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Trophic influences on survival, development and reproduction of *Hyperaspis notata* (Col., Coccinellidae)

B. Stäubli Dreyer[1], P. Neuenschwander[2], J. Baumgärtner[3] and S. Dorn[1]
[1]Institute of Plant Sciences, Applied Entomology (ETH-Zentrum), Zürich, Switzerland; [2]Plant Health Management Division, International Institute of Tropical Agriculture (IITA), Bénin, Cotonou, République du Bénin; [3]current address: Institute of Insect Physiology and Ecology, Nairobi, Kenya

Abstract: The coccinellid, *Hyperaspis notata* Mulsant, is associated with the mealybugs *Phenacoccus manihoti* Mat.-Ferr. and *P. herreni* Williams, on cassava in southern Brazil and the highlands of Colombia. Brought to Africa to help control the accidentally introduced *P. manihoti*, its range of target prey and plant food sources as well as its performance under conditions of food scarcity were investigated in the laboratory. *H. notata* showed a moderately narrow food spectrum which should allow survival in periods when *P. manihoti* is scarce without threatening a broad range of insects species: *H. notata* survived, completed larval development and reproduced on *P. madeirensis* (Green) and *Ferrisia virgata* (Cockerell), which are alternate prey species of the family Pseudococcidae and occur abundantly in cassava fields and on ornamental plants in southern Benin. By contrast, development was not possible on less related taxa of the Sternorrhyncha, namely on *Aphis craccivora* Koch which occur on cowpea often intercropped with cassava and on the spiralling white fly *Aleurodicus dispersus* Russel infesting cassava, and many other food crops and ornamental plants. These alternate food sources allowed survival of the larvae and adults for a limited period only and neither moulting nor egg production were observed. Cassava pollen was unsuitable as a food source since it did not allow larvae to develop, females to oviposit, nor did it extend longevity of larvae and adults. Honey prolonged the life span of adults without allowing egg production, and is thus a suitable food substitute for adult *H. notata* during shipment to release destinations. The coccinellid larvae completed their development to the adult stage when fed from a range of *ad libitum* supply (consuming up to 6 mg per day) of cassava mealybugs to a minimal daily amount of 1 mg (consuming only ≈0.8 mg per day). Females even laid eggs when fed with a minimal amount of 1.2 mg per couple and day. Larvae of the Colombian strain gained more weight before pupation, and the tolerance of larvae and adults to starving was more marked than in the Brazilian strain.

1 Introduction

The cassava mealybug, *Phenacoccus manihoti* Matile-Ferrero (Hom., Sternorrhyncha, Pseudococcidae), is a dry season pest on cassava in Africa. Since the introduction of the exotic parasitoid, *Apoanogyrus* (*Epidinocarsis*) *lopezi* De Santis (Hym., Encyrtidae), population peaks are much reduced and occur at irregular intervals, most often towards the end of the dry or at the beginning of the rainy season (HAMMOND and NEUENSCHWANDER, 1990). During the long rainy season, the natural enemies are then challenged with a period of scarcity of their preferred prey (SCHULTHESS et al., 1991).

Hyperaspis notata Mulsant (Col., Coccinellidae), an exotic predator of *P. manihoti* from South America has been introduced to complement *A. lopezi* in the control of the cassava mealybug and is now established locally in East Africa (HERREN and NEUENSCHWANDER, 1991; NEUENSCHWANDER and ZWEIGERT, 1994).

Among the many empirically desirable characteristics of natural enemies, a narrow host range is considered advantageous (MESSENGER et al., 1976). Food selectivity, acquisition and conversion are important in the interpretation of the dynamics of interactions between predator populations and their prey (BEDDINGTON et al., 1976; HASSELL et al., 1976). Little information is, however, available on the host range of *H. notata* and its response to different host stages or to food scarcity.

The first purpose of this study is the evaluation of the host ranges of *H. notata* of two origins, Brazil and Colombia. Three pseudococcids, *Phenacoccus manihoti* Mat.-Ferr., *P. madeirensis* (Green) and *Ferrisia virgata* (Cockerell), as well as *Aphis craccivora* Koch (Hom., Sternorrhyncha, Aphididae) and *Aleurodicus dispersus* Russel (Hom., Sternorrhyncha, Aleurodidae) were tested for their suitability as prey for *H. notata*; honey and pollen were used as alternative food sources. These different food sources were selected for the following reasons: *P. manihoti*, the main prey of *H. notata* in Brazil, *P. madeirensis*, belonging to the same genus, and *F. virgata* are three representatives of the Pseudococcidae commonly found in cassava fields as well as on ornamentals throughout Africa. Since some species of coccinellids can prey on aphids as well as on mealybugs (DREA and GORDON, 1990), *A. craccivora,*

