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THE EFFECT OF PREY SPECIES ON SELECTED FITNESS ATTRIBUTES OF *Nephaspis bicolor* (COLEOPTERA: COCCINELLIDAE), A PREDATOR OF ALEYRODIDAE

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Abstract: Laboratory studies were carried out to assess the effects of feeding on different prey species either individually or in a sequential combination, on the development, survival and reproduction of *Nephaspis bicolor* Gordon (Coleoptera: Coccinellidae). Three species of Aleyrodidae were used as prey, two from the subfamily Aleurodicinae (*Aleurodicus cocois* Curtis and *Aleurodicus pulvinatus* Maskell on coconut and seagrape, respectively), and one from the subfamily Aleyrodinae (*Aleurothrixus floccosus* Maskell on guava). Based on development rate and the size of adults, *A. floccosus* was the most suitable prey for larvae. Prey species affected lifetime fecundity with beetles ovipositing significantly more eggs when fed *A. floccosus*. Rearing *N. bicolor* on *A. floccosus* and *A. cocois* produced the fittest adults in terms of population growth statistics. Prey substitution in larval stages did not affect survival or the duration of development. However, switching newly-emerged adults to a prey different from that fed on as larvae resulted in an increased preoviposition periods. Based on these data, it is concluded that the *N. bicolor* is adapted to utilize prey from both whitefly subfamilies and can readily switch between prey types in accordance with changes in their availability. Thus, any biological control programme that plans to introduce the coccinellid as a predator of Aleyrodidae needs to take this into consideration in the risk analysis / decision-making process.

Key words: Nephaspis bicolor, Aleurodicus cocois, Aleurodicus pulvinatus, Aleurothrixus floccosus, biology, prey species, prey switching

INTRODUCTION

During the last 2-3 decades of the twentieth century, several species belonging to *Aleurodicus* (Homoptera: Aleyrodidae) were expanding their distribution range, either via accidental introduction e.g. *A. dispersus* Russell (Anonymous, 1993), or via expansion of geographic area e.g. *A. dugesii* Cockerell and *A. pulvinatus* Maskell (Martin and Watson, 1998; Zolnerowich and Rose, 1996). *Aleurodicus* spp. are generally difficult to control because they are polyphagous on woody (tree) species, have a relatively short life cycle and, in the absence of natural enemies, become rapidly entrenched in new environments that are favourable (Kajita *et al.,* 1991). Hence classical biological control i.e. introduction of specific natural enemies from the pests' native range, is often the only long-term sustainable solution for their management.

Predators belonging to the genus *Nephaspis* (Coleoptera: Coccinellidae) are among the known natural enemies of Aleyrodidae, particularly *Aleurodicus* spp. (Cock, 1985; Lopez and Kairo, 2003). Two species, *N. bicolor* Gordon and *N. indus* Gordon, were successfully used during the 1980s for the biological control of the exotic *A. dispersus* in Hawaii and some Pacific countries

(Kumashiro *et al*., 1983; Suta and Esguerra, 1993; Tauili'-ili and Vargo, 1993). Since *Nephaspis* spp. were considered specific to Aleyrodidae (Gordon, 1985), they were potential candidates for introduction to control exotic Aleyrodidae, particularly *A. dispersus* which was rapidly spreading in Africa (M'Boob and van Oers, 1994) and Asia (Alam *et al.,* 1997; Mani and Krishnamoorthy, 1996; Wen *et al*., 1994). Australia was also on alert for its invasion (Lambkin, 1999).

Increased concerns regarding nontarget effects of introduced natural enemies have resulted in the requirement of a rigorous host range testing of arthropod natural enemies being considered in a classical biological control programme, so that their potential host/prey range in new environments and associated risks to nontarget species can be predicted (FAO, 2005). There is little information on the prey range of *Nephaspis* spp. and their potential for attacking nontarget species, except for a preliminary study in Hawaii (Yoshida and Mau, 1985). Since *Nephaspis* is native to Trinidad, studies on prey range, focusing on *N. bicolor*, were conducted at the Caribbean Regional Centre of CAB International. Field and laboratory investigations on the prey range of *N. bicolor* revealed that the coccinellid was indeed specific to Aleyrodidae, with a marked preference for wax-producing species (Lopez and Kairo, 2003). However, the suitability of various Aleyrodidae as prey of *N. bicolor* was not known. The study reported belwo was therefore undertaken to determine the impact of three Aleyrodidae on the biology of *N. bicolor*. The effect of prey switching on the biology of the coccinellid was also investigated.

