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Feeding behaviour and food preferences of the pest species comprising the *Epilachna vigintioctopunctata* (F.) complex (Col., Coccinellidae)

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Abstract

Food acceptance trials involving 34 species belonging to five plant families confirm *Epilachna cucurbitae* Richards feeds exclusively on Cucurbitaceae and both *E. 26-punctata 26-punctata* (Boids.) and *E. 28-punctata pardalis* (Boisd.) feed exclusively on Solanaceae. Leaves and fruit are preferred by the two solanivorous species. Flowers, especially pollen, are preferred by *E. cucurbitae*, with beetles acting as pollinating agents. This is the first record of such behaviour in a phytophagous coccinellid. Food preference is influenced by odour, taste, vision and age of plant. It is also influenced by thickness of leaves and the proportion of crude fibres, parenchymatous tissue and water content present. Feeding positions on the same or different plant species vary in darkness and daylight, but *E. cucurbitae* prefers the abaxial and *E. 26-punctata* the adaxial side of leaves. With *E. cucurbitae*, there is no specific feeding period, but with *E. 26-punctata* night feeding is preferred. In food preference trials, *E.-cucurbitae* eat faster and can consume more food than *E. 26-punctata* in a limited period of time, with one exception – potato *(Solanum tuberosum)* is the most preferred of all food plant species offered to the three epilachnine species. Complex trench-cutting behaviour by *E. cucurbitae*, to isolate specific feeding areas of leaf from chemical defences produced by cucurbitaceous host plants, is recorded for the first time. This is the first record of such behaviour in Asian and Australasian epilachnines.

1 Introduction

The phytophagous Coccinellidae of the subfamily Epilachninae occur throughout tropical and subtropical parts of the world. *Epilachna* Dejean, the most widespread genus, contains species which attack crops belonging to the Solanaceae, Cucurbitaceae, Fabaceae, Convolvulaceae and Malvaceae. Many species also feed on weeds belonging to the Solanaceae, Cucurbitaceae and Asteraceae. The wild thistle (*Cirsium* spp.) is an important food plant in Japan (Shirai 1987). The food preferences of individual *Epilachna* species are usually confined to one family of plants. Some species exhibit marked host specificity and have been named after their favourite food as, for example, *E. varivestis* Mulsant (Mexican bean beetle), *E. elaterii* (Rossi) (melon ladybird) and *E. vigintioctopunctata* (Fabricius) (potato ladybird).

Three of the most widespread and important epilachnine pest species comprising the *E. vigintioctopunctata* complex, all occur in Australia. Two of them, *E. vigintioctopunctata pardalis* (Boisduval) and *E. vigintisexpunctata vigintisexpunctata* (Boisduval) attack members of the Solanaceae, while *E. cucurbitae* Richards is a pest of the Cucurbitaceae (Richards 1983). Recent studies on the biology of these 3 species (referred to here as *pardalis, 26-punctata* and *cucurbitae*) have compared the effect of several species of crops and weeds on their bionomics (Richards and Filewood 1988; Richards and Filewood 1990). They have highlighted the differences between the two solanivorous species and *cucurbitae*. They have also shown that the plant family usually influences the duration of their preoviposition period, while specific food plant species influence the length of their oviposition period. Because of the many contradictions in the literature (Agricultural

Gazette of N.S.W. from 1890 onwards; Olliff 1890; Froggatt 1923), this study investigates under laboratory conditions the food preferences of all 3 species when exposed to a wide range of species from several plant families. It also examines feeding behaviour, about which little is known. Both are important factors in the control of these pests.

2 Materials and methods

Cultures of *cucurbitae*, *26-punctata* and *pardalis* were established in the laboratory from adults or egg batches collected in the field and were used in all food preference experiments. All plant material was grown in the University garden or under glasshouse conditions.

In food acceptance trials, the 3 species of *Epilachna* were tested against 35 plant species belonging to 5 families (table 1). Each replicate consisted of 6 teneral beetles or 6 first instar larvae, all belonging to the same species, which had been starved for 24 h since emergence to prevent the development of a preference for any particular plant species. They were placed in a perspex cage together with a supply of fresh leaves, flowers and fruit (if available) of a selected plant species and left for several hours, after which they were re-examined. All cages were kept in the laboratory under normal room conditions. A scale from 1–5 in order of preference was applied to each species tested.

To evaluate host plant selection by *cucurbitae* and *26-punctata*, a stainless steel tube-punch was used to cut 2 cm diameter discs from leaves of different species. The discs were prevented from wilting by being placed above moistened filter paper covering the cardboard floor of a 15 cm diameter glass crystallizing dish. Each disc was supported by a 4 mm diameter plastic disc, the two discs being pinned together with a stainless steel pin and then positioned 4 mm above the filter paper. The crystallizing dish was covered with a thin transparent sheet of plastic to retain moisture throughout the experiment.

Pumpkin*(Cucurbita maxima)*, marrow *(C. pepo)*, button squash *(C. pepo)*, cucumber *(Cucumis sativus)* and loofah or vegetable sponge *(Luffa cylindrica)* were used in food preference trials with *cucurbitae*; while potato *(Solanum tuberosum)*, egg plant *(S. melongena)*, nightshade *(S. nigrum)*, devils apple *(S. capsicoides)*, tomato *(Lycopersicon esculentum)*, common thornapple *(Datura stramonium)*, apple of Peru *(Nicandra physalodes)*, kangaroo apple *(S. vescum)*, and capsicum *(Capsicum frutescens)* were used with *26-punctata*. Four plant species were used in each trial.

Two different methods were used for assessing food preference in *cucurbitae* and *26-punctata*. Initially, (trial A in each case), discs were arranged in a circle inside the circumference of a crystallizing dish and 6 teneral beetles, starved for 24 h since emergence and all of the same species, were placed in the centre of the dish and allowed to crawl in any direction (Jermy 1961). Results from these trials were discarded from most analyses, being considered not sufficiently accurate. In the second method (Bongers 1970), 12 leaf discs, 3 from each of 4 selected species, were placed inside a crystallizing dish in a pseudo-random schedule without replacement. Six teneral beetles, starved since emergence, were then introduced to the dish, each beetle being placed between 4 leaf discs, one from each species, so that it received equal stimulation from each of the 4 plant species. By walking in any direction, it would have equal chances of reaching any of the discs, and the chance of it climbing onto a disc by random movement would be equal for all beetles and all plant species. This second method was used in trials 1–7 for both *cucurbitae* and *26-punctata*. Because of their similarity with results in trials 1–7 assessing the amount of disc eaten per beetle per hour, results from trial A were included in table 5. Concurrent trials with *cucurbitae* and *26-punctata* were carried out in December under normal daylight hours, with temperatures ranging between 22–28 °C and a daylength of 14 h 18 min. Trials with *26-punctata* were repeated in April when temperatures ranged between 21–25 °C and daylength was 11 h 16 min. Six different food plants were used in each of the two groups of trials. To evaluate the amount of food eaten at intervals throughout the trials, each disc was divided into 8 portions for quick assessment so as not to disturb the beetles. A single bite was regarded as a nibble. The number of beetles on dorsal or ventral sides of each disc was also recorded.

