

AN ABSTRACT OF THE THESIS OF

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Title: Improvement of Biological Control Agents: Laboratory Selection for Fast Larval Development in the Convergent Lady Beetle, *Hippodamia convergens* Guérin-Méneville (Coleoptera: Coccinellidae)

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Hippodamia convergens Guérin-Méneville was selected for rapid development through five generations at four constant temperatures (18, 22, 26, and 30°C). Two levels of selection were used: intense and moderate. Differences in developmental rate, survivorship, live adult weight, aphid consumption, adult longevity, and fecundity were measured for both groups and an unselected line.

The two selected lines exhibited significant differences in developmental rate after the first generation of selection. The differences increased by the fifth generation of selection. Average differences between selected lines at 18, 22, 26, and 30°C in development from egg to adult were 4.9, 3.0, 1.0, and 1.5 days, respectively. Individuals from the intense selected line had a lower developmental threshold (11.3°C) than the moderate selected line (12.0°C). Also, degree-day requirements from egg to adult were lower in the intense (266 DD°) than moderate (277 DD°) line. Wild type

beetles accumulated 231 degree-days above a threshold of 13.6°C.

Survivorship at cold temperatures significantly increased with selection for fast development. In addition, no significant differences occurred in either live adult weight, total larval consumption of prey, fecundity, or adult longevity. Larvae selected for fast growth consumed higher numbers of aphids per day and were more efficient metabolically in converting prey mass into body mass than slow growing larvae.

Because of a lower developmental threshold and lower degree-day requirements, for complete development, beetles from the intense selected line may accumulate more degree-days throughout a year compared to a moderate selected line. Predictions of population growth, based on an equation for intrinsic growth rate, showed that beetles from the intense selected line would produce 1.6 and 1.4 times more individuals in a 60-day period than beetles from the moderate selected and unselected lines, respectively. The results suggest that intense selected beetles would develop faster earlier in the season and would produce higher population numbers under optimum conditions. Thus, selection of *H. convergens* produced superior beetles for future introductions in biological control.

Improvement of Biological Control Agents: Laboratory
Selection for Fast Larval Development in the Convergent
Lady Beetle, *Hippodamia convergens* Guérin-Ménéville
(Coleoptera: Coccinellidae)

By

Cesar Ramiro Rodriguez-Saona

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TABLE OF CONTENTS

CHAPTER I: INTRODUCTION	1
CHAPTER II: LITERATURE REVIEW	3
Biological Control	3
Unintentional Selection	4
Artificial Selection	6
Selection for Time of Development	7
The Family Coccinellidae	9
Effect of Temperature on Developmental Rate	12
<i>Hippodamia convergens</i>	13
CHAPTER III: SELECTION FOR FAST DEVELOPMENT IN THE CONVERGENT LADY BEETLE <i>HIPPODAMIA CONVERGENS</i> (COLEOPTERA: COCCINELLIDAE)	16
Abstract	16
Introduction	16
Materials and Methods	19
Degree-day Requirements by Wild Type Female Source	19
Selection Trials	20
Degree-day Assessment after Selection	22
Results and Discussion	22
Degree-day Requirements by Wild Type Female Source	22
Selection Trials	23
Degree-day Assessment after Selection	25
References Cited	34
CHAPTER IV: EVALUATION OF CERTAIN LIFE HISTORY TRADE-OFFS IN <i>HIPPODAMIA CONVERGENS</i> (COLEOPTERA: COCCINELLIDAE) SELECTED FOR FAST DEVELOPMENT	37
Abstract	37
Introduction	37
Materials and Methods	39
Weight and Mortality	39
Larval Consumption	40
Fecundity and Adult Longevity	42
Results and Discussion	43
Weight and Mortality	43
Larval Consumption	45
Fecundity and Adult Longevity	46
References Cited	55
CHAPTER V: IMPACT OF SELECTION FOR FAST DEVELOPMENT IN <i>HIPPODAMIA CONVERGENS</i> (COLEOPTERA: COCCINELLIDAE) ON BIOLOGICAL CONTROL	57
Abstract	57
Introduction	57
Materials and Methods	59
Population Growth	60
Number of Generations	61
Results and Discussion	62

Population Growth	62
Number of Generations	63
References Cited	70
SUMMARY	72
BIBLIOGRAPHY	74

LIST OF FIGURES

<u>Figure</u>	<u>Page</u>	
I.1	Difference in development time between intense and moderate selected <i>H. convergens</i> at 18, 22, 26, and 30°C through five generations of selection.	28
I.2	Difference in percentage of adult emergence between intense (■) and moderate (+) selected <i>H. convergens</i> at 18, 22, 26, and 30°C.	29
I.3	Accumulative development time at different preimaginal stages of development for individuals from the intense (■) and moderate (+) selected <i>H. convergens</i> .	30
I.4	Temperature dependent development rate regression lines for the intense (■) and moderate (+) selected <i>H. convergens</i> .	31
II.1	Live adult weight for intense (black bars) and moderate (white bars) selected lines of <i>H. convergens</i> at different temperatures.	49
II.2	Mortality for intense (black bars) and moderate (white bars) selected lines of <i>H. convergens</i> at different temperatures.	50
II.3	Age specific mortality for intense (black bars) and moderate (white bars) selected lines of <i>H. convergens</i> at 18°C.	51
II.4	Differences in weight between the intense (■) and moderate (+) selected lines of <i>H. convergens</i> during development from third instar to pupation.	52
II.5	Efficiency in consumption by <i>H. convergens</i> at different development times from third instar to pupa ($r^2=0.45$).	53
III.1	Degree-days accumulated by the intense selected <i>H. convergens</i> throughout an average year in Corvallis, OR (heavy solid line) and Hermiston, OR (solid line).	66
III.2	Degree-days accumulated by the intense (heavy solid line) and moderate (solid line) selected <i>H. convergens</i> throughout a year in Corvallis, OR.	67
III.3	Degree-days accumulated by the intense (heavy solid line) and moderate (solid line) selected <i>H. convergens</i> throughout a year in Hermiston, OR.	68

LIST OF TABLES

<u>Table</u>		<u>Page</u>
I.1	Developmental threshold (Dth), degree-day (DD°) requirements, and predicted developmental times at 18 and 30°C for fourteen field collected females of <i>H. convergens</i> in Oregon.	32
I.2	Development threshold (Dth), degree-day (DD°) requirements and predicted development times at 18 and 30°C for the intense and moderate selected <i>H. convergens</i> after five generations of selection.	33
II.1	Total consumption, 7-day consumption, and daily consumption by <i>H. convergens</i> at different times of development from third instar to pupation.	54
II.2	Adult longevity, fecundity, and oviposition rate for intense and moderate selected lines of <i>H. convergens</i> .	54
III.1	Mean period over which progeny are produced (T), net replacement rate per generation (R_0), intrinsic rate of increase (r_m), population growth, and doubling time for intense line, moderate line, and wild type <i>H. convergens</i> at 22°C.	69

DEDICATION

To my wonderful parents, Luis and Ana.

You are the best, I love you.

IMPROVEMENT OF BIOLOGICAL CONTROL AGENTS: LABORATORY
SELECTION FOR FAST LARVAL DEVELOPMENT IN THE CONVERGENT
LADY BEETLE, *HIPPODAMIA CONVERGENS* GUERIN-MENEVILLE
(COLEOPTERA: COCCINELLIDAE)

CHAPTER I: INTRODUCTION

The convergent lady beetle, *Hippodamia convergens* Guérin-Méneville, is an important component in aphid population suppression. It is one of the most abundant and widespread species within the genus *Hippodamia* in North America. Although the species is polyphagous, it has a preference for aphids, and is known to feed upon many species of aphids that are pests in agroecosystems.

The convergent lady beetle is widely distributed in the United States and has been introduced for biological control in many different countries to control aphid populations. Mass rearing programs for its introduction have been based on field collected individuals obtained from masses of individuals at overwintering sites. Selection for an improved biotype of *H. convergens* for biological control has never been attempted. The following are steps to improve a biological control agent:

1. Choose trait for selection
2. Do selection trials
3. Assess differences after N generations
4. Check for trade-offs
5. Model potential of "new" selected biocontrol agent
6. Assess potential of "new" selected biocontrol agent.

The questions of interest in the current study were: Can

H. convergens be selected for faster development? If fast development results from artificial selection, what changes occur in the development threshold and degree-day requirements of the beetle? What life history trade-offs (such as survivorship, adult live weight, larval consumption, adult longevity, and fecundity) occur in association with selection for fast development? Are *H. convergens* that have been selected for fast development better biological control agents?.

To answer these questions, the study was divided into three chapters. The objective of each was: 1) select for fast development in *H. convergens*, 2) after selection check for possible trade-offs in mortality, weight, consumption, adult longevity, and fecundity, and 3) assess the potential of the "new" selected biocontrol agent by predictions on population growth and number of generations per year.

CHAPTER II: LITERATURE REVIEW

Biological Control

DeBach (1964) defines biological control as "the action of parasites, predators, or pathogens in maintaining another organism's population density at a lower average than would occur in their absence". The concept of biological control encompasses both the introduction and manipulation of natural enemies by man to control pests (applied biological control) and control that occurs without man's intervention (natural biological control) (Van den Bosch et al. 1982).

New natural enemies are introduced for biological control based on the fact that many, if not most, agricultural pests have been accidentally introduced into the area concerned while their indigenous natural enemies have been left behind. However, the possibilities of controlling indigenous pests by introducing natural enemies of related exotic pests are not excluded (DeBach 1964). Some advantages of biological control programs are that it can be directed at a particular pest, a single program may be effective in keeping down a pest for many years, and in the long term it is one of the least expensive, safest, and most efficient methods of pest control (Samways 1981).

Classical biological control begins with determining whether the target pest is a native or exotic species and then passes through a series of steps involving foreign exploration, quarantine processing of collected material, mass

propagation of the natural enemies, their field colonization, and finally the evaluation of their impact on the pest population (Van den Bosch et al. 1982). Insectary rearing of biological control agents is a critical component of classical biological control. Most natural enemy species are reared at least one generation to ensure that secondary parasites and pathogens are excluded (Hoy 1979). During this phase in biological control programs, the collected material can undergo genetic alteration.

Unintentional Selection

Successful classical biological control programs have evolved in the introduction and establishment of insect natural enemies. Some of the failures in the establishment of predators and parasitoids imported in classical biological control programs from a foreign country can be attributed to genetic alterations during collection, colonization, propagation, release, or establishment. Genetic bottlenecks, inbreeding drift, and inadvertent selection are often suspected to be deterrents to the establishment of natural enemies (Hoy 1979).

Insectary propagation involves more than the maintenance of the stock or increase of populations. Laboratory populations undergo changes in response to selection forces of the environment (Mackauer 1972). Only a limited number of individuals can be collected and processed during foreign exploration; therefore, only a fraction of the total genetic

variation of the original population will be sampled (Roush 1990). In addition, a small source colony results in a greater potential that random processes will cause unintended change. Therefore, there is a greater probability that descendent populations will differ from the parent species, and a higher probability that descendent populations will consist of genetically similar individuals (Mackauer 1972).

Genetic variation is necessary if the newly colonized population must adapt to achieve success. A critical issue for biological control is whether the reduction in variation during mass propagation decreases the chance for success (Roush 1990). Quarantine and mass-rearing phases also produce genetic drift. If the initial sample is small there is an increased likelihood of divergence between the laboratory population and the parent population. Because of this change, the first few generations will suffer the greatest impact (Mackauer 1976).

Inbreeding increases homozygosity. It changes genotypic frequencies by decreasing the proportion of heterozygotes in the population. One way to minimize laboratory selection is to minimize the genetic variance available for selection by inbreeding several lines for each colony and by keeping the strains in the laboratory for as few generations as possible. The establishment's success will be improved by releases of individuals reared from collections made at several sites (Roush 1990).

Artificial Selection

Artificial selection is the alteration over time of phenotypic characteristics in organisms through intervention. The two major categories of traits are discrete (or qualitative) and continuous (or quantitative). With discrete traits, such as number of hairs and eye/body color, there may be one or only a few major genes controlling its expression (Collins 1984).

Most traits that interest breeders are quantitative. In quantitative traits, many genes influence the phenotypic expression of the trait. Thus, clear-cut dominance relationships and modes of inheritance are not seen (Collins 1984).

