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## Emphasizing Behavioural Host-Range: The Key to Resolving Ambiguous Host-Specificity Results on *Lantana camara* L.

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### Abstract

The host-range extension by natural enemies under laboratory conditions continues to plague the interpretation of host-specificity results. Candidate biocontrol agents presently under evaluation for release on *L. camara* in South Africa accept closely related native plant species. The host-range results of two natural enemies, *Falconia intermedia* (Hemiptera: Miridae) and *Coelocephalapon* sp. (Coleoptera: Brentidae) are analyzed to determine a feasible method for interpreting host-range extensions. Results for standard no-choice and multi-choice trials for both species were compared, to determine the influence these trials have on the interpretation of the accepted host-range. The lantana mirid showed a highly significant difference between the target weed and test plants during multi-choice trials but survival and development was similar in no-choice nymphal survival trials. This indicated that its physiological host-range included a wider range of species than that largely determined by behavioural factors stimulated during multi-choice trials. *Coelocephalapon* sp. showed a significant difference in oviposition performance between the target weed and the test plants during both no-choice and choice trials. The similarity in results during these trials is attributed to the specific oviposition behaviour, which limited host utilization. Similar no-choice trials conducted on *Teleonemia scrupulosa* (Hemiptera: Tingidae), an agent established in the field in South Africa, resulted in an extended host-range. Preliminary results however indicate that this host-range extension does not occur under field conditions. The natural host-range of a candidate biocontrol agent is best determined through the focus on behavioural factors influencing host acceptance. The implications, of using trials that incorporate insect behaviour, during host-specificity screening and risk analysis are discussed.

**Keywords:** extended host-range, host-specificity, no-choice, multi-choice, insect behaviour, risk analysis

### Introduction

An increase in concern for possible effects natural enemies have on native plants has encouraged much discussion on the interpretation of the results of host-specificity experiments in weed biological control (Cullen 1990; Marohasy 1998). The recent inclusion of taxonomically closely related plant species during the screening process (Wapshere 1989) has emphasized the phenomenon of host-range extension under laboratory conditions. Laboratory based screening tends to impose restrictions on an organisms host finding and selection procedure (Cullen 1990; Harris and McEvoy 1995), which usually leads to an extension in the accepted (or real) host-range (Zwölfer and Harris 1971). Predicting an organism's natural host-range as opposed to that obtained during laboratory screening is

receiving much attention (Balciunas *et al.* 1996; Cruttwell Mcfadyen 1998), and has become increasingly important in the safe execution of classical weed biological control.

Forecasting the accepted host-range under field conditions has largely been a matter of judgement, assessing the results from host-specificity screening (Cullen 1990; McClay 1996, Wan and Harris 1997). This information, although prescribed screening procedures vary with the target and natural enemy species, is usually based on results from no-choice and choice conditions broadly representing the physiological and behavioural host-range respectively (Cullen 1990). Motivation for release based on this information usually involves the assessment of the risks (Wan and Harris 1996), and weighing the benefits and possible negative effects (Hill *et al.* 1999). During this process, inadequate discussion has been given to the mechanisms of host selection by different agents, and the degree of emphasis that should be placed on results from no-choice versus choice conditions. In a system where host-range is determined by the adult female host selection process, results from no-choice and choice conditions may vary. Risk assessments in biocontrol programmes should be adjusted to emphasize results which best determine the natural host-range. Where specific behavioural mechanisms restrict the number of acceptable hosts, the results should be accepted to better represent the natural host-range.

This paper analyses the phenomenon of host-range extension of natural enemies under evaluation as possible biocontrol agents on *Lantana camara* in South Africa. The two candidate agents, *Falconia intermedia* (Distant) and *Coelocephalapion* sp. both rely on the female adult for host selection with relatively immobile immature stages. The former is dependent on the adult host selection process to define the acceptable host-range, whereas the later has a behavioural mechanism that restricts the number of acceptable hosts. Host-specificity results for no-choice and multi-choice tests are analyzed to determine factors that influence the interpretation of laboratory host-ranges. The implications for risk assessments in biocontrol are discussed. *Teleonemia scrupulosa* Stål, an established agent of *L. camara* in South Africa, is brought back into the laboratory to determine how the laboratory host-range, under similar screening conditions differ from the realized host-range in the field.

