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Prey range of **Nephaspis** bicolor Gordon (Coleoptera: Coccinellidae), a potential biological control agent of **Aleurodicus dispersus** and other **Aleurodicus** spp. (Homoptera: Aleyrodidae)

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Prey range of *Nephaspis bicolor* Gordon (Coleoptera: Coccinellidae), a potential biological control agent of *Aleurodicus dispersus* and other *Aleurodicus* spp. (Homoptera: Aleyrodidae)

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Abstract. *Nephaspis bicolor* Gordon is a potential candidate for the biological control of *Aleurodicus dispersus* Russell. Its prey range was assessed based on the published literature, and field and laboratory studies. Tests were carried out to assess the suitability of 20 potential prey species selected based on a modified centrifugal system and/or perceived importance by importing authorities. In general, *Nephaspis* spp. were only associated with non-aleyrodid prey when these occurred together with aleyrodid prey. On all prey except Aleyrodidae, survival of *N. bicolor* adults and larvae was similar or lower than controls (no food) suggesting that these were unsuitable as a food resource. Generation survival and reproduction occurred only on Aleyrodidae and the presence of wax appeared to be an important cue for oviposition. As expected, no feeding occurred on honeybees, silkworms or predatory mites. *N. bicolor* adults attacked parasitized whitefly prey but they appeared to recognize and avoid prey with mature parasitoid larvae or pupae. Based on the information adduced, it was concluded that *N. bicolor* was an aleyrodid predator. Within the Aleyrodidae, the prey range could not be delimited without doing specific tests on individual species, but there was ample field and laboratory evidence that *N. bicolor* was specialized to attacking wax-producing species, in particular *Aleurodicus* spp. and *Aleurothrixus flocossus* Maskell.

1. Introduction

Coccinellids are an important component of the natural enemy complex of many homopteran pests. As a consequence, they are often considered as candidates for introduction against such pests. According to Obrycki and Kring (1998), 'coccinellids will continue to play a role in naturally occurring and human-assisted biological control and they will be considered as possible natural enemies for importation whenever a homopteran pest invades a new region'. They also acknowledge that the understanding of prey specificity in coccinellids is a critical research area. Prey range in predatory coccinellids varies quite extensively (Majerus and Kearns 1989), from one or two prey species (e.g. *Hyperaspis pantherina* Fürsch) to a range of related prey (e.g. *Harmonia axyridis* Pallas) and finally to completely unrelated species (e.g. *Cryptolaemus montrouzieri* Mulsant) (Gordon 1985, Booth *et al.* 1995, LaMana and Miller 1996). Nechols *et al.* (1992) applied the terms 'host-specific', 'oligophagous' and 'polyphagous', respectively, to the three groups above. Acknowledging some of the concerns of environmentalists, Nechols *et al.* (1992) suggested that a

common ground be found for cooperation among various groups involved in classical biological control programmes. Among their recommendations was the need to choose species that have acceptably narrow host ranges rather than those known to be polyphagous. However, few studies have been carried out on the prey range of predatory Coccinellidae since the methodologies for undertaking such studies have not been completely developed. Obrycki *et al.* (2000) concluded that 'our present knowledge of coccinellid ecology does not allow for predictions of the interactions and effects of an introduced coccinellid species'. The development of such approaches is therefore vital and urgent. The present study focuses on work carried out on *Nephaspis bicolor* Gordon a candidate agent for control of the spiralling whitefly *Aleurodicus dispersus* Russell in Africa.

The spiralling whitefly was reported for the first time in Nigeria (Akinlosotu *et al.* 1993). In a relatively short time it spread to several neighbouring countries in West Africa, including Togo (Anon. 1993, Kiyindou 1993), causing damage to a wide range of fruit and forest trees, food crops, and ornamental and shade trees (M'Boob and van Oers 1994). As an exotic pest, *A. dispersus* was a good target for classical biological control. Indeed, this strategy had been used successfully for control of the pest in Hawaii and several Pacific islands where the species had also been accidentally introduced (Kumashiro *et al.* 1983, Suta and Esguerra 1993, Tauili'-ili and Vargo 1993). The principal natural enemies used in these countries were a parasitoid, *Encarsia* sp. nr *haitiensis* Dozier and coccinellids in the genus *Nephaspis*, notably *N. bicolor* and *N. indus* Gordon (table 1). There was some confusion about the taxonomy and nomenclature of *N. indus*. The species was introduced into Hawaii as *N. amnicola* Wingo (Kumashiro *et al.* 1983). A few years later, Gordon (1985) synonymized it with *N. oculata* (Blatchley) and a decade later described it as a new species (Gordon 1996).

In West Africa, *E.* sp. nr *haitiensis* and another parasitoid, *Encarsia guadeloupae* Viggiani, were fortuitously introduced together with *A. dispersus* and this was noted to provide some degree of control in some countries (M'Boob and van Oers 1994, Neuenschwander 1994). However, the parasitoid did not provide the desired level of control in all situations. Hence,

Table 1.   Introductions of natural enemies for biological control of Aleurodicus dispersus *based on the BIOCAT database (Greathead and Greathead, 1992)*

Locality	Natural enemy	Year	Origin of natural enemy	Status of programme[1]
Hawaii	*Nephaspis bicolor* Gordon	1980	Trinidad	S
	Nephaspis indus (=*N. amnicola*	1979,	Trinidad,	
	Wingo=*N. oculata* (Blatchley))	1984	Honduras	S
	Delphastus pusillus (Le Conte)	1980	Trinidad	S
	Encarsia ?haitiensis Dozier	1980	Trinidad	S
	Encarsia sp.	1980, 1982	Trinidad	E
Marianas	*N. indus*	1981	?	S
	E. ?haitiensis	1981	?	S
Florida	*N. indus*	1982	?	?
	E. ?haitiensis	1982	Caribbean	?
American Samoa	*N. bicolor*	1984	Trinidad	S
	N. indus	1984	Trinidad	S
	D. pusillus	1984	Trinidad	S
	E. ?haitiensis	1984	Trinidad	S
Caroline Islands (Palau)	*E. ?haitiensis*	1986	Trinidad	S
Caroline Islands (Ponpei)	*E. ?haitiensis*	1987	Trinidad	S
Cook Islands	*N. bicolor*	1985, 1987	Trinidad	F
	E. ?haitiensis	1985, 1987	Trinidad	N
Fiji	*N. bicolor*	1987	Trinidad	S
	Nephaspis sp.	1987	Trinidad	S
	E. ?haitiensis	1987	Trinidad	S

[1]The outcome of the programme is denoted as S when there is substantial control after the introduction of several agents; N, when the result unknown; E, when the natural enemy is permanently established; and F, when the natural enemy fails to become established.

introduction of additional biological control agents particularly *Nephaspis* spp. was recommended. In accordance with the code of conduct for the introduction and release of exotic biological control agents (FAO 1996), it was necessary to determine the natural and potential prey range of the selected agent as well as assess the impending risks of its introduction into Africa. Thus, as part of a Technical Cooperation Project (TCP/TOG/4557) funded by the Food and Agriculture Organization of the United Nations, a study focusing on *N. bicolor* was carried out in Trinidad, the country of origin of the *Nephaspis* spp. used in biological control of *A. dispersus* (table 1).