As fresh weight may differ from one disc to another, due to variation in thickness of leaves, the dry weight of discs was also measured. Fresh discs of all trial species were individually weighed, reweighed after 24 h in a moist enclosed container to estimate weight loss, and then dried for a further 24 h in an oven set at 55 °C. After exposure to air for 1 h, the discs were reweighed and percentage water content calculated (table 6).

A further series of trials using the second method of disc arrangement, measured the amount of food (in mg) consumed by one beetle in an hour. The same food plant was used for all 12 discs to eliminate food preferences. Six beetles were used in each trial, which was run for 24 h. All discs were weighed individually before and after each trial, and the amount of food eaten assessed. They were then dried for 24 h in an oven at 55 °C and reweighed to estimate total weight of food eaten, allowing 5 % weight-loss, and water content of uneaten residue. Dry weight of food eaten was calculated and the percentage of inedible tissues (table 7).

3 Results

3.1 Food acceptance trials

Of the 34 plant species offered as food to adults and larvae of *cucurbitae, 26-punctata* and *pardalis* (table 1), those belonging to the Euphorbiaceae, Malvaceae and Fabaceae were rejected. Only members of the Cucurbitaceae were readily eaten by *cucurbitae*, while

Table 1. **Food preferences of three *Epilachna* species**

	26-punctata		*pardalis*		*cucurbitae*	
	Adult L Fl Fr	Larva L Fl Fr	Adult L Fl Fr	Larva L Fl Fr	Adult L Fl Fr	Larva L Fl Fr
CUCURBITACEAE						
Citrullus lanatus †	– – 0	– – 0	– – 0	– – 0	5 – 2	5 – 2
Citrullus lanatus ††	0 0 0	0 0 0	0 0 0	0 0 0	5 3 1	5 3 1
Cucumis melo	0 0 0	0 0 0	0 0 0	0 0 0	3 3 2	4 2 2
Cucumis myriocarpus	0 0 –	0 0 –	0 0 –	0 0 –	5 3 1	5 3 1
Cucumis sativus	0 – 0	0 – 0	0 – 0	0 – 0	5 5 3	5 5 3
Cucurbita maxima	0 0 0	0 0 0	0 0 0	0 0 0	5 5 5	5 5 5
Cucurbita pepo	0 0 0	0 0 0	0 0 0	0 0 0	5 5 5	5 5 5
Luffa cylindrica	0 0 –	0 0 –	0 0 –	0 0 –	5 5 –	5 5 –
Sechium edule	0 – 0	0 – 0	0 – 0	0 – 0	2 – 5	2 – 5
EUPHORBIACEAE						
Ricinus communis	0 – –	0 – –	0 – –	0 – –	0 – –	0 – –
FABACEAE						
Glycine max	1 – –	0 – –	1 – –	0 – –	0 – –	0 – –
Phaseolus vulgaris	1 – –	0 – –	0 – –	0 – –	0 – –	0 – –
MALVACEAE						
Gossypium sp.	0 – –	0 – –	0 – –	0 – –	0 – –	0 – –
SOLANACEAE						
Brugmansia suaveolens	4 – –	4 – –	4 – –	4 – –	0 – –	0 – –
Capsicum frutescens	2 – 3	– – 3	– – 3	– – –	0 – 1	0 – 0
Cestrum parqui	2 – –	1 – –	1 – –	– – –	0 – –	0 – –
Datura ferox	– – –	– – –	4 – –	– – –	0 – –	– – –
Datura stramonium	5 5 –	5 5 –	5 5 –	5 5 –	0 0 –	0 0 –
Lycopersicon esculentum	3 – 4	3 3 2	2 – 4	2 – 5	0 0 –	0 0 –
Nicandra physalodes	5 5 –	5 5 –	5 5 –	5 5 –	0 0 –	0 0 –
Nicotiana sp.	1 – –	0 – –	1 – –	0 – –	0 – –	0 – –
Nicotiana debneyi	0 – –	0 – –	1 – –	0 – –	0 – –	0 – –
Nicotiana glauca	2 – –	2 – –	– – –	– – –	0 – –	0 – –
Physalis peruviana	5 5 0	5 5 0	5 5 –	5 5 –	0 – –	0 – –
Solanum capsicoides	5 5 5	5 5 5	5 5 5	5 5 5	0 – 0	0 – 0
Solanum mauritianum	5 – –	5 – –	– – –	– – –	0 – 0	0 – 0
Solanum melongena	5 5 5	5 5 5	5 5 5	5 5 5	0 0 0	0 0 0
Solanum nigrum	5 5 5	5 5 5	5 5 5	5 5 5	0 0 0	0 0 0
Solanum nitidibaccatum	5 5 –	5 – –	5 5 –	5 – –	0 – –	0 – –
Solanum nodiflorum	5 – –	5 – –	– – –	– – –	0 – –	0 – –
Solanum opacum	– – –	– – –	5 – –	5 – –	– – –	– – –
Solanum torvum	– – –	– – –	5 – –	5 – –	– – –	– – –
Solanum tuberosum	5 5 –	5 5 –	5 5 –	5 5 –	0 – –	0 – –
Solanum vescum	5 – –	5 – –	– – –	– – –	0 – –	0 – –

0 not eaten; 1 nibbled ... 5 eaten avidly; – not tested
† Water Melon, †† Camel Melon
L, Fl, Fr = leaf, flower, fruit

solanaceous species were the exclusive choice of both *26-punctata* and *pardalis*. Food preferences of *26-punctata* and *pardalis* were very similar.

Leaves, flowers and fruit of some species were offered in sampling trials. Both *26-punctata* and *pardalis* preferred leaves and fruit, especially the purple berries of *S. nigrum*, while *cucurbitae* preferred flowers, especially those of *C. pepo* and *C. maxima*. In the latter case, petals, pollen and nectar were eaten. As a result, beetles and larvae often became covered with sticky pollen grains (fig. 1). By moving from male to female flowers beetles acted as pollinating agents. No comparable role was observed with epilachnines feeding on solanaceous flowers.

