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The effect of agricultural crops and weeds on the bionomics of the pest species comprising the *Epilachna vigintioctopunctata* complex (Col., Coccinellidae)

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Abstract

Feeding experiments on the 3 pest species of the *Epilachna vigintioctopunctata* complex show that marrow *(Cucurbita pepo)* is the preferred food of the cucurbitophagous *E. cucurbitae* Richards, while potato *(Solanum tuberosum)* is the preferred food of the 2 solanivorous species *E. vigintisexpunctata vigintisexpunctata* (Boisduval) and *E. vigintioctopunctata pardalis* (Boisduval). *E. vigintisexpunctata vigintisexpunctata* can survive on weeds for long periods, often with reduced fecundity. The plant family influences the duration of their preoviposition period, while specific food plant species influence the length of their oviposition period. In *E. cucurbitae* the development rate is the fastest in the 3 species and the mortality is the highest. Of the 2 solanivorous species, *E. v. pardalis* is the more successful. In both species, egg hatch, fecundity and generation time *T* are higher than in *E. cucurbitae*. Both *E. cucurbitae* and *E. v. vigintisexpunctata* exhibit a temperate reproductive pattern, while *E. v. pardalis* retains a tropical pattern. *Epilachna cucurbitae* has a development rate, and preoviposition and oviposition periods similar to other cucurbitophagous species outside Australia, but has a longer life span and higher fecundity. Of all epilachnine species studied, the 2 Australian solanivorous species have the slowest development rate, longest preoviposition, oviposition and postoviposition periods, longest life span and highest fecundity.

1 Introduction

The phytophagous Coccinellidae of Australia belong to the tropical and semitropical subfamily Epilachninae. Some are important pests of agricultural crops, particularly in eastern Australia, and their distribution extends both eastward to Oceania and north to South-east Asia, Japan, China, India and Pakistan. The taxonomy of the 3 most widespread and important pest species comprising the *Epilachna vigintioctopunctata* complex has recently been studied (Richards 1983). They are now known as *E. vigintioctopunctata pardalis* (Boisduval), *E. vigintisexpunctata vigintisexpunctata* (Boisduval) and *E. cucurbitae* Richards (referred to here as *pardalis, 26-punctata* and *cucurbitae*). Records of their damage to crops, both as larvae and adults, can be found in many articles in the Agricultural Gazette of N. S. W. from 1890 onwards, where they are recorded as pests of pumpkin, potato, tomato (Olliff 1890), tobacco, nightshade, trumpet flower weed *(Brugmansia suaveolens)*, cucumber, melon and cotton (Froggatt 1923). Usually it is the leaves of plants that are skeletalized, but flowers and fruit may also be eaten. *E. cucurbitae* has been recorded as a transmitter of cucurbit viruses (Greber 1969). Both *26-punctata* and *pardalis* feed exclusively on Solanaceae, while *cucurbitae* feeds only on Cucurbitaceae (Richards 1983).

Descriptions of the biology of the immature stages of the 3 species have all been given under the name *E. vigintioctopunctata* (F.) (Olliff 1890; Temperley 1928; Stride and Warwick 1960). So far no detailed information has been published on their biology, and nothing is known of the biology of *26-punctata.*

Until recently, the effect of temperature, photoperiod, and food plants on the biology

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of the Epilachninae was not known. Ali (1979) has studied this in the alfalfa ladybird *Subcoccinella vigintiquatuorpunctata* (L.) in Europe, and also in the melon ladybird [*E. elaterii* (Rossi) (= *E. chrysomelina* sensu auct. not (Fabricius) (Fursch 1964)] in Egypt (Ali and El-Saedy 1981, 1982). (Fursch showed the true *chrysomelina* (F.) to be a synonym of *E. sparsa* (Herbst), which in turn has recently been synonomized with *E. vigintioctopunctata* (F.) (Richards 1983)). More recently, Nakamura et al. (1984) have described development, fecundity and mortality in 2 unidentified species of *Epilachna* from Sumatra. Both Egyptian and Sumatran species feed on cucurbitaceous crops. Only limited information is available on species which attack solanaceous crops (Sachan and Rathore 1979; Kono 1979, 1982). This study investigates under laboratory conditions the effects of food plants, both solancaeous and cucurbitaceous, both crop plants and weeds, on development, mortality, fecundity, fertility and longevity in the 3 species which form the *Epilachna vigintioctopunctata* complex.

2 Materials and methods

Cultures of the 3 *Epilachna* species were established in the laboratory from adults or egg batches collected in the field. In the fecundity trials *E. cucurbitae* was fed on pumpkin *(Cucurbita maxima)*, marrow *(C. pepo)*, and cucumber *(Cucumis sativus)*; *26-punctata* was fed on potato *(Solanum tuberosum)*, nightshade *(S. nigrum)*, tomato *(Lycopersicon esculentum)*, apple of Peru *(Nicandra physalodes)* and common thornapple *(Datura stramonium)*; and *pardalis* was fed on *S. nigrum*. Wherever 20 or more adult beetles were kept together in culture, the rate of oviposition drastically declined, so isolated pairs of adults were used in all fecundity experiments. Initially, 10 replicates were used for each food trial, but not all adults proved capable of mating successfully. Each replicate consisted of a pair of teneral adults (first generation in culture) placed in a perspex cage and provided with a regular supply of fresh leaves from the selected food plant. The cages were kept in cabinets maintained at 25 °C, 75% R. H., and a 14:10 h L:D photoperiod. Food plants were checked each day for eggs. All egg batches were removed, eggs counted, and hatchings recorded. Each experiment was continued until the death of all insects on a particular food plant. Males that died before females in the early stages of the experiment were replaced, but only the initial male was included in the longevity results.

To assess development rate and mortality on different food plants, newly hatched larvae of the 3 species were placed individually in a series of glass phials with cottonwool stoppers. They were inspected each day and fed on a particular food plant until emergence of the adult beetle, when they were sexed. The same food plants were used for *cucurbitae* as in the fecundity experiments. *D. stramonium* was not used for *26-punctata*, while *S. tuberosum* was added for *pardalis*.

3 Results

3.1 Duration of developmental stages

The duration of developmental stages in the 3 species of *Epilachna* is given in tables 1, 2, 3. In *cucurbitae* variations in total development time on *C. maxima*, *C. pepo* and *Cu. sativus* (table 1) were not significant [$p > 0.05$; Hochberg GT_2 test, Spjotvoll Stoline T^1 test and Tukey Kramer test (Sokal and Rohlf 1969)]. However, in the prepupal and most larval instars, those fed on *C. maxima* were significantly different ($p < 0.01$ or $p < 0.05$) from those on the other 2 food plants. Although no specific patterns in duration of individual instars were evident in relation to type of food, total larval development was longest on *C. maxima* and shortest on *C. pepo*. Duration of pupal development appeared to be affected by larval diet, being longer on *C. pepo* than on the other two food plants.