The only reported study on the prey range of a *Nephaspis* sp. was carried out on *N. indus* in Hawaii (Yoshida and Mau 1985). It was of a preliminary nature and suggested that this species fed on three aleyrodids and at least one non-aleyrodid prey. Thus, while all prey records of *Nephaspis* spp. are on Aleyrodidae (Gordon 1996), it is quite possible that these coccinellids can use prey from other families for short- or long-term survival and even reproduction. The present study was therefore undertaken with a view to assess the prey range of *N. bicolor* and *Nephaspis* spp., based on published literature as well as field and laboratory studies. Interactions with other natural enemies particularly parasitoids were also studied.

2.   Materials and methods

2.1.   Field occurrence of Nephaspis spp. on Aleyrodidae and association with other natural enemies

Field surveys were undertaken throughout Trinidad and Tobago. At each location, potential host plants of *Aleurodi-*

cus spp., namely guava, coconut and other palms, mango, citrus, cassava, avocado, ficus, banana and seagrape, as well as surrounding trees/plants, were examined for the presence of whitefly and their natural enemies. When whitefly were encountered, a qualitative assessment of their population levels was carried out based on a scale of 0–3, where 0=no infestation, 1=low infestation (<30% leaf surface/leaves infested), 2=medium infestation (30–70% leaf surface/leaves infested) and 3=high infestation (>70% leaf surface/leaf area infested). A maximum of three to five plants harbouring mixed stages of the aleyrodids were assessed depending on the number of plants available at each location.

Whitefly pupae as well as associated natural enemies (*Nephaspis* spp. and other predators, parasitoids and microbial control agents) were collected on various host plants. Where necessary, material was sent to taxonomists at CABI Bioscience, UK, for identification. Since it was not possible to identify easily field-collected *Nephaspis* adults to species (with the exception of female *N. bicolor* (Gordon 1996), these were identified to genus. The percentage parasitism of whiteflies was computed based on a randomly collected sample of whitefly pupae. Parasitized pupae were generally larger and black in colour while unparasitized insects were smaller and pale greenish or yellow, with the eyes of the whitefly visible on the ventral surface. Three to five batches (300–500 pupae) were assessed for each location. Mean percentage parasitism and standard errors were computed for that location on that sampling date and the data were used to compare levels of parasitism in the presence and absence of *Nephaspis* spp. Batches of parasitized pupae were also placed individually in clear plastic

capsules to rear out parasitoids. Emerging parasitoids were sent for identification.

2.2. Field occurrence of Nephaspis spp. on non-aleyrodid prey

At several locations, populations of other Homoptera such as Aphididae, Pseudococcidae, Diaspidae and Psyllidae were examined for the presence of *Nephaspis* spp., together with Aleyrodidae on the same plants or separately. These included plants both in agricultural and natural systems. At each location, insects were identified to species (or genus) and the number of trees/plants examined recorded.

2.3. Prey feeding tests

Potential test prey species were selected based upon similar principles as those used for centrifugal testing of weed biological control agents. This procedure is based on the phylogenetic relationships between the target species and potential hosts (Harley and Forno 1992, Cruttwell-McFadyen 1998). Thus, testing starts with species belonging to the closest relatives of the hosts attacked in the field in the area of origin. Testing continues with representatives of higher systematic categories, e.g. subfamilies and families within the same order. Additionally, phytophages are also tested against quite unrelated but valuable plants, either crop plants or ornamentals. This system, when extrapolated for *N. bicolor*, involved testing species belonging to:

- the two subfamilies of Aleyrodidae (Aleyrodinae, Aleurodicinae);
- families within Homoptera closely related to Aleyrodidae;
- unrelated families; and
- three groups of beneficial insects (silkworms, honeybees and predatory mites).

The choice of beneficial insects was based on the presence of the three groups of insects, and their perceived importance, on the African continent. The prey species used in the tests and stages tested are given in table 2. Adult and larvae of *N. bicolor* were tested in separate experiments. In all tests, the adults were starved for 24–30 h and larvae for 4–5 h before being used.

For tests with adult *N. bicolor*, leaf sections harbouring large numbers of various prey were placed on moist filter paper in Petri dishes of 4-cm diameter. The number of replications depended on the availability of the prey. However, in most cases, 10 replications were set up for each test prey. One pair of *N. bicolor* adults was released in each Petri dish and observations made on the response of the coccinellids to the prey immediately after release, and at other times when they appeared to have settled on the leaf discs to determine if they were feeding. The filter paper was kept moist and observations on adult survival recorded daily for 7 days when the experiment was terminated. Leaf sections were observed daily and leaves changed or prey added to ensure that there was always sufficient supply of prey. Two types of controls were set up with *N. bicolor*, the first comprising suitable prey (Aleyrodidae) and the second, no prey.

Ten eggs and five newly hatched first instar larvae of the silk moth, *Bombyx mori* L., were placed on a moistened filter paper in a 3-cm diameter dish and replicated 10 times. From a brood frame of the honeybee, *Apis mellifera* L., various stages (larvae and pupae) were collected and placed in 8-cm diameter Petri dishes. Based on the size of the larvae, they were divided into three groups and based on numbers available five to 10 replications were set up, each with one to three larvae and one pupa. Adults of the predatory mite, *Typhlodromus* sp., were set up with the prey (*Mononychellus* sp.) on cassava leaves placed on a moist filter paper. Five replications were set up on cassava leaves in 3-cm Petri dish, with five mites per replication. One pair of *N. bicolor* adults was released in each Petri dish and

Table 2. Prey species and stages tested to determine the prey range of N. bicolor

Order/Family	Species	Prey stage used in tests
Homoptera		
Aleyrodidae/Aleurodicinae	*Aleurodicus maritimus* Hempel	immatures
	Aleurodicus cocois Curtis	immatures
	Lecanoideus mirabilis (Cockerell)	immatures
Aleyrodidae/Aleyrodinae	*Aleurothrixus floccosus* Maskell	immatures
	Bemisia tabaci B Gennadius	immatures
Psyllidae	*Heteropsylla cubana* D. L. Crawford	
Diaspidae	*Aspidiotus destructor* (Signoret)	nymphs and adults
Aphididae	*Aphis gossypii* Glover	nymphs and adults
	Toxoptera citricida Kirkaldy	nymphs and adults
Pseudococcidae	*Maconellicoccus hirstutus* Green	nymphs
	Planococcus citri (Risso)	nymphs
Diptera	*Liriomyza trifolii* Burgess	larvae
Lepidoptera	*Plutella xylostella* L.	larvae
	Bombyx mori Linnaeus	eggs and first instar pupa
Coleoptera	*Nephaspis bicolor* Gordon	eggs
Hymenoptera	*Encarsiella noyesi* Hayat	larvae
	Encarsia guadeloupae Viggiani	pupae
	Apis mellifera L.	larvae and pupae
Acari/Phytoseiidae	*Tetranychus* sp.	nymphs and adults
	Mononychellus sp.	nymphs and adults
	Typhlodromus sp.	adults

observed immediately after release as well as daily for 2 days to record prey feeding by the coccinellids.

