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Leptinotarsa decemlineata (SAY), ON HORSENETTLE,
Solanum carolinense L., IN MICHIGAN

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Jaime Mena-Covarrubias

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ECOLOGY OF THE COLORADO POTATO BEETLE, *Leptinotarsa decemlineata* (SAY), ON HORSENETTLE, *Solanum carolinense* L., IN MICHIGAN.

By

Jaime Mena-Covarrubias

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ABSTRACT

ECOLOGY OF THE COLORADO POTATO BEETLE, *Leptinotarsa decemlineata* (Say), ON HORSENETTLE, *Solanum carolinense* L., IN MICHIGAN.

By

Jaime Mena-Covarrubias

Population dynamics of Colorado potato beetle (CPB), *Leptinotarsa decemlineata* (Say) on horsenettle was determined through field experiments. Development rate and survival on two host plants was evaluated in a laboratory study. The optimum sample size for studying CPB on horsenettle is calculated. A technique for estimate an error term for Southwood's stage-specific mortality is presented. Accumulated mortality for CPB egg and larvae stages was higher than 90%. Predators with chewing mouthparts were more abundant early in the season, and predators with sucking mouthparts late in the season.There were no differences in development rate, pupal weight or survival for two beetle populations on potato or horsenettle foliage. CPB has been very selective for laying its eggs on horsenettle. The CPB has been able to feed efficiently on horsenettle plants while keeping its ability to exploit potato plants, but a probable difference in oviposition behavior is developing.

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INTRODUCTION

The Colorado potato beetle (CPB), *Leptinotarsa decemlineata* (Say) is one of the most important pests of potatoes in many regions of the United States, Canada, Europe, USSR, and Turkey (de Wilde and Hsiao 1981). The genetic variability of the insect along with the mismanagement that have characterized commercial potato areas during the last 100 years, have made of this insect one of the best known cases in the entomological literature. The first commercial insecticide sprayers were developed for control this insect in the 1870's (Casagrande 1987). CPB is also a classical case for explaining the potential of an insect to develop resistance to insecticides. After its introduction in Europe, CPB forced the creation of an organization for dealing with this insect exclusively. However, the CPB was an unknown insect to the entomologists before 1800. When Thomas Say collected the specimens for the description of the species, he reported it as a rare insect feeding on buffalo burr *Solanum rostratum* , on the hills of the Rocky Mountains. It took about 40 years of exposure to potato plants before the beetle become one of the most destructive insects in agriculture (Casagrande 1985).

The CPB probably evolved in southern Mexico, feeding upon *S. rostratum* (Tower 1906) a weed common to disturbed areas of North America and also native to Mexico (Whalen 1979). Host and beetle dispersed northward, invading the eastern slopes of the Rocky mountains (Casagrande 1985, 1987). In this habitat, CPB also feeds on *S. elaeagnifolium* (Hsiao 1986). Beetles, intraspecific variation in response to host species has been noted for geographically widely separated populations (Hsiao 1978, 1981, de Wilde and Hsiao 1981, Hare and Kennedy 1986). Populations from Europe, parts of Asia, and North America vary in growth and survival on different host plants. Shifts to feeding on closely related hosts of the pest may not require major genetic changes in physiology or behavior (Tabashnik 1983), specially if the genetic make up of the population includes some sort of "all purpose" genotype having high fitness simultaneously on several host species (Mitter and Futuyama 1983). The host shift of the CPB from *S. rostratum* to *S. tuberosum* probably occurred without major changes in physiology or behavior (Hsiao 1978, Horton et al 1988).

At the Michigan State University Kellog Biological Station (KBS) at Hickory Corners, MI. a population exist that fed on potatoes before 1954, but since then, horsenettle has been the host plant for the beetles. I investigated the population dynamics of KBS beetles as well as its natural enemies on horsenettle, its new host for the last 34 years. Additionally, the possible differences in host plant use between the KBS population and a CPB population that has been feeding on potatoes (Montcalm population) were evaluated under laboratory conditions. The sample size needed to study the CPB on horsenettle was also calculated.

LITERATURE REVIEW

CPB is an oligophagous beetle that feeds on members of the Solanaceae, and primarily on plants in the genus *Solanum* (Hsiao 1981, 1986). Throughout Colorado, New Mexico, Texas, Oklahoma, and Mexico, *S. rostratum* is the predominant host, followed by *S. elaeagnifolium* . In Arizona, where *S. rostratum* is not prevalent, *S. elaeagnifolium* is the principal host. In several central and south eastern states, *S. carolinense* is an important native host. Several introduced or cultivated plants, including *S. dulcamara* , *S. melongena* , *Lycopersicum esculentum* , *S. villosum* , and *Hyoscyamus niger* are minor or occasional hosts (Hsiao 1978).

Different geographic populations of CPB in North America use different local hosts. Varying degrees of specialization in larval digestive efficiency (Hsiao 1978) and adult food-plant preference have evolved (Harrison 1987, Harrison and Mitchell 1988, Horton et al 1988). The existence of a CPB population from southern Arizona that is uniquely adapted to a native host, *S. elaeagnifolium* , is reported by Hsiao (1978). Due to the ecological conditions that limited the species of host plants available, a CPB population was adapted to *S. carolinense* in North Carolina, and it is reported as an example of host expansion rather than host shift (Hare and Kennedy 1986) . Horton et al (1988) indicate that the success of CPB on *S. sarracoides* in Canada is also due to a diet expansion by this population. This variability has a strong genetic component, and it may be a major factor in the CPB success in colonizing new areas (Jacobson and Hsiao 1983).

CPB HOST FINDING

The first step in host plant selection is the orientation of an insect while walking or flying (Visser and Thiery 1984). As early as 1926, McIndoo used a Y-tube olfactometer to demostrate attraction to unbruised potato foliage. In a series of detailed studies, J. H. Visser and his colleagues have shown that CPB adults orient to solanaceous plants by sensing complex blends of "green leaf volatiles" (Visser and Nielsen 1977, Ma and Visser 1978, Visser and Ave 1978). Through olfactory discrimination over a long range, exploration is to some extent confined to a relevant part of the vegetation. Complexes of the general "green leaf volatiles" form a predominant aspect of all leaf odors, discernible in the different and particular ratios (Ma and Visser 1978, Visser and Ave 1978, Visser and de Wilde 1980). An essential part of the "green volatiles" is a complex of C_6 alcohols, aldehydes, and corresponding derivates generally distributed in green leaves (Visser et al 1979, Thiery and Visser 1987).

The presence of a mixture of components can be detected by the antennal receptors. These receptors transfer information to the deutocerebrum where two classes of neurons are present: one class containing neurons which are not very specific for the tested compounds, and another class with highly specialized neurons (de Jong and Visser 1988a). Their different responses suggest two channels for the processing of olfactory information in the antennal lobe: one channel for the detection of the presence of "green leaf odor" components, and another one for an evaluation of the component ratios. A study of the antennal receptor responses indicates that this mechanism is also present at the peripheral level of the CPB's nervous system (de Jong and Visser 1988b). The presumed separation of olfactory information by these groups is more obvious at the deutocerebral than peripheral level (de Jong and Visser 1988b).

From some field observations on flying CPB it would seem that odor of potato plants may have an arrestant effect (de Wilde 1976). Odor-conditioned anemotaxis is much more likely to be of practical significance for orientation at a distance in the field (Kennedy 1977a, 1977b). In the field, however, wind turbulence will blend volatiles from a mixed stand of plants (Stanton 1983, Visser 1983). It is expected therefore, that the beetle's range of attraction to host-plant odor is reduced in mixed cropping systems. Masking the attractive host-plant odor will then hinder the beetle's searching for host plants (Thiery and Visser 1987). *S. rostratum* and many of the other *Solanum* hosts occur in large patches may have eased the problems of olfaction and detection by providing a wide and intense odor plume that would not be completely disrupted by small-scale turbulence (May and Ahmad 1983). For the anemotactic response, the presence of the four terminal antennal segments is essential. As 99% of the trichoid chemoreceptors are located on these four segments (Schnatz 1953 in May and Ahmad 1983) it is intriguing to think that these sensilla have at the same time a anemoreceptor function (May and Ahmad 1983). In western Europe, host-finding by the CPB happens mainly while the beetle is walking (de Wilde 1979, 1981 observations in Thiery and Visser 1987). Under field conditions, walking CPB find potato plants from a distance of 6 m when these plants were located up wind (de Wilde 1976). If potato rows were absent or at a long distance, the tracks often bore no relation to the wind direction, but were directed towards the nearest green vegetation (de Wilde 1976). Caprio (1987) also indicates that olfactory and visual cues in CPB are not active over a distance of 15 m.

The capacity to perceive the food-plants exists with larvae. They are able to locate host plants from a very short distance by smell (Chin 1950 in Hsiao 1969) and sight (de Wilde 1958). However, the perceptive ability of the larvae is limited to a distance of less than 5 cm (Hsiao 1969). When larvae fall to the ground during heavy rains or run out of food, they search in a random until guided by olfactory and optic stimuli (Hsiao 1969, Visser and de Wilde 1980).

CPB HOST SELECTION BEHAVIOR

Prior to feeding or oviposition, many insect herbivores show stereotyped sequences of sampling behavior (Miller and Strickler 1984) and subtle variations in these behavior patterns can be correlated with differences in plant characteristics (Harrison 1987). Food plant acceptance involves complex set of stimuli as well, and beetles may be capable of discriminating among closely related *Solanum* species by examining the surface of their leaves (Harrison 1987, Harrison and Mitchell 1988). Behavioral categories with functional significance in terms of plant perception and regulation of meal size in CPB adults are:

Examine: It is the time spent by the beetles on the leaf surface beginning with first physical contact with the leaf and ending with transition to *macerate* . Active movements include walking, palpating (repetitive contacts by maxilari palpi on the leaf surface) and antennal waving. Sensory input may be received by sensilla located on the antennae, maxilary palps, labial palps, and tarsi (Harrison 1987).

Macerate: A period following *examine* during which the leaf edge is "squeezed" with repetitive movements of the mandibles .On acceptable host plants this piercing action of mandibles release visible droplets of plant fluid bringing gustatory sensilla on the beetle's mouth parts (Mitchell and Harrison 1984) into direct contact with leaf saps. On plants that are not eaten, action of the mandibles is often less vigorous, and gentle pressing of the leaf edge does not result in apparent breaks of leaf tissue. Antennae are actively drawn towards the leaf surface during *macerate* , suggesting that plant volatiles may be released (Harrison 1987).

Small bite: A bite is noted when a visible fragment of leaf is taken into the oral cavity. Beetles typically took one or two bites before resuming feeding (Harrison 1987).

Sweep feed: Rapid feeding characterized by repetitive bites along the leaf edge. Feeding bouts normally terminated in one or more of the following: grooming, rest or further examination of the leaf surface (Harrison 1987).

On preferred species, beetles usually sampled and fed at a single site on the leaf before ending the feeding bout with a long period of grooming and rest. On less-preferred plants, fewer insects proceeded directly through the sequence, and many re-initiated sampling and feeding at different sites on the leaf before stopping to rest or groom (Harrison 1987). A similar pattern of time allocation on different hosts has been described by de Wilde (1958) for larvae of the CPB. Individuals that feed on marginal hosts sample them less prior to feeding, and selection for these feeders may establish local populations with broader feeding preferences that are capable of exploiting novel host plants (Harrison 1987).

CPB HOST PLANT SELECTION FOR OVIPOSITION

Oviposition by adult females is the point at which the most important host-selection behavior takes place. To some degree this is influenced by different stimuli than feeding (May and Ahmad 1983). In this process, the physical characters of the plant seem to play a ,minor role, since the female lays on surfaces as diverse as hairy and spiny leaves, glass dishes, copper screens, or paper towels (Hsiao and Fraenkel 1968). Chemical stimuli received from the plant appear to be decisive. Both positive and negative chemical stimuli influence the selection of a plant. Thus in *Capsicum annum* , egg laying never occurs (Hsiao and Fraenkel 1968). The black night shade, *S. nigrum* was superior to potatoes and *S. rostratum* in eliciting egg laying, with twice the percentage of eggs laid on this plant that on potato (Hsiao and Fraenkel 1968). However, this plant does not support larval growth and it is eaten only occasionally, and the adults rarely feed on this plant. These data indicate that acceptability and suitability of a plant for feeding are not primarily related to the act of oviposition (Hsiao and Fraenkel 1968). This conclusion resembles a case described by de Wilde et al (1960) where *S. luteum* a toxic plant to larvae was prefered to potato for oviposition. Jermy and Szentesi (1978) when working with the insects *Acanthoscelides obtectus*, *Bruchus pisorum* and *Pieris rapae* concluded that chemoreceptors presumably located on the ovipositor of the insects studied play only a subordinate role in governing egg-laying behavior. Thus, the information on oviposition site selection is probably perceived by chemoreceptors located on other parts of the body such as the legs and head appendages (Jermy and Szentesi 1978). Hsiao and Fraenkel (1968), Latheef and Harcourt (1972) demostrated that feeding conditioning does not alter the CPB oviposition preference. Waldbauer (1962) showed that feeding on non solanaceous plants did not modify the tabaco hornworm's innate preference for the tomato plant.

DIAPAUSE

Adult CPB enter diapause primarily in response to short day lenghts. However, low temperatures, senescent foliage, or a non preferred host greatly enhance the diapause-inducing effects of photoperiod (de Wilde and Ferket 1967, Hsiao 1978, Hare 1983). This phenotypic variability allows the beetles to adapt to local conditions even under day lengths that would consistently prevent diapause (Tauber at al 1988a). Fifty five years after CPB introduction and first establishment in Europe, the beetle has spread throughout almost all of continental Europe and had developed a substantial degree of photoperiodic differentiation. Northern populations exhibit a larger critical photoperiod than southern populations, the difference being approximately 1.5 hours (de Wilde and Hsiao 1981). This range of variability is less than that found among North American populations. Among the later, the critical photoperiod ranges from about 15 hours (Logan, UT) to fewer than 13 hours (Benson, AZ) and a population from Roma-Los Saenz, TX., shows very little response to photoperiod (de Wilde and Hsiao 1981). However, comparisons between North American and European populations are complicated by the fact that food quality and species play an important role in diapause induction (de Wilde et al 1969, Hsiao 1978, Hare 1983). European beetles are largely restricted to cultivated potato, whereas North American beetles have several wild solanaceous hosts to which they are variously adapted (Hsiao 1978, de Wilde and Hsiao 1981, Jacobson and Hsiao 1983). The restricted availability of food plants could strongly influence the phenology and adaptation of European populations. The enormous flexibility of CPB in diapause and voltinism characteristics has undoubtedly contributed to its success in invading new habitats (Ushatinskaya 1966, Tauber et al 1986, Horton and Capinera 1988).

CPB leave the food plant, move to the edges of fields, and burrow 10 to 70 cm in the soil to hibernate (Minder 1966); positive geotaxis and negative phototaxis guide movements during this period (de Wilde 1954 in Tauber et al 1986). In the state of New York, many CPB first generation adults enter diapause. A substantial number of these do it after ovipositing briefly (Tauber et al 1988a). In the USSR, approximately one-half of the females oviposit, one fifth oviposit some eggs and one fifth enter diapause without ovipositing (Ushatinskaya 1966).

HOST PLANT RESISTANCE

Feeding deterrents are responsible for the resistance of the majority of solanaceous and non solanaceous plants (Hsiao and Fraenkel 1968c). Extensive screening by Schalk et al (1970) of over 1500 clones of the ancestral *S. tuberosum* subspecies *andigena* failed to detect any resistance to CPB. Hence, it appears unlikely that *S. tuberosum* will provide any genetic sources that might be of value in breeding for CPB resistance (Dimock and Tingey 1985). CPB tolerate the glycoalkaloids found on *S. tuberosum* foliage (Melville et al 1985). *S. chacoense* is one of the most resistant of the wild tuber-bearing *Solanum* species to CPB, but the level of resistance varies widely within the species (Sinden et al 1986). *S. chacoense* clones with high leptine (glycoalkaloids) are highly resistant to larvae and nearly immune to CPB adults (Sinden et al 1986). Trichome exudate of *S. polyadenium* , a wild mexican species with type A hairs only, encased the tarsi of first instar CPB larvae, interfering with their ability to grip the plant (Gibson 1976b in Dimock and Tingey 1985). Only 14% of dead larvae collected from *S. berthaultii* sufferred from tarsal encasement by the trichome exudate, compared to 96% on *S. polyadenium* and one on potato. The highest mortality on *S. polyadenium* occurred during the first instar, young larvae being highly susceptible to entrapment in the trichome exudate (Dimock and Tingey 1985). High mortality in CPB first instars due to chronic intoxication or malnutrition is reported for *S. berthaultii* (Groden and Casagrande 1986).