Quantitative traits have been artificially selected in a wide number of insect species. Laboratory selection to develop resistance in insects has been widely practiced. The beet armyworm *Spodoptera exigua* (Hubner) has been selected for resistance to fenvalerate, permethrin, and methomyl (Brewer et al. 1990). Brown & Payne (1988) selected species of *Aedes*, *Culex*, *Musca*, and *Heliothis* for resistance to DDT, permethrin, malathion, parathion, and other acetylcholinesterase inhibitors, to determine how fast the insects developed resistance to these insecticides.

Parasitoids have also been selected for resistance to pesticides (Pielou & Glasser 1952, Hoy et al. 1990, Javier et al. 1991, and Ke et al. 1991). Similarly, predators, like the

green lacewing, have been selected for resistance to carbaryl (Grafton-Cardwell & Hoy 1986). Field and Hoy (1986) selected for a non-diapausing pesticide-resistant strain of the predaceous mite *Metaseiulus occidentalis* (Nesbitt) to control *Tetranychus urticae* Koch on roses. Their selected strain can be integrated into a rose pest control system without being seriously affected by chemicals and can be an effective predator of *T. urticae* on roses throughout the year. Reproductive potential and humidity tolerance were not affected after selection.

Other traits that have been selected in insects include non-diapausing strains in the gypsy moth (Hoy 1976), thorax length in *Drosophila melanogaster* L. (Partridge & Fowler 1993), life span in *D. melanogaster* (Luckinbill & Clare 1985), body weight (Hillesheim & Stearns 1991), and postponed senescence in *D. melanogaster* (Rose 1984).

Selection for Time of Development

Some *Drosophila* sp. have been selected for fast and slow development rate (Clarke et al. 1961, Prout 1962, Sang 1962, Van Delden & Kamping 1979, Cavener 1983, Knibb et al. 1987). Clarke et al. (1961) found an asymmetrical response of *Drosophila suboscuro* Collin to selection for fast and slow development, they also found a more rapid progress in the slow than the fast line. They concluded that the difference was due to a "development barrier" (epistatic interactions) which prevented development in less than a certain minimum time. In

contrast, Bradley & Saunders (1985) found a more rapid response for fast development rate in the flesh fly *Sarcophaga argyrostoma* (Robineau-Desvoidy), concluding that the fast strain contained fewer alleles or a more homogeneous collection of alleles than the slow strain.

Development time is a polygenic trait (many genes control the expression of the trait) and requires many generations of laboratory selection to obtain individuals with faster development. Van Delden & Kamping (1979), Cavener (1983), and Knibb et al. (1987) have discussed the effect of selection for fast development time on different genes in *D. melanogaster*. Van Delden and Kamping (1979) and Cavener (1983) found evidence that selection for fast development may affect allele frequencies of three polymorphic enzymes (Adh, Gpdh, and 6Pgd).

Tribolium castaneum (Herbst) has also been selected for fast development (Englert & Bell 1969, Englert & Bell 1970). A response to selection for early and late pupation time after six generations resulted in an average response of -0.34 and 0.70 days per generation for early and late pupation respectively. The asymmetrical response was greater for early pupation than for late. There was a high and negative correlation between pupation time and 13-day larval weight, but it was not consistent between pupation time and pupal weight (Englert & Bell 1970).

The honey bee, *Apis mellifera* L., has been selected for shorter development time in an attempt to reduce parasitization by the mite *Varroa jacobsoni* Oudemans (Harbo 1992). Fast development of the honey bee may provide the colony with some resistance to the mite by allowing the mite less time to reproduce. The results showed a rapid development in workers, but stocks with rapidly developing workers did not always produce rapidly developing queens.

Henrich & Denlinger (1982) studied the effect of selection for late pupation and diapause incidence in *Sarcophaga bullata* Parker. They found that individuals artificially selected for greater duration of larval stage were more likely to enter diapause and remained in diapause considerably longer than do unselected individuals.

Selection for fast development has also been practiced in insect natural enemies. Weseloh (1986) selected *Cotesia melanoscela* (Ratzeburg), a parasite of the gypsy moth *Lymantria dispar* (L.), for fast development to improve the synchronization of adults with host larvae of the proper size. The results showed a reduction in the number of days from oviposition to first emergence during selection, but the trend was not significant.

The Family Coccinellidae

Coccinellids are world-wide in distribution and, because of their habits, they are the most frequently encountered of the predaceous Coleoptera (Clausen 1940). The species in the

family are extremely diverse in their habitat and the majority are beneficial because of their predaceous nature, with the exception of some species in the subfamily Epilachninae that are foliage feeders (Hagen 1962). They occur frequently on the leaves of garden plants, and the adults vary in color from red or yellow, sometimes with black spots, to black, sometimes with red or yellow spots. Their shape is usually nearly hemispherical, but some species are more elongate-oval and less convex (Dillon & Dillon 1972).

Predaceous coccinellids have a wide range of accepted food. Apart from feeding on Homoptera and phytophagous mites, they often prey on young instars of Lepidoptera, Coleoptera, Hymenoptera, small nematoceros Diptera and Thysanoptera. Because of their preference for aphids and scales, coccinellids play an important role in the development of biological control (Hodek 1973).

Some characteristics in the Coccinellidae appear to indicate that they are effective predators. Such characteristics include a high searching capacity, an ability to occupy all the habitats and niches of their prey, a generally high fecundity, and a degree of host specificity connected with dependence on certain aphid species for breeding, the latter associated with considerable polyphagy in terms of alternative food for the adults (Hodek 1973).

Coccinellids are holometabolous, they have complete metamorphosis, and pass through the following stages: egg, 4

larval instars, pupa, and adult. The eggs are usually oval or spindle-shaped, vary in color from yellowish to reddish orange and are mostly laid in clusters with each egg attached to the substrate by the narrow end. These clusters are laid on the underside of a leaf or in bark-crevices. A few days before hatching the eggs become greyish. After hatching, the larvae stay on the egg shells for up to one day, and often eat unfertilized nonviable eggs or larvae from later hatching eggs. They then crawl about in search of their normal food. Usually three larval ecdysis separate the four instars. For several days before ecdysis to pupa, the fourth instar remains immobile and does not feed. Some authors separate this stage ("prepupa") from the other instars (Hodek 1973).

Pupation usually takes place *in situ* on the foliage or bark at the point where feeding was completed (Clausen 1940). The pupa is not entirely immobile. If irritated, the head region raises several times. At emergence, adults have the elytra soft and light in color. They acquire their normal appearance only gradually (Hodek 1973).

There is abundant evidence that coccinellids are often a major cause of mortality of aphids, coccids, and spider mites. In regions where coccids are serious pests, particular coccinellid species with high degree of prey specificity are important in the biological control of a pest (Hodek 1973). And, although coccinellids on their own are usually unable to check aphid infestations effectively, they are an important

component of natural control (Hodek 1967). In the list of "cases of biological control of pest insects by imported entomophagous insects" (DeBach 1964), coccids make up about 40 per cent of the species controlled. This contrast with only seven species of aphids in which control has been achieved, in five cases by parasites and in two cases by a complex of parasites and predators (Hodek 1967).

Lady beetles have played a significant role in the development of biological control with the introduction of the vedalia beetle, *Rodolia cardinalis* Muls., into California during the 1880's from Australia. The vedalia beetle saved the citrus industry in California by controlling the cottony cushion scale *Icerya purchasi* Mask. Also, augmentation of natural enemy populations has been practiced by growers and gardeners that collect or buy native lady beetles to release against aphids. Private individuals for years have been collecting the convergent lady beetle from mountain aggregations and selling them to farmers and gardeners (Hagen 1960).

Effect of Temperature on Developmental Rate

In common with all other insects, the development rate of coccinellids depends on the ambient temperature and nutrition (prey spp.). Within the favorable range, the developmental rate of all stages increases with temperature. As the upper threshold of thermal tolerance approaches, further temperature increases produce only a slight increase in development rate.

Above a certain thermal limit, this rate decreases and is followed by complete mortality.

A simple linear relationship between temperature and development rate holds only through the middle range of favorable temperatures. At either end of the range the relationship is not linear. When a straight line is superimposed on development rate and temperature, it intersects the x-axis at the temperature threshold (Campbell et al. 1974). A classic formula that relates temperature and developmental rate is based on the theory that completion of any given stage in development requires the accumulation of a definite amount of heat energy. Because energy is difficult to measure, the effective temperature (i.e. the temperature above the developmental threshold) accumulates as degree-days.

The theoretical assumption that the product of the effective temperature and time is always constant may be written $D (T - a) = C$, where D is the duration of the developmental stage at temperature T , a is the developmental threshold, and C are the degree-day requirements (Hodek 1973). In a linear model, the number of degree-days required by an insect to complete its development above a developmental threshold is measured by the reciprocal of the slope in the linear equation (Campbell et al. 1974).

Hippodamia convergens

The convergent lady beetle, *Hippodamia convergens* Guérin-Méneville, is the most abundant and widespread of *Hippodamia*

in North America. The range of *H. convergens* is from Ontario and British Columbia to the Antilles and Central and South America. The adults vary in length from 4.20 to 7.30 mm, and from 2.50 to 4.90 mm in width. The pronotum has convergent pale spots and the elytra ranges from a full complement of discrete black spots to a nearly immaculate form (Gordon 1985).

Although the species is polyphagous, it prefers aphids. Its importance in suppressing homopteran pests has been extensively reported. Rice & Wilde (1988) considered *H. convergens* as an important predator in suppressing greenbugs *Schizaphis graminum* (Rondani) in sorghum and winter wheat in Kansas. Goodarzy & Davis (1958) reported *H. convergens* as the most beneficial, numerous, and widely distributed predator of the spotted alfalfa aphid in Utah. And, Kring & Gilstrap (1986) found *H. convergens* and *H. sinuata* the most abundant predators of corn leaf aphid *Rhopalosiphum maidis* (Fitch) in grain sorghum in Texas.

Before hibernation, *H. convergens* often joins other *Hippodamia* spp. in valley aggregations. The aggregation of vast numbers of coccinellid beetles in mountainous regions, far removed from the areas in which feeding and reproduction take place, is the result of a pronounced tendency toward migration. This migration has been attributed to several influences, among which are food scarcity, temperature, and air currents (Clausen 1940). *H. convergens* enters hibernation

in late autumn, where diapause is induced mainly by photoperiod and temperature (Hodek 1973).

The development time of *H. convergens* at different temperatures has been widely studied in the United States (Butler & Dickerson 1972, Obrycki & Tauber 1982, Miller 1982). A linear regression model for development rate on temperature has been applied to determine its lower developmental threshold and the degree-day requirements. Miller (1992) calculated the degree-day requirements and developmental threshold for *H. convergens* collected in Arizona and Oregon. The results were compared with two other populations from New York (Obrycki & Tauber 1982) and Texas (Michels & Behle 1991). No difference in the development threshold and degree-day requirements for *H. convergens* were found in populations from different places in the United States. The degree-day requirements for the development of *H. convergens* from egg to adult are 228 heat-units above a threshold of 12.5°C.

CHAPTER III
SELECTION FOR FAST DEVELOPMENT IN THE
CONVERGENT LADY BEETLE *HIPPODAMIA CONVERGENS*
(COLEOPTERA: COCCINELLIDAE)

ABSTRACT

Individuals of the convergent lady beetle, *Hippodamia convergens* Guérin-Ménéville, were selected for fast larval development through five generations at four constant temperatures. Two levels of selection, intense and moderate, were applied, creating two laboratory cultures for comparison with wild type beetles. Statistical analysis comparing development times, developmental thresholds, and degree-days showed that intense and moderate selected individuals after selection, belonged to two significantly different populations ($p < 0.001$). Intense selected beetles developed 11%, 11%, 5%, and 7% faster than moderate selected individuals at 18, 22, 26, and 30°C, respectively. Individuals from the intense selected line had a lower developmental threshold (11.3°C) than individuals from the moderate selected line (12.0°C). Degree-day requirements from egg to adult were also lower in the intense (266 DD°) than the moderate selected line (277 DD°). Wild type beetles required 231 degree-days above a threshold of 13.6°C.

INTRODUCTION

Selection for specific attributes has been practiced on a wide range of traits in plants and animals (Hill & Caballero 1992). For instance, selecting for resistance to pesticides

and environmental stress has been studied for many insect species (Brown & Payne 1988, Brewer et al. 1990). Also, certain life history traits such as adult longevity, thermal sensitivity, and body weight have been selected in *Drosophila melanogaster* L. (Rose 1984, Luckinbill et al. 1984, Huey et al. 1991). Many species of biological control agents have been chosen for "improvement" by selecting for higher fecundity, field parasitism, host acceptance, adult longevity, temperature preference, and temperature tolerance (Hopper et al. 1993). Selection for specific traits in insect natural enemies may provide a better biological control agent for future introductions (Hoy 1976, Hoy 1979).