MATERIALS AND METHODS

Two sets of studies were carried out in a controlled-temperature (CT) room, on the development and reproduction of *N. bicolor* using three whitefly species reared on their respective host plants: two Aleurodicinae - *Aleurodicus cocois* Curtis on coconut and *A. pulvinatus* on seagrape - and *Aleurothrixus floccosus* Maskell (Aleyrodinae) on guava. The first study compared suitability of the three aleyrodids as prey species of *N. bicolor* while the second study examined adaptability of the coccinellid when reared on one prey species and then transferred to the other two species.
Cultures of *A. cocois* were maintained outdoors under sleeve cages while *A. pulvinatus* and *A. floccosus* were cultured in CT rooms under mesh cages. Temperatures of 26±2° C and RH 60±10% were maintained in the CT rooms. Artificial lighting was provided in the form of 4-6 fluorescent bulbs and 2-4 incandescent bulbs suspended 20-30 cm above the cages. The lighting regime used was 12 h light and 12 h dark. Coconut plants with *A. cocois* were brought into the CT rooms for acclimatization at least 48 h prior to being used.

Prey suitability studies

For prey suitability studies, *N. bicolor* females reared for at least 3 generations on the respective whitefly species were used. In each case, 30-40 mated females reared on a whitefly host were released on the respective host plant to obtain eggs. On each host / host plant, the adults were allowed to oviposit for 12 h in order to obtain uniform-age eggs. The eggs were gently detached from the leaf with a fine paintbrush and placed individually on new leaf discs harbouring the same prey species. A total of 57 eggs were thus set up on coconut with *A. cocois*, 43 on seagrape with *A. pulvinatus* and 28 on guava with *A. floccosus* as prey. The leaf discs with the eggs were placed on moist filter paper in a 4-cm diameter petri dish and observed daily for egg-hatch. Development of *N. bicolor* larvae was followed through to adult stage. Observations were recorded daily on survival and moulting. Leaf discs were changed as required, ensuring an adequate supply of food at all times. Once pupae were formed, they were gently detached from the leaf and placed on a dry filter paper in the petri dish. The date of adult emergence and sex of the emerging adults were recorded. The following measurements were made: Egg and adult - length and width along the longest and widest part, respectively; Larval stages - width of the head capsule along the widest part; Pupa - width along the widest part.

To study reproductive biology, 20 newly-emerged adults (14 pairs for *A. pulvinatus*) obtained above were paired. Each pair was released in a 4-cm diameter petri dish with the respective whitefly species. Mortality was recorded daily and dead males were replaced with mature adults from laboratory cultures. Leaf discs were changed at three day intervals and the number of eggs oviposited were counted. The experiment was terminated when all the females were dead.

Adaptability studies

To study larval adaptability, about 50 uniform-age eggs oviposited on *A. cocois* by *N. bicolor* females (reared on this prey species for at least 3 generations) were used. The emerging larvae were fed on *A. cocois* until day 9 after oviposition. On day 10, thirty-two 1st instar larvae were used in setting up the experiment. Leaf discs with the three whitefly prey species on their respective host plant were each placed in 3-cm diameter petridishes. Larvae were transferred (one per petridish) as follows: 10 larvae on *A. cocois* and 11 each on *A. pulvinatus* and *A. floccosus*. All other details, including observations on size, were the same as described above for the experiment on prey suitability.

To study the adaptability of adults, pupae of *N. bicolor* were collected from a cohort that had been reared on *A. cocois* under CT Room conditions for at least 3 generations. Forty newly-emerged adults were paired and ten pairs each were transferred to leaf discs harbouring *A. pulvinatus* or *A. floccosus*, @ one pair per petridish and the oviposition was studied until all the females died. All other details were the same as described above for the prey suitability studies.

Data analysis

For both studies, standard errors and analysis of variance (ANOVA) were computed for all developmental and reproductive biology parameters. Paired t-tests were performed only where the F-ratio from the ANOVA showed significant differences. Data on female survival and egg production were used to compute life table parameters according to Birch (1948), as follows:

net reproductive rate = $\sum_{0}^{\infty} l_x m_x$; mean generation time GT = $\ln R_0/r_m$; intrinsic rate of increase

$r_m = \sum e^{-r_m x} l_x m_x = 1$; finite rate of increase $\lambda = e^{r_m}$, and doubling time DT = $\ln 2/r_m$.

