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Movement and feeding patterns of *Epilachna cucurbitae* Richards (Coleoptera:Coccinellidae) on pumpkin and zucchini plants[2]

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Abstract

The oviposition patterns of adults and the movement and feeding patterns of larvae of Epilachna cucurbitae *on two species of cucurbits,* Cucurbita maxima *cv Queensland Blue and* C. pepo *cv Blackjack, were studied in the field and laboratory. The physical and nutritional characteristics of host plant leaves of different ages were described. Younger leaves had higher nitrogen contents but were less abundant, smaller and had higher trichome densities than older leaves. The development of first instar larvae was delayed by the leaf hairs on young and mature pumpkin leaves which prevented larvae from reaching the leaf surface to feed. First instar larvae developed more quickly on leaves rich in nitrogen. Neither the total developmental time of larvae nor the size of pupae was affected by leaf age because larvae on poor quality leaves compensated by eating more. Female beetles oviposited on all but the youngest and oldest leaves of the host plant. The trichomes on young leaves prevented females from attaching eggs to the leaf surface. First instar larvae remained where they hatched, but older larvae were more mobile, changing feeding sites frequently and moving progressively to younger, more nutritious leaves. Final instar larvae moved onto adjacent vegetation to pupate. The adaptive significance of these patterns is discussed in relation to the nutritional value, hairiness and abundance of host plant leaves of different ages and the physical limitations of different larval instars.*

Introduction

Epilachna cucurbitae (Richards) is a phytophagous coccinellid, belonging to the subfamily Epilachninae. Previously *E. cucurbitae* was grouped with two other coccinellid species as *Epilachna vigintiocto-punctata*, the "28-spotted ladybird beetle" (Richards 1983). Adults and larvae of *E. cucurbitae* feed on the leaves, flowers and fruits of their cucurbit host plants, and are a pest of commercial cucurbit crops such as pumpkin and zucchini (Richards 1983). Females of *E. cucurbitae* deposit eggs in batches, usually between 20 and 40 eggs, on the underside of host plant leaves. Larvae develop through four instars, pupate and emerge as adults.

Adults of many phytophagous insect species have well developed locomotory powers while those of their larvae are often limited (Ives 1978; Mitchell 1981). The choice of oviposition site by adults, both between and within host plants, often largely determines early larval food quality and may profoundly affect larval survival (Mitchell 1981). Within individual plants there can be substantial variation in the nutritional value, water content, size, and physical and chemical defenses of leaves of different ages. Older larvae of many phytophagous insect species are more mobile than young larvae, enabling them to move to other parts of their host plants, or even to new plants, to feed. Larvae moving to feeding sites of better nutritional quality may achieve faster growth rates, and reduced feeding rates (Scriber & Slansky 1981; Slansky & Feeny 1977).

In this study the oviposition patterns of

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[2] Abbreviations used: MZ = mature zucchini; OP = old pumpkin; MP = mature pumpkin; YP = young pumpkin; N = total nitrogen content; CR = tissue consumption rate; NCR = nitrogen consumption rate; NUE = nitrogen utilization efficiency; S = shaved.

females of *E. cucurbitae* and the movement and feeding patterns of their larvae on pumpkin and zucchini host plants were examined. To evaluate the adaptive significance of these patterns, two further aspects of this insect–plant relationship were studied:

(1) The effects of leaf age and presence of trichomes on larval development.

(2) The nutritional value and abundance of host plant leaves of different ages.

Materials and methods

A laboratory culture of *E. cucurbitae* was maintained on pumpkin leaves to provide a reliable source of eggs, larvae and adults. A small field plot of pumpkin and zucchini plants was established in an enclosure at James Cook University to provide plant material for laboratory and field experiments. Twenty-five pumpkin plants, *Cucurbita maxima* Duchesne ex Lam cv Queensland Blue, were planted in a 5×5 m grid and grown for 3 months. Nearby there were six zucchini plants, *C. pepo* L. cv Blackjack, 6 months old which were grown for an earlier experiment. All plants were fertilized fortnightly with Aquasol (Hortico, Aust.); the zucchinis thrived but the pumpkin plants grew poorly and are unlikely to be nutritionally representative of healthy pumpkin plants. However, they still provided a useful comparison with the nutritional quality of the zucchini plants. The experiments were conducted between June and September 1981.