For tests with larvae, first- to second-instar *N. bicolor* were placed on leaf discs harbouring various test species on moist filter paper in 3-cm diameter Petri dishes. It was ensured that sufficient numbers of prey were available on each leaf disc for larval feeding. Observations were recorded daily for 5 days on survival of the larvae. Other experimental details including data analysis were the same as for adults.

Data from the prey range tests was pooled separately for adults and larvae before analysis. Survival data were analysed using the SPSS® statistical package. Survival of *N. bicolor* on various prey species was subject to the Kaplan–Meir technique, which allowed for inclusion of censored cases (i.e. the insects that were still alive at the end of the experimental period of 7 days). For this technique, the standard error (se) of cumulative proportion surviving at time *k* was:

$$\text{se}(t_k) = S(t_k)\sqrt{\sum_{i=1}^{k}\frac{d_i}{n_i(n_i - d_i)}},$$

where $S(t_k)$ is the cumulative survival probability, d_i is the number of deaths or censored cases at time t_i and n_i is the number of cases alive before time t_i. Paired comparison of the survival of *N. bicolor* on various prey species and control was computed using the Breslow statistic, also known as the generalized Wilcoxon test. The test is based on computing the weighted difference between the observed and expected number of deaths at each point. In this experiment, the weights are the number of *N. bicolor* at risk at each time point. The Breslow Statistic (U) is computed using:

$$U = \sum_{i=1}^{k} w_i - (O_i - E_i),$$

where w_i is the weight for the time point i and k is the number of distinct time points (Norusis 1993).

2.4. Feeding tests with parasitized prey

The study focused on understanding the feeding behaviour of *N. bicolor* when offered unparasitized and parasitized prey as a first step in evaluating the ability of the predator to be complementary to parasitoids. Immature stages of *Aleurodicus cocois* Curtis on coconut, parasitized by *Encarsiella noyesi* Hayat, were used in the experiment. Feeding of the coccinellid adults was recorded on unparasitized and two categories of parasitized prey based upon the approximate age of the parasitoid larvae. Both categories were clearly visible under the ventral surface of the host. The first category comprised young parasitoid larvae which were small, often curled, and there was a substantial amount of host tissue yet to be fed upon. In the late stages, parasitoid larvae were oval, large and occupied nearly the entire body of the host having fed upon nearly all the host tissues. Individual immature aleyrodids, parasitized and unparasitized, were detached from the leaf and placed on a moist filter paper in a 4-cm diameter Petri dish. Five treatments (T1–5) were set up as follows: T1 = four unparasitized *A. cocois* pupae; T2 = two early stage parasitized and two unparasitized hosts; T3 = two late stage parasitized and two

unparasitized hosts; T4 = four early stage parasitized hosts; and T5 = four late stage parasitized hosts. Each treatment was replicated nine times. One pair of *N. bicolor* adults (one male, one female) was released in each Petri dish and left undisturbed for 2 days except for moistening the filter paper on day 1. When the beetles were removed, the number of whitefly fed upon was recorded. Aleyrodids from the various replicates were then pooled and further development of the parasitized insects was recorded on day 6.

2.5. Generation survival and reproduction in N. bicolor

To provide semi-natural conditions, live host plants harbouring large numbers of six potential prey species were set up in cages of varying size. Three plants per cage constituted one replication and in the case of potatoes with *Maconellicoccus hirsutus* Green, three sprouted tubers placed in a clear plastic container formed one replication. Each treatment was replicated three times and five pairs of adult *N. bicolor* were released on each plant or potato tuber. The number of adults settling on each prey species for feeding and/or oviposition was observed 24 h later. Adult *N. bicolor* mortality was recorded 7 and 21 days after release. Live adults were left undisturbed for 30 days. On day 30, all plants (except those with *Aleurothrixus floccosus* Maskell where immature stages of the coccinellids were observed) were destructively sampled and observed under the microscope for eggs and immature stages of *N. bicolor*. The plants with *A. floccosus* were maintained for a further 3 weeks to allow the development of the immature stages of *N. bicolor* to continue. Emerging adults were collected and sexed and the experiment was terminated.

3. Results

3.1. Field occurrence of Nephaspis spp. on Aleyrodidae and association with other natural enemies

On guava, *N. bicolor* and at least two other species were commonly associated with whitefly. However, *N. bicolor* often accounted for >90% of total coccinellid population (table 3). *Nephaspis bicolor* was also the predominant species attacking *A. cocois* (on coconut and other palms) and *Aleurodicus pulvinatus* Maskell (on seagrape and guava) in Trinidad, particularly when prey populations were high. *Nephaspis nigra* Gordon was the predominant species attacking whitefly in Tobago. These consisted of *A. pulvinatus* on seagrape and a combination of *Aleurodicus maritimus* Hempel, *A. pulvinatus* and *A. floccosus* on guava. Identification of *Nephaspis* spp. (based on the morphology of *N. bicolor* females) is shown in table 3 together with the prey species and host plants recorded from various locations in Trinidad. Based on the occurrence of adult and immature stages *Nephaspis* spp., a list of prey species that supported reproduction and development of the beetle is compiled in table 4.

The field studies also showed that *Nephaspis* spp. coexisted with a range of parasitoids. In total, 15 species of parasitoids were recorded on various Aleyrodidae (table 5). At most locations, the parasitoids were found associated with *Nephaspis* spp. and often, high levels of parasitism were recorded even in the presence of the coccinellid (figures 1 and 2).

Table 3. *Occurrence of* Nephaspis bicolor *and other* Nephaspis *spp. and their prey in various locations in Trinidad*

| | | | | Number of coccinellids collected | | |
| | | | | Female | Unidentified *Nephaspis* spp. | |
Date	Location	Host plants	Prey species*	*N. bicolor*	Females	Males
March 1996	Las Lomas	Guava	*A. maritimus*	10	0	14
			A. floccosus			
April 1996	Cunupia	Guava	*A. maritimus*	13	6	8
			A. floccosus			
April 1996	Balandra	Seagrape	*A. pulvinatus*	1	2	3
			A. maritimus			
May 1996	Las Lomas	Guava	*A. maritimus*	2	4	4
			A. floccosus			
May 1996	San Juan	Guava	*A. maritimus*	1	1	0
			A. floccosus			
May 1996	Santa Cruz	Guava	*A. maritimus*	0	3	1
May 1996	Trincity	Guava	*A. maritimus*	2	1	0
			A. floccosus			
June 1996	Cane farm	Guava	*A. maritimus*	3	0	10
			A. floccosus			
June 1996	Cane farm	Guava	*A. maritimus*	6	0	10
			A. floccosus			
July 1996	St. Augustine	Guava	*A. maritimus*	17	7	16
			A. floccosus			
August 1996	Manzanilla	Coconut	*A. cocois*	60	0	27
September 1996	Bamboo	Coconut	*A. cocois*	14	0	7
September 1996	Manzanilla	Coconut	*A. cocois*	2	0	7
October 1996	Sangre Grande	Guava	*A. maritimus*	300	25	200
November 1996	St. Helena	Guava	*A. maritimus*	1	0	2
			A. floccosus			
November 1996	Maracas	Coconut	*A. cocois*	8	1	12
December 1996	Manzanilla	Coconut	*A. cocois*	8	0	5