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the common aphid on cowpea (*Vigna unguiculata*, Walp.), often intercropped with cassava, was also tested. Recently, the spiralling whitefly, *A. dispersus*, was introduced accidentally into Nigeria and southern Benin, Togo and Ghana (AKINLOSOTU et al., 1993) where it attacks, among other crops, cassava. In Hawaii the coccinellid *Nephaspis amnicola* Wingo was established for the control of *A. dispersus* (KUMASHIRO et al., 1983). Thus, *A. dispersus* was considered as a possible alternate prey for *H. notata* and included into this suitability study. Pollen of plants was found in the guts of the coccinellid *Adalia bipunctata* (L.) (HEMPTINNE and DESPRETS, 1984). Therefore, cassava pollen was tested as an alternative food source, together with honey as a potential food substitute for *H. notata* when they are shipped to their release sites.

The second purpose of this study is the assessment of the response to food restriction. Larvae of coccinellids respond by lengthening their developmental time or by pupating at a lower weight, though with higher mortality, as was observed, e.g. in *Adalia bipunctata* (L.) (DIXON, 1970). In addition, prey density influences the predator's fecundity and thus its population dynamics (BEDDINGTON et al., 1976).

2 Material and methods

2.1 Rearing of the predator

H. notata (Brazilian origin = BB and Colombian origin = CC) was reared in the insectary at 27°C ± 2°C on *P. manihoti* on potted cassava plants. The plants were kept in wooden cages (44 cm × 45 cm × 58 cm) with fine screen sides and glass tops. Cohorts of *H. notata* BB and *H. notata* CC were obtained by rearing the larvae from daily laid egg batches on an unlimited food supply in a Petri dish. Freshly emerged larvae and adults were used for the experiments carried out in incubators at 25 ± 1°C and 70–90% RH.

2.2 Preference for and suitability of different food sources

Seven different food sources were offered in Petri dishes to *H. notata* of both origins BB and CC: (1) *P. manihoti*; (2) *P. madeirensis*; (3) *F. virgata* (all reared on potted cassava); (4) the spiralling whitefly, *A. dispersus*, collected in the field from different host plants; (5) *A. craccivora* reared on cowpea; (6) pollen of cassava flowers, collected in the field; and (7) pure honey. The food supply was offered *ad libitum*.

Freshly hatched first instar larvae (L1) and newly emerged adults of *H. notata* of both origins were fed with one of the above mentioned prey or food sources. Larvae were observed daily for survival time and moulting, adults for egg deposition. Dead individuals were removed. Since *H. notata* adults usually live for a long period of time (up to 425 days at 25°C, B. STÄUBLI DREYER, unpubl. data) longevity could not be assessed and preoviposition time was recorded instead. All experiments were replicated 10 times, every replicate representing data from one *H. notata* individual.

The data were subjected to an analysis of variance evaluating the main effect and all possible interactions, followed by a *t*-test according to Tukey for mean separation.

In an additional experiment, pairwise-choice test were performed to assess the predator's preference for one of the two prey stages, ovisacs or L3. A liberal amount of cassava mealybug ovisacs and L3 was weighed on small pieces of aluminium foil. The two food sources were placed into a Petri dish on the same piece of aluminium foil and an individual L2 or L4 of either *H. notata* BB or CC was added. After 24 h the remaining cassava mealybug ovisacs and L3 were weighed. The proportion of ovisacs in the diet was calculated. Ten replicates were carried out for each of the four combinations.

2.3 Consumption of different instars of *Phenacoccus manihoti* by different predator stages

For the no-choice experiment, liberal amounts of cassava mealybug ovisacs, first instar crawlers, third instar larvae, or adults were weighed on small pieces of aluminium foil on a Mettler balance UM3 (± 0.003 mg) and subsequently transferred to a Petri dish. Cassava mealybug crawlers were offered a cassava petiole, the other prey instars did not receive a plant support. One individual of each of the different stages of either *H. notata* BB or CC was introduced into the Petri dish, which was then sealed with Parafilm® to prevent the prey from escaping. After 24 h, larvae and adults of *H. notata* were removed and the remaining cassava mealybugs weighed.

For calibration purposes, cassava mealybug ovisacs were weighed, dried at 105°C for 3 h, and then weighed again. Percentage dry weight was also calculated for crawlers, L3 and non-ovipositing females of the prey, in 15 replicates. The consumption of the different prey stages by the different *H. notata* instars could thus be expressed as dry matter.

An analysis of variance was carried out, followed by a *t*-test according to Tukey for mean separation.