Although it has been recognized that food-plant selection in CPB is based on a complex of stimuli, several studies have stressed an important role for alkaloids as feeeding deterrents and toxins. The alkaloids are thought to restrict the host range of beetles and reduce feeding on "resistant" plants (Hsiao and Fraenkel 1968, Hsiao 1974, Sinden et al 1978, 1980, Dimock and Tingey 1985). In several papers, authors imply, or explicitly state, that alkaloids act directly on the chemosensory system to inhibit feeding. As a result, it has become generally accepted that alkaloids exert a strong influence on the host choice behavior of CPB. However, variable acceptance of host plants among regional populations of CPB has evolved independently of adaptations to alkaloids at the sensory level (Harrison and Mitchell 1988).

Plant resistance in *Solanum* plants slows population increase through negative impacts on growth and reproduction. In general, larvae fed on *S. tuberosum* developed more rapidly, had lower mortality, and higher size and weight, than did those fed on wild *Solanum* species (Latheef and Harcourt 1972, Hsiao 1974, 1978, de Wilde and Hsiao 1981, Melville et al 1985, Horton et al 1988). Some exceptions to this rule had been found by Hsiao (1978), Hare and Kennedy (1986), and Cappaert (1988), as a result of the great variability in the CPB populations. For example, Tauber et al (1988b) report that under field conditions, the development rate of CPB larvae is substantially different even among individuals of the same egg mass. One of the factors affecting this variability in development rate is larvae feeding on its egg shells. Hsiao (1976) indicates that the larvae deprived of feeding on egg shell invariably initiated feeding sooner but required a longer overall feeding period to reach the second instar, especially when reared on less acceptable plants. Retarded development not only reduces the number of generations that can be completed within a growing season, but might also lead to increased susceptibility to insecticides and protracted exposure of vulnerable larvae to the controlling influence of natural enemies and adverse environmental conditions (Brown et al 1980, Dimock and Tingey 1985). Populations of CPB feeding on tomato, a suboptimal host species, appear to be more affected by the parasitoid *Myiopharus doryphorae* than populations feeding on potato (Latheef and Harcourt 1974).

The potential of CPB populations to overcome plant resistance is high. Casagrande (1982) indicates that *S. berthaultii* deter oviposition to CPB. After two generations of confinment on *S. berthaultii* in the field, the beetles no longer demostrate reluctance to oviposit on this host (Groden and Casagrande 1986). Furthermore, there is no difference in survival between these larvae that complete its third generation on *S. berthaultii* and larvae that had been consistently reared on *S. tuberosum* (Groden and Casagrande 1986).

Host plant resistance could also have negative impacts on CPB natural enemies. Under greenhouse conditions, there is a direct relationship between the density of glandular trichomes in aphid resistant potato clones (*S. tuberosum* x *S. berthaultii* ,F_3, and S. *berthaultii*) and adverse effects on aphidiophagous species (eight coccinellids, two chrysopids and one parasitoid) (Obrycki and Tauber 1984). These negative effects include a reduction in adult coccinellid searching time and a corresponding increase in the rapid movements of the adults (Obrycki and Tauber 1984). The mobility of newly hatched coccinellid and chrysopid larvae is inversely related to the density of glandular trichomes (Obrycki and Tauber 1984). The highest number of larvae dropped from leaves with medium densities of pubescence, while few larvae escaped from S. berthaultii leaves bearing high densities of glandular trichomes (Obrycki and Tauber 1984). The severe negative effects observed under greenhouse conditions are attenuted in the field (Obrycki and Tauber 1984). In the laboratory, *Edovum puttleri* readily attacks and parasitizes CPB eggs on *S. tuberosum* , but it is entrapped by the glandular trichomes on *S. berthaultii* . Not only is the parasitism higher on *S. tuberosum* , but a great number of eggs are killed (possible due to feeding or superparasitism) on *S. tuberosum* than on *S. berthaultii* (Obrycki et al 1985). Natural enemies and moderate levels of glandular pubescence are compatible mortality factors in the management of aphids and CPB on potatoes (Dimock and Tingey 1985, Obrycki et al 1985).

NATURAL ENEMIES

Natural enemies of the CPB are mainly predators. Only two tachinid parasitoids are found naturaly in the United States. The most common pentatomid predators of the CPB in the northern states are *Perilus bioculatus* Fabricius and *Podosius maculiventris* Say. Both have been reported to be relatively ineffective in controlling CPB densities in conventional grown potatoes (Tamaki and Butt 1978, Drummond et al 1984). Another pentatomid (*Oplomus dichrous*) has a considerable disadvantage in development in relation to the CPB, especially below 28°C (Drummond et al 1987). *Coleomegilla maculata* DeGeer is a polyphagous predator associated with crops supporting aphids (Wright and Laing 1978). In Michigan, both adults and larvae prey on eggs and small larvae (Groden 1988). For the foliar searching carabid, *Lebia grandis* Hentz, adults are predaceous on eggs and larvae of CPB, and the larvae are solitary ectoparasitoids on CPB pupae (Groden 1988). She considers this insect as the most significant predator of CPB in Michigan, and predation on CPB is strongly density dependent. The tachinid parasitoid, *Myiopharus doryphorae* main limitation with its host (CPB) is the lack of population syncrony (Harcourt 1971, Tamaki et al 1983, Horton and Capinera 1987, Groden 1988). For the CPB egg parasitoid, *Edovum puttleri* , an inverse relationship between incidence of parasitism and age of the host has been reported (for both the Colombian and Mexican biotypes) (Rubertson et al 1987). An extensive literature review of the CPB natural enemies is reported in Groden (1988).

HORSENETTLE

Horsenettle, *Solanum carolinense* L., is a prickly, perennial plant, 30-100 cm, having a very extensive and deeply penetrating root system which permits storage of large reserves (Darlington et al 1951, Illnicki et al 1962). It is normally disseminated by means of seeds, creeping roots, and root cuttings (Illnicki et al 1962). Seeds are capable of germination from depths of 10 cm, and producing seedlings from May through August (Illnicki et al 1962). Plants may arise from small vegetative root cuttings less than 3 cm long and 0.5 cm in diameter (Wehtje et al 1987). Shoots may arise from adventitious buds found on the tap root section from depths of 30 cm (Illnicki et al 1962). Roots of horsenettle act a the major sink for photosynthate accumulation at the 0.2 to 0.5 bloom growth stages (Garrel et al 1988), while the starch content of the storage roots was about 36% prior to emergence in the spring, declined to 13% at flowering, and increased by late summer to the original level (Pagano 1974).

Horsenettle is a native of the southern part of the United States, but is spreading northward, where it is becoming common in places. Horsenettle distribution is through all the eastern half of the United States except Maine, north into southern Ontario, west from Oregon and California east to the Rockies in southern Idaho and Arizona (Illnicki et al 1962, Pagano 1974, Allan 1978). This plant was of occasional occurrence in Michigan by 1904, but is becoming a serious weed in parts of the state, and is gradually spreading from the south to the north (Darlington et al 1951).

Horsenettle acts as an important host for insects of economic important crop plants. It is a host plant for the potato psyllid (*Paratrioza cockerelli* Sulc.). Other important insects harbored by this plant are as follows: potato flea beetles (*Epitrix fuscula* Crotch and *E. cucumeris* Harris), Colorado potato beetle (*Leptinotarsa decemlineata* Say), potato stalk borer (*Trichobaris trinolata* Say), onion thrips (*Thrips tabaci* Lind) and greenhouse red spider mite (*Tetranychus telarius* L.) (Illnicki et al 1962). Snapbean yield is reduced 14 to 74% when infested with horsenettle (Frank 1988).

The major problem in controlling this weed is the regrowth potential of the storage roots which can repeatedly produce new shoots as tops are removed (Pagano 1974, Wehtje et al 1987). The results of some researchers (Illnicki et al 1962, Bradbury 1956 in Pagano 1974) indicate that cultivation actually enhanced the problem since the weed is capable of reproducing from small root sections. Bradbury (1954) in Pagano (1974) observed differences in growth patterns between disturbed and undisturbed infestations of the weed. The older undisturbed areas were less thickly populated with horsenettle than were cultivated. Under non-agricultural environments, horsenettle is found in open, sparsely vegetated areas, forming fairly large but often widely dispersed patches (M. L. May unpublished observations 1981 in May and Ahmad 1983), where grass competition is minimal (Pagano 1974).

This plant is likely to persist along the edges of cultivated fields, along roadsides, and in waste ground (Darlington et al 1951), but it has been noticed most frequently in corn, followed by pastures, alfalfa, potatoes, and tomatoes, with the most intensive infestations occurring in fields where corn had been grown for several years (Illnicki et al 1962, Pagano 1974).

In the eastern of the United States, the native horsenettle, has served as an important alternate host for the Colorado potato beetle, and it is a natural host for a related *Leptinotarsa* species, *Leptinotarsa juncta* (Hsiao 1985).

MANUSCRIPT I

DEVELOPMENT AND SURVIVAL OF TWO POPULATIONS OF COLORADO POTATO BEETLE (COLEOPTERA : CHRYSOMELIDAE) ON HORSENETTLE, *Solanum carolinense* L.

ABSTRACT

The Colorado potato beetle (CPB), *Leptinotarsa decemlineata* (Say) has been very successful in exploiting a variety of native and cultivated solanaceous plants in a wide range of habitats. The population dynamics of CPB on horsenettle was determined through field experiments. Development rate and survival on two host plants was evaluated in a laboratory study. The optimum sample size for studying CPB on horsenettle is calculated. Accumulated mortality for CPB egg and larvae stages was higher than 90%. Predators with chewing mouthparts were more abundant early in the season, and predators with sucking mouthparts late in the season.There were no differences in development rate, pupal weight or survival for two beetle populations on potato or horsenettle foliage. CPB has been very selective for laying its eggs on horsenettle. CPB has been able to feed efficiently on horsenettle plants while keeping its ability to exploit potato plants, and a probable difference in oviposition behavior is developing.

The Colorado potato beetle (CPB) ,*Leptinotarsa decemlineata* (Say), has been very successful in exploiting a variety of native and cultivated solanaceous plants in a wide range of habitats (Hsiao 1982). It is believed that buffalo bur ,*Solanum rostratum* L., was the principal North American host of CPB before the introduction of potato ,*S. tuberosum* L. in the 1800's (Tower 1906, Hsiao 1981, May and Ahmad 1983, Casagrande 1986,1987). While the majority of CPB in the north, central and eastern United States feed on cultivated potatoes, many found in the southern states feed on native hosts (Hsiao 1978). In the Great Plains of the United States, buffalo bur is the predominant host. Silver night shade, *S. elaeagnifolium* is a secondary host in the southern plains, and a principal host in Arizona, where buffalo bur is not prevalent (Hsiao 1978). In several central and south eastern states, the horsenettle, *S. carolinense* is an important native host (Hsiao 1978).

The CPB is highly adaptable and capable of further expanding its host range and geographic distribution (Hsiao 1982). Distinct differences exist among local geographic CPB populations. For example, their ability to survive on several wild hosts, particularly *S. elaeagnifolium*, has been determined by Hsiao (1978, 1981), Hare and Kennedy (1986). In a comparative study of eleven United States and European beetle populations, Hsiao (1982) indicates that Arizona beetles have a unique ability to survive on *S. elaeagnifolium* . All populations survived uniformly well on potato, suggesting that the ability of southwestern CPB populations to survive on wild hosts is independent of their ability to survive on potato (Hsiao 1978, 1982). Substantial geographic variation in host species utilization suggests that New England *L. decemlineata* populations differ from populations in the southwestern U.S.A and Europe in their ability to utilize *S. dulcamara* (Hare 1983). There were clear differences in the ability of Colorado potato beetles collected from different commercial potato-growing regions along the east coast of the United States to survive on horsenettle. For example, North Carolina CPB exhibited significantly greater rearing success than

Connecticut beetles. The North Carolina population has expanded its host range to include horsenettle without losing its ability to survive on potato (Hare 1986). Host-adapted populations are developing among geographic populations of the CPB in North America (de Wilde and Hsiao 1981, Hsiao 1978, 1982), but this is likely to occur only when populations are isolated from each other and from normally preferred optimal hosts (Hsiao 1978).

At the Michigan State University Kellogg Biological Station (KBS), Hickory Corners, MI the CPB population utilizes horsenettle, and has probably been restricted to this host since 1954, when farmers quit growing potatoes in the area. This population provides an opportunity for investigating the possible existence of a host-adapted population. The purpose of this study was to investigate the population dynamics of the CPB in Michigan on its wild host plant, horsenettle. A second objective was to determine whether development and survival rate differ between Michigan CPB populations originating from potato and horsenettle plants. Using the variability of the sampling data of CPB on horsenettle, the sampling size for studing this insect was calculated.

MATERIALS AND METHODS

Site description: All field work was conducted at the Bird Sanctuary of KBS, Hickory Corners, MI during the summer of 1987 and 1988. In 1987, CPB were monitored in contiguous three different horsenettle stands: 1) the Weed Field (2 ha) had been uncultivated since harvest of a corn crop the previous year. Horsenettle plants were successful early in the season, but were overshadow or weaken by competition with other weeds like lambsquarter, red dock and rag weed by the beginning of July. Horsenettle density represented 20-30% of the weed population in that field. 2) The

Corn Field (5 ha) was planted with corn in 1986, 1987, and 1988. The variety used was Great Lakes 579, sown at a density of 60000 plants/ha, and 90 cm distance between rows. Horsenettle was the dominant weed and only a small population of velvetleaf was present (less than 10% of weed population). Finally, 3) the Grass field (10 ha) was sown with a mixture of timothy grass (2 kg/ha) and orchard grass (3kg/ha) on May 1987. This field had been fallow for the two previous growing seasons. Due to poor germination of the grass seed, this field could be considered a second weed field. Velvetleaf and pig weed were the other weeds present in this field, with velvetleaf overgrowing the others by the middle of July. Horsenettle density represented approximately 50% of the total weed population. In 1988, the Corn field(2) was the only study site. No pesticides were used in the study area in 1987 or 1988.

Stage-specific survival: In order to evaluate the impact of environmental factors on the development of the CPB under field conditions, age-specific survival was calculated from CPB measurements. In 1987, weather data were obtained from the climatological station located about 500 m east of the research plots. During 1988, a hygrothermograph in a standard meteorological weather shelter was located between the Corn and the Grass fields. It was used to gather daily temperature and humidity data. Degree-day accumulations were calculated from weather data using the direct method. A lower threshold of 10° C was used to calculate the mean accumulated degree days (DD_{10}) for CPB development (Logan and Casagrande 1980). Residence time for eggs was estimated as 72 DD_{10} (Logan et al. 1985), 41 DD_{10} for 1st instars, 39 DD_{10} for 2nd instars, 49 DD_{10} for 3rd instars, and 76 DD_{10} for 4th instars (Groden and Casagrande 1986).

The mortality estimate was calculated with Southwood's graphical method as described by Helgensen and Haynes (1972). This involved estimating the absolute density of each instar in the field until all larvae had pupated. Since the instars occur simultaneously over a relatively long period of time, a population curve for each instar was made by plotting the absolute densities against time (in DD_{10}). Numerical trapezoidal integration was used to calculate the area under the curve (total incidence). The actual number to enter a specific instar was calculated by dividing the total incidence of that instar by its residence time. Using the actual number entering each instar, survival for a specific instar (S_x) was calculated by dividing the number entering instar (x+1) by the number entering instar (x).

Field sampling: CPB and its natural enemies were monitored by direct observation of 100 randomly selected stems. Sampling began with the emergence of the beetles and horsenettle plants and ended when no insects were found on the plants.

In 1987, plots were sampled weekly between May 29 and July 25. Samples were taken from a 2 ha area in each field. To estimate parasitism by tachinids, 100 4th instars were taken from each field on June 25 and dissected in the lab.

In 1988, sampling was conducted every 2 to 4 days from May 24 through July 29. The sampled area was 4 ha. Tachinid parasitism was determined for 100 4th instars collected on June 14, 24, July 3 and 12. These larvae were kept in petri dishes filled with wet vermiculite until they pupated or parasitoids emerged. To study survival and development of CPB cohorts, individual plants were flagged when an egg mass was discovered, and sampled every 2 to 4 days. Seventy cohorts were sampled from May 24 to July 15. CPB oviposition rate was also studied. All CPB egg masses found on horsenettle, corn or other weeds were collected from a 150 m^2 area (50 x 3 m) every 2 to 4 days from May 28 to July 18.

Development rate: The effect of host plant species on development and survival of the CPB was evaluated in the laboratory. Two beetle populations were used: one collected from the Michigan State University Potato Research Farm, Entrican MI

(Montcalm population) under continuous potato cropping; and one collected from KBS on horsenettle (KBS population).

In experiment one, egg masses from potato (Montcalm population) and horsenettle plants (KBS population) were collected from the field during the summer of 1988. The egg masses were held in plastic petri dishes (90 x 15 mm) lined with moist paper. Excessive leaf material was trimmed from the egg mass to reduce food available to the larvae at hatching time (Groden and Casagrande 1986). Egg masses were checked daily for 1st instars hatching. Both egg hatching and larval development were measured at room temperature conditions (26.8 ± 2.2°C). In this experiment, a total of 280 1st instars (2 populations X 2 host plants X 7 replications X 10 larvae per replication) were used. The number of newly molted or dead individuals was recorded every 24 h and fresh leaves (potato cv Atlantic, or horsenettle) provided. Pupae were weighed within 24 h after molting, and adults were sexed. Because survival differed between treatments and replications, data analysis was as an unbalanced design (SAS GLM procedure, SAS 1982).