Host plant characteristics

Three pumpkin plants (3 months old) and the one zucchini plant (6 months old) with no larvae on it were analysed to provide data on the size, availability and nitrogen content of differently aged leaves. The plants were cut at the base and transported on ice for 200 m to the laboratory. Each leaf was cut from the stem at the top of the petiole, its length and width measured and its area determined using an area estimator (Paton Industries, Australia). The fresh and oven dry weights of each leaf were recorded and leaf water contents determined.

For each species the dried leaves were grouped into age classes for further analysis. Leaves were classified as young leaves, the three smallest leaves from each plant; intermediate leaves, not fully expanded, but excluding young leaves; mature leaves, no longer increasing rapidly in size; old leaves, yellowing and senescent, usually partially covered with powdery mildew. For each leaf class the dried leaf tissue was pulverized, and three 0.2 g subsamples were taken. The young and intermediate zucchini leaf classes were combined to yield sufficient material for analysis (0.1 and 0.09 g subsamples). The subsamples were digested using the micro-Kjeldahl technique and their total nitrogen contents were determined using a Technicon Auto-analyzer II (Alkaline phenate reaction).

Oviposition sites, larval movement and survival

Wild females of *E. cucurbitae* oviposited on the zucchini plants but not on the pumpkin plants, although they do normally oviposit on pumpkin plants (Wilson, pers. obs.). To obtain eggs on the pumpkin plants, pairs of laboratory-reared female beetles were caged with single pumpkin plants for 24–48 h during which oviposition usually occurred. For both host plant species the length and position of each leaf, counted from the base of the plant, was recorded on every third day after oviposition so that leaves could later be assigned to leaf age classes. The survival of eggs and larvae and the position and instar of larvae were recorded daily. Larvae were not marked and observed individually because they are covered in branched spiny tubercules that are easily damaged and make them difficult to mark.

Effect of leaf age and trichomes on larval development and food consumption

To determine whether the development of larvae was affected by either leaf age or leaf hairiness, larvae were raised on host plant leaves of several ages, and on leaves from which trichomes had been removed. Groups of 17 larvae were raised on mature zucchini leaves (MZ) and three ages of pumpkin leaves: old (OP), mature (MP), and young (YP). A further two groups of 17 larvae were raised on either MP or YP leaves which had trichomes removed using a razor. Resources did not permit a full experimental design including larvae raised on young or old zucchini leaves. Larvae were confined individually in 9 cm petri dishes kept humid by moist filter paper. Photoperiod was 14L:10D, and temperature was 26 ± 1°C. Day old leaf discs were removed and replaced with fresh discs. Instar duration, pupation time and pupal weight (±0.01 mg) were recorded for each larva. Dead larvae were replaced with larvae of the same age where possible, and recording for these larvae began after the next ecdysis. There were 22 such replacements. The partially eaten leaf discs for larvae raised on normal leaves were photocopied. The area and weight of the photocopy pages was determined and the area (cm^2) of leaf tissue consumed by each larva was estimated from the weights of the cut-out, photocopied leaf scars. The dry weight:area ratio was calculated for each age class of leaves for both pumpkin and zucchini, which enabled leaf consumption by larvae to be converted from area eaten to dry weight (mg) of leaf tissue eaten.