## Materials and Methods

Cultures were maintained on potted plants, and host-specificity experiments were conducted in glasshouse conditions, with temperatures fluctuating between 20 and 30°C. Cultures and experiments were subject to a natural summer photoperiod of about 14 h, at the quarantine facilities of the Plant Protection Research Institute, South Africa. Culture and test plants were maintained in pots and large bags under drip and overhead irrigation, under 50 percent shadenet and fertilized regularly. Although there are four native *Lippia* species described (Arnold *et al.* 1993), two additional entities with different morphological characteristics and chemical composition were treated as separate species and referred to as *Lippia* sp.A. and B. One way ANOVA, Dunn's multiple range tests were conducted to determine the significant difference ( $P < 0.05$ ) of results.

## LIFE HISTORY

### *Falconia intermedia* (Hemiptera: Miridae)

The active, sap-sucking lantana mirid, *F. intermedia*, is endemic to Central America (Palmer and Pullen 1998). Live material was collected in Jamaica, in 1994 (Baars and Nesar 1999), and laboratory based host specificity testing was initiated in 1995. Adults

and nymphs feed on the leaves, causing leaf chlorosis, characterized by the stippling of the dorsal leaf surface. Eggs are semi-embedded into the leaf tissue and partly covered by a faecal deposit.

#### ***Coelocephalopion* sp. (Coleoptera: Apionidae)**

The leaf-petiole and flower-peduncle galling apionid, *Coelocephalopion* sp., is an undescribed species (D. Kissinger, personal communication 1998) first collected from Cárdenas, Mexico in 1997. The adult is a leaf-feeder, and the eggs are oviposited into the leaf-petiole or flower-peduncle. The specific mechanism that governs oviposition appears to operate on a threshold basis (J.R.B., unpublished data) and may limit the range of acceptable host plants (Baars and Nesar 1999). The larvae burrow a short distance into the plant tissue and induce a gall, where it predominantly feeds on proliferated tissue. Feeding damage severs the transport system to the leaf and reduces the flow of solutes.

#### ***Teleonemia scrupulosa* (Hemiptera: Tingidae)**

The sap-sucking tingid, *T. scrupulosa*, is one of the most effective agents established on lantana in South Africa (Baars and Nesar 1999). The general biology of *T. scrupulosa* is well known (Khan 1945; Harley and Kassulke 1971) and it has a heavy impact on lantana in South Africa (Cilliers 1987), and causes periodic defoliation. Releases were made from material imported from Mexico via Hawaii in 1961, and subsequently from other countries (Baars and Nesar 1999). Permission to release was granted on the basis of their performance in Hawaii (Oosthuizen 1964), and minimal additional testing was conducted on plants indigenous to South Africa, prior to their release.

#### **Host specificity**

Host-ranges were determined using no-choice and choice conditions. Under no-choice conditions, nymphal survival trials with relatively mobile immature stages of *F. intermedia* and *T. scrupulosa* were used, whereas adult isolation trials were used for *Coelocephalopion* sp. Choice conditions using multi-choice trials were used to expose *F. intermedia* and *Coelocephalopion* sp. to a more natural situation to stimulate behavioral mechanisms governing host-range acceptance.

#### **No-choice**

Ten 1st instar nymphs of *F. intermedia* were exposed to 68 plant species in 19 families. Nymphs were transferred to potted plants, and development was monitored on a daily basis. Naïve adult *Coelocephalopion* sp. (25 males and 25 females) were isolated on single large potted plants for two consecutive exposures of 14 days, totaling 2 plants per species per replicate. Exposed plants were isolated and development was monitored till adult progeny emerged.

Field collected material of *T. scrupulosa* was reared in quarantine, and nymphs were exposed to 51 plant species in 14 families (10 nymphs per replicate). Nymphal survival to the adult stage was recorded on a daily basis.