Experiment two was designed to determine the effect of horsenettle foliage quality (new versus old foliage) on the development and survival of CPB from the KBS population. New foliage was obtained from the upper part of the horsenettle plants. The foliage was 1-2 weeks, tender, and of a green light color. Old foliage refers to leaves located at the lower part of the horsenettle plants, with an age of 4-5 weeks. The leaves were thicker, harder, and the color was dark green. A total of 120 1st instars (2 foliage conditions x 6 replications x 10 larvae per replication) were used. This experiment was conducted under the same conditions as experiment one and the same variables were reported. The t-statistic was used to test for differences between treatments (TTEST procedure, SAS 1982).

CPB sampling : The first step to estimating mortality of the insect on horsenettle, was to choose a basic population unit to compare densities of the different life stages. For potato plants, an appropriate sample unit for the above ground stages of CPB is a single stalk (Harcourt 1964). He also suggests sampling 150-200 potato stalks for adult beetle estimation and 100 for eggs and larva. Because no sample unit or sample size has been determined for CPB on horsenettle, the sample unit was defined as one horsenettle stem (a single stem coming from the ground), and the sample size was 100 stems.

In order to estimate optimum sample size for future studies of CPB on horsenettle, mean and variance of density were calculated for each sampling date to determine spatial pattern. Taylor (1961) has shown that the spatial pattern of a large number of plants and animals can be described with the variance being proportional to a fractional power of the mean :

$$s^2 = a * m^b$$

where "a" is related to sampling methods, and "b" is a measure of aggregation ("b" has a value of 1.0 when the population is randomly distributed, greater than 1.0 when it is a contagious disribution, and smaller than 1.0 when it is a uniform distribution). Estimated values of "a" and "b" are obtained from the regression of $\log(s^2)$ on $\log(m)$ (Taylor 1961).

Additionally, Taylor's equation can be used to calculate sample size. For this purpose, antilog(m) and antilog(s^2) are substituted into a sample size formula (Karandinos 1976, Logan 1981). Because the arithmetic mean is underestimated when predicted from the regression equation of a logarithmic plot (Finney 1941, Morris 1955, Bliss 1967 in Ruesink and Haynes 1973), the antilog(s^2) has to be computed from the equation :

$$s^2 = (a + b \log m + 1.1513 EMS^2)$$

where EMS^2 is the error mean square from analysis of variance table of regression (Bliss 1967). Logan (1981) reports that using the negative binomial to fit the distribution of CPB egg and larval densities did not produce very good results. He prefers to calculate the optimum sample size with Karandinos formula (Karandinos 1976). The same formula was thus chosen for this study, but using a fixed percentage of the mean instead of the coefficient of variation as shown below:

$$N=(Z_{a/2} / D)^2 s^2 / m^2$$

where: $Z_{a/2}$ = Value from the Z table

D = Fixed proportion of the mean

s^2 = Antilog of variance from Taylor's regression

m = Antilog of sample mean

The first step to define optimum sample size was to determine if data from both years could be pooled, since sampling size was fixed to 100 stems in 1987 and 1988. Regression equations (log s^2 on log m) were calculated as well as a confidence interval for the slope using a t-value (Sokal and Roelf 1960). The data could be pooled if the confidence intervals overlap ($p = 0.05$), otherwise it would be necessary to analyze each year separately.

Horsenettle sampling: In order to support data from beetle sampling, the spatial distribution and sample size of horsenettle plants was determined following the methodology described for the insects (spatial distribution estimated with Taylor's power law, and sample size with Karandinos formula). Horsenettle density was estimated by counting the number of stems in randomly-selected 1 m^2 quadrats. Horsenettle density in 1987 was sampled in the Weed Field on May 29, June 15 and July 5, and in the Grass and Corn Fields onJune 20 and July 22. Horsenettle density in 1988 was recorded on May 24, June 4, June 15, June 28 and July 15. In order to estimate CPB density per m^2, the mean number of insects per horsenettle stem was multiplied to horsenettle density at each particular sampling date.

RESULTS AND DISSCUSSION

Stage-specific survival 1987

The degree day (DD_{10}) accumulation started on May 26, three days before the first adult beetles were observed in the fields. The numbers of insects per horsenettle stem were multiplied by the stems per meter square to obtain beetle density. Horsenettle density was sampled twice in the Corn and Grass fields, at 270 and 760 DD_{10}, and three times in the Weed field, at 60, 270 and 540 DD_{10} (Figure 1). A linear increment of plant density was assumed between sampling points. This linear increment was observed again in 1988 during the first 500 DD_{10} (Figure 2). Horsenettle sampling started one week earlier in 1988 than in 1987; the sampling in 1988 was done only in the Corn field.

Adult beetle populations from overwintering peaked at 130 DD_{10}, and summer adults at 380 DD_{10} for the Weed and Grass fields (Figure 3). However, the summer generation in the Corn field peaked at 800 DD_{10} (Figure 3). Beetle densities were similar between the Weed and Corn fields, while the densities in the Grass field were about four times lower. This low density was related to fewer horsenettle plants on the Grass field (Figure 1). The higher egg densities for the three fields were found at 130 and 500 DD_{10}, and the lower densities observed between 300 and 400 DD_{10} (Figure 4a, b, c). The Weed and Grass fields had similar egg densities (Figure 4a, c), and they were about four times lower than in the Corn field (Figure 4b). Even though the horsenettle density was similar in the Corn and Weed fields, the egg input was different. This maybe explained by the resource concentration hypothesis of Root (1973). In the Corn field, horsenettle represented over 90 % of the weed population. In the Weed field , horsenettle plants were only 20-30 % of the weeds present. This may facilitate CPB finding of its host plants among the Corn plants, while the mix of other weeds made oviposition on the horsenettle more difficult. The odor of solanaceous plants releases the upwind locomotory response in CPB, and attracted the beetles in the vicinity of these plants (de Wilde 1976, Visser and Ave 1978). Visser and Ave named this odor "green leaf volatiles" and considered the concentration ratios of these volatile components decisive for the release of a positive anemotactic response in the CPB. This odor is probably directing flight behavior but clearly directs walking activity (de Wilde 1976). Under field conditions, walking CPB find potato plants from a distance of 6 m when these plants are located up wind (de Wilde 1976). In mixed vegetation, however, interaction of the different odors might prevent the long-range olfactory orientation. Hiding the host from insects in this way (Visser and de Wilde 1980), leads to associational resistance (a plant odor being masked by another plant odor, Cromartie 1981). The disruption of olfactory orientation by the mixing of odors occurs independently of the beetle's behaviors after emergence and could have important implications in the population dynamics of CPB (Latheef and Harcourt 1967, Hsiao and Fraenkel 1968 c, Thiery and Visser 1986, 1987) (see also egg input discussion below).

The larvae densities kept the same relationship among fields as that reported for the egg stage (Figures 4a, b, c, and 5a, b, c).

Mortality for eggs, and third instars was higher in the Weed and Grass fields than in the Corn field, as well as the cumulative mortality (Table 1). These mortalty differences were small though. Cappaert (1988) reported similar cumulative mortalities for CPB on *S. angustifolium* in Mexico. But Groden (1988) found that in commercial planted potatoes, early in the season at the Montcalm Potato Research Farm, the within generation survival was 0.51. This situation indicated that mortality of the CPB under undisturbed conditions is very high, but not under the common agricultural environment. The negative mortality reported for the second instar in the Corn field (Table 1) was probably due to sampling error and therefore is inconclusive. Also Southwood's method requires at least seven non zero points for each different instar sampled in order to have accurate estimation of mortality (Ruesink 1975). This requirement was not fulfilled in 1987. Therefore, the data were used only as a preliminary evaluation of CPB mortality.

Natural enemies of the CPB found in 1987 on the horsenettle plants were: phalangids (probably *Phalangium opilio*), cocinellids (*Coleomegilla maculata* and less commonly *Coccinella septempunctata*), pentatomids (*Perilus bioculatus* and less commonly *Podosius maculiventris*) and nabids (*Nabis* spp). In the Weed field, coccinelids and nabids were more abundant early in the season, and pentatomids late in the season (Figure 6a). Pentatomid populations were well correlated with the second generation egg stage (Figures 5a and 6a), and it was further supported by the agreement with the number of egg masses destroyed on the last 400 DD_{10} (Figures 6a and 7). In the Corn field, predator counts were low during the first 400 DD_{10} (Figure 6b). Their populations were not associated with egg mass number destroyed (Figures 6b and 7). In the Grass field, pentatomids and nabids represented over 90 % of the predator counts (Figure 6c). Their population were closely related to the number of egg masses preyed upon by predators (Figures 6c and 7).

Stage-specific survival 1988

Degree day (DD_{10}) accumulation started on May 23, one day before the first adult beetles were observed in the field. Beetles began to emerge about 3 to 4 days before the horsenettle plants. Apparently, that is a common situation both under agricultural (Lashom 1981 in May and Ahmad 1983) and non agricultural environments (de Wilde 1969, Hsiao 1969). Overwintered beetles peaked at 150 DD_{10}. The first summer adult was observed at 400 DD_{10}, and numbers peaked at 600 DD_{10} (Figure 8). Beetle densities were 3 to 5 times higher in 1988 than in 1987 (Figures 3 and 8). Egg density was approximately three times higher in 1988 than in 1987 during the first generation, and about the same size for the second generation (Figures 4b and 9). For the larvae stage only the first instars had two well defined peaks (Figure 10). The larval densities between years were about twice that of 1988 (Figures 5b and 11).

Mortality during the first instar wasvery similar in 1987 and 1988, but not during the second and third instars (Table 1). The lack of correspondence could be due in part to the sampling frequency, there were ca. three fold increase in the number of sampling points in 1988. This inaccuracy of the 1987 data is also reflected in the negative mortality observed for the second instar (Table 1) and the size of the confidence intervals for mortality estimation as reported in Appendix A.

Soil splashed by rain drops had little or no effect on egg masses (16 egg masses observed in the field all hatched). The impact of soil splash on the numbers of first instars hatched, on the other hand, was not quantified. Harcourt (1964) reported rain as the main cause of the first instar mortality, but it was not found in this study. There were only 5.88 mm of rain accumulated from April 1 to July 8 during the 1988 season and therefore rain was not responsible for the 70 % first instar mortality recorded (Table 1).

Among the natural enemies of CPB found on the horsenettle plants, phalangids were the most common (Figure 11). During the first 150 DD_{10}, 41 plants with an egg mass also had a phalangid on the same plant. Of the egg masses, 23 had some or all of the eggs chewed. Phalangids are one of the CPB mortality factors early in the season. However, in the literature they are reported as a minor mortality factors. Phalangids are general predators, and there is a lack of syncrony of their population with the CPB population (Drummond et al. 1988). Coccinellids (mainly *C. maculata*) were sampled from150 to 400 DD_{10} period (Figure 11), and was coincident with the higher egg densities (Figure 9). *C. maculata* are reported as predators of eggs and small larvae of the CPB, and their populations are well correlated with the first generation of CPB on potatoes in Michigan (Groden 1988). A carabid (*Lebia grandis*) and pentatomids (mainly *P. bioculatus*) were also important mortality factors, both for egg masses and larvae. Some *Lebia* were observed searching on horsenettle plants (Figure 11). They actualy overlap the 4th instar population of CPB (Figures 10 and 11). Parasitism by tachinids (*Myopharus doryophorae*) was also important (17, 21, 8, and 11 % parasitism at 200, 343, 426, and 562 DD_{10} respectively). The maximum parasitism corresponded with the peak of the 4th instars (Figure 10).

Egg input

CPB egg mass size differed significantly during the season. They were smaller earlier and late in the sampling period ($F(10, 1253) = 9.83$, $p > 0.0001$, Table 2). On potato plants, Groden (1988) reports similar findings. However, the size of the egg mass was greater on potato than on horsenettle plants in her study. This could be an effect of host plant quality, with horsenettle as a sub-optimal host plant for egg mass size. De Wilde et al (1969), Brown et al (1980), Casagrande (1982), Melville et al (1985) and Groden and Casagrande (1986) reported reduced fecundity of CPB when it was fed on plants other than potatoes.

Total egg input provided an absolute count of eggs laid by the CPB. When this value was compared with the number of eggs from a random sampling of 100 horsenettle stems, seasonal trends and number of egg per m^2 were closely related (Figures 9 and 12). The exception was for the sampling point at 350 DD_{10}. This egg input data (better estimation than data from random sampling) reflected a closer relationship between the number of eggs and the total population of the natural enemies (Figures 11 and 12). Total number of natural enemies were closely related to the CPB egg density.

Some insight on the oviposition behavior of the CPB was also obtained from the egg input study. The Corn field sampled consisted of corn, horsenettle and a low density of velvet leaf (less than 10 % of the total weed population). During the first 100 DD_{10}, CPB laid more eggs on corn than on horsenettle plants. After 138 DD_{10} until the end of the season more eggs were laid on horsenettle than corn (Table 3). Oviposition on other weeds was low during the entire sampling period. Oviposition of CPB egg masses on non-host surfaces is a common phenomenon (May 1981, in May and Ahmad 1983). Groden (1988) found that about 60% of CPB oviposition was on weeds. Cappaert (1988) reported ca. 30 % of the oviposition of a CPB population from *S. angustifolium* was on the cage screening. He suggested as the possible reason, that host discrimination occurs, in part, prior to the alighting of the beetles on the host plant. CPB appears to have poor short range host recognition. The results shown in Table 3 for the first two sampling dates, are in agreement with these findings. However, from 138 DD_{10} on and especially after 217 DD_{10}, the CPB seemed very selective as indicated by laying more than 90 % of its eggs on horsenettle (Table 3).

During the first 50 DD_{10}, when the horsenettle was less than 5 cm, CPB adults were efficient in finding the plants prior to oviposition. It is reported that oogenesis only starts after a period of food intake (de Wilde et al 1969). If the selection of an oviposition site is the first and primary step of host selection by CPB as stated by Hsiao and Fraenkel 1968c, Hsiao 1969, Visser and de Wilde 1980, and Ahmad and May 1983, there are four possible explanations for the results presented on Table 3. One, feeding and oviposition behaviors are governed by different mechanisms and the small horsenettle plants do not provide adequate oviposition cues. In the CPB selection process for an oviposition site, the physical characteristics seem to play a minor role. Female lays eggs on surfaces as diverse as hairy and spiny leaves, glass dishes, copper screens, or paper towels (Hsiao and Fraenkel 1968). Hsiao and Fraenkel (1969) found that black night shade, *S. nigrum* , gets twice the number of eggs as potato or *S.*

rostratum plants. However, *S. nigrum* does not support larval growth and adults rarely feed on this plant. This observation resembles a case described by de Wilde et al (1960), and Bongers (1970) in Visser and de Wilde (1980), where *S. luteum* , a toxic plant to larvae was preferred to potato for oviposition. Therefore, acceptability and suitability of a plant for feeding are not primarily related to the act of oviposition (Hsiao and Fraenkel 1968, Hsiao 1969, and May and Ahmad 1983). Chemical stimuli received from the plant appear to be decisive for selection of an oviposition site (Hsiao and Fraenkel 1968, Hsiao 1969). Small horsenettle plants may not release enough chemicals to stimulate oviposition.

An alternate explanation was that the Corn field was a simpler environment that consisted of corn plants, horsenettle, and a small population of non solanaceous weeds. Therefore, after the horsenettle reached a certain density and size, CPB females became more efficient in finding the host plants and the plant cues were appropriate for the CPB to lay the eggs. A third explanation could be that early in the season, the horsenettle density had less than 6 stems / m^2 (Figure 2) and over 90 % of the stem sizes were lower than 5 cm (Figure 13). On the other hand, the corn density and size (6 plants / m^2 and 10 cm in height) represented a bigger leaf area in the field. Although the beetles were able to locate the plants for feeding, they had to move frequently to another plant, and their residence time on the horsenettle plants was smaller . Due to the size and density of the corn plants, probably the CPB had a higher residence time on them, and just by chance the females laid more eggs on the corn plants. The last explanation (less likely) would be to avoid predators that target on the host plant. However, of 41 egg masses sampled on corn and 36 on horsenettle plants, 48 and 52 % respectively were preyed upon by predators, indicating that the egg masses on the corn plants did not have an advantage in escaping predation. Also Groden (1988) did not find differences in CPB egg predation on potato and weed plants. First instars had to move from the corn plants to horsenettle, and that could lead to high mortality.