Intraspecific differences in duration of developmental instars in *26-punctata* fed on *S. nigrum*, *S. tuberosum*, *L. esculentum* and *N. physalodes* were in most cases highly significant ($p < 0.01$) (table 2). The egg to adult period was also highly significant ($p < 0.01$) in all food plant comparisons except that between *N. physalodes* and *L. esculentum* where $0.01 < p < 0.05$. The development rate was fastest on *S. tuberosum* (32.6

Table 1. Duration of life stages in *E. cucurbitae* at 25 °C, LD 14:10

Food Plant	*Cucurbita maxima*			*Cucurbita pepo*			*Cucumis sativus*		
	n	Mean (days)	SEM	n	Mean (days)	SEM	n	Mean (days)	SEM
Incubation	45	6.15	0.15	54	6.62	0.31	31	6.59	0.35
1	45	5.27	0.10	54	3.96	0.12	31	3.77	0.09
2 Larval	43	4.47	0.17	53	3.62	0.11	30	3.53	0.10
3 Instars	42	4.00	0.17	50	3.80	0.12	30	3.80	0.12
4	42	3.83	0.14	43	4.26	0.25	29	5.28	0.20
Prepupa	41	1.51	0.11	30	2.46	0.12	27	1.77	0.10
Pupa	39	4.54	0.09	28	4.71	0.09	25	4.28	0.09
Preoviposition	6	12.50	4.51	3	9.33	2.19	4	9.75	4.75
Oviposition	6	47.50	12.15	3	72.33	17.23	4	44.00	21.11
Postoviposition	6	36.00	16.22	3	38.00	22.52	4	24.00	13.14
Generation *T*		60.78			68.56			72.46	

days), 0.9 of that rate on *S. nigrum*, 0.85 of it on *L. esculentum* and 0.67 of it on *N. physalodes*. Strangely, duration of total pupal development was fastest on *N. physalodes*, the least preferred food plant, and slowest on *L. esculentum*.

In *pardalis*, except for larval instar 2, the duration of each developmental instar on *S. tuberosum* was significantly different from that on *S. nigrum* ($p < 0.01$) (table 3). The total development rate on *S. tuberosum* was 1.3 times that on *S. nigrum*, and both larval and pupal development rates were also faster.

When both, *pardalis* and *26-punctata* were fed on *S. nigrum*, differences in the development rate were significant in larval instar 1 and the prepupa ($p < 0.05$), and highly significant in larval instar 4 and the pupa ($p < 0.01$). The total development rate in *pardalis* was 0.9 the rate in *26-punctata*. When both were fed on *S. tuberosum*, only larval instar 2 and the total development period were significantly different ($p < 0.05$), and the total rate

Table 2. Duration of life stages in *E. 26-punctata 26-punctata* at 25 °C, LD 14:10

Food Plant	*Solanum nigrum*			*Solanum tuberosum*			*Lycopersicon esculentum*			*Nicandra physalodes*			*Datura stramonium*[1]		
	n	Mean (days)	SEM	n	Mean (days)	SEM	n	Mean (days)	SEM	n	Mean (days)	SEM	n	Mean (days)	SEM
Incubation	44	6.48	0.22	50	6.48	0.22	50	4.59	0.05	47	3.77	0.02	29	5.01	0.44
1	44	6.90	0.17	50	4.36	0.08	47	4.94	0.12	29	9.48	0.41			
2 Larval	42	4.10	0.14	48	4.71	0.09	45	3.82	0.10	27	6.26	0.36			
3 Instars	40	5.40	0.11	47	4.19	0.08	44	6.57	0.15	27	5.67	0.34			
4	39	5.10	0.14	45	5.11	0.10	40	6.85	0.23	27	6.30	0.57			
Prepupa	35	3.23	0.17	45	2.77	0.08	32	3.22	0.14	25	2.52	0.22			
Pupa	35	5.29	0.10	44	5.45	0.08	30	5.43	0.15	23	4.83	0.10			
Preoviposition	10	26.90	2.95	8	32.40	1.87	6	20.83	2.98	5	50.80	4.78	4	35.50	14.52
Oviposition	10	72.10	4.17	8	76.00	13.10	2	28.50	6.50	5	44.20	10.45	4	39.00	21.12
Postoviposition	10	7.00	2.32	8	2.88	0.95	2	8.00	3.00	5	56.40	11.35	4	27.00	11.12
Generation *T*		92.41			98.84			93.37			145.72			132.14	

1. No data for immature stages on *D. stramonium*.

Table 3. Duration of life stages in *E. 28-punctata pardalis* at 25 °C, LD 14:10

Food Plant	*Solanum nigrum*			*Solanum tuberosum* [1]		
	n	Mean	SEM	n	Mean	SEM
Incubation	35	5.48	0.28	50	5.00	0.00
1	35	6.11	0.27	45	4.78	0.10
2 Larval	35	4.37	0.43	44	3.82	0.11
3 Instars	35	5.91	0.34	44	4.30	0.14
4	32	6.56	0.20	44	4.55	0.11
Prepupa	26	4.00	0.27	41	2.80	0.11
Pupa	25	5.92	0.08	41	5.20	0.07
Preoviposition	5	31.20	4.08			
Oviposition	5	128.40	13.40			
Postoviposition	5	34.40	21.85			
Generation *T*		143.03				

1. No data for adult stages on *S. tuberosum*.

from egg to adult in *26-punctata* was 0.96 that in *pardalis*. In both species, the total development rate was faster on *S. tuberosum* than on any of the other solanaceous food plants tested. Length of total development on all food plants was comparable in the 2 species and, except for those feeding on *S. tuberosum*, was much longer than in *cucurbitae*. In most cases, interspecific variation was highly significant ($p < 0.01$) irrespective of food plant, the main exceptions being when *26-punctata* and *pardalis* were reared on *S. tuberosum*.

3.2 Mortality

Mortality rates per day were calculated using the formula

$$m = 1/T \log_e (N_1/N_0)$$

In all 3 species of *Epilachna*, the level of mortality was influenced by the type of food plant on which the larvae were reared. The mean daily rate in immatures of *cucurbitae* was 0.026, being 2.9 times that in *pardalis* and 1.8 times that in *26-punctata*.

Intraspecifically the total rate in *cucurbitae* was highest on *C. pepo* (0.038), being 1.5 times the rate on *C. maxima*, and 2.8 that on *Cu. sativus*. On each of the 3 food plants, the larval rate in the 1st instar was higher than in the other 3 larval instars combined, being 0.084 on *C. maxima* (15 times higher), 0.054 on *C. pepo* (2.8 times higher), and 0.025 on *Cu. sativus* (4.7 times higher). The total larval rate on *C. maxima* and *C. pepo* was in each case 0.03, being 2.9 times that on *Cu. sativus*. The total larval rate on *C. maxima* was 2.4 times the total pupal rate, but on *C. pepo* and *Cu. sativus* the total pupal rate was 0.060 and 0.025 respectively, more than double the total larval rate. Prepupal mortality was greater than pupal mortality, being 0.016 (1.5 times the pupal rate) on *C. maxima*, 0.062 (6.2 times it) on *Cu. sativus*, and 0.146 (9.7 times it) on *C. pepo*.