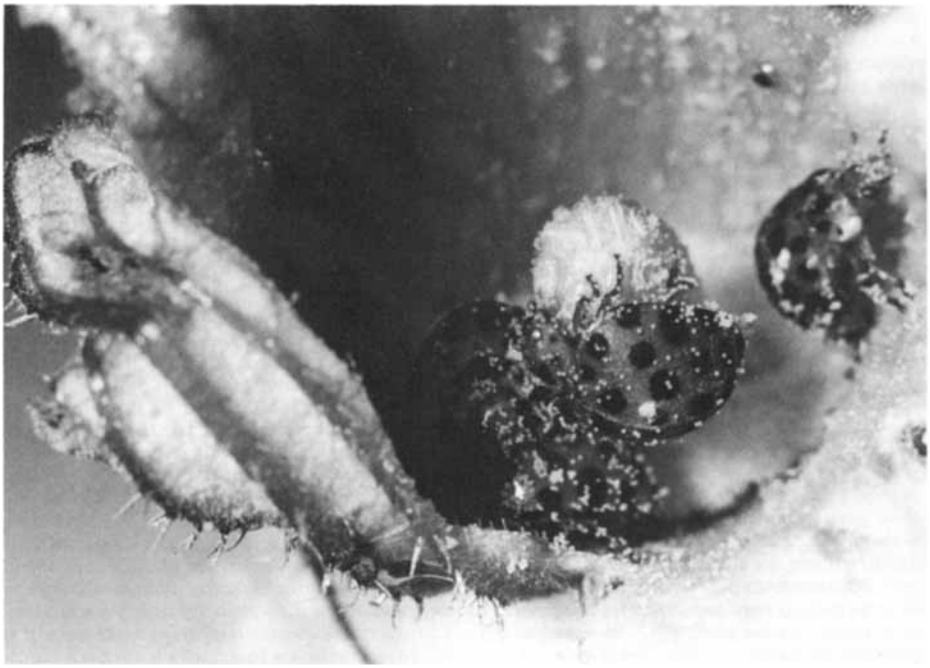

Fig. 1. Four *Epilachna cucurbitae* beetles feeding on anther and petals of *Cucurbita pepo*. All beetles are covered with sticky pollen grains. (Photo: R. Arnett)

Both crops and weeds were accepted from within the selected families, with varying levels of preference. If leaves of *C. maxima* or *S. tuberosum* (essential food) were offered to epilachnines already feeding on paddy melon *(Cu. myriocarpus)* or *N. physalodes* (alternative food), they readily transferred from weeds to crops. If weeds were offered to crop-feeders, most remained on crops. In the laboratory, transfer from essential to alternative food often led to starvation and death of both larvae and adults.

3.2 Trench-cutting behaviour

Before feeding on a *C. maxima* or *C. pepo* leaf, adult *cucurbitae* frequently used their large, pointed apical mandibular teeth (Richards 1983) to cut arcuate trenches around an area at the edge of the leaf. Both adaxial and abaxial surfaces were used for cutting. On one occasion, the arc was adjacent to the mid-vein. Arcs took about 10 min or less to complete. They were variable in size and shape, ranging from completely circular, to flattened semicircular or spiral. They often overlapped, and smaller ones were frequently cut inside

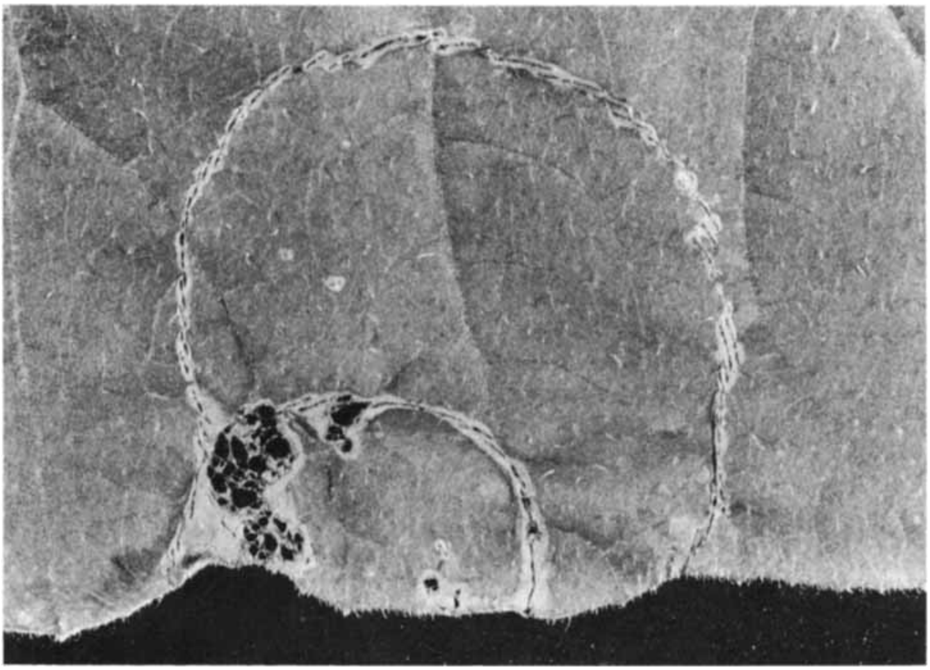

Fig. 2. Two overlapping arcuate trenches cut by *Epilachna cucurbitae* into leaf of *Cucurbita maxima*. Note mandibular slashes which form the trenches, also feeding at overlap of arcs. (Photo: R. MURPHY)

Fig. 3. Two *Epilachna cucurbitae* beetles feeding inside arcuate trench on leaf of *Cucurbita pepo* in market garden, Cowan. (Photo: L. W. FILEWOOD)

larger ones. Areas where 2 or 3 arcs of different size overlapped (fig. 2) were preferred for feeding. In each case, a narrow strip of leaf was partly eaten by a single beetle, and a series of closely-linked deep tooth slashes were made along the centre of the strip leaving only a few veins and parts of the epidermis to hold the isolated portion in place. On some leaves one or more beetles fed on the encircled tissues, either on the same side of the leaf (fig. 3) or on both sides. Some areas left intact after trench-cutting, were subsequently selected for feeding. No feeding took place outside the trenches. On three occasions, female beetles were observed cutting trenches while copulating. After separation, both beetles fed within the isolated area. In the laboratory, all leaves were undamaged before beetles were introduced, but the petioles had been cut and then placed in water. In the field, both perfect and damaged leaves were attacked by beetles (fig. 3). No such trench-cutting behaviour was observed in either solanivorous species.