Comparing the oviposition behavior of the Montcalm CPB population on potatoes (Groden 1988) with the results obtained in this experiment on horsenettle (KBS), it is tempting to say that both populations have been under different selection regimes for egg laying behavior. Larvae hatching from an egg mass laid on a non-host plant by Montcalm beetles would have a better chance to find its host plant than a larva under the same conditions for the KBS beetles. Therefore, there was a strong selection for KBS beetles to oviposit efficiently on its host plant, than for Montcalm beetles.

Using the egg input data, it was possible to evaluate the intensity of egg predation. The percentage of egg masses destroyed on horsenettle was low at the begining of the season and increased through time (Figure 14). Comparing the data from the random sampling (Figure 14), the mortality trends were similar, but the estimates were always lower under the egg input study. The residence time of the egg mass exposed to predation and the residence time of the egg mass after predation were different between sampling methods. In the egg input study, all the egg masses were removed from the field at each sampling date. As an average they were collected from the field at 52.6 DD_{10} (the residence time is 72 DD_{10}), therefore, they were exposed to predation for only 73 % of residence time. In the random sampling, the egg masses were not collected and remained on the plants. After an egg mass is fed upon by a predator, it remains visible in the field for a certain period of time. If the egg mass was destroyed by a predator with sucking mouth parts (as it was the case for the majority of egg input data), it would last in the field for about 173 DD_{10} (see cohort study below). Because all the egg masses preyed upon were collected for the egg input study but not for the random sampling, a sucked egg mass would be exposed to being sampled 3.3 times more in the random sampling than in the egg input study.

Cohort study

Egg mortality was estimated at 49.8% (n = 78 egg masses). When comparing this mortality with Southwood's stage-specific estimation, Southwood's estimate was 14 % higher (Table 1), probably due to the assumption of the distribution of mortality through the stage. Southwood's method assumes that mortality is light at the beginning and heavy at the end of the stage. From the cohort study, it was found that the accumulated 50% mortality for individual eggs was observed when the egg mass age was about half of its residence time, and the mortality rate was constant through the stage (Figure 15). Constant mortality for the egg stage seems reasonable, unless the predators have some preference for egg masses of a certain age. This preference has not been reported in the literature.

The last part of the cohort study was related to the natural enemies. Chewing predators destroyed 12 of 13 egg masses during the first three weeks of sampling. Predators with sucking mouth parts consumed 14 of 15 egg masses over the next four weeks. After an egg mass is consumed it remains on the plant for several days and could be recounted on subsequent sampling dates. Data from 28 egg masses indicated that the average residence time on horsenettle for a chewed egg mass was 82.8 DD and 178.5 DD for a sucked egg mass. These findings were similar to the data reported by Groden (1988) on potato plants.

Development rate

The effect of host on larvae development was significant ($F(1,229) = 896.2$, $p > 0.0001$, Table 4). Beetles feeding on potatoes developed faster than those feeding on horsenettle (Table 4). The slower development on horsenettle must increase larval exposure to predation and pathological infection. This could account for the higher CPB mortality on horsenettle than on potatos. Since they may be nutritionally deficient, insects on horsenettle may also be more susceptible to to insecticides (Brown et al 1980). Potato plants were also a better food source when evaluated by pupal weight. Male and female pupae weight were similar in relation to the host plant effect(Table 4). Host plant effect was significant for survival of first to adult stages ($F(1,24) = 3.05$, $p < 0.01$and $F(1,24) = 7.93$, $p < 0.01$ respectively, Table 5). Better survival was observed when potato was the host plant, independently of the beetle population. Working with three beetle populations from potato fields, Hare and Kennedy (1986) report differences for survival on horsenettle, with the North Carolina population better adapted to survive on horsenettle. Because the last two of the three generations in North Carolina must seek out and feed on alternate hosts, mainly *S. carolinense* , the beetles were conditioned to horsenettle.

Development rate (7.24 vs 7.57% per day), pupal weight (136.2 vs 128.2 mg for females and 111.5 and 107 mg for males), and survival (68.6 vs 83.3%) in Montcalm and KBS beetles were not significantly different when they fed on horsenettle (Tables 4 and 5). This implies that Montcalm and KBS beetles belong to the same population, and 30 years have not been sufficient for the KBS population to adapt to the horsenettle plants. The majority of research reports indicate that CPB population are better adapted to potato than to any of its native host plants (Hsiao 1978, Brown et al 1980, de Wilde and Hsiao 1981, Hsiao 1982, Groden and Casagrande 1986, Hare and Kennedy 1986). However, Hsiao (1978) indicates that in Arizona CPB is better adapted to *S. angustifolium* , more than to any other plant. Cappaert (1988) reports that a CPB population from Morelos, Mexico, where its native host is *S. angustifolium* , rarely feeds on potato plants.

In the experiment about the impact of foliage age on development and survival of the KBS beetles (experiment two), no significant differences were found for larval deveolpment ($t(48) = 1.3$, $p > 0.37$, Table 6) or survival from the first to fourth instar ($t(5) = 1.86$, $p > 0.51$, Table 6). There was a slight indication that on new foliage, beetles developed faster (8.84 vs 7.41% per day) and survived better (80 vs 75%). Observations on the amount of foliage consumed, indicated that larvae consumed about 40% less foliage when fed on old foliage. Besides the metabolic effect, feeding also has a behavioral aspect (Visser and de Wilde 1980). When fed on suitable host plants, CPB larvae spend most of the time feeding with only short periods of rest. When fed on unsuitable plants, the larvae spend most of its time wandering and resting, and feed only for short periods (Hsiao 1969). In feeding tests, de Wilde et al (1969) reported that CPB adults can detect the age of its host plant. Pupal weight was significantly different both for females ($F(1,30) = 16.8$, $p > 0.0003$, Table 6) and males ($F(1,56) = 16.9$, $p > 0.0001$, Table 6). The insects had heavier pupal weights when fed on new foliage than on old foliage (128 vs 114 mg and 110 vs 101 mg for females and males respectively, Table 6). As pointed out by Rafes (1967) pupal weight may be regarded as an index of larval food consumption. The distribution of the larvae on the horsenettle plants in the field, also indicates that they were feeding mainly on the new foliage. Harcourt (1964) observed that newly hatched larvae feed on the egg chorions for a short period of time, as a rule showing little discrimination between hatched and unhatched eggs. They then attack the foliage near to the edge of the egg mass before moving to the top of the plants to complete their development. Young foliage could have a lower glykoalkaloid concentrations. Hsiao (1986) found that young foliage in *Lycopersicum hirsutum* had 50 % less glykoalkaloids than mature foliage.

Beetle sampling

Mean densities of all stages were well below the typical population levels of CPB on potato plants (Tables 7 and 8). Adult and egg masses per stem had lower standard error, while first instars had the highest. Since this insect lays eggs in clusters, first instars dispersing away from the egg masses would have the highest degree of clustering.

Spatial distribution based on Taylor's power law analysis (*b* values) for egg masses, larvae and adults were very consistent among fields (Table 9) and between years (Table 10). Spatial patterns for eggs and adults in 1987 and 1988, showed a pattern best described by a Poisson distribution based on the *b* values around 1.0 (Table 9 and 10). By contrast, larvae had *b* values greater than 1.0, indicating a negative binomial distribution (Table 9 and 10). Standard errors were higher in 1987 than in 1988. Because of the lower sampling frequency, only half as many sampling dates were taken in 1987 as in 1988 (Table 7 and 8). The non-significance of the regression line for the larval stage in the Corn Field (b = 1.606, a = 0.908, r^2= 0.573, Table 9) could be related to the high standard error of the mean for first instars (0.51). This standard error was twice as high as the highest standard error found for any of the other stages sampled during this study.

Egg mass and larval *b* values (0.95-1.09 for eggs, and 1.52-1.57 for larvae, Table 10) were comparable to those reported for potatoes by Harcourt (1963) (1.12 for eggs and 1.45 for larva), and Logan (1981) (1.07 for egg masses and 1.31-1.45 for larvae). This is an indication that host plant does not affect the aggregation pattern of this insect. However, the spatial distribution of adults (b = 1.06-1.16 Table 10) was different than the patterns described by Taylor (1961) (b=1.48) or Harcourt (1963) (b=1.53). The *b* values of this study suggested a Poisson distribution for the adult beetles, while Taylor and Harcourt report as a negative binomial. However, Taylor (1961) and Logan (1981) mention that lower slope values reflect the fitting of samples from a lower-density population. The mean range for Colorado potato beetles at KBS was from 0.01 to 0.29 adults per stem, a low density in relation to the beetle densities on potato plants. Notably, similar random distribution for adult beetles was observed by Harcourt (1963) for densities lower than 0.5 beetles per potato stem. In fact, this may apply to other insects like the cereal leaf beetle, *Oulema melanopus* where the mean and variance are nearly equal at densities ranging from 0.01 to 0.5 insects per sample, fitting a Poisson distribution (Ruesink and Haynes 1973, Logan 1980).

Spatial distribution can be used not only to describe the aggregation pattern characteristic of the species, but also to determine the sample size required to estimate population parameters. Confidence intervals for each stage indicate that all slopes (*b* values) overlap when comparing the different fields (Table 9) and years (Table 10). Therefore data was pooled. Pooling the data decreased the magnitude of variation both between fields (Table 9) and between years (Table 10). The optimum sample size analysis for egg masses or adult densities below 0.5 per horsenettle stem, indicated that 100 stems per sampling date resulted in a 30% precision (Figure 16a and 16b). However, the larval stage would require at least twice the sample size for similar precision with the densities of the CPB on the horsenettle stems (Figure 16c).

Optimum sample size for estimation of beetle densities on horsenettle plants was about 3 fold higher for eggs (Figure 16b), and 10 fold higher for larvae (Figure 16c), than reported for the beetles on tomato (Latheef and Harcourt 1973) or potato plants (Logan 1981). The suggested optimum sample size for adult beetles was 3 fold higher in relation to the sample size indicated for this insect on tomato plants (Latheef and Harcourt 1973). Even though the aggregation patterns of CPB egg masses and larvae were similar in horsenettle and potato plants, the sample size required to estimate the same population level was much higher on horsenettle. The spatial pattern of the host plant may have a considerable impact on the aggregation pattern of the insect, because the potato plants were uniformly distributed while horsenettle plants were not.

Horsenettle sampling

Horsenettle density in 1988 changed from 2 plants per m^2 on May 24 to 15 plants per m^2 on June 28 (Figure 2). The plant density through time could be described with the following equation obtained with the mean stem densities of the six sampling dates:

$$y = 0.88979 + (1 / 4.6151\ e^{2x}) - (1 / 3.7164\ e^{5x^{**}2})$$

where y = horsenettle stems / m^2, and

x = time in degree days (base 10)

with an $r^2 = 0.977$. The slope (*b*) for horsenettle density during 1988 was 1.68, indicating an aggregation pattern. This could be explained in part by the ability of the plants to reproduce through rhizomes or by seeds that are not moved too far away from the mother plants (Illnicki et al. 1962, Pagano 1974, Wehtje et al 1987). Taking 50 samples of the horsenettle stem density with the 1 m^2 quadrat, produced an estimation of the horsenettle density within 30% of the mean in 1988 (Figure 17).

CONCLUSIONS

Mortality estimation higher than 90% for the CPB egg and larval stages observed during the two years of study, indicates that CPB populations are better regulated under non-agricultural conditions.

The principal biotic agents for control of CPB populations early in the season are insects with chewing mouth parts, especially the coccinellid *Coleomegilla maculata* , and the carabid *Lebia grandis* . Their populations being closely associated with the higher CPB egg input.

Late in the season, the pentatomid *Perilus bioculatus* is one of the more important predators on CPB eggs, and along with *Lebia* beetles, are a strong mortality factor for CPB fourth instars. Also, the tachinid *Doryophorophaga doryphorae* is responsible for 8-21% mortality for CPB fourth instar and prepupae.

Mortality during the egg stage due to predation is constant through the egg mass age. The residence time for a chewed egg mass is 83 DD_{10} and for an egg mass preyed upon by sucking predators, is 179DD_{10}.

Better development rate, pupal weight and survival were found for beetles feeding on potatoes when contrasted to feeding on horsenettle plants. Beetles from a potato population (Montcalm) had similar larval growth as a beetle population from horsenettle (KBS) when feeding on horsenettle foliage. This supports the idea that CPB has been able to feed efficiently on horsenettle plants while keeping its ability to exploit potato plants. However, there was a slight indication that KBS beetles have been under a strong selection pressure for laying the majority of its eggs on host plants and that could be the first step for initiating the development of a CPB biotype on the horsenettle population. It would be worthwhile to test this hypothesis further.

Table 1. Southwood's stage-specific mortality for the Colorado potato beetle on horsenettle at Kellogg Biological Station, Hickory Corners, MI.

FIELD	EGG	L-1	L-2	L-3	ACCUM. MORT.
WEED	0.8511[a]	0.3977	0.8491	0.5715	0.9942
CORN	0.7313[a]	0.5922	-0.1407	0.0968	0.8870
	0.6582[b]	0.4715	0.2784	0.4368	0.9201
GRASS	0.8529[a]	0.4246	0.8420	0.5715	0.9943

[a] Mortality within the stage, date from 1987.

[b] Mortality within the stage, data from 1988.

[c] ACCUM. MORT. = Accumulated mortality from egg stage to third instar.

Table 2. Changes in the Colorado potato beetle egg mass size on horsenettle at the Kellogg Biological Station, Hickory Corners , MI in 1988.

DD[a]	N[b]	EGG MASS SIZE ± S.E[c]		F value[d]	p
57	16	14.9 ± 2.2	a[e]	(10, 1253) = 9.83	0.0001
100	38	25.1 ± 1.7	b		
561	10	28.1 ± 2.1	b c		
464	88	29.2 ± 1.4	b c d		
415	54	29.4 ± 1.5	b c d		
267	244	30.5 ± 0.6	b c d		
217	227	32.1 ± 0.8	c d		
138	106	32.2 ± 1.2	c d		
171	249	33.5 ± 0.7	c d e		
319	142	34.4 ± 1.1	d e		
371	90	37.9 ± 1.3	e		

[a] DD = Degree days base 10°C, accumulated since May 24.

[b] N = Number of egg masses collected from 130 m^2.

[c] Average number of eggs per egg mass.

[d] F value based on GLM test.

[e] Means followed by the same letter are not significantly different, Duncan test (p = 0.05).

Table 3. Egg mass distribution on different plants from a Colorado potato beetle population adapted to horsenettle at Kellogg Biological Station, Hickory Corners MI in 1988.

	NUMBER OF EGG MASSES LAID ON [b]		
DD[a]	HORSENETTLE	CORN	OTHER PLANTS[c]
57	20	113	28
100	45	90	23
138	106	52	44
171	249	54	18
217	224	12	8
267	239	3	1
319	145	1	2
371	90	1	1
415	56	1	2
464	78	2	3
561	10	0	0
636	0	0	0

[a] DD = Degree days base 10°C, accumulated since May 26.

[b] Egg masses collected from an area of 130 m^2.

[c] Mainly velvet leaf. A few egg masses were laid on dry sticks.

Table 4. Larvae development and pupae weight of two populations of the Colorado potato beetle on potato and horsenettle plants in 1988.

BEETLE POPULATION	HOST PLANT	DEVELOPMENT RATE (% /DAY ±S.E)[a]	PUPAE WEIGHT (mg±S.E) FEMALES	MALES
Montcalm	Potato	9.99 ± 0.39[b]	153.4 ± 3.2[c]	139.1 ± 2.3[d]
Montcalm	Horsenettle	7.24 ± 0.68	136.2 ± 2.8	111.5 ± 2.6
KBS	Potato	9.89 ± 0.51	149.0 ± 2.2	127.9 ± 2.3
KBS	Horsenettle	7.57 ± 0.95	128.2 ± 2.9	107.0 ± 2.3

[a] From the first to the fourth instar.

[b] Significant differences only for the host plant effect. GLM test ($F(1, 229) = 896.2$, $p < 0.0001$).

[c] Significant differences for beetle populations. GLM test ($F(1, 112) = 10.17$, $p < 0.0002$); and host plant effect ($F(1, 112) = 99.91$, $p < 0.0001$).

[d] Significant differences for beetle populations. GLM test ($F(1, 105) = 4.77$, $p < 0.03$); and host plant effect ($F(1, 105) = 44.29$, $p < 0.0001$.

Table 5. Survival of two populations of the Colorado potato beetle fed on two different host plants under laboratory conditions in 1988.

BEETLE POPULATION	HOST PLANT	SURVIVORSHIP (% ± S.E)[a] L1 - L4	L1 - ADULT
Montcalm	Potato	91.43 ± 2.61[b]	87.14 ± 4.20[c]
Montcalm	Horsenettle	68.57 ± 9.86	67.14 ± 9.69
KBS	Potato	96.25 ± 2.63	93.75 ± 3.24
KBS	Horsenettle	83.33 ± 7.60	78.33 ± 7.03

[a] Insects reared in petri dishes under room temperature (26 ± 2.4°C).

[b] Significant difference only for the host plant effect ($F(1, 24) = 3.05$, $p < 0.001$). GLM test, data transformed to Arc Sin Square Root of Percentage (Bliss 1967).