In *26-punctata* the daily mortality rate was highest (0.024) on *N. physalodes*, being 1.4 times that on *L. esculentum*, 2.4 times that on *S. nigrum* and 4.9 times that on *S. tuberosum*. Larval mortality on each of the 4 food plants was very variable with no obvious pattern. The total larval rate was highest (0.024) on *N. physalodes* due to a very high 1st instar mortality, being 2.4 times that on *L. esculentum*, 2.8 times that on *S. nigrum*, and 4.2 times that on *S. tuberosum*. Total pupal mortality was variable, being confined to the prepupal stage on *S. nigrum* and to the pupal stage on *S. tuberosum*. The pupal rate on *N. physalodes* (0.017), was 1.1 times the prepupal, and on *L. esculentum* the prepupal rate

(0.069) was 5.8 times the pupal. The total pupal rate was highest (0.033) on *L. esculentum*, being 1.5 times that on *N. physalodes*, 2.6 times that on *S. nigrum* and 12.3 times that on *S. tuberosum*. The last was the smallest pupal mortality rate on any plant during the experiment, being 0.003 per day. The total larval and total pupal mortality rates on the same plants were variable. The total larval rate on *S. tuberosum* (0.006), was 1.9 times the pupal, and that on *N. physalodes* (0.026), was 1.6 times the pupal, while the pupal rates on *S. nigrum* (0.013) and on *L. esculentum* (0.033), were 1.2 times and 3.3 times the larval rate.

In *pardalis* the total mortality rate on *S. nigrum* was 0.011, double that on *S. tuberosum*. In the 1st instar on *S. tuberosum* the larval rate was 0.014, and in the 4th instar on *S. nigrum* 0.016, but it was almost negligible in the other 3 instars. While the total larval rate was 0.005 on both food plants, the total pupal rate (0.027) was 3.3 times higher on *S. nigrum*. On both food plants, mortality rates for pupae were higher than those for larvae, being 1.6 times higher on *S. tuberosum* and 5.3 times higher on *S. nigrum*. On *S. tuberosum* pupal mortality was confined to the prepupal stage, while on *S. nigrum* the prepupal rate (0.052) was 6.5 times the pupal.

In the 2 solanivorous species the total mortality rates on *S. tuberosum* and *S. nigrum* were very similar. In *26-punctata* on *S. tuberosum* the rate (0.004) was the smallest on any plant throughout the experiment. Total larval rates for the 2 species on the same food plants ranged between 0.005 and 0.012 per day. High mortality in a particular instar influenced the overall result on a food plant, as in the high 1st instar mortality on *N. physalodes* and the high prepupal mortality on *L. esculentum*. In the solanivorous species, the total larval plus total pupal rate was highest (0.024) on *N. physalodes*. In *cucurbitae* on *C. maxima* it was 1.04 times the rate on *N. physalodes*, even higher at 1.38 times it on *C. pepo*, but only 0.58 of the rate on *Cu. sativus*.

3.3 Sex ratio

In all 3 species of *Epilachna* the sex ratio of reared teneral adults was about 1:1. Although chi-square tests were not significant ($p > 0.05$), females tended to outnumber males. The ratio of males to females was 48:54 in *cucurbitae*, 53:79 in *26-punctata* and 8:8 in *pardalis*. In all 3 species when fed on different food plants, intraspecific comparison of the sex ratio also proved to be non-significant.

3.4 Fecundity

The effect of different food plants on fecundity [measure of total egg production (SOUTHWOOD 1978)] varied both intra- and interspecifically.

In *cucurbitae* the total number of eggs laid per female when fed on *C. maxima*, *C. pepo* or *Cu. sativus* (table 4) did not differ significantly ($p > 0.05$). However, the mean total number of eggs laid on *C. pepo* (1145) was 1.5 times that on *Cu. sativus* and twice that on *C. maxima*, suggesting a preference for *C. pepo*. The number of times a population will multiply per generation is described as the net reproductive rate R_0, that is the average number of female eggs produced per female beetle. This parameter was calculated using the formula

$$R_0 = l_x m_x$$

(SOUTHWOOD 1978). Analysis of R_0 based on the survivorship and fertility figures in table 4, showed that those beetles fed on *C. pepo* had the highest reproductive rate, followed closely by those on *Cu. sativus*, with those on *C. maxima* approximately 0.66 those on *C. pepo*. The mean total number of eggs laid per female (table 4) was 5.2 times the value of R_0 on *C. pepo*, 4.4 times its value on *C. maxima* and 4.1 times its value on *Cu. sativus*. Figure 1 shows that the frequency distribution of egg batch size in *cucurbitae* was

Table 4. Fecundity of three *Epilachna* species on different food plants at 25 °C, LD 14:10

Species	Food Plant		Eggs laid		Eggs/day		Eggs hatched		R_o	r
		n	Mean	SEM	Mean	SEM	Mean	SEM		
cucurbitae	*C. maxima*	6	590.8	145.1	15.2	3.1	437.5	120.9	134.2	0.08
	C. pepo	3	1144.7	202.0	16.6	1.8	688.0	157.4	219.5	0.08
	Cu. sativus	4	758.5	518.0	18.9	5.7	308.0	194.8	186.1	0.07
pardalis	*S. nigrum*	5	1692.4	405.1	13.7	2.7	831.8	246.2	325.2	0.04
26-punctata	*S. nigrum*	10	1019.6	135.1	14.0	4.2	490.3	88.5	290.8	0.06
	S. tuberosum	8	1259.3	176.2	17.6	1.4	621.0	120.0	384.0	0.06
	N. physalodes	5	126.4	24.6	3.4	1.0	64.0	15.9	32.0	0.02
	D. stramonium	4	212.3	68.1	13.0	8.1	74.8	25.6	65.3	0.03
	L. esculentum	2	372.5	17.5	13.6	2.5	210.0	40.0	64.9	0.04

variable on the 3 food plants, with about 1.3 times more egg batches laid on *C. pepo* than on the other two. While the distribution between the number of egg batches versus the number of eggs per batch was not significant on *C. pepo* and *Cu. sativus*, the distribution on *C. maxima* was significantly different from that on the other two ($p < 0.01$, log likelihood ratio test). Similar tests between *cucurbitae* on all 3 food plants and *pardalis* on *S. nigrum* were not significant, but those between it and *26-punctata* on *S. nigrum*, *S. tuberosum*, *D. stramonium* and *N. physalodes* were significant ($p < 0.05$). The number of egg batches per female in *cucurbitae* was significantly different from that in *pardalis* ($p < 0.01$) (GT_2 test), and from that in *26-punctata* ($p < 0.05$).