*A=*Aleurodicus* except *Aleurothrixus floccosus*

Table 4. *Prey which will support reproduction and development of* Nephaspis *spp. In the field based on presence of various developmental stages*

| | | Occurrence of *Nephaspis* spp. | | |
Prey sp.	Host plants	Larvae	Pupae	Adult
Aleurodicus cocois	*Cocos nucifera* (coconut)	✓	✓	✓
	Ficus benjamina	✓	✓	✓
	Vietchia merrillii (manila palm)	✓	✓	✓
Aleurodicus maritimus	*Psidium guajava* (guava)	✓	✓	✓
	Cajanus cajan (pigeonpea)	✓	✓	✓
Aleurodicus pulvinatus	*Coccoloba uvifera* (seagrape)	✓	✓	✓
	Guava	✓	✓	✓
	Terminalia catappa (tropical almond)	✓	✓	✓
Paraleyrodes urichii,	Coconut	✓	✓	✓
Paraleyrodes sp.		✓	✓	✓
Lecanoideus mirabilis	*Ficus benjamina*	✓	✓	✓
	Polyalthia longifolia	✓	✓	✓
Aleurothrixus floccosus	Guava	✓	✓	✓
	Citrus sp.	✓	✓	✓

3.2. Field occurrence of *Nephaspis* spp. on non-aleyrodid prey species

Nephaspis spp. were never found associated with any of the 12 species of alternative prey examined in the field but some other coccinellids were (table 6). *Nephaspis* spp. were encountered in association with some non-aleyrodid Homoptera like Aphididae, Diaspididae and Pseudococcidae, but only when these occurred together in mixed population with an aleyrodid prey and never when they occurred alone.

3.3. Prey feeding tests

Although adult beetles were starved up to 30 h before each test, their immediate reaction after release was to move to the top of the Petri dish towards light. However, they moved towards the aleyrodid prey a few minutes to a few hours later and began to feed. Although they moved around within the Petri dish between feeding episodes, they continued to return to the prey periodically for feeding. In contrast, on non-aleyrodid prey, coccinellids were rarely observed attempting to feed. In a few cases, they were able to puncture the cuticle of, and even kill,

Table 5.   Occurrence and association of Nephaspis spp. with 15 parasitoid species on various Aleyrodidae in Trinidad and Tobago

Species	Ex: host	Host plant	Location
Encarsia cubensis Gahan	Aleurothrixus floccosus	Guava	Carrera Island, Curepe*, San Juan*
Encarsia guadeloupae Viggiani	Aleurodicus maritimus	Guava	Curepe
	Aleurodicus cocois	Manila palm	Maloney*
	Aleurodicus pulvinatus	Seagrape	Manzanilla*
	Lecanoideus mirabilis	Ashoka tree	St. Augustine*
Encarsia hispida DeSantis	A. floccosus	Guava	Curepe, St. Augustine*
Encarsia sp. nr.meritoria Gahan	A. maritimus	Pigeonpea	Curepe*
sp. A. (=E. sp. nr. ?haitiensis Dozier)		Guava	St. Helena*
	A. cocois	Manila palm	Maloney*
	Aleurothrixus floccosus	Spondias dulcis	Tunapuna*
		Citrus, guava, Pimenta sp.	Cunupia
Encarsia sp. nr.meritoria Gahan	A. cocois + Paraleyrodes sp.	Coconut	San Fernando
sp. B	A. maritimus	Guava	Curepe*
Encarsia sp. nr. variegata Howard	A. floccosus	Guava	Carrera Island
Encarsiella sp. D	A. cocois	Coconut	Arima*, Icacos*, Maloney*, San Raphael*
	A. maritimus	Guava	Curepe*, Las Lomas*, St. Helena*
		Pigeonpea	Tunapuna*,Curepe*
	A. pulvinatus	Seagrape	Manzanilla*
Encarsiella noyesi Hayat	A. cocois	Coconut	Arima*, Bamboo*, Moruga*, Warrenville
	A. maritimus	Guava	Curepe*
	A. pulvinatus	Seagrape	Lowlands*, Pigeon Pt.*, Charlotteville* (Tobago)
Entedononecremnus sp.	L. mirabilis	Ficus	St. Augustine*
Metaphycus sp. 1	Aleurotrachelus sp.	Coconut	Caroni
Metaphycus sp. 2	A. cocois	Coconut	Bamboo settlement*
	A. maritimus	Guava	Curepe*, San Juan*, Carrera Island
	A. floccosus	Guava	Curepe*, Tunapuna*
Amitus spiniferus (Brèthes)	A. floccosus	Guava	Curepe*
Signiphora xanthographa Blanchard	A. floccosus	Guava	Carrera Island
Signiphora spp.	?A. cocois	Coconut	Blanchiseusse
	Aleurotrachelus sp.	Capsicum sp.	Curepe

*Nephaspis spp. present.

some young Aphis gossypii Glover, Aspidiotus destructor (Signoret) and M. hirsutus. In most instances, however, there was no settlement or attempted feeding on these species beyond the initial probing/puncturing. Thus, the coccinellids were usually found on the top of the Petri dishes, away from the prey.

The mean survival of adults over the 7 days is shown in figure 3. The beetles survived without food for 2 days. Thereafter, they began to succumb gradually and a mortality rate of 100% was recorded on day 6 after release. Similar results were obtained for all test prey except where aleyrodids were offered. On day 6, the survival rates on aleyrodids were 72% on A. cocois, 75% on Bemisia tabaci B Gennadius and 80% on A. floccosus. Statistical comparison of the survival of adult N. bicolor revealed significant differences between the aleyrodids and all other prey species as well as the control (see appendix 1).

On the three beneficial arthropod species (honey bee, silk moth and predatory mites), the immediate reaction of N. bicolor adults after release was to fly to the top of the Petri dish. After a while, they moved around and probed the prey. They soon lost interest, however, and moved back to the top of the Petri dish. At the end of 24 and 48 h, no feeding had occurred on any stage of the test prey.

Twenty-four hours after release, all larvae were alive on all aleyrodid prey (except B. tabaci B) with good settlement and feeding while some mortality was observed on all other prey. Newly moulted larvae wandered around, often leaving the leaf discs to move on the moist filter paper, resulting in drowning of younger stages. A 100% mortality rate was recorded on Tetranychus sp. by day 2. Like adults, larvae were seen attempting to feed on A. gossypii and A. destructor and digging into the flocculent material of M. hirsutus, but by day 2 they had stopped feeding on these prey. Larval survival was poor on B. tabaci B. Five days after release, survival on A. cocois, A. maritimus and A. floccosus was 70, 68 and 80%, respectively, on B. tabaci B 18% and on A. gossypii 5%. The pattern of survival of larvae offered different test prey is shown in figure 4. The Breslow statistic and significance for survival of N. bicolor larvae in different treatments (see appendix 2) was similar to that of adults.