[c] Significant difference only for the host plant effect ($F(1, 24) = 7.93$, $p < 0.01$). GLM test, data transformed to Arc Sin Square Root of Percentage (Bliss 1967).

Table 6. Larvae development and pupae weight of a Colorado potato beetle population on two different foliage conditions of horsenettle plants in 1988.

FOLIAGE AGE[a]	DEVELOPMENT RATE (% / DAY ± S. E)[b]	PUPAE WEIGHT (mg ± S.E) FEMALES	MALES	SURVIVAL (% ± S. E)
NEW	8.84 ± 0.9[c]	128.8 ± 2.7[d]	114.0 ± 2.7[e]	80.0 ± 6.8[f]
OLD	7.41 ± 1.06	110.0 ± 3.8	100.5 ± 2.0	75.0 ± 6.7

[a] New foliage was obtained from the upper part of the horsenettle plants. Its age was 1-2 weeks, tender texture and the color was light green. The old foliage refers to leaves located at the lower part of the horsenettle plants. Its age was 4-5 weeks, the leaves were thicker and harder, and the color was green dark.

[b] Reared in petri dishes under room temperature (26.6 ± 2.4°C).

[c] Differences non significant. T-test ($t(48) = 1.30$, $p > 0.37$).

[d] Differences significant. GLM test ($F(1, 30) = 16.8$, $p < 0.001$).

[e] Differences significant. GLM test ($F(1, 56) = 16.9$, $p < 0.0001$).

[f] Differences non significant. T-test ($t(5) = 1.86$, $p > 0.51$). The data was transformed to Arc Sin Square Root of Percentage (Bliss 1967).

Table 7a. Mean, variance and standard errors of the different stages of the Colorado potato beetle on horsenettle during the summer of 1987. Weed Field.

DATE	STATISTIC	EGG MASSES	L-1	L-2	L-3	L-4	ADULTS
MAY 29	MEAN[a]	0.01	0.0	0.0	0.0	0.0	0.01
	VARIANCE	0.01	0.0	0.0	0.0	0.0	0.01
	STD. ERROR	0.01	0.0	0.0	0.0	0.0	0.01
JUN 04	MEAN	0.07	0.09	0.02	0.0	0.0	0.01
	VARIANCE	0.07	0.14	0.02	0.0	0.0	0.01
	STD. ERROR	0.03	0.04	0.01	0.0	0.0	0.01
JUN 10	MEAN	0.02	0.27	0.14	0.06	0.04	0.01
	VARIANCE	0.02	5.37	0.85	0.11	0.04	0.01
	STD. ERROR	0.01	0.23	0.09	0.03	0.02	0.01
JUN 16	MEAN	0.01	0.07	0.05	0.08	0.05	0.0
	VARIANCE	0.01	0.21	0.11	0.14	0.05	0.0
	STD. ERROR	0.01	0.05	0.03	0.04	0.02	0.0
JUN 23	MEAN	0.0	0.0	0.0	0.02	0.06	0.01
	VARIANCE	0.0	0.0	0.0	0.02	0.06	0.01
	STD. ERROR	0.0	0.0	0.0	0.01	0.02	0.01
JUL 05	MEAN	0.03	0.36	0.0	0.0	0.0	0.0
	VARIANCE	0.03	6.04	0.0	0.0	0.0	0.0
	STD. ERROR	0.02	0.03	0.0	0.0	0.0	0.0

[a] Mean number of insects per horsenettle stem, 100 horsenettle stems sampled per sampling date

Table 7b. Mean, variance and standard errors of the different stages of the Colorado potato beetle on horsenettle during the summer of 1987. Corn Field.

DATE	STATISTIC	EGG MASSES	L-1	L-2	L-3	L-4	ADULTS
MAY 29	MEAN[a]	0.01	0.0	0.0	0.0	0.0	0.01
	VARIANCE	0.01	0.0	0.0	0.0	0.0	0.01
	STD. ERROR	0.01	0.0	0.0	0.0	0.0	0.01
JUN 04	MEAN	0.15	0.02	0.0	0.0	0.0	0.05
	VARIANCE	0.13	0.04	0.0	0.0	0.0	0.05
	STD. ERROR	0.03	0.02	0.0	0.0	0.0	0.02
JUN 10	MEAN	0.10	1.48	0.14	0.16	0.03	0.03
	VARIANCE	0.09	26.31	0.49	0.34	0.03	0.03
	STD. ERROR	0.03	0.51	0.07	0.06	0.02	0.02
JUN 16	MEAN	0.05	0.80	0.31	0.23	0.06	0.01
	VARIANCE	0.05	13.25	0.94	0.60	0.08	0.01
	STD. ERROR	0.02	0.36	0.10	0.08	0.03	0.01
JUN 23	MEAN	0.05	0.02	0.07	0.05	0.28	0.03
	VARIANCE	0.05	0.02	0.09	0.05	0.63	0.03
	STD. ERROR	0.02	0.01	0.03	0.02	0.08	0.02
JUL 02	MEAN	0.06	0.12	0.06	0.19	0.26	0.05
	VARIANCE	0.06	0.83	0.08	0.40	0.34	0.05
	STD. ERROR	0.02	0.09	0.03	0.06	0.06	0.02
JUL 20	MEAN	0.0	0.0	0.0	0.0	0.0	0.05
	VARIANCE	0.0	0.0	0.0	0.0	0.0	0.05
	STD. ERROR	0.0	0.0	0.0	0.0	0.0	0.02

[a] Mean number of insects per horsenettle stem, 100 horsenettle stems sampled per sampling date

Table 7c. Mean, variance and standard errors of the different stages of the Colorado potato beetle on horsenettle during the summer of 1987. Grass Field.

DATE	STATISTIC	EGG MASSES	L-1	L-2	L-3	L-4	ADULTS
MAY 29	MEAN[a]	0.02	0.0	0.0	0.0	0.0	0.06
	VARIANCE	0.02	0.0	0.0	0.0	0.0	0.06
	STD. ERROR	0.02	0.0	0.0	0.0	0.0	0.02
JUN 04	MEAN	0.14	0.09	0.05	0.0	0.0	0.16
	VARIANCE	0.18	0.24	0.07	0.0	0.0	0.18
	STD. ERROR	0.04	0.05	0.03	0.0	0.0	0.04
JUN 10	MEAN	0.18	0.56	0.31	0.06	0.05	0.09
	VARIANCE	0.17	4.94	6.34	0.06	0.05	0.12
	STD. ERROR	0.04	0.22	0.25	0.02	0.02	0.04
JUN 17	MEAN	0.11	0.56	0.15	0.03	0.01	0.03
	VARIANCE	0.12	10.13	0.35	0.03	0.01	0.03
	STD. ERROR	0.04	0.32	0.06	0.02	0.01	0.02
JUN 25	MEAN	0.12	0.0	0.09	0.01	0.01	0.17
	VARIANCE	0.11	0.0	0.81	0.01	0.01	0.26
	STD. ERROR	0.03	0.0	0.09	0.01	0.01	0.05
JUL 05	MEAN	0.07	0.29	0.0	0.0	0.0	0.06
	VARIANCE	0.07	4.39	0.0	0.0	0.0	0.06
	STD. ERROR	0.03	0.21	0.0	0.0	0.0	0.02

[a] Mean number of insects per horsenettle stem, 100 horsenettle stems sampled per sampling date

Table 8. Mean, variance and standard errors of the different stages of the Colorado potato beetle on horsenettle during the 1988 sampling in the Corn Field.

DATE	STATISTIC	EGG MASSES	L-1	L-2	L-3	L-4	ADULTS
MAY 24	MEAN[a]	0.0	0.0	0.0	0.0	0.0	0.04
	VARIANCE	0.0	0.0	0.0	0.0	0.0	0.04
	STD. ERROR	0.0	0.0	0.0	0.0	0.0	0.02
MAY 26	MEAN	0.04	0.0	0.0	0.0	0.0	0.06
	VARIANCE	0.04	0.0	0.0	0.0	0.0	0.08
	STD. ERROR	0.02	0.0	0.0	0.0	0.0	0.03
MAY 28	MEAN	0.07	0.0	0.0	0.0	0.0	0.02
	VARIANCE	0.06	0.0	0.0	0.0	0.0	0.02
	STD. ERROR	0.04	0.0	0.0	0.0	0.0	0.01
MAY 31	MEAN	0.05	0.01	0.0	0.0	0.0	0.04
	VARIANCE	0.05	0.01	0.0	0.0	0.0	0.04
	STD. ERROR	0.03	0.01	0.0	0.0	0.0	0.02
JUN 04	MEAN	0.03	0.10	0.01	0.0	0.0	0.06
	VARIANCE	0.03	0.68	0.01	0.0	0.0	0.57
	STD. ERROR	0.02	0.08	0.01	0.0	0.0	0.02
JUN 06	MEAN	0.07	0.08	0.04	0.02	0.0	0.05
	VARIANCE	0.06	0.30	0.08	0.04	0.0	0.09
	STD. ERROR	0.04	0.05	0.03	0.02	0.0	0.03
JUN 09	MEAN	0.10	0.08	0.15	0.06	0.0	0.06
	VARIANCE	0.09	0.64	0.63	0.18	0.0	0.10
	STD. ERROR	0.03	0.08	0.08	0.04	0.0	0.03
JUN 12	MEAN	0.18	0.49	0.15	0.21	0.01	0.03
	VARIANCE	0.17	6.43	0.29	0.90	0.01	0.03
	STD. ERROR	0.04	0.25	0.05	0.09	0.01	0.02
JUN 14	MEAN	0.17	0.91	0.09	0.11	0.05	0.02
	VARIANCE	0.20	18.26	0.12	0.24	0.17	0.02
	STD. ERROR	0.05	0.43	0.04	0.04	0.04	0.01
JUN 18	MEAN	0.16	0.98	0.28	0.31	0.11	0.03
	VARIANCE	0.16	19.05	3.36	2.56	0.16	0.03
	STD. ERROR	0.04	0.44	0.18	0.16	0.04	0.02
JUN 21	MEAN	0.15	0.22	0.34	0.12	0.17	0.03
	VARIANCE	0.15	1.55	2.81	0.15	0.47	0.03
	STD. ERROR	0.04	0.12	0.17	0.04	0.07	0.02

a Mean number of insects per horsenettle stem, 100 horsenettle stems per sampling date.

Table 8 (cont'd.).

DATE	STATISTIC	EGG MASSES	L-1	L-2	L-3	L-4	ADULT
JUN 24	MEAN[a]	0.19	0.04	0.46	0.41	0.32	0.0
	VARIANCE	0.25	0.06	4.33	1.07	0.54	0.0
	STD. ERROR	0.05	0.02	0.21	0.10	0.07	0.0
JUN 27	MEAN	0.16	1.34	0.28	0.32	0.37	0.06
	VARIANCE	0.24	34.75	0.79	0.54	0.88	0.12
	STD. ERROR	0.05	0.29	0.06	0.07	0.10	0.01
JUN 29	MEAN	0.13	0.52	0.16	0.25	0.39	0.02
	VARIANCE	0.11	8.52	0.40	0.55	1.05	0.02
	STD. ERROR	0.03	0.29	0.06	0.07	0.10	0.01
JUL 04	MEAN	0.16	0.14	0.21	0.06	0.23	0.10
	VARIANCE	0.24	1.46	1.34	0.06	0.52	0.11
	STD. ERROR	0.05	0.12	0.12	0.02	0.07	0.03
JUL 08	MEAN	0.12	0.32	0.01	0.08	0.15	0.06
	VARIANCE	0.13	5.90	0.01	0.11	0.13	0.06
	STD. ERROR	0.04	0.24	0.01	0.03	0.04	0.02
JUL 16	MEAN	0.09	0.0	0.0	0.03	0.01	0.29
	VARIANCE	0.81	0.0	0.0	0.03	0.01	0.41
	STD. ERROR	0.09	0.0	0.0	0.02	0.01	0.06
JUL 22	MEAN	0.0	0.36	0.0	0.0	0.0	0.28
	VARIANCE	0.0	8.86	0.0	0.0	0.0	0.24
	STD. ERROR	0.0	0.30	0.0	0.0	0.0	0.05
JUL 29	MEAN	0.0	0.0	0.0	0.0	0.01	0.10
	VARIANCE	0.0	0.0	0.0	0.0	0.01	0.09
	STD. ERROR	0.0	0.0	0.0	0.0	0.01	0.03
AUG 05	MEAN	0.0	0.0	0.0	0.0	0.0	0.05
	VARIANCE	0.0	0.0	0.0	0.0	0.0	0.05
	STD. ERROR	0.0	0.0	0.0	0.0	0.0	0.02

[a] Mean number of insects per horsenettle stem, 100 horsenettle stems sampled per sampling date

Table 9. Spatial pattern analysis of the Colorado potato beetle on horsenettle in 1987, based on Taylor's power law regression.

STAGE	FIELD	N	SLOPE (b) ± S.E	INTERCEPT(a)	R^2	p[a]
EGG	WEED	4	0.967 ± 0.009	-0.062	0.999	< 0.01
MASSES	CORN	5	0.835 ± 0.158	-0.193	0.903	0.01
	GRASS	5	0.705 ± 0.159	-0.241	0.868	< 0.01
	POOLED	14	0.949 ± 0.043	-0.069	0.976	< 0.01
LARVAE	WEED	4	1.836 ± 0.232	1.060	0.969	0.01
	CORN	5	1.606 ± 0.800	0.908	0.573	N.S[b]
	GRASS	5	1.573 ± 0.300	1.256	0.902	0.01
	POOLED	14	1.573 ± 0.224	1.034	0.804	< 0.01
ADULTS	WEED	3	N.P[c]			
	CORN	6	1.290 ± 0.144	0.544	0.952	< 0.01
	GRASS	6	1.049 ± 0.170	0.189	0.905	< 0.01
	POOLED	15	1.156 ± 0.056	0.317	0.971	< 0.01

[a] p = Statistical significance probability of the log s^2 on the log m regression.

[b] N.S = Non statistically significant.

[c] N.P = Not possible to make the calculations.

Table 10. Spatial pattern analysis of the Colorado potato beetle on horsenettle in 1987 and 1988, based on Taylor's power law regression.

STAGE	YEAR	N	SLOPE (*b*) ± S.E	INTERCEPT(*a*)	R^2	p[a]
EGG	1987	14	0.949 ± 0.043	-0.069	0.976	< 0.01
MASSES	1988	13	1.094 ± 0.074	0.120	0.952	< 0.01
	POOLED	27	1.009 ± 0.040	0.018	0.962	< 0.01
LARVAE	1987	14	1.573 ± 0.224	1.034	0.804	< 0.01
	1988	13	1.516 ± 0.195	1.000	0.847	< 0.01
	POOLED	27	1.543 ± 0.141	1.014	0.828	< 0.01
ADULTS	1987	15	1.156 ± 0.056	0.317	0.971	< 0.01
	1988	19	1.060 ± 0.77	0.131	0.917	< 0.01
	POOLED	34	1.096 ± 0.046	0.199	0.946	< 0.01

[a] p = Statistical significance probability of the log s^2 on the log m regression.

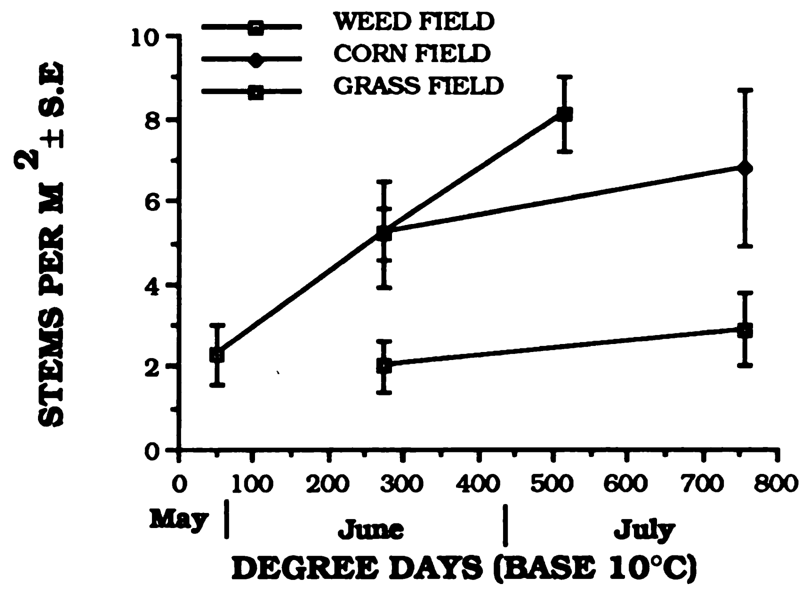

Figure 1. Horsenettle density in three different fields at the Kellog Biological Station during 1987. DD_{10} measurements beginning on May 26.

