

Host Specificity and Impacts of *Platyptilia isodactyla* (Lepidoptera: Pterophoridae), a Biological Control Agent for *Jacobaea vulgaris* (Asteraceae) in Australia and New Zealand

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Abstract

Jacobaea vulgaris Gaert. (ragwort) is a serious noxious weed of high fertility pastures in high rainfall regions of southern Victoria and Tasmania in Australia. Biological control of *J. vulgaris* in Australia has been underway since the 1930s. Overseas explorations in Europe identified the ragwort plume moth, *Platyptilia isodactyla* Zeller as a potential biological agent. The host specificity of *P. isodactyla* was tested to determine its safety. Seventy-three plant taxa were screened for *P. isodactyla* phytophagy and survival. *P. isodactyla* development and survival was restricted to a few taxa in the tribes Senecioneae and Asterae, but was negligible on species other than *J. vulgaris*. *P. isodactyla* showed only weak oviposition preference for *J. vulgaris* but this behavior may have been affected by confined test conditions. Only *J. vulgaris* was able to support continued *P. isodactyla* population growth. *P. isodactyla* was released for biological control of *J. vulgaris* in Australia during 1999 and in New Zealand during 2005. Field site damage assessments have shown that *P. isodactyla* can have substantial impact on *J. vulgaris* flowering and survival. A survey of *Senecio* species in close proximity with *J. vulgaris* attacked by *P. isodactyla* during 2004 showed no off-target impacts. *P. isodactyla* is well established in both Australia and New Zealand. Its ability to survive on *J. vulgaris* in wetter habitats is expected to complement other biological control agents enabling it to make a significant contribution to *J. vulgaris* suppression in Australia and New Zealand.

Introduction

Ragwort, *Jacobaea vulgaris* Gaertn. (Asteraceae) is a biennial, perennial or occasionally annual herb that is native to Europe and western Asia (Schmidl, 1972) and has become a serious noxious weed of high fertility pastures in Victoria and Tasmania (Parsons and Cuthbertson, 1992). Annual costs

of *J. vulgaris* control have been estimated at more than \$4 million per year to Australia (McLaren and Micken, 1997). *Jacobaea vulgaris* is also naturalised in New Zealand, Canada, South Africa and the Americas (Walsh, 1999). Several biological control agents have been introduced and released in Australia in an attempt to control *J. vulgaris*. These include the cinnabar moth, *Tyria jacobaeae* L., a seed fly, *Botanophila jacobaeae* (Hardy), two

flea beetle species *Longitarsus flavicornis* Stephens and *L. jacobaeae* Waterhouse and the crown-boring moth *Cochylis atricapitana* (Stephens) (McLaren et al., 1999). This paper describes host specificity testing of the most recently introduced species *Platyptilia isodactyla* Zeller that was originally collected from near Lugo in Spain (43.07°N, -7.27°W). It also documents the damage caused by *P. isodactyla* to *J. vulgaris* and its establishment and impacts in Australia and New Zealand.

Materials and Methods

No-Choice Tests

Overseas exploration by CSIRO had previously identified *P. isodactyla* as a potential biological control agent for *J. vulgaris* in Australia as it was host specific (Cullen et al., 1985) and its larvae caused considerable damage to *J. vulgaris* (Vayssières and Rahola, 1985). *P. isodactyla* larvae could be easily reared using cut leaves and petiole plant samples in Petri-dishes kept hydrated with moistened filter paper in an insectary with temperatures fluctuating between 15°C-25°C and a photoperiod of 12L: 12D. Plants selected for host specificity testing were either purchased from commercial nurseries or grown from seeds, cuttings or whole plants collected from the field. In no-choice feeding tests, neonate larvae that had hatched from eggs were collected and stored in Petri-dishes on moist filter paper. Larvae were placed onto an individual test plant leaf and petiole in a separate Petri-dish and their survival was monitored at five-day intervals. All observations on final larval development were made after five to six weeks. Fresh plant segments were made available to the larvae at all times. In total forty-two plant species were tested using Petri-dish treatments (Table 1).

Whole plant no-choice host specificity tests were conducted in a quarantine facility at the Victorian Department of Primary Industries Frankston, Australia. All tests were carried out on comparably sized whole plants growing in 15 cm pots. Tests were conducted by placing 10 unfed neonate *P. isodactyla* larvae on each test taxon and the plants were enclosed separately in nylon gauze cages maintained in a CT room kept at a constant photoperiod of 16L: 8D and temperature of 26:18°C respectively. *P. isodactyla* adults were collected upon emergence from cages and their emergence times

recorded. Test plants were examined for *P. isodactyla* one week after emergence from the control test plant (*J. vulgaris*) had ended or had become irregular.