2.4 The effect of *Phenacoccus manihoti* density on larval growth and development of *Hyperaspis notata*

The following amounts of cassava mealybug ovisacs, expressed as fresh weight, were daily offered to a freshly hatched first instar larvae of either *H. notata* BB or *H. notata* CC: 1.0, 1.5, 2.0, 2.5, or 3.0 mg. In addition, food was offered *ad libitum* (at least 7 mg per day) in one treatment. The ovisacs were first weighed alone on a Mettler balance UM3 (± 0.003 mg) on a small piece of aluminium foil of known weight and then together with the larvae. This set-up (larva + ovisac(s) on foil) was kept in a Petri dish for 24 h at 25 ± 1°C and then weighed again. The larva was then removed and the weight of the foil plus the residual ovisacs recorded. This procedure was repeated until the larva had developed to the prepupal stage, defined in this study by complete cessation of feeding.

For each experimental group, developmental times, daily consumption, and larval mortality were observed. The wet weight as a function of the age (in hours) was described by:

$$W = \frac{a}{1 + e^{(b-cx)}} \qquad [1]$$

where W is the larval wet weight (in mg) at the age x (in hours), and *a*, *b* and *c* are parameters to be estimated. The parameters defining the curve for the *ad libitum* feeding regimes were compared by introducing a dummy variable for each parameter to separate the effect of the origins. The asymptotic confidential interval indicated whether the parameters were significantly different or not. For all other regimes means were used to estimate the parameters by the least square method implemented in the SPSS soft-ware package.

2.5 The effect of *Phenacoccus manihoti* density on oviposition of *Hyperaspis notata*

During an experimental period of 11 days, 1.2, 1.4, 1.7, 2.0 or 2.8 mg cassava mealybug ovisacs were placed every day into a Petri dish containing an about eight-week-old female and a male of *H. notata* BB or CC, held at 25 ± 1°C. The eggs laid per female were counted daily and cumulated. The experiment

Table 1. *Mean development time in days from freshly emerged first instar larvae up to adult emergence and mean preoviposition time of freshly emerged females of* Hyperaspis notata *of two origins on different food sources at 25°C. Ten replicates for each food source and origin*

Food source	Mean development time		Mean preoviposition time	
	Origin			
	Brazil	Colombia	Brazil	Colombia
Phenacoccus manihoti	32.5 a	33.0 a	8.1 c	8.4 ce
Phenacoccus madeirensis	34.3 a	28.0 b	20.4 d	11.3 e
Ferrisia virgata	28.5 ab	28.0 b	8.3 ce	11.2 ce

Means of both columns followed by the same letter do not differ at P = 0.05; $\sqrt[2]{MSE} = 3.217$ for the mean development time; $\sqrt[2]{MSE} = 3.018$ for the mean preoviposition time.

was carried out in 10 replicates. The mean numbers of eggs laid by females for each origin under different regimes was tested separately according to a two-way factor analysis of variance followed by a Tukey test separating the mean number of eggs laid at the different food regimes.

3 Results and discussion

3.1 Preference for and suitability of different food sources

3.1.1 Larval development and longevity on different food sources

Complete larval development of *H. notata* was only possible on *P. manihoti* and the two other mealybug species, *P. madeirensis* and *F. virgata*, but not on the aphid, *A. craccivora* or on the spiralling whitefly, *A. dispersus* (tables 1, 2). Thus, only closely related Sternorrhyncha, namely mealybugs, were found to serve as alternative prey. The survival of the freshly hatched coccinellid larvae to the pupal moult decreased from 76 and 82% for BB and CC, respectively, when feeding on *P. manihoti* to 60% for the larvae of both origins when these were fed P. *madeirensis* and still further to 20 and 50% for BB and CC larvae, respectively, when feeding on *F. virgata*. Survival times were very short on those food sources on which no moulting was observed (table 2). The shortest survival times were noticed on pollen or honey.

The strains of the different origins, BB and CC, showed very similar patterns regarding larval development and longevity on different the food sources tested in this experiment. Both strains developed faster on *F. virgata* than on *P. manihoti*, but this difference was only significant for strain CC (table 1). When feeding on *P. madeirensis*, BB larvae needed more time to complete their development than the CC larvae. This effect might be due to the fact that the supply with *P. madeirensis* for the larvae of *H. notata* BB was not always optimal, due to some problems with the rearing of this special prey. This may also explain the significant interaction (P = 0.05) found in the analysis of variance, but not reported here, between food source and origin. Survival of both strains was low on *F. virgata* but especially low in strain BB.