In *26-punctata* the total number of eggs laid per female, the number of egg batches, the number of eggs per day and the number of eggs that hatched on *D. stramonium* and

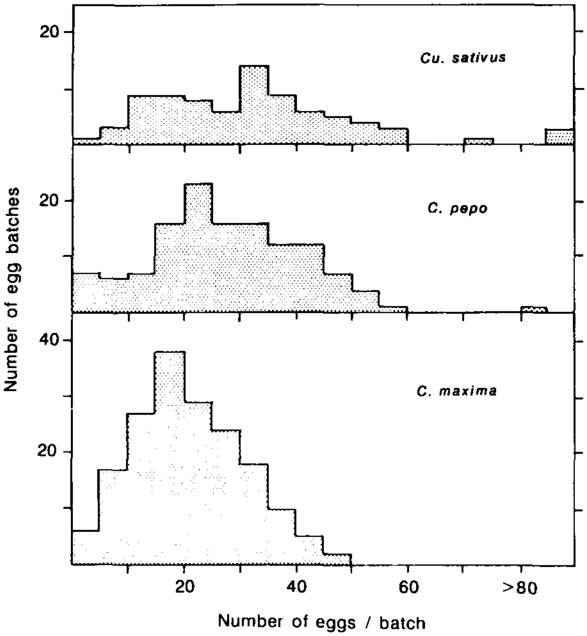

Fig. 1. The frequency distribution of egg batch size in *E. cucurbitae* on different food plants. The number of egg batches is 80 on *Cu. sativus*, 128 on *C. pepo* and 175 on *C. maxima*

N. physalodes were not significantly different. Apart from the number of egg batches, the results on *S. nigrum* and *S. tuberosum* were also not significantly different (table 4). This separated fecundity on the 4 food plants into 2 groups, differences between which were in most cases highly significant ($p < 0.01$, GT_2 test). While *L. esculentum* results were not included in the tests because female numbers were too small, they appeared to be closer to those obtained when fed on the first group. The net reproductive rate (table 4) was highest on *S. tuberosum* followed by *S. nigrum*, while on the other 3 food plants there was a dramatic decrease in egg production. Fecundity was highest on *S. tuberosum*, being 1.2 times that on *S. nigrum*, 3.4 times that on *L. esculentum*, 5.9 times that on *D. stramonium* and 10.0 times that on *N. physalodes*. The mean total number of eggs laid per female was 5.7 times the value of R_0 on *L. esculentum*, 3.9 times it on *N. physalodes*, 3.5 times it on *S. nigrum* and 3.3 times it on both *S. tuberosum* and *D. stramonium*. Figure 2 shows that the frequency distribution of egg batch size in *26-punctata* was divisible into 3 groups, with *S. tuberosum* in one, *S. nigrum* in a second and *D. stramonium* and *N. physalodes* in a third. On *S. tuberosum* the mean number of egg batches (43.75) was 1.8 times that on *S. nigrum*, 5.8 times that on *D. stramonium* and 8.4 times that on *N. physalodes*. On the 4 different food plants, the relationship between the number of eggs per batch and the number of egg batches was not significantly different ($p > 0.05$; log likelihood ratio test). Similar results were obtained when *26-punctata* on *S. nigrum* was compared with *pardalis* on the same food plant. Compared with the number of egg batches per female laid by *pardalis* on *S. nigrum*, those laid by *26-punctata* on *S. nigrum*, *D. stramonium* and *N. physalodes* were all significantly different ($p < 0.01$, GT_2 test), but those laid on *S. tuberosum* were not. The net reproductive rate in *26-punctata* on *S. tuberosum* was double that in *cucurbitae* on *C. maxima*, *C. pepo* and *Cu. sativus*.

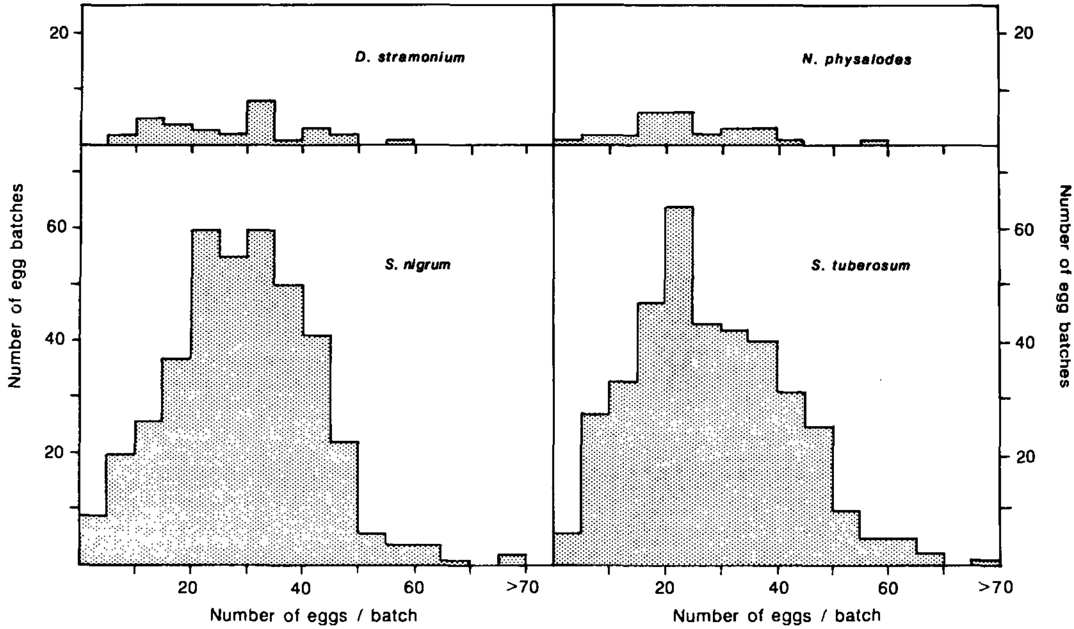

Fig. 2. The frequency distribution of egg batch size in *E. 26-punctata 26-punctata* on different food plants. The number of egg batches is 27 on *N. physalodes*, 31 on *D. stramonium*, 381 on *S. tuberosum* and 396 on *S. nigrum*

Fecundity results for ***pardalis*** on *S.* ***nigrum*** (table 4) were 1.1 times those for *26-punctata* on the same food plant. The net reproductive rate per female was 1.7 times that in *cucurbitae*. The mean total number of eggs laid per female was 5.2 times that of R_0 on *S.* ***nigrum*** (table 4). Figure 3 shows that the frequency distribution of egg batch size was similar to, but slightly less than in *26-punctata* on the same food plant.

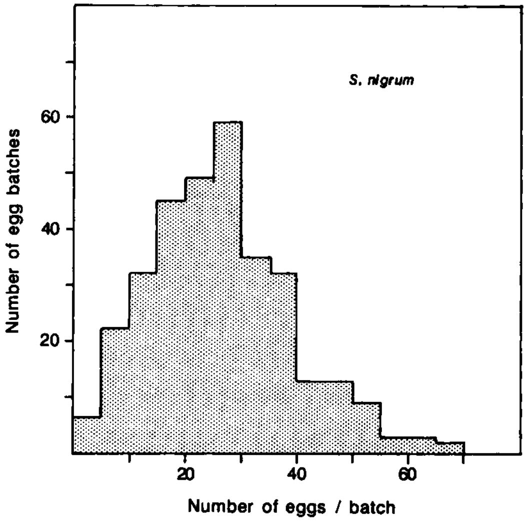

Fig. 3. The frequency distribution of egg batch size in *E. 28-punctata pardalis* on *S. nigrum*. The number of egg batches is 336

3.5 Survivorship and fertility

Survivorship, the falling of numbers with time (l_x) (Southwood 1978) in both male and female adults of the 3 species on different food plants is shown in fig. 4, 5, 6. The age-specific fertility, expressed as the change in the number of eggs laid per female per day, is also shown. As a sex ratio of about 1:1 was obtained in all 3 species, the age specific fertility for the populations in all cases equals $2m_x$ [twice the number of living females born per female/unit time (Southwood 1978)].

