and Temperature

Lifespan

Males and females differed in longevity patterns with respect to *Tm*. For males, there was a linear relationship between development rate and temperature from 17°C to 32°C (Fig. IV-2), while for females the *Tm* occurred at 25°C. Females lived longer than males, especially at lower temperatures. At 10°/24°C (mean temp.=17°C), female ECB survived an average 32.2 days, while males lived only 15.9 days. At 25°C, females lived 7.6 days and males lived 7.3 days (see Appendix 2). The estimated t_o for lifespan did not differ significantly (Weighted ANOVA: $df=1$, $X^2=0.89$, $P=0.30$) between females (14.6±1.54°C) and males (12.2±1.90°C). *K*, which is an indirect measure of the slope of the regression, was nearly equal between sexes. Mean female lifespan was 71.7±12.74 DD, while the *K* for male lifespan was 70.6±9.78

DD.

PRE, POST, and REP

Development rate was determined for each of the three periods associated with female lifespan. Rate for PRE was linearly related to temperature from 17°C to 27°C (Fig. IV-3). Mean development time was recorded as 7.7 days at 17°C and 2.3 days at 27°C (see Appendix 2).

Temperature and 1/POST were linearly related (Fig. IV-3) from 17°C (development time=6.0 days) to 25°C (time=1.0 days, see Appendix 2). The calculated thresholds t_o for POST and PRE were 11.6±4.04°C and 14.6±2.79°C respectively. The number of DD above the threshold t_o (*i.e.* K) were computed as 11.9±4.36 DD and 20.3±5.45 DD for POST and PRE respectively.

Although I had observed significant differences in REP between valley and plains ECB at 15°/29°C, when their development rate curves were regressed on temperature, no significant differences were noted (comparison of adjusted means: MS=0.8364; df=2,44; F=1.09; P=0.30). The adjusted mean for plains ECB was 0.50±0.578, and for valley ECB was 0.42±0.566. Therefore development times and rates may be pooled (see Appendix 2) for the two populations. The development rate curve was linear between 20°C and 32°C (Fig. IV-4). Mean development time was highest at 17°C (17.7 days) and lowest at 32°C (1.6 days). K was estimated as 15.8±2.56 DD, and t_o was estimated as 18.8±1.46°C. Differences in t_o between the three variables related to

lifespan (PRE, POST, REP) were significant at $P=0.05$ (Weighted ANOVA: $df=1$, $X^2=3.99$).

Fecundity and Oviposition Rate

A negative linear relationship between fecundity and temperature occurred over the range of temperatures tested (Fig. IV-5). Fecundity was greatest at 17°C and lowest at 32°C. Analysis of covariance demonstrated significant differences between the regression lines of plains and valley ECB (comparison of adjusted means: $MS=1.65 \times 10^5$; $df=2,70$; $F=4.04$; $P=0.02$). The adjusted mean for plains ECB (279±40.4 eggs/female) was significantly less than that for valley ECB (412±29.5 eggs/female).

The effect of these differences was clearly shown in the rate of oviposition (Fig. IV-6), which is simply fecundity/REP. No significant differences were observed between populations from 20° to 25°C (Fig. IV-6). At 27°C however, oviposition rate was significantly less ($T=-3.10$, $df=10$, $P=0.011$) for plains ECB than for valley ECB. Thus valley ECB had a higher Tm than did plains ECB for oviposition rate. The regression of oviposition rate on temperature showed a linear relationship from 17°C to the Tm (Fig. IV-4), with a t_o of 11.5±4.93°C.

Valley ECB also had a higher optimum range (25-27°C) for laying viable eggs than did plains ECB (22°C), when reared under constant temperatures (Table IV-3). Under these optimum temperatures 89% of valley ECB and 83% of plains ECB

laid viable eggs. Egg viability increased for valley ECB when subjected to the variable temperature (95% viable eggs) as compared to when placed at a constant temperature of 22°C (60% viable eggs, Table IV-3). The temperature at which the laying of viable eggs would theoretically cease (34.1±1.71°C) was approximately equal for both populations. Average oviposition/female/day for constant temperatures is given in Table IV-4, and for variable temperatures is given in Table IV-5.

Patterns of Reproduction and Lifespan

To explain why a considerable amount of variation was observed for some reproductive variables, partial correlations between selected variables were examined. Strong negative correlations between lifespan and percentage of total eggs laid on either the first or last day of life (Table IV-6) indicate that individuals which oviposited heavily during these periods had a shorter life. Short-lived females also produced less offspring, since the correlation between fecundity and lifespan was positive (Table IV-6). Oviposition rate was negatively correlated with lifespan (Table IV-6), suggesting that those females that produce many offspring over a short period do not live long. As well, REP was positively correlated with fecundity (partial correlation=0.816, $P<0.01$), while oviposition rate was not (Table IV-6). Together these observations suggest that the large number of offspring associated with long-lived

individuals is mainly achieved by reproducing at a low rate over many age classes. Short-lived individuals, in contrast, reproduced at a high rate over few age classes, with less total fecundity.

Wet pupal mass of females was related to their subsequent reproductive pattern. Both fecundity and lifespan were positively associated with pupal mass (Table IV-6), suggesting that heavier females live longer and produce more offspring. The percentage of total eggs laid on either the first or last day of life was negatively associated with pupal mass (Table IV-5), which suggests that lighter females concentrated their oviposition in fewer age classes.

Reproductive effort is best measured in sexually reproducing species by comparing average survival and fecundity in groups of genetically diverse individuals (Bell 1980). Consequently reproductive cost was determined for valley ECB at 22°C by plotting survival against oviposition rate (Fig. IV-7). The data was best described (r^2=0.77; df=1,22) by a quadratic equation ($Y=14.605+0.000017X^3$) that is convex downward (Fig. IV-7). Thus, as daily fecundity increases, survival diminishes rapidly at first, but does so more slowly as daily fecundity becomes very great. A tangent to this line at the equilibrium point (Fig. IV-7) is described by the regression equation $Y=20.959-0.1079X$ (r^2=0.67; df=1,22). The equilibrium point, where survival cost is balanced by fecundity, occurred where lifespan was ca. 10 days, and oviposition rate was ca. 75 eggs per day.

D. Discussion

Differences Observed

Differences Between Populations

We found significant differences between valley and plains ECB with respect to REP at 15°/29°C, and with respect to fecundity over all temperatures. Partial correlations demonstrated that females with higher wet pupal mass generally lived longer and gave birth to more offspring. We also found in another study (see Chapter II) that valley larvae weighed significantly more in the spring than did plains larvae. These differences resulted mainly from environmental (*i.e.* temperature) differences between sites. Because I used pupae from the field, and because valley borers weighed more on average than did plains borers (see Chapter II), valley females had greater fat resources to lay more eggs.

While differences in REP and fecundity were correlated with pupal mass, other differences between the two populations were not. Plains ECB had a lower *Tm* than valley ECB for both oviposition rate and optimum egg viability, and this is likely related to physiological differences between the two populations. We have also found that plains ECB have a lower *Tm* for the fourth and fifth larval instars (see Chapter III), and have explained these differences in terms of evolution of physiological time parameters as proposed by

Taylor (1981).

Differences Between Regimes

Differences in development time between fluctuating and constant temperatures, such as I observed with male and female longevity, have been documented for many insects (Hagstrum and Hagstrum 1970, Hagstrum and Leach 1973). Although I cannot confirm Spark's assertion (1963) that mating frequency increases under fluctuating temperature regimes, I did note that the number of valley females laying viable eggs increased by 35%. Loughner (1971) found that ECB mating success ranged from 56-75% under a fluctuating temperature of 18.3°/29.4°C. With the system of adult rotation that I used, successful mating was higher (80-95% of all females laid viable eggs) under a similar temperature regime (15°/29°C).

Developmental rate was not adversely affected when moths were exposed to a thermoperiod with a cryophase (10°C) below the t_o. Values at 10°/24°C for most reproductive variables fit the straight line through the other points on the development rate curve (Figs. 2,3). The only exception was for REP, because the t_o (18.8°C) was actually higher than the mean temperature (17°C) of the regime (Fig. IV-4). Yeargan (1980) also found that successful development of *Telenomus podisi* occurred at 14°/22°C, when the cryophase was below the t_o.

Reproductive Traits

Longevity and Oviposition

Results for ECB development differed in some respects from studies of other insects. Mack and Backman (1984) and Mason and Mack (1984), who studied that lesser cornstalk borer and the soybean looper respectively, found that female longevity decreased linearly with temperature. Female ECB lifespan in contrast decreased with temperature in a non-linear fashion, forming a typical 'J-shaped' curve. The authors cited above also observed that total fecundity/female increased with temperature in a non-linear manner. For the ECB fecundity/female decreased linearly with temperature.

Similar to insects studied by Greenfield and Karandinos (1976), Bari and Lange (1980), and Mason and Mack (1984), daily egg production in the ECB at lower temperatures was less than that at higher temperatures, but extended for a longer duration. As well, temperature apparently affected rate of oogenesis in ECB, because the rate of oviposition changed with temperature (Fig. IV-6). With some Lepidoptera (Greenfield and Karandinos 1976), oogenesis is not completed by the end of the pupal stage, but continues during adult life, and is therefore affected by temperature. This probably applies to the ECB as well. If this is the case, then higher temperatures would increase oogenesis rate and subsequent oviposition rate.

Reproductive Strategies of the Sexes

The fact that adult female ECB live longer than males raises questions about life history stategies. Would it not be more advantageous for polygamous male moths to have long lifespans, to enhance their reproductive success? Because reproductive success in male insects is proportional to the number of females mated (Wade and Arnold 1980), this question is bound to that of optimal timing of male eclosion. Males which emerge close to the peak for the population clearly have greater potential reproductive success, because more females are available (Fagerstrom and Wiklund 1982). ECB populations conform to the optimization model proposed by Fagerstrom and Wiklund (1982), whereby males emerge slightly before females, and the eclosion period is about equal for both sexes (see Chapter II). I suggest that selection for male ECB reproductive success is based mainly upon selection for optimal timing of eclosion and not upon longevity. Female reproductive success however depends upon several factors (Fagerstrom and Wiklund 1982), one of which is reduced mortality both before and during oviposition. Mortality of female ECB is very low during these periods (Tables 4 and 5), suggesting that maximum reproductive success is achieved by extended longevity. These data suggest that differences in male and female lifespans arose in response to selection for different reproductive strategies in each sex.

Reproductive Cost

The two types of reproductive patterns I have observed, *i.e.* that of concentrated reproduction in a few age classes vs. that of low-level reproduction over a long time period, can be explained in terms of resource limitation theory (Snell and King 1977). Individuals which oviposit at a high rate limit their resources available for growth and maintenance, and therefore die early.

In reproductive cost theory, semelparity may evolve either through selection toward a stable equilibrium or selection away from an unstable equilibrium (Bell 1980). The latter route occurs when the graph of fecundity on survival is convex downward, as was observed for valley ECB (Fig. IV-7). This suggests that selection away from an unstable equilibrium is correlated with evolution of semelparity in valley populations of Alberta ECB.

Existence of an unstable equilibrium between present fecundity and future survival in Alberta ECB may explain why natural selection for differences in fecundity and REP occurred within five years between valley and plains populations. Since there are no forces acting to stabilize the equilibrium, the environmental differences could rapidly be reflected as differences in fecundity and longevity between ECB populations.

Table IV-1. Comparison of valley and plains ECB populations[1], with respect to reproductive variables, at a fluctuating temperature of 15°C/29°C.

Variable	Mean ±S.D. (and CV for some cases)[2]	Test for Equal Variances	T-test for differences in Means	Mann-Whitney U-test[3]
Male Life-span	V=11.8±5.21 P= 9.9±4.65	F=1.26 P=0.32 df=30,18	T=-1.30 P= 0.21 df=48	
Female Life-span	V=14.1±6.11; CV=43.4 P=11.1±2.36; CV=21.3	F=6.72 P=0.008 df=20,7	-	T=1.68 P=n.s.[3] df=27
PRE	V=2.9±2.74; CV=94.5 P=2.9±1.13; CV=39.0	F=5.91 P=0.011 df=20,7	-	T=-1.17 P=n.s. df=27
REP	V=9.1±4.66; CV=51.2 P=5.1±2.47; CV=48.4	F=3.55 P=0.046 df=20,7	-	T=2.10 P=<0.05 df=27
POST	V=2.2±3.40 P=3.1±3.14	F=1.18 P=0.44 df=20,7	T=0.68 P=0.51 df=27	-
Fecundity	V=559±252.5; CV=45.2 P=267±132.5;	F=3.66 P=0.044 df=20,7 CV=49.6	-	T=2.73 P=<0.05 df=27

[1]V refers to valley populations; P refers to plains populations. PRE refers to Prereproductive Period; REP refers to Reproductive Period; and POST refers to Postreproductive Period.

[2]CV refers to coefficient of variation.

[3]Test statistic is compared to á significance level of 5%; n.s.=not significant.

Table IV-2. Reproductive variables of Alberta ECB populations compared at a constant temperature of 22°C and at a variable temperature[1] of 15°C/29°C.

Variable	Mean ±S.D. (and CV for some cases)	Test for Equal Variances	T-test for differences in Means	Mann-Whitney U-test
Male Lifespan	F=11.1±5.05; CV=45.5 C=8.8±3.70; CV=42.0	F=1.85 P=0.032 df=47,33	-	T=4.38 P<0.05 df=80
Female Lifespan	F=13.3±5.46; CV=41.1 C=9.1±2.36; CV=25.9	F=5.38 P=0.014 df=28,7	-	T=2.26 P=<0.05 df=35
PRE	F=2.9±2.38; CV=82.1 C=2.4±1.06; CV=44.2	F=5.04 P=1.017 df=28,7	-	T=0.34 P=n.s. df=35
REP (plains)	F=5.1±2.48 C=4.6±2.61	F=1.11 P=0.423 df=4,7	T=0.37 P=0.72 df=11	-
POST	F=2.4±3.30; CV=137.5 C=1.3±0.89; CV=68.5	F=13.87 P=0.001 df=28,7	-	T=0.42 P=n.s. df=35
Fecundity (plains)	F=267±132.5 C=278±180.7	F=1.86 P=0.22 df=4,7	T=-0.13 P= 0.90 df=11	-

[1]F refers to fluctuating temperature regime; C refers to constant temperature regime; other abbreviations as in Table IV-1.

Table IV-3. Percentage of females tested which oviposited, and the percentage which laid viable eggs.

Temperature Regime	Percentage of Females Ovipositing		Percentage of Females Laying Viable Eggs		Sample Size	
	Valley	Plains	Valley	Plains	Val.	Plns.
10/24	75	-	75	-	4	-
20	80	80	40	60	5	5
22	80	100	60	83	5	6
15/29	95	90	95	80	21	10
25	88	78	88	44	8	9
27	100	100	89	50	9	8
32	75	64	33	50	12	14

Table IV-4. Survivorship and fertility table for the ECB, for constant temperatures

Adult Age (days)	20°C			22°C			25°C			27°C			32°C		
	l_x[1]	m_x[2] V[3]	P	l_x	m_x V	P	l_x	m_x V	P	l_x	m_x V	P	l_x	m_x V	P
0	1.0	-	-	1.0	-	-	1.0	-	-	1.0	-	-	1.0	-	-
1	1.0	-	-	1.0	-	-	1.0	-	-	1.0	-	-	1.0	0	2
2	1.0	-	-	1.0	0	13	1.0	13	0	1.0	31	0	1.0	47	24
3	1.0	-	-	1.0	53	26	1.0	36	85	1.0	45	8	1.0	25	6
4	1.0	26	15	1.0	45	3	1.0	38	18	1.0	33	27	0.9	5	4
5	1.0	37	29	1.0	47	40	0.9	9	34	0.9	13	6	0.9	4	1
6	1.0	24	20	0.9	4	4	0.8	4	17	0.8	29	0	0.8	0	2
7	1.0	62	22	0.8	29	25	0.8	6	20	0.8	9	7	0.7	18	1
8	1.0	18	41	0.8	19	13	0.5	12	6	0.4	5	0	-	-	-
9	1.0	46	39	0.6	5	4	0.3	5	5	0.3	5	0	-	-	-
10	1.0	25	27	0.5	8	10	0.3	4	0	-	-	-	-	-	-
11	1.0	10	23	-	-	-	0.1	3	0	-	-	-	-	-	-
12	1.0	14	12												
13	1.0	6	8												
14	0.8	4	8												
15	0.7	3	9												
16	0.6	0	2												
17	0.3	-	7												
18	0.2	-	3												
19	0.1	-	4												

[1]Proportion of adult females surviving to age x.

[2]Mean number of female offspring per female aged x per day.

[3]V=valley ECB; P=plains ECB.

Table IV-5. Survivorship and fertility table for the ECB, for variable temperatures. Abbreviations as in Table IV-4.

	10/24°C		15/29°C		
Adult Age (days)	*Lx*	*Mx* V	*Lx*	*Mx* V	P
0	1.0	-	1.0	4	-
2	1.0	-	1.0	21	-
3	1.0	-	1.0	28	15
4	1.0	-	1.0	28	28
5	1.0	-	0.95	30	24
6	1.0	-	0.91	34	27
7	1.0	-	0.86	28	22
8	1.0	26	0.81	27	10
9	1.0	23	0.76	14	11
10	1.0	18	0.76	21	4
11	1.0	24	0.76	13	1
12	1.0	29	0.71	13	-
13	1.0	19	0.67	7	-
14	1.0	14	0.62	4	-
15	1.0	24	0.52	3	-
16	1.0	32	0.43	3	-
17	1.0	28	0.29	1	-
18	1.0	3	0.19	.9	-
19	1.0	17	0.14	.3	-
20	1.0	0			
21	1.0	17			
22	0.83	14			
23	0.83	11			
24	0.83	3			
25	0.83	7			
26	0.83	3			
27	0.83	2			
28	0.83	4			

Table IV-6. Partial correlation coefficients of reproductive variables with pupal weight, oviposition rate and lifespan of female ECB (linear effects of the remaining variables have been removed).

	Fecundity	Lifespan	Eggs Laid on First Day, as % of Total	Eggs Laid on Last Day, as % of Total
Wet Pupal Mass	0.225 P<.05	0.267 P<.05	-0.191 not sig.	-0.232 P<.05
Oviposition Rate	0.088 not sig.	-0.280 P<.05	0.894 P<.01	0.125 not sig.
Lifespan	0.992 P<.01	-	-0.327 P<.01	-0.346 P<.01

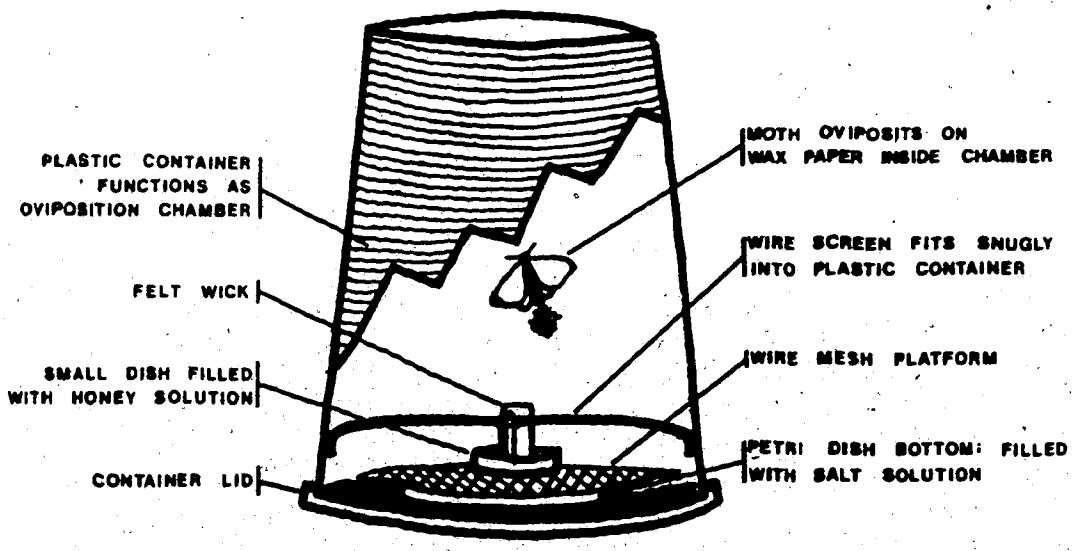

Figure IV-1. Diagram of oviposition chamber used for experiments, cut away to expose the interior.

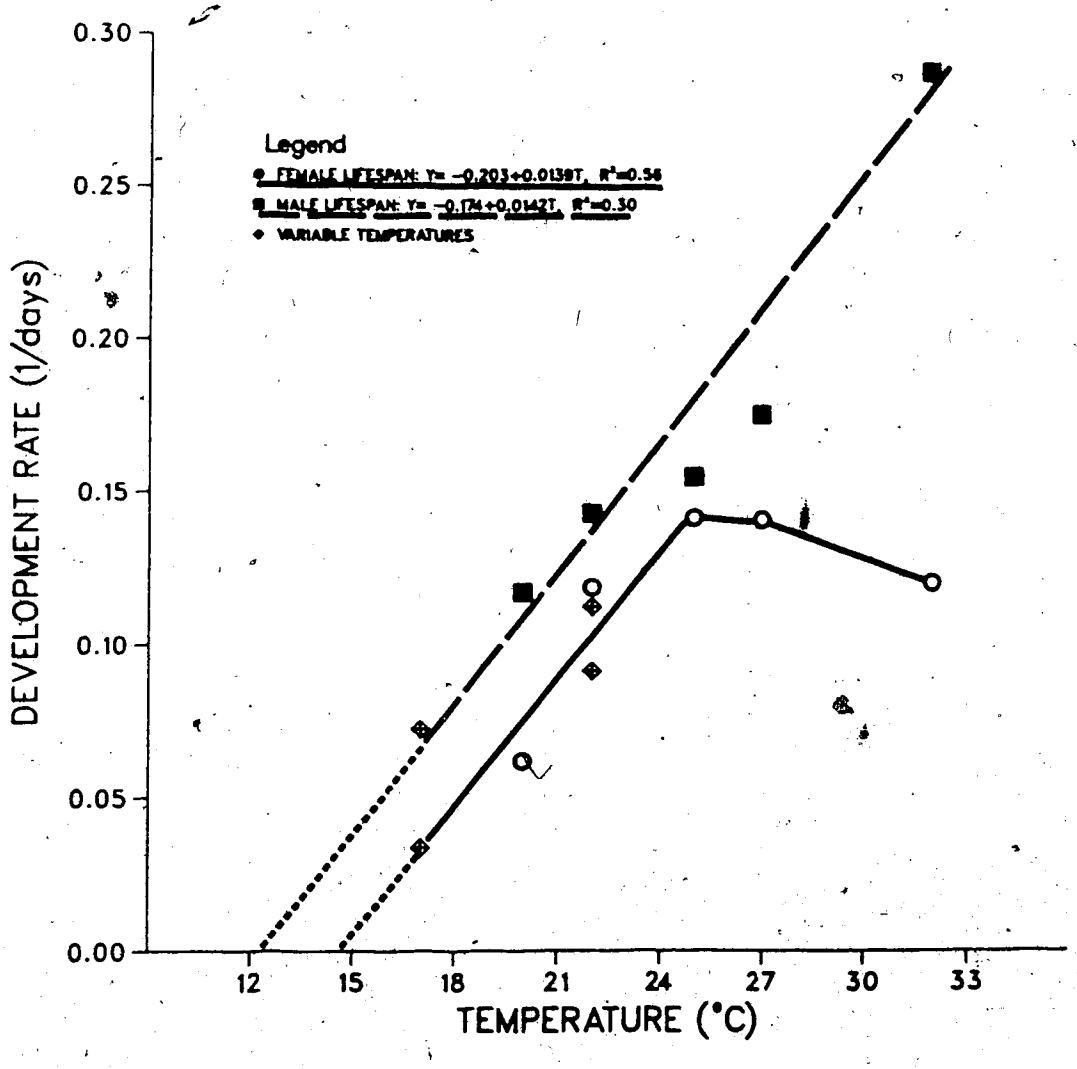

Figure IV-2. Rate of development (% development/day) for adult male and female longevity of Alberta ECB. Interpolated values are represented by dashed lines.