#### **Multi-choice**

Experienced adult *F. intermedia* (about 7-10 days) were exposed to 11 to 13 plant species inter-dispersed (minimum overlap) in a choice condition in a gauze cage. The adults (25 males and 25 females) were released from four containers and the trial continued for a period of 18 days. Adults were collected and the plants were isolated for about 7 days, after which the number of fertile eggs (fully distended) deposited per plant, were counted using a dissecting microscope.

Experienced adult *Coelocephalopion* sp. (about 15-20 days) were exposed to ten plant

species with overlapping foliage, which were assigned random positions in a large gauze cage. Adults (50 males and 50 females) were released onto two suspended platforms above the test plants. Trials ran for 21 days, after which adults were collected, plants isolated and larval development and emerging adult progeny was recorded. To promote host selection, choice trials with *F. intermedia* and *Coelocephalapion* sp., included four and two plant species, respectively, which had proved to be unsuitable for adult feeding and immature development.

## Results

Since the biological control programme on *L. camara* was resumed in 1994, no-choice host-specificity screening results indicated that the host-range of natural enemies under laboratory conditions included closely related plant genera (Table 1). Nymphal survival and development and adult feeding and oviposition under no-choice conditions, occurred on other *Lantana* species and on several species in the native, closely related genus *Lippia*. Performance of the natural enemies on other species in the Verbenaceae, was generally poor and were mostly considered to be unacceptable hosts. *Omophoita albicollis* Fabricius, proved to be the exception and accepted unrelated plant species in related families and was rejected as a biocontrol agent (Table 1).

**Table 1.**  
**Preliminary trends in nymphal survival and development and adult feeding and oviposition under no-choice conditions: an indication of the laboratory host-range of natural enemies under evaluation as biocontrol agents on *Lantana camara* (Verbenaceae) in South Africa.**

Order: Family	Insect Species	Congeneric species	<i>Lippia</i> spp.	Other Verbenaceae	Species in other plant families
<b>Acari:</b> Eriophyidae	<i>Aceria lantanae</i> (Cook)	0	0	-	-
<b>Hemiptera:</b> Miridae	<i>Falconia intermedia</i> (Distant)	+	+++ (4)	++	0
Tingidae	<i>Teleonemia vulgata</i> Drake and Hambleton	+++ (3)	+++ (4)	++	+
Membracidae	<i>Aconophora compressa</i> Walker	+	+++ (3)	+	0
<b>Coleoptera:</b> Apionidae	<i>Coelocephalapion</i> sp.	++	+++ (4)	+	0
Chrysomelidae	<i>Alagoasa ?quadrilineata</i> (Harold)	++	+++ (4)	+++ (4)	0
	<i>Omophoita albicollis</i> Fabricius	++	+++ (3)	+++ (4)	+++ (8)
	<i>Charidotis pygmaea</i> Buzzi	+++ (3)	+++ (4)	++	0
<b>Diptera:</b> Agromyzidae	<i>Ophiomyia camarae</i> Spencer	+	+++ (3)	0	0
Tephritidae	<i>Eutreta xanthochaeta</i> Aldrich	-	++	-	-

+ indicates no. of species; + 1 sp., ++ 2 spp., +++ 3 or more spp. with no. of species represented in parenthesis, 0 no survival and development of immature stages, - no test results available.

***Falconia intermedia***

Similar rates of nymphal survival occurred on *Lantana camara* as on several indigenous *Lippia* species (Table 2) during no-choice nymphal survival trials. Significantly low survival rates occurred on *Lantana trifolia* and *Priva cordifolia* and are considered relatively unsuitable as host plants. No survival and development occurred on the native *Lantana rugosa* and the introduced *Lantana montevidensis*. During multi-choice trials adults consistently preferred to feed and oviposit on *Lantana camara* (Table 2). Significantly fewer eggs were deposited on related *Lippia* species, and even less on *Lantana trifolia*, *Alloysia triphylla* and *Priva cordifolia*.

**Table 2.**  
No-choice nymphal survival and adult multi-choice laboratory host-specificity results of *Falconia intermedia*.