Tables 1, 2, 3 give the overall mean longevity for each of the 3 species, together with the length of generation time *T*. The longevity of males and females was variable on different food plants (GT_2, T^1 and Tukey Kramer tests). In *cucurbitae* there was a slight tendency for males to live longer than females (fig. 4), but this was not significant between food plants. With both sexes combined, those reared on *C. pepo* lived an average of 117 days, being 1.2 times longer than those reared on *C. maxima*, and 1.4 times longer than those reared on *Cu. sativus*. In *26-punctata* longevity in males and females was variable on different food plants (fig. 5, 6A). Females reared on *N. physalodes* lived longest (153 days), while survival was shortest in those on *L. esculentum* (66 days). The lifespan in those reared on the other 3 food plants was approximately half way between these extremes. Longevity in males formed a series of semi-equal steps between those reared on *D. stramonium* (174 days) and those reared on *L. esculentum* (90.5 days). In both sexes survival was shortest on *L. esculentum*. Male longevity on *S. tuberosum* (158 days) was significantly greater than that in both males (109 days) and females (107) on *S. nigrum*, and in females on *S. tuberosum* (104) and *D. stramonium* (103). Females on *N. physalodes* lived significantly longer than females on *S. tuberosum* ($p < 0.05$, GT_2 test).

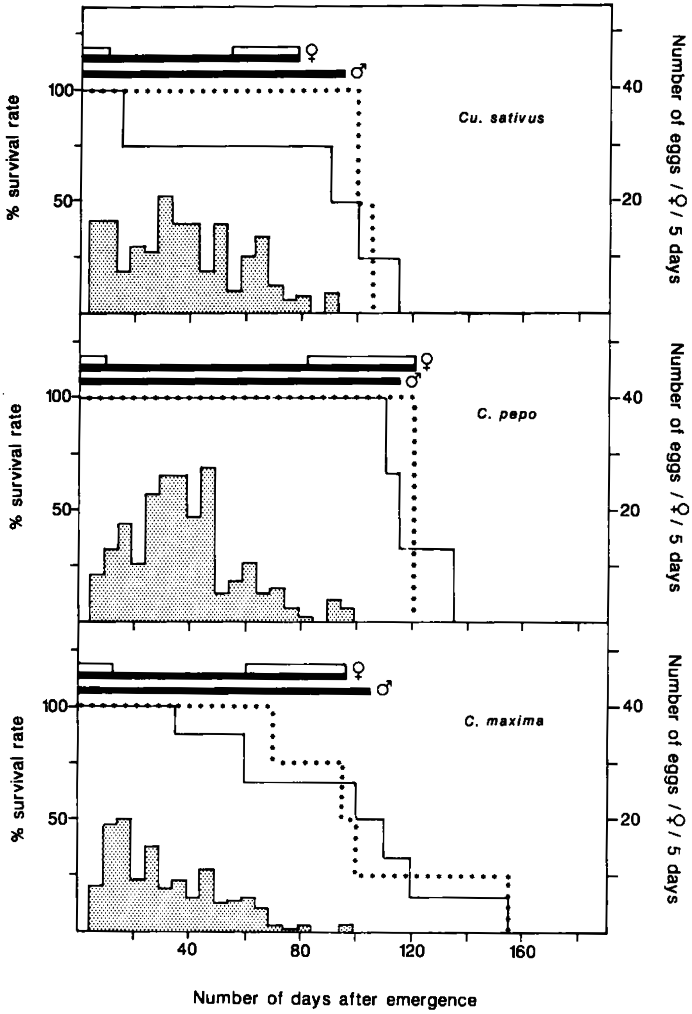

Fig. 4. $l_x m_x$ schedules in *E. cucurbitae* on different food plants. Solid and starred lines are survivorship curves for females and males respectively. The histogram shows the number of eggs laid per female/ 5 days. The horizontal bars show the mean longevity for both sexes. The boxes above the female bar depict the duration of pre- and postoviposition periods

In *pardalis*, females tended to live longer than males (fig. 6B), but the difference was not significant ($p > 0.05$, GT_2 test). They lived significantly longer ($p < 0.01$) than females in *cucurbitae* and *26-punctata*, and also longer than males in *cucurbitae* and *26-punctata* on *S. nigrum*. Longevity in *cucurbitae* females was significiantly less ($p < 0.01$) than in males of *26-punctata* on *S. tuberosum*. Other interspecific differences were non-significant, including the lifespan in males of all 3 species.

In *cucurbitae* the preoviposition period was short, and there was little variation on different food plants (fig. 4). In both *26-punctata* and *pardalis*, it was approximately 3 times that in *cucurbitae* (fig. 5, 6). On each food plant differences from that in *cucurbitae* were highly significant ($p > 0.01$), except in *26-punctata* on *S. nigrum* ($p < 0.05$). In *26-punctata*, preoviposition was shortest on *L. esculentum* (21 days), and longest on

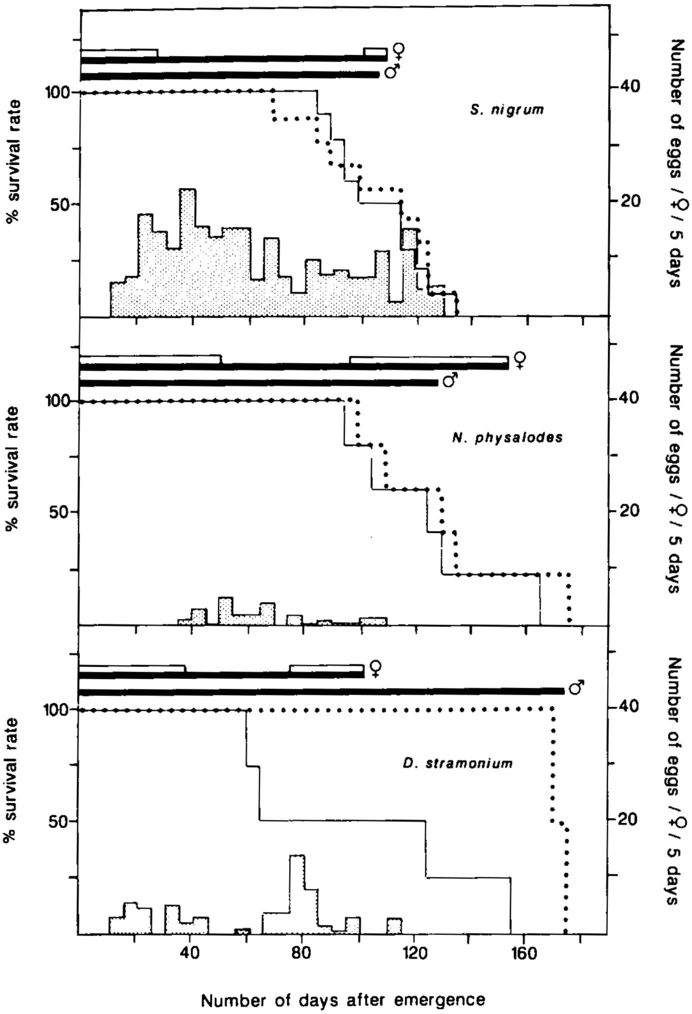

Fig. 5. $l_x m_x$ schedules in *E. 26-punctata 26-punctata* on different food plants. Solid and starred lines are survivorship curves for females and males respectively. The histogram shows the number of eggs laid per female/5 days. The horizontal bars depict the mean longevity for both sexes. The boxes above the female bar show the duration of pre- and postoviposition periods

N. physalodes (51 days) (table 2); that on *S. nigrum* was significantly different from that on *N. physalodes* ($p. < 0.05$). There was no significant difference between the preoviposition periods in *pardalis* and *26-punctata* on any food plant.