The developmental rates of an insect may serve as a useful trait for selection. Many insect species have been selected for fast and slow development time (Sang 1962, Englert & Bell 1969, Ochieng'-Odero 1990, Harbo 1992). Weseloh (1986) selected for fast development in *Cotesia melanoscela* (Ratzeburg), a parasite of the gypsy moth, *Lymantria dispar* (L.), to improve synchronization of adults with host larvae of the proper size. He obtained a reduction of the number of days for oviposition to emergence during selection but the trend was not significant.

The introduction of non-indigenous coccinellids for biological control of homopteran pests, in particular aphids and scales, has been widespread (Clausen 1978). The convergent lady beetle, *Hippodamia convergens* Guérin-Ménéville

is one of the most common and widely distributed species in North America (Gordon 1985) and has been introduced in many countries for biological control. The species, although polyphagous, has preference for aphids and constitutes an important component in the suppression of aphid populations (Hagen 1962).

The development of *H. convergens* at different constant temperatures has been well studied (Butler & Dickerson 1972, Obrycki & Tauber 1982, Michels & Behle 1991, Miller 1992), and contributes to our understanding of its function in biological control and the dynamics of predator-prey interactions. Miller (1992) calculated the degree-day requirements (228 DD°) and developmental thresholds (12.5°C) for *H. convergens* collected in Arizona and Oregon. These data were compared to similar studies conducted by Obrycki & Tauber (1982) regarding a population from New York, and Michels & Behle (1991) for a population from Texas. No differences occurred in the development time of the convergent lady beetle between populations collected from these various sources in the United States. Miller (per comm.) noted a wide range in the development of family lines according to individual female sources. Thus, artificial selection for development rate may result in a population with faster development time. If fast development is selected in lady beetles, then what changes occur in the degree-day requirements? Does the developmental threshold change to a lower value in concert with reduced

degree-day requirements in beetles exhibiting fast development?

The objectives of the current study were to: 1) determine the amount of variation in development time occurring within a population of *H. convergens*; 2) select for fast development in the convergent lady beetle; and 3) determine the developmental threshold and degree-day requirements for each of the selected lines.

MATERIALS AND METHODS

The study was divided into three sections: 1) degree-day requirements by wild type female source; 2) selection trials; and 3) degree-day assessment after selection.

Degree-day Requirements by Wild Type Female Source

Adults of *H. convergens* were collected in Oregon during July and August, 1992. Field-collected females were held at room temperature in 1-oz plastic creamers with cardboard lids to obtain egg masses. The egg masses from each female ($n > 5$) within 24 h oviposition were randomly placed into one of four constant temperatures (18, 22, 26, 30°C). A minimum of four egg masses from each female were placed at all temperatures. Each temperature treatment was conducted at a photoperiod of 16:8 (L:D) in 50-70% RH.

First instars were placed individually into single plastic creamers within 8 h of egg hatch. At least twenty first instars from each female were placed at all

temperatures. Larvae were fed daily with pea aphid, *Acyrtosiphum pisum* (Harris), cultured on fava bean. The pea aphid was reared as described by James & Lighthart (1990). Individuals were checked daily at cold temperature (18 and 22°C), and twice a day at the warmer temperatures (26 and 30°C), for time of molting, pupation, and adult emergence. Development times (days) from oviposition to adult emergence were recorded for each offspring of specific field-collected females.

Linear regression models of development rate (1/days) on temperature (X) were used to estimate the lower developmental threshold and the degree-day requirements for the family of progeny from each field-collected female. The lower developmental threshold was determined as the x-intercept of the linear equation, and the degree-day requirements were determined as the inverse of the slope. Estimates for the standard error of the two parameters were calculated as described by Campbell et al. (1974). Predicted days of development were obtained from the formula $Y = k/(T-t)$, where k represents the degree-day requirements, T is the temperature, and t is the developmental threshold.

Selection Trials

Individuals from the field-collected parents completed development at all temperatures in October 1992, and were selected for fast and slow development based on their pre-imaginal development times. There were two levels of

selection: an intense and a moderate selected line.

The intense selected line included individuals with relatively fast development times, individuals that had development times shorter than the group mean. The moderate selected line included individuals with relatively slow development times, individuals that had development times longer than the group mean.

Five males and five females from the first generation were selected from each selected line, and successfully mated. At least five eggs from each female were placed into one of the temperatures. A minimum of twenty eggs per female were placed at all temperatures. A temperature range from 18 to 30°C was used because the preimaginal developmental rate is not linear above temperatures of 30°C (Obrycki & Tauber 1982). The lowest temperature, 18°C, was used because Miller (1992) reported no larval survival beyond the third instar at 13°C and high mortality (83%) at 17°C. Also, Michels & Behle (1991) observed that larvae failed to develop past the first instar at 15°C.

Development times from egg to adult emergence were recorded for the second generation. After adult emergence, beetles were ranked from the slowest to the fastest based on their average development times at each temperature. Selection occurred by continuing the cultures with beetles from parents in the intense line that had development times shorter than the mean or beetles from parents in the moderate

line with development times longer than the grand mean. The same selection procedure was followed for the next three generations of selection. Differences in developmental rate between selected lines were assessed by using t-test comparisons from the Statgraphics (manufactured by STSC, Inc.) computer package.

Degree-day Assessment after Selection

An important aspect of using four different temperatures for this study was to determine if changes occur in the developmental threshold and degree-day requirements before and after selection for fast development in *H. convergens*. To calculate the lower developmental threshold and the degree-day requirements for the intense and moderate selected lines after five generations of selection, a linear model of development rate (Y) on temperature (X) was applied. The lower developmental threshold, degree-day requirements, and predicted development times for both selected lines were determined as previously explained.

RESULTS AND DISCUSSION

Degree-day Requirements by Wild Type Female Source

Miller (1992) reported no differences in the developmental threshold and degree-day requirements among populations of *H. convergens* from Oregon, Arizona, Texas, and New York. Overall, *H. convergens* required 228 degree-days above a threshold of 12.5°C. In the current study, degree-day

requirements and developmental thresholds were calculated for fourteen field-collected females in Oregon (Table I.1), to compare variation within a population. Developmental thresholds ranged from 13.1°C to 13.8°C. Degree-day requirements ranged from 223.2 to 272.6. Predicted development times at 18°C ranged from 47.4 days for a fast female, characterized by a degree-day requirement of 229 above a threshold of 13.2°C, to 55.5 days for a slow female characterized by a degree-day requirement of 273 above a threshold of 13.1°C.

These data demonstrated the existence of significant variation in developmental rates based on isofemale lines. Therefore, individuals of *H. convergens* were chosen on the basis of fast and slow development for an experiment on selecting beetles for fast developmental rates.

Selection Trials

Field-collected individuals of *H. convergens* were selected for fast and slow development times through five generations. The difference in development times between both selected lines was progressively increased through selection at different temperatures (Fig. I.1). Before selection individuals showed no difference in their development times, but after selection the difference became highly significant. The difference in development times between the intense and moderate selected lines five generations after selection were 4.9 days at 18°C ($t = -8.7$, $p < 0.001$), 3.0 days at 22°C ($t =$

-6.9, $p < 0.001$), 1.0 days at 26°C ($t = -4.9$, $p < 0.001$), and 1.5 days at 30°C ($t = -7.5$, $p < 0.001$). With an average increment in the difference per generation of 3.5 ± 0.2 , 1.3 ± 0.3 , 0.5 ± 0.2 , and 0.7 ± 0.1 at 18, 22, 26, and 30°C respectively.

Individuals selected for fast development exhibited a shorter generation time than the moderate selected line (Fig. I.2). All individuals from the intense selected line completed their immature development within 43, 26, 19.5, and 15 days at 18, 22, 26, and 30°C, respectively. In contrast, only 70%, 30%, 60%, and 70% of the individuals from the moderate selected line had emerged at the time of 100% emergence in the fast selected line.

The differences in the development between the intense and moderate selected lines at different temperatures occurred throughout all larval instars, and became more significant at the fourth instar (Fig. I.3). Ochieng'-Odero (1990) also found an overall faster development in the five larval instars of *Cnephasia jactatana* (Walker) selected for fast rate of pupation. Englert and Bell (1969) suggested that individuals of *Tribolium castaneum* (Herbst) selected for early pupation experienced an early depletion of juvenile hormone (JH), while individuals selected for late pupation had a sustained but low output of JH and molting hormone.

A problem commonly reported after selection for specific traits in insect natural enemies is the reduction of genetic

variability (σ^2) in the selected population. Such a reduction may affect establishment of populations in new environments (Roush, 1990). Through selection for fast development time the SE (σ/\sqrt{n}) for development time among all individuals, was reduced from 0.74 to 0.20 at 18°C, from 0.33 to 0.15 at 22°C, from 0.20 to 0.10 at 26°C, and from 0.17 to 0.07 at 30°C.

Degree-day Assessment after Selection

An objective of the study was to determine what changes in the developmental threshold and degree-day requirements had occurred after selection for fast development in *H. convergens*. It was of interest to determine whether selection had either: a) increased the developmental threshold and degree-day requirements; b) decreased the developmental threshold and degree-day requirements; c) increased the developmental threshold and decreased the degree-day requirements; or d) decreased the developmental threshold and increased the degree-day requirements.

After five generations of selection, the intense and moderate selected lines showed to be two different populations (Fig. I.4). Regression of development rate versus temperature for both selected strains demonstrated that the two lines exhibited significantly different slopes ($p < 0.001$). The best fit model for the development rate by temperature for the selected lines was $Y = -0.04 + 0.004*T - 0.0002*T*D$ ($r^2 = 97.7$). Where Y is the expected rate of development (1/days), T is the temperature, and D is the selected line (0 = intense;

1 = moderate). The intense selected line exhibited a lower developmental threshold and lower degree-day requirements than the moderate selected line (Table I.2). The developmental threshold decreased from 13.6°C in the initial unselected generation of *H. convergens* to 11.3°C in the intense selected line. The degree-day requirements from egg to adult development were 266.2 and 276.8 for the intense and moderate selected lines, respectively.

Beetles selected for fast development may have an advantage over non-selected lines because of their lower developmental threshold, as they can be active earlier in the season and can tolerate lower temperatures. Bernal & Gonzales (1993) suggested that parasites of *Diuraphis noxia* (Mordvilko) with lower developmental thresholds would have greater population densities following the winter season, and thus have greater potential as effective biological control agents. In the current study, lower degree-day requirements should allow for a more rapid accumulation of physiological heat units, therefore faster development rates in the intense selected line.

H. convergens has been used in many circumstances for biological control programs of aphids, and has been successfully established in many countries where it was introduced. The purpose of this study was to produce an improved natural enemy for future introductions by selecting for faster development time in *H. convergens*. The results

suggest that lady beetles can be selected for fast development time because of the genetic variability within populations. Also, selection produced a population with a reduced developmental threshold and degree-day requirements. The following chapter will report on studies conducted to determine whether trade-offs in fitness of *H. convergens* had occurred after selection for fast development time.