RESULTS

Prey suitability studies

The means for the developmental period of different stages of *N. bicolor* on the three whitefly prey are summarized in Table 1 together with the results of the ANOVA. Egg incubation and duration of 1st and 2nd instars and prepupae were on par on the three species. Duration of development of 3rd and 4th instars was significantly shorter on *A. floccosus*. This was reflected in the total larval period and total duration of development, which were shorter by 3 and 2 days, respectively, on this prey (Table 1). Conversely, the pupal stage on *A. floccosus* lasted significantly longer (0.7 days). Males generally developed faster than females, except on *A. floccosus* where the duration of development for males and females was the same (20.3 days).

Table 1. Analysis of variance (ANOVA) for the duration of development (days ± SE) of various life stages of *N.bicolor* on three aleyrodid prey species

Life stage	A. cocois	N	A. pulvinatus	N	A. floccosus	N	F (F critical)	P
Egg	5.42±0.09	55	5.32±0.12	37	5.50±0.10	28	0.61 (3.07)	NS
1st instar	2.15±0.07	54	2.42±0.16	36	2.11±0.08	27	1.25 (3.08)	NS
2nd instar	2.39±0.18	54	2.19±0.15	36	1.88±0.11	27	1.93 (3.08)	NS
3rd instar	3.06±0.19**	52	3.00±0.26	34	1.72±0.12	25	10.11 (3.08)	9.45 E-05
4th instar	3.82±0.21**	51	3.70±0.34**	30	2.48±0.13	25	7.41 (3.08)	9.91 E-04
Total larval stage	11.39±0.32**	51	11.10±0.47**	30	8.24±0.19	25	19.3 (3.08)	7.79 E-08
Prepupa	1.65±0.11	48	1.55±0.14	29	1.64±0.14	25	0.16 (3.09)	NS
Pupa	4.19±0.08**	47	4.27±0.11**	29	4.96±0.10	24	17.53 (3.00)	3.09 E-07
Total duration	22.45±0.39**	47	22.28±0.60**	29	20.33±0.20	24	5.52 (3.09)	NS
Male	21.20±0.54	20	21.85±1.05	13	20.38±0.31	14	1.12 (3.21)	NS
Female	23.37±0.48**	27	22.88±0.70**	16	20.30±0.21	10	6.35 (3.18)	0.00378

*, ** Denotes values that are significantly different from corresponding values for *A. floccosus*
There were no significant differences between values for *A. cocois* and *A. pulvinatus*; NS = not significant

Differences in growth parameters became evident from the 2nd instar when *N. bicolor* larvae reared on *A. cocois* and *A. pulvinatus* had significantly ($p<0.01$) wider head capsules compared to those on *A. floccosus* (Table 2). As development continued, the trends changed, and in the end, head capsules adults reared on *A. floccosus* were found to be the widest and those on *A. pulvinatus* the least wide (Table 2). Adult females were larger than males on all three prey species.

Table 2. Means and ANOVA for measurements (in mm) of various life stages of *N. bicolor* reared on three aleyrodid prey species

Life stage	A. cocois	N	A. pulvinatus	N	A. floccosus	N	F (F critical)	P-value
Egg –	0.402±0.002	57	0.400±0.002	4	0.404±0.002	2	0.363	NS
length	0.202±0.001		0.203±0.002	3	0.205±0.002	8	(3.069)	NS
Egg –							0.949	
width							(3.069)	
1^{st} instar[a]	0.143±0.002	55	0.147±0.002	3	0.141±0.003	2	1.871	NS
				8		8	(3.073)	
2^{nd} instar	0.225±0.003 **	55	0.227±0.003**	3	0.214±0.002	2	4.694	0.011
				6		7	(3.075)	
3^{rd} instar	0.292±0.004 **	54	0.319±0.007(**)	3	0.305±0.003	2	7.900	0.000
				6		7	(3.076)	6
4^{th} instar	0.398±0.003 **	52	0.405±0.004**	3	0.425±0.004	2	14.47	2.71
				4		5	(3.080)	E-06
Pupa –	1.040±0.007 **	47	1.029±0.011**	3	1.132±0.010	2	31.92	2.00
width				0		5	(3.089)	E-11
Adult	1.478±0.013 **	47	1.420±0.010**	3	1.516±0.004	2	11.87	2.40
length			0.964±0.010(*), **	0	1.056±0.010	4	(3.089)	E-05
Adult	0.994±0.010 **						17.09	4.30
width							(3.089)	E-07

a. values correspond to the width of the head capsule for instars 1 to 4.
** denotes values that are significantly different (p<0.01) from corresponding values for *A. floccosus*
(*), (**) denote values that are significantly different (p<0.05, p<0.01) between *A. cocois* and *A. pulvinatus*

Newly-emerged adult *N. bicolor* mated 5-10 days after emergence. Thereafter, mating occurred repeatedly throughout life. The mean preoviposition period ranged from 10.0-10.4 days on the three aleyrodids. Average longevity of 74, 51 and 66 days and a life-time fecundity of 92, 51 and 85 eggs were recorded on *A. cocois, A. pulvinatus* and *A. floccosus*, respectively. Significant differences (p<0.05) occurred only between the oviposition on *A. pulvinatus* and the other two species (Table 3). Average number of eggs oviposited per day by *N. bicolor* females on *A. cocois* and *A. pulvinatus* was significantly (p<0.05) lower than those oviposited on *A. floccosus*.