Results

Host plant characteristics

The total nitrogen content (N) of cucurbit leaves decreased as they aged. The zucchini leaves contained more N than the pumpkin leaves. Zucchini N values were: young and intermediate leaves 4.47%, mature leaves 4.03% and old leaves 2.97%. Pumpkin N values were: young leaves 2.89%, intermediate leaves 2.70%, mature leaves 2.24% and old leaves 1.69%. Water contents of leaves were between 79 and 83% of fresh weight for all leaf ages for both plant species.

For both pumpkin and zucchini plants, old and mature leaf tissue is more abundant than young or intermediate leaf tissue. For the zucchini plants, young and intermediate leaves represented 6.6% of the total plant leaf area, mature leaves 41.7% and old leaves 51.7%. For the pumpkin plants, young leaves represented 4.3% of the total plant leaf area, intermediate leaves 16.5%, mature leaves 42.5% and old leaves 36.7%.

Oviposition sites, larval movement and survival

The distribution of eggs and larvae on the pumpkin and zucchini plants is shown in Figs 1 and 2. Oviposition on both host plant species occurred on leaves of all ages except the oldest and youngest leaves. Thirty-two egg batches were laid, 22 on pumpkin plants ($\bar{x}$ = 19.9 eggs/batch, s.e. = 1.98) and 10 on zucchini plants ($\bar{x}$ = 31.2 eggs/batch, s.e. = 3.26). A chi-square test showed that after allowing for leaf abundance, old pumpkin leaves received fewer eggs than expected while mature, intermediate and young leaves received more eggs than expected ($P < 0.05$). The oviposition data for zucchini was too sparse for reliable analysis. Eggs were usually laid on the underside of leaves. Both sides of the youngest leaves of both pumpkin and zucchini plants were densely covered with trichomes which probably prevented females from attaching eggs firmly to the leaf surface. In the laboratory females given only young leaves oviposited on the dense layer of trichomes above the leaf surface and the eggs were poorly attached and easily dislodged.

Larvae were not followed individually so larval movement was scored as the minimum number of shifts necessary to account for changes in the distribution of larvae on their plant between observations. A shift occurred when a larva changed leaves between observations and was measured as the number of leaves moved past; thus if a larva moved from leaf 9 to

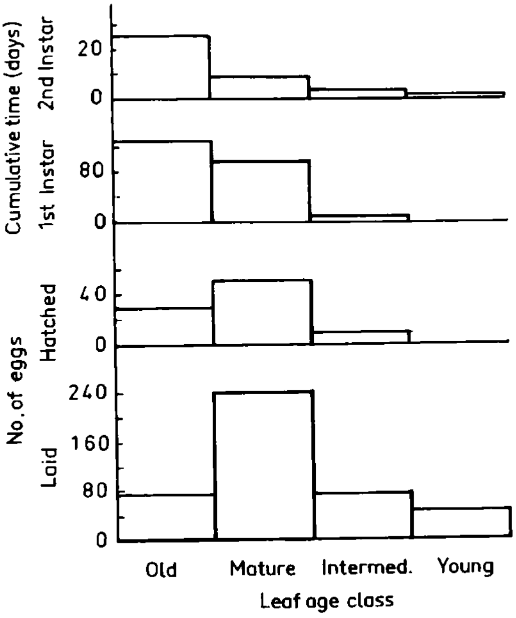

FIG. 1. The distribution of eggs and larvae of *E. cucurbitae* on pumpkin plants.

II, then one shift of two steps was scored. Larvae were assigned a particular shift between consecutive observations, and the shift length, direction (towards younger or older leaves) and age of leaves of origin and destination was determined. This technique is conservative and may underestimate larval movement. The distribution of larvae was scored as the cumulative number of days that larvae of each instar spent on each age class of leaves. Larval movement patterns are shown in Table 1 and distribution in Figs 1 and 2; both are summarized below. Few larvae survived to third and fourth instar on pumpkin so no data for these are shown in Fig. 1. To compare the movement of differently aged larvae, adjacent instars were sometimes pooled to allow valid chi-square tests.