Plant species	No-choice Nymphal survival $\xi$ survival/10 $\pm$ SE <sup>a</sup>	No. reps.	Multi-choice Adult oviposition $\xi$ no. eggs $\pm$ SE <sup>a</sup>	No. reps.
<i>Lantana camara</i> *	8.73 $\pm$ 0.3a	15	877.6 $\pm$ 40.5a	9
<i>L. montevidensis</i> *†	0d	5	0d	9
<i>L. trifolia</i> *	1.75 $\pm$ 1.2d	8	2.6 $\pm$ 0.9d	9
<i>Lippia javanica</i>	8.27 $\pm$ 0.4ab	11	28.7 $\pm$ 13.0d	6
<i>L. rehmannii</i>	7.45 $\pm$ 0.31ab	11	39.3 $\pm$ 14.1d	8
<i>L. scaberrima</i>	4.11 $\pm$ 1.0c	9	18.4 $\pm$ 8.3d	9
<i>L. wilmsii</i>	8.43 $\pm$ 0.5ab	7	49.3 $\pm$ 9.3cd	3
<i>Lippia</i> 'Sp. A'	7.60 $\pm$ 0.5ab	5	96.3 $\pm$ 21.4c	3
<i>Lippia</i> 'Sp. B'	8.00 $\pm$ 0.5ab	5	209.7 $\pm$ 16.8b	3
<i>Alloysia triphylla</i> *†	4.33 $\pm$ 0.3c	3	7.5 $\pm$ 4.4d	4
<i>Priva cordifolia</i>	1.70 $\pm$ 0.7d	10	8.9 $\pm$ 5.6d	8

<sup>a</sup> = Means within columns followed by the same letter are not significantly different ( $p < 0.05$ , ANOVA, Dunn's multiple range test). \* = plant species introduced to South Africa (Arnold and de Wet, 1993), † = plant species of ornamental and/or economic value in South Africa.

***Coelocephalopion* sp.**

During no-choice and choice conditions, significantly more adult progeny of *Coelocephalopion* sp., emerged from *Lantana camara* than on any other of the test plants (Table 3). No significant difference in the number of emerged progeny was found to occur between the various test plants.

***Teleonemia scrupulosa***

Nymphal survival and development of *T. scrupulosa*, was similar on *L. camara*, *L. trifolia*, three *Lippia* species tested and *Priva cordifolia* (Table 4). Relatively good nymphal survival occurred on *L. rugosa*, *L. montevidensis*, *Verbena bonariensis* and *Alloysia tri-*

**Table 3.**  
**No-choice adult isolation and multi-choice laboratory host-specificity**  
**results of *Coelecephalopion* sp.**

Plant species	No-choice Adult isolation $\xi$ progeny $\pm$ SE <sup>a</sup>	No. reps.	Multi-choice Adult oviposition $\xi$ progeny $\pm$ SE <sup>a</sup>	No. reps.
<i>Lantana camara</i> *	<b>143.2 <math>\pm</math> 14.3a</b>	<b>5</b>	<b>156.3 <math>\pm</math> 23.4a</b>	7
<i>L. rugosa</i>	2.3 $\pm$ 1.2b	3	1.4 $\pm$ 0.6b	5
<i>L. montevidensis</i> *†	6.5 $\pm$ 1.9b	4	1.7 $\pm$ 0.6b	7
<i>L. trifolia</i> *	6.3 $\pm$ 0.9b	3	5.0 $\pm$ 1.4b	5
<i>Lippia javanica</i>	0.3 $\pm$ 0.3b	3	2.3 $\pm$ 0.5b	3
<i>L. rehmannii</i>	5.3 $\pm$ 2.4b	3	6.3 $\pm$ 1.1b	3
<i>L. scaberrima</i>	12.3 $\pm$ 2.0b	3	2.5 $\pm$ 1.2b	4
<i>L. wilmsii</i>	3.3 $\pm$ 2.0b	3	3.4 $\pm$ 0.7b	5
<i>Lippia</i> 'Sp. A'	4.3 $\pm$ 0.8b	3	11.8 $\pm$ 2.1b	5
<i>Lippia</i> 'Sp. B'	4.3 $\pm$ 0.9b	3	10.3 $\pm$ 3.5b	4
<i>Alloysia triphylla</i> *†	3.7 $\pm$ 0.9b	3	4.0 $\pm$ 1.3b	3
<i>Priva cordifolia</i>	0.0b	3	0.2 $\pm$ 0.2b	5

<sup>a</sup> = Means within columns followed by the same letter are not significantly different ( $p < 0.05$ , one way ANOVA, Dunn's multiple range test). \* = plant species introduced to South Africa (Arnold and de Wet, 1993), † = plant species of ornamental and/or economic value in South Africa.