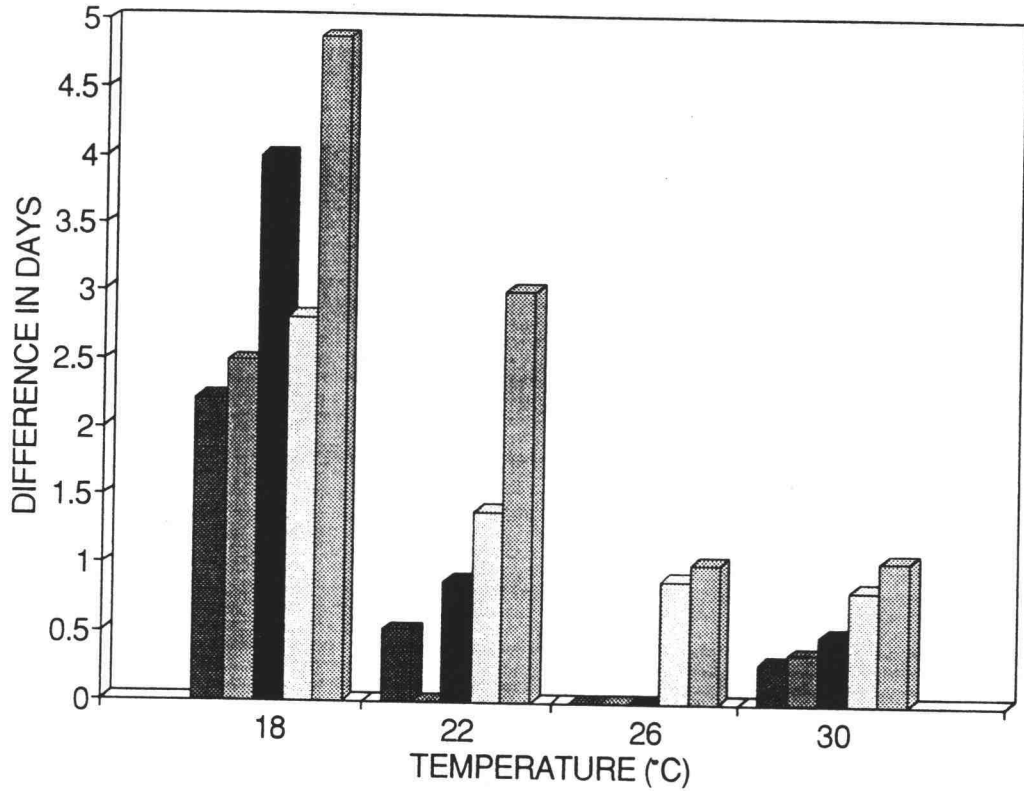


Fig. I.1 Difference in development time between intense and moderate selected *H. convergens* at 18, 22, 26, and 30°C through five generations of selection.

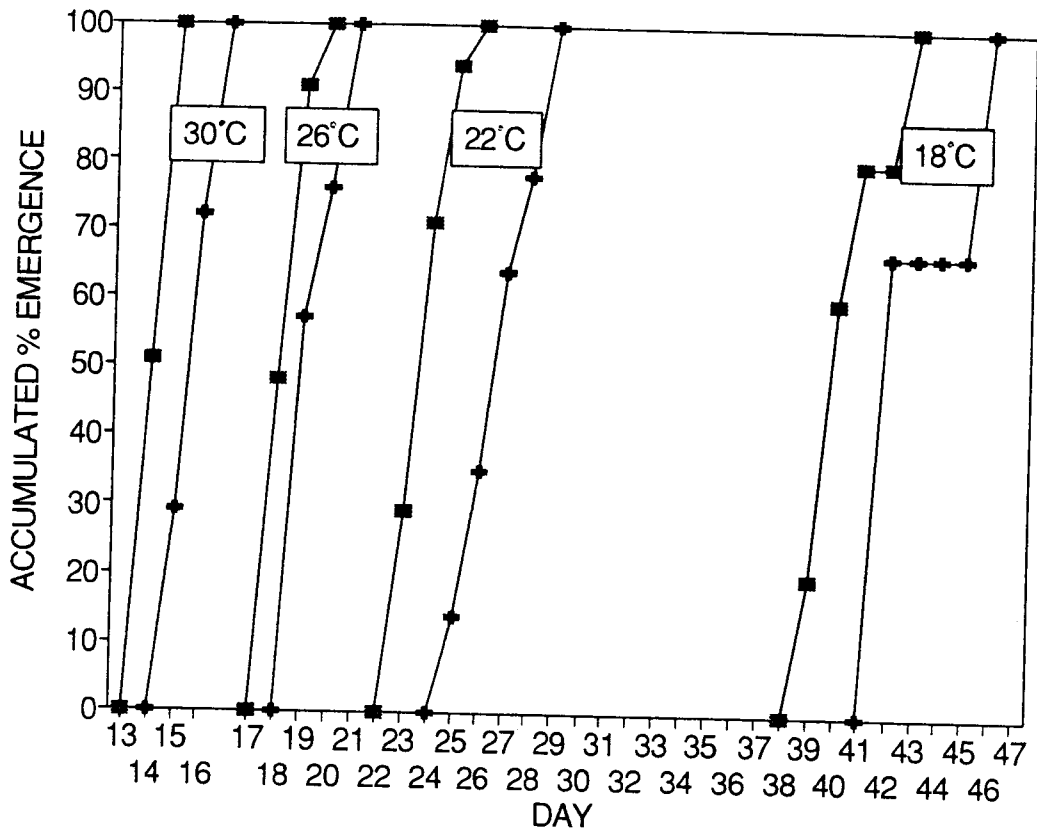


Fig. I.2 Difference in percentage of adult emergence between intense (■) and moderate (+) selected *H. convergens* at 18, 22, 26, and 30°C.

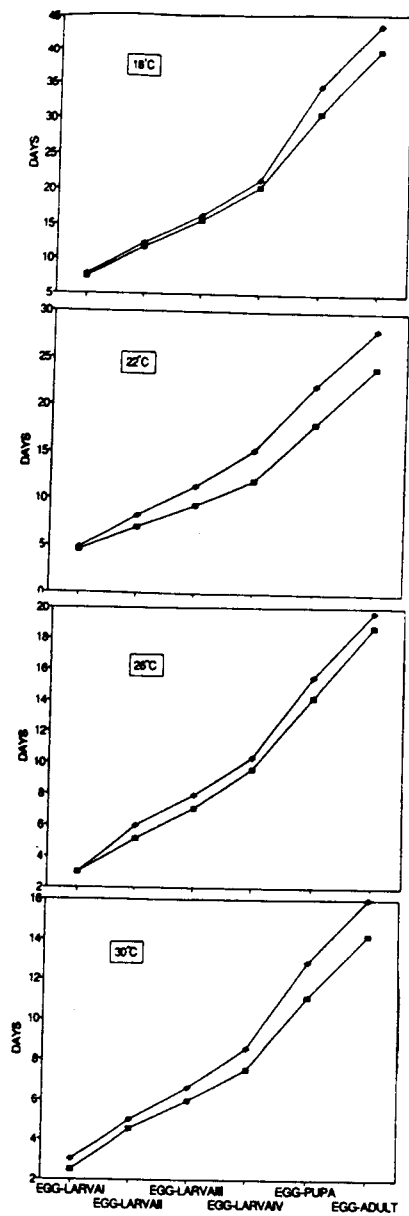


Fig. I.3 Accumulative development time at different preimaginal stages of development for individuals from the intense (■) and moderate (+) selected *H. convergens*.

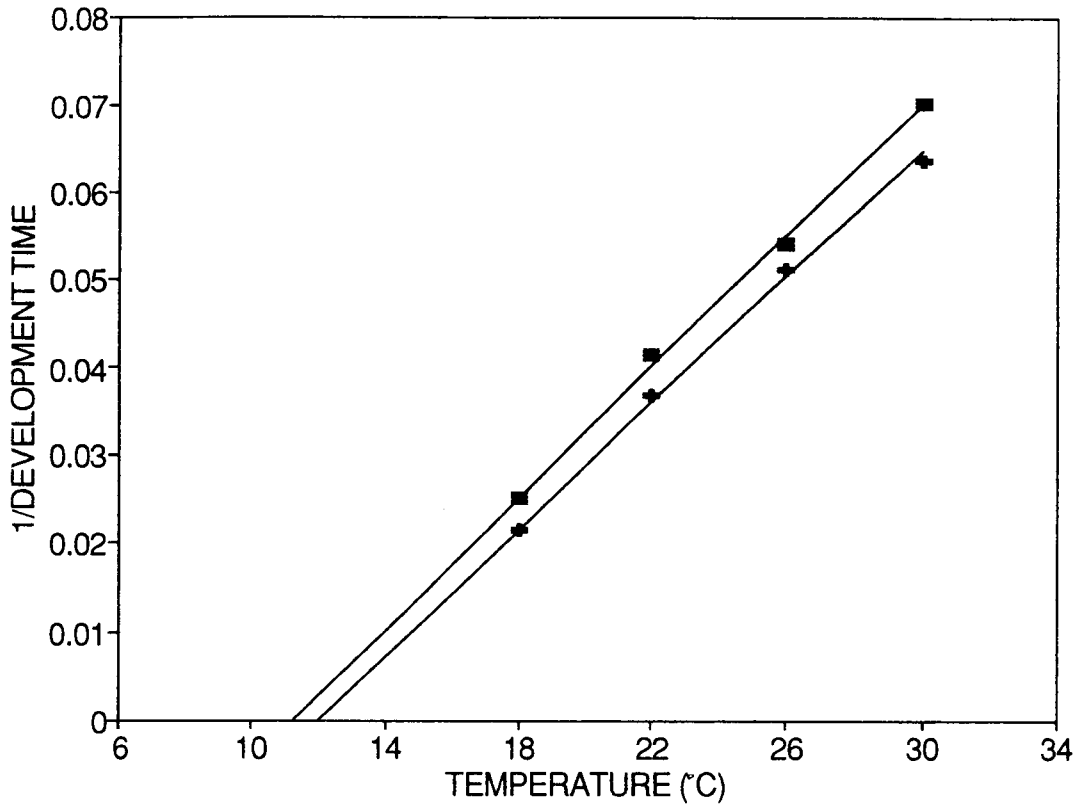


Fig. I.4 Temperature dependent development rate regression lines for the intense (■) and moderate (+) selected *H. convergens*.

Table I.1 Developmental threshold (Dth), degree-day (DD°) requirements, and predicted developmental times at 18 and 30°C for fourteen field collected females of *H. convergens* in Oregon.

Female	n	r ²	Dth	DD°	Predicted days at	
					18°C	30°C
A	34	0.97	13.2±0.4	228.7± 7.6	47.4	13.6
B	24	0.99	13.2±0.3	236.8± 6.0	49.2	14.1
C	39	0.98	13.6±0.2	225.8± 5.1	51.1	13.8
D	43	0.99	13.5±0.2	231.2± 3.7	51.1	14.0
E	15	0.99	13.2±0.3	251.6± 5.8	52.2	15.0
F	31	0.97	13.8±0.3	223.2± 7.0	52.6	13.7
G	22	0.99	13.8±0.2	224.9± 3.5	53.0	13.8
H	8	0.99	13.3±0.3	255.0± 9.3	53.8	15.2
I	11	0.97	13.2±0.5	260.6±14.6	54.4	15.5
J	12	0.99	13.8±0.3	229.0± 5.7	55.0	15.2
K	19	0.99	13.7±0.2	236.1± 3.6	55.2	14.2
L	10	0.99	13.8±0.4	232.9± 7.8	55.3	14.5
M	14	0.97	13.1±0.4	272.6±12.6	55.5	16.1
N	9	0.99	13.3±0.2	259.9± 8.4	55.6	15.6
All	305	0.97	13.6±0.1	230.9± 2.3	53.2	14.1

Table I.2 Development threshold (Dth), degree-day (DD°) requirements and predicted development times at 18 and 30°C for the intense and moderate selected *H. convergens* after five generations of selection.

Selection	Dth	DD°	Equation	r ²	Predicted days at	
					18°C	30°C
Intense						
E	12.2±0.7	43.4± 2.6	-0.28+0.023X	0.99	7.5	2.4
I-IV	10.2±1.3	171.1±15.0	-0.59+0.006X	0.98	21.9	8.6
P	12.3±1.6	56.7± 7.1	-0.22+0.018X	0.95	9.9	3.2
E-A	11.3±0.2	266.2± 4.3	-0.04+0.004X	0.97	39.7	14.2
Moderate						
E	12.6±1.0	46.6± 3.6	-0.29+0.023X	0.98	7.9	2.4
I-IV	11.0±0.1	187.8± 1.9	-0.59+0.005X	0.99	26.8	9.9
P	12.0±0.7	57.4± 3.0	-0.21+0.017X	0.99	9.6	3.2
E-A	12.0±0.5	276.8±10.1	-0.04+0.004X	0.96	46.1	15.4

E - egg stage

I-IV - from first to fourth instar

P - pupal stage

E-A - from egg to adult emergence

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CHAPTER IV
EVALUATION OF CERTAIN LIFE HISTORY TRAITS
IN *HIPPODAMIA CONVERGENS* (COLEOPTERA: COCCINELLIDAE)
SELECTED FOR FAST DEVELOPMENT

ABSTRACT

Individuals of the convergent lady beetle *Hippodamia convergens* Guerin-Meneville, selected for fast development rates (intense selected line) through five generations, were assessed for unintended affects on adult body weight, survivorship, consumption, fecundity, and adult longevity. Individuals from the intense selected line were compared with individuals from a moderate line and field-collected wild type beetles. After selection, survivorship at 18, 22, and 26°C was improved 9.4%, 8.5%, and 22.2%, respectively, in the intense selected line compared to a moderate selected line. Selection for fast development did not affect adult body weight (19.6 mg at 22°C), larval consumption (106 mg of pea aphids), fecundity (344 eggs), or adult longevity (53 days).