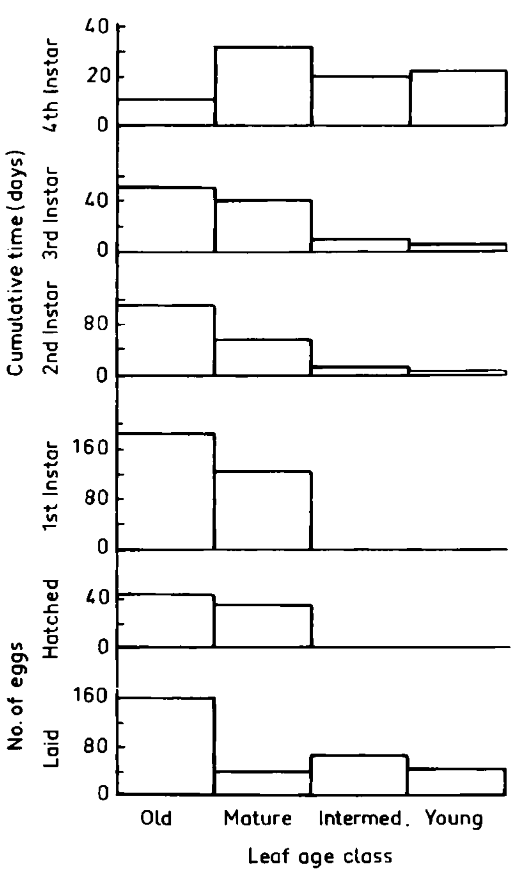

FIG. 2. The distribution of eggs and larvae of *E. cucurbitae* on zucchini plants.

On pumpkin and zucchini most first instar larvae hatched on mature or old leaves. Eggs took 7–9 days to hatch. Leaves aged during this interval and some were reassigned to older leaf classes. First and second instar larvae moved little, often remaining on the leaf where they hatched. Leaf death was a major cause of movement for first and second instar larvae ($P<0.001$) on zucchini but not on pumpkin. Leaf death had no detectable effect on the movement of older larvae. Larvae moved preferentially towards the plant tip rather than toward the base. This was true for all instars on zucchini ($P<0.025$ for all instars) and for second ($P<0.005$) and third ($P<0.05$) instars on pumpkin. Older larvae shifted more frequently than young larvae; on zucchini third and fourth instar ($P<0.001$) and on pumpkin, second and third instar ($P<0.001$) shifted more frequently than younger larvae. On zucchini this resulted in older larvae moving progressively to younger, more nutritious leaves. Replete fourth instar larvae moved onto nearby small weeds to pupate. Vegetation within a 1 m radius around each host plant was searched to establish whether larvae pupated successfully.

TABLE 1. Movement of larval instars of *E. cucurbitae* on pumpkin or zucchini plants. See text for explanation of analysis of larval movement. Percentages are shown in brackets after actual counts

Plant species	Larval instar	No. moves off dead or live leaves				No. steps moved towards plant's		Total % of larvae either	
		Dead leaves		Live leaves					
		not moved	moved	not moved	moved	base	tip	moved	not moved
Pumpkin	I	32 (91)	3 (9)	172 (96)	7 (4)	6 (50)	6 (50)	4.7	95.3
	II	12 (63)	7 (37)	18 (75)	6 (25)	9 (24)	29 (76)	30.2	69.8
	III	1 (33)	2 (66)	3 (43)	4 (57)	1 (10)	9 (90)	60.0	40.0
Zucchini	I	4 (80)	1 (20)	296 (98)	7 (2)	6 (24)	19 (76)	2.6	97.4
	II	21 (57)	16 (43)	106 (79)	28 (21)	68 (39)	106 (61)	25.7	74.3
	III	9 (50)	9 (50)	52 (58)	38 (42)	20 (17)	97 (83)	43.5	56.5
	IV	0 (0)	1 (100)	34 (42)	46 (58)	40 (35)	73 (65)	58.0	42.0

The survival of eggs, larvae and pupae on the pumpkin and zucchini plants is shown in Table 2. Chi-square tests indicated that mortality was similar for eggs but was proportionately higher on pumpkin than on zucchini plants for first ($P<0.001$) and second ($0.01<P<0.05$) instar larvae. Survival of older larvae on the two species of host could not be compared due to insufficient sample sizes on pumpkin. On both species of host, mortality was highest in eggs and first instar larvae.