3.4.   Tests on parasitized prey

The results of the experiment assessing whether the N. bicolor fed upon parasitized hosts are summarized in table 7. Although 12 early parasitized prey had apparently not been attacked by coccinellids in T2, further development occurred only in five. Corresponding figures in T3 were 20 and 16 pupae, respectively. When offered only parasitized prey, consumption of early stages of the parasitoid larvae in T4 (eight completely, 16 partially) was much higher compared with late stages of
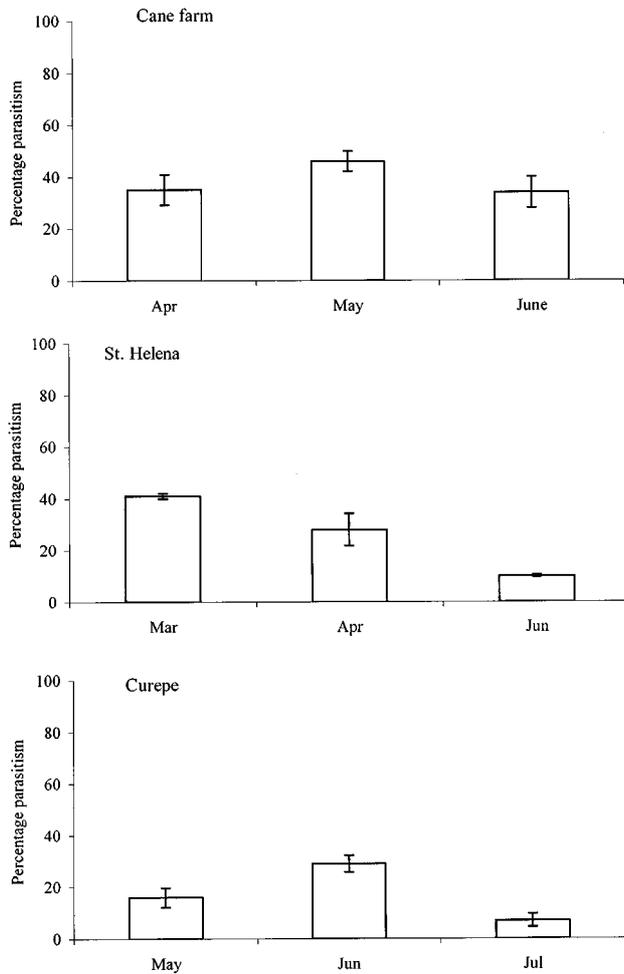
Figure 1.   Percentage parasitism of Aleurodicus maritimus *at three sites where* Nephaspis *spp. were also present during 1996.*
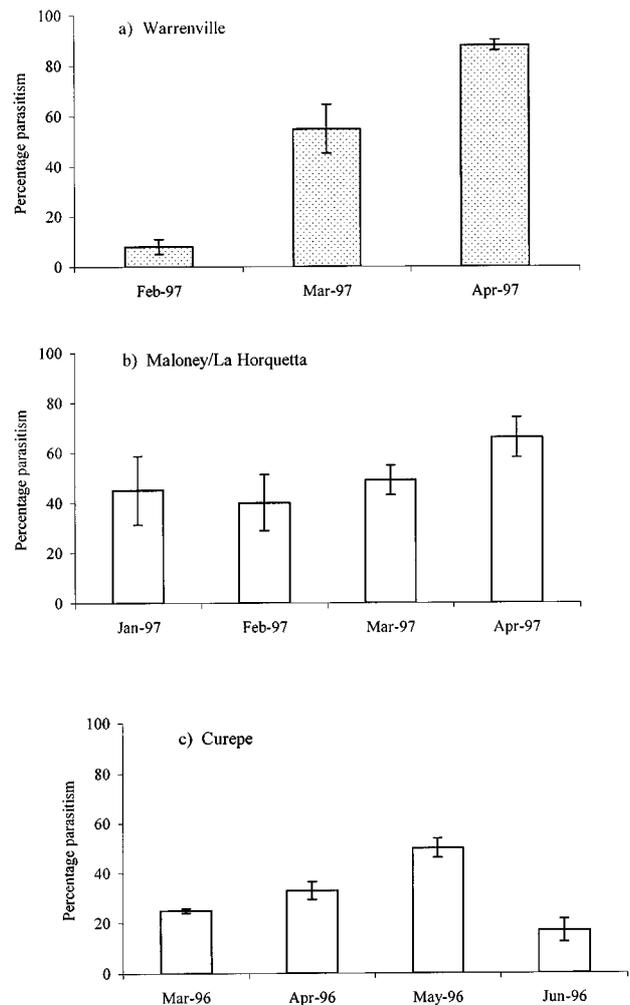

Figure 2.   *Percentage parasitism of* Aleurodicus cocois *(a, b) and* Aleurothrixus floccosus *(c) at three sites where* Nephaspis *spp. were present (clear bars) or absent (shaded bars) during 1996/97.*

parasitoid larvae in T5 (two completely, 12 partially). The coccinellids often attacked early stages of parasitized prey, even in the presence of available unparasitized prey. A greater proportion of early stage parasitized prey was thus partially or completely consumed compared with those in the late stages. In the early stages of parasitization, the developing parasitoid larvae had consumed only a part of the body contents and the unconsumed portion was available to the beetles for feeding. In the late stages, on the other hand, nearly all the body contents of the host were used up, often leaving only the clear larval/ pupal skin intact. Therefore, there was very little for the beetles to feed on. In spite of this, there was evidence of coccinellids rupturing the host skins of, and damaging, late parasitized hosts, particularly when no unparasitized insects were offered.

3.5.   Generation survival and reproduction

Adults tended to move to top of the cages towards light immediately after release. At the end of 24 h, there was no mortality on any prey. At the end of 7 days, a 100% mortality rate was recorded on *H. cubana* and *P. xylostella*. On other prey, surviving adults were recorded feeding on prey only on *A. floccosus* and *B. tabaci B* (table 8). At the end of 3 weeks, one female each was alive on these prey species. During destructive sampling 30 days after the start of the experiment, one female
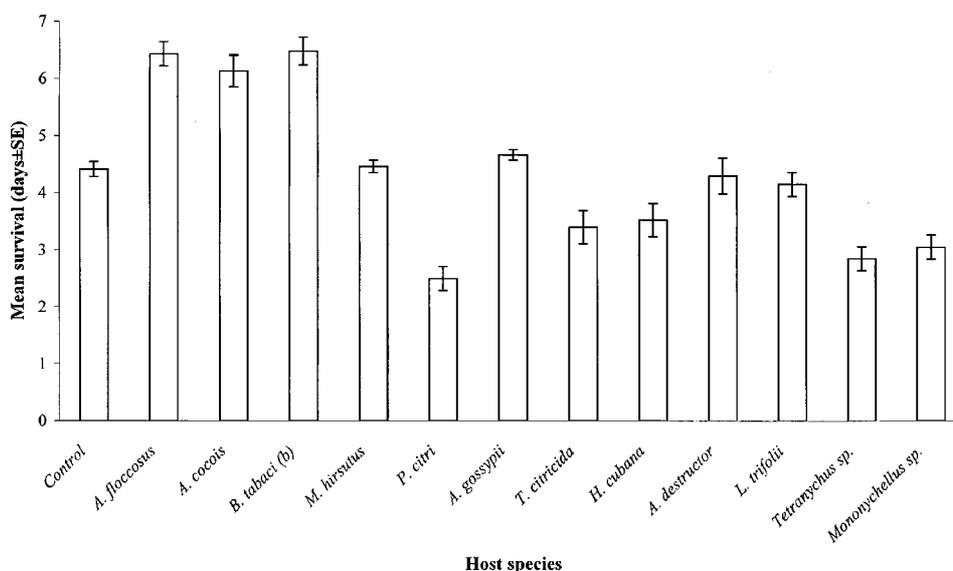
was still alive on *B. tabaci B* but no eggs or progeny were observed despite the presence of large numbers of mixed prey stages. Emergence of first-generation progeny was recorded on *A. floccosus* from day 28 after release of adults and continued for 3 weeks (table 8).