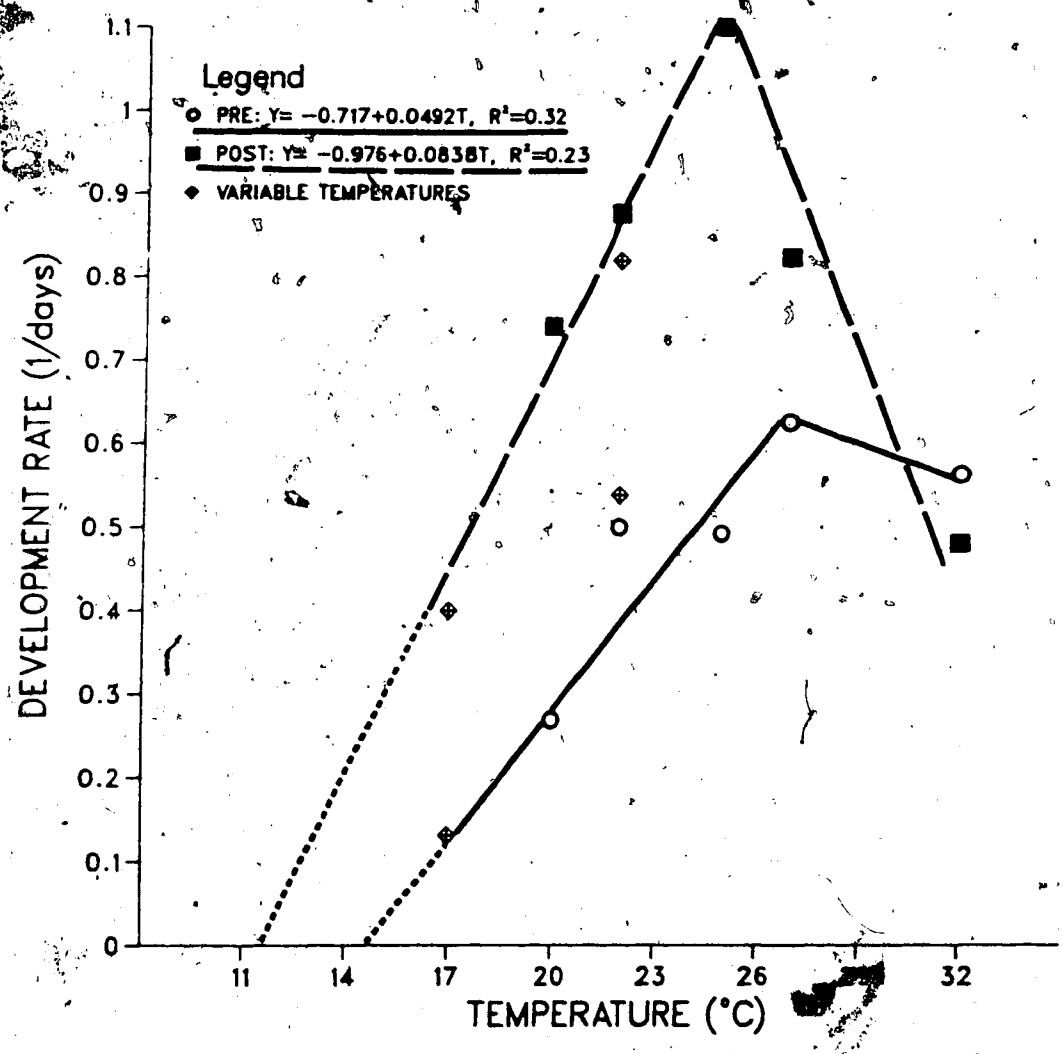

Figure IV-3. Rate of development (% development/day) for pre- and post-reproductive periods of Alberta ECB. Interpolated values are represented by dashed lines.

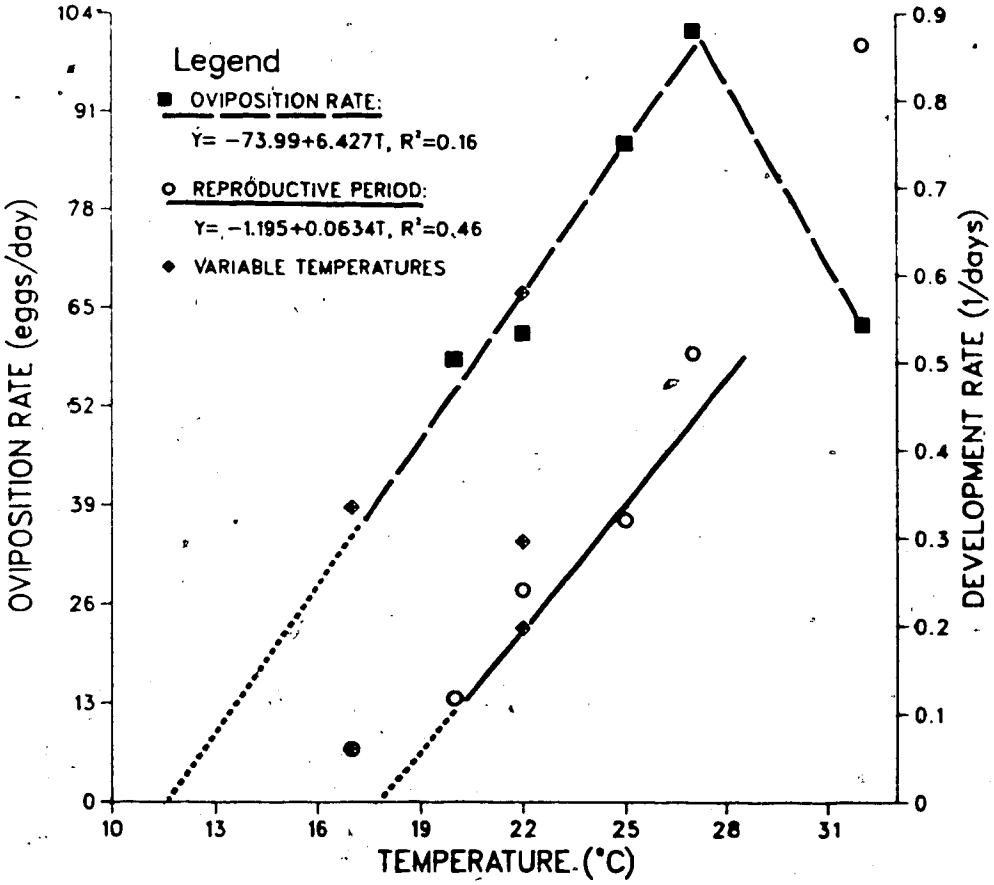

Figure IV-4. Rate of oviposition, and development rate (% development/day) for the reproductive period of Alberta ECB. Interpolated values are represented by dashed lines.

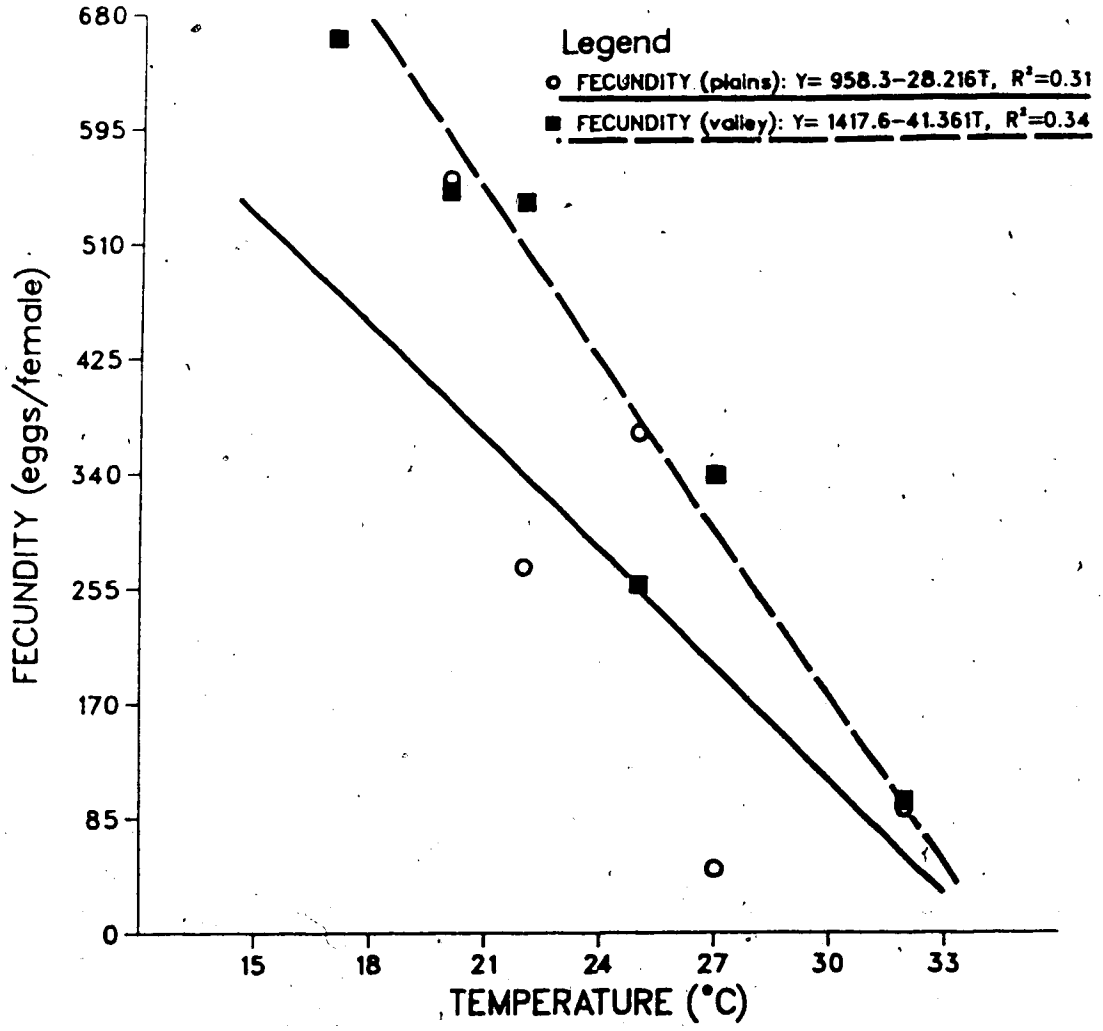

Figure IV-5. Regression of fecundity (total eggs laid/female) against temperature, for plains and valley populations of Alberta ECB.

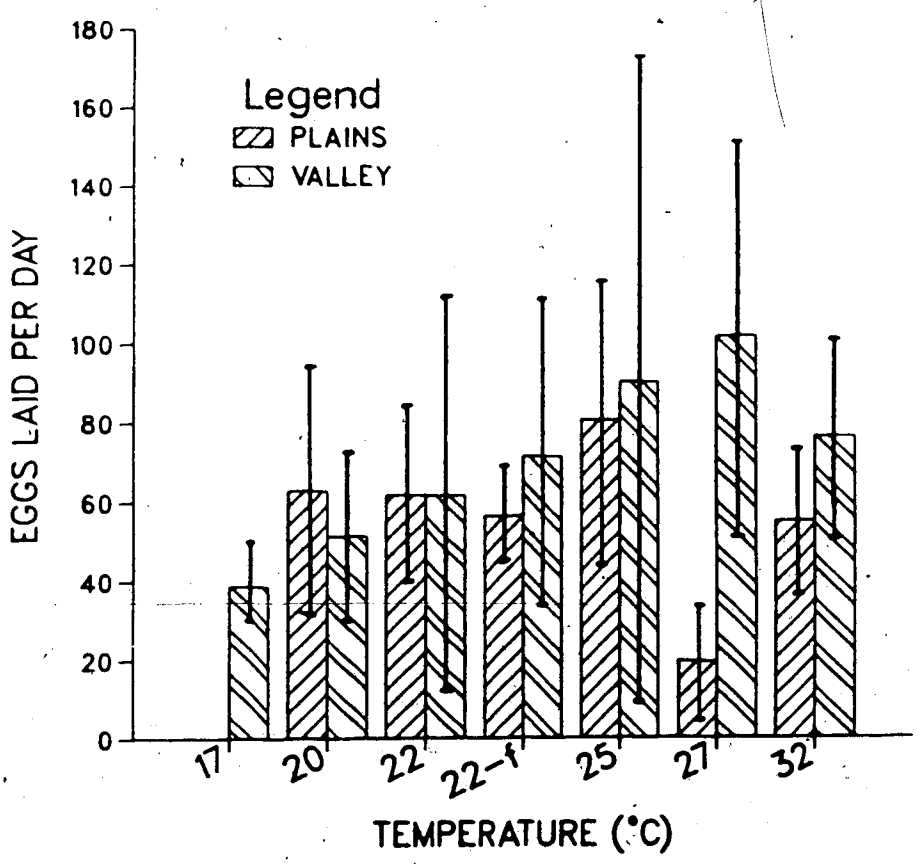

Figure IV-6. Bar diagram comparing oviposition rate of plains and valley ECB at various temperatures. The fluctuating temperature of 15°C/29°C (mean=22°C) is represented as 22-f.

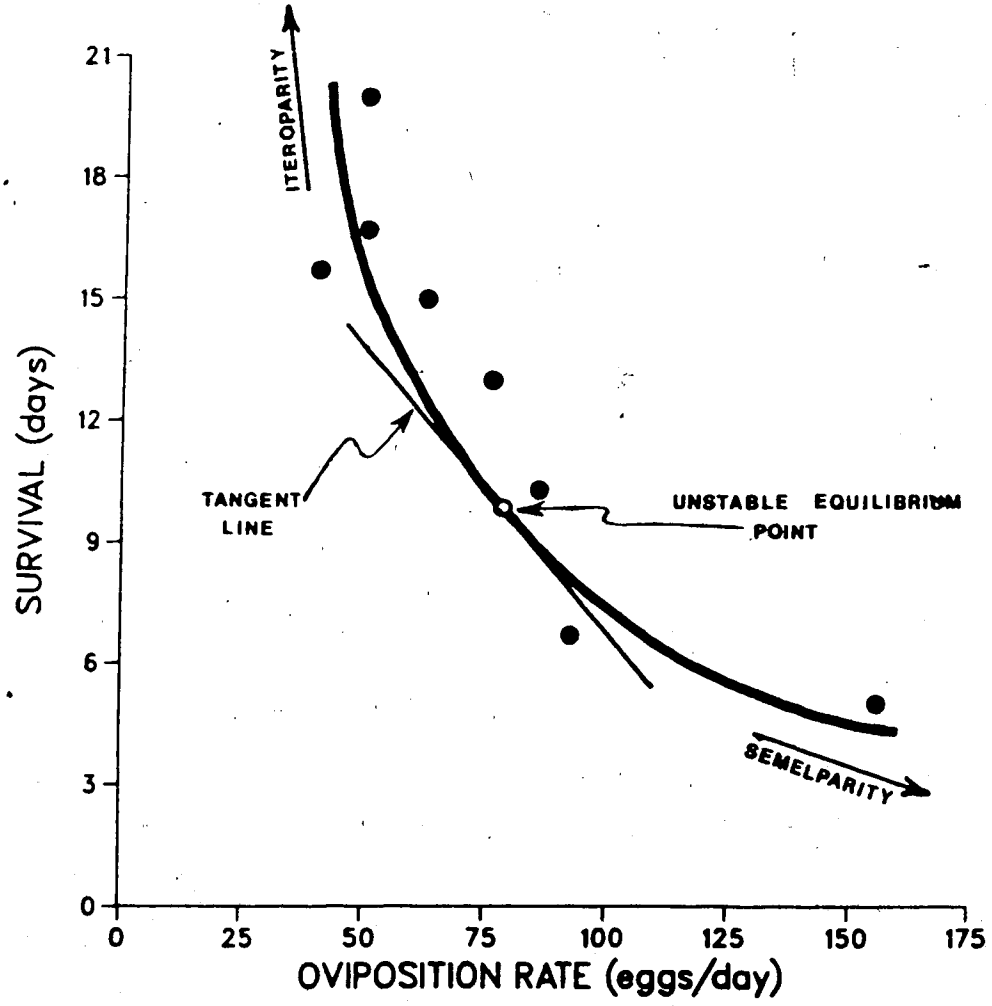

Figure IV-7. Regression of survival of valley ECB female moths against oviposition rate, at a temperature of 22°C. Data taken from both constant and variable temperatures. Each data point is based on three individuals. Refer to text for regression equations.

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V. LARVAL DISPERSAL AND FORAGING PATTERNS

A. Introduction

The study of insect dispersal and habitat selection has often been considered a trivial exercise, until recently (Stinner *et al.* 1983). However, it is now realized that effective control of an insect pest depends upon accurate knowledge of it's feeding habits and dispersal patterns. The European corn borer (ECB) is a good case in point. Growing larvae can attack all parts of the corn plant, depending upon plant growth stage (Hudon *et al.* 1982). Interplant dispersal of mature larvae in the fall is a strategy for overwinter survival of ECB (Barber 1924, Worthley 1927, Hodgson 1928, Huber *et al.* 1928). Information gained by monitoring movement of larvae throughout the plant (Caffrey and Worthley 1927, Crawford and Spencer 1928, Huber *et al.* 1928, Patch 1943) has been applied to the development of corn and sorghum varieties that are resistant to leaf and sheath feeding by corn borers (Guthrie *et al.* 1960, 1970, 1971, 1984).

Several aspects of ECB dispersal however have been inadequately described or quantified. Information about movement patterns of newly hatched larvae is lacking. Several questions are addressed by the present study. What types of dispersal routes are followed, and are some routes preferred over others? Do newly-hatched larvae drop from leaves solely to avoid predators, or is this also a

dispersal tactic? What microhabitats are colonized by early-instar larvae, and how quickly does this colonization occur? Why do so many early-instar larvae die (see Chapter VII)? Because early-instar mortality is a major component of ECB lifetable analysis, an understanding of how this mortality occurs is important.

Larval selection of microhabitats within the corn plant (*i.e.* intraplant dispersal) has not yet been described as to larval stage, but only as the percentage of larvae found in a particular location, in relation to the number of days growth from a specified starting date (Huber *et al.* 1928, Patch 1943, Guthrie *et al.* 1984). Results may not apply to other regions, because of differences in larval and/or corn growth rate. Therefore, in this study, habitat selection by different larval instars is related to specific plant growth stages. Because insecticide application is ineffective once larvae have bored into the stalk (Clement *et al.* 1981), it is important to determine which instar begins boring.

Finally, interplant dispersal needs to be effectively measured. In this study, the pattern of interplant dispersal at a given egg density has been determined in a cornfield. I also hypothesized that survival of larvae which dispersed across corn rows would be less than that for larvae which dispersed between rows.

To summarize all aspects of ECB dispersal, I constructed a flow diagram, which may be useful in modelling (*cf.* Stinner *et al.* 1983) ECB larval dispersal.

B. Methods and Materials

Corn Plant Phenology

The distinguishable stages of growth in a corn plant have been defined by Barber (1943) and the Alberta Corn Committee (1982). Those stages relevant to this study are the pre-whorl (1-5 leaves fully open),early whorl (6 leaves open), mid-whorl (8 leaves open; tassel enclosed in whorl), late whorl (tassel visible in whorl cup), early green tassel (10 leaves open; tassel tip above whorl; ear buds forming), mid-green tassel (tassel as a clump of folded branches), late green tassel (12 leaves open; tassel unfurled), early silk (14 leaves open; silks emerging, anthers dehiscing), mid-silk (maximum pollen shedding), and late silk (silks dried at tips, anthers gone) stages.

Dispersal After Hatching

Field Trials

Field trials were conducted to determine dispersal routes chosen by newly-hatched larvae, and their speed of movement. Larvae were obtained from egg masses laid on wax paper by laboratory-reared female moths. Masses were incubated at 26°C until the blackhead stage, then placed at 16°C and checked daily for hatching. When a few larvae had hatched, egg masses were transported in a cooler to the field plot. When egg masses were removed from the cooler,

most larvae began hatching immediately.

Three or four larvae were brushed onto the underside of a corn leaf, 15 to 20 cm from the ligule. Mean distance from naturally-laid egg masses to the ligule is 18.4 cm (see Chapter VI). Larvae were placed only on leaves in the midsection (leaf nos. 5-9) of the plant. The dispersal route of each larva was charted until it entered the ligule or fell off the leaf. Care was taken not to disturb larvae during observation. The experiment was replicated 34 times (a total of 105 larvae were observed) over eight windless days. During trials sweet corn was in the mid-silk to late silk stages. Mean temperature during trials was 27.5±4.44°C.

Laboratory trials

Dispersal of newly-hatched larvae was monitored on artificial corn plants, to investigate why larvae drop from leaves, causes of larval mortality, and rate of colonization. One meter high plant stems were made from doweling (diameter=2 cm), and painted white. Stems were nailed to a 0.37 m^2 square plywood base, which was also painted white. Leaves were cut from 4-mil clear polyethylene to the approximate dimensions (see Appendix 3) of corn leaves. Plastic leaves were made rigid by interweaving wire down the midrib. The end of the wire was wound around the stem to attach the leaf.

Blackhead egg masses were pinned to the middle (at 13±3 cm from the ligule) of the ninth leaf (45±2 eggs/plant), on the underside. Prior to egg placement, artificial medium

(BioServ, Frenchtown, N.J.) was poured into the leaf ligules and tassel. Tangle-trap® was placed around the perimeter of the stem base and plant stand. Use of artificial plants was advantageous because all dispersing larvae could be seen against the white wood, and through the plastic leaves, without disturbing the plant. Larvae dropping to the plant base were caught in Tangle-trap®, and counted.

First-instar larval mortality and dispersal to food sites was monitored at 3-hour intervals for 7.5±0.25 degree-days (DD). DD calculations were based upon a lower threshold of 11.5°C (see Chapter III). Eight replicates were used in a controlled temperature chamber at 17±1°C and 98±2% relative humidity (RH). To simulate field conditions, trials were repeated under a fluctuating temperature (range=16°-23°C, mean=19.5°C) and humidity (range=44%-66% RH). At the end of each trial, food sites and leaf surfaces were carefully examined for larvae.