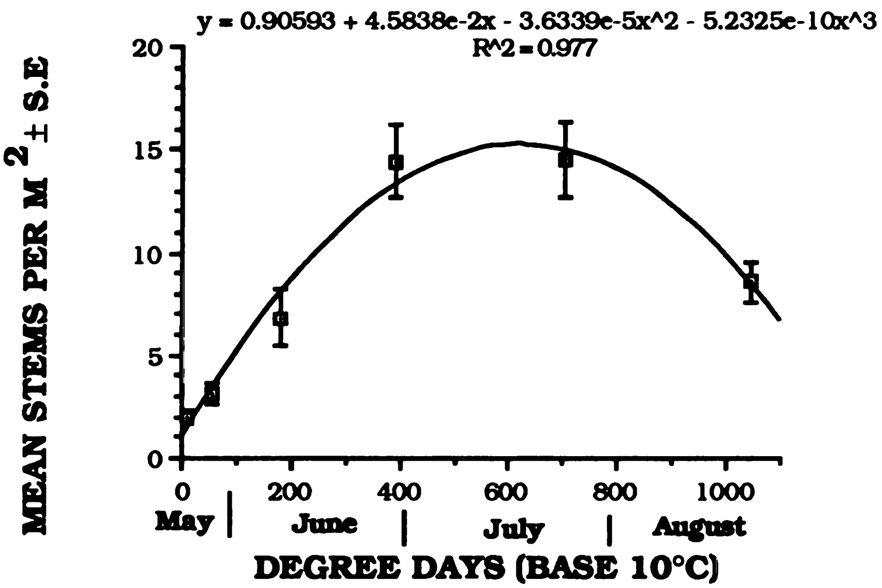

Figure 2. Relationship between horsenettle stem density and sampling date in the Corn field at the Kellogg Biological Station in 1988. DD_{10} measurements started on May 22.

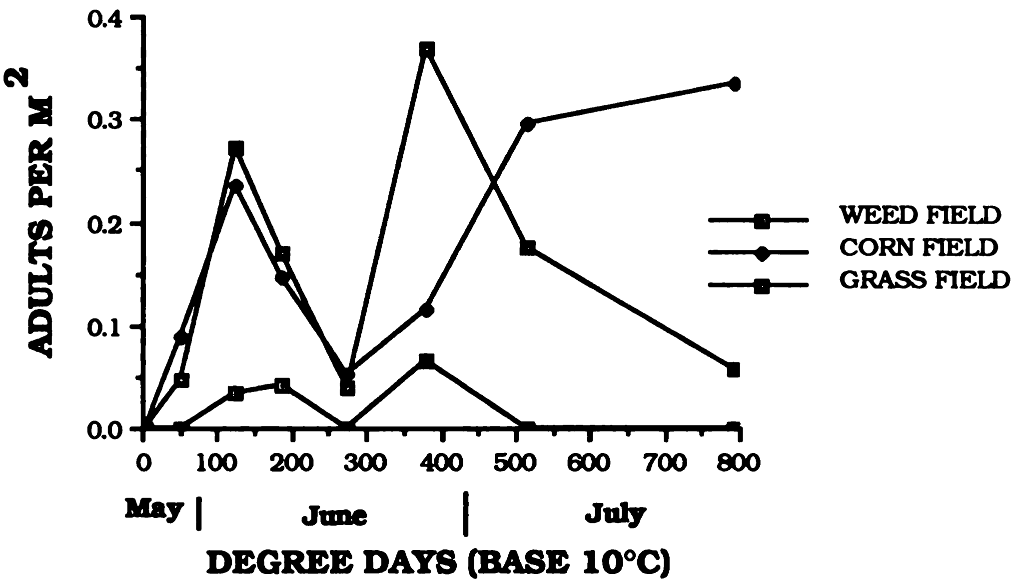

Figure 3. Population density of Colorado potato beetle adults on horsenettle at the Kellogg Biological Station in 1987. DD_{10} accumulation started on May 26.

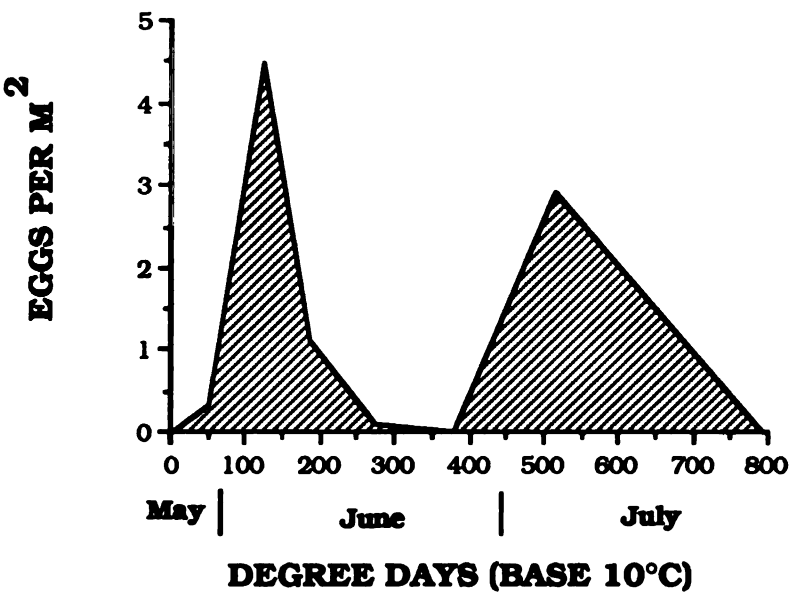

Figure 4a. Population density of Colorado potato beetle eggs on horsenettle at the Kellogg Biological Station in 1987. Weed Field. DD_{10} measurements starting on May 26.

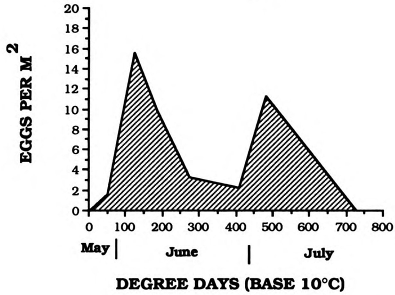

Figure 4b. Population density of the Colorado potato beetle eggs on horsenettle at the Kellogg Biological Station in 1987. Corn Field. DD_{10} accumulation started on May 26.

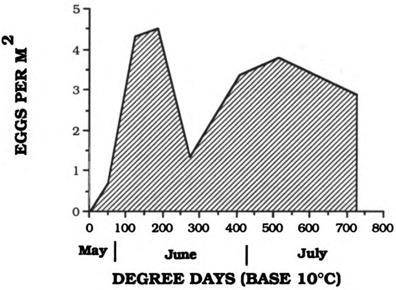

Figure 4c. Population density of the Colorado potato beetle eggs on horsenettle at the Kellogg Biological Station in 1987. Grass Field. DD_{10} accumulation started on May 26.

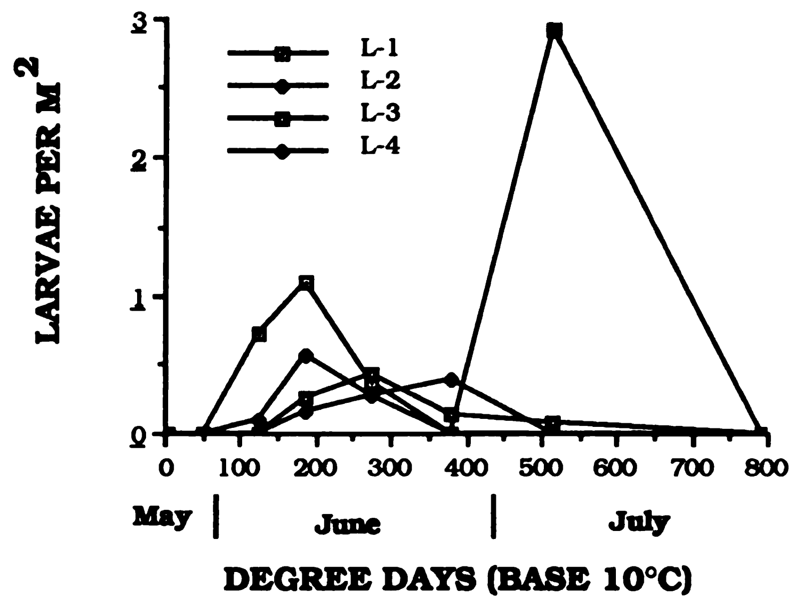

Figure 5a. Population density of Colorado potato beetle larvae on horsenettle at the Kellogg Biological Station in 1987. Weed Field. DD_{10} measurements beginning on May 26.

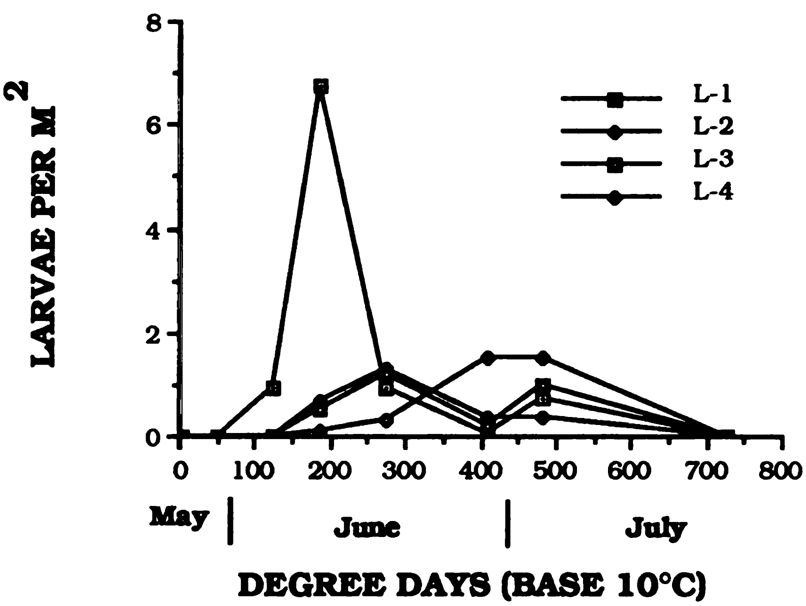

Figure 5b. Population density of Colorado potato beetle larvae on horsenettle at the Kellogg Biological Station in 1987. Corn Field. DD_{10} accumulation started on May 26.

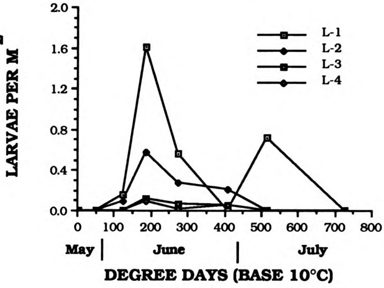

Figure 5c. Population density of Colorado potato beetle larvae on horsenettle at the Kellogg Biological Station in 1987. Grass Field. DD_{10} accumulation started on May 26.

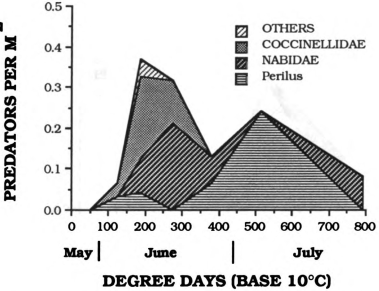

Figure 6a. Population density of Colorado potato beetle natural enemies on horsenettle at the Kellogg Biological Station in 1987. Weed Field. DD_{10} measurements beginning on May 26.

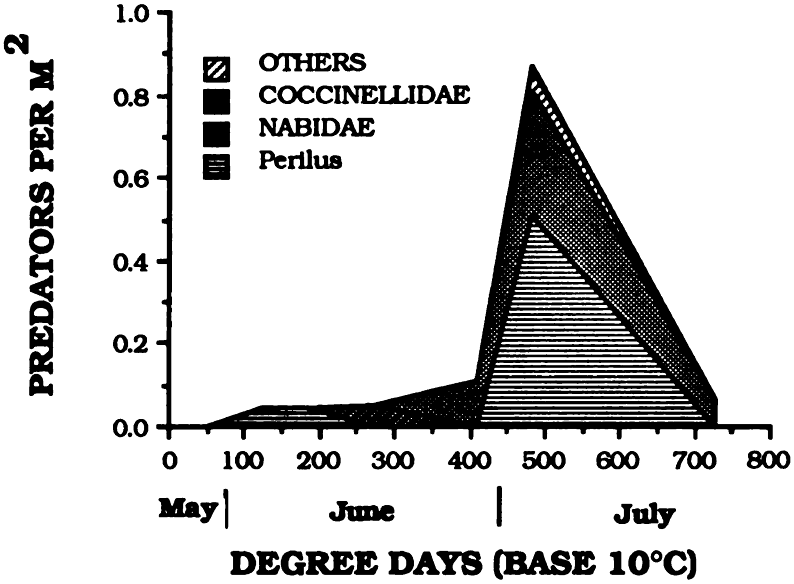

Figure 6b. Population density of Colorado potato beetle natural enemies on horsenettle at the Kellogg Biological Station in 1987. Corn Field. DD_{10} accumulation started on May 26.

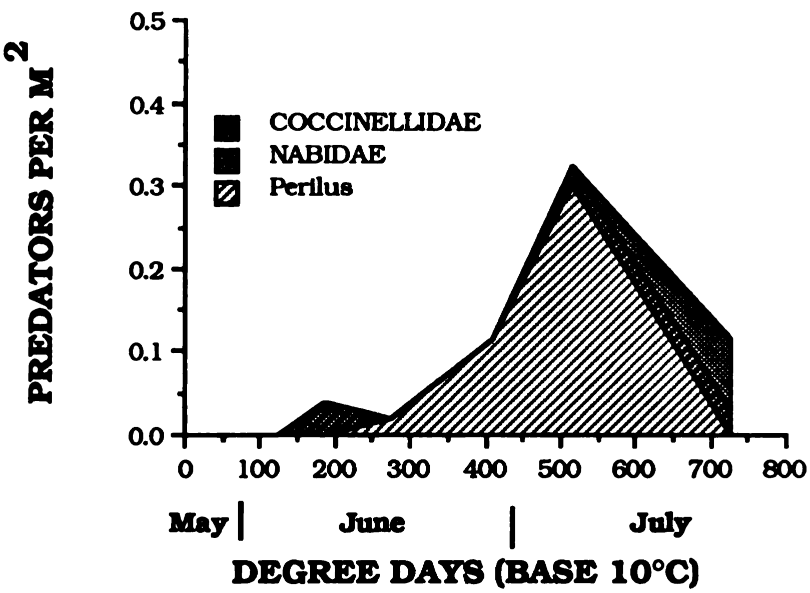

Figure 6c. Population density of Colorado potato beetle natural enemies on horsenettle at the Kellog Biological Station in 1987. Grass Field. DD_{10} accumulation started on May 26.

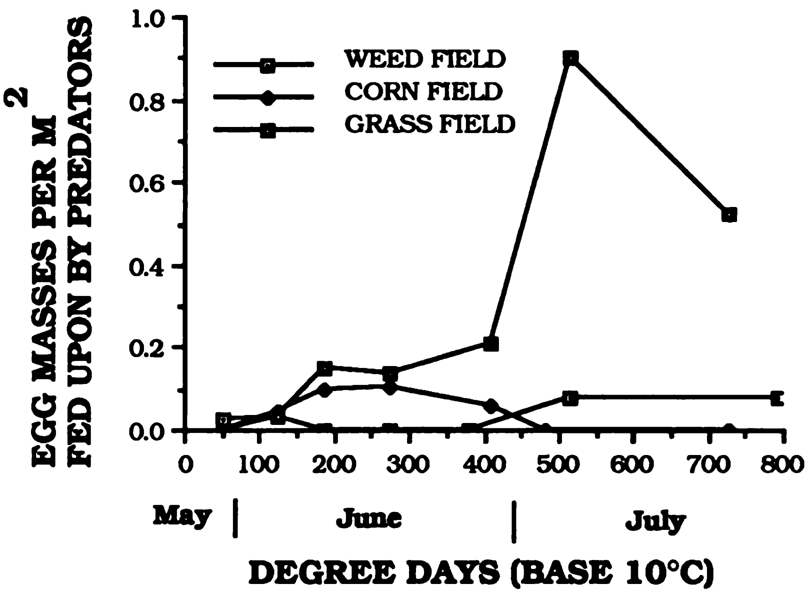

Figure 7. Egg masses preyed upon by Colorado potato beetle predators on horsenettle at the Kellogg Biological Station in 1987. DD_{10} accumulation started on May 26.