Table 3. Analysis of variance (ANOVA) for four reproductive biology parameters[a] of *N. bicolor* on three aleyrodid prey species

Parameter	A. cocois[b]	A. pulvinatus[c]	A. floccosus[d]	F[e,f]	P-value
Preoviposition period (range)	10.2±0.65 (7-13)	10.4±0.47 (7-13)	10.0±0.52 (8-13)	0.79	NS
Longevity (range)	74.5±11.65 (39-164)	50.6±7.82 (23-115)	66.0±7.57 (24-113)	1.91	NS
Fecundity (range)	93.2±11.83 (47-164)	51.0±8.68* (16-124)	84.7±13.01 (29-179)	4.37	0.02
Mean no. of eggs /day	1.12±0.07	1.12±0.06	1.43±0.08*	4.19	0.017

a. Reproductive biology parameters = preoviposition period (in days), longevity (in days) and fecundity (mean no. of eggs per female), and mean no. of eggs / day
b. *A. cocois* (N = 10); c. *A. pulvinatus* (N = 14); d. *A. floccosus* (N = 10)
e. F critical = 3.305 for preoviposition period, longevity and fecundity
f. F critical = 3.071 for mean no. of eggs per day
* denotes values significantly different ($p < 0.05$) from corresponding values for the other two aleyrodid species

Like many coccinellids, *N. bicolor* females were synovigenic and produced eggs in batches of 3-4 throughout life. The eggs were inconspicuous and usually laid flat. Most were oviposited in the flocculent material produced by the whiteflies. Although eggs were mostly found singly, two or three eggs laid closely together were also recorded on a few occasions. Life table parameters of *N. bicolor* on the three aleyrodids are summarized in Table 4 and survival and age-specific fecundity is depicted in Figure 1. Values of several parameters (r_m, DT and λ) were very similar for *N. bicolor* reared on *A. cocois* and *A. floccosus*, but on *A. pulvinatus* were much lower for r_m and λ and correspondingly higher for DT.

Adaptability studies

Larvae of *N. bicolor* reared on *A. cocois* and transferred to *A. pulvinatus* and *A. floccosus* readily adapted to the new prey species. They began feeding within a short time and continued to develop normally. Small differences in the duration of development of various stages were not significant. Similarly, small non-significant differences were noted in the size of the head capsule of the 4th instar, width of pupa and length and width of adults reared on the three prey species. There was no mortality in larvae reared on *A. cocois* and *A. pulvinatus*. One pupa failed to develop on *A. floccosus*. Sex ratio (male : female) of *N. bicolor* adults was female-biased on *A. cocois* (1.0 : 1.5) and *A. pulvinatus* (1.0 : 1.75) and male-biased on *A. floccosus* (1.5 : 1.0)

Table 4. Life table statistics of *Nephaspis bicolor* on three aleyrodid prey species

Parameter	***A. cocois***	***A. pulvinatus***	***A. floccosus***
Net reproductive rate (R_O) (females per female per generation)	38.42	17.17	37.80
Intrinsic rate of increase (r_m) (female progeny/female/day)	0.0689	0.0530	0.0692
Generation time (G) (days)	67.80	63.38	64.15
Doubling time (DT) (days)	10.06	13.08	10.02
Innate capacity for increase (λ) (females per female/day)	1.071	1.054	1.072