4.   Discussion

Gordon (1996) described 43 species of *Nephaspis*, of which 34 were new species. All species of the genus *Nephaspis* are restricted to the Western Hemisphere, the nearest European counterpart being *Clitostethus* Weise (Gordon 1985). The natural range of *Nephaspis* spp. thus appears to be Central and South America and the Caribbean (table 9), the region where most Aleurodicinae and *Aleurodicus* spp. are believed to have evolved (Mound and Halsey 1978). Based on published literature and records from the British Museum of Natural History (BMNH), the prey range of *Nephaspis* spp. is apparently restricted to Aleyrodidae (Cock 1985, Gordon 1985 and 1996, Greathead and Greathead 1992). However, for most *Nephaspis* spp. the prey range is restricted to only a few species (table 9). Gordon (1985) cited *A. dispersus* and *A. cocois* as specific prey of the genus *Nephaspis*. There is some evidence that suggests

Table 6. Occurrence of Nephaspis spp. on non-aleyrodid prey

Site/no. of plants observed	Host plant	Prey insect	Nephaspis present	Other coccinellid species Identified	Unidentified
Curepe:					
200–250 plants	Hibiscus sabdariffa	Aphis gossypii Glover	no	Cryptolaemus montrouzieri Mulsant	1 species
200–250 plants	H. rosa-sinensis	Maconellicoccus hirsutus Green	no		
2 trees	Annona sp.	M. hirsutus	no		
		Ferrisia sp.	no		
25 plants	Solanum esculenta	Liriomyza trifolii Burgess	no		
Warrenville/Hedge—20 yards	H. rosa-sinensis, other ornamentals	A. gossypii, M. hirsutus	no no	C.montrouzieri	1 species
Manzanilla/50–100 trees	Coconut	Aspidiotus destructor (Signoret)	no	Cryptognatha nodiceps Marshall	1 species
Trinicity/50 trees		Parlagena bennetti Williams	no	Pseudazya trinitatis (Mulsant)	
Bamboo/20 trees		Aonidiella orientalis (Newstead)	no	Zagloba aenipennis (Sicard)	
Longdenville/50 trees	Leucaena leucocephala	Heteropsylla cubana D.L. Crawford	no	no	2 species
Mt. Hope/10 trees	L. leucocephala	H. cubana	no	no	
Piarco/15–20 trees	Anacardium occidentale	Thrips sp.	no	no	1 species
St. Helena/1 tree	Psidium guajava	Ferrisia sp.	no	no	1 species
Cunupia/1 tree	Malpighia glabra (Barbados cherry)	Anthonomus sp. (cherry weevil)	no	no	no
10–15 plants	Cajanus cajan (pigeonpea)	M. hirsutus	no	no	no
5 stools	Saccharum officinarum (sugarcane)	Sacharicoccus sachari (Cockerell)	no	no	no
3 trees	Citrus spp.	Toxoptera sp.	no	no	no
1 tree	Annona sp.	Aphis sp.	no	no	no
Arouca/1 tree	Citrus sp.	Toxoptera sp.	no	no	

Figure 3. Survival of Nephaspis bicolor adults on various prey.

some degree of prey specificity within Aleyrodidae in N. oculata in the USA (Meyerdirk et al. 1980). However, the field studies reported here as well as records from literature (table 9) suggest that although prey specificity of Nephaspis spp. and N. bicolor is limited to the family Aleyrodidae, the number of species attacked within this family can be wide.
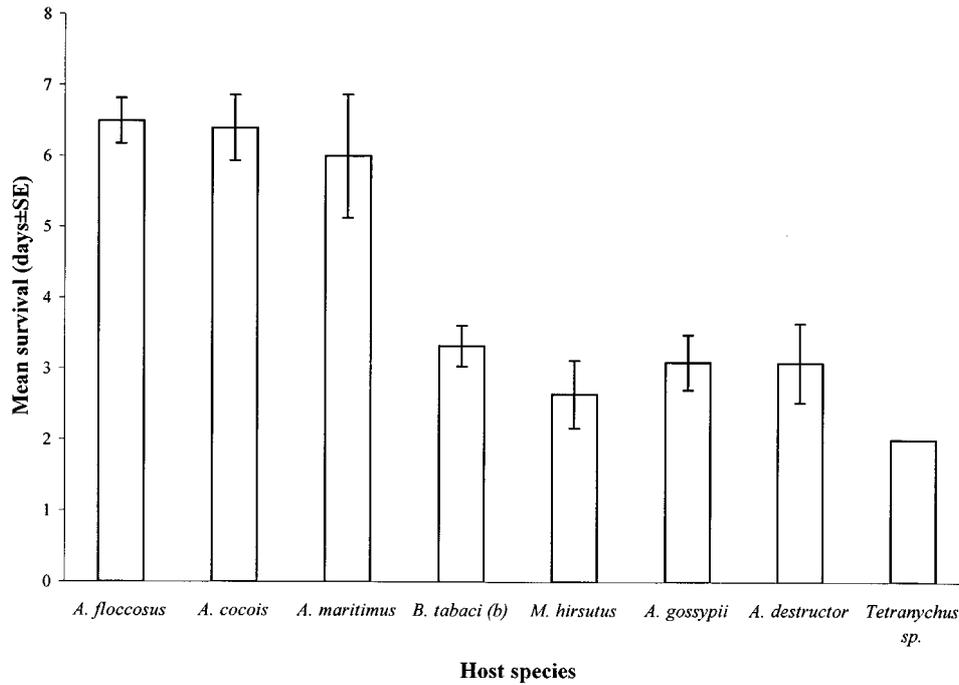
Figure 4.   Survival of Nephaspis bicolor *larvae on various prey.*

Table 7.   *Patterns of feeding by* Nephaspis bicolor *on parasitized and unparasitized* Aleurodicus cocois *in choice and no choice situations*

Treatment	No. of *A. cocois* offered		No. fed upon by day 2			Parasitoids developed[2]	
	Parasitized[1]	Unparasitized	Complete	Partial	None	Number	%
T1	0	36	11	8	17	1	–
T2	18 (early)	18	19	5	12	5	28
T3	18 (late)	18	9	7	20	16	89
T4	36 (early)	0	8	16	12	13	36
T5	36 (late)	0	2	12	22	20	56

[1]Insects denoted early contained very young larvae, and those denoted late, mature larvae of *Encarsiella noyesi*.
[2]All whitefly material was kept to determine if parasitoid larvae were damaged by assessing formation of parasitoid pupa.