It was observed that many coccinellids fed on different prey species under laboratory conditions, but disperse when placed on the same hosts in the field (DREA and GORDON, 1990). Under laboratory conditions, even toxic prey may be consumed. BLACKMAN (1967) showed that larvae of *Adalia bipunctata* (L.) feed on *Megoura viciae* Buckt. even in the presence of their favourite prey *Acyrthosiphon pisum* Harris. The larvae of *A. bipunctata* feeding on *M. viciae* were able to moult, but this consumption then caused high larval mortality. The high mortality rate of *H. notata* feeding on *F. virgata* might indicate that this specific prey is suboptimal and would be generally avoided under field conditions, though it could be accepted as supplement.

Table 2. *Mean survival time in days from freshly hatched first instar larvae of* Hyperaspis notata *of two origins on different food sources on which no moulting was observed at 25°C, based on ten larvae each*

Food source	Origin	
	Brazil	Colombia
Aphis craccivora	4.6 a	4.2 ab
Aleurodicus dispersus	4.2 ab	3.4 ab
Pollen	1.8 b	2.5 ab
Honey	2.3 b	3.4 ab

Means of both columns followed by the same letter do not differ at P = 0.05; $\sqrt[2]{MSE} = 1.855$

3.1.2 Adult longevity and preoviposition period on different food sources

Females of both origins were able to lay fertile eggs when preying on either *P. manihoti, P. madeirensis*, or *F. virgata*, but preovipositing periods varied (table 1). On *P. madeirensis*, the preoviposition period of the CC females was only half as long as that of the Brazilian females. This might be due to the fact that some problems occurred in the rearing of this special food source and the supply was not always unlimited, this may explain the significant interaction that showed up in the analysis of variance. Two CC females but no BB female laid eggs when feeding on *A. dispersus*.

Honey allowed *H. notata* adults to survive for at least one month at 25°C (table 3). In table 3, the food source 'honey' was excluded from the analysis of variance because the standard error of the mean was 10 times higher than the standard errors of the other means and were therefore compared with a *t*-test. On honey, males of both strains survived longer, but this was not sig-

Table 3. Mean survival time in days of adult females and males of Hyperaspis notata *of two origins on different food sources at 25°C, based on ten couples, each. For the analysis of variance the data for the food source 'honey' was excluded. The analysis of variance was done for each sex separately*

	Sex			
	Females		Males	
Food source	Brazil	Colombia	Brazil	Colombia
Honey	39.7	28.1	43.9	34.2
Aleurodicus dispersus	15.1 a	19.5 b	15.4	17.6 a
Aphis craccivora	9.4 c	10.5 c	8.9 b	8.7 b
Pollen	7.7 cd	9.8 c	7.7 b	6.2 b
No food	5.5 d	8.9 c	4.6 bc	6.4 b

Means of both columns followed by the same letter do not differ at $P = 0.05$; $\sqrt[2]{MSE} = 2.861$ for the mean survival time of the females; $\sqrt[2]{MSE} = 3.390$ for the mean survival time of the males.

nificant. For the other food sources, the mean survival times for females were tested separately from the ones of the males.

3.1.3 Preference for different host instars

The results of the pairwise choice experiments (third larval instar vs. ovisacs) are summarized in table 4. The proportion of the consumption of the second and fourth cassava mealybug instars indicate that, in general, more ovisac mass than L3 were consumed. Larvae of the fourth instar of CC origin, however, consumed more L3 than cassava mealybug ovisacs. Nevertheless, experiments with variable proportions of different prey stags are considered necessary to adequately analyse the preference.

3.1.4 Concluding remarks

P. manihoti, *P. madeirensis* and *F. virgata* occur on cassava throughout almost all of Africa and they appear nearly simultaneously in the fields. *P. manihoti*, the only species originating from South America, must be considered the main prey of *H. notata*. Assessments in cassava fields of the Congo showed that *P. manihoti* appeared between July and December (KIYINDOU et al., 1990). Thus, the predator *H. notata* must either find alternative food sources on cassava or on different plants in periods of low occurrence of *P. manihoti*. A suitable alternative prey is *F. virgata*, which also is found on ornamentals. As a food source for adult *H. notata*, it is nearly equivalent to *P. manihoti* under laboratory conditions. This is in contrast to what was found for *H. notata* larvae. Sternorrhyncha other than mealybugs proved unsatisfactory alternative prey.

This limitation in the range of hosts allowing reproduction is an asset for biological control. Certain other coccinellids such as *Coccinella septempunctata* L. are generalists with a wide host range (BLACKMANN, 1967). These species, when introduced, either feed on all available and suitable hosts or affect associated species including non-target species. They would thus pose a risk if released in a biological control program (HOWARTH, 1991). The relatively narrow range of *H. notata*, in contrast, still offers the possibility of exploiting alternative food sources, but probably does not endanger extended taxonomic groups of non-target insects.