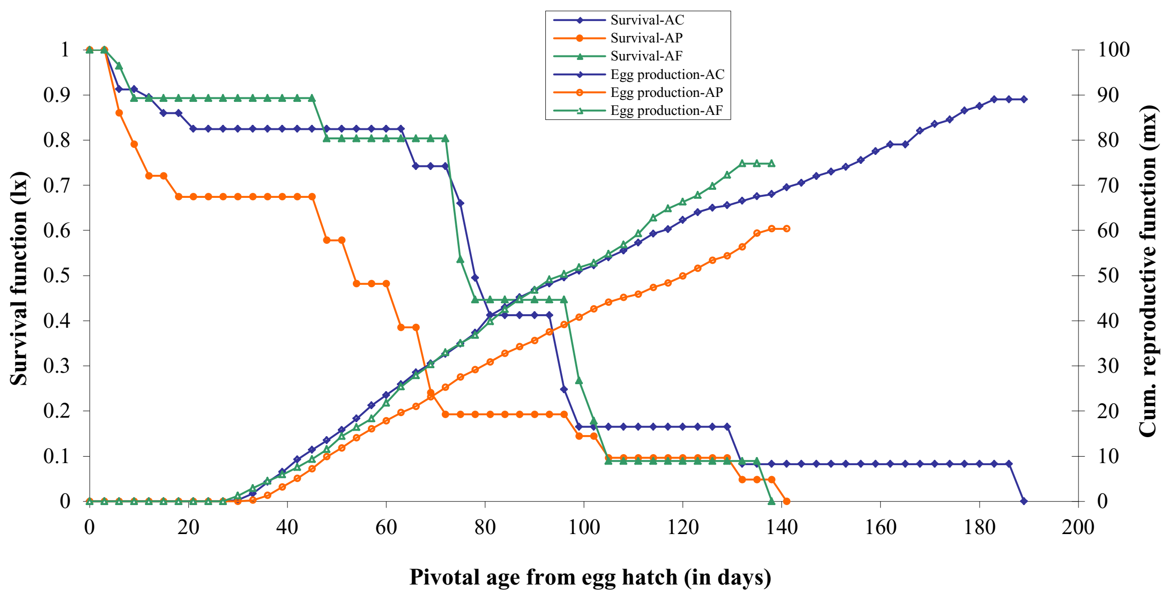


Figure 1. Comparison of survival and age-specific fecundity of female *N. bicolor* reared on *Aleurodicus cocois* (AC), *A. pulvinatus* (AP) and *Aleurothrixus floccosus* (AF).

Nephaspis bicolor reared on *A. cocois* to pupal stage and transferred as newly-emerged adults to *A. pulvinatus* and *A. floccosus* had significantly longer preoviposition period, compared to those transferred to *A. cocois* (Table 5). Adult longevity was on par on the three prey species, however, significantly more eggs were oviposited on *A. floccosus* and *A. cocois*, compared to *A. pulvinatus*.

Among the reproductive biology parameters, only the preoviposition period was significantly affected when the prey species were switched, while longevity and fecundity were on par (Table 6). Although prey switching increased longevity and fecundity of *N. bicolor* on *A. pulvinatus*, there was a reduction of about 2.6% in the average daily egg production in the *N. bicolor* females switched to *A. pulvinatus*. On *A. floccosus*, increased longevity and fecundity translated into a 4.3% increase in daily egg production in the switched females. Life table parameters of *N. bicolor* transferred to the three Aleyrodidae are presented in Table 7. Transfer from *A. cocois* to *A. pulvinatus* resulted in a reduction in the overall performance of the predator when compared to *A. cocois*. On *A. floccosus*, although values of R_0 were higher than those on *A. cocois*, a reduction in r_m led to an increase in GT and DT and a corresponding decrease in λ.

Table 5. Analysis of variance (ANOVA) for four parameters[a] of the reproductive biology of *N. bicolor* reared on *A. cocois* and switched as newly-emerged adults to *A. cocois*, *A. pulvinatus* and *A. floccosus*

Parameter	A. cocois[b]	A. pulvinatus[c]	A. floccosus[d]	F[e,f]	P-value
Preoviposition period (range)	10.2±0.65 (7-13)	16.0±1.11** (12-24)	14.8±0.94** (10-20)	11.13	0.0003
Longevity (range)	74.5±11.66 (39-164)	71.2±0.13.09 (24-152)	80.9±0.23 (53-119)	0.30	0.743
Fecundity (range)	93±12.6 (47-164)	61±0.14.5 (11-154)	104±12.0 (58-171)	2.86	0.075
Mean no. of eggs/ day	1.12±0.07**	1.09±0.05**	1.45±0.07	8.37	0.0004

a. Reproductive biology parameters: as in Table 3
b, c, d N=10 for A. cocois, A. pulvinatus and A. floccosus each
e. F critical = 3.354 for preoviposition period, longevity and fecundity
f. F critical =3.064 for mean no. of eggs per day
** denotes that values are significantly different (p<0.01) from corresponding values for *A. cocois* (for preovipostion period) and for *A. floccosus* (for mean no. of eggs per day)

Table 6. Analysis of variance (ANOVA) for four parameters[a] of the reproductive biology of *N. bicolor*, comparing adults reared on the same aleyrodid prey species and those switched from another aleyrodid