Choice Tests

Taxa on which feeding and subsequent emergence of moths occurred during no-choice tests were included in oviposition choice tests (Figure 1). *Senecio linearifolius* A. Rich. and *S. quadridentatus* Labill. were also included in choice tests because of their sympatric distribution with *J. vulgaris* in Australia and the development of *P. isodactyla* larvae on them in no-choice tests. Thirteen choice tests were conducted. Each test comprised one plant of four different test taxa plus the target species, *J. vulgaris*. Choice tests were conducted in a large insect screen cage (2m x 2m x 1.5m) within a quarantine glasshouse receiving natural summer daylight. *P. isodactyla* was being routinely reared on ragwort plants in smaller cages in the same quarantine glasshouse while these tests were being conducted. Two unmated pairs of adult *P. isodactyla* were released into the cage for each test. Test plants were assigned random positions using a Latin square design within the cage and care was taken to ensure test plants did not come in contact with the sides of the cage or each other. Plants were monitored daily for oviposition until both female *P. isodactyla* had died. Plants were then removed and individually caged in a CT room maintained at 16L: 8D photoperiod, and 26°C-18°C temperature to monitor *P. isodactyla* development. Adult emergence was recorded and plants carefully dissected and examined for attack by *P. isodactyla* 60 days after the trial began. To compare the relative development of *P. isodactyla* in this experiment, an arbitrary index of development on each taxon was calculated by scoring a 1 for each first instar found through to a score of 6 for emergence of each adult (Figure 1).

Generation Trials

A generation trial was undertaken to determine whether large populations of the host specificity test species *Senecio lautus lanceolatus* (Benth.) Ali (66 plants), *S. linearifolius* (20 plants) and *Arrhenechthites mixta* (A. Rich.) Belcher (20 plants) and the target species *J. vulgaris* (20 plants) could

sustain two or more generations of *P. isodactyla*. Large screen cages (2m x 2m x 1.5m) were used to test each taxon separately in a quarantine glasshouse at temperatures ranging from 18-25°C with *J. vulgaris*, *S. lautus lanceolatus*, *S. linearifolius* and *A. mixta* being inoculated with 34, 141, 34 and 40 *P. isodactyla* respectively (Table 2). First generation moths emerging from the *S. lautus lanceolatus* treatment were then used to inoculate taxa of *J. vulgaris*, *S. lautus lanceolatus*, *S. lautus maritimus* Ali using eight plants in separate smaller screen cages (inoculation rate of 20, 20 and 18 *P. isodactyla* respectively). The number of *P. isodactyla* that emerged and plant survival were recorded (Table 2).

Field Non-Target Impacts

Three sites (Travers - 38.57°S, 146.38°E, Beech Forest - 38.14°S, 143.34°E, Kemps - 38.36°S, 146.62°E) where *P. isodactyla* had been released three years previously were assessed to determine post-release host specificity of *P. isodactyla*. Whole plants of 30 *J. vulgaris* and 30 native *Senecio* plants were collected at each site during late summer 2003 (all sites) and 2004 (Kemps). At each site, plants were selected at random using two 30m linear transects to sample plants at two meter intervals. In total, 120 native *Senecio* species and 90 *J. vulgaris* were collected, returned to a laboratory, dissected and examined in detail for *P. isodactyla* impacts. Specimens of native *Senecio* species were sent to the National Herbarium for identification.

Insecticide exclusion trial

A field site at Foster North, in Australia (38.59°S, 146.19°E) where *P. isodactyla* had been released three years previously was used to assess *P. isodactyla* impacts on *J. vulgaris*. Vegetation comprised grasses and forbs, including *J. vulgaris*. *P. isodactyla* was well established at the site with approximately 40% of *J. vulgaris* plants showing signs of *P. isodactyla* attack (n=100). No other biological control agent of *J. vulgaris* was present at the site.