INTRODUCTION

Selection for "beneficial" traits in insect natural enemies can enhance the effectiveness of biological control agents (Hoy 1979). However, populations selected for a specific trait provide an improved biocontrol agent only if other important life history traits are not affected negatively. For instance, a trait such as

developmental time could be shortened through selection and provide a superior biocontrol agent if body weight, consumption, fecundity, and adult longevity were not adversely affected.

Selection for fast development can produce some unexpected changes (pleiotropic effects) in other genes that can reduce the fitness of the selected line. Van Delden & Kamping (1979) and Cavener (1983) found that selection for fast development affected allele frequencies of three enzyme polymorphisms in *Drosophila melanogaster* L. Selection for early and late pupation time in *Tribolium castaneum* (Herbst), resulted in a negative correlation between pupation time and 13-day larval weight (Englert & Bell 1970). Also, selection for fast larval development in the flesh-fly, *Sarcophaga argyrostena* (Robineau-Desvoidy), produced a reduced incidence of pupal diapause in short daylengths (Bradley & Saunders 1985).

Individuals of *Hippodamia convergens* Guérin-Méneville selected for fast development time (intense selected line) completed development from egg to adult 11%, 11%, 5%, and 7% faster than a moderate selected line at 18, 22, 26, and 30°C, respectively (see Chapter I). In addition, individuals from the intense selected line had a lower developmental threshold (11.3°C) and lower degree-day requirements (266 DD°) than the moderate line

(277 DD° above a threshold of 12.0°C). The objective of the current study was to check for unintended affects on body weight, mortality, consumption, adult longevity, and fecundity after selection for fast development in *H. convergens*.

MATERIALS AND METHODS

Populations of *H. convergens* previously selected for fast (intense selected line) and slow (moderate selected line) development rates were used for the experiments. Details of the selection experiment are explained in Chapter I. Individuals from the fifth generation of the intense and moderate selected lines were assessed for live adult weight, mortality, daily and total consumption, fecundity, and adult longevity.

Weight and Mortality

A comparison of live adult body weight and pre-imaginal mortality was conducted using selected and unselected beetles. Live adults from the intense and moderate selected lines were weighed within 24 h after emergence from the fifth generation of selection. Weights were measured to the nearest 0.1 mg using a Fisher Scientific Electronic Balance. Also mortality from first instar to adult emergence at 18, 22, 26, and 30°C was compared between intense and moderate selected lines. Mortality within each instar was compared between

both selected lines at 18°C.

Larval Consumption

Possible effects of selection for fast development concerning the total number of prey consumed by third and fourth instars, and consumption rates were assessed in two experiments. The first experiment consisted of observing consumption over a 24 h period by third and fourth instars for the two selected lines and a field-collected wild type line. Third instars were used to initiate the consumption study. Larvae (N = 15) were randomly taken from the intense selected strain, moderate selected strain, and field-collected individuals. First and second instars were not used because consumption could be more accurately determined in third and fourth instars. Also, the third and fourth instars exhibited higher differences in development rate between the selected lines.

The experiment was conducted at $21 \pm 1^\circ\text{C}$ in a controlled temperature chamber. Each third instar larva was fed a daily allotment of 15 full grown pea aphids, *Acyrtosiphum pisum* (Harris). Fourth instars were fed 20 aphids each on a daily basis. Pea aphids were cultured on fava bean as described by James & Lighthart (1990). Aphids were weighed as a group before the experiment. An individual larva and aphids were placed in 5-oz containers. A terminal stem of fava bean was placed into

a glass tube containing water to maintain turgid leaves and live aphids. After 24 h, the total weight of aphids in the container was recorded. Control trials consisting of identical quantity of aphids and plant material, but with no beetles, were kept under the same conditions.

Consumption throughout the third and fourth instars was recorded daily. Total consumption was obtained from the summation of daily consumption from the third instar to the day of pupation. Also, weights of the third and fourth instars after molting, the pupa, and the adult were recorded for each individual. Efficiency in consumption was measured as the amount of aphids consumed from the third instar to pupation divided by the pupal weight of the beetle.

The second experiment was conducted to compare the increase in body size, within a seven day period, for the intense and moderate selected individuals allowed to search for aphids on a plant. Pots (8 inch dia.) were planted with approximately 30 fava bean seeds per pot (N = 30). One week after germination the plants in each pot (ca. 25 plants/pot, 2.5 inches tall, and 2-3 opened leaves) were inoculated with 250 mg of aphids. A single third instar was added to the aphid-plant microcosm 24 h after inoculation with aphids. Ten control cages contained aphids but no beetle larva. The pots were covered with a 25cm x 35cm cloth mesh screen. All cages

were maintained at a constant temperature of approximately $21 \pm 1.5^\circ\text{C}$.

The larvae and aphids remained undisturbed on the cages for one week. Beetle larvae were then removed and weighed. Each larva was then reared individually at $21 \pm 1.5^\circ\text{C}$ until pupation in 1-oz plastic creamers. The development time from the third instar to pupation was recorded. Larval weight-gain during the seven days of encagement were compared between the intense and moderate selected line. These data were used to compare differences in weight-gain between the selected lines during a fixed period of time before pupation.

Fecundity and Adult Longevity

Fecundity and adult longevity were compared among selected and unselected beetles to determine possible changes in these traits following selection for fast development time. Individuals ($N = 15$) were randomly taken from each of the selected lines. Ten adult wild type females were collected from the field.

After emergence males and females from the intense selected line were placed together for two days to allow mating. The same procedure was followed for moderate selected individuals. After an opportunity to mate, females and males from both selected lines and field-collected females were placed individually into 1-oz plastic creamers with cardboard lids. From emergence to

death, all females were kept at room temperature ($21 \pm 1.5^\circ\text{C}$) and fed daily with pea aphids. The number of eggs laid per female was recorded daily. Eggs were kept at 26°C until hatch to check for viability. Longevity was recorded for males and females of the two selected lines. Beetles were fed daily with pea aphids from the time of adult emergence and checked daily for time of death.

RESULTS AND DISCUSSION

Weight and Mortality

Live adult weight was compared between unselected beetles and beetles from the intense selected line five generations after selection. The results demonstrated that live adult body weight was not affected after selection. Adults from the intense selected line weighed on average 19.3, 19.5, 19.5, and 18.5 mg at 18, 22, 26, 30°C , respectively. Adult weight in the intense selected line remained constant before and after selection at 18°C ($t = -1.1$, $p = 0.3$), 22°C ($t = -0.8$, $p = 0.4$), 26°C ($t = 1.5$, $p = 0.1$), and 30°C ($t = 1.1$, $p = 0.3$). Live adult weight was also compared between the intense and moderate selected lines. Adult weights from the intense selected line were higher than the moderate selected line at all temperatures tested (Fig. II.1). Differences in adult weight between selected lines were 2.3, 1.9, 2.7, and 4.4

mg at 18, 22, 26, and 30°C, respectively. The difference was significant at 26 and 30°C ($p < 0.001$).

The results also showed a significant negative correlation between development time and body weight after selection. The shorter the development time, the higher the body weight. The correlation was significant at 18°C ($t = -2.3$, $p = 0.05$), 22°C ($t = -2.9$, $p = 0.005$), 26°C ($t = -3.5$, $p = 0.001$), and 30°C ($t = -4.5$, $p < 0.001$). Similarly, Ochieng'-Odero (1990) found no significant effect on pupal weight of *Cnephasia jactatana* (Walker) selected for a fast development rate.

Larval survivorship improved at cold temperatures after selection for fast development ($t = 19.9$, $p = 0.03$) (Fig. II.2). Mortality in the intense selected line was 73.1%, 25.2%, and 35.4% at 18, 22, and 26°C, respectively, while mortality in the moderate selected line was 82.5%, 33.7%, and 57.6% at the same temperatures. Miller (1992) reported a high mortality of 83% at 17°C for nonselected individuals. The lower mortality at cold temperatures in the intense selected line may be attributed to the reduction in the lower developmental threshold after selection (see Chapter I).

Improvement in survivorship at low temperatures after selection for fast development occurred during the first instar of development. Percent mortality at 18°C

during the first instar was three times higher in the moderate selected line than the intense line (Fig. II.3).

Larval Consumption

The total consumption, 7-day consumption, and daily consumption were compared from third instar to pupation for the two selected lines and wild type beetles (Table II.1). There was no relationship between total consumption and development time ($t = -0.01$, $p = 0.9$). Individuals from the intense selected line ate the same total amount of aphids as the other lines. Larvae consumed an average 105.8 (SE = 1.6) mg of pea aphids during the third and fourth instars.

Within a 7-day period individuals that developed faster consumed more aphids (by weight) than slow individuals ($t = -5.4$, $p < 0.001$). The result was confirmed in the second experiment, where larvae were able to search for aphids in the plant. Intense selected individuals gained significantly more weight within a 7-day period ($t = -2.6$, $p = 0.02$) than individuals of the moderate line (Fig. II.4). After a 7-day period, larvae from the intense selected line weighed 27.7 mg, 8.7 mg more than the moderate selected line. As expected, individuals from the intense selected line were nearer pupation than individuals from the moderate selected line.

A negative relationship occurred between development

time and feeding rate ($t = -5.0$, $p < 0.001$). Larvae exhibiting fast development ate 0.9 mg more aphids per day than slow individuals. However, fast individuals of *H. convergens* ate fewer aphids per milligram of weight ($t = 5.1$, $p < 0.001$) than slow individuals (Fig. II.5). Daily, larvae with fast development ate 0.6 mg fewer aphids per milligram of weight than slow growing larvae. Thus, feeding efficiency was higher in fast individuals than slow individuals. Sharma & Norris (1993) also found fast growing larvae of *Trichoplusia ni* (Hubner) to be more efficient in converting consumption mass into body mass.

The results suggest that physiological differences in consumption between the intense and moderate selected lines allow fast individuals to eat more aphids daily and reach a critical body mass in a shorter period of time. On the other hand, fast individuals may require a higher number of aphids daily in order to complete their development. This would be disadvantageous for them in situations where aphids are scarce and would favor slower growing individuals.

Fecundity and Adult Longevity

Longevity and fecundity were compared among the intense line, moderate line, and wild type beetles. No significant differences were found in adult longevity between the selected lines of *H. convergens* ($t = -0.8$, p

= 0.4) (Table II.2). Average longevity of adult lady beetles was 52.8 days (SE = 3.8). Also, there was no difference in adult longevity between males and females of the convergent lady beetle ($t = 0.1$, $p = 0.9$). Females and males lived an average of 50.5 (SE = 5.1) and 56.2 (SE = 5.8) days, respectively. Ochieng'-Odero (1990) reported that adult longevity was longer in the fast strain than the slow strain of *C. jactatana*.

No significant differences were observed between selected lines in the fecundity of *H. convergens* ($t = -0.52$, $p = 0.6$) (Table II.2). On average a female laid approximately 344 (SE = 49.1) eggs during its life span. Clausen (1915) reported an average of 358 eggs laid for a *H. convergens* female, and Peckman & Wilde (1993) an average of 361 eggs per female. Likewise, there was no difference in the oviposition rate between intense and moderate selected lines ($t = 0.1$, $p = 0.9$), and between intense and unselected females ($t = -1.15$, $p = 0.3$). On average, a female lady beetle laid 11.3 (SE = 0.8) eggs daily. Clausen (1915) and Peckman & Wilde (1993) reported an average daily oviposition of 8.9 and 14.7 eggs, respectively. Thus, selection for fast development in *H. convergens* had no negative effects on fecundity. Ochieng'-Odero (1990) found that fecundity was significantly less in slow selected *C. jactatana*.

Overall, the results indicated that no negative

effects occurred in certain life history traits of *H. convergens* following five generations of selection for fast development. In fact, survivorship improved when *H. convergens* was selected for fast development. No negative effects were observed in body weight, consumption, fecundity, and adult longevity after selection for fast development. Studies on population dynamics are needed to further assess the potential of beetles selected for fast development. The next chapter will predict population growth and number of generations per year for the intense and moderate selected lines.