**Table 4:**  
**Laboratory no-choice nymphal survival host-specificity**  
**results of *Teleonemia scrupulosa*.**

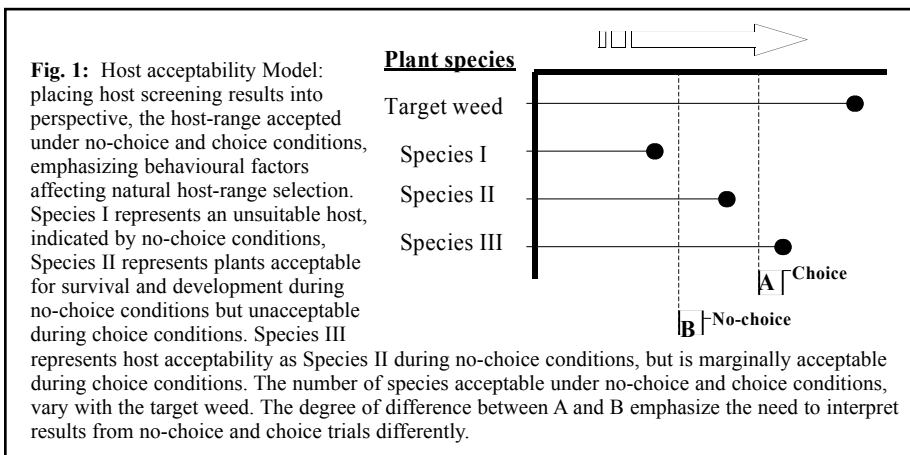
Plant Family	Plant species	No-choice Nymphal survival $\xi$ survival/10 $\pm$ SE <sup>a</sup>	No. reps
Verbenaceae	<i>Verbena brasiliensis</i> *	6.3 $\pm$ 0.8bc	7
	<i>Verbena bonariensis</i> *	2.0 $\pm$ 0.4de	7
	<i>Lantana camara</i> *	<b>8.8 <math>\pm</math> 0.3a</b>	13
	<i>L. rugosa</i> *	6.6 $\pm$ 0.7bc	5
	<i>L. montevidensis</i> *†	6.1 $\pm$ 0.6c	8
	<i>L. trifolia</i> *	7.8 $\pm$ 0.5abc	9
	<i>Lippia javanica</i>	7.4 $\pm$ 0.6abc	8
	<i>L. rehmannii</i>	8.4 $\pm$ 0.4ab	5
	<i>L. scaberrima</i>	7.6 $\pm$ 0.5abc	9
	<i>Phyla nodiflora</i>	3.4 $\pm$ 0.7d	10
	<i>Alloysia triphylla</i> *†	6.3 $\pm$ 0.7bc	3
	<i>Priva cordifolia</i>	6.9 $\pm$ 0.3abc	7
	<i>Holmskioldia titensis</i> †	0.8 $\pm$ 0.2e	4
	Lamiaceae	<i>Teucrium trifidum</i>	2.8 $\pm$ 0.6d
<i>Mentha spicata</i> *		0.4 $\pm$ 0.2e	4
Scrophulariaceae	<i>Buchnera reducta</i>	1.8 $\pm$ 0.6de	6
	<i>Mazus repens</i> *†	0.2 $\pm$ 0.2e	6

<sup>a</sup> = Means within columns followed by the same letter are not significantly different ( $p < 0.05$ , one way ANOVA, Dunn's multiple range test). \* = plant species introduced to South Africa (Arnold and de Wet, 1993), † = plant species of ornamental and/or economic value in South Africa.