Intraplant Dispersal

Progress of larval dispersal throughout individual corn plants was monitored in the field in 1983 and 1984. Wax papers containing blackhead egg masses (*ca.* 40 eggs/plant) were stapled to the undersides of corn leaves at mid-plant level. Larvae generally hatched within a few hours. Each plant was tagged as to date of egg placement and the number of eggs placed (±2 eggs). In 1983 eggs were placed on field corn at *ca.* 3-day intervals from July 13 to Aug. 8, while in

1984 eggs were placed on sweet corn at 5-day intervals from July 5 to Aug 9.

Treatment groups (those plants which received eggs all on the same day) were separated from each other by plastic sheeting barriers coated with Tangle-trap® on top, to prevent dispersal between treatments. Every 5 days after egg placement, two plants from each treatment group were cut at the roots, put in plastic bags and transported to the laboratory, where they were carefully dissected. Larvae were noted as to instar (based upon head capsule width) and location within each corn plant.

Two methods were used to prevent larval escape from plots and to prevent natural infestation. In 1983 the plot was enclosed by a meter-high 6-mil plastic fence, coated with Tangle-trap® at the bottom. The plot was located at the periphery of the corn borer infestation, so that chances of natural egg-laying were unlikely. In 1984 the plot was again enclosed by a plastic fence. However, above the plastic was another meter of screening, and the enclosure top was also screened. Temperature, humidity and rainfall were recorded continuously at mid-plant level within the field plots. Both plots were irrigated.

Larval development was described as to instar, and as to the number of DD from egg placement. DD were accumulated using a computer program based upon a sine-wave model (Gilbert *et al.* 1976). Calculations were based upon lower development thresholds of 11.5°C, 10.2°C, 11.9°C, 15.3°C,

and 11.9°C for the first, second, third, fourth, and fifth instars respectively (see Chapter III).

Inter-plant Dispersal

Larval dispersal between corn plants was examined in 1984 by erecting a series of screen cages around groups of corn plants, and artificially infesting the centre plant with 60±2 eggs. Six replicates of cages along a single row of corn contained 9 plants each, while each of six cages across five rows contained five plants (one plant/row). To simulate actual dispersal over a large area, four cages of 45 plants (9 plants/row X 5 rows) were erected, with the centre plant again infested with 60±2 eggs. The plots of field corn were planted according to standard practise, with 76.2 cm between rows, and *ca.* 15 cm between plants within a row.

To determine how dispersal occurs, in three cages (of 9 plants/cage) all leaves were tied to the corn stalks, so that larval dispersal from the centre plant could only occur by ground, while in three other cages plastic traps were used to prevent dispersal by ground. These traps were circular in shape, similar to a cross-sectioned donut. Trough diameter was six cm, and diameter of the hollow core was 12 cm. Each trap was positioned over the centre plant and dug into the ground, so the that edges of the trap trough were level with the ground at the plant base. This trap, which completely encircled the plant base, was filled

with glycol, and examined for larvae on 27 August.

To prevent larvae from dispersing outside of cages, they were enclosed by a meter-high plastic fence with Tangle-trap® spread along the bottom. The top portion of cages was screened. Egg masses were placed from 11-14 August, after moths had ceased flying. Plants were checked for naturally-laid eggs and larvae before placement of egg masses.

To determine numbers and locations of larvae that successfully dispersed from the centre plant, wax papers were checked for eggs that did not hatch. For each cage, numbers of eggs or larvae thus accounted for were tallied. The difference between this figure and the number of eggs placed on the plant, (*i.e.* those unaccounted for), was assumed to represent those first or second instar larvae that died during dispersal, from weather, pathogens or predators. This assumption is reasonable because dead instars above the second are unlikely to disintegrate over a long time span, and therefore can readily be observed upon dissection of stalks. Plants inside smaller cages were dissected for larvae on 27 August, while plants inside larger cages were examined 28 September.

C. Results

Dispersal After Hatching

Movement Patterns

Seven distinct patterns of movement by newly hatched larvae were identified from field trials (Fig. V-1). Three of these routes accounted for 74.2% of all travel (Table V-1), whereby larvae travelled down the midvein to the ligule on either the upper or lower leaf surfaces, or moved along the leaf edge. Larvae travelling by these routes reached the ligule in less time then larvae travelling by other routes (Table V-1).

The majority of larvae (71.4%) travelled to the upper leaf surface during a portion of their route. When larvae were first placed on the leaf, the initial direction of movement was also mainly upward (36.2%). 34.3% of larvae initially moved basally towards the ligule, 19.0% moved distally towards the leaf tip, while 15.2% initiated a circling pattern. Once larvae reached the upper leaf surface, they invariably travelled along the depression formed by the midvein, in a downward direction. If larvae entered this depression where the leaf drooped down towards the tip, then they usually followed the midvein to the leaf tip, and dropped off.

Larval Drop

The percentage of larvae falling off the leaf by means of a silken thread was related to the type of travel. Larval drop increased as the amount of time spent on the leaf edge increased. While those larvae that remained on the lower leaf (route 2) had the lowest rate of falling (3.7%), larvae that moved to the upper surface had higher drop rates (route 1=10%, route 7=14.3%). Drop rates for larvae which either remained on the leaf edge or repeatedly crossed it had still higher drop rates (route 3=33.3%, route 6=42.9%). 100% of larvae that travelled to the leaf tip (routes 4 and 5) fell off the leaf. A total of 24.8% of all larvae dropped off the leaf in field trials. In laboratory trials, the percentage of larvae which dropped to the ground (instead of to a lower leaf) was similar (t=-1.33, df=14, P=0.20) for both constant (11.9±6.73%) and variable (17.4±9.51%) regimes.

Mortality

Newly-hatched larvae were observed dying during dispersal in laboratory trials by dropping to the ground (see previous section), by dessicating (variable regime), or by drowning when they entered water droplets on leaves (constant regime). Mortality of first-instar larvae did not differ significantly (t=0.59, df=14, P=0.56) between constant (41.9±15.54%) and variable (36.2±22.40%) regimes. However, significantly more larvae (t=2.78, df=14, P=0.01) were found dead on leaves under the constant humidity regime (22.4±21.13%) than under the variable regime (1.3±2.94%).

This was likely because drowned larvae remained on the leaf, whereas dessicated larvae disintegrated. Despite precautions to observe the fate of all larvae, 12.9±8.73% of all larvae that hatched under a constant regime and 20.8±20.64% of larvae at a variable regime were missing at the end of the trials. These larvae were presumed dead, and included in the mortality counts.

Intraplant Dispersal

Larval Distribution and Colonization Rate

Distribution of newly-hatched larvae along nodes of artificial corn plants (Fig. V-2) was significantly different between temperature and humidity regimes (Rank-sum Test: $F=3.69$; $df=205,223$; $P<0.05$). After 7.5 DD, most larvae (56% at a constant RH and 38% at a variable RH) were still within the ninth ligule (which was the closest ligule to where eggs had been placed). Of those larvae that moved to other ligules, a greater percentage (53% to 78%) were found in food sites above the ninth ligule, even though there were less food sites above the ninth ligule than below it.

Field trials showed that frequency distribution of larvae along corn plant nodes was similar for the first four instars (Fig. V-3A), indicating that colonization was completed in the early instars. For these four instars, most larvae (17.0±3.16% of all larvae) were found on the fifth node. Slightly more larvae were found above the sixth node

than below it, and a large proportion of the total were found in the tassel during the first and second instars. Distribution of fifth-instar larvae along the plant varied over time (Fig. V-3B). Larvae moved towards the base of the plant between 300 and 500 DD.

The colonization rate for each plant node (*i.e.* (occupied/non-occupied+occupied)x100) was similar to the larval distribution along the plant (Fig. V-3A). Almost all tassels examined had been colonized by early instar larvae. Colonization of nodes (including leaves, ligules and ears) varied. Nodes in the centre of the plant were highly colonized, while those near the extremites were not.

Microhabitat Selection

Distribution of larvae within microhabitats in a corn plant varied depending upon larval development. First-instar larvae were fairly evenly distributed among the tassel buds, ligules, sheaths, and ear buds (Fig. V-4A, 1984 data only). Throughout the second and third instars, the proportion of larvae in the tassel buds decreased (Figs. V-4B,C). During the third instar, larvae began feeding in the stalk, while numbers of larvae in the ligule and sheath dropped (Fig. V-4C). Larvae stopped feeding in the ligule and sheath during the fourth instar, and the proportion of larvae in the cobs and stalk increased (Fig. V-4D). The percentage of larvae in stalks continued to increase during the fifth instar (Fig. V-4E), with a corresponding decline in larvae found in cobs. Numbers of larvae found in the leaves and

tassel were low and constant during the fourth and fifth instars. Larvae in the tassel were feeding in the pith, not in tassel buds. Larvae found in leaves were in the prepupal stage, seeking a refuge for metamorphosis.

The proportion of larvae in the ears and tassel appeared to fluctuate between 50 and 280 DD. Larval distribution data depended upon whether egg masses were placed either before or after the formation of ear buds (in the eary green tassel stage). When eggs were placed before ear buds appeared (Fig. V-5A, 1983 and 1984 data), then larvae fed in tassel buds, ligules, sheaths and leaves. However, when egg masses were placed after ear buds had formed, then a large proportion of young larvae moved to and fed on these ears (Fig. V-5B).

Inter-plant Dispersal

Larvae dispersed equally well in cages where leaves were tied (with no traps), or in cages with a trap around the centre plant (leaves not tied). The percentage of larvae found on plants other than the centre plant was equal (t=0.51, df=4, P=0.63) for cages with corn leaves tied (60.0±7.10%) and for cages with traps (63.1±7.29%). Larval survival was not significantly different (t=-0.27, df=4, P=0.80) for cages with corn leaves tied (39.6±9.42%) and for cages with traps (37.1±13.10%).

Only two larvae (instars two and four) were captured in glycol traps. For larvae to evade the traps, they would have

to crawl along a leaf and drop to the ground by a silken thread. Obviously, most larvae crawled further along a leaf than the 12 cm diameter of the trap, before they dropped.

Significant differences in larval survival were observed between cages placed along rows and cages placed between rows. Larval survival in cages along corn rows was 38.3±10.29%, while larval survival in cages across rows of corn (23.48±10.16%) was much lower (t=2.51, df=10, P=0.03). The amount of dispersal was equal for both groups of cages, because numbers of larvae remaining in the centre stalk were not significantly different between groups (t=0.53, df=10, P=0.61). 7.8±2.99 larvae (48% of all larvae found) were found in centre plants of cages along rows, while 6.8±3.55 larvae (60% of all larvae found) were found in centre plants of cages across rows.

For dispersal in cages along rows, larval density per corn plant decreased exponentially as the distance of travel from the centre plant increased (Fig. V-6). The polynomial regression equation describing this relationship accounted for 63.7% of the total variation. Larval counts in the large cages confirmed this dispersal trend (Fig. V-7). Most larvae moved along the centre row to infest new plants. By the end of September 1984, 83.7±2.18% of all larvae had left the original plant where eggs were placed, to disperse to new plants.

D. Discussion

Pyke *et al.* (1977) have defined three levels of insect foraging in the environment: the habitat, the patch (*i.e.* the microhabitat), and the food item. A 'patch' is a "spacial subunit of the foraging area in which aggregations of food items occur" (Hassel and Southwood 1978). A species' foraging pattern evolves by natural selection, which acts to minimize survival risks and to maximize nutrient gain from feeding (Hassel and Southwood 1978). Therefore, my examination of ECB foraging patterns focused on patch selection, and on survival risks during dispersal.

Dispersal After Hatching

Movement Patterns

My studies of ECB larval dispersal do not entirely support the statement by Huber *et al.* (1928) that ECB larvae are negatively geotropic. Although most larvae began crawling upward to the upper leaf surface, they then travelled downward to reach the ligule (Fig. V-1). Possibly larvae are not actually negatively geotropic, but rather are positively heliotropic.

Because larvae are positively thigmotropic (Huber *et al.* 1928), they preferred travel routes that led through folds or depressions in leaf tissue, such as convoluted leaf edges and the midvein. Larvae quickly travelled to the ligule to hide (Table V-1), without stopping to feed on the

leaf. This short exposure time on plant surfaces may explain why predation of ECB larvae (see Chapter VII) was low.

Larval Drop

The large percentage (24.8%) of newly hatched larvae which dropped off leaves during field trials, and the high proportion of larval drop in laboratory trials, suggests that this behaviour is a dispersal strategy in the ECB. Since artificial leaves in the laboratory were absolutely motionless, clearly larval drop was not due to leaf disturbance.

Is dropping off a leaf a successful strategy for larval survival? Because larvae are negatively geotrophic, they do not usually crawl downward. Dropping off leaves is the only means of dispersing to lower portions of the plant. In laboratory trials, numerous larvae were observed hanging from leaves. A large proportion of these newly-hatched larvae dropped to the ground instead of to a lower leaf. Only 48.6±28.06% (N=174 larvae, 16 artificial plants) of all larvae that dropped actually landed on a lower leaf. Those larvae which fall to the ground in the field would almost certainly die, since it is unlikely that small larvae could crawl back to safety.

This wandering behaviour of first-instar larvae may be advantageous because of changes in the spatial-temporal distribution of resources on the corn plant. Corn grows rapidly, and a new patch (such as ear buds) may become available to larvae within days. Because early-instar larvae

have a great range of food items, some of which are preferred (see next section), exploratory behaviour may improve foraging efficiency.

Mortality

My observations of larval mortality during dispersal in laboratory trials confirmed field observations of Huber *et al.* (1928) that newly hatched larvae are very susceptible to drowning and dessication. In field trials, average mortality over all larval instars was 64.2% (see Chapter VII). Laboratory results suggest that most of this mortality (39.0±18.85%) occurred within the first 7.5 DD of hatching.

Intra-plant Dispersal

Larval Distribution and Colonization Rate

Observations of ECB dispersal suggest that newly-hatched larvae first disperse to food sources that are closest to the leaf where eggs were laid, and that they only disperse to other food items when populations exceed the available food supply. For example, in laboratory trials artificial medium remained in good condition at a humidity regime of 98% RH, and larval density in the ninth node was high (13.5). Under the variable humidity regime, however, medium began to dry out and larval density in the ninth node dropped to 8.1, because of larval dispersal to other nodes (Fig. V-2).

According to foraging theory (Pyke *et al.* 1977), the attractiveness of a resource decreases as dispersal distance increases, because of increased danger from predators. Thus larval density per node should decrease in proportion to the distance separating that node from the egg mass. Laboratory (Fig. V-2) and field data (Fig. V-3A) did show that the preferred patches were those closest to where eggs were deposited, since larval densities were highest in these sites. Because ECB moths lay most egg masses on the sixth (Huber *et al.* 1928) or seventh leaves (see Chapter VI), it is reasonable to expect the mid-section of the corn plant to be the most highly colonized.

However, field trials demonstrated a 92% colonization rate of the tassel, which is at the extremity of the plant, in comparison to lower colonization rates of the nodes below it. Clearly the tassel buds are a food item that is preferred over the nodes of the upper leaves. Protected from predators and insecticides within the tassel buds, the larvae remained there until the third instar, at which time they burrowed into the stalk (Fig. V-4C).

Distribution of first- to fourth-instar larvae also depended upon the growth stage of the corn plant. When eggs were placed before cob formation, many larvae fed in tassel buds (Fig. V-5A). However, when eggs were placed after cob formation, over twice as many larvae were seen in cobs than in the tassel (Fig. V-5B), possibly because larvae encountered cobs before tassel buds while wandering. Beard

and Turner (1942) also observed that although both tassel and ear buds were very attractive to ECB larvae, attractiveness of tassel buds dropped sharply in the late green whorl stage. My studies showed that numbers of early-instar larvae in the tassel decreased dramatically after 188 DD (Fig. V-5A), when pollen shedding began.

Observed larval distributions were likely maintained by territoriality. Feeding territorities are established when larvae spin webs around the food item (Huber *et al.* 1928). Once feeding territories were established, ECB larvae usually remained there until the third instar, when they then bored into the stalk. When eggs were placed before cob formation (Fig. V-5A), larval density on cobs remained low during the early instars, even though this resource was underutilized.

Microhabitat Selection

Resource utilization graphs (Figs. V-4A-E) demonstrated that different larval instars fed in different microhabitats. First and second instars did not feed in stalks, and fourth and fifth instars did not feed in tassel buds and ligules. Early-instar larvae fed on a wider range of food items than did the later instars. Foraging behaviour of early-instar larvae was "opportunistic" (Rosenzweig 1981), because they fed in all available microhabitats. Although the leaves were less utilized than other habitats, this was likely due to lateness of planting dates in Alberta. In Iowa, first-generation ECB larvae begin feeding

mainly on leaves (Guthrie *et al.* 1960).

The cob was the only habitat shared by all instars. However, different instars fed in different areas within the cob. Fourth and fifth instars fed in the core and in kernels, while early-instar larvae fed on the soft inner leaves and silks.

Differences in habitat choice were likely because diets of early and late-instar larvae were different. Early-instar larvae feed on pollen (Guthrie *et al.* 1969), on plant parts with high concentrations of embryonic or dividing tissue, such as in leaves, tassel or ear buds, or in ligules and sheaths, where elongation of leaves and stems occurs. These soft tissues are easily masticated, and they are rich in amino acids and nitrogen, which favour insect survival (Kimmins 1971). Late-instar larvae feed in stalk pith and in cobs, which have large amounts of roughage and glucose.

Interplant Dispersal

Mature diapausing larvae dispersed towards the base of stalks and roots (Fig. V-3B), where winter snowcover lessens injury from freezing (see Chapter VII). Diapause sites for the ECB, as with most insects, are different from feeding sites (Southwood 1978). In Alberta, many larvae even overwinter underground in the roots (see Chapter VII). Huber *et al.* (1928) found 60%-90% of all larvae to be below 61 cm in stalks by October. Dispersal behaviour is likely 'triggered' (Hassel and Southwood 1978) by changing

photoperiod.

Lower larval survival rates (39% lower) in cages across rows of corn than in cages along rows suggests that predators such as ground beetles and spiders prey upon larvae which disperse over ground. Previous references to predatory ground beetles (Sparks *et al.* 1966) and spiders (Barber 1926) have not measured their influence on larval survival.

Mature larvae disperse during the night for distances up to six metres (Barber 1924). Migration also occurs (Hassel and Southwood 1978) when larvae leave the corn habitat to overwinter in bordering vegetation (Barber 1924). In Alberta, larvae dispersing from a partially plowed corn field overwintered in Showy Sunflower (*Helianthus annuus* L.).

Model for ECB Larval Dispersal

ECB larval dispersal is summarized by a flow diagram (Fig. V-8). The first major dispersal decision occurs just after hatching, when the larva searches for a hiding place to "satisfy it's tropisms" (Huber *et al.* 1928). A second dispersal choice occurs as larvae define their territories on different patches within the corn plant. Finally, larvae disperse within the corn habitat, or migrate outside it, when diapause begins. For non-diapausing generations, mature larvae spin a hibernaculum within a protected spot, in the stalk, a cob, or on a nearby leaf. I suggest that these

three critical paths in the dispersal process have adaptive value, which minimize survival risks and maximize nutrient gain from feeding.

Table V-1. Movement patterns, travel time, and % of first-instar larvae using each movement pattern. Refer to Figure V-1 for illustration of movement pattern

Route or Movement Pattern	Sample Size	Travel Time (seconds)	% of Larvae
1. Crawls to upper leaf surface, then down midvein to ligule	35	15.8±8.53 a[1]	37.1%
2. Crawls along lower leaf surface to ligule.	27	17.4±10.13 ab	25.7%
3. Crawls to leaf edge, and walks along edge to ligule.	12	15.3±7.12 a	11.4%
4. Crawls along lower leaf surface to leaf tip.	5	22.2±15.96 ab	4.8%
5. Crawls to upper leaf surface, then down midvein to leaf tip.	8	27.3±12.12 b	7.6%
6. Crawls to upper leaf surface, then to lower surface and walks to ligule	7	24.2±9.70 b	6.7%
7. Crawls to upper leaf surface, then down midvein towards tip; then reverses direction and walks to ligule.	7	22.3±6.68 ab	6.7%

[1]Means with different letters are significantly different from each other at $P<0.05$, using Sheffe's Test

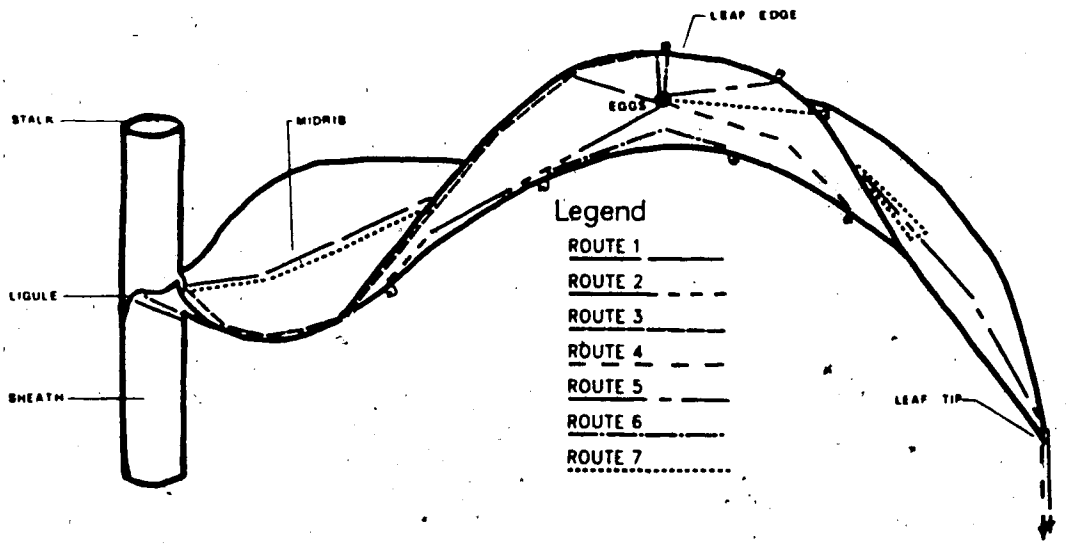

Figure V-1. Movement patterns of newly hatched larvae. For description of routes, see Table V-1.