Honey prolonged the life of adults. This validates the routine use of honey as food source during shipments of *H. notata* to the different release sites in Africa (HERREN and NEUENSCHWANDER, 1991; NEUENSCHWANDER and ZWEIGERT, 1994).

3.2 Consumption of different instars of *Phenacoccus manihoti* by different predator stages

The food consumption of various *H. notata* instars is shown in fig. 1. The daily consumption of cassava mealybug by fourth instars was much higher than that of the other larval instars or of the adults and concerned mainly eggs. Similarly, fourth instars of the coccinellids *Hyperaspis marmottani* Fairm. (UMEH, 1982), *H. raynevali* Mulsant, *Diomus hennesseyi* Fürsch and *Exochomus flaviventris* Mader (KANIKA-KIAMFU et al.,

Table 4. Mean consumption per day in mg wet weight [±SE] of cassava mealybug (CM) ovisacs and third instar larvae (L3) by Hyperaspis notata *originating from Brazil (BB) and Colombia (CC) with excessive supply of both prey stages at 25°C and the calculated proportion of ovisacs consumed*

	Predator instar			
	L2		L4	
Prey instar origin	BB	CC	BB	CC
CM ovisacs	0.4008 ± 0.0704	0.4874 ± 0.1016	2.4233 ± 0.4092	1.0028 ± 0.2966
CM L3	0.2743 ± 0.0604	0.3733 ± 0.0443	1.8899 ± 0.2994	1.3969 ± 0.2542
Proportion ovisacs consumed	0.5938	0.8897	0.5618	0.4179

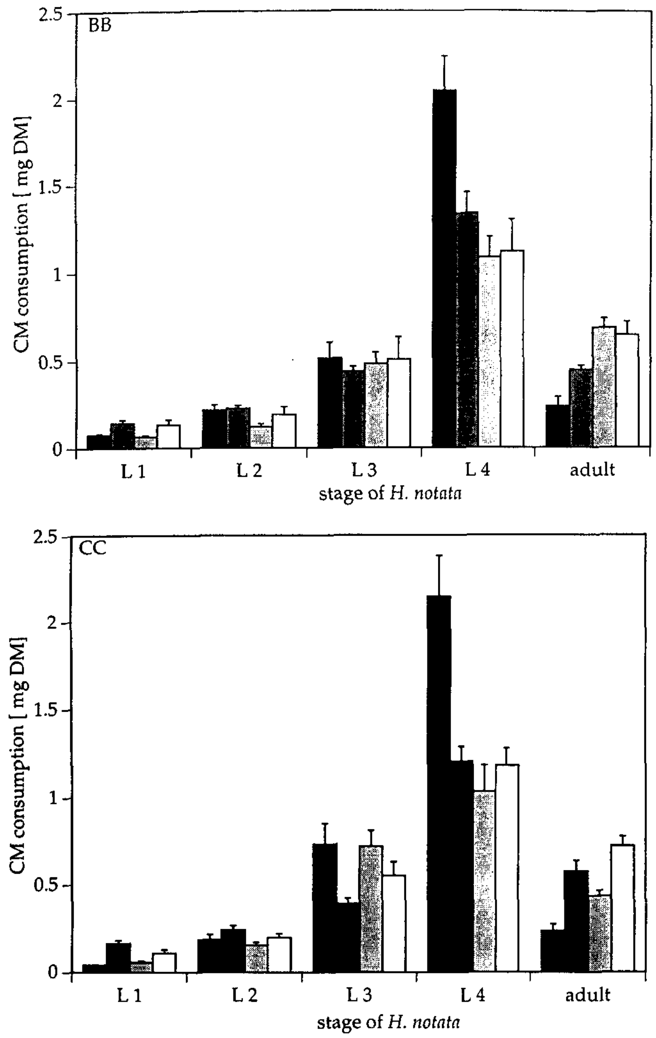

Fig. 1. *Consumption [in mg dry matter (DM), ± SE] of different cassava mealybug prey stages (■ CM eggs, ▩ CM crawlers, □ CM L3, □ CM adults) by four instars and by adults of* Hyperaspis notata *of Brazilian origin (BB) and of Colombian origin (CC) within 24 h at 25°C*

1992), and *Coccinella septempunctata* L. (ASGARI, 1966) also consumed the largest quantities of prey in comparison to the other predator stages. Interestingly, the first instar of *H. notata* fed on more cassava mealybug crawlers than on ovisacs. The egg chorion may be too hard and therefore difficult to handle for the young larvae. Adults, by contrast, consumed more young females than egg masses (fig. 1). Adults and third instar larvae of *H. notata* of both origins consumed about the same amount of prey in mg per day, but the larvae did not show any preference for a certain prey stage.