Effect of leaf age and trichomes on larval development and food consumption

The effect of food quality on larval development and food consumption is shown in Table 3 and Fig. 3. First instar larvae developed significantly faster when fed MZ leaf tissue than when fed YP or OP leaves (Fig. 3a). However, there was no significant difference in the developmental rates of larvae raised on normal pumpkin leaves of different ages (Duncan's multiple range test, 0.05 level). Analysis of variance showed that first instar larvae raised on leaves with no trichomes developed more quickly than those raised on normal leaves ($F=6.02$, 1×52 df, $0.05>P>0.01$). Neither the developmental rates of other instars nor the pupal weights were affected by leaf tissue type or trichomes. The complete developmental rate of larvae was greater for those raised on MZ leaves than for those raised on OP leaves (Duncan's multiple range test, 0.05 level). However, this was attributable to the differences in the developmental rates of first instar larvae, as developmental rates were statistically similar if they were excluded.

The mortality of larvae raised on each leaf class was tested. Data for all instars were pooled for each leaf class in order to perform valid chi-square tests. No significant difference in larval mortality between age classes of leaves was found.

The leaf areas consumed by fourth instar larvae were converted to dry weight leaf tissue consumed and dry weight N consumed. From these the leaf tissue consumption rate (CR) and N consumption rate (NCR) were estimated as follows (mg/day):

$$\mathrm{CR}=\frac{\text{Leaf tissue consumed}}{\text{Developmental time}}$$

$$\mathrm{NCR}=\frac{\text{N consumed}}{\text{Developmental time}}$$

TABLE 2. The survival of eggs, larvae and pupae of *E. cucurbitae* on pumpkin and zucchini plants

Developmental stage	Pumpkin plants Number	Mortality	Percentage survival	Zucchini plants Number	Mortality	Percentage survival
Egg	438	348	20.55	312	234	25.0
I	90	79	2.74	78	34	14.1
II	12	8	0.91	44	9	11.22
III	4	3	0.23	35	17	5.77
IV	1	1	0	18	8	3.20
Pupae	0	0	0	10	4	1.92
Adult	0	0	0	6	—	—

TABLE 3. Mean developmental rates for fourth instar larvae, total larval developmental rates and pupal weights of *E. cucurbitae* raised on pumpkin or zucchini leaves of different ages. Sample sizes (*n*) changed due to larval deaths

Leaf type fed to larvae	*n*	Fourth instar developmental rate (1/days) Mean	(s.e.)	*n*	Total developmental rate (1/days) Mean	(s.e.)	*n*	Pupal weight (mg) Mean	(s.e.)
Mature zucchini leaf	12	0.168	(0.006)	10	0.049[a]	(0.001)	12	42.26	(1.610)
Young pumpkin leaf	14	0.169	(0.010)	11	0.047	(0.001)	14	39.74	(1.130)
Shaved young pumpkin leaf	14	0.168	(0.017)	13	0.047	(0.003)	14	42.96	(1.157)
Mature pumpkin leaf	13	0.172	(0.009)	9	0.048	(0.002)	13	42.69	(1.107)
Shaved mature pumpkin leaf	12	0.168	(0.014)	11	0.048	(0.003)	12	41.16	(1.064)
Old pumpkin leaf	15	0.165	(0.009)	12	0.046[b]	(0.001)	14	42.42	(0.712)

[a,b]Significantly different 0.05 level, Duncans Multiple Range test.