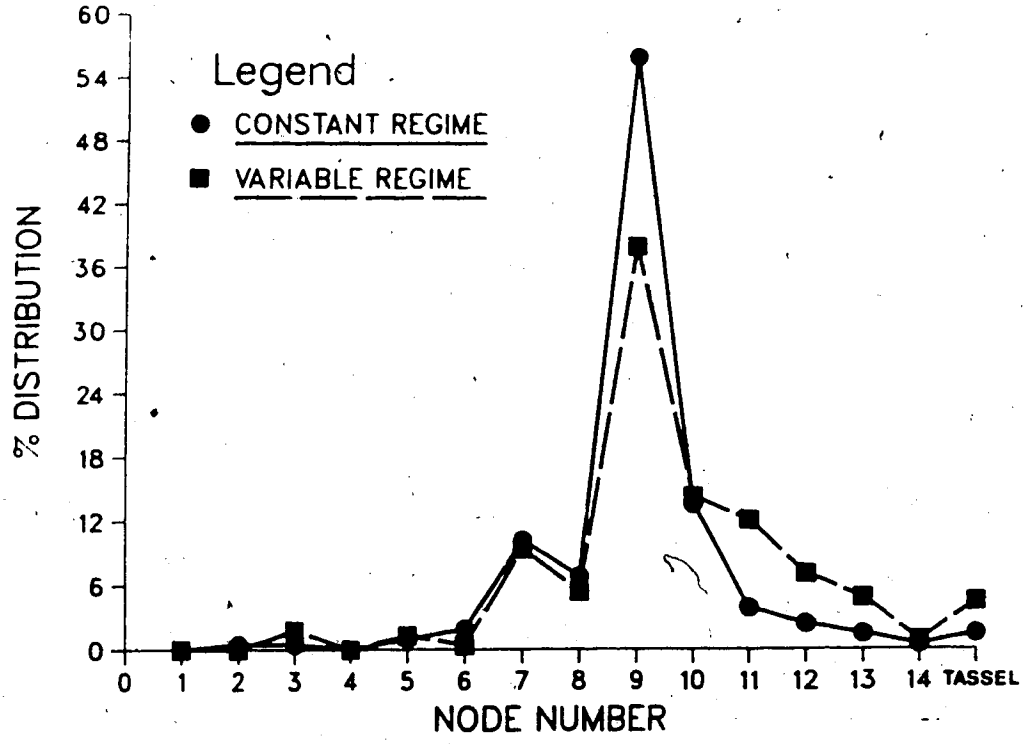

Figure V-2. Frequency distribution of first-instar larvae along food sites (nodes) of artificial corn plants during laboratory trials, after 7.5 degree-days (DD).

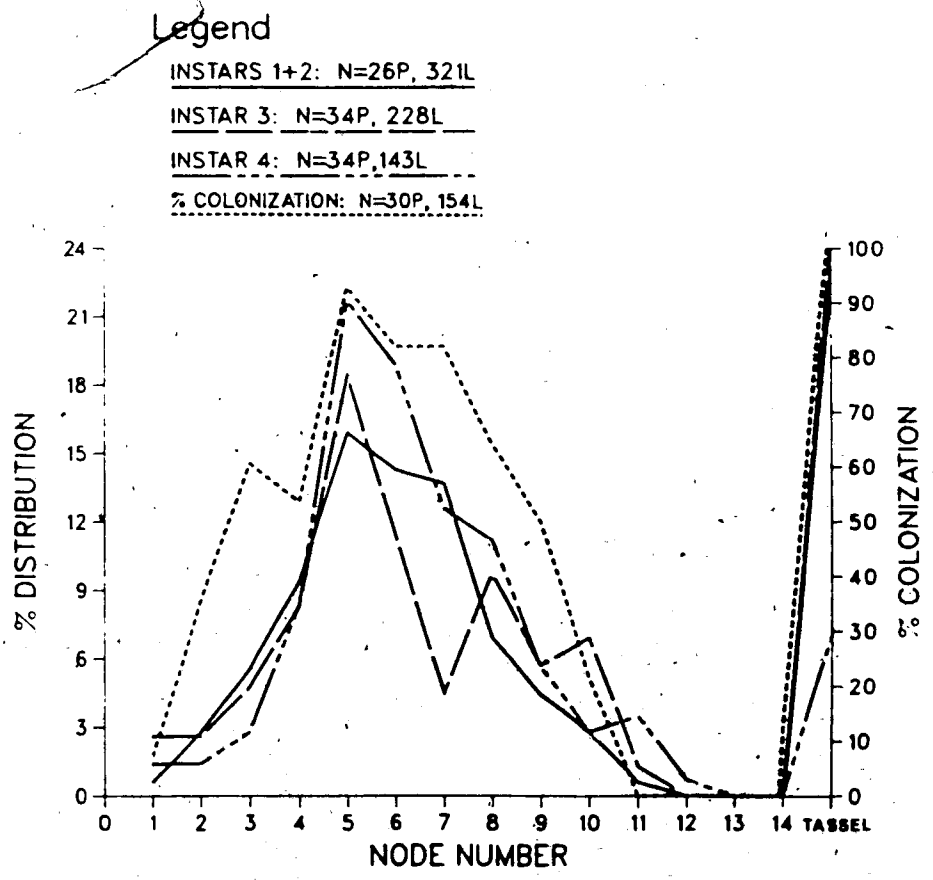

Figure V-3A. Frequency distribution of first to fourth-instar larvae (left-hand side of graph), plotted for each node of corn plants dissected in 1984 field trials. The colonization rate per corn plant node (right-hand side of graph) is also plotted. Abbreviations: N=sample size; P=#plants; L=#larvae.

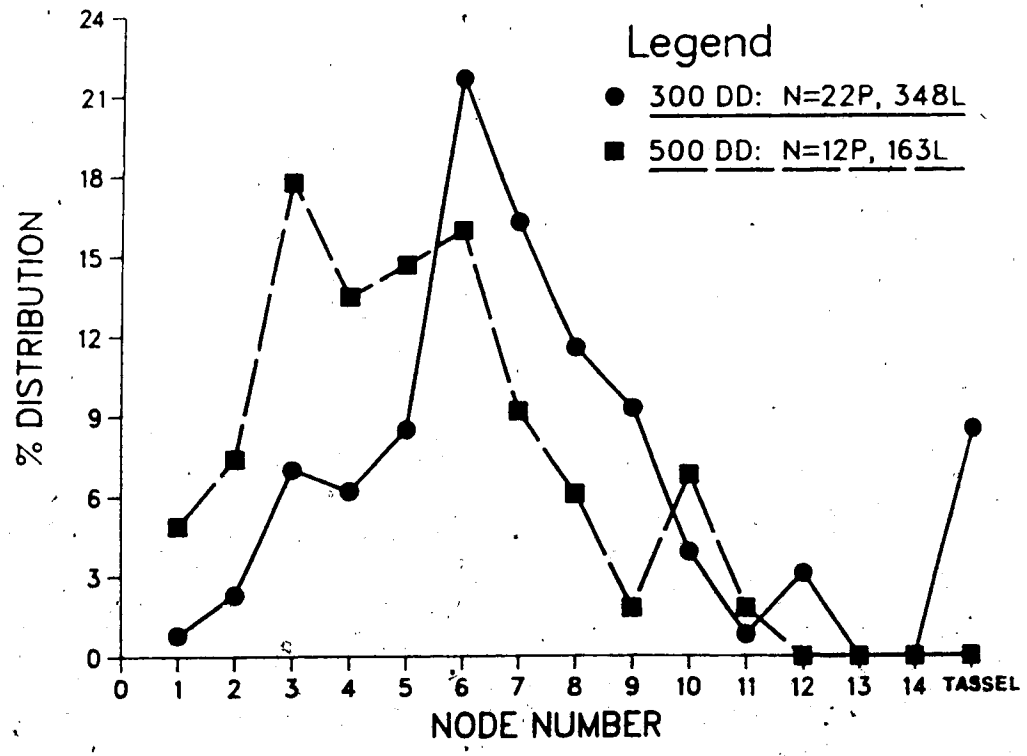

Figure V-3B. Frequency distribution of fifth-instar larvae, plotted for each node of corn plants dissected in 1984 field trials. Degree-days (DD) were calculated using a lower threshold of 11.9°C.

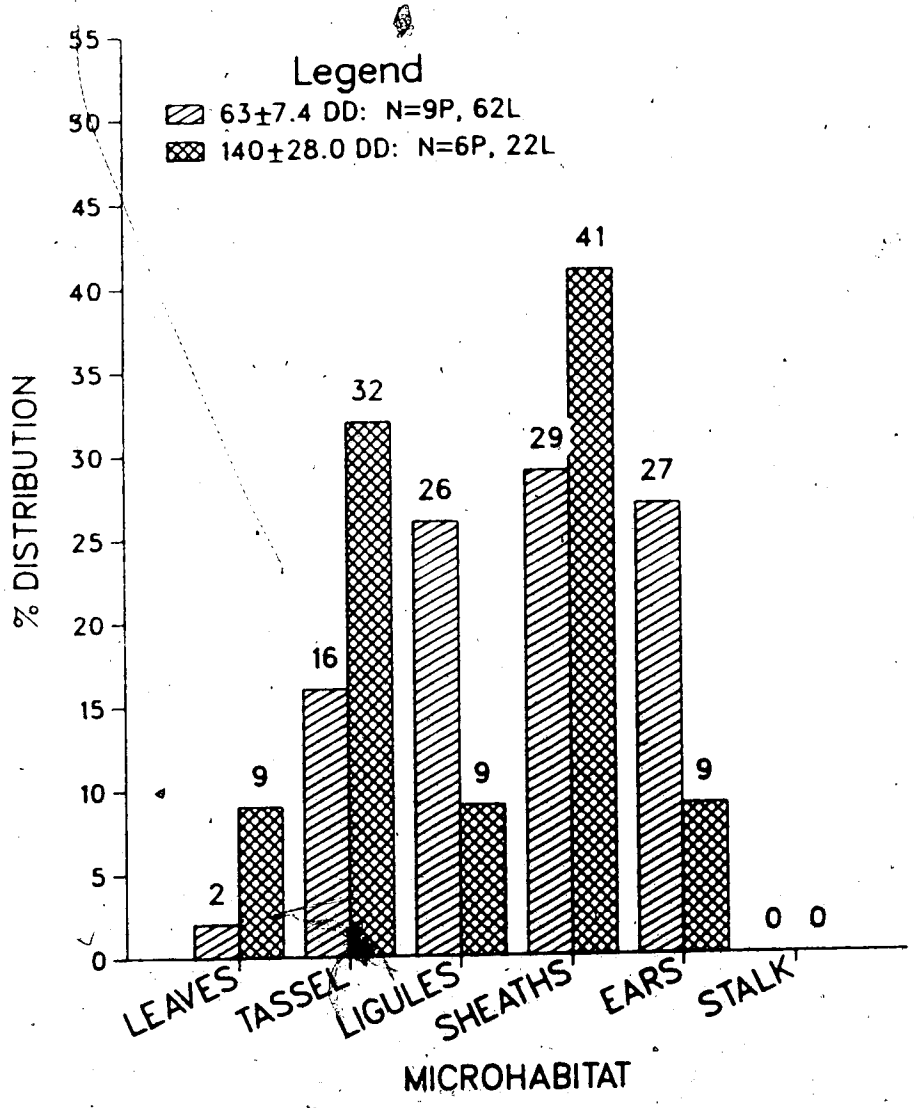

Figure V-4A. Frequency distribution of first-instar larvae in microhabitats of a corn plant during 1984 field trials. A lower threshold of 11.5°C was used to calculate DD. Abbreviations as in Figs. V-3A,B.

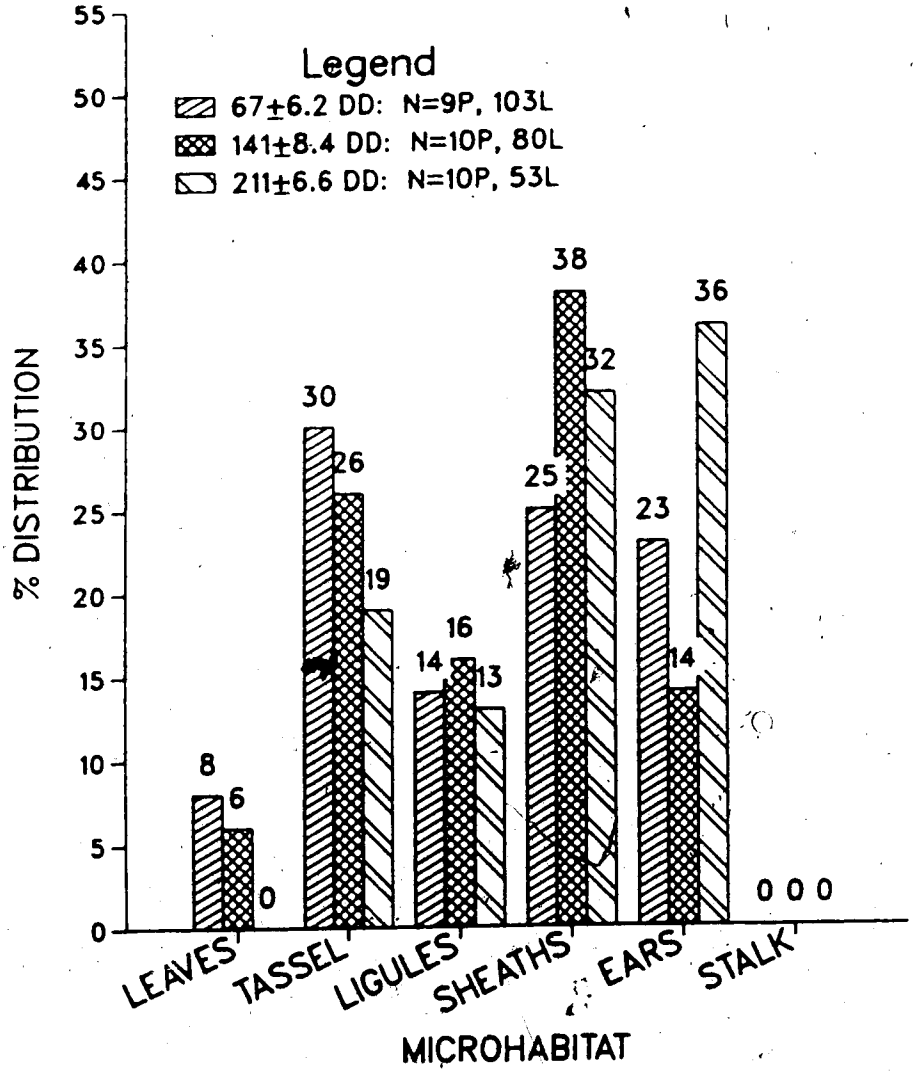

Figure V-4B. Frequency distribution of second-instar larvae in microhabitats of a corn plant during 1984 field trials. A lower threshold of 10.2°C was used to calculate DD. Abbreviations as in Figs. V-3A,B.

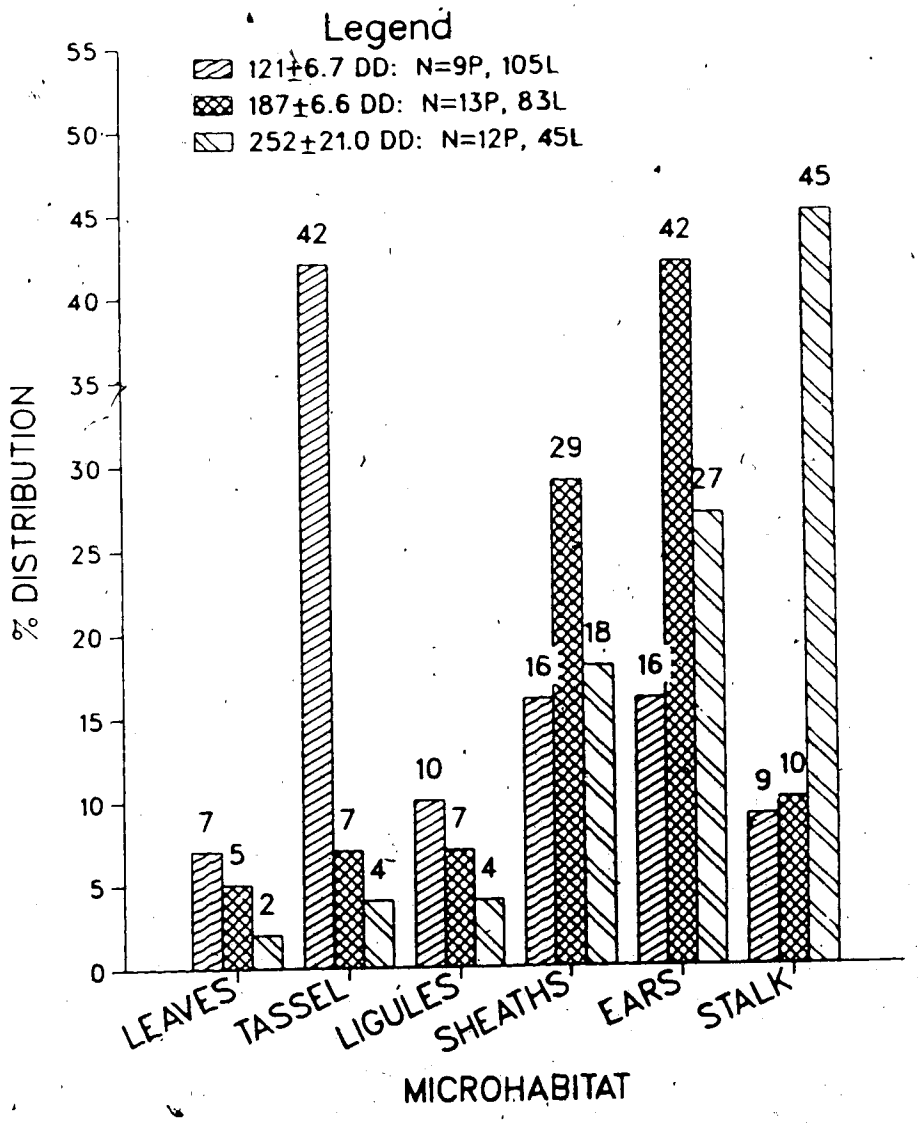

Figure V-4C. Frequency distribution of third-instar larvae in microhabitats of a corn plant during 1984 field trials. A lower threshold of 11.9°C was used to calculate DD. Abbreviations as in Figs. V-3A,B.

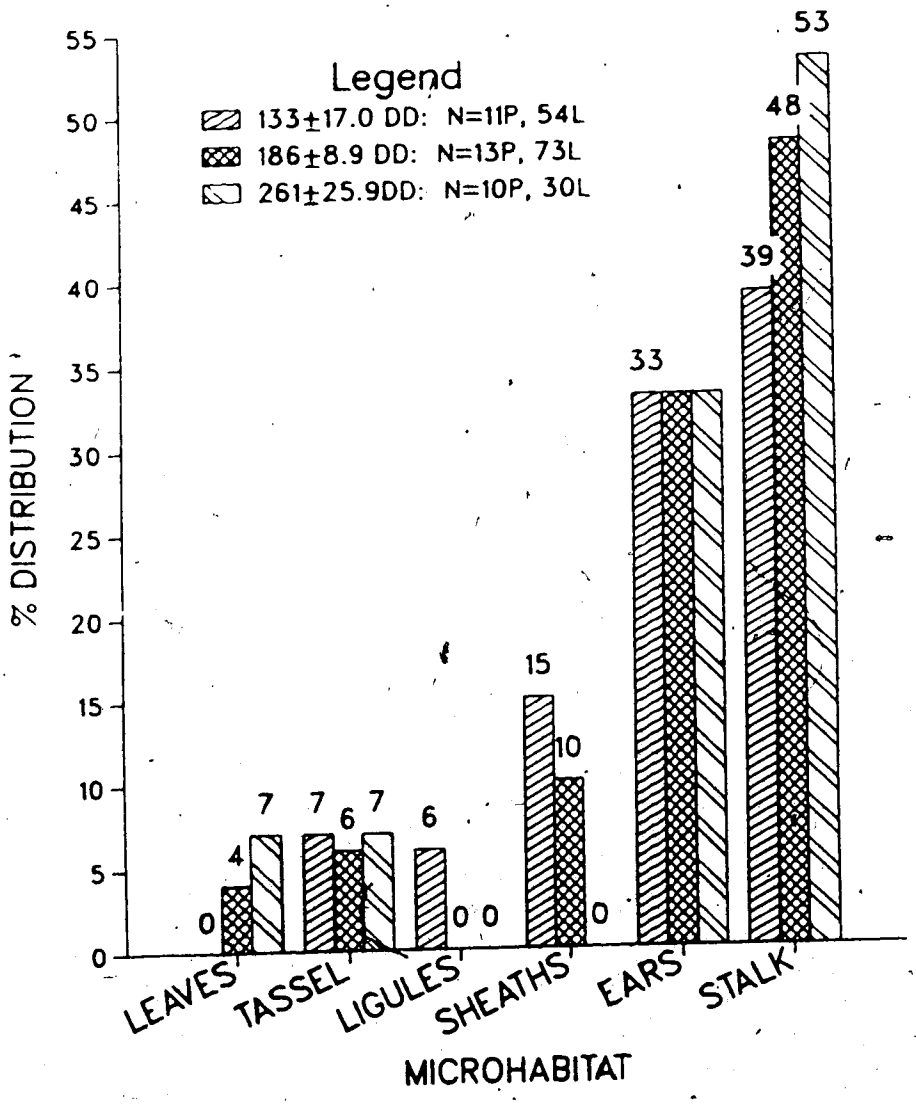

Figure V-4D. Frequency distribution of fourth-instar larvae in microhabitats of a corn plant during 1984 field trials. A lower threshold of 15.3°C was used to calculate DD. Abbreviations as in Figs. V-3A,B.

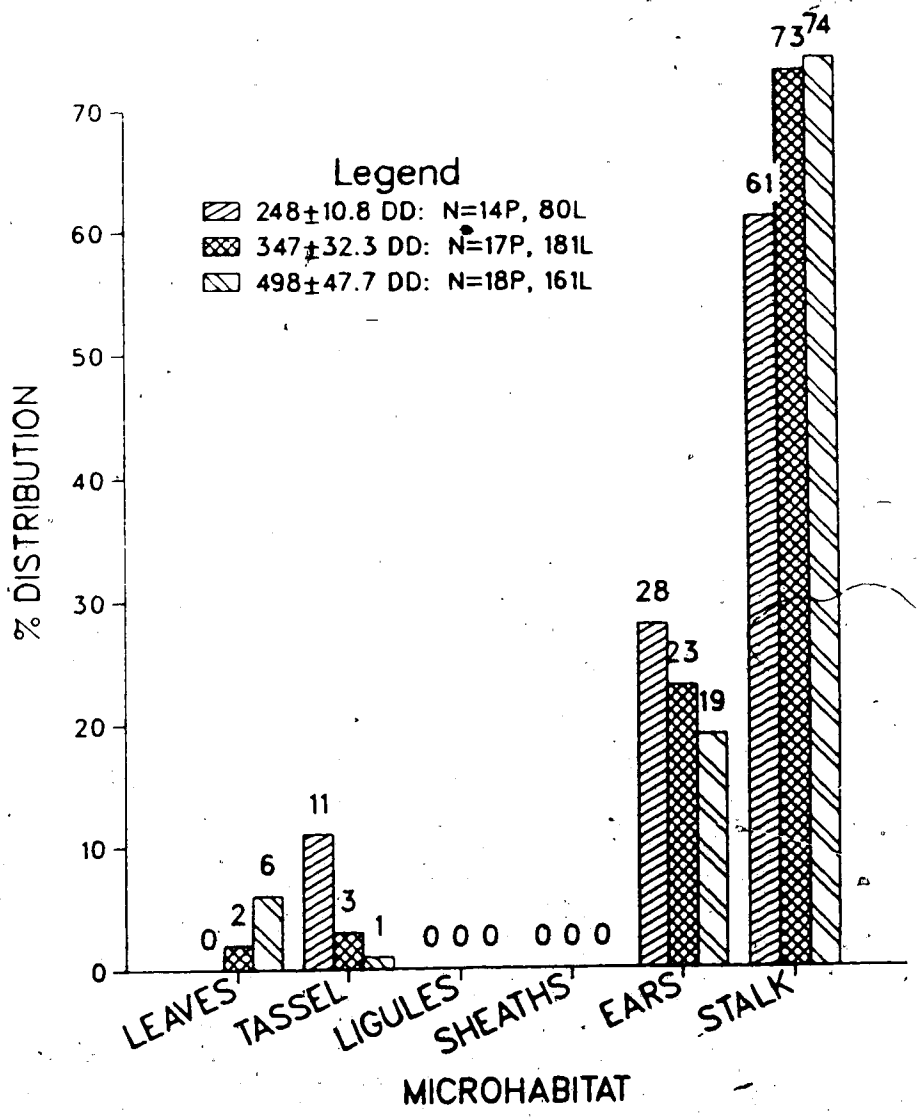

Figure V-4E. Frequency distribution of fifth-instar larvae in microhabitats of a corn plant during 1984 field trials. A lower threshold of 11.9°C was used to calculate DD. Abbreviations as in Figs. V-3A,B.