3.3 Behaviour during leaf disc trials

In both *cucurbitae* and *26-punctata*, changes in food preference and feeding behaviour often occurred during a trial. Although all leaf discs were inspected and crawled over, many remained untouched, including some of preferred food (fig. 4). The number of times a disc was encountered was not necessarily related to the quantity of food eaten. Beetles

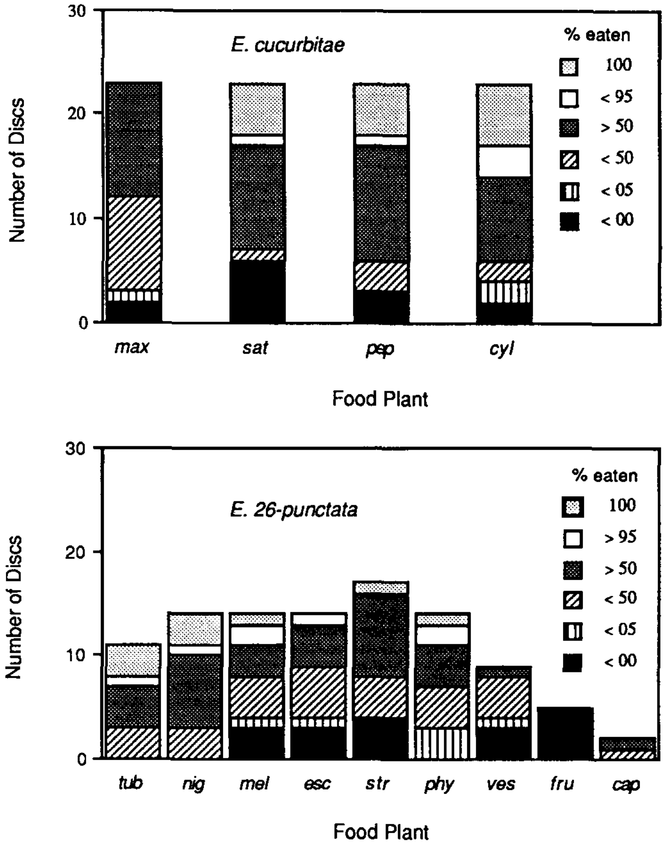

Fig. 4. Percentage of food plant leaf discs eaten by *Epilachna cucurbitae* and *E. 26-punctata* during food preference trials

either climbed onto and remained on a disc feeding until it was 100 % eaten; sat on a disc without feeding; sat beside a disc; wandered randomly between discs; or sat on the substrate for up to 60 min at a time. When a hungry beetle encountered another beetle feeding on a disc, this sometimes stimulated the newcomer to commence feeding and remain there until the disc had been completely skeletalized.

This behaviour varied in the two species when the total number of observations for all trials was compared (261 in *cucurbitae* and 318 in *26-punctata*). In *26-punctata*, the number of beetles not on discs (14.4 %) was 2.6 times that in *cucurbitae* and significantly higher ($p < 0.01$, chi-square test); while the number on the sides or beside discs (7.6 %) was 9.8 times greater and also significantly different ($p < 0.01$). The majority of beetles, 93.8 % in *cucurbitae* and 78.0 % in *26-punctata*, were on the upper or lower surfaces of discs, and of these 35.1 % of *cucurbitae* were in groups of two, 2.6 times more than in *26-punctata* and significantly higher ($p < 0.01$). Exceptions to this were a group of 3 *cucurbitae*, two above and one beneath, on a *Cu. sativus* disc, and a group of 4 *26-punctata* all on top of a *S. tuberosum* disc. On the 23 discs used for each of the four cucurbitaceous species, the number of pairs of beetles range from 16 (69.6 %) on *Cu. sativus,* 12 (52.2 %) on *C. pepo* and *L. cylindrica*, to 5 (21.7 %) on *C. maxima*; these differences were non-significant ($p > 0.05$). The number of discs used for each of the nine solanaceous species varied, not all species being available for each of the trials. The number of pairs of beetles ranged from 6 (54.6 % on 11 discs) on *S. tuberosum* and 6 (35.5 % on 17 discs) on *D. stramonium* to no pairs on discs of *S. vescum* and *C. frutescens.* Three pairs on two discs of *S. capsicoides* (150.0 %) gave an anomalous result, as this species was one of the least favoured food plants. These differences were non-significant ($p > 0.05$).

3.4 Feeding positions on leaf discs

In *cucurbitae*, over a 24 h period, the number of beetles (245) on dorsal or ventral sides of all cucurbitaceous discs was significantly different ($p < 0.01$, chi-square test), with 60 % preferring the ventral side (table 2). The same pattern occurred at night, with 70 % of beetles preferring the ventral side and again it was significantly different ($p < 0.01$). During daylight, preference for the ventral side of discs (52.8 %) was only marginal and nonsignificant. Feeding positions on discs of each of the four food plants were variable. On *L. cylindrica* the pattern was as for all food discs combined with significantly more beetles ($p < 0.01$) on the ventral side both at night (80.7 %) and for the full 24 h period (70.5 %). On *C. pepo,* significantly more beetles ($p < 0.05$) also preferred the ventral side (68.6 %) during darkness; but on *C. maxima* and *Cu. sativus* positions were not significantly different ($p > 0.05$), even though 66.6 % and 64.7 % respectively of all beetles preferred the ventral surface. On all food plants, there were significantly more beetles ($p < 0.01$) on the dorsal side in daylight (61.1 %) than in darkness, and conversely there were significantly more beetles ($p < 0.01$) on the ventral side of discs in darkness (56.7 %) than in daylight. Similar comparisons on individual food plants were non-significant ($p > 0.05$), although following the same trends.