3.3 The effect of prey density on larvae

For all feeding regimes, the wet weight of the larvae of *H. notata* BB and CC was satisfactorily described by equation [1] (see fig. 2). *H. notata* CC gained more wet weight than BB. Comparison of the parameters *a*, *b* and *c* (table 5) for the case of the unlimited food supply showed that the parameter *a* for the curve of BB differed from that for CC. This indicates that the larvae of the Colombian strain grew heavier before pupation than the larvae of the Brazilian strain. However, parameter *b*, which describes the lag phase, i.e. the time needed to approach the maximum weight *a*, and parameter *c*, which controls the curve's ascent, were identical for BB and CC.

After 11 days, the means of the wet weight of BB larvae feeding on 1.5, 2.0 or 2.5 mg cassava mealybug ovisacs per day did not differ significantly from each other. For the CC larvae, the corresponding values were also similar at the supply levels of 2.0, 2.5 and 3.0 mg ovisacs per day (table 6a and b). In comparison to the lowest ovisac supply studied (i.e. 1.0 mg per day), the larvae of both origins fed *ad libitum* were about 2.5 times heavier when they pupated. It is noteworthy that larval development could be completed, even with the most restrictive feeding regimes of 1 mg ovisacs per day, which covered about 33% of the maximal food consumption at the surplus feeding method. Moreover, the larvae never consumed all ovisacs offered.

In this study mortality did not increase under low food supply. However, when less food was offered the larvae developed more slowly (table 7).

The total biomass of ovisacs consumed during the development of the larvae of *H. notata* BB and CC is summarized in table 6a and 6b. Fed *ad libitum*, BB and CC consumed 24.2 and 23.1 mg of ovisacs, respectively. HODEK et al., (1965) state that constant temperatures can inhibit the feeding capacity of coccinellids. Therefore the voracity of *H. notata* could be even greater under field conditions with variations in temperatures. The comparison of the daily consumption (table 6a and table 6b) and the daily weight gain according to eqn 1 indicates that a great proportion of food ingested is converted into body mass. This aspect will be discussed in a further study.

KANIKA-KIAMFU et al., (1992) describe the consumption of three different coccinellids preying on *P. manihoti*. *H. raynevali* (Mulsant) consumed 17.74 mg, *Diomus henneseyi* (Fürsch) 1.69 and *Exochomus flaviventris* (Mader) 71.82 mg of prey biomass during their development. Thus, the voracity of *H. notata* was only surpassed by *E. flaviventris*, which is a far bigger species.

3.4 The effect of prey density on oviposition

The food dependent oviposition by *H. notata* of both origins is shown in fig. 3. When feeding 1.2 mg per couple and day, oviposition of *H. notata* BB and CC was negligible. With 1.4 mg, CC females produced three times more eggs than the BB females; at the 2.8 mg level oviposition of CC females exceeded that of their BB counterpart by a factor 2. If the ratios between the numbers of eggs laid at the highest (2.8 mg) and the lowest (1.2 mg) amount of food offered are considered, the respective increments were 12-fold for BB and 28-fold for females of the CC strain. This is an interesting fact because the biomasses of the BB and CC females as well as the biomasses of the BB and CC eggs are virtually the same. We conjecture that the Brazilian and the Colombian strains may show differences in their egestion and conversion or prey exploitation rates.