Parameter	Same prey[b]	Prey switched[c]	F value[d,e]	P-value
A. *pulvinatus*				
Preoviposition period (range)	(N=10) 10.5±0.47 (7-13)	(N=14) 16.0±1.11 (12-24)	25.97	4.2E-05
Longevity (range)	50.6±7.82 (23-115)	71.2±8.40 (24-152)	1.607	0.220
Fecundity (range)	51.0±8.7 (16-124)	61.8±14.49 (14-154)	0.434	0.517
Mean no. of eggs / day	1.12±0.059	1.09±0.046 (-2.6%)	0.105	0.747
A. *floccosus*	(N=10)	(N=10)		
Preoviposition period (range)	10.0±0.52 (8-13)	14.8±0.94 (10-20)	20.01	0.0003
Longevity (range)	66.0±7.6 (24-113)	80.9±8.05 (53-119)	1.817	0.194
Fecundity (range)	84.70±13.01 (29-179)	104.10±12.02 (58-171)	1.198	0.288
Mean no. of eggs per day	1.39±0.08	1.45±0.07 (+4.3%)	0.329	0.568

a. Reproductive biology parameters: same as in Table 3
b. Newly emerged adults transferred to same prey species i.e. from *A. pulvinatus* to *A. pulvinatus*, and *A. floccosus* to *A. floccosus*, respectively
c. Larvae reared on *A. cocois* and switched as newly-emerged adults to *A. pulvinatus* or *A. floccosus*
d. F. critical = 4.301 (*A. pulvinatus*) and 4.414 (*A. floccosus*) for preoviposition period, longevity and fecundity
e. F critical = 3.96 (*A. pulvinatus*) and 3.98 (*A. floccosus*) for mean no. of eggs per day

Table 7. Life table statistics of *N. bicolor* upon transfer from *A. cocois* to the same and two other aleyrodid prey species.

Parameter	***A. cocois* to *A. cocois***	***A. cocois* to *A. pulvinatus***	***A. cocois* to *A. floccosus***
Net reproductive rate (R_o) (females/female/ generation)	38.43	25.48	42.92
Intrinsic rate of increase (r_m) (female progeny/ female/day)	0.0689	0.0515	0.0555
Generation time (G) (days)	67.82	79.10	79.10
Doubling time (DT) (days)	10.06	13.46	12.49
Innate capacity for increase (λ) (females/female/day)	1.071	1.053	1.057

A comparison of the survival and reproductive functions of *N. bicolor* on three aleyrodids (transferred from *A. cocois* as newly-emerged adults) is provided in Figure 2. The effect of prey switching on the survival and reproduction on *A. pulvinatus* and *A. floccosus* are depicted in Figures 3 and 4, respectively.

Longevity was the key factor in the observed fecundity on all three prey species, since the longer the adults lived, the more eggs they laid. Oviposition rate was quite similar on same and switched prey species for both *A. pulvinatus* and *A. floccosus*.

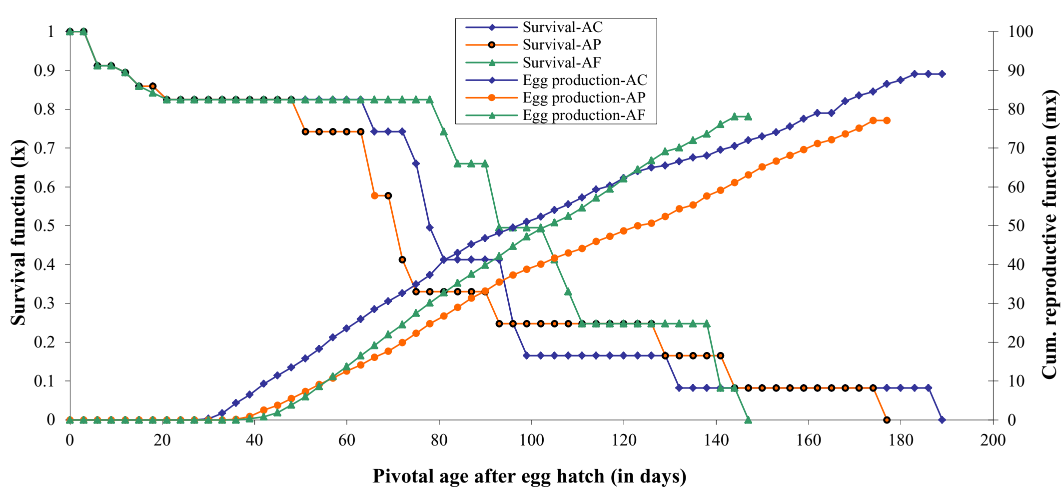


Figure 2. Comparison of age specific survival and cumulative reproduction (females/females) of *N.bicolor* reared on *A. cocois* and transferred *A. cocois* (AC), *A. pulvinatus* (AP) and *Aleurothrixus floccosus* (AF).