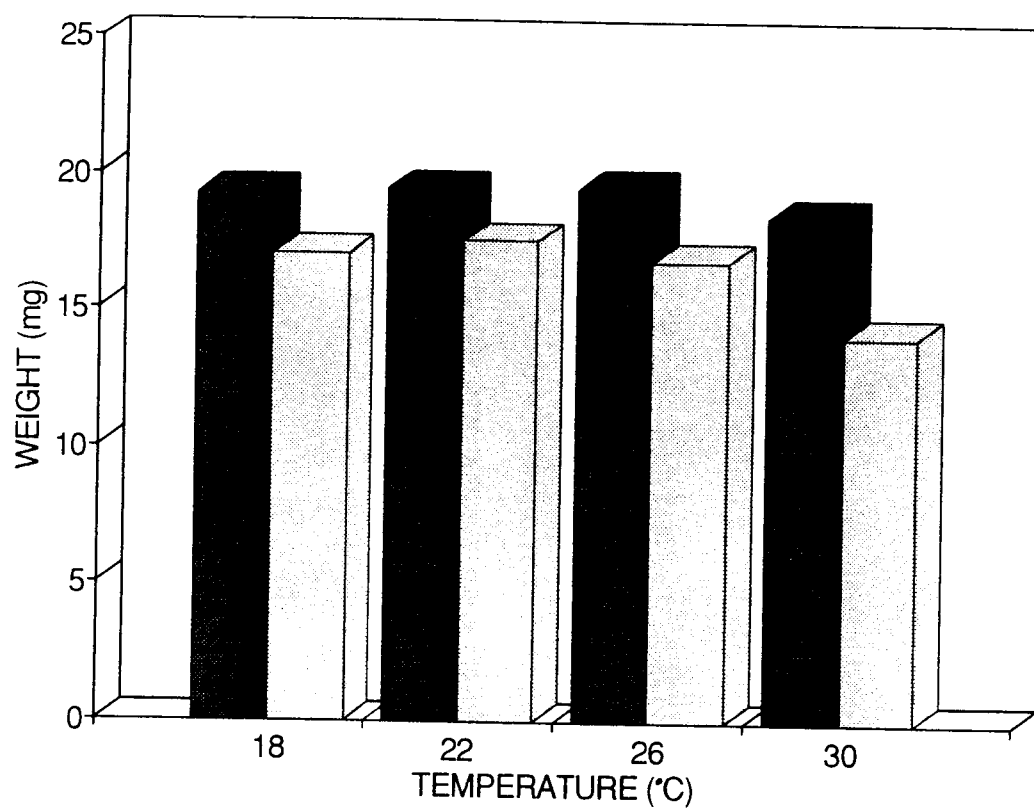


Fig. II.1 Live adult weight for intense (black bars) and moderate (white bars) selected lines of *H. convergens* at different temperatures.

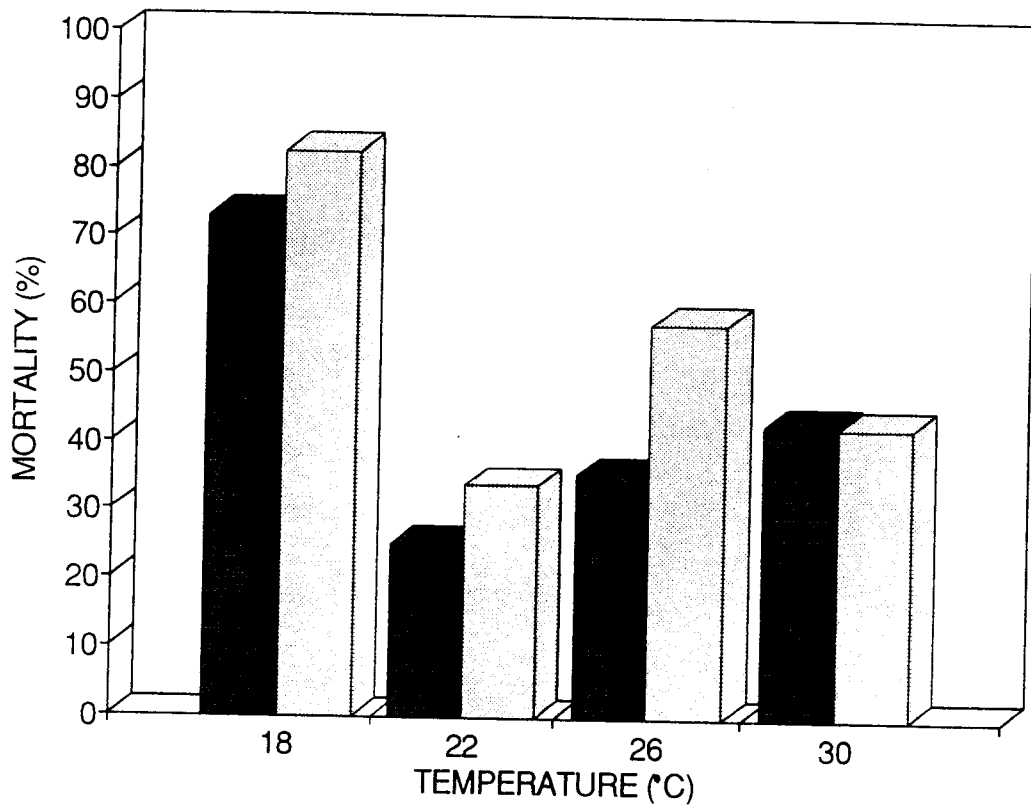


Fig. II.2 Mortality for intense (black bars) and moderate (white bars) selected lines of *H. convergens* at different temperatures.

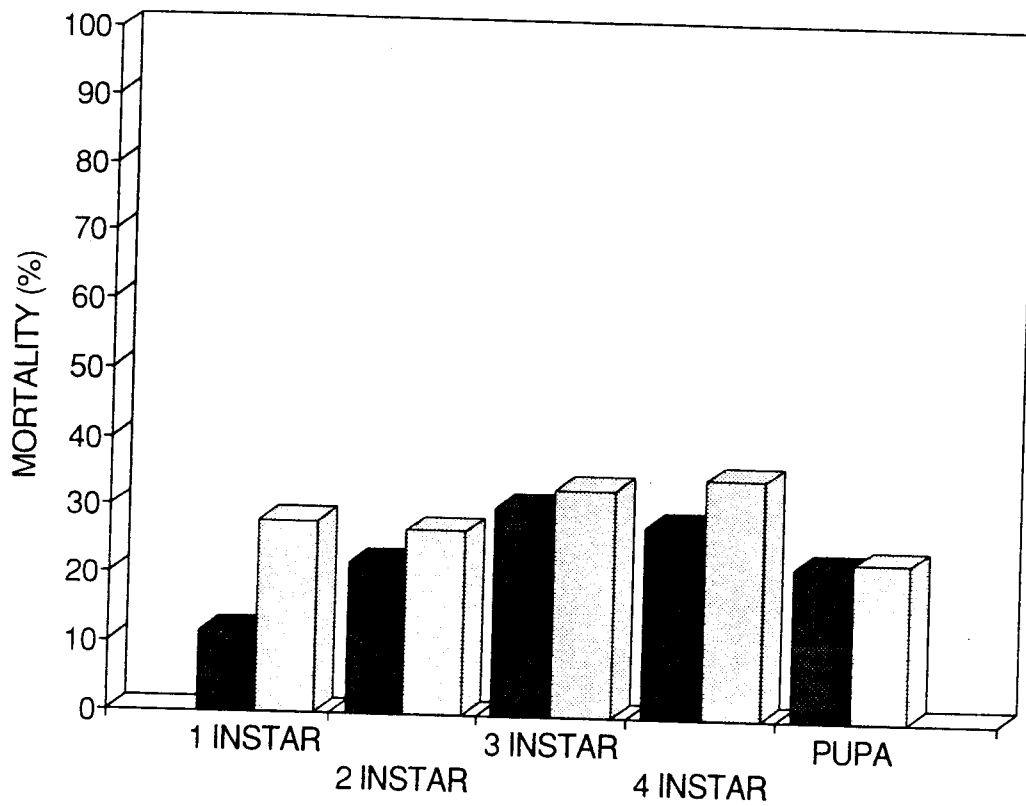


Fig. II.3 Age specific mortality for intense (black bars) and moderate (white bars) selected lines of *H. convergens* at 18°C.

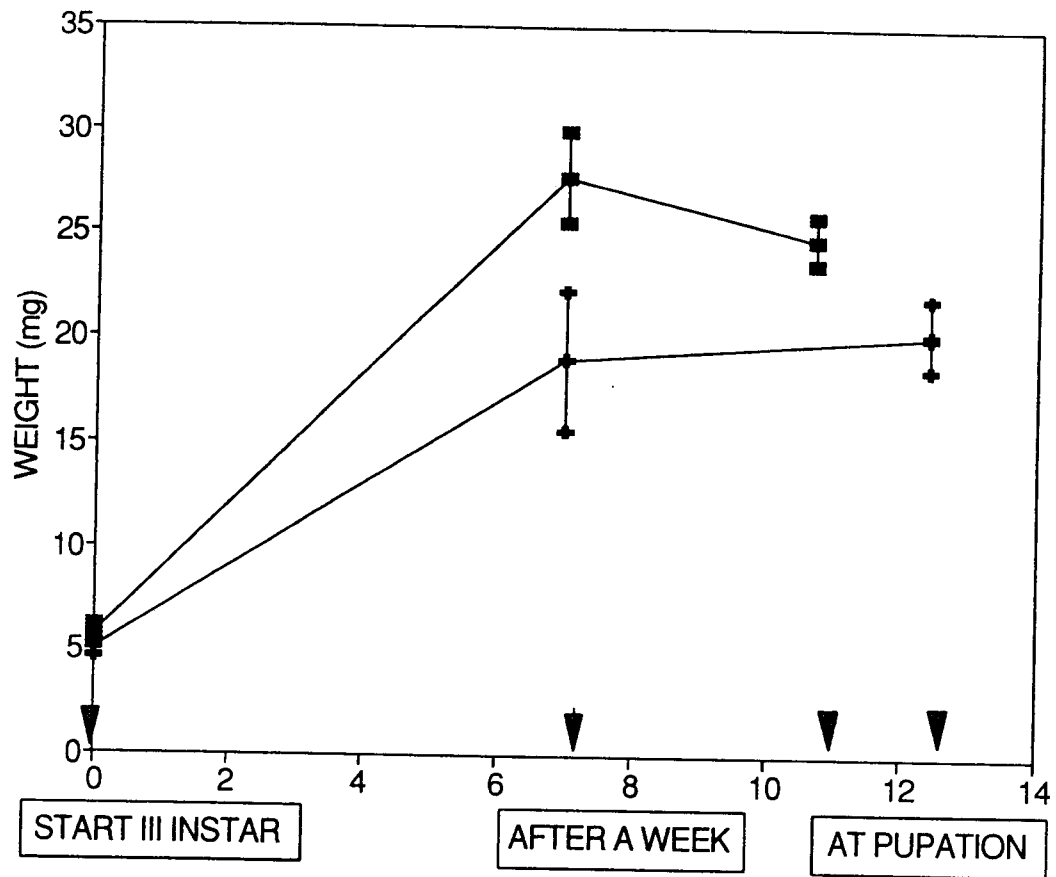


Fig. II.4 Differences in weight between the intense (■) and moderate (+) selected lines of *H. convergens* during development from third instar to pupation.