The oviposition periods in *26-punctata* and *cucurbitae* were similar, but that in *pardalis* was significantly longer ($p < 0.01$) (tables 1, 2, 3; fig. 4, 5, 6). Although the oviposition periods in both the former species were much longer on their preferred food plants (tables 1, 2), intraspecific differences were not significant. In *26-punctata,* oviposition was of similar duration on *D. stramonium* and *N. physalodes,* but twice as long on *S. nigrum* and *S. tuberosum* (76 days), while in *cucurbitae* oviposition on *C. pepo* (72 days) was approximately 1.5 times longer than on *C. maxima* and *Cu. sativus.* The histograms of age-specific fertility (fig. 4, 5, 6A) show that in *cucurbitae* on all food plants, and *26-punctata*

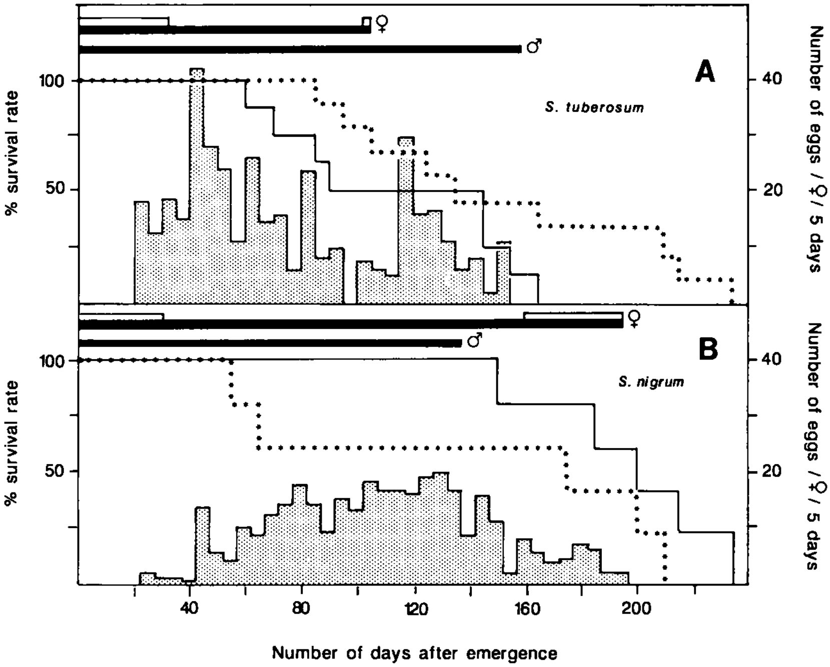

Fig. 6. A: $l_x m_x$ schedules in *E. 26-punctata 26-punctata* on *S. tuberosum.* B: $l_x m_x$ schedules in *E. 28-punctata pardalis* on *S. nigrum.* Solid and starred lines are survivorship curves for females and males respectively. The histogram shows the number of eggs laid per female/5 days. The horizontal bars show the mean longevity for both sexes. The boxes above the female bar show the duration of the pre- and postoviposition periods

on *S. tuberosum* and *S. nigrum* fertility reached a peak fairly early in the oviposition period and then declined, in some cases quite sharply, over the rest of the period. Fertility in *26-punctata* on *N. physalodes* and *D. stramonium* was too low for a definite pattern to emerge. In contrast, in *pardalis* after a slow start eggs were produced at a fairly constant rate throughout the greater part of the reproductive period (fig. 6B). Because of the variation in length of the preoviposition period, both intra- and interspecifically, Kendall's rank correlation coefficients τ were used to test whether females with shorter preoviposition periods completed oviposition earlier, and if they died earlier than those with a longer preoviposition period. Differences were significant ($p < 0.05$) only in *26-punctata* on *S. nigrum.* Here the female's age at first oviposition was significantly correlated with her age at final oviposition ($p < 0.01$), and with her age at death ($p < 0.05$).

The postoviposition period in *cucurbitae* was 3 times longer than the preoviposition period (fig. 4). That on *Cu. sativus* was shortest, being 0.66 the length on the other 2 food plants (table 1), and all differences were non-significant ($p > 0.05$, GT_2 test). In contrast, in *26-punctata* postoviposition was extremely short (3 days) on *S. tuberosum,* slightly longer on *S. nigrum* and *L. esculentum,* (7–8 days), 4 times longer on *D. stramonium* and double that again on *N. physalodes.* On the latter it was 56 days, about 20 times longer than on *S. tuberosum.* Differences in postoviposition periods between the 5 food plants were significant ($p < 0.01$) in only 2 cases – between *S. nigrum* and *N. physalodes,* and between *S. tuberosum* and *N. physalodes.* On *N. physalodes* and *D. stramonium* both pre- and postoviposition periods were of similar length (table 2; fig. 5, 6A). The latter was also true for ***pardalis*** and *S. **nigrum*** (table 3; fig. 6B). Postoviposition on *S. **nigrum*** was about 5 times longer in ***pardalis*** than in ***26-punctata.***

The intrinsic rate of natural increase r describes the growth potential of a population under given climatic and food conditions. Under a stable age distribution with the population still growing in an unlimited environment and using the $l_x m_x$ values obtained from table 4, r can be determined using the expression

$$e^{-r} l_x m_x = 1$$

(SOUTHWOOD 1978). For this both immature and adult stages are involved. In the 3 *Epilachna* species, the r value per individual/day was 0.08 in ***cucurbitae***, 0.04 in ***pardalis*** and between 0.02 and 0.06 in ***26-punctata*** depending on the food plant. It should be stressed that these conditions rarely occur naturally.

Another parameter, generation time T was obtained using the expression $T = \log R_0/r$ (SOUTHWOOD 1978). In ***cucurbitae*** it varied between 60.8 and 72.5 days on different food plants, being shortest on *C. **maxima*** and longest on *Cu. **sativus*** (table 1). In ***26-punctata*** it ranged between 92.4 and 145.7 days, being shorter on crop plants and *S. **nigrum*** and longer on other weeds (table 2). A generation took between 1.3 to twice as long as in ***cucurbitae.*** In ***pardalis*** a generation took 143 days on *S. **nigrum*** (table 3), about 1.5 times longer than in ***26-punctata*** on the same food plant, due to a much longer oviposition period. It was twice as long as in ***cucurbitae.***