In November 2003, 90 *J. vulgaris* rosettes were paired by leaf number and size of the smallest ellipse that could encircle the rosette. Leaf numbers ranged from 4 to 14 and ellipse areas ranged from 19 to 636 cm². Plants showing *P. isodactyla* damage were

not used. Forty-five pairs were designated. Each plant size index (S_w) was calculated by multiplying its rosette ellipse area by leaf number. The 45 pairs of *J. vulgaris* rosettes were ranked by mean S_w . The smallest plant in each successively larger pair was alternately assigned as either treatment or control. S_w ranged from 113 to 6616 for treatment plants and from 110 to 6361 for control plants. A matched pairs t-test (StataCorp 2009) did not suggest that the two sets were from different S_w populations ($p>0.3$).

The insecticide treatment was applied to the treated *J. vulgaris* rosettes using 0.22 g/L a.i. thiocloprid insecticide plus 0.2 mL/L alcohol alkoxyolate surfactant sprayed to runoff using a hand-pressurised sprayer. Applications were made every 3-4 weeks from spring to autumn during 2003-4 and 2004-5. These applications prevented *P. isodactyla* damage on treated plants. The control plants were treated with surfactant only and this gave no protection against *P. isodactyla* damage. Assessments of *J. vulgaris* survival and capitula number were made during February 2005. Treatment effects on survival and flowering were assessed using McNemar's exact test (StataCorp 2009). Pairs were excluded from the analysis if either member flowered during 2004 (could affect survival for following season) or was destroyed by wildlife. Thirty-eight pairs were included in the analysis.

Dispersal and distribution of *P. isodactyla*

The distribution of *J. vulgaris* and establishment of *P. isodactyla* in Australia is shown in Figure 2. Mapped *P. isodactyla* distributions include those from release sites at least two years after release and from sightings of *P. isodactyla* that have spread more than 500 m away from release sites.

Results

No-Choice Tests

No choice host specificity trials showed that survival and development of *P. isodactyla* was greatest on the target species, *J. vulgaris* (55%) and there was no survival of *P. isodactyla* on any species from plant families outside the Asteraceae (Table 1). Within the Asteraceae, several species

within the tribe Senecioneae supported relatively low survival percentages of *P. isodactyla* including *S. madagascariensis* Poir., *S. lautus maritimus*, *S. lautus lanceolatus*, *S. lautus dissectifolius* Ali, *S. lautus alpinus* Ali, *Jacobaea maritima* (L.) Pelser & Meijden, *A. mixta* and *Emilia sonchifolia* (L.) DC. ranging from 5.8% to 1.3%. (Table 1). *Callistephus chinensis* (L.) Nees (Astereae) was the only species to support survival (0.5%) of *P. isodactyla* outside of the Senecioneae tribe. Some *P. isodactyla* larval development was recorded from species within the Tageteae and Cynareae tribes, but no survival was recorded. Even when feeding was evident, the narrow woody nature of the stems of most of the Australian native *Senecio* species tested precluded survival of the *P. isodactyla* larvae. Larvae would bore in and feed initially, but would then exit the plant and not re-enter it.

Choice tests

A summary of results of oviposition choice tests and development index are presented in Figure 1. Though there was substantially more *P. isodactyla* eggs laid on *J. vulgaris*, oviposition preferences were inconclusive. In one of five choice tests conducted for both *S. lautus maritimus* and *S. lautus lanceolatus*, *P. isodactyla* laid more eggs on these species than on the target species, *J. vulgaris*. *P. isodactyla* are sexually mature at emergence and are active at night when mating occurs with moths laying on average 101 eggs (Masri, 1995). In this experiment, only 6% of the expected oviposition occurred on plant foliage suggesting that cage size and/or experimental conditions may not have been conducive to natural *P. isodactyla* oviposition. Pre-alighting cues used in host location often rely heavily on the sensory modality of olfaction (Heard 2000). These trials were undertaken in quarantine glasshouse without air movement which may have restricted *P. isodactyla* searching capacity and partially explain low oviposition rates on test species.

The development index for *P. isodactyla* on *J. vulgaris* (46.9) was more than six times greater than on any other taxon (Figure 1). Other than *J. vulgaris*, the taxa with the next highest *P. isodactyla* development indices were *S. lautus lanceolatus*, *S. lautus maritimus* and *S. linearifolius* (6.6, 2.8 and 2.5 respectively). *P. isodactyla* development was observed on *S. linearifolius* and *J. maritimus* when

no oviposition was observed on the leaves of these species suggesting that eggs may have been laid elsewhere within the cage and larvae have then made their way onto these plants subsequently.