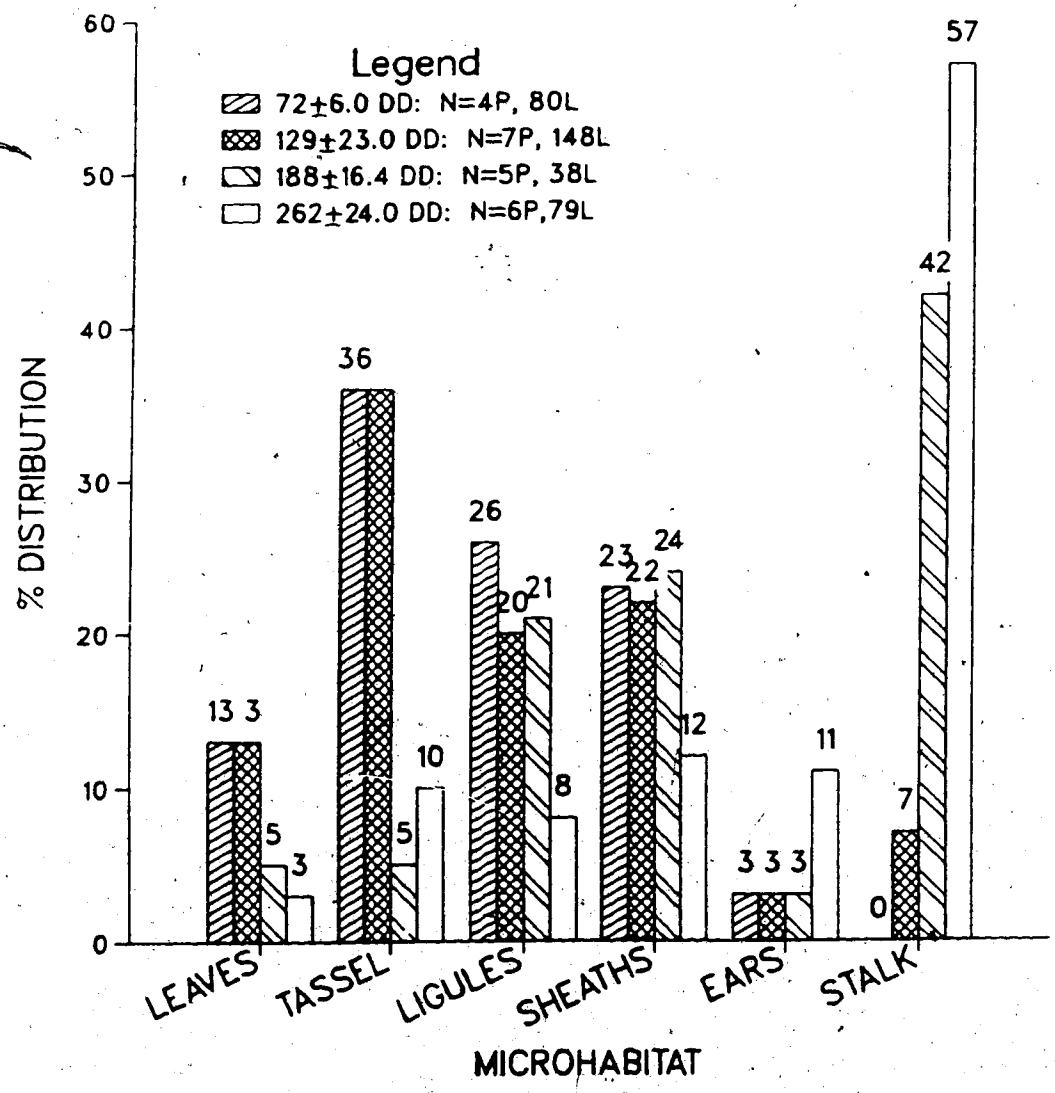

Figure V-5A. Frequency distribution of larval instars in microhabitats of a corn plant, when larvae hatched before ear buds appeared. Data was combined from 1983 and 1984 field trials. A common lower temperature threshold of 10°C was used to calculate DD. Abbreviations as in Figs. V-3A,B.

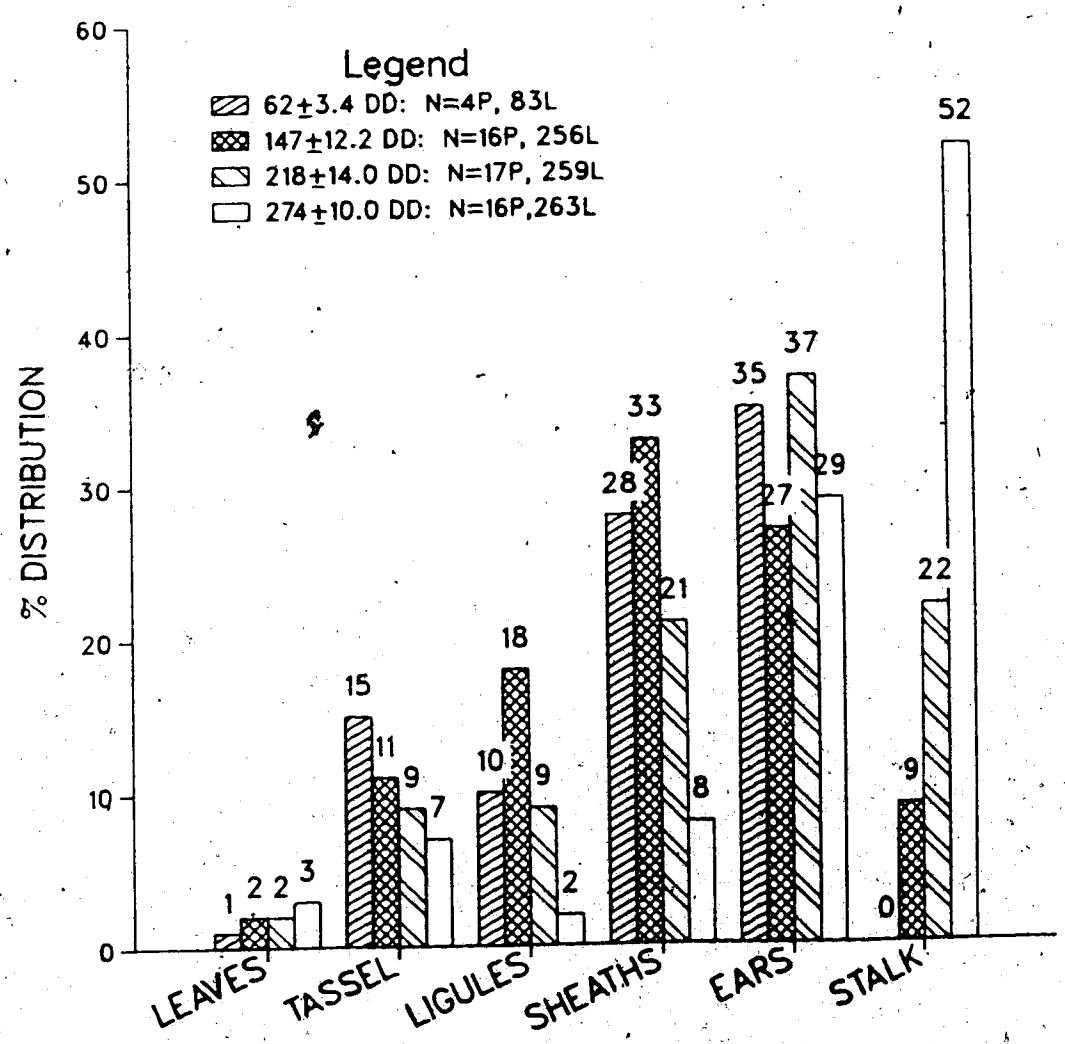

Figure V-5B. Frequency distribution of larvae in microhabitats of a corn plant, when larvae hatched after ear buds appeared. Data was combined from 1983 and 1984 field trials. A common lower temperature threshold of 10°C was used to calculate DD. Abbreviations as in Figs. V-3A,B.

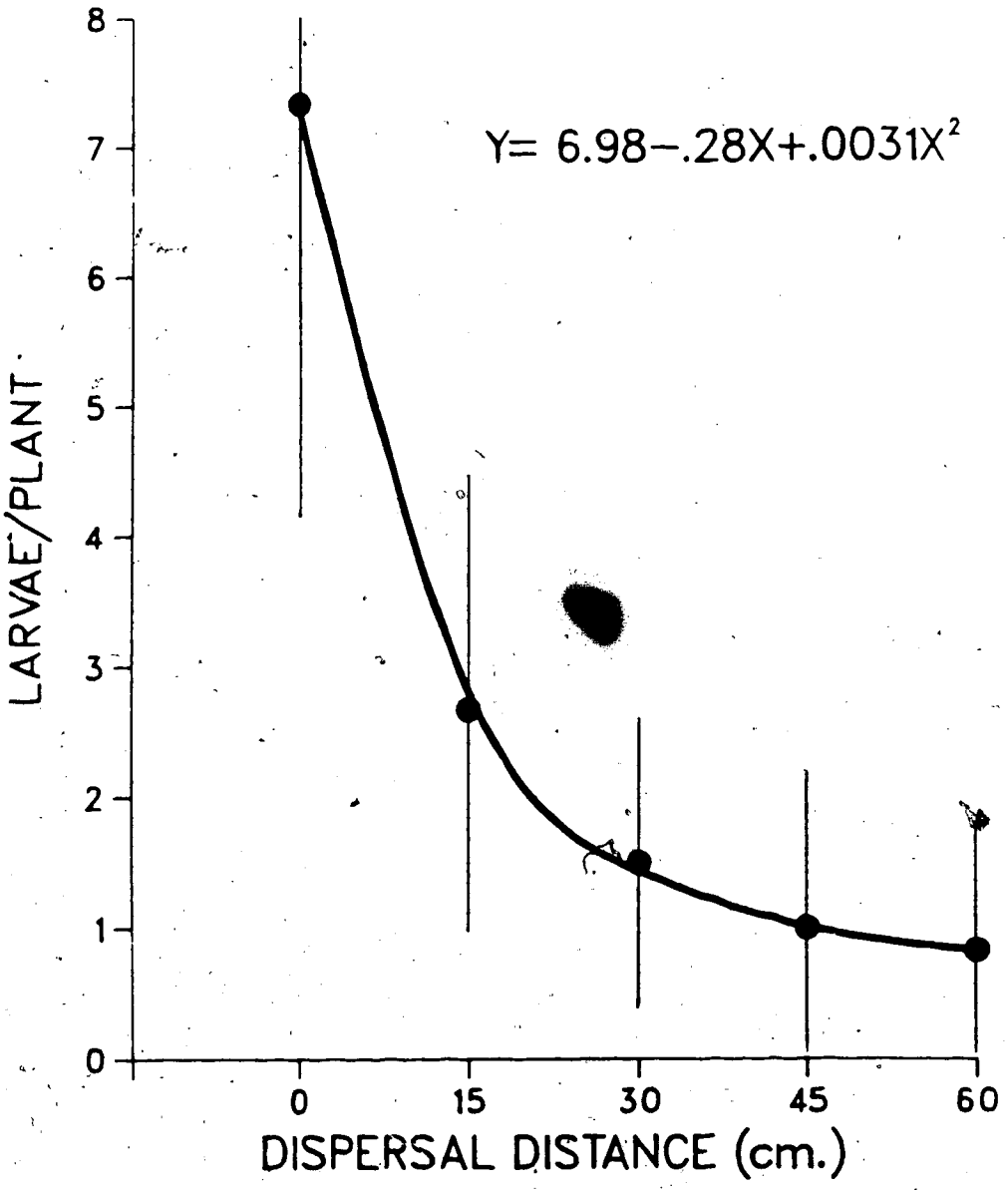

Figure V-6. Larval density (#larvae/plant) in relation to the distance larvae dispersed from the centre plant, where eggs were placed. Data taken for cages along rows.

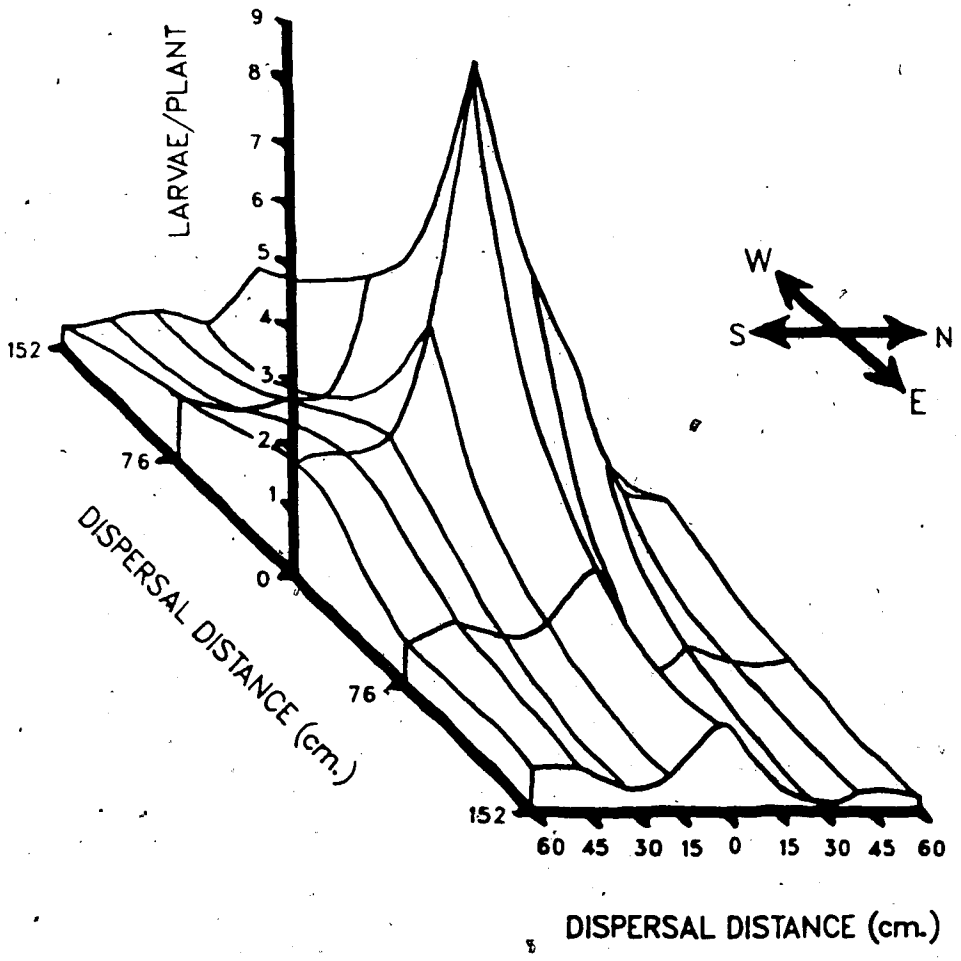

Figure V-7. Larval counts per plant in large cages, with 60 eggs placed on centre plant. Results presented as an average of four trials. Rows were spaced 76 cm apart; plants in a row were spaced *ca.* 15 cm apart.

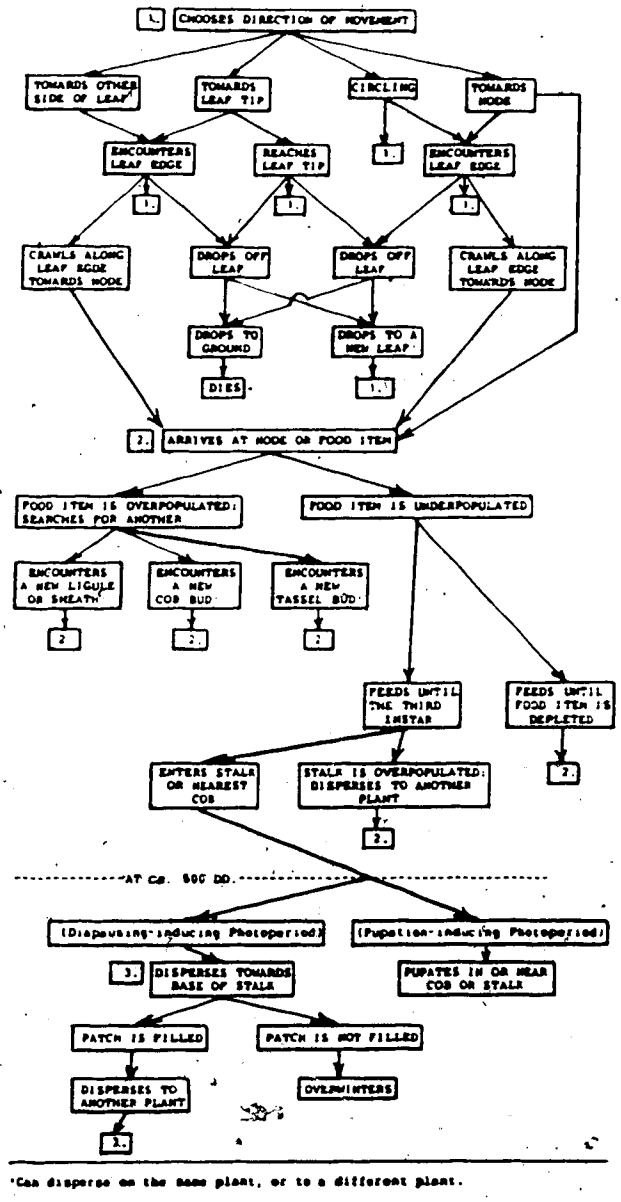

Figure V-8. Flow diagram for modelling ECB larval dispersal. Decisions during phase 1 (top) occur just after hatching. Decisions during phase 2 (centre) occur during larval growth, and during phase 3 (bottom) when larvae are mature.

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VI. MOTH DENSITY AND OVIPOSITION PATTERNS

A. Introduction

Adult European corn borer (ECB) moths are known to aggregate in patches of dense vegetation. Showers *et al.* (1976) reported that most sexual activity occurs up to 100m from the nearest cornfield, in areas of dense foxtailgrass. DeRozari *et al.* (1977) found that the presence of free water in the form of dew or rain is a prerequisite for sexual activity, and that high amounts of dew on dense foxtailgrass contributed to the aggregation of ECB moths in these "action sites". Treatment of dense grasses bordering cornfields with carbaryl significantly reduced ECB egg-laying within the cornfield (Showers *et al.* 1980).

Climatic conditions and native vegetation in southeastern Alberta, where the ECB has recently become established (Lilly and Harper 1982), differ considerably from Iowa where studies of moth aggregation have been conducted. While southeastern Alberta has a dry steppe climate, the climate of Iowa is that of humid-and-warm summers (Muller 1982; after C. Troll and K. H. Paffen). Vegetation also differs between the two regions. Southeastern Alberta is dominated by perennial grasses, interspersed with low annual or root-perennial plants. Iowa is within the grassland-deciduous forest transition zone (Livingstone and Shreve 1921).

Because Alberta ECB moths inhabit a different natural environment than do those in Iowa, I hypothesized that action sites and areas of oviposition within corn fields would also differ. Monitoring of moths and oviposition sampling demonstrated greater moth density and oviposition in the centre of Alberta corn fields, rather than near the edges.

B. Materials and Methods

ECB Moth Density

Population density of male moths was monitored with commercial pheromone traps (Pherocon® 1-C traps by Zoecon Corp.) containing a 97%(Z)+3%(E) mixture of 11-tetradecenylacetate, which was impregnated in a rubber dispensor cap (also supplied by Zoecon Corp.). ECB populations in the mid-western United States possess pheromones of this isomer ratio (Klun *et al*. 1975), and Alberta populations also have this pheromone type (D.L. Struble, personal communication). Preliminary trials (see Appendix 4) indicated that maximum trap captures were obtained by placing the dispensor in the sticky glue (as recommended by Fletcher-Howell 1983), and by changing both the dispensor and trap every 2-4 days (as recommended by McLeod and Starratt 1978).

Two types of trials were used to examine differences in moth captures between the edges and the centre of corn

fields. In 1983, eight traps were set up in a grid pattern at the corner of a silage corn field (Fig. VI-1A). Four traps located along the field edges were spaced 100m apart. Four traps inside the field were 100m apart from each other, and at least 100m away from the field edges. One of the field edges was bordered by alfalfa, and the other was bordered by summerfallow. Both traps and dispensors were replaced every 2-4 days from July 17 to Aug. 10. Adult males captured were counted every 2 days. Traps were hung just below crop height from cross-braces attached to wooden posts. The braces were moved up the posts as the corn grew.

In 1984 traps were placed in field corn along two separate test lines that ran in a north-south direction. Ten traps were placed 40m apart along a service road to the pivot in the field centre. The trap close to the edge of the field was *ca.* 150m inside the field. Ten traps similarly were positioned along the edge of the field, 500m east of the service road. The field was bordered by native grasses. Every three days captured moths were counted and all traps were replaced. Three traps at the edge were later excluded from the dataset, because the pivot did not irrigate there and the corn plants died.

To examine moth abundance in habitats within the centre of corn fields, traps were set up in 1984 for a 4-day period in a separate field, in stands of dense corn, in thin stands of corn, and in areas of thick green foxtail (*Setaria viridis*) weeds. Traps were placed *ca.* 30m apart, close to a

service road leading to the pivot in the field centre.

For trials conducted in 1984, live females were used as well as pheromone dispensors. A newly emerged virgin female was placed inside a small screen cage (5cm x 3cm x 2cm), which was then placed in the sticky glue in the centre of a Pherocon® trap. The cage contained a food dispensor with 10% sugar solution. Live females or pheromone dispensors were randomly allocated to trap sites.

Density of both male and female ECB moths within daytime resting sites was monitored in 1984 (between 0700 and 1300 MST) by the flush bar technique (Sappington and Showers 1983a,b), whereby vegetation was disturbed with a 1m-long bar, causing moths to fly and thus be counted. Counts were taken during oviposition sampling (see below), and were recorded as numbers of moths flushed per 100 corn plants while walking between two rows.