Multiple regression analysis showed that the CR of fourth instar larvae decreased significantly as leaf N increased ($F = 100.77$, d.f. $= 1\times52$, $P<0.001$). Addition of leaf water content to the regression made no significant improvement. The equation:

$$CR = 1/(\text{leaf N } 19.66 + 27.39)$$

explained 66% of the variation in CR (Fig. 3b). In contrast, the NCR of fourth instar larvae increased significantly as leaf N increased ($F = 28.6$, d.f. $= 1\times52$, $P<0.001$) and addition of leaf water content did not improve the regression. The equation:

$$NCR = (\text{Leaf N } 0.418 + 2.23)\times10^{-4}$$

explained 35% of the variation in NCR (Fig. 3c).

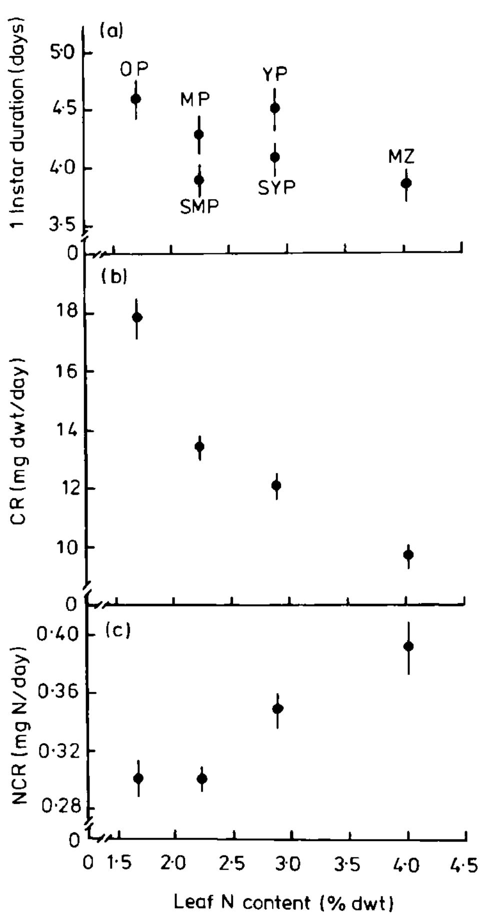

FIG. 3(a). The effects of leaf nitrogen content and leaf hairs on the duration of I instar *E. cucurbitae* larvae. Leaf types are: OP, old pumpkin; MP, mature pumpkin; YP, young pumpkin, and MZ, mature zucchini (S indicates shaved leaves). Values are $\bar{x}\pm$s.e. (b) The effect of leaf nitrogen content on the food consumption rate (CR) of IV instar *E. cucurbitae* larvae. Leaf types as in Fig. 3(a) except no SYP or SMP. Values are $\bar{x}\pm$s.e. (c) The nitrogen consumption rate (NCR) of IV instar *E. cucurbitae* larvae raised on leaf tissue of different nitrogen content. Leaf types as in Fig. 3(a) except no SYP or SMP. Values are $\bar{x}\pm$s.e.

Discussion

Leaf trichomes and larval development

The effectiveness of trichomes in preventing insect attack on plants is well documented. Levin (1973) reviewed this topic, finding numerous species for which a negative correlation was reported between trichome density and feeding, ovipositional responses and larval nutrition of insects. In this study trichomes affected the development of first instar larvae on mature and young pumpkin leaves. Trichomes acted as a mechanical barrier both to ovipositing females and to first instar larvae which had difficulty reaching the leaf surface on hairy leaves. Older larvae were apparently unaffected by trichomes.