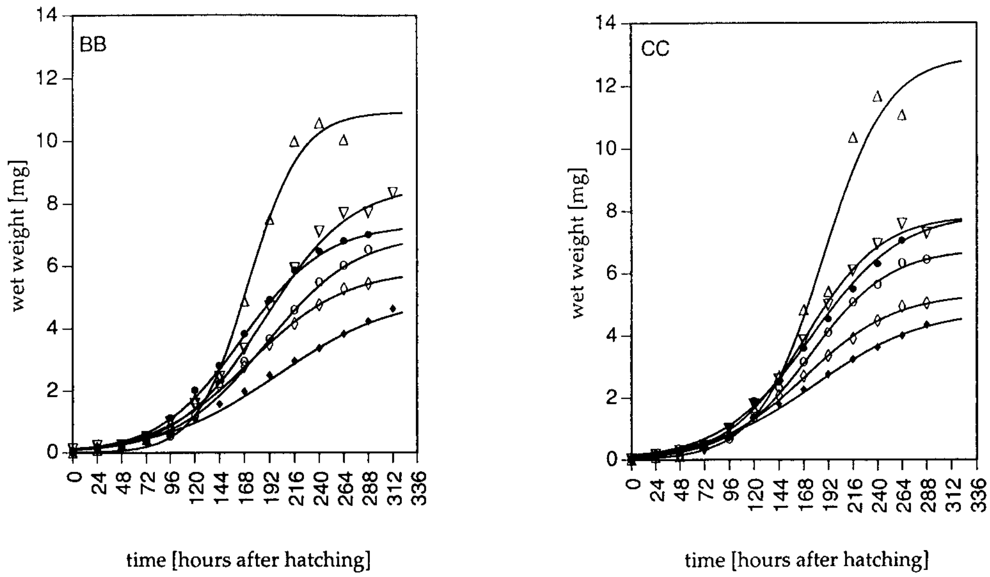

Fig. 2. Effect of prey density on age-specific cumulative wet weights of larvae of Hyperaspis notata *of Brazilian origin (BB) and of the Colombian origin (CC) as a function of various feeding regimes:* ◆ *1.0 mg,* ◇ *1.5 mg,* ○ *2.0 mg,* ● *2.5 mg,* ▽ *3.0 mg, and* △ *ad libitum per day*

Table 5. Effect of prey density on larval growth. Estimates of the parameters a, b *and* c *of equation 1 and the coefficient of determination* R^2*. The values relate to* Hyperaspis notata *of Brazilian origin (BB) and* Hyperaspis notata *of Colombian origin (CC) supplied with various amounts of prey. For statistical comparisons only the ad libitum data were used*

		Parameter			
		a	b	c	R^2
BB	1.0 mg/day	5.021	3.593	0.018	0.996
	1.5 mg/day	5.872	3.818	0.022	0.998
	2.0 mg/day	7.032	4.342	0.023	0.997
	2.5 mg/day	7.341	4.143	0.025	0.999
	3.0 mg/day	8.629	4.498	0.024	0.998
	ad libitum	10.939a	6.882a	0.040a	0.889
CC	1.0 mg/day	4.835	3.398	0.019	0.997
	1.5 mg/day	5.358	3.893	0.023	0.997
	2.0 mg/day	6.788	4.539	0.026	0.999
	2.5 mg/day	7.947	4.035	0.023	0.998
	3.0 mg/day	7.842	4.574	0.087	0.998
	ad libitum	13.293b	5.913a	0.031a	0.889

Means in one column followed by the same letter do not differ at the P = 0.05 level.

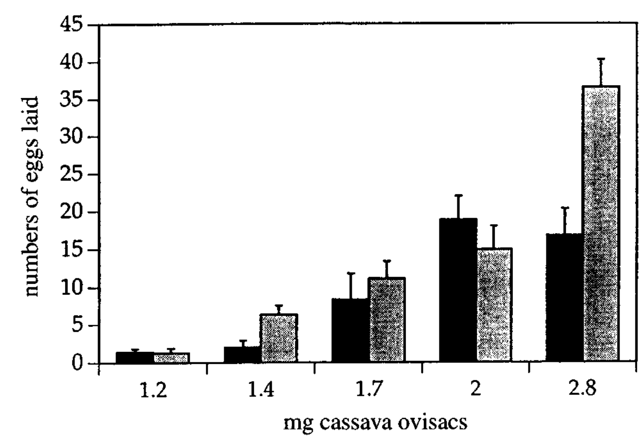

Fig. 3. The effect of prey density on oviposition. The columns represent the mean total number (± SE) of eggs laid per Hyperaspis notata *female (■ Brazilian origin and ▒ Colombian origin) at the indicated daily food supply levels [mg cassava mealybug ovisacs] offered to each couple of* H. notata *during 11 days*

4 Conclusion

A prey can be regarded as essential if it allows completion of the larval development and oviposition (Hodek, 1973). Since *P. manihoti, P. madeirensis* and *F. virgata* allow the larvae of *H. notata* to complete their development and the females to produce eggs, all three species are considered to be essential prey for *H. notata*. These insects occur on ornamentals as well as on cassava in Benin. *P. madeirensis* and *F. virgata* could serve as alternative food sources, provided they can be found efficiently. *A. dispersus* by contrast did not allow completion of larval development nor full egg production, although it prolonged the lives of larvae and adults. *A. craccivora*, however, prolonged only the life span of adult *H. notata*. Thus, *A. dispersus* and *A. craccivora* can be useful substitutes to bridge limited periods of food shortage. Honey increases the longevity of *H. notata* and is thus useful as an additive for shipments of adult *H. notata* for planned mass release. Pollen, finally, did not even prolong the life of *H. notata* adults; it is therefore doubtful whether the predator consumed it at all. The present laboratory studies with *H. notata* originating from two ecologically different zones aimed at evaluating *H. notata* as a model predator for controlling *P. manihoti*. Larvae of the CC strain gained