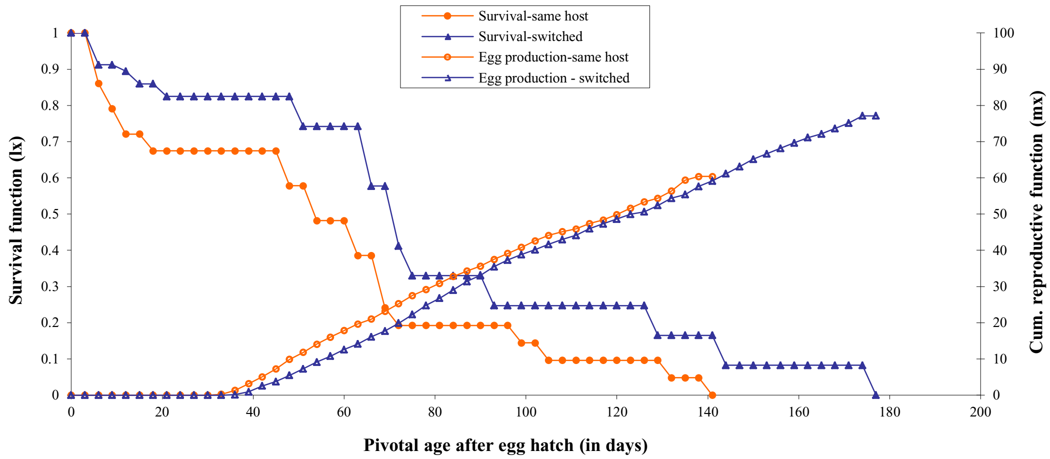
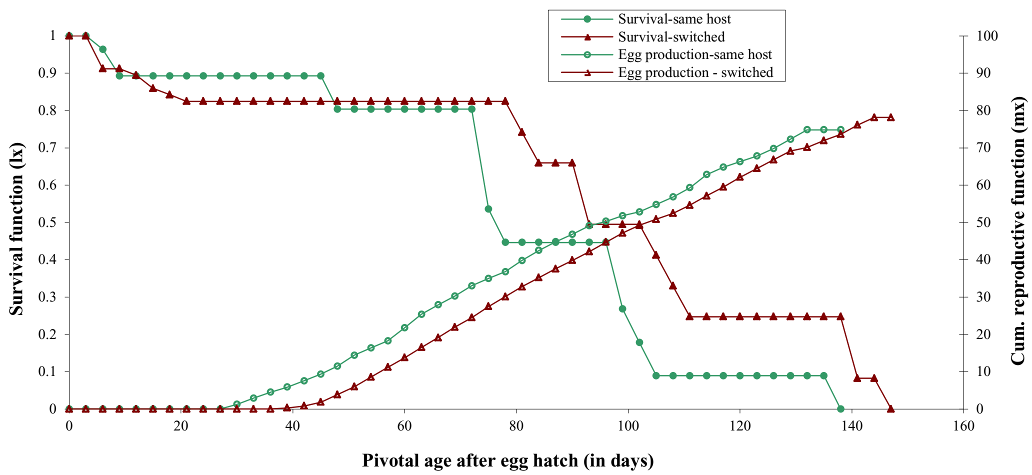


Figure 3, Comparison of age specific survival and cumulative reproduction (females/females) of



Nephaspis bicolor reared on *A. pulvinatus* and switched from *A. cocois*

Figure 4. Comparison of age specific survival and cumulative reproduction (females/females) of *N bicolor* reared on *A. floccosus* and switched from *A. cocois*

DISCUSSION

Results from the present study suggest that the whitefly prey species do have an impact on several biological parameters of *N. bicolor*, in particular duration of development, sex ratio, size, longevity and life-time fecundity. Among the three aleyrodids studied, *A. floccosus* was the most suitable prey in terms of developmental period of *N. bicolor* while *A. pulvinatus* and *A. cocois* were on par. This was, however, counteracted to some extent by the sex ratios, which were female-biased on *A. cocois* (1.0:1.35) and *A. pulvinatus* (1.0 : 1.23) but were in favour of males on *A. floccosus* (1.5:1.0). However, the number of insects used in the experiment was too small to draw any firm conclusions on the effect of prey species on the sex ratio.