In *26-punctata*, over a 24 h period, the number of beetles (249) on dorsal or ventral sides of all solanaceous discs was significantly different ($p < 0.01$), with 58.6 % preferring the dorsal side (table 2). The same pattern also occurred at night, with 61.3 % preferring the dorsal side, and again it was significantly different ($p < 0.01$). During daylight, preference for the dorsal side (53.9 %) was only marginal and non-significant. Feeding positions on each of the 9 food plants were variable. On *S. nigrum* and *S. melongena*, the pattern was as for all food discs combined, with significantly more beetles ($p < 0.01$) on the dorsal side both at night (78.6 % and 89.3 % respectively) and for the full 24 h period (83.3 % and 79.5 % respectively). On *S. nigrum* significantly more beetles ($p < 0.01$) were also on the dorsal side in daylight (92.9 %). On all other species preferences were variable

Table 2. **Feeding positions of *Epilachna* species on discs in light and darkness**

Food	Beetle Observations												Disc Observations		
	T	B[1]	T	B	T	B	L	D	L	D	L	D	L	D	L+D
	L		D		L+D		T		B		T+B				
cucurbitae															
C. max.	15	15	9	18	24	33	15	9	15	18	30	27	51	54	105
C. pep	16	17	11	24	27	41	16	11	17	24	33	35	51	54	105
Cu. sat.	17	18	12	22	29	40	17	12	18	22	35	34	51	54	105
L. cyl.	10	15	5	21**	15	36	10	5	15	21	25	26	51	54	105
	58	65	37	85**	95	150**	58	37**	65	85**	123	122	204	216	420
26-punctata															
S. nig	13	1**	22	6**	35	7**	13	22	1	6	14	28	36	54	90
S. mel.	6	5	25	3**	31	8**	6	25**	5	3	11	28**	39	54	93
S. tub.	3	7	17	15	20	22	3	17**	7	15	10	32**	24	39	63
D. str.	8	14	12	15	20	29	8	12	14	15	22	27	48	69	117
L. esc.	5	5	7	7	12	12	5	7	5	7	10	14	30	48	78
N. phy.	9	5	11	11	20	16	9	11	5	11	14	22	42	54	96
S. ves.[2]	2	2	4	0	6	2	2	4	2	0	4	4	21	53	96
S. cap.[2]	2	1	0	3	2	4	2	0	1	3	3	3	12	6	18
C. fru.[2]	0	1	0	2	0	3	0	9	1	2	1	2	12	15	27
	48	41	98	62**	146	103**	48	95	41	62	89	160**	264	372	636

*$p<0.05$,
**$p<0.01$
[1] T,B: beetles on Top, Bottom of disc. L/D: Light/Dark
[2] Insufficient data for significance tests

but non-significant, favouring the dorsal on *N. physalodes*, the ventral side on *D. stramonium*, both surfaces equally on *L. esculentum*, and on *S. tuberosum* the ventral side (52.4 %) over 24 h, the dorsal side (53.1 %) in darkness and the ventral side (70 %) in light. On all food plants, significantly more beetles ($p < 0.05$) were on the dorsal side in darkness (66.4 %) than in light; conversely there were 60.2 % more beetles on the ventral side at night than in daylight, but the difference was non-significant. Similar comparisons on individual food plants were variable. On both *S. tuberosum* and *S. melongena* there were significantly more beetles ($p < 0.01$) on the dorsal side in darkness (85.0 % and 80.6 % respectively) than in light. Total data on these two plant species also showed significantly more beetles ($p < 0.01$) on discs during darkness than in light (76.2 % and 71.8 % respectively). Comparisons for other food plants were non-significant, or insufficient data was available for tests.

3.5 Food preference trials using leaf discs

In *cucurbitae*, changes in food preference occurred at various times throughout the 24 h of a trial. Of the 4 food plants used in the 7 trials (21 discs per species) (table 3), *C. pepo* was consistently favoured and had the highest proportion of discs eaten, with its first disc completely skeletalized after 8 h. *Cu. sativus* ranked similarly for the first 18 h, with its first disc 100 % skeletalized after 5 h and its second after 8 h, but the final amount eaten was only 0.66 that for *C. pepo*. *L. cylindrica* was rejected for the first 6 h, but after 18 h the amount eaten had almost equalled *C. pepo*, with 3 discs completely skeletalized, a position that was maintained with the proportion eaten being only 0.06 less than for *C. pepo*, *C. maxima* was the least favoured, with the total amount eaten approximately 0.5 that for *C. pepo*. Of the 92 discs offered to *cucurbitae* (including discs from trial A), 14.1 % were

Table 3. **Proportion of discs eaten through time by *E. cucurbitae***

Food Plant	Time (hrs)‡ 1.0	3.0	5.0	6.0	8.0	18.5	24.0
C. pepo	0.05	0.07	0.12	0.21	0.31♦	0.48♦	0.77♦♦
C. maxima	0.01	0.05	0.05	0.07	0.15	0.26	0.41
Cu. sativus	0.04	0.10	0.16♦	0.24	0.24♦	0.35♦	0.55♦
L. cylindrica	0.00	0.01	0.01	0.01	0.10	0.45♦♦♦	0.73♦♦
Trials	1-3	1-7	4-7	4-7	1-7	1-7	1-3
Beetles (n)	18	42	24	24	42	42	18
Discs (n)	9	21	12	12	21	21	9

♦ Disc totally eaten (non-cumulative)
‡ Time 0 = 17:00

rejected, 19.6 % between 0.05–0.5 eaten, 43.5 % between 0.5–0.93 eaten and 22.8 % completely skeletalized (fig. 4). Approximately 66 % of the discs were between 0.5 and 1.0 eaten. *C. maxima* was the only species with no discs completely eaten, the maximum amount being 0.75 of a disc; approximately 43.5 % of its discs belonged in the 0.05–0.5 consumed range, 3.75 times more than in the other 3 species. *Cu. sativus* had 26.1 % of its discs rejected, 2.6 times more than in the other species. *L. cylindrica* had most discs skeletalized, 39 % of its total discs and 1.5 times more than *C. pepo* and *Cu. sativus*. From these results, *L. cylindrica* ranked as the preferred food, with *C. pepo* and *Cu. sativus* equal second and *C. maxima* fourth. When the total data from the food preference trials was converted into the quantity of plant disc eaten by a beetle in an hour, results for the different trial groupings were remarkably similar (table 5). They made little change to the preference rankings, except that *C. pepo* moved to third place. When the amount eaten was converted into mg, *Cu. sativus* supplanted *L. cylindrica* as the preferred food.