Leaf nitrogen and larval development

Taylor (1984) found that larval *Samea multiplicalis* (Guenee) developed more rapidly and had one less larval instar when the food plant of the first two instars, *Salvinia molesta* Mitchell, was richer in nitrogen. First instar *E. cucurbitae* larvae also developed more rapidly on the N-rich MZ leaves than on the OP leaves. However, larvae on YP leaves developed more slowly than those on MP leaves, indicating that something other than N is affecting their development. It is possible that YP leaves have higher concentrations of chemical defenses and that young larvae are more sensitive to the levels of these chemicals than are older larvae, explaining why a similar result was not found with older larvae.

Adjustment of the rate of food consumption by phytophagous insects in response to the levels of nutrients, particularly nitrogen, in host plants is well documented (Slansky & Feeny 1977; McNeil & Southwood 1978; Scriber & Slansky 1981). Adult insects or their larvae consumed more food when fed nitrogen-poor plants or diets than when fed nitrogen-rich plants or diets. Fourth instar larvae of *E. cucurbitae* raised on the N-rich MZ or YP leaves had lower CR but higher NCR than larvae raised on the N-poor MP or OP leaves. Slansky and Feeny (1977), working with fifth instar *Pieris rapae* larvae found that nitrogen utilization efficiency (NUE) declines as NCR increases. They demonstrated that *P. rapae* larvae adjusted their NCR so as to achieve a relatively stable rate of N accumulation into larval biomass. If *E. cucurbitae* larvae respond similarly then larvae raised on MP or OP leaves probably increased their CR to achieve a sufficient rate of N accumulation for normal biomass production. However, they had lower NCR and consequently higher NUE than larvae raised on MZ or YP, which allowed them to achieve similar developmental rates and pupal weights. In contrast, larvae raised on MZ or YP leaves may reduce their CR in an attempt to reduce their NCR from the unacceptably high levels and subsequent decline in NUE that would result if their CR was maintained at a similar level to that of larvae on MP or OP leaves.

Oviposition, larval movement and survival

Wild female bettles only oviposited on the zucchini plants in the field plot thereby perhaps discriminating against the low quality pumpkin plants as oviposition sites, since they readily oviposit on healthy pumpkin plants. Oviposition occurred on all but the oldest and youngest leaves on both species of host. The youngest leaves were most likely avoided because they are densely covered with trichomes (see above). The distribution of oviposition between the leaves of a plant may also be related to leaf availability. Younger leaves are a much scarcer resource than are larger mature leaves. However, young, intermediate and mature leaves received more eggs than expected while old leaves received fewer. Old leaves are usually yellow and often covered with mildew which combined with their low N content and nearness to death may make them unattractive to *E. cucurbitae*. Eggs laid on old leaves often shrivelled and died, probably due to dehydration as the leaf senesced and dried out. Eggs frequently disappeared before they were due to hatch, possibly due to predation, although no predators were observed taking eggs.

The survival of first and second instar larvae was lower on the pumpkin plants than on the zucchini plants. This may be explained by the lower nutritional value of the pumpkin plants, thus supporting the hypothesis of White (1978) that a relative shortage of nutritionally adequate food, particularly nitrogenous food, is one of the main factors affecting the survival of young herbivores. However, differences in mortality may also occur because the pumpkin plants were small and had no overlap between leaves so that larvae on pumpkin plants were more exposed than those on the zucchini plants which had larger, often overlapping leaves. Cohen and Brower (1982) suggested that larger plants with more overlapping leaves and stems may offer greater protection against biotic and physical mortality factors than do smaller plants.

Most first instar larvae remained on the leaf on which they hatched, shifting only if forced to by death of the leaf. It would appear advantageous for larvae on old leaves to move to more nutritious leaves. Poor mobility may be responsible for their sedentary nature. However, Chew and Robbins (1984) in a review reported evidence that gregarious larvae feed more efficiently in groups. If larvae of *E. cucurbitae* respond similarly then they may have evolved a behavioural pattern to keep young larvae from egg clusters together. Mobility increased with age and older larvae dispersed and moved progressively from old leaves to the more nutritious mature and intermediate leaves.