All stages of *N. bicolor,* except the egg and pupa, fed on all stages of the whiteflies. Younger instars preferred eggs and early stages of the prey while older instars preferred later stages and pupae. The developmental biology of *N. bicolor* on *A. cocois* was comparable to three other *Nephaspis* spp.: *N. cocois* Gordon*, N. indus* Gordon and *N. oculata* Blatchley reared on *A. cocois*, *A. dispersus* and *B. tabaci B*, respectively (Carvalho, 1976; Liu *et al*., 1997; Yoshida and Mau, 1985). Preferred prey stages for *N. oculata* were eggs of *B. tabaci B* (Liu *et al*., 1997) and for *N. indus* nymphs of *A. dispersus* although all stages were fed upon (Yoshida and Mau, 1985).

Reproductive parameters of *N. bicolor*, *N. indus* and *N. oculata* were also comparable. Females were synovigenic and oviposition occurred throughout life. Longevity of the adults was thus a key factor, since the longer they lived, the more eggs they oviposited. An average of 67-75% of eggs was oviposited by *N. bicolor* during the first 50 days after the commencement of oviposition, compared to *N. indus* females which laid 'most of their eggs' within 49 days of an ovipositional period of 131±35 days (Yoshida and Mau, 1985). Rate of oviposition in both *N. oculata* and *N. indus*, averaging 3 eggs per day, was however much higher than the average of 1.12 - 1.45 recorded for *N. bicolor* (Liu *et al.*, 1997; Yoshida and Mau, 1985). Based on the fecundity life table analysis, the overall performance of *N. bicolor* on *A. cocois* and *A. floccosus* was on almost on par and was superior compared to that on *A. pulvinatus*. The r_m values of 0.0689, 0.053 and 0.0692 on the three species, though lower that of *N. oculata* (0.078), was well within the expected range of 0.05-0.08 for species feeding on aleyrodids and scales.

Based on the present study, *N. bicolor* larvae and adults are clearly adaptable to new aleyrodid prey species. Switching of larvae reared on *A. cocois* to *A. pulvinatus* or *A. floccosus* did not impact on feeding, survival and duration of development of the larvae or size of the emerging adults. Such was not the case with *Chilocorus nigrata* (Fabricius) where prey switching to (normally) suitable prey species resulted in significantly retarded larval development rate and produced smaller adults (Hattingh and Samways, 1992). According to Iperti (1978), the true effects of prey preferences in predacious coccinellids can only be determined from the extent to which progeny are produced. Prey switching had little or no effect on the longevity and fecundity of the adults of *N. bicolor*. The only parameter affected was the preoviposition period, which was significantly longer in the switched adults. Prey switching of ovipositing adults to normally suitable prey resulted in short-term suppression in oviposition and feeding rates in adult *Chilocorus nigritus* (Hattingh and Samways, 1992). The changes in the life table parameters of *N. bicolor* after prey switching reflected slight, insignificant enhancements or reductions in the overall performance of the predator.

CONCLUSIONS

The present study confirms *N. bicolor* as an oliphagous predator that is able to adapt with little difficulty to new prey species, both in subfamily Aleurodicinae and Aleyrodinae. Indeed, during field surveys in Trinidad and Tobago, *N. bicolor* and *Nephaspis* spp. were consistently found on several wax-producing aleyrodids and it is suggested the presence of waxes may be an important factor that determines the suitability of a prey species for oviposition (Lopez and Kairo, 2003). If chemical cues from waxes are used for oviposition, then this narrows down the range of potential prey species that may be attacked by *N. bicolor*. But is also means that if and when introduced, *N. bicolor* can adapt to attacking and feeding on a fairly wide range of wax-producing Aleyrodidae. In Hawaii, *N. indus* was found attacking *A. floccosus* and *O. mammaeferus*, both Aleyrodinae, following its introduction (Yoshida and Mau, 1985). There are other instances where predatory coccinellids introduced for the control of one prey species were found attacking other species. Usually these consisted of members of the same family (e.g. *Hyperaspis notata* (Mulsant) and *Rodolia cardinalis* Mulsant) Ragab, 1995; Staubli *et al*., 1997), but occasionally other families were also attacked (e.g. *Cryptolaemus montrouzieri* Mulsant) (Mani and Krishnamoorthy, 1999). Sands (1997) contends that the development of an exotic natural enemy on native species may be acceptable, provided the benefits achieved from the control of the pest species are considered worth the risk of reduced numbers of indigenous flora or fauna. It is recommended that the above factors should be considered in any evaluation of *N. bicolor* and decision-making for its introduction.

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