4 Discussion

The food preference experiments reported here have demonstrated the influence of food plants on the development rate, fecundity and mortality of epilachnines when kept under conditions of constant temperature and photoperiod. They have shown that the preferred food of both ***26-punctata*** and ***pardalis*** is *S. **tuberosum,*** while that of ***cucurbitae*** is *C. **pepo.*** These plants have promoted accelerated rates of development, highest egg production and, in the solanivorous species, lowest levels of mortality. Both ***26-punctata*** and ***pardalis*** have demonstrated their ability to survive for long periods of time on an alternative diet of solanaceous weeds, even though this has led to retarded growth, very low levels of fecundity and high mortality. Similar trials using cucurbitaceous weeds were not carried out on ***cucurbitae,*** although it is known to feed on the South African paddy melon *(Cucumis myriocarpus).*

Comparative trials using the same solanaceous food plants, *S. **nigrum*** and *S. **tuberosum*** have given a faster development rate in ***pardalis*** than in ***26-punctata.*** Although maturation of gonads is slower in ***pardalis,*** the oviposition period is almost double that in ***26-punctata*** and fecundity and egg hatch are correspondingly higher. Whilst r, the intrinsic rate of natural increase per female/day, is lower in ***pardalis,*** it is again compensated for by the much longer oviposition period. On *S. **nigrum*** the reproductive rate per female is much higher in ***pardalis*** than in ***26-punctata.*** On *S. **tuberosum*** it is even higher in ***26-punctata,*** and it is expected that this could again be exceeded if experiments were carried out with *pardalis* on this food plant. Generation time T is a third longer in *pardalis*, but the potential for fewer generations per year is compensated for by the greater reproductive capacity of females, leading to the production of far more offspring per female over a much longer period. Based on these results, *pardalis* is the more successfvul species.

Irrespective of food plant, the development rate in *cucurbitae* is the fastest of the 3 species. As well, the preoviposition period and generation time T are the shortest. During the oviposition period more eggs are produced per day than in the solanivorous species, although over a shorter period. The rate of hatching is higher than in *26-punctata*, but not as high as in *pardalis*, and the fecundity is much lower than in the 2 solanivorous species. In spite of a higher mortality rate, *cucurbitae* has the potential to build up numbers of larvae and adults at a greater rate than either of the solanivorous species, as it has the highest intrinsic rate of natural increase per female/day. Thus it has the potential to produce more generations per year.

Ali and El-Saeady (1981) selected similar environmental conditions to those used here for studies on *E. elaterii*, and they also used *C. pepo* and *Cu. sativus* as 2 of their 4 trial food plants. Nakamura et al. (1984) carried out their experiments at temperatures ranging between 24 and 32 °C, with no information given on photoperiod. *Cucurbita* sp. was used as the food plant for *Epilachna* sp. "D", and bitter gourd *(Momordica charantia)* for *Epilachna* sp. "C".

The duration of developmental stages in *elaterii* (Ali and El-Saeady 1981) is similar to that in *cucurbitae*, but in the Sumatran species it is 2–3 days shorter (Nakamura et al. 1984), perhaps influenced by higher temperatures. Depending on food plant, total larval development in all 3 species is between 2–4 days shorter than in *cucurbitae*. Duration of pupal development in *cucurbitae* is midway between *elaterii* and the other 2 species. Development rates in the Mexican bean beetle (*E. varivestis* Mulsant) on beans [*Phaseolus vulgaris* (Papilionaceae)] (Kogan 1977) are comparable with those in *cucurbitae*.

In contrast, development rates in the 2 Australian solanivorous species are much longer and more variable, and are sharply at variance with studies on *28-punctata 28-punctata* in India and Japan. At 27 °C and a 12:12 h photoperiod, the latter's mean development rate on brinjal *(S. melangena)* and several solanaceous weeds (Sachan and Rathore 1979) is strangely only 0.58 that in *28-punctata pardalis* and *26-punctata*, and about 0.76 that in the 4 cucurbitophagous species; while at 24–27 °C and a 16:8 h photoperiod, its rate on *S. tuberosum* (Kono 1979) is unchanged. Even allowing for higher temperatures and in one case a longer photoperiod, the discrepancy in results between the 2 subspecies using the same food is quite remarkable.

The claim by Nakamura et al. (1984) that there was no mortality in the immature stages of the 2 Sumatran species during the experimental period is in direct contradiction to the results of Ali and El-Saeady (1981) and it cannot be substantiated here. The total immature mortality rate per day on all food plants averaged 0.017 in *elaterii* (Ali and El-Saeady 1981), 0.026 in *cucurbitae*, 0.014 in *26-punctata* and 0.009 in *pardalis*. Larval real mortality in almost all cases was higher than pupal mortality, but using the daily rate this was reversed. Further, the species of food plant on which the larvae were reared directly influenced the level of mortality.

The length of the preoviposition period in epilachnines is influenced by the family of plants on which they feed, and to a lesser extent by particular plant species within the family. Those beetles feeding on Cucurbitaceae require a comparatively short period for maturation of the gonads and, in most cases, different plant species have little influence on this. In *cucurbitae* on 3 plant species it averages 10.9 days; in *elaterii* on 4 plant species 11.4 days (Ali and El-Saeady 1981), in *Epilachna* sp. "D" 15.5 days and in *Epilachna* sp. "C" 18.9 days (Nakamura et al. 1984), giving a mean for all 4 species of 14.2 days. A similar period of 12.5 days occurs in *varivestis* on Papilionaceae (Bernhardt and Shepard 1978; Kogan 1977). Australian epilachnines feeding on Solanaceae require a much longer preoviposition period and there is much greater variation depending on the plant species. In *26-punctata* on 5 plant species it averages 33.3 days, while in *pardalis* on *S. nigrum* it is 31.2 days, giving a mean for the 2 species of 32.3 days, more than double that in the cucurbitophagous species and almost triple that in the papilionivorous species. These results on Solanaceae are again at marked variance with findings by Kono (1979, 1982) and Sachan and Rathore (1979) for *28-punctata 28-punctata*, both reporting a preoviposition period of about 11 days.

The length of the oviposition period is influenced by specific plant species rather than by a particular plant family, indicating that selection of the correct food plant is of prime importance to a gravid female. Oviposition is highest on preferred food plants and lowest on those weeds regarded as alternative food. In *cucurbitae, Epilachna* spp. "C" and "D", (NAKAMURA et al. 1984), *26-punctata, 28-punctata 28-punctata* (SACHAN and RATHORE 1979), and *varivestis* (BERNHARDT and SHEPARD 1978) the oviposition period ranges between 33 and 76 days on different food plants, averaging about 50 days. The exception is *pardalis* with a period averaging 128 days.

The duration of the postoviposition period is very variable both inter- and intraspecifically, and, in most cases, appears to be independent of plant species. Provided food is plentiful, it has little effect on larval survival.

Irrespective of food plant, adults in all 3 species of Australian epilachnines live longer than their relatives from other parts of the world. The adult female life span in *cucurbitae* and *26-punctata* is approximately 1.5 times that in *varivestis* (BERNHARDT and SHEPARD 1978), *Epilachna* spp. "C" and "D" (NAKAMURA et al. 1984) and *28-punctata 28-punctata* (SACHAN and RATHORE 1979), while in *pardalis* it is about 2.5 times longer than in *28-punctata 28-punctata*, and approximately 3 times longer than in the other 3 species. Similarly *pardalis* and *26-punctata* males live about 1.5 times longer than those in *Epilachna* sp. "D" and *28-punctata 28-punctata*, and twice as long as those in *Epilachna* sp. "C", while *cucurbitae* males live slightly longer than those in *Epilachna* sp. "D" and *28-punctata 28-punctata*, and about 1.5 times longer than those in *Epilachna* sp. "C". The discrepancy in length between *28-punctata 28-punctata* and its subspecies *pardalis* is quite remarkable. With the exception of *pardalis*, males in all these species live longer than females.