With *26-punctata*, 9 plant species were used in 7 trials involving 84 discs, the number per species varying in different trials (table 4). Changes in food preference occurred throughout the trials both intra- and interspecifically. In December, *S. tuberosum* was the preferred food in all trials with the highest proportion of discs per species eaten, while after 16 h *L. esculentum* replaced *S. melongena* to rank second, the total amounts eaten being 0.7 and 0.42 respectively that for *S. tuberosum*. *D. stramonium* ranked fourth, with the amount eaten 0.38 that for *S. tuberosum*. *C. frutescens* was consistently rejected and remained untouched at the end of the trials. Usually 30 h were required for complete skeletalization of a disc, but with *S. tuberosum* it ranged between 5 and 30 h up to 6 times as fast as for other species (table 4). The increased quantities of food eaten in April necessitated separation of the total data into two groups, but the ranking remained very similar. Compared with the December trials, the quantity of *S. melongena* eaten over 30 h increased 2.85 times, that of *D. stramonium* 2.28 times and of *L. esculentum*, 1.68 times. Without *S. tuberosum*, *S. nigrum* and *S. melongena* ranked equal first as the preferred food, with *L. esculentum* at only 0.05 less eaten, a close third. *D. stramonium*, *N. physalodes* and *S. vescum* ranked fourth, fifth and sixth, and, compared with the preferred species, the total amounts eaten were 0.73, 0.53 and 0.26 respectively. Although the December trials with *S. nigrum* were not completed, the December and April results for comparable time spans were very similar. Of the 100 discs offered to *26-punctata* in both December and April, and including discs from an extra trial in December (trial A), 18 % were rejected, 34 % were between 0.05–0.5 eaten, 32 % between 0.5–0.93 eaten and 16 % completely skeletalized (fig. 4). Approximately 48 % of the discs were between 0.5 and 1.0 eaten. Four species had no discs 100 % eaten; the maximum amounts were 0.94 of a disc (7 % of total discs) on *L. esculentum*, 0.6 of a disc (11 % of total discs) on *S. vescum*, 0.5 of a disc (50 %

Table 4. **Proportion of discs eaten through time by *E. 26-punctata***

December Trials (1-3)

Food	Beetles	Discs	Time (hrs)†					
Plant	n	n	3.0	5.5	7.5	16.0	24.0	30.0
S. tuberosum	19	9	0.15	0.42♦	0.50	0.55♦	0.63	0.65♦
S. melongena	12	6	0.00	0.13	0.13	0.18	0.22	0.27
L. esculentum	19	9	0.00	0.08	0.08	0.18	0.27	0.44
D. stramonium	12	6	0.00	0.06	0.06	0.15	0.18	0.25
S. nigrum	7	3	0.00	0.25	0.32	-	-	-
C. frutescens	7	3	0.00	0.00	0.00	0.00	0.00	0.00

April Trials (4-7)

Food	Beetles	Discs	Time (hrs)††								
Plant	n	n	2.0	3.5	5.0	6.0	14.0	16.0	19.0	25.0	30.0
S. nigrum	18	9	0.16	0.23	0.28	0.28	0.48	0.48	0.49	0.63	0.78♦♦♦
S. vescum	18	9	0.00	0.04	0.06	0.08	0.08	0.08	0.12	0.19	0.20
S. melongena	12	6	0.08	0.17	0.42	0.52	0.55	0.55	0.58	0.62	0.77♦
D. stramonium	18	9	0.06	0.12	0.12	0.12	0.31	0.34	0.34	0.43	0.57♦
N. physalodes	24	12	0.02	0.04	0.16	0.17	0.21	0.22	0.27	0.30	0.41
L. esculentum	6	3	0.05	0.10	0.43	0.43	0.60	0.63	0.74	0.74	0.74

♦ Disc 100% eaten (non-cumulative)
† Time 0 = 18:00; †† 0 = 20:00

of total discs) on *S. capsicoides* and zero on *C. frutescens*. *S. tuberosum* and *S. nigrum* had most discs 100 % skeletalized, 27.3 % of total discs in the former and 21.4 % in the latter, 3 times as many as *S. melongena* and *N. physalodes*. Apart from *S. capsicoides*, they were also the only species with no less than 0.125 of a disc eaten – 0.3 of a disc (27.3 % of total discs) on *S. tuberosum* and 0.26 of a disc (21.4 % of total discs) on *S. nigrum*. *C. frutescens* had the highest number of discs (80 %) rejected, *S. vescum* was second with 33.3 %, *D. stramonium* third with 23.5 % and *S. melongena* and *L. esculentum* equal fifth with 21.4 %. *S. tuberosum* and *S. nigrum* ranked equal first as preferred food, with *N. physalodes* third, *S. melongena* fourth, *D. stramonium* fifth, *L. esculentum* sixth, *S. vescum* seventh, *S. capsicoides* eighth and *C. frutescens* ninth. When the total data from food preference trials was converted into the quantity of food eaten by a beetle in an hour, the results for the different trial groupings were remarkably similar (table 5). These changed the preference rankings of half the species. *S. tuberosum* remained the most preferred food, with *S. nigrum* second, *S. melongena* third, *D. stramonium* fourth and *N. physalodes* fifth. The other rankings remained unaltered. When the amount eaten was converted into mg, *L. esculentum* replaced *N. physalodes* in fourth place. The amount of *S. tuberosum* eaten was 1.86 times that of second placed *S. nigrum*.

During the trials, the total food eaten by *cucurbitae* easily exceeded that eaten by *26-punctata*. The number of discs 100 % skeletalized by *cucurbitae* was 1.93 times that by *26-punctata*, with the time taken to eat them 0.71 less. When the quantity of each plant species consumed was reduced to the proportion of disc eaten by a beetle in an hour (table 5), the amount eaten in 3 out of the 4 cucurbitaceous species exceeded that for all the solanaceous species. Only with *S. tuberosum* did *26-punctata* exceed the amount of *C. maxima* eaten by *cucurbitae*, with *S. nigrum* equalling it. When the quantity of disc eaten was converted into mg, the amount of *S. tuberosum* eaten exceeded all other species.

Uneaten discs of food plants were used to assess their fresh weight, dry weight and

Table 5. **Food eaten by *Epilachna* spp.**

Food Plant	Means of Trials						Amount Eaten
cucurbitae	A		1-3	4-7		1-7+A	(mg)[1]
Cu. sativus	0.015		0.011	0.012		0.013	1.1
L. cylindrica	0.015		0.015	0.014		0.015	0.8
C. pepo	0.010		0.016	0.012		0.012	0.7
C. maxima	0.011		0.008	0.008		0.009	0.5
26-punctata	A	1-2	3	4-5	6-7	1-7+A	
S. tuberosum	0.003	0.011	0.019	-----	-----	0.011	1.3
S. nigrum	0.002	-----	0.008	0.014	0.013	0.009	0.7
S. melongena	0.000	0.004	-----	0.011	0.015	0.008	---
D. stramonium	0.002	0.004	-----	0.010	0.010	0.007	---
N. physalodes	0.006	-----	-----	0.007	0.007	0.007	0.4
L. esculentum	0.000	0.007	0.002	-----	0.012	0.006	0.5
S. vescum	-----	-----	-----	0.003	0.004	0.004	---
S. capsicoides	0.002	-----	-----	-----	-----	0.002	---
C. frutescens	0.000	-----	0.000	-----	-----	0.000	0.0

1 wet weight

water content (table 6). Fresh weight was very variable due to different thickness of leaves, that of *Cu. myriocarpus* and *S. edule* being particularly high. In most cases, dry weight and water content were similar. In all species except *L. cylindrica*, water content exceeded 80 %, averaging 84.0 % in other cucurbits and 84.1 % in solanaceous species. It was highest in *S. tuberosum*. While fresh weight of *L. cylindrica* was comparable with that of *C. pepo* and *C. maxima*, water content was 9 % lower.