Table 8.   *Generation survival and reproduction of* N. bicolor *on six prey*

Test prey	Percentage settlement after 24 h	Percentage mortality rate		Progeny recovered	
		after 7 days	after 21 days	Males	Females
Aleurothrixus floccosus Maskell	70	83	97	18*	31*
Bemisia tabaci B Gennadius	16	95	95	0	0
Maconellicoccus hirsutus Green (sorrel)	10	90	100	0	0
M. hirsutus (potato)	not recorded	30	40	0	0
Aphis gossypii Glover	80	95	100	0	0
Heteropsylla cubana D.L. Crawford	23	100	–	0	0
Plutella xylostella Linnaeus	0	100	–	0	0

*Recovered up to 7 weeks after release of the adults.

Female oviposition behaviour is an important determinant of prey range in *N. bicolor* since eggs are laid on or in close association with the host. Chemical cues associated with the wax are likely to be important in this process. The importance of chemical cues emanating from prey waxes for oviposition has been demonstrated in other coccinellid species like *H. patherina* (Booth *et al.* 1995) and *C. montrouzieri* (Merlin *et al.* 1996). *Nephaspis bicolor* readily oviposited on several aleyrodid hosts (table 4). In Hawaii, *N. indus* oviposited within the flocculent

material produced by *A. dispersus* and under field conditions was found on *A. floccosus* and *Orchamoplatus mammaeferus* Quaintance & Baker (Yoshida and Mau 1985). While all three species produce white, flocculent wax, the texture, chemistry and constitution of the waxes varies considerably (G. W. Watson, personal communication, 2000). It could be speculated that the lack of such waxes in *B. tabaci B*, perhaps deterred *N. bicolor* females from ovipositing on the species. If such waxes were important, their effects may even act at the species level

Table 9.   Records of Nephaspis with prey species, host plant and distribution from the literature

Species	Prey sp./host plant	Distribution	Author
N. aries Gordon	Aleyrodes sp.	Panama	Misidentified as N. amnicola Gordon (1972)
N. bicolor Gordon	Aleurodicus dispersus* Russell	Trinidad	Gordon (1982)
N. cocois Gordon	Aleurodicus cocois Curtis on cashew	Brazil	Carvalho (1976)
	Paraleyrodes citri, P. proximus on citrus	Argentina	Teran and Frias (1984)
N. capricornus Gordon	Aleurodicus cocois Curtis eggs	Brazil	
N. carina Gordon	A. cocois eggs	Brazil	females not known
N. convexa (Nunenmacher) (=Scymnus convexa)	Aleurothrixus sp. Paraleyrodes sp.	Argentina	new combination; Misidentified as N. cocois (Gordon 1996)
N. cygnus Gordon	Aleurodids on cocoa	Trinidad	externally similar to N. indus
N. dispar (Sicard)	Whiteflies	British Guyana	Gordon (1972)
N. gemini Gordon	Trialeurodes vaporariorum Westwood	Brazil	?Biocontrol of T. vaporariorum in greenhouse
N. lacerta Gordon	A. cocois eggs	Brazil	Gordon (1996)
N. magnopunctata Gordon	Trialeurodes variabilis Quaintance	Puerto Rico	Gordon (1996)
N. oculata Blatchley (=amnicola Wingo)	Paraleyrodes citri on citrus	Texas	Meyerdirk et al. (1980)
		West Indies, North and Central America	Gordon (1972)
	Bemisia argentifolii	Florida	Liu and Stansly (1996)
N. picturata Gordon	Aleyrodidae on citrus	Argentina	Teran (1989)

*Aleurodicus dispersus does not occur in Trinidad: these collections were most likely on A. cocois, A. pulvinatus or A. maritimus on coconut, guava/seagrape and guava, respectively.

since at least one Nephaspis spp. is known to exploit B. tabaci effectively. Indeed, in Florida, N. oculata has been examined for inclusion into a biological control programme for B. tabaci B (Liu and Stansly 1996). It is also noteworthy that N. bicolor and other Nephaspis spp. were not found on large field populations of the recently introduced citrus blackfly, Aleurocanthus woglumi Ashby in Trinidad (Parkinson et al. 2000, unpublished). The citrus blackfly produces very little wax except as tiny droplets and a slight fringe around the pupal margin.

Under field conditions, Nephaspis spp. were only ever found associated with non-aleyrodid prey when these occurred in close association with Aleyrodidae. From the prey feeding tests, it was clear that N. bicolor survived better only aleyrodid prey. Although attempts at adult and larval feeding were recorded on some prey (A. gossypii, M. hirsutus and A. destructor), these did not provide suitable food, as survival on these species was also very poor. This suggests that non-aleyrodid prey species are unsuitable for feeding and survival of both larvae and adult coccinellids and are therefore unlikely to be attacked under field conditions, except perhaps for short-term feeding. Longer survival of N. bicolor adults on M. hirsutus and A. gossypii was attributed to the honeydew secreted by these insects, which may have provided suitable food for survival but not for reproduction. Female coccinellids begin to oviposit only when they have fed on a sufficient number of prey, in excess of their metabolic requirement (Frazer 1988). Although adults fed and survived for long periods on B. tabaci B, no reproduction was observed on this aleyrodid. Survival of N. bicolor larvae on this prey species on cabbage and cucurbit leaves was poor, but on tomato leaves a 60% survival rate was recorded 5 days after release, suggesting some plant-mediated effects.

Under field conditions, three distinct patterns of distribution of Nephaspis spp. and parasitoids were recorded: (1) both natural enemies were consistently encountered together (figure 2b; Maloney/La Horquetta); (2) parasitoids were the predominant natural enemy and Nephaspis spp. were not found (figure 2a; Warrenville) and (3) parasitoids were rare and Nephaspis spp. (mainly N. bicolor) were solely responsible for keeping whitefly populations in check. Thus, under field conditions, Nephaspis spp. and parasitoids, either alone or in apparent complementarity with each other, appeared to be the most important natural enemies controlling aleyrodid populations in Trinidad. It could be hypothesized that these natural enemies have evolved mechanisms allowing them to coexist. Such mechanisms, however, can be quite complex involving a number of factors. For instance, predation of parasitized prey can result in significant reductions in parasitoid levels (Nelson and Parella 1992). The ability of a predator to avoid parasitized prey and select unparasitized prey may thus be a useful attribute when the two are present, or used together, in pest management programmes (Hoelmer et al. 1994).