Again, irrespective of food plant, fecundity in Australian epilachnines is higher than in related species in other parts of the world, with crop feeding solanivorous species having a higher egg production than cucurbitophagous species. The highest recorded fecundity (2882 eggs) and highest mean fecundity (1692 eggs) occurs in *pardalis* on *S. nigrum*. In *28-punctata 28-punctata* (SACHAN and RATHORE 1979) the highest fecundity and highest mean fecundity are both only about 0.25 that in *pardalis*. Amongst the cucurbitophagous species, the highest fecundity (2300 eggs) and highest mean fecundity (1145 eggs) occurs in *cucurbitae* on *Cu. sativus* and *C. pepo* respectively. In *elaterii* (ALI and EL-SAEADY 1981) the mean fecundity is only 0.16 and 0.2 of that in *cucurbitae* on the same food plants. In the Sumatran species (NAKAMURA et al. 1984), mean fecundity levels are close to those in *cucurbitae* on *C. maxima* and *Cu. sativus*, but 0.6 those in *cucurbitae* on *C. pepo*. Their highest fecundity is only half that in *cucurbitae*. Mean fecundity in the papilionivorous *varivestis* (BERNHARDT und SHEPARD 1978) is about 0.5 that in the Sumatran species and *cucurbitae* on *C. maxima* and *C. pepo*. It is just under 0.25 that in *cucurbitae* on *Cu. sativus* and *26-punctata* on *S. tuberosum*, and a little over 0.25 that in *pardalis* on *S. nigrum*.

Although variable, the intrinsic rate of natural increase in Australian epilachnines is approximately half that in the Sumatran species (NAKAMURA et al. 1984). This can be explained in part at least by NAKAMURA ignoring natural mortality in his specimens. As a result, his calculations of R_0 and r have become inflated causing his estimation of generation time T to be artificially low and therefore not comparable with results obtained for the Australian species.

Many insects living in temperate regions have a marked peak in their age specific fertility curves near the beginning of their reproductive period, while those living in tropical environments have a more prolonged reproductive period with a less conspicuous peak, a smaller total egg production and a lower value of r (BIRCH et al. 1963; LANDAHL and ROOT 1969; PEFEROEN et al. 1981; ZALUCKI 1981). While admitting that up till then no studies had been carried out on development rates, fecundity and fertility schedules on related epilachnines under laboratory conditions, NAKAMURA et al. (1984) suggested that the prolonged reproductive periods in the 2 Sumatran species had an adaptive value for living in tropical environments where they claimed Cucurbitaceae are available throughout the year. In the Australian species, *cucurbitae* and *26-punctata* conform to a typical temperate reproductive pattern (fig. 4, 5, 6), while *pardalis* has a prolonged tropical reproductive pattern (fig. 6), except that the reproductive period is 2.5 times longer than in the Sumatran species, and egg production is the highest yet recorded.

As the Australian species were studied under identical conditions, variations in temperature and day length cannot explain the different reproductive patterns and nor can food, for *pardalis* and *26-punctata* were both fed on *S. nigrum* throughout the experiment. Comparison of the distribution of the 3 species suggests that the differences may be genetic: *pardalis* is widespread throughout tropical areas from south-east Asia to Oceania, and extends from tropical into temperate Australia, while *26-punctata* is confined to temperate eastern Australia (RICHARDS 1983). The continuous availability within Australia of solanaceous crops and weeds, indigenous and introduced, must be a major factor influencing the ability of the 2 species to survive for long periods, as it reduces the need for rapid maturation of the gonads and allows prolonged reproductive periods, while also promoting high fecundity. Alternative food can support the species for long periods when preferred food is not available, encouraging adult longevity. As crops are affected by seasonality in more temperate regions, this may explain the pronounced early peak in the fertility curve of *26-punctata*.

Unlike the other 2 species, *cucurbitae* is very widely distributed throughout most of Australia (RICHARDS 1983), showing it is the most adapted to the Australian environment. Although there are very few endemic Cucurbitaceae, there are many native and introduced species, particularly in the more arid parts of the continent. Nevertheless the marked seasonality and unreliablity of food in many areas must influence the behaviour of *cucurbitae*. This could explain the rapid maturation of its gonads, its temperate reproductive pattern, and its winter diapause (RICHARDS, in prep.).

While Australian cucurbitophagous epilachnines have a development rate, preoviposition and oviposition periods similar to related species in other parts of the world, their postreproductive period is much longer leading to a longer adult life span. Their most distinctive characteristics are their higher fecundity and temperate reproductive pattern. In contrast, Australian solanivorous species exhibit many differences. Of all epilachnine species studied, they have the slowest known development rate and the longest preoviposition, oviposition and postoviposition periods, leading to the longest total life span. Although slow to mature, they have the highest recorded fecundity. Unfortunately there is no reliable information for epilachnine species outside Australia on the net reproductive rate, the intrinsic rate of natural increase per female per day, or generation time to act as a guide in assessing the performance of Australian species. Of particular interest would be studies on the development, fecundity and fertility schedules of other solanivorous species.

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Zusammenfassung

Zum Einfluß von Feldfrüchten und Unkräutern auf die Bionomie der Schädlinge des Epilachna-vigintioctopunctata-Komplexes

Fütterungsexperimente mit 3 Unterarten von *Epilachna vigintioctopuncata* zeigen, daß Zucchinis *(Cucurbita pepo)* das bevorzugte Futter des Zucchinischädlings *E. cucurbitae* Richards, während Kartoffeln *(Solanum tuberosum)* das bevorzugte Futter der beiden Kartoffelschädlinge *E. vigintisex-*

punctata vigintisexpunctata (Boisduval) und *E. vigintioctopunctata pardalis* (Boisduval) sind. *E. vigintisexpunctata vigintisexpunctata* kann eine lange Zeit von Unkraut leben, oft mit verminderter Fruchtbarkeit. Bei allen 3 *Epilachna*-Arten wird die Zeitdauer vor der Eiablage von den konsumierten Pflanzenfamilien bestimmt, während die Länge der Eiablagephase von spezifischen Futterpflanzenarten bestimmt wird. Von allen 3 Arten hat *E. cucurbitae* die schnellste Entwicklung und auch die höchste Sterblichkeitsrate. *E. vigintioctopunctata pardalis* ist die erfolgreichere von den beiden Kartoffelschädlingen. *Epilachna cucurbitae* gleicht in der Entwicklung sowie in der Zeitdauer vor und während der Eiablage anderen Arten außerhalb Australiens, hat aber eine längere Lebenserwartung und eine größere Fruchtbarkeit. Die beiden australischen Kartoffelschädlinge zeigen unter allen untersuchten *Epilachna*-Arten die langsamste Entwicklung, die längste Zeitspanne vor, während und nach der Eiablage, die längste Lebenserwartung und die größte Fruchtbarkeit.

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