Oviposition

Egg-laying was monitored in 1984, on a heavily-infested quarter-section within 1 km of the field where pheromone traps were located. The field was divided into six zones running east-west: two on the outside edges of the field, two in the centre and two intermediate zones (Fig. VI-1B). Each zone was 176 rows of corn in width, and about one third of the size of the field in length. Only the centre portion of the field was sampled, because corn plants in the corners were impoverished due to lack of water from the pivot

irrigation system. Egg sampling procedure ensured random allocation of effort among rows and among plants within a row. On each sampling day three rows were sampled from each zone, and 30 plants were sampled from each row. At each of the ten randomly-chosen sampling sites per zone, nine plants per sampling site were checked for egg masses: 3 adjacent plants in the sample row, and 3 adjacent plants in each row on either side of the sample row. All leaves and stems of corn plants were carefully examined. A total of five samples were taken, about every 5 days from 11 July to 14 August. Each sampling site was rated (before the sample was taken) comparatively as to corn density and weediness, on a scale of 1-5. Sites in the field with healthy plants showing the greatest height and development received the highest corn density rating of five. Similarly, higher weediness ratings were given to sites with weeds of greater height and density relative to other sites in the field.

Egg masses found were described as to their position on the leaf (top or bottom surface), and to their relative position on the plant. The number of eggs per field-laid mass was compared to egg mass size for a laboratory colony reared at room temperature (20°C).

C. RESULTS

Pheromone traps in the field centre captured significantly more moths than did those placed near field edges, in both 1983 and 1984 (Table VI-1). For 1983, the two

traps placed on the border with summerfallow were not included in the dataset, because no moths were caught in these traps. Within the field centre in 1984, trap captures also varied significantly between different habitats (Table VI-1). Greatest captures were recorded in traps placed in weeds (mainly *Setaria* sp.).

Numbers of moths flushed and egg masses found also varied significantly between zones (Table VI-1), with progressively more eggs and resting moths found from the edge to the centre zones. Numbers of egg masses per sample site increased exponentially with corn density (Fig. VI-2). The polynomial regression equation describing this relationship accounted for 44% of the variation in egg-laying patterns. The correlation between corn stand density and oviposition was positive and significant (r=0.637; df=1,178; P<0.01). The linear regression describing the relationship between weediness and oviposition (Fig. VI-2) explained only 17% of the variability in egg-laying (r=-0.412; df=1,178; P<0.01). Corn stand density and weediness were negatively correlated (r=-0.573; df=1,178; P<0.01).

Eggs sampled on 19 and 21 July 1984 were found on leaves 3-13 (n=90 egg masses). More eggs were found on the seventh leaf than on any other, and 95% of all eggs were found on leaves 5-9. The mean distance from the egg mass to the whorl was 18.4±10.05 cm (range=1.3-45.7 cm, N=90 masses). Only 4.4±0.66% of all egg masses (n=4 sample dates,

319 plants) were found on the top surface of leaves. 11.5±5.23% of all eggs (n=5 samples, 347 plants) were laid on tiller leaves rather than on leaves from the main stalk. 2.3±1.70% of all eggs were found with another egg mass on the same leaf, and 10.5±3.54% of masses were found with one or more egg masses on the same plant (n=5 samples, 347 plants). The mean number of eggs in a field-laid mass (19.3±10.68, n=136 egg masses) was similar to the mean number of eggs/mass in laboratory-laid eggs (21.6±13.49, n=71; see Chapter IV).

D. Discussion

Pheromone trap trials demonstrated that ECB males were more abundant in the centre of corn fields than at field borders. This same trend occurred for both male and female adults resting during the day, and for female oviposition within the corn field. As Sappington and Showers (1983a) have pointed out however, a major requirement in interpreting data is to separate the effects of population abundance and activity. To accurately define ECB moth activity would require nightly monitoring of both males and females at several sites within a cornfield (*cf.* Sappington and Showers 1983).

Although I have not used these methods, I argue that for ECB populations in the Alberta environment, population abundance is a strong indicator of actual flight activity. Southern Alberta, with a semi-desert environment, has few

patches of natural vegetation outside the cornfield (within 100m) that are tall enough (57.5-117.5 cm) and dense enough (covering 45% of surface, and over 5 m wide) to provide high humidity and retain free water which the adults require (Showers *et al.* 1976, 1980; deRozari *et al.* 1977, Sappington and Showers 1983b). Corn, on the other hand, is a crop with high evapotranspiration of *ca.* 500mm/season (Alberta Corn Committee 1982). Moreover, infestation of cornfields with *Setaria* weeds is a common problem in southern Alberta. In addition, many Alberta farmers leave crop margins fallow to prevent grasshopper infestations. Waterways are often concrete-lined, which prevents water loss and subsequent weed growth. Therefore I propose that most Alberta ECB moths aggregate in "action sites" within the cornfield. This contention is supported by pheromone trap counts which show that within a cornfield, highest numbers of males were found in weeds and in dense stands of corn (Table 4-1). Showers *et al.* (1980) found a high correlation between daytime population densities of adult ECB in *Setaria* weeds and ECB egg masses laid in nearby corn.

Because ECB oviposition data has not previously been collected according to zones within a field, egg-laying patterns of Alberta ECB could not be compared in this respect with those elsewhere. However, the percentage of eggs laid on upper leaf surfaces was similar to that (6.3%) noted by Stirrett (1933). My results were also similar to those of Huber *et al.* (1928), who found that most eggs were

laid close to the sixth leaf. The strong positive correlation between corn stand density and egg masses found suggests that female ECB selectively oviposit in dense, healthy corn stands. Everett *et al.* (1958) have also noted that infestation levels were related to corn maturity at the time of ECB flight. It is not surprising that corn stand density was negatively correlated with weed density, because corn stands with more weeds are not able to compete as effectively for nutrients, and are thus likely to be less healthy than weed-free stands.

These results suggest that more effective management of ECB in Alberta would be obtained by spraying for early instar larvae within the field (Clement *et al.* 1981), than by spraying for moths along the field edges.

Table VI-1. Means for each treatment.

Comparison	Site	Sample Size	Mean	SD	ANOVA df	ANOVA Mean Sq.	ANOVA F	ANOVA P
A. Pheromone Trap Trials								
Edge vs. Centre 1983	Edge	16	0.31	0.479	1	0.417	12.38	0.001*
	Centre	32	1.81	1.874	45	0.036		
Edge vs. Centre 1984	Edge	43	2.5	3.60	1	36.702	24.08	0.0001*
	Centre	55	11.1	12.46	96	1.524		
Field Centre 1984	Thin Stands of Corn	20	1.00a*	1.717	2	20.545	27.28	0.0001*
	Dense Stands of Corn	9	5.78b	5.805	34	0.753		
	Weeds Between Rows	8	14.13c	8.626				
B. Flush Bar Sampling								
Areas in Field	Edge Zones	8	0.83a*	0.544	2	5.816	7.10	0.044*
	Intermediate Zones	8	3.28bc	3.948	21	0.819		
	Centre Zones	8	5.21c	4.231				
C. Oviposition Sampling								
Areas in Field	Edge Zones	10	4.90a*	3.381	2	5.495	3.96	0.031*
	Intermediate Zones	10	10.80ab	8.483	27	1.389		
	Centre Zones	10	14.60b	11.711				

'For pheromone trap trials, N=(#traps)x(#times traps checked) . For flush bar and oviposition sampling, N=(#zones)x(#dates sampled). 90 plants/zone were sampled each sample date.

'For pheromone trap trials, mean=(#moths)/trap/examination.
For flush bar sampling, mean=(#moths flushed)/100 plants
For oviposition sampling, mean=(#egg masses)/90 plants.

'Test performed after data was transformed to a normal distribution'

'Test performed after data was transformed: log(X+0.5)

'Test performed after data was transformed: sqrt(X+0.5)

'Means with different letters are significantly different from each other at P=0.05, using Sheffe's Test

Fig.1a

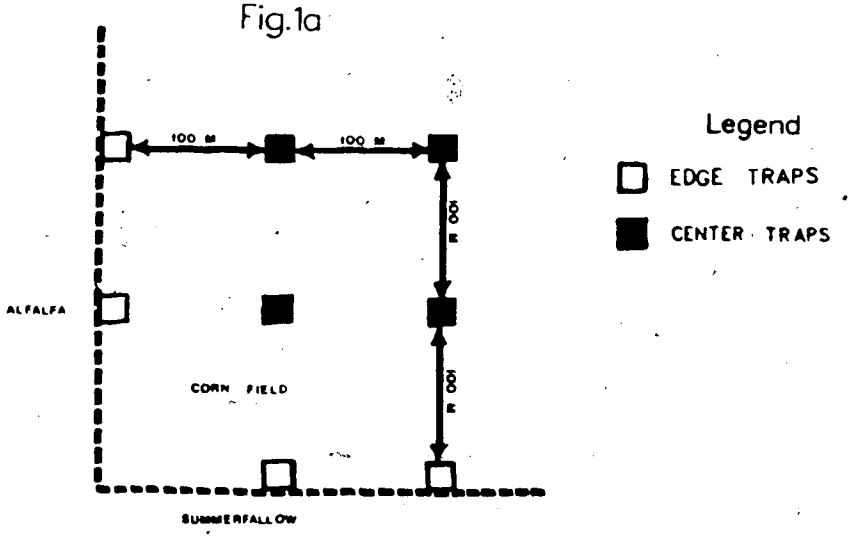

Fig.1b

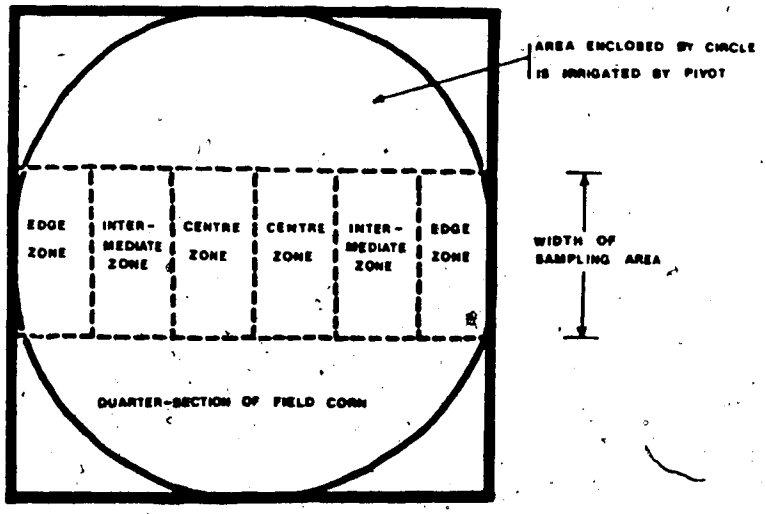

Figure VI-1. Schematic diagrams explaining design of experiments. (a.)pheromone trap grid for sampling ECB moth numbers in 1983, (b.)quarter-section of field corn that was sampled for ECB oviposition in 1984, showing the partitioning of the field into six zones.

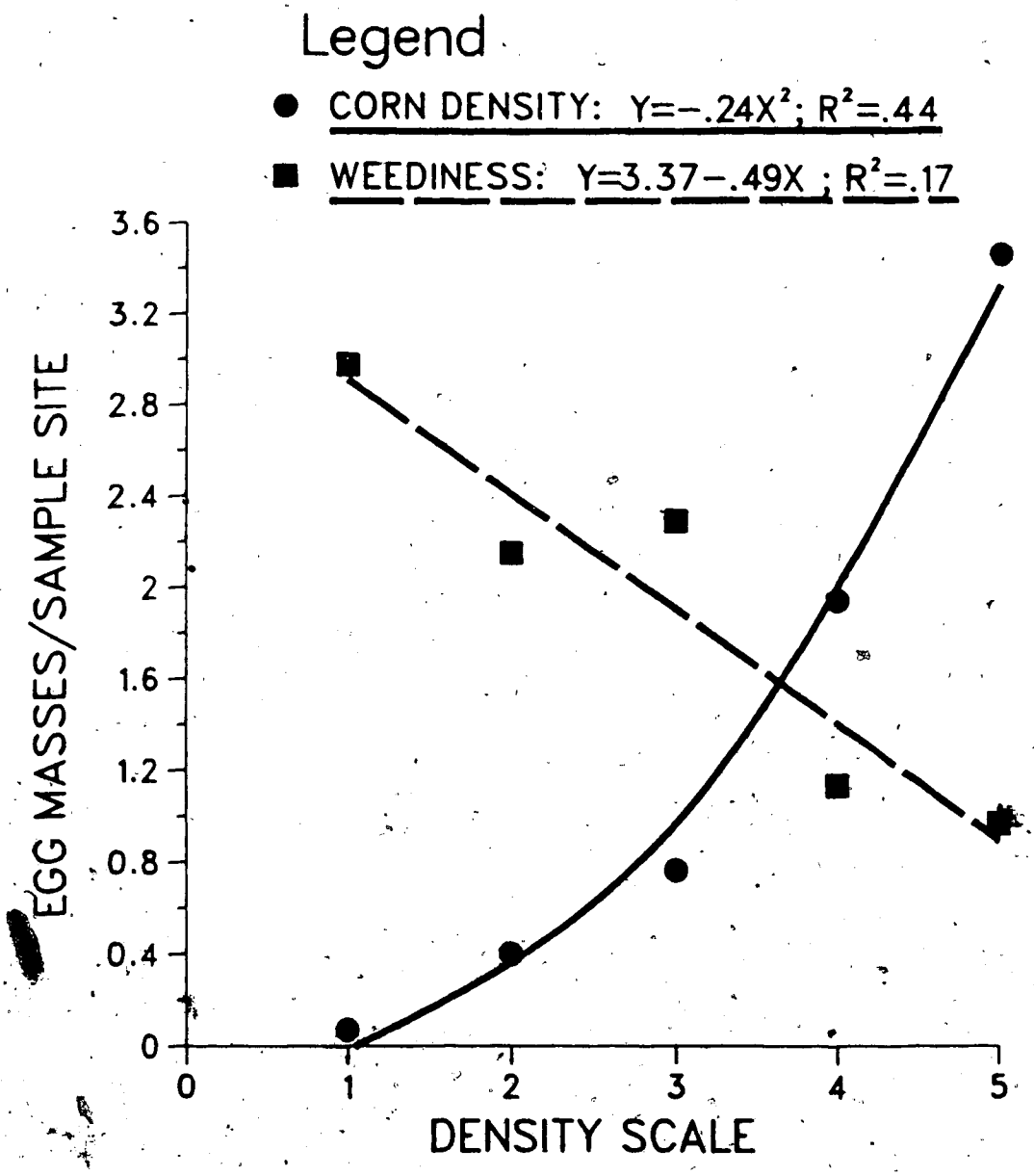

Figure VI-2. Relationship between ECB oviposition and corn stand density or weediness density.

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VII. MORTALITY FACTORS

A. Introduction

The affect of mortality factors on ECB survival has been determined for field populations in eastern North America (reviewed by Barber 1926, Hudon and Leroux 1961, Chiang and Hodson 1972 and Brindley *et al.* 1976), and a life table for the ECB has been constructed (Leroux *et al.* 1963). Results of these studies suggest that natural enemies usually play a minor role in regulation of population levels of the ECB, and that weather extremes can seriously reduce populations during larval diapause, during adult flight, and during growth of immature larvae.

An infestation of ECB was first discovered in Alberta in 1980 (Lilly and Harper 1982), and it's population size has increased dramatically since then. To determine the causes of population increase, I examined mortality during all life stages of Alberta ECB in the field. I hypothesized that mortality rates of ECB in Alberta would be lower than those in other regions, because of lower mortality rates of early instar larvae, and lower rates of parasitism and predation. I also examined the effect of abiotic factors upon mortality of developing eggs and larvae, and upon diapausing larvae in the field.

B. Methods and Materials

Spring Mortality

Factors affecting mortality (except predation) in spring 1983 and 1984 were monitored by dissecting diapausing larvae from corn stalks at various locations around Medicine Hat (see Chapter II). Larvae were placed in Petri dishes (4 larvae/dish) lined with moist filter paper to provide free moisture for pupation (Beck 1967). In 1983, 150 larvae were also repositioned in their stalk tunnels, and the stalks taped together. Both treatments were placed in an outdoor screen cage. When fungi were found on dead borers, the fungal species were isolated and identified. Parasitoids found emerging from pupae were identified, and percent parasitism recorded.

Mortality During Development From Biotic Factors

Egg Parasitism

ECB egg masses randomly collected (see Chapter VI) from a heavily infested field corn plot (Legal Descr.: 11-6-18-2, near Medicine Hat) from 19 July to 5 August 1984 were examined for parasitism. Corn leaf cut-outs containing egg masses were placed in Petri dishes (10 egg masses/dish), inside a sealed plastic bag at 25°C. Egg masses were monitored daily for larval hatching and emergence of parasitoids.

Larval Predation

The influence of natural enemies on larval mortality was studied by comparing ECB survival in completely screened cages to survival in open cages. In an experiment similar to that of Sparks *et al.* (1966), each of three completely enclosed cages (1m X 1m X 1.5m high) were placed over *ca.* 12 corn plants when artificial infestation occurred, at the end of July 1984. Cages were completely enclosed with nylon screening (6.7 meshes/lineal cm), except for the first 0.5m above the ground, which was covered with 6-mil clear polyethylene. Top edges of this sheeting were coated with Tangle-trap®, to prevent larval escape. Cages were spaced at least 10 m apart in a field of silage corn, which was in the centre of the Alberta ECB range.

Wax papers containing blackhead egg masses were stapled to the undersides of leaves (*ca.* 45 eggs/plant), on 30 July. Each plant was tagged as to the sample size (±2 eggs). Plants were checked for naturally-laid egg masses and larvae, and for predators, prior to placement of eggs. In late August plants inside the cages were dissected and the wax papers collected. Numbers of surviving larvae and eggs that failed to hatch were noted for each plant.

On the same day, eggs were similarly placed in the three control cages, which were made with both an inner and outer frame, spaced 0.5m apart. The inner frame was 1m X 1m X 1.5m high. Screened portions of the cage alternated between the inner and outer frames. Thus plants in these

double-framed cages were exposed to physical conditions similar to those of plants in the regular cages, yet they were accessible to predators (Sparks *et al.* 1966). Because the test was conducted when few if any ECB moths were flying, natural infestation of the open cages was very unlikely.

Predation intensity was calculated using Sparks's formula (1966); where predation intensity=(ECB survival in closed cages)-(ECB survival in open cages)x 100/(ECB survival in closed cages)).

To further observe the effect of predators on ECB survival, 18 adult coccinelids (species included *Adelia bipunctata*, *Coccinella novemnotata*, and *Hippodamia convergens*) were placed into each of three completely enclosed cages on 1 August. Sparks *et al.* (1966) have noted that coccinelids are the main insect predators of ECB larvae. Coccinelids were collected in the field up to a week prior to placement, and stored at 10°C until needed.

Abiotic Mortality During Development

To test the effect of relative humidity (RH) on egg survival, newly laid egg masses were placed in dessicators (Winston and Bates 1960) at 75% RH (using NaCl saturated salts), at 53% RH (using $Mg(NO_3)_2.6H_2O$ saturated salts) and at 32.5% RH (using $MgCl_2.6H_2O$ saturated salts). Dessicators were one-litre inverted plastic containers (see Chapter IV), with the salt solution placed in a dish on the container

lid. Petri dishes (with screened lids) containing 5-8 egg masses/dish were stacked above the salt solution between spacers. Treatments were placed in Precision® incubators at 22±1°C and 27±1°C. All eggs in a Petri dish were taken as a single sample. Egg masses were monitored daily for hatching. Infertile eggs were excluded from counts.

Egg and larval mortality in the field was examined during 1983 and 1984, and related to weather conditions during the growth period. Egg masses laid on wax paper by laboratory-reared females were placed at 26°C in Petri dishes with moistened filter paper, until they reached the blackhead stage. They were then stapled to the undersides of corn leaves at mid-plant level. Larvae generally hatched within a few hours. 30 to 50 eggs were placed on each corn plant, which was tagged as to date and sample size (±2' eggs). In 1983 eggs were placed at *ca.* 3-day intervals on field corn from July 13 to Aug. 8, while in 1984 eggs were placed at 5-day intervals on sweet corn from July 10 to Aug 4.

Treatment groups (those plants which received eggs all on the same day) were separated by plastic sheeting barriers coated with Tangle-trap® on top. Two methods were used to prevent larval escape from the plot area and to prevent egg laying by wild adults. In 1983 a 1-m high 6-mil plastic fence was erected around the plot, which was located at the periphery of the corn borer infestation where chances of natural infestation were unlikely. In 1984 the plot was

enclosed on the top and sides by a 2-m high screen cage, with 1-m high plastic encircling the cage bottom. In both years a layer of Tangle-trap® was applied to the plastic to prevent larval escape. Temperature, humidity and rainfall were recorded continuously at mid-plant level. The 1983 plot was irrigated regularly by pivot, but the 1984 plot was irrigated only twice by flooding.

About every five days after egg placement, two plants from each treatment group were cut at the roots and transported to the laboratory in plastic bags. Plants were dissected and both live and dead larvae noted as to instar (based upon head capsule width). Wax papers were checked for dead eggs. For each corn plant the number of eggs and larvae thus accounted for were tallied. The difference between total larvae found and the number of eggs that hatched (*i.e.* those unaccounted for) was assumed to represent first or second instar larvae that died. This assumption is reasonable because dead larvae above the second instar were unlikely to disintegrate over the test period, and therefore could readily be observed.

Winter Mortality of Diapausing Larvae

The effect of freezing temperatures on diapausing larvae in stalks on the ground surface was examined by placing infested stalks gathered 25 August 1983 at ground level in a screen cage. Stalks were dissected the following spring, and numbers of dead larvae counted.

Similar information was obtained for larvae within stalks on the ground of a heavily infested quarter section of field corn. Plowing operations in fall 1983 had failed to bury all stalks. Corn debris on the ground surface was sampled for larvae in June 1984. Twenty 1-m^2 quadrat samples were randomly taken at each of 19 sampling sites evenly distributed along a diagonal transect of the field. All corn debris was collected and bagged as to sampling site, taken to the laboratory, and dissected for ECB.

The relationship between winter mortality and larval location within the stalk was examined in spring 1985 in the same field, which had been harvested but not yet plowed under. Ten stalks were sampled at six randomly selected points in the field. Stalks were split open in the field, and larval position noted as to internode. Mortality of larvae within cobs was determined in another plot left unharvested.

Life Table

Mortality data gathered in the field was supplemented by some laboratory data, to construct a life table for Alberta ECB. This laboratory data included egg mortality due to hatching failure and infertility (see Chapter III), non-performing females (see Chapter IV), and larval death due to dropping from leaves (see Chapter V). Initial egg density (# eggs/100 plants) was determined by sampling for eggs from 11 July to 14 August 1984, on the quarter-section

of field corn mentioned previously. Every 6±1.6 days, corn plants were randomly monitored (see Chapter VI) for newly-laid (in the "whitehead" stage) egg masses. Because eggs in the field hatch within four to seven days (Hudon *et al.* 1982), almost all egg masses counted per sample date were newly-laid since previous sampling. Total egg density over the season was determined by summing egg densities over all sample dates.