The interaction between predators and parasitoids attacking the same host is expected to be complex in nature. However, simple feeding trials provide a useful insight into the nature of such interactions. In laboratory tests, adult N. bicolor did not feed on mummies of L. mirabilis containing pupae of the parasitoid E. guadeloupae. When unparasitized A. cocois were offered together with parasitized ones, a lower proportion of parasitized prey were consumed compared with when only parasitized prey were offered. The coccinellids often attacked early stages of parasitized prey, even in the presence of available unparasitized prey. A greater proportion of early stage parasitized prey was thus partially or completely consumed compared with that in the late stages. What the study suggested was that adult N. bicolor did in fact recognize and avoid feeding on whitefly that contained late stages of parasitoids in the

presence of unparasitized prey. However, they were unable to discriminate between unparasitized and early parasitized stages of the aleyrodid. Nelson and Parella (1992) and Hoelmer *et al.* (1994) reported similar observations for parasitoids of *B. tabaci* B in relation to the predatory coccinellid *Delphastus pusillus* (Le Conte). They also noted that the tendency of *D. pusillus* and parasitoids to attack different stages of the whitefly increased temporal separation and enhanced the options for their use together in pest management programmes.

Based on information from published and unpublished data, Lynch *et al.* (2001) deduce that <10% of classical biological control introductions have led to population changes in non-targets. While they acknowledge that there is little evidence for extinction caused principally by insect introductions from the 1960s onwards, they also caution against interpreting lack of evidence as a reason for complacency. In Hawaii where *N. bicolor* was introduced nearly 20 years ago, the coccinellid continues to be present and controls occasional outbreaks of *A. dispersus* populations (M. Ramadan, Hawaii Department of Agriculture, personal communication, 1997). There are no reports or evidence of *N. bicolor* causing disruption to, or leading to the extinction of, indigenous Aleyrodidae either in Hawaii or in other Pacific islands where it was introduced. This is significant because disruptions and/or extinctions are more likely to occur in small island situations (Howarth 1991).

Based on field and laboratory data, the following species, all Neotropical in origin, were considered suitable to support reproduction and development of *N. bicolor*: *A. cocois*, *A. maritimus*, *A. pulvinatus*, *A. floccosus*, *L. mirabilis* and *Paraleyrodes* sp. This suggests that *N. bicolor* is a predator of Aleyrodidae. In Africa, 190 species belonging to Aleyrodidae in 46 genera are recorded, of which 133 species in 42 genera are represented in West Africa (G. W. Watson, personal communication, based on BMNH collection, Mound & Halsey 1978, Bink-Moenen 1983, M'Boob and Van Oers 1994). At least some of these species are likely to be attacked by *N. bicolor* when it is introduced. While the prey range of *N. bicolor* within Aleyrodidae cannot be predicted without tests on individual species, there is a weight of evidence to suggest that the species specializes to feed on *Aleurodicus* spp. and *A. flocossus*. There is also some evidence that the prey range may be restricted to Aleyrodidae that produce flocculent waxes. The evidence from Hawaii and elsewhere suggests that it is unlikely that the introduction of *N. bicolor* into Africa will lead to extinction of indigenous species of Aleyrodidae. However, use of the predator in biological control would have to acknowledge that there is a risk that it could feed on certain Aleyrodidae. Whether or not this risk is sufficient to preclude introduction would depend on particular circumstance, e.g. presence of an endangered species within the vulnerable group, environmental implications as well as cost and effectiveness of other methods of control. Sands (1997) suggested that 'for an exotic agent, some development on indigenous flora or fauna may be acceptable, provided that the benefit gained by controlling a pest outweighs any slight risks on the abundance of indigenous species'.

Acknowledgements

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Appendix 1: Breslow Statistics to compare adult *N. bicolor* survival on 12 prey species

Prey species	Control	*A. floccosus*	*A. cocois*	*B. tabaci* B	*M. hirsustus*	*A. gossypii*	*H. cubana*	*A. destructor*	*L. trifolii*	*T. citricida*	*Planococcus* sp.	*Tetranychus* sp.	*Mononychellus* sp.
Control													
A. floccosus	29.8 / <0.001												
A. cocois	14.29 / <0.0001	0.98 / NS											
B. tabaci B	19.92 / <0.0001	0.00 / NS	0.79 / NS										
M. hirsutus	0.05 / NS	29.56 / <0.0001	14.82 / <0.0001	21.15 / <0.0001									
H. cubana	1.38 / NS	24.77 / <0.0001	10.42 / <0.001	17.11 / <0.0001	2.83 / NS	8.12 / <0.01							
A. gossypii	4.71 / <0.05	34.48 / <0.0001	19.93 / <0.0001	23.28 / <0.0001	4.14 / <0.05								
A. destructor	0.68 / NS	27.55 / <0.0001	12.93 / <0.0001	17.63 / <0.0001	0.99 / NS	0.42 / NS	4.26 / <0.05						
L. trifolii	9.62 / 0.005	34.32 / <0.0001	21.13 / <0.0001	24.53 / <0.0001	9.53 / <0.001	16.59 / <0.0001	0.33 / NS	6.09 / <0.05					
T. citricida	37.46 / <0.0001	48.25 / <0.0000	35.87 / <0.0001	33.78 / <0.0001	42.23 / <0.0001	43.43 / <0.0001	6.62 / <0.010	10.76 / <0.001	5.68 / <0.01				
Planococcus sp.	28.37 / <0.0001	44.16 / 0.0001	31.41 / 0.0001	31.76 / 0.0001	30.83 / 0.0001	35.82 / 0.0001	3.70 / 0.05	8.88 / 0.005	2.49 / NS	0.93 / NS			
Tetranychus sp.	21.82 / 0.0001	46.75 / <0.0001	31.34 / <0.0001	31.87 / <0.0001	22.53 / <0.0001	25.81 / <0.0001	2.31 / NS	7.66 / <0.01	1.40 / NS	1.70 / NS	0.11 / NS		
Mononychellus sp.	0.93 / NS	27.43 / <0.0001	14.59 / <0.0001	19.01 / <0.0001	0.90 / NS	3.96 / <0.05	1.37 / NS	0.87 / NS	3.37 / NS	19.26 / <0.0001	13.88 / <0.0001	9.95 / <0.001	

NS, not significant.

Appendix 2:   Breslow Statistics to compare larval survival of *N. bicolor* on seven prey species

Prey species	A. floccosus	A. cocois	B. tabaci b	A. maritimus	M. hirsutus	A. gossypii	A. destructor	Tetranychus sp.
A. floccosus								
A. cocois	0.30							
	NS							
B. tabaci b	13.89	11.34						
	<0.0001	<0.0001						
A. maritimus	10.91	8.95	0.57					
	<0.001	<0.01	NS					
M. hirsutus	14.32	12.58	0.23	0.55				
	<0.001	<0.001	NS	NS				
A. gossypii	12.51	11.37	0.07	0.31	0.05			
	<0.001	<0.001	NS	NS	NS			
A. destructor	19.00	17.00	4.90	0.12	0.99	0.42		
	<0.0001	<0.0001	<0.05	NS	NS	NS		
Tetranychus sp.	0.69	0.17	2.02	2.32	4.04	3.3	11.00	
	NS	NS	NS	NS	<0.05	NS	<0.001	

NS, not significant.