Table 6. **Fresh weight and water content of food plant discs**

Food Plant	n	Fresh Weight (mg)	%24-hr Weight Loss	Dry Weight (mg)	% Water
cucurbitae					
C. maxima	20	54.0	5.5	10.4	81.7
C. pepo (Marrow)	17	53.1	3.9	10.2	84.7
C. pepo (Squash)	6	74.5	14.9	11.7	84.3
Ct. lanatus	10	83.4	2.0	12.4	85.1
Cu. myriocarpus	10	115.6	4.6	18.3	84.1
Cu. sativus	15	76.8	---	12.8	83.3
S. edule	10	102.5	3.1	14.9	85.0
L. cylindrica	12	56.5	---	11.8	75.8
26-punctata					
S.nigrum	15	68.5	1.9	10.9	84.1
S. tuberosum	20	85.0	3.4	10.8	87.3
S. melongena	6	98.5	2.9	14.7	85.1
L. esculentum	17	65.6	---	13.5	80.0
C. frutescens	15	67.7	---	10.4	84.7
N. peruviana	10	81.4	1.5	13.4	83.5

1 wet weight

Table 7. **Food eaten by *Epilachna* species over 24 hours**

Food Plant	***cucurbitae*** *C. maxima*	 *C. pepo* (Marrow)	 *C. pepo* (Squash)	***26-punctata*** *S. tuberosum*	 *S. nigrum*	***pardalis*** *S. melongena*
Fresh weight/disc (mg)	39.3	108.5	72.9	95.9	43.3	124.4
Amount eaten/disc (mg)[1]	13.4	16.2	15.2	28.6	51.2	10.7
Water content of residue (%)	76.5	84.1	81.7	89.9	82.6	85.4
% eaten[2]	68.9	25.8	38.9	48.3	66.0	28.6
% inedible[2]	50.7	51.7	55.5	38.3	46.7	69.0
Amount eaten/beetle/hour (mg)[1]	1.11	1.35	1.26	2.38	1.27	0.90
Dry weight/beetle/hour (mg)[1]	0.26	0.22	0.23	0.24	0.22	0.13

1 allowing 5% water-loss
2 assessed

A further series of trials over a 24 h period estimated the amount of food (in mg) consumed by one beetle in an hour in all three epilachnine species (table 7). In the three trials with *cucurbitae, C. pepo* (marrow) had the greatest amount eaten (1.35 mg), 1.07 times more than *C. pepo* (button squash) and 1.22 times more than *C. maxima*. When converted into dry weight, the order was reversed and the amount of *C. maxima* eaten became heaviest (0.26 mg), 1.13 times heavier than *C. pepo* (button squash) and 1.18 times heavier than *C. pepo* (marrow). In the two trials with *26-punctata S. tuberosum* had the greater amount eaten (2.38 mg), 1.87 times more than *S. nigrum*. When converted to dry weight, the amounts eaten were much closer, that of *S. tuberosum* being 1.09 times heavier than *S. nigrum*. The amount of *S. melongena* eaten by *pardalis* ws the smallest for all trials, being 0.38 that for *S. tuberosum*; its dry weight was also the lightest, being 0.54 that for *S. tuberosum*. However it had the highest inedible material (69 %), 1.8 times more than *S. tuberosum* and 1.5 times more than *S. nigrum*. The amount of *S. tuberosum* eaten exceeded that in all other trials, with 1.92 times more eaten by weight than for the 3 cucurbit species combined, but when converted to dry weight the amounts eaten were identical. After the trials, the percentage water content of *S. tuberosum* was 9.1 % higher than in the 3 cucurbit species combined.

4 Discussion

Food preferences of insects that are major pests of agricultural crops are very important in any aspect of their control. In the Epilachninae, interspecific similarities in size and appearance, overlapping distribution and similar food habits have led to wrong identifications and confusion over food preferences. The *Epilachna vigintioctopunctata* complex is a typical example, and although it is now known that *E. 28-punctata* (Fabr.) feeds exclusively on Solanaceae (Richards 1983), it continues to be confused with other species which feed exclusively on Cucurbitaceae (Singh and Phaloura 1987; Sinha and Chandra 1988). For the purposes of the present paper, in cases where the correct use of this name is questionable, it is placed in quotation marks.

In previous studies on food preference in epilachnines, all beetles used were mature adults either collected in the field or taken from culture and starved for 24 h. The length of each trial varied, ranging from one hour (Krishna and Sinha 1969), 2 h (Sinha and Sahni 1979), 6 h (Sinha and Krishna 1969), two days (Ali 1976), to one month (Ganga and Nagapann 1983). The shortness of some trials and the use of mature adults make some results questionable, as with later larval instars and mature adults it is often difficult or impossible to induce changes from one plant species to another. While starving may increase the appetite, it does not eliminate previous food preferences within a particular instar. In results reported here, teneral adults and first instar larvae, all starved since emergence, were used for all trials. As the prereproductive period is a time of concentrated feeding associated with maturation of the gonads, use of starved teneral adults should maximise feeding and eliminate any concentration of energy towards mating, or possible changes in food preference associated with selection of a suitable oviposition site. Compared with *26-punctata*, the greater attraction of *cucurbitae* to plant discs, faster rate of eating and far greater quantity of food consumed in a limited period, can all be related to its much shorter preoviposition period (RICHARDS and FILEWOOD 1988). Only with *S. tuberosum* did *26-punctata* exceed the amount of food eaten by *cucurbitae*.