Third and fourth instar larvae changed their position on the plant more frequently than did younger larvae. Frequent movement takes larvae away from sites of recent feeding which may be used by predators and parasites as a cue to locate their prey. Heinrich and Collins (1983) found that black-capped chickadees, *Parus atricapillus*, learned to forage preferentially in trees with leaves damaged by caterpillars. Carroll and Hoffman (1980) found that larvae of *E. tredecimnota*, a similar cucurbit-feeding coccinellid, also moved frequently on their host plants, avoiding leaves with fresh feeding scars. They suggested that frequent movement, rather than serving to avoid predators, serves to avoid areas where previous feeding has caused the plant to increase the level of chemical feeding-deterrents, probably cucurbitacins. In the field, fourth instar *E. cucurbitae* larvae move off the host plant and pupate on neighbouring vegetation. This behaviour may also be a mechanism of predator/parasite avoidance, since obligate parasites of many insects search initially for their hosts' food plants (Price 1975).

The feeding and movement patterns of *E. cucurbitae* larvae are affected by age-related differences in the nutritional value and trichome density of leaves of the host plant. Further studies to determine the diel patterns of feeding, rest and movement would be useful in defining the benefits accruing to larvae that move to feed on younger leaves. Differences in size and mobility impose physical limitations on differently aged larvae and this emphasizes the importance of regarding the host plant as a place for the insect to live as well as something for it to eat (Dethier 1966).

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References

Carroll C. R. & Hoffman C. A. (1980) Chemical feeding deterrent mobilized in response to insect herbivory and counteradaptation by *Epilachna tredecimnota. Science* **209**, 414–6.

Chew F. S. & Robbins R. K. (1984) Egg-laying in butterflies. In: *The Biology of Butterflies* (eds R. I. Vane-Wright and P. R. Ackery) pp. 65–79. Academic Press, London.

Cohen J. A. & Brower L. P. (1982) Oviposition and larval success of wild Monarch Butterflies (Lepidoptera: Danaidae) in relation to host plant size and cardenolide concentration. *J. Kans. Entomol. Soc.* **55**, 343–8.

Dethier V. G. (1966) Feeding behaviour. *Royal Ent. Soc. London Symposium on Insect Behaviour.* **3**, 46–58.

Heinrich B. & Collins S. L. (1983) Caterpillar leaf damage, and the game of hide and seek with birds. *Ecology* **64**, 592–602.

Ives P. M. (1978) How discriminating are Cabbage Butterflies? *Aust. J. Ecol.* **3**, 261–76.

Levin D. A. (1973) The role of trichomes in plant defense. *Quart. Rev.Biol.* **48**, 3–15.

McNeil S. & Southwood T. R. E. (1978) The role of nitrogen in the development of insect/plant relationships. In: *Biochemical Aspects of Plant and Animal CoEvolution* (ed. J. B. Harbourne) pp. 77–98. Academic Press, London.

Mitchell R. (1981) Insect behaviour, resource exploitation, and fitness. *Ann. Rev. Entomol.* **26**, 373–96.

Price P. W. (1975) *Insect Ecology.* John Wiley, New York.

Richards A. M. (1983) The *Epilachna vigintioctopunctata* complex (Coleoptera:Coccinellidae). *Int. J. Entomol.* **25**, 11–41.

Scriber J. M. & Slansky F. Jr (1981) The nutritional ecology of immature insects. *An. Rev. Entomol.* **26**, 183–211.

Slansky F. Jr & Feeny P. (1977) Stabilization of the rate of nitrogen accumulation by larvae of the Cabbage Butterfly on wild and cultivated food plants. *Ecol. Monogr.* **47**, 209–28.

Taylor M. F. J. (1984) The dependence of development and fecundity of *Samea multiplicalis* on early larval nitrogen intake. *J. Insect Physiol.* **30**, 779–85.

White T. C. R. (1978) The importance of a relative shortage of food in animal ecology. *Oecologia* **33**, 71–86.

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