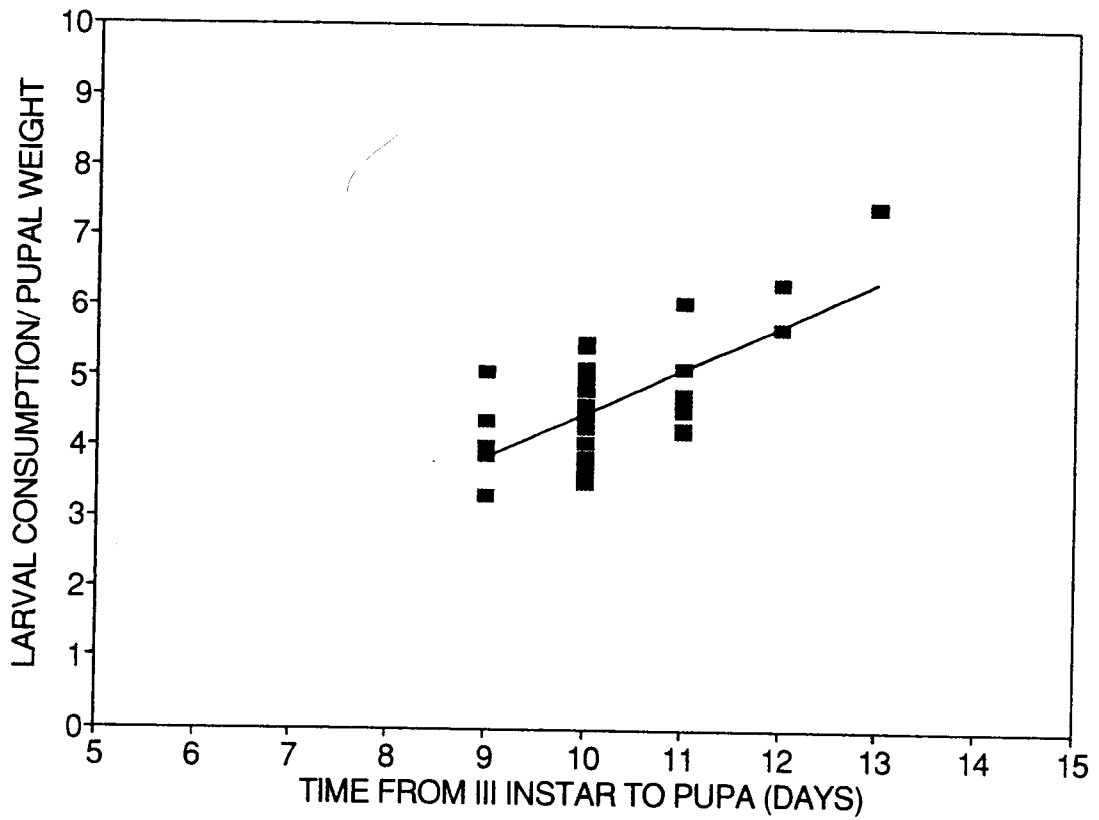


Fig. II.5 Efficiency in consumption by *H. convergens* at different development times from third instar to pupa ($r^2=0.45$).

Table II.1 Total consumption, 7-day consumption, and daily consumption by *H. convergens* at different times of development from third instar to pupation.

Number of days from third instar to pupation	Total consumption (mg) \pm SE	7-day consumption (mg) \pm SE	Daily consumption (mg) \pm SE
9	100.6 \pm 4.1 ^a	96.1 \pm 4.6 ^a	11.2 \pm 0.4 ^a
10	106.3 \pm 4.8 ^a	95.1 \pm 5.4 ^a	10.6 \pm 0.5 ^a
11	106.8 \pm 5.4 ^a	80.5 \pm 6.1 ^b	9.7 \pm 0.5 ^b
12	109.6 \pm 8.1 ^a	64.5 \pm 9.3 ^b	9.1 \pm 0.8 ^b
13	85.0 \pm 10.7 ^a	41.4 \pm 12.2 ^b	6.5 \pm 1.0 ^b

Numbers with indices of different letters are significantly different (t-test, $p < 0.05$)

Table II.2 Adult longevity, fecundity, and oviposition rate for intense and moderate selected lines of *H. convergens*.

	Longevity \pm SE	Fecundity \pm SE	Oviposition rate \pm SE
Intense selection	55.4 \pm 6.5	362.8 \pm 59.6	12.1 \pm 1.2
Moderate selection	50.4 \pm 4.2	308.0 \pm 91.5	12.3 \pm 2.3
Unselected	-----	-----	9.8 \pm 1.4
Average	52.8 \pm 3.8	343.5 \pm 49.1	11.3 \pm 0.8

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CHAPTER V
IMPACT OF SELECTION FOR FAST DEVELOPMENT
IN *HIPPODAMIA CONVERGENS* (COLEOPTERA:
COCCINELLIDAE) ON BIOLOGICAL CONTROL

ABSTRACT

Individuals of the lady beetle, *Hippodamia convergens* Guérin-Ménéville, previously selected for different developmental rates (intense selected line) were compared for their potential as natural enemies of aphids. The intrinsic rate of increase (r_m) and number of generations per year were calculated for an intense selected line and compared to a moderate selected line and wild type beetles. The r_m was higher for the intense (0.099) than the moderate selected line (0.091) and wild type (0.092). Over a 60-day period the intense selected line can produce 37,993 individuals; 1.6 and 1.4 times more than the moderate and wild type lines, respectively. Also, the intense selected line can accumulate more degree-days and produce 0.5 and 0.7 more generations throughout a year in Corvallis, OR and Hermiston, OR, respectively than the moderate line. Thus, data on r_m and temperature records from two distinct locations suggest that a population of *H. convergens* selected for fast development rate may perform as a superior biological control agent.

INTRODUCTION

Temperature has a major effect on the appearance and dynamics of insect populations in the field. Therefore heat

accumulations (commonly expressed in degree-days) above a given temperature threshold have been widely used to predict the effect of temperature on biological processes (Arnold 1960, Baskerville & Emin 1969). For this purpose, many degree-day methods have been proposed for predicting insect development and biological events critical in insect pest management (Pruess 1983). Degree-day models have been used in predicting the field occurrence of *Myzus persicae* (Sulz.) (Whalon & Smilowitz 1979), *Rhagoletis pomonella* (Reissig et al. 1979), *Heliothis virescens* (F.) (Tingle & Mitchell 1988), *Parabemisia myricae* (Kuwana) (Walker & Aitken 1993), and *Harrisina brillians* Barnes & McDunnough (Roltsch & Mayse 1993). Degree-day models are also applied in predicting optimal time for chemical control. Such applications are optimal spray dates of fenvalerate and dimethoate to control *Rhyacionia frustrana* (Comstock) (Gargiullo et al. 1985) and diazinon and azinphosmethyl to control *Grapholitha molesta* (Busck) (Rice et al. 1984).

In general, development rates in insect natural enemies are slower than their host/prey. The degree-day requirements and developmental thresholds of natural enemies are higher than those of their hosts. The build-up of a natural enemy population is delayed until average temperatures increase and the host has become established. Any adult natural enemy that emerges from diapause before the host/prey will find no food at all (Campbell et al. 1974).

Hippodamia convergens Guérin-Méneville, is multivoltine. In late autumn adult beetles migrate to the mountains, where they enter diapause for the winter. In early spring the overwintered beetles become active and start accumulating degree-days. Selection for fast development in *H. convergens* resulted in a decrease in the lower developmental threshold. Individuals selected for fast development (intense selected line) required 266 degree-days to complete development from egg to adult above a threshold of 11.3°C. A moderate selected line required 277 degree-days above a threshold of 12.0°C. And field-collected wild type beetles required 231 degree-days above a threshold of 13.6°C (see Chapter I).

The purpose of this study was to compare individuals from cultures of *H. convergens* that had been selected for fast development rate. The beetles were compared for their potential as biological control agents of aphids. The beetles were assessed relative to their rate of population growth and the number of generations throughout a year.

MATERIALS AND METHODS

The intense selected line was compared with a moderate selected and unselected lines to determine whether individuals selected for fast development time (intense selected line) were better for biological control programs. Two parameters were evaluated: 1) population growth 2) number of generations per year.

Population Growth

Population growth in *H. convergens* from two selected lines, intense and moderate, and from an unselected wild type line were compared over a 60-day period.

A mathematical equation for calculating population growth was used to measure the potential population increase in both selected lines. The formula used was $N_t = N_0 e^{rt}$, where N_0 is the initial number of organisms, r is the intrinsic rate of increase under optimal conditions, t is the amount of time elapsed, and e is the constant 2.72.

The intrinsic rate of increase (r_m) was measured using the following formula: $r_m = \log_e R_0 / T$. Where R_0 is the net replacement rate per generation and T is the mean of the period over which progeny are produced. The net replacement rate (R_0) was calculated assuming that half of the total number of eggs laid by a single female will produce female offspring. The value for R_0 (175 eggs) was then multiplied by the total mortality from first instar to adult emergence at 22°C for the intense (0.25) and moderate selected lines (0.33). Obrycki & Tauber (1982) reported a total mortality of 14% at 21.1°C for wild type beetles, the value was used to estimate the R_0 for unselected individuals. Population doubling time was obtained by deriving t from $e^t = 2$.

All estimates were based on data from a constant temperature of 22°C. A temperature of 22°C was used because temperature has an effect on the total number of eggs laid per

female (Ratte 1985). And the data for fecundity were conducted at $21 \pm 1.5^\circ\text{C}$.

Number of Generations

The number of generations per year were estimated based on total degree-day accumulations from two field sites. Maximum and minimum daily temperatures for the past fifteen years (1979-1993) were collected from the Corvallis Oregon Weather Station located 70.1 meters above sea level ($123^\circ 11'$ Long. and $44^\circ 38'$ Lat.) and Echo Oregon Weather Station (10 miles from Hermiston) at 231.6 meters above sea level ($119^\circ 21'$ Long. and $45^\circ 42'$ Lat.). Corvallis and Hermiston were two collecting sites for wild-type beetles used in the selection experiment. Both locations are important in Oregon's agriculture and have different weather patterns during the year. Average temperatures were entered in a degree-day model by Baskerville & Emin (1969) to obtain the number of degree-days accumulated by intense and moderate selected lines throughout a year.

Degree-days were accumulated above a lower developmental threshold of 11.3°C for the intense selected line, 12.0°C for the moderate selected line, and 13.6°C for wild type unselected beetles (see Chapter I). The number of generations per year for the two selected lines and field-collected wild type line were obtained by dividing the total number of accumulated degree-days in an average year by the degree-days required for development from egg to adult.

RESULTS AND DISCUSSION

Population Growth

The intrinsic rate of increase (r_m) is a useful statistic for describing population growth rates. Estimates of r_m have been used to assess the potential effectiveness of natural enemies. For instance, Obrycki et al. (1993) compared the intrinsic rate of increase, net reproductive rates, and preoviposition periods of *Propylea quatuordecimpunctata* L. from populations collected in Canada, France, and Turkey. He found no differences in the values of the three parameters among populations. Also, Force & Messenger (1964) estimated the net reproductive rate and innate capacity of increase for three species of hymenopterous parasitoids of the spotted alfalfa aphid, *Therioaphis maculata* (Buckton), to assess the effectiveness of each species as an aphid natural enemy.

The r_m value for the intense selected line was higher (0.099) than moderate selected (0.091) and wild type (0.093) individuals. Therefore, a population founded by individuals from the intense selected line will increase more rapidly than a population founded by individuals from the moderate selected and wild type lines. The intense selected line can produce 1.6 and 1.4 times more individuals than the moderate selected line and wild type beetles, respectively, after 60 days. Doubling time was shorter in the intense selected line (7.0 days) than the moderate (7.6 days) and unselected (7.5 days)

lines (Table III.1).

The results suggest that the intense selected line has a greater potential for increasing population numbers because of their higher survivorship and shorter development time from egg to adult. This is an important aspect for biological control programs, especially during mass production, where high numbers of a natural enemy may be needed in a short period of time and where production costs are high.

Number of Generations

In general, Hermiston has colder winters and warmer summers than Corvallis. During summer, beetles accumulated a higher number of degree-days in Hermiston than in Corvallis. The intense selected line accumulated 1048.0 degree-days in Corvallis and 1405.6 degree-days in Hermiston throughout the season (Fig. III.1).

Eggs from the intense selected line started accumulating degree-days on Julian-day 56 at Corvallis and Hermiston. In Corvallis, eggs from the moderate selected line started accumulating degree-days also on Julian-day 56. But in Hermiston eggs from the moderate selected line, because of their higher developmental threshold, started accumulating degree-days 10 days later than the intense selected line. After a cold winter (eg. in Hermiston), immature development in the intense selected line is active earlier in the season than the moderate line. Eggs from a wild type population started accumulating degree-days on Julian-day 66 and 69 in

Corvallis and Hermiston, respectively (10 and 13 days later than the intense selected line).

The intense selected line accumulated higher degree-days than the moderate selected (Fig. III.2 & III.3) and unselected lines in both locations. The moderate selected line accumulated 937.5 and 1284.6 degree-days in Corvallis and Hermiston, respectively. And, wild type beetles accumulated 731.7 and 1046.4 degree-days in Corvallis and Hermiston, respectively. At the end of one year, the number of generations completed by the intense selected line were higher than the moderate selected and unselected lines. In Corvallis, the intense selected line can complete 3.9 generations compared to 3.4 and 3.2 generations by the moderate selected and unselected wild type lines, respectively. In Hermiston, the intense selected line can complete 5.3 generations (1.4 more than in Corvallis), while only 4.6 and 4.5 generations can be completed by the moderate selected line and wild type beetles, respectively. Bernal & Gonzales (1993) found that *Aphidius matricariae* Haliday, with a low developmental threshold, may complete more generations than *Aphelinus asychis* W., with a higher developmental threshold, at three localities in California.