Food preferences in epilachnines are influenced by odour, taste and age of the food plant. The basis for discrimination is chemical with scent being detected by olfactory and gustatory sensilla on maxillary palps and antennae (FISCHER and KOGAN 1986). Restriction to a particular plant family and species selection within the family is dependent on both odour and taste. Although SRIVASTAVA (1957) contended that the age of the food plant was not important in food selection trials with *E. "vigintioctopunctata"*, our trials showed that softer, younger leaves were usually preferred. Vision must also play a role. The attraction of epilachnines to flowers and fruit of certain species has also been observed in Indian species. *E. "vigintioctopunctata"* and *E. dodecastigma* Wied. feed on the yellow flowers of *Luffa aegyptiaca* and *L. cylindrica* (KRISHNA and SINHA 1969; SINHA and KRISHNA 1969; SHUKLA and UPADHYAY 1987), while *E. "vigintioctopunctata"* also attacks the purple fruit of *S. melongena* (SINHA and SAHNI 1979; SINHA and CHANDRA 1988). In the former case, it is the petals that are eaten, with the stamens and gynoecium remaining almost untouched. The role of *cucurbitae* as a pollinating agent has not previously been recorded for a phytophagous coccinellid, although many other species of Coccinellidae feed on pollen. In the leaf disc trials, intraspecific varieties of food plant, especially those of *C. pepo, C. maxima* and *L. esculentum* produced different responses from *cucurbitae* and *26-punctata*, ranging from full acceptance to total rejection. The Mexican bean beetle (*E. varivestis* Mulsant) also exhibits distinct preferences among varieties of soybean *(Glycine max)* (FISCHER and KOGAN 1986).

Plants are known to produce chemical defences in response to herbivore attack. Mechanical damage to *L. esculentum* and *S. tuberosum* leaves induces the production of proteinase inhibitors (GREEN and RYAN 1972), while damage to leaves of squash *(Cucurbita moschata)* and *C. pepo* caused by insect mandibles, induces rapid mobilization of cucurbitacins (within 40 min) to the damaged site. These act as feeding deterrents for epilachnines (CARROLL and HOFFMAN 1980; TALLAMY 1985). The rapid circular trench digging behaviour of *E. borealis* (F.) and *E. tredecimnotata* (Latreille), and now also *cucurbitae* on *C. maxima* and *C. pepo*, serves to isolate areas of leaf from cucurbitacins thus permitting feeding on uncontaminated tissues within the protected area. The different shaped trenches, cutting of trenches within trenches and overlapping of trenches has not been recorded for the North American epilachnines. As yet the significance of this complex behaviour has not been determined, but if cucurbitacins succeeded in invading the protected area via uncut veins, this could stimulate further trench cutting with each successive trench becoming smaller in size. Under field conditions, *E. borealis* and *E. tredecimnotata* are solitary feeders within the protected area, but this is not always so with *cucurbitae* (fig. 3). The time response for insect related induced resistance is very variable (CARROLL and HOFFMAN 1980), and this may partly explain changes in food preference shown by *cucurbitae* and *26-punctata* during trials, and their acceptance or rejection of discs cut from the same leaf.

Although SRIVASTAVA (1957) observed that larvae of *E. "vigintioctopunctata"* fed on the abaxial and adults on the adaxial surface of solanaceous leaves, the feeding positions adopted by epilachnines on species belonging to different plant families has not previously been recorded. While positions on the same or different plant species varied in darkness and daylight, *cucurbitae* larvae and adults usually preferred the ventral side of discs or leaves, while *26-punctata* larvae and adults preferred the dorsal side. SINHA and SAHNI (1974) noted that in daylight *E. "vigintioctopunctata"* preferred yellow flowers of *L. aegyptiaca* to leaves, while in darkness flowers and leaves were equally accepted. Similar preferences were observed with *cucurbitae*.

The 24 h and 30 h food preference trials showed that both *cucurbitae* and *26-punctata* alternately fed or rested throughout the whole period. With *cucurbitae* there was no particular feeding time, but with *26-punctata* night feeding was preferred. These long feeding periods contrast with that for *E. tredecimnotata*, which lasts for only one or two hours each morning (CARROLL and HOFFMAN 1980).

The large quantity of food eaten by epilachnines is due to their preference for soft parenchymatous tissues and their avoidance of indigestible crude fibres, leaving leaves skeletalized. When assessing the amount of fresh food eaten, intraspecific variations in thickness of leaves, the amount of parenchymatous tissue and fibres present and water content must all be considered. The higher fibre content in leaves of *L. cylindrica* might explain its complete rejection by *cucurbitae* early in the preference trials (table 3). The smaller quantity of parenchymatous tissue in each disc and the lower water content might also explain why by the end of the trials *L. cylindrica* had the highest number of discs completely skeletalized, yet the amount eaten in mg was 0.73 that for *Cu. sativus* (table 5). Conversely, the very high water content and low inedible fibre content in *S. tuberosum* (table 7) might explain why the amount eaten for this species was almost double that for all other trial species, both in the food preference trials (table 4) and the food weight trials (table 7).

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Zusammenfassung

Ernährungsverhalten und Nahrungsbevorzugung bei den Marienkäfern des Epilachna vigintioctopunctata (F.)-Komplexes (Col., Coccinellidae)

Ernährungsversuche mit 35 Pflanzenarten aus 5 Familien ergaben, daß *Epilachna cucurbitae* Rich. ausschließlich an Cucurbitaceen und *E. 26-punctata 26-punctata* (Boisd.) sowie *E. 28-punctata pardalis* (Boisd.) ausschließlich an Solanaceen fressen. Dabei werden von den beiden Solanaceen-Spezialisten die Blätter und Früchte bevorzugt. Blüten, vor allem Pollen, bevorzugt dagegen *E. cucurbitae*, deren Käfer somit als wichtige Blütenbestäuber fungieren. Diese Erkenntnis wurde erstmals zum Verhalten phytophager Coccinelliden gewonnen. Die Nahrungswahl wird bestimmt durch Riech-, Tast- und Sehsinn des Käfers sowie das Alter der Pflanze. Sie wird weiterhin beeinflußt durch die Blattdicke sowie durch das Verhältnis zwischen Rohfasern, Parenchymgewebe und Wassergehalt. Das Ernährungsverhalten an denselben oder verschiedenen Pflanzenarten variiert je nach Dunkelheit und Tageslicht, doch bevorzugt *E. cucurbitae* die abaxiale und *E. 26-punctata* die adaxiale Seite der Blätter. Bei *E. cucurbitae* gibt es keine spezifische Nahrungsaufnahme-Periode, jedoch bevorzugt *E. 26-punctata* die Nacht. Bei Nahrungswahlversuchen fraß während einer gegebenen Zeit *E. cucurbitae* schneller und konsumierte mehr Nahrung als *E. 26-punctata* – mit einer Ausnahme: die Kartoffel *(Solanum tuberusom)* wurde von allen 3 *Epilachna*-Arten gleich schnell und stark befressen. Sie bildete die eindeutig und allgemein bevorzugte Nahrung. Zum ersten Mal wurde bei *E. cucurbitae* ein komplexes Blattschneide-Verhalten festgestellt. Es dient zum Schutz spezifischer Nahrungsareale am Blatt vor chemischen Abwehrreaktionen, die von Cucurbitaceenblättern produziert werden.

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