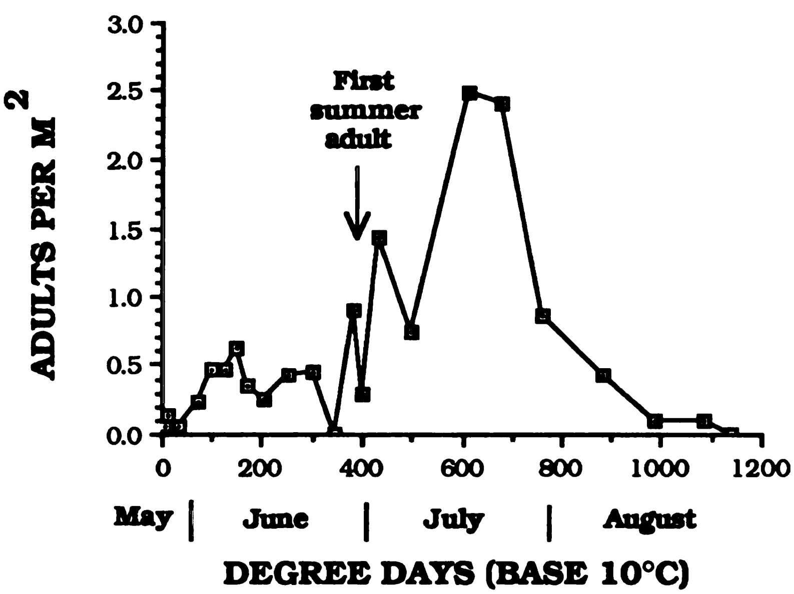

Figure 8. Population density of Colorado potato beetle adults on horsenettle at the Kellogg Biological Station in 1988. DD_{10} measurements beginning on May 22.

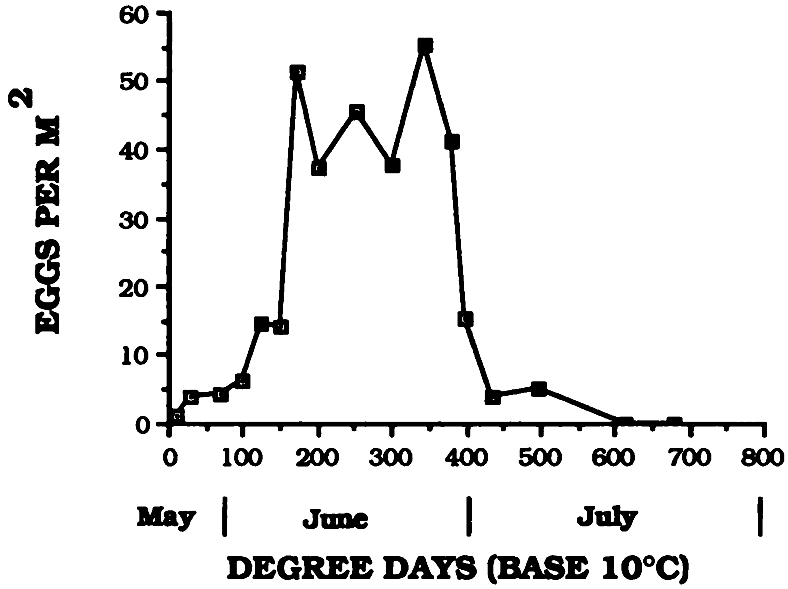

Figure 9. Population density of Colorado potato beetle eggs on horsenettle at the Kellogg Biological Station in 1988. DD_{10} measurements beginning on May 22.

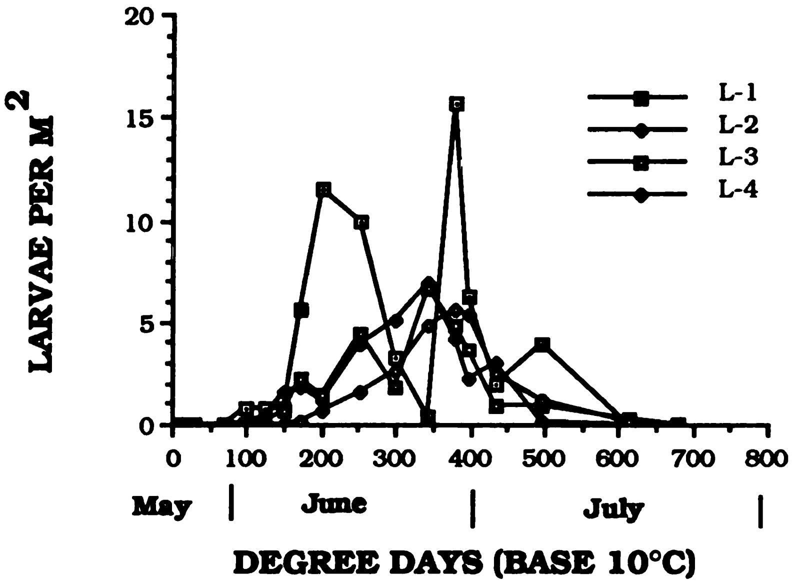

Figure 10. Population density of the Colorado potato beetle larvae on horsenettle at the Kellogg Biological Station in 1988. DD_{10} accumulation started on May 22.

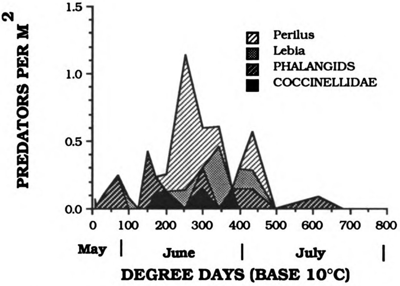

Figure 11. Population density of CPB natural enemies on horsenettle at the Kellogg Biological Station in 1988. DD_{10} accumulation started on May 22.

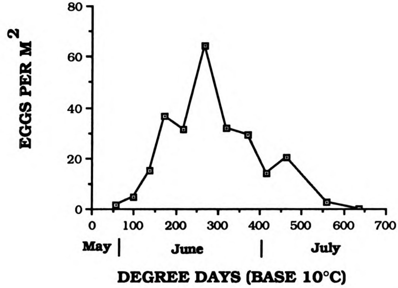

Figure 12. CPB egg density on horsenettle as obtained from sampling an area of 130 m^2.

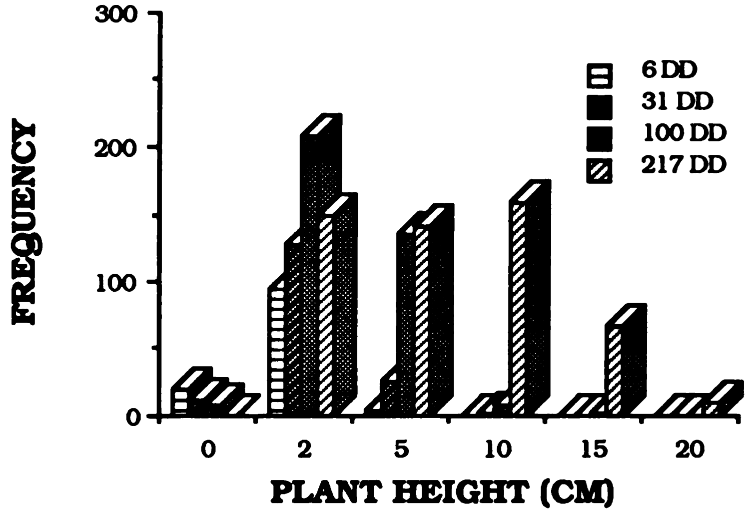

Figure 13. Relationship between horsenettle size and sampling date at the Kellogg Biological Station in 1988.

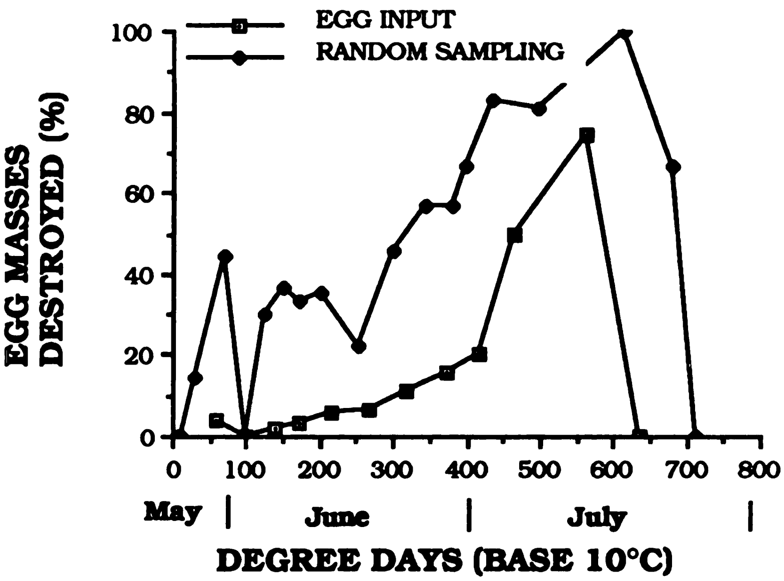

Figure 14. Estimation based on two sampling methods of the percentage of egg masses preyed upon by CPB predators on horsenettle at the Kellogg Biological Station in 1988.

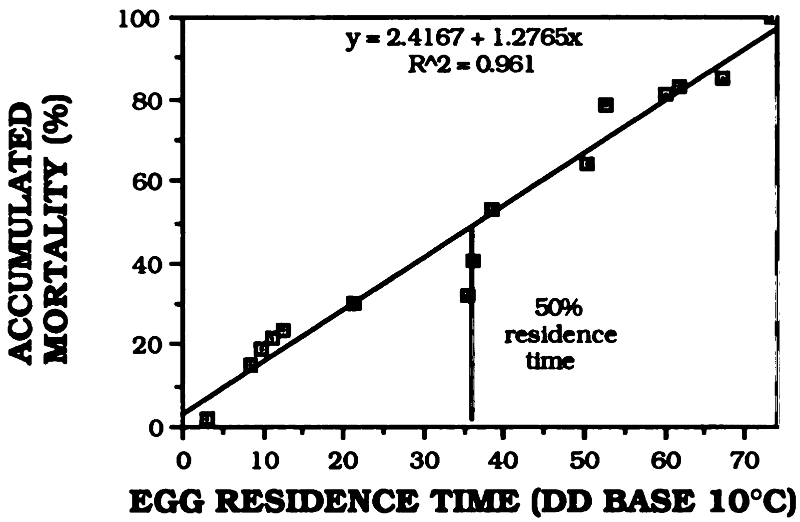

Figure 15. CPB egg mortality distribution in relation to the egg mass age on horsenettle at the Kellog Biological Station in 1988.

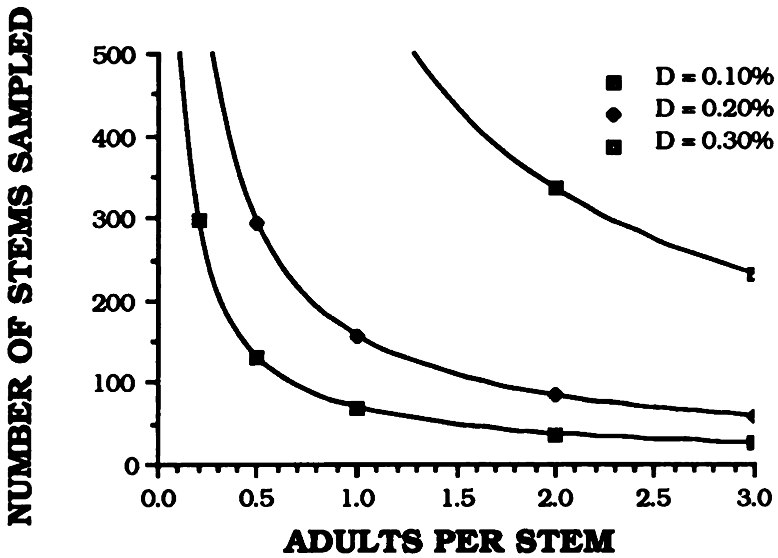

Figure 16a. Sample size needed to estimate CPB adult density on horsenettle.

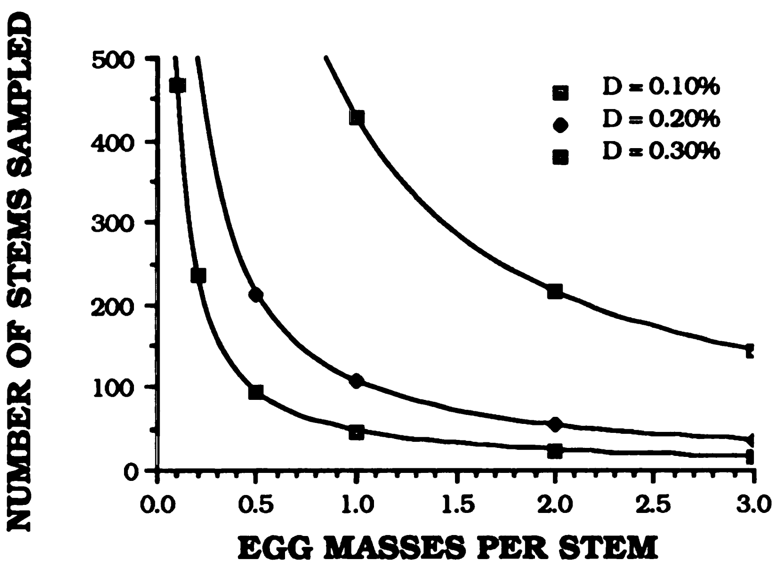

Figure 16b. Sample size needed to estimate CPB egg mass density on horsenettle.

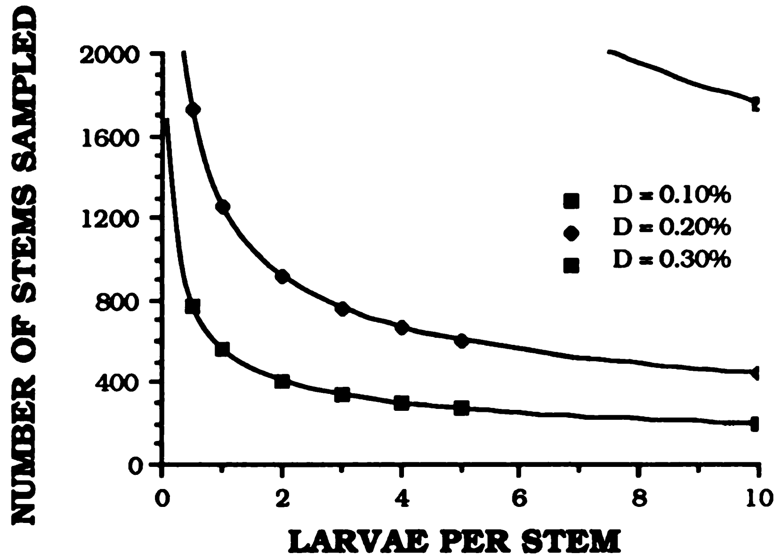

Figure 16c. Sample size needed to estimate CPB larvae density on horsenettle.

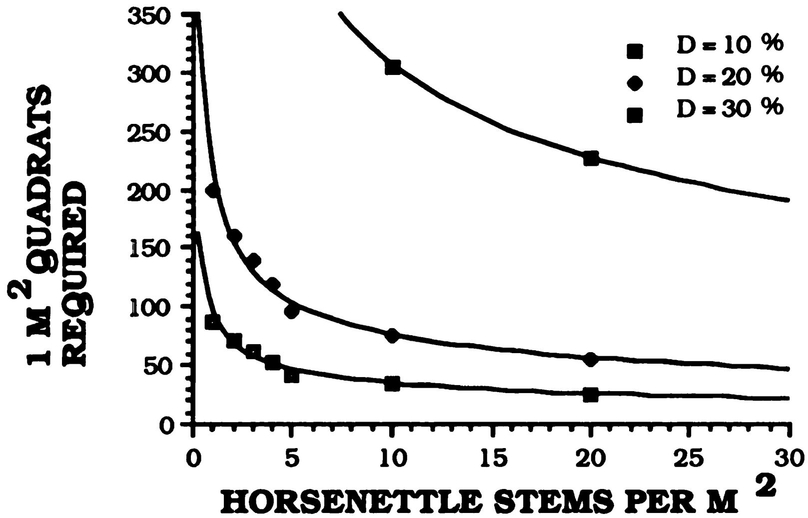

Figure 17. Sample size needed to estimate horsenettle density based on number of stems per m^2.

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APPENDIX

APPENDIX

THE JACKNIFE APPROACH TO VARIANCE ESTIMATION FOR SOUTHWOOD'S STAGE-SPECIFIC MORTALITY.

ABSTRACT

One of the shortcomings of Southwood's method of stage-specific mortality estimation is the lack of an error term. The Jacknife technique was applied to the estimation of the variability associated with stage specific mortality calculation for Colorado potato beetle on horsenettle. Removing up to 20 observations did not affect greatly the Standard Error / Mean relationship, and it was chosen as the size of the subsample removed for the Jacknife. Except for recruitment to the first and second instar in 1987, and the second instar in 1988, population estimates had a coefficient of variation approximating 10%. Except for the second instar in 1988, the Jacknife estimates of mortality were not significantly different from the estimates calculated from the entire data set in the standard way. The Jacknife consistently underestimated the value of mortality compared to the standard Southwood's method which also underestimates stage mortality whenever mortality is not occurring at the end of the stage. Jacknife is an acceptable method to estimate the variability of the stage-specific mortality calculation with Southwood's method.