Table 6a. *The effect of prey density on the daily consumption in mg wet weight of different amounts of cassava mealybug ovisacs of the Brazilian strain of* Hyperaspis notata *larvae*

Hours after hatching	Daily food supply in mg 1.0	1.5	2.0	2.5	3.0	*ad libitum*
24	0.1604	0.1820	0.2526	0.3061	0.4550	0.1698
48	0.1644	0.1115	0.1451	0.2900	0.1706	0.2230
72	0.2781	0.4207	0.3539	0.4501	0.5490	0.4110
96	0.4352	0.5553	0.5991	0.7700	0.6882	0.6320
120	0.7041	1.0943	0.9590	1.4726	1.0320	1.3751
144	0.7733	1.0419	1.3208	1.4398	1.5123	1.5074
168	0.7163	1.2242	1.3114	1.8770	1.6817	4.3136
192	0.7447	1.2130	1.4523	1.7535	2.2609	5.4401
216	0.7807	1.1802	1.6140	1.7473	2.3690	5.9869
240	0.7794	1.2017	1.4050	1.6458	2.4438	3.0935
264	0.8253	1.1293	1.3028	1.2149	1.6291	1.0514
288	0.7817	0.6938	1.1891	0.7848	0.9706	1.1615
312	0.7976					
Total	7.9411	10.0477	11.9052	13.7518	16.9236	24.2038
Residual not consumed	5.0589	7.9523	12.0948	16.2482	22.0764	
Total consumption as % of total supply	61.1	55.8	49.6	45.8	43.4	
Total consumption as % of total consumption with ad libitum feeding	32.8	41.5	49.2	56.8	70.0	(100.0)

Table 6b. *The effect of prey density on the daily consumption in mg wet weight of different amounts of cassava mealybug ovisacs of the Colombian strain of* Hyperaspis notata *larvae*

Hours after hatching	Daily food supply in mg 1.0	1.5	2.0	2.5	3.0	ad libitum
24	0.1511	0.1994	0.1626	0.4648	0.3130	0.1195
48	0.1963	0.0833	0.2987	0.1978	0.2906	0.1219
72	0.3727	0.3070	0.3539	0.4255	0.3494	0.4439
96	0.4593	0.6128	0.5207	0.7214	0.7806	0.5480
120	0.6542	1.0184	0.9211	1.4508	1.3043	1.3589
144	0.7412	0.9894	1.4304	1.1239	1.3613	1.5854
168	0.7471	1.0978	1.4535	1.8048	2.1875	4.0937
192	0.7697	1.1530	1.4458	1.7658	2.2975	3.1528
216	0.7207	1.1344	1.5377	1.6722	2.1372	6.2947
240	0.8044	1.1662	1.3327	1.6988	2.1855	4.8429
264	0.7411	1.0098	1.2663	1.9054	1.8639	0.5418
288	0.7064	0.7091	0.6940	0.7454	0.7712	
312	0.6377					
Total	7.7091	9.4805	11.4172	13.9766	15.8419	23.1034
Residual not consumed	5.2909	8.5195	12.5828	16.0234	20.1581	
Total consumption as % of total supply	59.3	52.7	47.6	46.6	44.0	
Total consumption as % of total consumption with ad libitum feeding	33.3	41.0	49.4	60.4	68.6	(100.0)

Table 7. Mean developmental times in days of ten larvae of Hyperaspis notata *of two different origins (Brazil, Colombia) given different amounts of cassava mealybug ovisacs per day*

Food quantity [mg per day]	Origin Brazil	Colombia
ad libitum	10.1 a	10.1 a
3.0	11.1 a	11.2 a
2.5	11.2 a	11.3 a
2.0	11.5 a	11.3 a
1.5	11.7 a	11.7 a
1.0	14.7 b	14.1 b

Means of both columns followed by the same letter do not differ at $P = 0.05$; $F = 49.61$; $\sqrt[2]{MSE} = 0.6594$.

more weight before pupation, and the tolerance of larvae and adults to starving was more marked.

BUFFONI et al. (1995) demonstrated that physiological and behavioural parameters permit the coexistence of predator and prey and affect the stability of the acarine system. The results of these experiments on prey range, food selection, acquisition and conversion by larvae and adults of *H. notata* are considered necessary but not sufficient to predict the dynamics of the interaction in the predator-prey system. To meet this objective further studies in the field and in the laboratory are required.

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Author's address: Prof. Dr S DORN (corresponding author), Institute of Plant Science, Division of Phytomedicine, ETH-Zentrum, CH-8092 Zürich, Switzerland