Unexplained losses in the adult stage were assumed to be either from adult migration or from loss in reproductive potential. This was estimated by comparing actual egg density in the field to an estimate of the potential egg density. Potential egg density (#eggs/plant) was calculated by estimating numbers of emerged females in spring 1984, multiplying this figure by the fecundity per female as determined in the laboratory (Chapter IV), and dividing by plant density.

C. Results

Spring Mortality

Mortality of ECB placed inside Petri dishes (n=412) in spring 1983 totalled 6.1% as diapausing larvae and 10.4% as pupae. Most larvae died as they were pupating, and formed larval-pupal intermediates. 4% of ECB larvae placed inside taped stalks were found dead, and 6% could not be located.

Fungi isolated from dead ECB inside taped stalks were identified as *Penicillium*, *Phoma*, *Rhizopus*, *Paecilomyces*, *Fusarium*, *Mucor*, *Cylindrocarpon*, *Cladosporium*, *Alternaria* and *Geomyces pannorus*. All species are common in the field (L. Sigler, personal communication).

Three species from the family Ichnuemonidae emerged from ECB pupae in the spring. *Trichiomutus* sp. caused 1.0% mortality in 1983 (n=303 ECB pupae) and 0.2% mortality in 1984 (n=518). A single specimen of *Phygadeuontinae* sp. (n=256 ECB pupae) was found in 1983, and an individual *Phaeogenes* sp. (n=518) in 1984. A parasitoid from the family Braconidae, *Meteorus* sp., caused 0.7% mortality in 1983 (n=150) and 0.2% mortality in 1984 (n=518). Only one parasitoid from the family Tachinidae was found in 1983 (n=412 ECB pupae), but could not be identified further. Sample sizes are different because sampling occurred in different years or in different locations. An unidentified cutworm feeding in close association with ECB was heavily parasitized by *Cotesia laeviceps* (Ash)., but none were observed emerging from ECB larvae.

Predation

Percent larval mortality in screened cages (65.5±18.29%) was not significantly different (t=0.73, df=64, P=0.47) from that in open cages (62.1±19.98%). Predation intensity (Sparks 1966) was calculated as 5.2%. Mean mortality of ECB in cages with introduced predators

(61.8±8.6%) was similar to mortalities for the other two treatments.

414 larvae were recovered from screened cages, 272 larvae from open cages, and 579 larvae from cages with introduced predators. However, differences in larval recovery rates between treatments were due to differences in egg mortalities. Highest mean egg mortality (47.4±36.38%), highest variance, and lowest coefficient of variation (76.8) were recorded for the screened cages. Lower means and variances, and higher coefficients of variation (CV) were recorded for open cages (22.4±26.72%, CV=119.3) and for cages with introduced predators (9.7±14.42%, CV=148.7).

Egg Mortality

In the laboratory, egg survival increased significantly with increasing RH at both of the temperatures tested (Table VII-1). For a given RH, egg survival was lower at 22°C than at 27°C. For example, survival at 35% RH was 15.7% at 22°C and 51.6% at 27°C (t=2.8, df=18, P=0.01). Lower survival at the lower temperature may be due to longer exposure time to low humidities. Survival values did not include egg mortality from infertiliy or cannibalism, because neither of these would be affected by changes in RH.

In the field, egg mortality due to dessication was low and constant (10.0±4.75%, n=6 sample dates) during mid-July (Fig. VII-1), when peak egg-laying occurred (unpublished data). However in late July and August egg mortalities were

usually much higher, and more variable. Maximum temperatures during this period were high, and mean RH fairly low (Figs. VII-2A and V-3B). No egg parasitoids emerged from the 270 egg masses collected in the field on six different days.

Mortality of Developing Larvae

During larval growth, very low mortalities were recorded for the third instar (0.85±2.69%, n=144 stalks sampled), fourth instar (0.35±1.34%, n=61) and fifth instar (0.79±2.72%, n=103).

Because 98% of all larval mortality occurred during the first and second instars, any change in early instar mortality would greatly affect total larval survival. Therefore early instar mortality was plotted against time for both 1983 and 1984, and related to weather data (Figs. VII-2 and V-3). In 1983, early instar mortality was lowest (55-67%) from 25-29 July (Fig. VII-2B). During this period maximum temperatures were not excessive (25-32°C), mean RH was average (53-67%) and rainfall was low (3.2 mm). Mortality was highest (79-91%) during 13-21 July, when rainfall was great (total of 70 mm) and RH was high (60-77%). For most of this time the mean dewpoint temperature was above the minimum temperature (Fig. VII-2A). This signifies that little evaporation occurred, so that rainwater remained in the ligules. Many small larvae likely drowned, since they are very susceptible to water on the plant (Painter and Fitch 1924). A period of high mortality

(68-77%) also occurred from 4-7 August, when maximum temperatures were high (39-44°C) and mean RH was low (37-58%).

During 1984, larval mortality increased over the season from a low of 45% on 10 July to a high of 72% of 4 August (Fig. VII-3B). This pattern was associated with gradually increasing moisture stress (Fig. VII-3A), caused by a severe drought. Corn plants sampled in 1984 were not irrigated regularly.

Winter Mortality of Diapausing Larvae

Mortality of larvae in stalks at ground level was 13.5% (n=37 ECB) during 1983/84. Mortality of larvae found within surface debris in spring 1984 was 21.7±11.81% (n=19 sites, 766 ECB). Density of live ECB was 1.579 borers/m^2. Net weight of corn debris was 2.0±0.85 kg/m^2.

Mortality of larvae in relation to location within stalks varied greatly, from 0% mortality in the roots to 100% mortality in locations higher than the fourth internode (Fig. VII-4). An 88% increase in the mortality rate occurred at the snowline (Fig. VII-4), between the first and second internodes. One or more larvae were found in the roots or first internode in 83% of all stalks sampled. Up to five larvae were found together in a single root. Larval density in the root (1.6±0.96 larvae, n=72) was higher than that in any other internode (mean=1.3±0.51 larvae, n=72). 49.5% of all larvae were found below the snowline. Mortality of

larvae within unharvested cobs was 62.5% (n=16 ECB).

Life Table

A lifetable (Table VII-2) for Alberta ECB showed generation survival as being 2.46%. The trend index (*lx* for eggs of the new generation expressed as a ratio of the old) was 3.28. Highest mortalities occurred during the first instar, from overwinter frosts and from migration.

Unexplained adult losses (migration and loss in reproductive potential) were calculated as follows. The area of the irrigated corn in the test plot was measured (by pacing) as 501,160m². Since live larval density in spring 1984 was 1.579 ECB/m², the total number of surviving ECB was 1.582×10^4 in the test plot. With larval mortality of 12.1% and pupal mortality of 10.4% (Table VII-2), the population was further reduced to 1.246×10^4. With a 50% sex ratio (see Chapter II), and with 20% female incompetency (Table VII-2), *ca.* 498,400 competent females emerged. Assuming there are *ca.* 3.84×10^4 plants per quarter section (Alberta Corn Committee 1982), 267 viable eggs laid per female (see Chapter IV), and 21.6 eggs per mass (see Chapter VI), the potential infestation level was 160.4 egg masses/100 plants. The actual infestation level was only 55.57 masses/100 plants (or 1200.2 eggs/100 plants), signifying a loss of 72.0%.

D. Discussion

Factors Associated With Low Mortalities

Mortality factors which show only small fluctuations in death rate over time are also those which have little impact on overall ECB mortality (Leroux *et al.* 1963). Such factors for the ECB in Alberta include parasitism and predation; egg infertility, dessication and dislodgement; mortality of third, fourth and fifth instars; and incompetence of female moths to lay viable eggs.

Winter mortality of diapausing larvae under snow cover and spring mortality of larvae and pupae were also small in 1983 and 1984. Stirrett (1930) observed that winter mortality of larvae at ground level ranged from 0 to 14.3%. I noted 13.5% mortality in 1983 and 21.7% in 1984. The latter figure likely included some larvae killed during harvesting and cultivation. The high survival rate of larvae in the ploughed field shows that cultivation is not an effective control measure unless all debris is buried. Huber *et al.* (1928) observed that only 6-10% of larvae are directly killed by crushing from tractor wheels, and Caffrey and Worthley (1927) showed that many shallow-buried larvae burrow back to the surface and reenter corn debris.

Mortality of diapausing larvae (4% to 6.1%) and pupae (10.4%) in the screen cage was only slightly greater than that observed under laboratory conditions (3.5% for larvae, 8.8% for pupae, Appendix 2). Hudon and Chiang (1977)

similarly reported 10% pupal mortality in the field.

I believe the 6% of larvae missing from the screen cage were killed by ants. I observed ants continually walking over stalks, and I once saw them dragging away a larva. Ants can destroy many ECB larvae in both spring and fall (Caesar 1925). Other predators active during these seasons were seagulls, which were observed searching for insects in corn debris. Although the effect of vertebrate predation on ECB mortality in Alberta is unknown, Graziano (1979) recorded 25.9% mortality from avian predators in North Dakota. The effectiveness of bird predation depends however upon low amounts of corn debris for the larvae to hide in (Huber *et al.* 1928).

Some of the fungi I found on ECB cadavers may be moderately pathogenic. In pathogenicity tests (Brooks and Raun 1965) *Fusarium* was moderately pathogenic to ECB, while *Penicillium*, *Rhizopus* and *Paecilomyces* were weakly pathogenic or saprophytic.

Total pupal parasitism was 2.3% in 1983 and 0.6% in 1984. Clearly ECB are only minor hosts for these native parasitoids. Caffrey and Worthley (1927) reported ECB parasitized by the native species *Meteorus loxostegei* (Vier.), and by an introduced species *Phaeogenes planifrons* (Wesm.). To my knowledge the other Ichneumonid species I found have not previously been reported parasitizing ECB. Parasitism of ECB in Alberta was lower than that in most sites examined in Ontario by Wressel (1973), in Conneticut

by Andreadis (1982), or in Delaware by Roming *et al.* (1985).

Egg mortality in the field during mid-July (10%, Fig. VII-1) was similar to that observed in the laboratory by Hudon and Chiang (10%, 1977) and myself (11.7%, see Chapter III). Leroux *et al.* (1963) observed 77-90% egg hatching in the field. The laboratory trials showing increasing egg dessication at lower humidities support the work of Huber *et al.* (1928), who observed that ECB eggs are susceptible to dessication in the field.

Differences in egg mortalities between treatments in the predation experiment were likely due to an artifact. Eggs used in screened and in open cages were held at 10°C in the blackhead stage for up to five days before placement, because laboratory-reared moths could not produce enough eggs in a single day. Eggs used for cages with introduced predators were held at 10°C for only one or two days.

The coccinelids deliberately introduced into cages may not have fed on ECB larvae because there was an abundant supply of their preferred prey, aphids. Aphids were not apparent at time of egg placement, but their large numbers were observed upon completion of the experiment. Caged coccinelids seemed to thrive, because several were still alive after 25 days. Their search behaviour was concentrated in the tassels, where aphids feed. Because the ECB larvae entered the leaf ligules in the centre of the plant, it is possible that coccinelids would rarely encounter ECB larvae. In another study (see Chapter V) I found that ECB larvae

spent little time feeding on the leaves, but quickly dispersed into the ligules.

Factors Associated With High Mortalities

Annual mortality rates are often large, but fluctuate greatly for ECB adults, early-instar larvae, and for overwintering larvae above the snowline (Leroux *et al.* 1963, Chiang and Hodson 1972). These mortalities are difficult to predict, since they greatly depend upon abiotic (*i.e.* weather) factors. For example, Stirrett (1930) noted that annual larval mortality above the snowline varied widely (0-100%). The high larval mortalities I observed in internodes above the snowline (Fig. 4) may have been caused by sudden prolonged frosts in early September 1984.

The 72.0% mortality due to adult dispersal and loss in reproductive potential (Table 2) was similar to that (93.6%) noted by Leroux *et al.* (1963), who observed that migration of adults accounted for 78% of population variance, by far the largest factor. Dispersal of ECB within the infestation area in Alberta is widespread, and all corn stands are likely to be affected yearly.

The only other studies which define moth dispersal, those of Hudon and Leroux (1961) and Leroux *et al.* (1963), do not explain how this dispersal was measured. The critical assumption underlying dispersal calculations for Alberta ECB was that fecundity and longevity rates determined under laboratory conditions (see Chapter IV) are the same in the

field. This is unlikely. Barlow (1971) noted that rainfall is a key factor in ECB population dynamics, since maximum longevity of adults and fecundity is attained when 25-76 mm rain/day is received. Semi-arid S.E. Alberta receives much less rainfall than this (*ca.* 25 mm/week) via irrigation (Alberta Corn Committee 1982). Therefore actual moth dispersal is probably less than 72%, the difference being due to a loss reproductive potential.

Variation in mortality of early instar larvae (45%-91%) was related to seasonal weather patterns. Showers *et al.* (1978) have shown that 81-93% of variation in ECB larval mortality is related to hot temperatures, moisture stress and evaporation. The very low mortalities of third, fourth and fifth instar larvae during growth are not unusual. Painter and Ficht (1924) similarly observed only 3-4% mortality of mid-sized larvae and 0.3-3% mortality of mature larvae.

Most ECB larvae are in the first and second instars during the last week in July (unpublished data). During this period, mean mortality for 1983 and 1984 was 62.2±4.18% (n=6 sample dates). When subsequent mortality of later instars is included, total larval mortality is only 64.2%. This is lower than mortalities for ECB in other areas. Caesar (1925, 1926) found overall larval mortality ranged from 79-97%, and Marshall (1926) documented mortality as 78-87%. Huber *et al.* (1928) noted mortality as 82-92%, while Chiang and Hodson (1972) observed 67-70% mortality. Lower larval mortalities

in Alberta may be due to lower predation and parasitism, and because only non-resistant varieties of corn can be grown. Chiang and Hodson (1977) determined that ECB survival was significantly higher on susceptible corn varieties, and Guthrie *et al.* (1960) reported 95% early instar larval mortality of first-generation ECB on resistant inbred hybrids.

The low mortality rates during most life stages of Alberta ECB suggests that populations are increasing. This was confirmed by the trend index (3.28), which indicates that the population increased over three times in one year. This figure is twice as high as that (1.70) obtained by Leroux *et al.* (1963) for ECB in Quebec. Not included in this index is mortality due to farming operations, which could have a major impact upon ECB survival. Further studies are needed to determine if this trend can be maintained over several years, and how the trend index varies as to locality.

Table VII-1. Effect of humidity on survival of ECB eggs. Treatments were compared by Analysis of Variance. RH=relative humidity; SD=standard deviation.

Temperature(°C)	Treatment	Sample Size	Mean % Survival	SD	F	P
22	35% RH	7	15.7	19.68	26.2	<0.001
	55% RH	6	57.2	18.75		
	75% RH	7	84.0	14.68		
27	35% RH	13	51.6	30.67	7.64	<0.002
	55% RH	11	71.6	28.20		
	75% RH	7	99.4	1.47		

Table VII-2. Lifetable for plains populations of the European corn borer in southern Alberta, 1984/85

Age Interval (x)	No. Alive at beginning of x, (lx)¹	Factor responsible for dx, (dxF)		No. Dying during x, (dx)¹	dx as a % of lx (100qx)
Eggs¹:	1200.2				
		Infertility		54.0	4.5
		Failed to Hatch		86.4	7.2
			TOTAL:	140.4	11.7
	1059.8				
Larvae¹:					
L1+L2		Dispersal		148.4	14.0
		Weather		455.7	43.0
		Predation		55.1	5.2
			TOTAL:	659.2	62.2
	400.6				
L3	397.4	Unexplained losses		3.2	0.8
L4	395.8	Unexplained losses		1.6	0.4
L5 (growth)	392.6	Unexplained losses		3.2	0.8
L5 (diapause)	167.3	Frost		225.4	57.4
		Fungi, larval-pupal transition		10.2	6.1
		Predation (by ants)		7.4	6.0
			TOTAL:	20.2	12.1
	147.0				
Pupae	131.7	Fungi, dessication, parasitism		15.3	10.4
Moths¹:					
	65.9	Sex ratio 50:50		65.9	50.0
	52.7	Moths that can't lay viable eggs		13.2	20.0
	14.8	Migration of moths, and loss in reproductive potential		37.9	72.0

¹per 100 plants.

'Mortalities due to infertility and hatching failure taken from Chapter III

'Death due to dispersal refers to larvae dropping to the ground (from Chapter V)

'Data for incompetent female moths taken from Chapter IV.

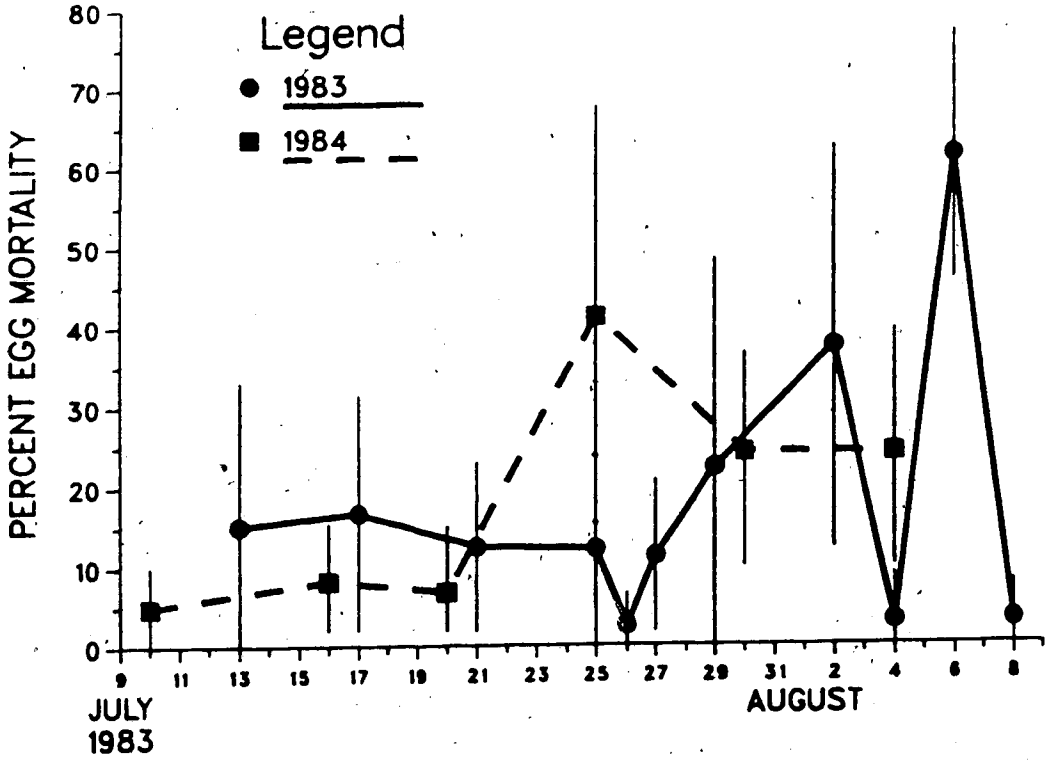
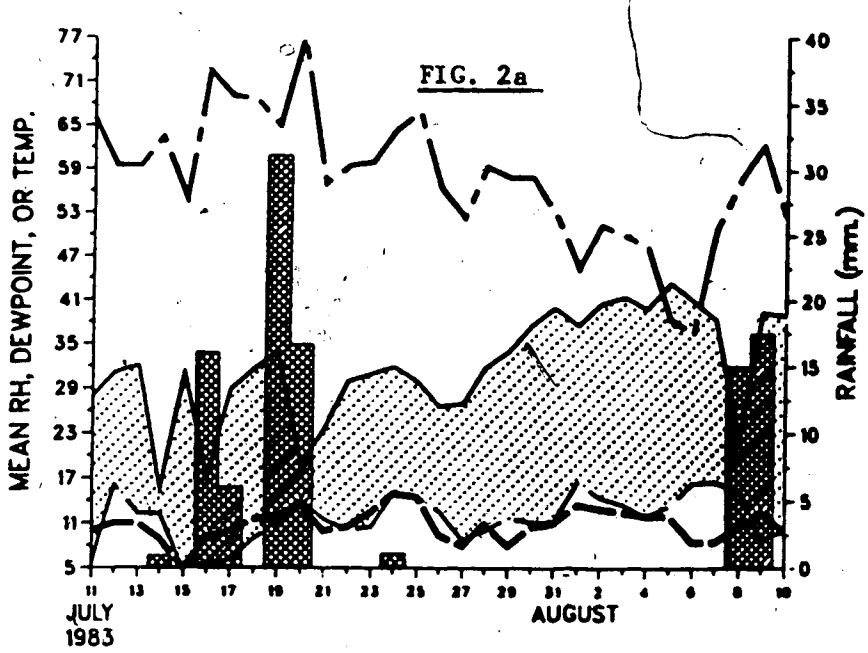
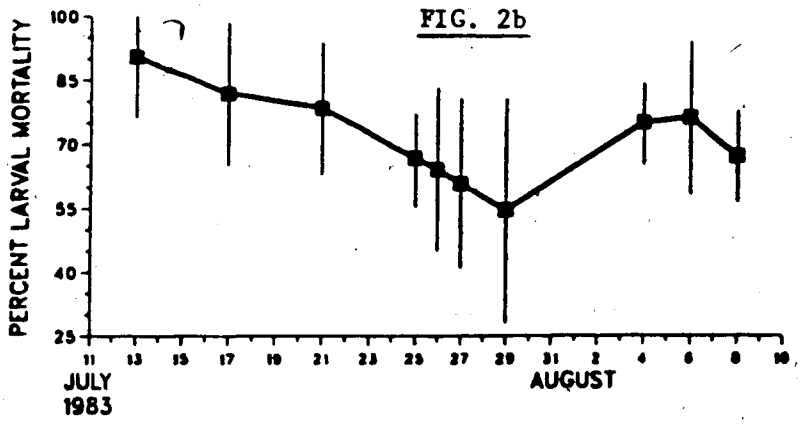


Figure V-1. Egg mortality in the field, for 1983 and 1984.