The study has shown that individuals resulting from selection for fast development can produce higher population numbers in a shorter period of time. This has an important application in mass propagation where high numbers of

individuals are required for release. The intense selected line will produce more individuals ready for release in a shorter period of time. Also, individuals selected for fast development, because of their lower threshold and lower degree-day requirements, will produce more generations throughout a year than a moderate selected line. Intense selected individuals can produce higher population numbers and therefore consume more aphids in a season, suggesting their greater efficiency as biological control agents.

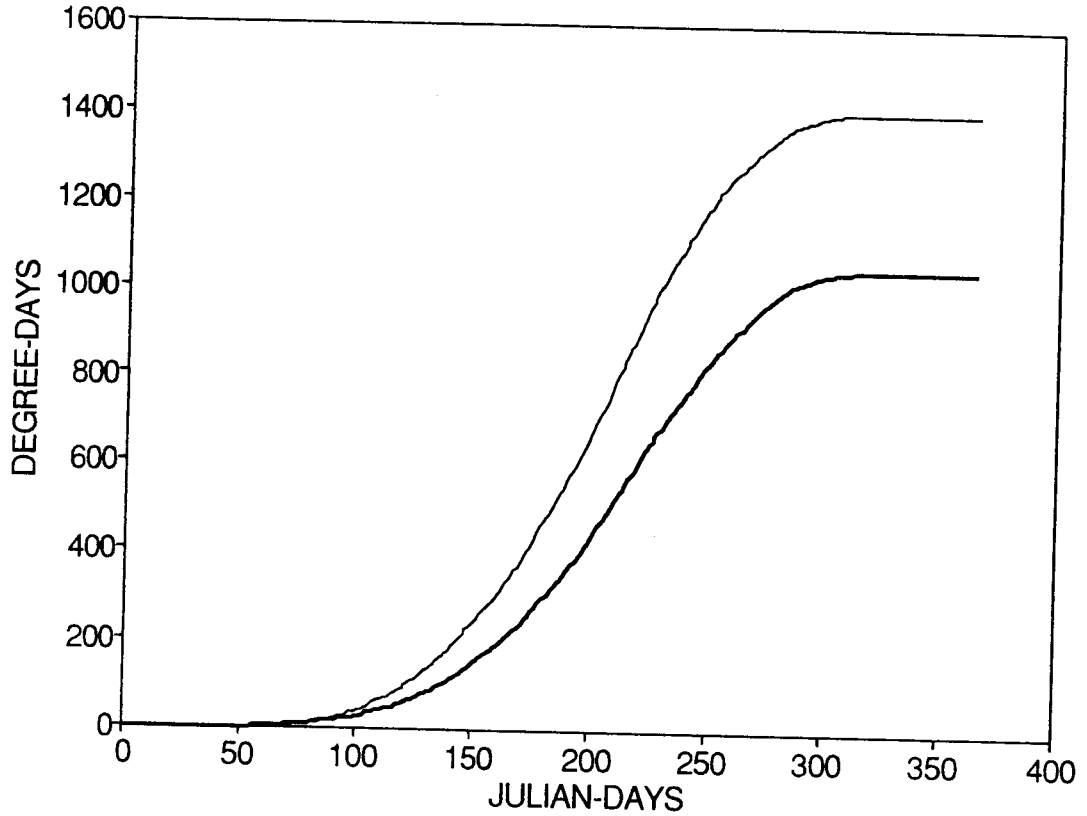


Fig. III.1 Degree-days accumulated by the intense selected *H. convergens* throughout an average year in Corvallis, OR (heavy solid line) and Hermiston, OR (solid line).

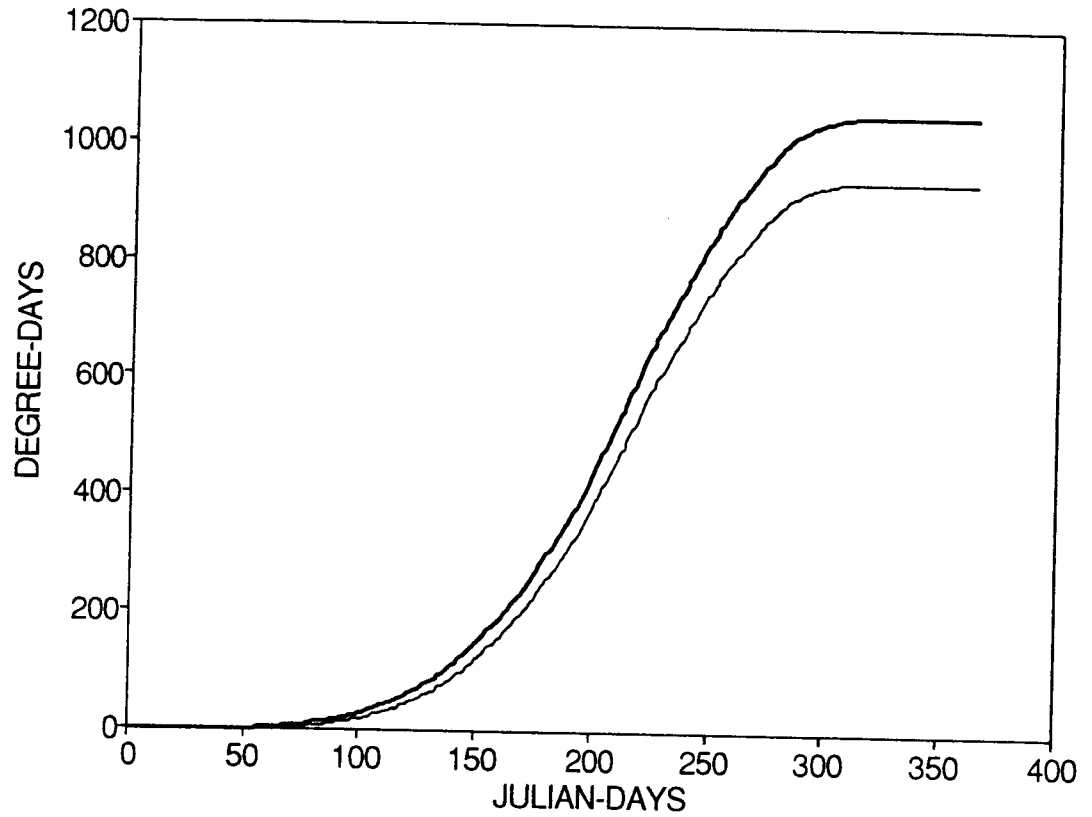


Fig. III.2 Degree-days accumulated by the intense (heavy solid line) and moderate (solid line) selected *H. convergens* throughout a year in Corvallis, OR.

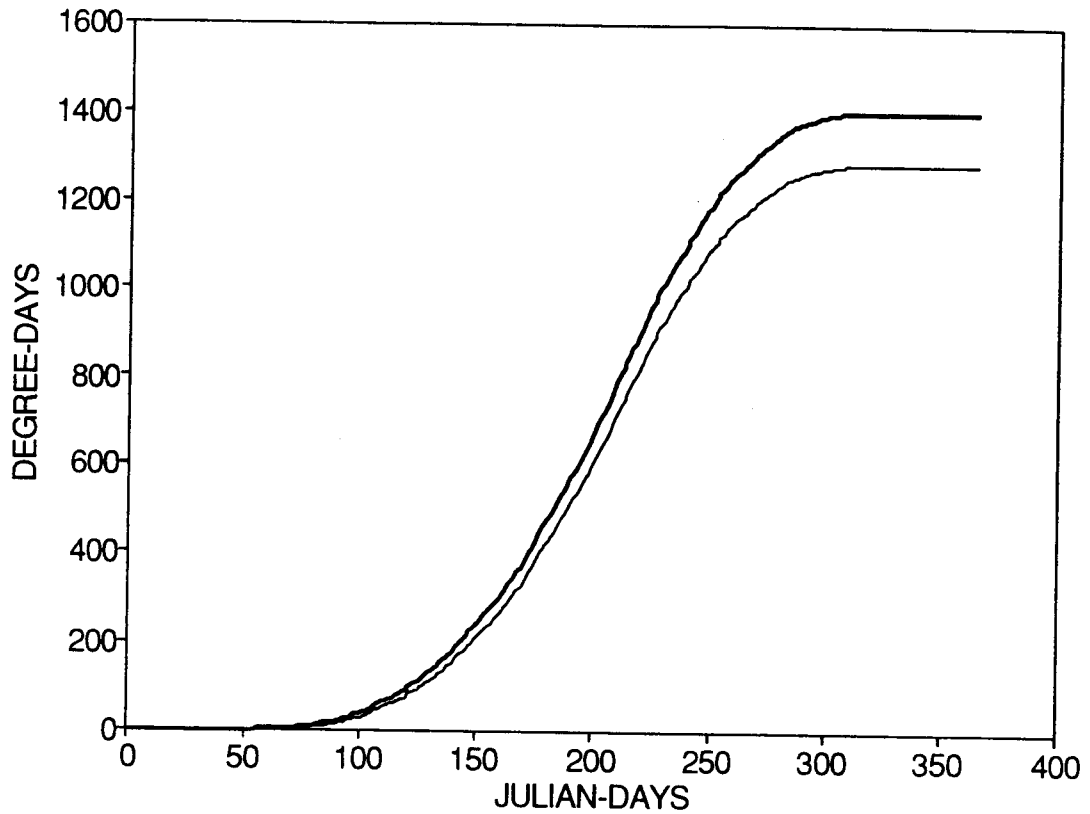


Fig. III.3 Degree-days accumulated by the intense (heavy solid line) and moderate (solid line) selected *H. convergens* throughout a year in Hermiston, OR.

Table III.1 Mean period over which progeny are produced (T), net replacement rate per generation (R_0), intrinsic rate of increase (r_m), population growth, and doubling time for intense line, moderate line, and wild type *H. convergens* at 22°C.

Variable	Intense	Moderate	Unselected
T (days)	49.1	52.1	53.8
R_0	131.3	117.3	150.5
r_m	0.099	0.091	0.093
Total production (60 days)	37,993	23,509	26,507
Doubling time (days)	7.0	7.6	7.5

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SUMMARY

Fast development in *Hippodamia convergens* Guérin-Méneville was selected through five generations at four constant temperatures (18, 22, 26, and 30°C). After selection individuals with fast development times, intense selected line, were compared to a moderate selected line (with longer development times) and to wild type beetles. Life traits such as survivorship, adult weight, larval consumption, fecundity, and adult longevity were tested for possible trade-offs after selection.

After five generations of selection, the intense selected line developed faster at all temperatures. Average development times from egg to adult at 18°C were 39.8 days for the intense selected line and 44.7 days for the moderate selected line. At 30°C, the intense selected line developed in 14.2 days, while the moderate line developed in 15.7 days.

Development thresholds and degree-day requirements for the two selected lines were compared after selection. The intense selected line had a lower developmental threshold and a lower degree-day requirements (266 degree-day requirements above a threshold of 11.3°C) than the moderate selected line (277 degree-day requirements above a threshold of 12.0°C).

Survivorship at 18°C improved in the intense selected line (73.1% mortality) after selection compared to the moderate selected line (82.5%). No trade-offs after selection were obtained in either body weight, total larval consumption,

fecundity, or adult longevity. Adult weights were the same before and after selection at all temperatures. Intense and moderate individuals consumed the same amount of aphids (ca. 100 mg) at the larval stage. Daily, fast-growing individuals consumed more aphids (11.2 mg) than a slow-growing larva (6.5 mg). Also, feeding efficiency was higher in fast-growing individuals. Fast individuals consumed fewer aphids per milligram of weight ($p < 0.001$).

Fecundity and longevity were not affected. A female lady beetle laid on average 344 eggs. The average life span of a beetle was 53 days.

The intense selected line can be a better natural enemy for biological control. In a 60-day period, the intense selected line can produce 1.6 and 1.4 times more individuals than the moderate selected and unselected lines, respectively, at 22°C. Additionally, because of a lower developmental threshold and a lower degree-day requirements, the intense selected line would accumulate more degree-days and have more generations per year. The intense selected line may produce 0.5 and 0.7 more generations in Corvallis, OR and Hermiston, OR, respectively, than a moderate selected line. Furthermore, larvae can be active earlier in the season during cooler temperatures.

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