One of the shortcomings of Southwood's method of stage-specific mortality estimation is the lack of an error term (Southwood 1978). This problem can be overcome using the Jacknife technique. Quenouiolle (1949) introduced this technique for reducing the bias of a serial correlation estimator based on splitting the sample into two half-samples. In his 1956 paper he generalized this idea, splitting the sample into g groups of size h each, so that $n = gh$, and explored its general applicability. Tukey (1958) broadened the applicability of the Jacknife technique when he used it for interval estimation. The variance of Jacknife estimates has an approximate t distribution (Miller 1974, Manly 1979) or, for large g, an approximate normal distribution (Miller 1974). The Jacknife is a robust technique, and it has been applied to infer S_1^2 / S_2^2 from s_1^2 / s_2^2, to estimate the variability of log s^2 or log s_1^2 - log s_2^2; and to establish a confidence interval on S^2 from s^2 (Miller 1974). The successful use of the Jacknife method for estimating variances on key factor analysis is reported by Manly (1979).

Most advocates of the Jacknife suggest using a variance stabilizing transformation on the estimator to keep the Jacknife on scale and thus prevent distortion of the results (Miller 1974). Using computer simulation Manly (1979) found that the Jacknife works best in mortality key factor analysis when it is applied to the $\log_e$ of estimates rather than with direct values.

Of the variety of methods that exist for the analysis of stage-specific frequency data reviewed by Southwood (1978), only Richard's and Manly's method have a formula (approximate) for standard error for stage-specific mortality estimation (Manly 1974). He also applied the Jacknife to the estimation of the standard error of stage-specific mortality for the Kiritani and Nakasuji's method (Manly 1977). He found that the standard error estimates were usually reasonable. Because there are no reports of variance estimation on Southwood's method, the objective of this paper was to apply the Jacknife technique for the estimation of the confidence limits associated with this stage-specific mortality calculation.

MATERIALS AND METHODS

The Jacknife estimate of variance was applied to mortality calculated for the Colorado potato beetle, *Leptinotarsa decemlineata* (Say) on horsenettle, *Solanum carolinense* L. at the Michigan State University Kellog Biological Station at Hickory Corners, MI. The beetles were sampled by direct observation of 100 randomly selected horsenettle stems. In 1987 the sampling frequency was approximately one week, and the area sampled was 2 ha. In 1988, the sampling frequency was 2 to 4 days and the sampled area was 4 ha. Insect counts were transformed to densities per m^2 based on the horsenettle density. Mortality estimates were calculated with Southwood's graphical method as described by Helgensen and Haynes (1972). A lower threshold of 10°C was used to calculate the mean accumulated degree days (DD_{10}) for Colorado potato beetle development (Logan and Casagrande 1980). Residence time was estimated as 72 DD_{10} for eggs (Logan et al. 1985), 41 DD_{10} for first instars, 39 DD_{10} for second instars, 49 DD_{10} for third instars, and 76 DD_{10} for fourth instars (Groden and Casagrande 1986). The Jacknife estimate is affected by the size of the subgroup used for the Jacknife process. The most precise form of Jacknife to use is to remove only one observation from the complete data set (Miller 1974, Drummond 1988). However, the estimate of the variance is not appreciably altered when removing 2, 3, ...5, etc observations (Miller 1974, Drummond 1988). Therefore, the size of the subsample removed for this study was defined by the percentage of the ratio Standard Error / Mean (Mosteller and Tukey 1977) from densities of eggs, first and fourth instars from five observation dates for the 1988 data set. These different densities and stages chosen were intended to represent the variability of the Colorado potato beetle sample data.

The variance of estimates was estimated by means of the Jacknife procedure (Manly 1977). The basic idea with the Jacknife technique is to divide sample data into h comparable sized subsamples. The first subsample is then removed from the full set of data and the mortality (q_{-i}) is estimated using the remaining data. This provides the first "partial estimate" (q_{-1}). The first subsample is then replaced , the second removed , and the second partial estimate (q_{-2}) is calculated. The process is continued in order to obtain all of the partial estimates $q_{-1}, q_{-2}, \ldots\ldots\ldots, q_{-n}$. These are then combined with the estimate q_{all} obtained using the full set of data to form the n "pseudovalues":

$$q_{\#j} = nq_{all} - (n-1)q_{-j}\,, \qquad j = 1, 2, 3, \ldots\ldots\ldots, n$$

The average of these pseudovalues is the Jacknife estimate for q :

$$JKq_{\#} = {}^{n}\text{Summatory}_{j=1} \ / \ n$$

The variance of $q_{\#}$ is estimated as :

$$Var(q_{\#}) = 1 \ / \ n(n-1) \ {}^{n}\text{Summatory}_{j=1} \ (q_{\#j} - q_{\#})^2$$

And the confidence limit (CL) of $q_{\#}$ is estimated as :

$$CL(q_{\#}) = JKq_{\#} \pm t_{df} \bullet (Var(q_{\#}) \ / \ n)$$

where t is a value from the t table with n-1 as degrees of freedom (see Manly 1977). In this study, the observations were removed systematically and 10 partial estimates of mortality were obtained.

RESULTS AND DISCUSSION

The Standard Error / Mean ratio was highest for first instars and lowest for the fourth instars (Figure 18). The higher variability observed for the first instar is due both to the dispersion of recently hatched larvae from the egg mass (Logan 1981) and to a higher sampling error (Groden 1988). For all stages there was an increase of about 4% in the variability of the data when one observation was removed from the data set (Figure 18). Removing up to 20 observations did not greatly affect the Standard Error / Mean relationship. However, when 40 observations were removed at once, there was a change of about 20% in the variability of the data (Figure 18). Based on these results, 20 observations was chosen as the size of the subsample removed for the Jacknife technique.

The estimates obtained with the Jacknife of the actual number of individuals entering the egg and larval stage exhibited a coefficient of variation (CV) of 7.1 to 23.8% in 1987 and 7.3 to 17.2% in 1988 (Table 11 and 12). Except for the recruitment to the first and second instar in 1987, and the second instar in 1988, population estimates had a CV approximating 10% indicating that with the Jacknife estimates, the level of uncertainty around the mean is small. The higher variability for the second instar in 1987 was due to estimates 2 and 7 that were about 50% lower than the others (Table 11). A similar situation was found for the same instar in 1988, when the estimates 3 and 8 were about 40% lower than the others (Table 12).

Survival was calculated by dividing the number of individuals that entered stage $i + 1$ by the number of individuals at stage i, and mortality was obtained by substracting survival from 1. The variance of the partial mortality estimates of the different life stages was higher in 1987 than in 1988, with first and second instars having higher variance in both years (Table 13 and 14). In 1987, one first instar mortality estimate (q_{-2} = - 0.0954) and another for second instar (q_{-1}= -0.1125) were negative, while only one negative estimate was found in 1988 (q_{-2} = -0.0349 for the second instar). These negative estimates of mortality were not considered for the Jacknife analysis. Negative estimates of mortality occur occasionally with specific methods due to sampling error, differential sampling efficiency of the various stages, or high mortality experienced early in a stage (Mills 1981, Sawyer and Haynes 1984, Groden 1988,).

The Jacknife estimates of mortality were not substantially different from the estimates calculated from the full data in the usual way, except for the second instar in 1988 (Table 15). It was found that the confidence limits of the estimates were large for the 1987 data, and for the second instar in 1988 (Table 15). Because of the size of the confidence limit for first instars in 1987 and second instars in 1988, the confidence limit extends beyond the lower limit of 0.0. However, the size of the confidence limit of the mortality estimates for the egg stage in both years or the mortality estimates for 1988 as an overall indicates a good reliability of the technique.

There was a slight indication that the Jacknife had decreased the estimated value of mortality (5 cases from 8 in Table 15), which is probably in the wrong direction. Southwood's method underestimates the number of individuals entering a life stage, whenever there is mortality occurring earlier than at the end of the life stage, therefore underestimates stage mortality (Sawyer and Haynes 1984). It is reported that at least the first and second instars of Colorado potato beetle on potato plants experience high mortality early in the stage (Groden 1988). These lowered Jacknife mortality estimates were due to number and size of the higher estimates of mortality with the partial estimates (q_{-i}'s) in relation to mortality estimate with the full data set (q) (Table 13 and 14).

One aspect that deserves attention from Table 15 is the size of the confidence intervals, specifically the first instars in 1987 and the second instar in 1988. The high variability was coming from two sources, the low estimations of mortality in relation to the mortality q or the mortality estimates higher than q that will lead to negative pseudovalues. This could be seen on the mortality estimates for first instars in 1987 ($q_{-2} = 0.6905$, $q_{-6} = 0.6717$, and $q_{-7} = 0.0386$ while estimate $q = 0.3640$) (Table 3). In the case of the second instars in 1988, only one observation is quite different from the others ($q_{-7} = 0.1107$ while $q = 0.5259$), but 6 of the 8 mortality partial estimates were higher than the mortality q, and therefore, they produced negative pseudovalues (Table 14).

These very low or high partial mortality estimations were possibly due to three factors:

1.- The size of the subsample removed from the data set led to the difference of about 8% of greater variability when removing 20 observations, than not removing any observation at all (Figure 18).

2.- The lower densities reached by the Colorado potato beetle led to a lot of zeros in the 100 observations per sampling date. The calculation of the mean when the 20 observations were removed was usually higher than the mean from the whole data set. The majority of these higher means were responsible for the higher partial estimates mortality, and therefore of the negative pseudovalues.

3.- The size of the subsample removed, defined from the ratio Standard Error / Mean was calculated using the data from 1988 but not 1987.

The majority of the Jacknife estimates of mortality were very similar to the normal estimate with Southwood's method. Due to the low densities of the beetles on horsenettle, this could be considered a though test for the technique. Therefore, the use of the Jacknife method for estimating an error term on the mortality calculated by Southwood's method is acceptable, but should be tested with simulation.

Table 11. Number of individuals entering each stage estimated with Southwood's method for estimate stage-specific mortality in Colorado potato beetle on horsenettle in 1987.

	EGGS[a]	L - 1[b]	L - 2[b]	L - 3[b]	L - 4[b]
1[c]	59.02	21.89	13.92	8.12	5.87
2[d]	61.75	24.00	7.43	8.26	6.45
3	64.43	14.59	15.98	8.56	6.59
4	66.99	22.84	15.32	7.78	5.19
5	57.71	22.39	15.67	8.83	5.74
6	43.66	25.24	15.39	7.50	5.46
7	69.27	23.82	7.82	7.06	6.45
8	59.58	16.21	15.59	8.57	5.86
9	67.29	22.93	14.82	8.36	5.45
10	49.73	22.30	15.10	8.39	5.74
11	50.02	23.89	15.36	8.77	5.97
C.V.[e]	14.7	16.1	23.8	7.1	8.1

[a] Based on 6 sampling dates.

[b] Based on 4 sampling dates.

[c] Number 1 refers to data using 100 observations per sampling date.

[d] Numbers 2 to 11 calculated using only 80 observations per sampling date.

[e] C.V. = Coefficient of Variation.

Table 12. Number of individuals entering each stage estimated with Southwood's method for estimate stage-specific mortality in Colorado potato beetle on horsenettle in 1988.

	EGGS[a]	L - 1[b]	L - 2[b]	L - 3[c]	L - 4[d]
1[e]	171.67	60.68	28.77	21.84	13.71
2[f]	176.63	60.04	32.38	21.99	13.74
3	167.82	56.32	19.79	20.48	11.29
4	156.53	50.35	28.71	20.41	13.96
5	165.80	69.79	32.01	22.47	13.28
6	190.99	66.53	30.79	22.55	16.16
7	182.07	68.24	32.55	22.50	12.63
8	150.91	56.29	19.79	17.60	12.03
9	164.51	50.76	28.71	22.17	13.37
10	180.94	56.36	30.35	23.53	14.97
11	180.19	61.82	32.38	22.73	15.50
C.V.[g]	14.7	16.1	23.8	7.1	8.1

[a] Based on 15 sampling dates.

[b] Based on 13 sampling dates.

[c] Based on 12 sampling dates.

[d] Based on 10 sampling dates.

[e] Number 1 refers to data using 100 observations per sampling date.

[f] Numbers 2 to 11 calculated using only 80 observations per sampling date.

[g] C.V. = Coefficient of Variation.

Table 13. Stage-specific mortality estimates for the Colorado potato beetle on horsenettle in 1987, calculated with the Jacknife technique.

	EGGS	L-1	L-2	L-3
q[a]	0.6291	0.3640	0.4166	0.2776
q-1[b]	0.6114	0.6905	-0.1125	0.2192
q-2	0.7736	-0.0954	0.4644	0.2303
q-3	0.6591	0.3294	0.4919	0.3334
q-4	0.6121	0.3000	0.4364	0.3502
q-5	0.4218	0.3905	0.5127	0.2721
q-6	0.6562	0.6717	0.0967	0.0867
q-7	0.7279	0.0386	0.4501	0.3163
q-8	0.6593	0.3538	0.4359	0.3475
q-9	0.5516	0.3227	0.4442	0.3164
q-10	0.5224	0.3570	0.4293	0.3192
Var($q_{\#}$) [c]	0.0839	0.2769[d]	0.1087[d]	0.0541

[a] Normal mortality estimate based on 100 observations per sampling date.

[b] Jacknife mortality estimates based on 80 observations per sampling date.

[c] Jacknife variance .

[d] Jacknife variance estimate based on 9 subsamples.

Table 14. Stage-specific mortality estimates for the Colorado potato beetle on horsenettle in 1988, calculated with the Jacknife technique.

	EGGS	L-1	L-2	L-3
q[a]	0.6465	0.5259	0.2409	0.3723
q_{-1}[b]	0.6601	0.4540	0.3239	0.3752
q-2	0.6644	0.6486	-0.0349	0.4487
q-3	0.6783	0.4298	0.2891	0.3160
q-4	0.5791	0.5413	0.2890	0.4090
q-5	0.6517	0.5372	0.2676	0.2834
q-6	0.6252	0.5230	0.3088	0.4387
q-7	0.6270	0.6484	0.1107	0.3165
q-8	0.6914	0.4344	0.2278	0.3969
q-9	0.6885	0.4615	0.2247	0.3638
q-10	0.6569	0.4762	0.2980	0.3181
$Var(q_{\#})$[c]	0.0094	0.0529	0.0316[d]	0.0262

[a] Normal mortality estimate based on 100 observations per sampling date.

[b] Jacknife mortality estimates based on 80 observations per sampling date.

[c] Jacknife variance .

[d] Jacknife variance estimate based on 9 subsamples.

Table 15. Comparison between the common and the Jacknife estimate of the stage-specific mortality rate using Southwood's method.

STAGE	MORTALITY WITHIN THE STAGE			
	1987	CONFIDENCE INTERVAL	1988	CONFIDENCE INTERVAL
EGGS	0.6291[a]		0.6465	
	0.7151[b]	± 0.2073[c]	0.5947	± 0.0649
FIRST	0.3640		0.5259	
INSTARS	0.2056	± 0.4045[d]	0.6200	± 0.1645
SECOND	0.4166		0.2409	
INSTARS	0.4058	± 0.2534[d]	0.0757	± 0.2880[d]
THIRD	0.2776		0.3723	
INSTARS	0.2638	± 0.1664	0.4233	± 0.1158

[a] Mortality calculated in the usual way with the Southwood's method. All the observations were considered for the mortality estimate (100 observations per sampling date).

[b] Jacknife mortality estimation based on 80 observations per sampling date.

[c] Jacknife confidence interval, t_9, alfa = 0.05.

[d] Jacknife confidence interval, t_8, alfa = 0.05.

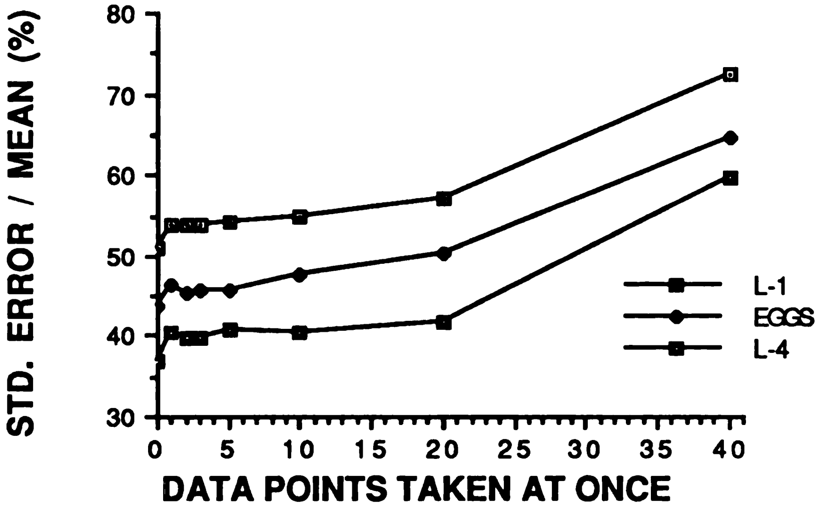

Figure 18. Relationship between the size of the subsample removed and the variability of the sampling data of the Colorado potato beetle on horsenettle.

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