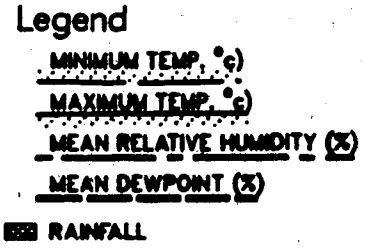
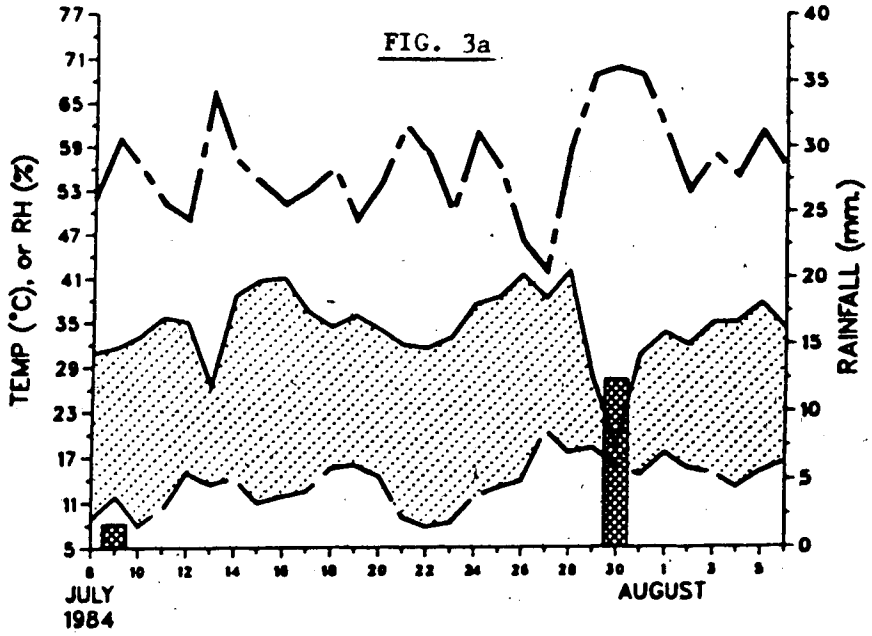
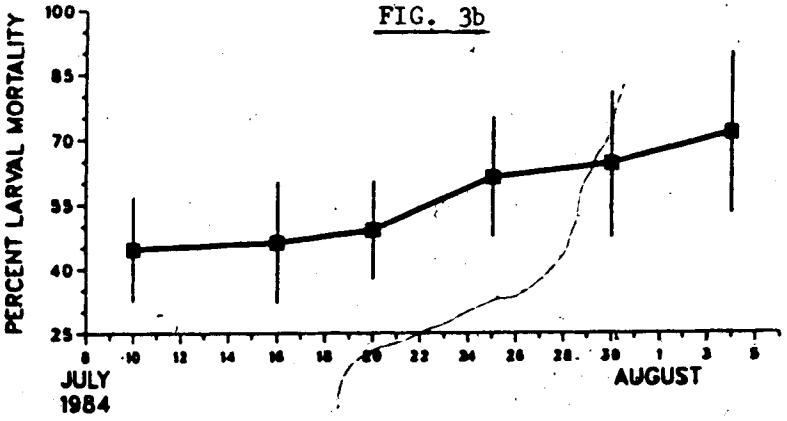


Figure V-2. Relation between weather factors in 1983 (Fig. 2a) and early-instar larval mortality (Fig. 2b).





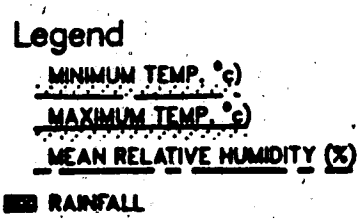


Figure V-3. Relation between weather factors in 1984 (Fig. 3a) and early-instar larval mortality (Fig. 3b).

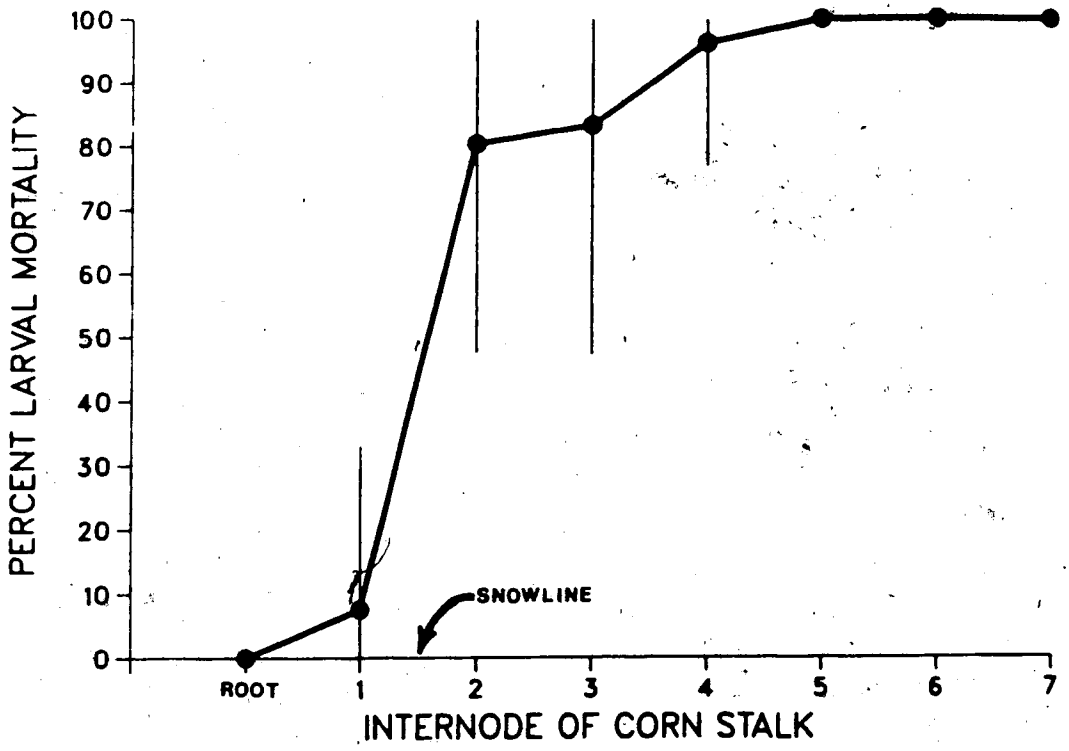


Figure V-4. Mortality of overwintering larvae in relation to their location in corn stalks in spring 1984. Sample sizes are as follows: root(39 larvae), 1st internode(33), 2nd internode(23), 3rd internode(36), 4th internode(27), 5th internode(17), 6th internode(14), 7th internode(9).

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VIII. General Discussion

For a colonizing species to become established in a new locality, it must be adaptable and "generalist" (Rosenweig 1981) in nature. Colonization is defined as "the establishment of a population of a species in a geographical or ecological space not occupied by that species" (Lewontin 1965).

New localities at the edge of a species' range, such as in Alberta for *O. nubilalis*, are often called "ecologically marginal habitats", in which "physical stresses tend to be both variable and extreme, so that resources tend to be unpredictable and short-lived" (Parsons 1983). The Alberta climate imposes physical restraints upon the ECB which are associated with observed phenology, physiological and behavioural characteristics. Also, mortality patterns in Alberta are different from those of ECB in the centre of it's North American range. Significant differences were also observed in some life history traits between plains and valley populations of Alberta ECB. These differences can be interpreted as adaptations to Alberta conditions by colonizing populations of *O. nubilalis*.

In this study I focused my research upon measurements of phenotypic variation. The next step in character analysis, which is beyond the scope of this study, would be a detailed measurement of genotypic variation by quantitative genetics (Falconer 1981, Parsons 1983). As Waddington (1965) has explained, "the natural selection

which guides evolutionary change acts primarily on phenotypes, and only secondarily on genotypes. Therefore, any agents which alter or limit phenotypes, *e.g.*, physiological adaptations, developmental canalization, *etc.*, may have evolutionary consequences". Therefore, I limited my research on genotypic variation to demonstrations that heredity was partially responsible for observed phenotypic traits.

Studies of ECB life history traits in eastern North America have been complicated by the presence of two different strains of *O. nubilalis*, which coexist and sometimes intermate. These strains are distinguished by separate pheromone isomers. Each strain also has different diapause and developmental characteristics, which have been shown to be inherited traits (McLeod 1978, Reed *et al.* 1981). Of course, geographical populations of each strain also differ in diapause and development traits (Apple and Beck 1961), which complicates matters greatly.

In Alberta, there is definitely only one strain, which has a pheromone composed of 97%(Z):3%(E) 11-tetradencylacetate (D.L. Strubble, personal communication). The closest source of the other strain (Ontario) cannot be seriously considered as a possible source for introduction of the pest to Alberta, since the ECB is a quarantine species. Therefore the observed differences between valley and plains ECB are those of different populations only. Some critics, however, may argue

that differences in life history traits for the two Alberta populations are due to two separate infestations. This is unlikely. Ever since the first infestation was discovered in a single field in the Medicine Hat area, corn fields have been carefully surveyed (Lilly and Harper 1982). The annual spread of the species, averaging 12 km., is indicative that the initial infestation arose from a single point source.

According to Parsons (1983), analyses of life history adaptation should proceed by (1) comparative studies of variation of several well-chosen traits, (2) the establishment of adaptive roles of these traits, (3) the demonstration of genetic changes under varying environments, and (4) the experimental demonstration of whether the outcomes represent adequate solutions to an adaptive challenge. Adaptation of ECB life history traits to Alberta conditions can be summarized by considering these four steps with respect to those traits in which differences between ECB populations were observed.

Phenological differences were noted between plains populations, which were univoltine, and valley ECB, which had a partial second generation in 1983. Mean pupation and emergence was five to seven days earlier for valley borers than for plains borers in both 1983 and 1984. A transplant experiment in 1984 demonstrated that phenological differences were patterned in accordance with a model of cogradient clinal variation (Gill *et al.* 1983), in which both heredity and the environment played a role. The

adaptive significance of these differences in phenology was demonstrated by examining the underlying physiological and behavioural differences between the two Alberta populations.

Physiological traits studied included larval and adult development rate, temperature thresholds for development, and fecundity. When both Alberta populations were grown under controlled temperatures, significant differences were observed in these traits for some life stages, thus confirming the existence of a genetic influence, that was initially observed in the transplant experiment. Profound differences were seen during the fifth larval instar, when plains ECB developed much slower than valley ECB or ECB from the United States. Development thresholds were higher for plains ECB than for valley ECB in this stage. Both these traits slowed down growth in plains ECB. Contrary to my expectations (see Chapter I), development thresholds for larval instars of Alberta ECB were generally much higher than those of ECB from the central States. This trend suggests that ECB adapt to cooler climates by selection for univoltinism.

Because valley ECB developmental traits were intermediate between those of plains ECB and those of United States populations, evidently selection for univoltinism is not as intense within valley populations as it is within plains ECB. Parsons (1983) observed that "any new and extreme genetic combination is likely to have lower overall fitness as measured by viability, fecundity, and hence, r".

The net reproductive rate, *r*, is important in determining the natural rate of increase (*rm*), which is often used as a measure of the relative "fitness" of a species (Andrewartha and Birch 1954). At an optimum temperature of 15°/29°C, plains ECB did indeed have lower egg viability (80%) and fecundity (267 eggs/female) than did valley ECB (95% viability, 559 eggs/female). This result again suggests that genetic selection is occurring in plains ECB.

Lower fecundity in plains ECB was correlated with lower pupal weight. Body size and ovariole number are known to vary both with temperature and altitude for *Drosophila melanogaster* (Parsons 1983, pg. 45). The transplant experiment I conducted in 1984 showed that both environmental and genetic influences affected ECB body mass. Studies in spring 1984 also suggested that differences in body mass between populations were related to differences in larval feeding behaviour. Wet larval weight of valley borers were not significantly different from those of plains borers during April and May, but during early June valley ECB larval mass increased significantly. This suggests that valley ECB entered a post-diapause feeding period, which plains larvae did not. This post-diapause feeding period delayed pupation, thus ensuring that most of the population remained univoltine.

Larval dispersal studies indicated that feeding behaviour of early-instar Alberta ECB larvae is less canalized than that of ECB in the United States. In Iowa,

first-generation borers begin feeding almost exclusively on the leaves and in the tassel buds. Newly-hatched second-generation borers feed primarily in the sheaths and on pollen (Guthrie *et al.* 1960, 1969, 1970). Alberta ECB larvae are more opportunistic, and will feed on whatever resource microhabitat of the corn plant that is available. Corn varieties grown in Alberta achieve rapid growth, therefore during the extended ECB oviposition and hatching period (up to one month long), newly-hatched larvae may be exposed to corn in various growth stages. Greater host plant heterogeneity thus necessitates greater behavioural adaptability for larval survival. Studies of food preferences of *Callosobruchus maculatus* larvae suggest that colonizing populations can make immediate behavioural adjustments of food preferences and foraging techniques (Wasserman and Futuyma 1981).

Population sampling of adults in the field also suggests that adult ECB in Alberta mate and rest in different habitat sites than do those in the United States. Iowa ECB moths mate and rest in "action sites" of dense foxtailgrass outside the cornfield, but Alberta moths choose such sites within the centre of the cornfield, probably because of the lack of dense vegetation outside the cornfield. The extended egg-laying period "spreads the risk" (den Boer 1968) for Alberta ECB, so that sudden adverse climatic conditions affect only a small proportion of the total population.

Because Alberta has such a short growing season compared to other areas within the ECB range, the low population levels of predators and parasites that were observed are unlikely to increase sufficiently over a season to have much affect upon ECB mortality and *rm*. ECB larval survival is also favoured in Alberta because resistant corn varieties cannot be grown in this climate. Harsh Alberta winters do not appear to increase larval mortality any more than in other areas, because many diapausing larvae disperse to the base of corn stalks in fall, where they are insulated by winter snowcover.

The ECB will continue to be a major economic pest of sweet corn in Alberta, because population levels will be maintained in field corn, where pesticides cannot be used economically to control the pest. Regional population levels will be influenced mostly by abiotic factors, because biotic control agents are limited, and because farming practises (cultural controls) will change little in response to the pest problem.

Parsons (1983) has pointed out that because the organism itself is the unit of natural selection, a comprehensive understanding of the adaptive process cannot be obtained by studying a single phenotypic trait. The ECB is a good example of how adaptive processes for phenological, physiological, and behavioural phenotypes are interrelated in a species that is colonizing new and marginal habitats.

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IX. Appendix 1: Development Data for Immature Stages

Mean number of days, standard deviation (SD), developmental rate and survivorship for various stages of Alberta strains of *Ostrinia nubilalis* at constant temperatures.

Stage	Strain	Temperature (°C)	Sample Size (N)	Mean Development Time (days)	SD	Mean Development Rate (1/days)	Survivorship (%)
Egg	P	17	455	14.16	0.917	0.0709	(is
		20	55	7.38	1.009	0.1374	com-
		22	2940	5.81	0.603	0.1743	bined
		25	202	5.34	0.738	0.1901	below)
		27	276	4.64	0.692	0.2220	-
		30	79	4.00	0.160	0.2500	-
		32	1122	3.45	0.538	0.2969	-
	V	17	2261	13.39	1.184	0.0755	-
		20	1746	6.82	0.389	0.1471	-
		22	5802	5.90	0.346	0.1701	87
		25	1769	4.96	0.240	0.2020	-
		27	1732	4.05	0.540	0.2513	-
		30	1153	3.77	0.542	0.2709	-
		32	2065	3.34	0.511	0.3066	85
First Instar	C	17	149	8.14	2.315	0.1305	75
		20	111	5.57	0.730	0.1822	76
		24	107	3.80	0.382	0.2652	89
		30	73	2.26	0.321	0.4503	91
		32.5	95	2.15	0.423	0.4817	92
		35	78	1.95	0.102	0.5245	98
Second Instar	C	17	148	6.78	1.087	0.1511	99
		20	110	4.49	0.735	0.2282	99
		24	106	2.99	0.403	0.3480	99
		30	73	2.26	0.404	0.4591	100
		32.5	90	1.96	0.307	0.5244	99
		35	77	2.12	0.275	0.4793	99
Third Instar	C	17	142	6.84	0.967	0.1494	96
		20	107	5.66	2.916	0.1945	97
		24	70	3.23	0.418	0.3141	100
		30	72	2.26	0.751	0.4675	99
		32.5	128	1.91	0.677	0.5744	100
		35	77	1.67	0.265	0.6160	100
Fourth Instar	C	17	141	7.62	1.648	0.1370	99
		20	106	7.26	1.696	0.1423	99

		24	68	3.39	0.494	0.3008	97
		30	71	2.28	0.519	0.4638	99
		32.5	171	2.25	0.859	0.5377	99
	P	32.5	47	1.58	0.147	0.6736	-
	V	32.5	74	2.67	0.817	0.4115	-
	C	35	77	2.39	0.753	0.4530	100
Fifth	P	17	26	16.88	4.411	0.0627	100
Instar		20	18	14.32	1.502	0.0706	100
		24	37	8.11	0.972	0.1250	97
		30	36	5.40	1.425	0.1950	97
		32.5	46	4.58	0.980	0.2276	100
		35	39	5.63	0.601	0.1795	97
	V	17	53	16.77	4.008	0.0625	100
		20	11	11.61	1.228	0.0871	100
		24	29	7.72	1.270	0.1326	97
		30	34	4.71	0.991	0.2201	100
		32.5	108	5.61	2.425	0.2003	87
		35	36	6.52	2.137	0.1633	100
Fifth	C	17	78	8.69	2.262	0.1238	-
Instar		20	105	10.09	2.753	0.1056	-
to		24	66	5.11	0.848	0.2008	-
Pre-		30	69	3.22	1.046	0.3457	-
pupal		32.5	146	3.38	1.738	0.3498	-
Phase	P	32.5	43	2.70	0.572	0.4031	-
	V	32.5	103	3.66	1.972	0.3276	-
	C	35	75	4.14	1.655	0.2693	-
Pre-	P	17	26	8.17	2.404	0.1301	-
pupal		20	3	6.67	1.155	0.1109	-
Phase		24	37	2.83	0.977	0.1972	-
		30	35	1.94	0.979	0.3363	-
		32.5	43	1.91	1.094	0.4031	-
		35	39	1.86	0.823	0.2846	-
	V	17	53	8.55	4.556	0.1372	-
		20	2	4.00	1.886	0.2813	-
		24	29	2.72	1.088	0.4320	-
		30	34	1.59	0.739	0.7598	-
		32.5	102	2.06	1.185	0.6576	-
		35	36	1.97	1.435	0.7192	-
Total	C	17	79	45.16	5.954	0.0225	-
Larval		20	27	37.28	7.347	0.0276	-
Devel-		24	66	21.03	1.949	0.0479	-
opment		30	70	13.98	1.591	0.0724	-
		32.5	112	14.10	3.543	0.0741	-
	P	32.5	46	12.29	1.123	0.0820	-
	V	32.5	66	15.36	4.080	0.0687	-
	C	35	75	14.15	2.112	0.0719	-
Pre-	C	17	75	30.63	2.415	0.0329	95
dia-		20	28	16.39	1.100	0.0613	-
pause		24	36	10.27	0.979	0.0984	97
Pupa-		30	65	6.95	1.224	0.1467	93
tion		32.5	84	6.12	0.613	0.1652	95
		35	58	6.67	0.709	0.1516	77
Post-	P	17	49	70.39	15.486	0.0149	100
dia-		22	45	37.58	10.385	0.0285	90

pause		26	55	31.26	14.552	0.0428	74
Pupa-		30	61	19.53	6.786	0.0570	90
tion		32	31	20.29	5.557	0.0541	81
		35	7	16.86	3.078	0.0614	19
	V	17	45	68.44	14.062	0.0153	96
		22	40	32.40	8.326	0.0327	92
		26	25	23.56	10.369	0.0528	86
		30	44	18.41	7.228	0.0620	88
		32	37	21.70	5.076	0.0492	88
		35	-	-	-	-	-
Post-	M	17	50	30.90	3.151	0.0327	(is
dia-		22	48	11.75	2.943	0.0932	com-
pause		26	48	9.17	1.589	0.1129	bined
Emer-		30	29	8.07	2.017	0.1304	below)
gence		32	13	7.15	0.555	0.1404	-
		35	-	-	-	-	-
	F	17	32	29.38	2.697	0.0343	90
		22	64	11.19	1.745	0.0917	92
		26	47	8.64	1.051	0.1174	90
		30	42	7.19	1.435	0.1451	87
		32	11	6.82	1.251	0.1503	70
		35	2	8.50	1.500	0.1177	40

' P=plains ECB; V=valley ECB; C=combined Alberta populations; M=males; F=females.

X. Appendix 2: Development Data for Adult Stage

Mean number of days, standard deviation (SD), and developmental rate for reproductive variables of Alberta strains of *Ostrinia nubilalis* at constant and variable temperatures.

Variable	Origin¹	Temperature (°C)	Sample Size (N)	Mean Development Time (days)	SD	Mean Development Rate(1/days)
Male	V	10/24	10	15.90	5.626	0.0725
Lifespan	C	20	21	9.76	3.520	0.1173
		22	34	8.77	3.701	0.1429
		15/29	48	11.13	5.039	0.1124
		25	24	7.25	2.383	0.1548
		27	26	7.50	2.687	0.1750
		32	34	4.59	2.258	0.2869
Female	V	10/24	3	32.33	11.015	0.0337
Lifespan	C	20	5	16.40	2.302	0.0620
		22	8	9.13	2.357	0.1188
		15/29	29	13.28	5.464	0.0915
		25	11	7.55	2.018	0.1413
		27	12	7.83	2.443	0.1406
		32	11	8.82	2.136	0.1202
Prereproductive	V	10/24	3	7.67	0.577	0.1310
Period	C	20	5	4.20	1.789	0.2686
		22	8	2.38	1.061	0.5000
		15/29	29	2.90	2.381	0.5379
		25	11	2.27	0.786	0.4924
		27	12	2.33	1.614	0.6250
		32	11	2.91	2.256	0.5639
Postreproductive	V	10/24	3	6.00	5.292	0.4000
Period	C	20	5	2.00	1.871	0.7400
		22	8	1.25	0.886	0.8750
		15/29	29	2.45	3.301	0.8183
		25	11	1.00	1.414	1.1091
		27	12	1.83	1.851	0.8225
		32	11	4.36	3.325	0.4818

Reproductive Period	V	10/24	3	17.67	5.508	0.0599
	C	20	5	10.40	3.782	0.1174
	C	22	8	5.50	2.391	0.2408
	P	15/29	8	5.13	2.475	0.2963
	V	15/29	21	9.05	4.664	0.1975
	C	25	11	4.27	1.954	0.3199
	C	27	12	3.67	2.807	0.5105
	C	32	11	1.64	1.567	0.8636

[1]V refers to valley populations; P refers to plains populations; C refers to combined data for both populations

XI. Appendix 3: Artificial Leaf Measurements

Leaf #	Length(cm)	Width(cm)
1	10	3.0
2	20	3.5
3	30	4.0
4	35	5.0
5	40	6.0
6	45	7.0
7	50	7.5
8	50	8.0
9	50	7.5
10	45	7.0
11	40	6.0
12	30	5.0
13	25	4.5
14	10	3.0

XII. Appendix 4: Results of Trap Efficiency Trials

	Treatment		
	Pheromone Dispensor in Sticky Glue; both Dispensor & Trap changed every 2-4 days	Pheromone Dispensor suspended in Trap; both Dispensor & Trap changed every 2-4 days	Pheromone Dispensor in Sticky Glue; neither trap nor Dispensor changed
(A)Total Captures	13	4	6
(B)# Times Traps Checked	3	5	5
Mean (A)/(B)	4.3 a	0.8 b	1.2 b'

'Differences in letters indicate differences in treatments at $P=0.05$, using the paired difference test for small sample sizes.