*phylla*. Although survival and development occurred on plant species in closely related plant families, survival rates are low and can be considered unsuitable as host plants on a sustainable basis.

## Discussion

Baars and Nesar (1999) argue that the host-range extension of natural enemies to include native *Lippia* species under laboratory conditions may limit the number of agents available for release on *L.camara*, and may jeopardize the success of the biocontrol programme in South Africa. Trends in the host-range extension to include closely related plant species (Table 1) under laboratory conditions emphasize these concerns. As an alternative, open field tests in the country of origin, as a complimentary role to laboratory based host specificity screening, have offered suitable solutions on other weeds (Balciunas *et al.* 1996; Clement and Cristofaro 1995). However this method remains impractical on the weedy entity of *Lantana camara* naturalized in South Africa, as it is a hybrid complex (Stirton 1977) which vaguely represents the original described species. Host-plant relationships of candidate biocontrol agents on the weedy form are thought to present a new association (Baars and Nesar 1999). Host selection by natural enemies in the country of origin will therefore possibly result in limited insight into the potential realized host-range following release in South Africa. As a short term solution to the better interpretation of the acceptable host-range of natural enemies under evaluation for release in South Africa, behavioural mechanisms which underlie host selection, has received deserved attention. It is an accepted phenomenon that laboratory based host specificity screening can lead to the extension in accepted host plants, and often over-estimate the range of plants suitable for survival under field conditions (Mayhew 1998). During no-choice trials, the *lantana* mirid *F. intermedia* survives on several closely related native plant species. Behavioural mechanisms, such as the oviposition behaviour of *Coelocephalopion* sp., limit the number of acceptable plants. For these reasons, amongst others, proposed changes in the screening procedures have been suggested, with a greater emphasis on insect behaviour (Marohasy 1998). A proposed host acceptability model (Figure 1) represents the acceptable host-range as determined by no-choice and choice conditions. The model indicates how the behavioural host-range largely determined by



choice conditions, better represents the natural host selection of candidate biocontrol agents on *Lantana camara*. The extent of difference between number A and B (Figure 1) varies with the natural enemy, as is the case with *Coelocephalopion* sp. where A and B will be close together. The number of plant species accepted under no-choice conditions varies with the target species tested.

Risk analysis using relative suitability scores resulting from no-choice and choice conditions have been afforded similar weighting in the calculation of risk indices (Wan and Harris 1997). Differences in the host-range results for *F. intermedia* during no-choice and choice conditions indicate the need for emphasis to be placed on those trials that predict the acceptable natural host-range (Figure 1; No. A). The effect of key behavioural mechanisms which limit the accepted host-range, as shown by *Coelocephalopion* sp. in no-choice and choice conditions and *F. intermedia* during choice conditions, emphasize the importance of incorporating these factors during risk analysis. Results obtained during no-choice trials should be carefully considered however, as variations in the methods of conducting these trials have led to important observations in broadening of host-range accepted by candidate agents under deprived conditions (Withers 1997).

Preliminary field observations (Baars and Nesar 1999), although conducted on an opportunistic basis, have indicated that the extension in the accepted host-range by *T. scrupulosa* during no-choice laboratory trials are not realized under field conditions. Detailed research has been initiated to determine the extent of the realized host-range of previously released biocontrol agents established in the field in South Africa. Limited nymphal survival of *T. scrupulosa* on unrelated species may explain the reported extension in host-range onto *Sesamum* spp. (Davies and Greathead 1967; Greathead 1968), as a short-term spillover effect.

## Conclusions

Behavioural factors form a key part in interpreting host-specificity screening results and aid in determining the probable natural host-range of a natural enemy under consideration. Where possible, emphasis should be placed on these factors during the consideration of a risk analysis. The host acceptability model (Figure 1) indicates the importance of putting screening results into perspective, and accepting and considering the correct information from each screening procedure. No-choice trials have a valuable role in the host-specificity screening procedure but usually give misleading information in terms of the accepted natural or realized host-range, and results from these trials should be carefully analysed.

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