Generation trials

A high inoculation rate of *P. isodactyla* on 66 *S. lautus lanceolatus* plants only resulted in emergence of 58 adults (Table 2). These moths were used to inoculate *J. vulgaris*, *S. lautus lanceolatus* and *S. lautus maritimus* in an attempt to generate a second generation. Only *P. isodactyla* on *J. vulgaris* produced a second generation showing that only *J. vulgaris* will sustain populations of *P. isodactyla*.

Field Non-Target Impacts

None of the 120 native *Senecio* plants (*S. lautus lanceolatus* 23%, *S. linearifolius* 18%, *S. glomeratus* Desf. Ex Poir. 3%, *S. minimus* Poir. 43%, unidentified 3%) examined in detail for *P. isodactyla* collected from three sites where *P. isodactyla* had been previously released in Australia were attacked. *P. isodactyla* was recorded attacking 7% of the 60 *J. vulgaris* plants assessed from the Kemp and Beech Forest sites. No *J. vulgaris* were found at the Travers site.

Insecticide exclusion trial

Field chemical exclusion of *P. isodactyla* from *J. vulgaris* resulted in a greater proportion of treated plants (30) surviving than control plants (23) ($p=0.065$) and more plants flowering (19) than the control plants (9) ($p=0.041$). Capitula production was 262% greater for the treated *J. vulgaris* (68.3 capitula/plant) than the untreated controls attacked by *P. isodactyla* (26.2 capitula/plant) ($p<0.017$).

Dispersal and distribution

Platyptilia isodactyla has been recorded surviving on *J. vulgaris* at more than 40 sites across south-eastern Australia where it is now impacting on *J. vulgaris* populations (Figure 2). The greatest detected dispersal from a release site has been 5.9 km.

In New Zealand, over 200 releases of *P. isodactyla* have been made primarily on the west coast of the South Island, but also throughout the rest of the

country since 2006. Approximately 70% of these releases have established. Monitoring of release sites for establishment and efficacy has shown that within 3 years *J. vulgaris* has been removed from sites where the moth had established (Caryl Coates pers comm.).

Discussion

P. isodactyla was selected as a potential biological control agent for *J. vulgaris* in Australia as *J. vulgaris* was believed to be its primary host. After host specificity trials were well under way it was discovered that *Jacobaea aquaticus* (Hill) Bonnier & Layens (marsh ragwort) was actually the primary host of *P. isodactyla* in Europe (Emmet and Heath 1989), but it also feeds and reproduces readily on *J. vulgaris* (Clifton 2008). *J. aquaticus* is very closely related to *J. vulgaris* as they hybridize and the F1 hybrids are fertile (Kirk et al., 2004). Given the extremely close taxonomic relationships of *J. vulgaris* and *J. aquaticus*, the positive results from host specificity testing and no evidence of *P. isodactyla* feeding on any other asteraceous species in Europe, host specificity testing of *P. isodactyla* was completed. Had *P. isodactyla* oligophagy been known prior to beginning these trials it is unlikely that *P. isodactyla* would have been selected as a biological control agent.

In the present study, some plants of economic importance, others related to the weed as suggested by Wapshere (1974), and representatives of Australian native flora were exposed to larvae of *P. isodactyla* in no choice tests. This was followed by choice tests of species showing some survival in no-choice tests and a generation trial to determine whether *P. isodactyla* could sustain a population on species other than *J. vulgaris*. To be at significant risk from *P. isodactyla*, a taxon needs to attract oviposition, support unretarded development of numerous larvae, sustain damage that impairs plant health and be able to support the growth of a *P. isodactyla* population. The host specificity testing conducted in this study show that *J. vulgaris* was the only species to exhibit all these factors for *P. isodactyla*. There was some survival of *P. isodactyla* in no choice tests but this was generally below 5% compared to survival

on *J. vulgaris* of 55%. It would be highly unlikely that any species could sustain a population with survival rates below 5%.

Following approval by Environment Australia and the Australian Quarantine and Inspection Service, *P. isodactyla* was first released as a biological control agent for *J. vulgaris* in Australia in December 1999. *P. isodactyla* was subsequently introduced and released in New Zealand during 2005. Field assessment of possible *P. isodactyla* off target impacts shows no attack on native Australian *Senecio* species, supporting the results obtained from the host specificity testing. *P. isodactyla* ability to survive on *J. vulgaris* in moist habitats (as with marsh ragwort), may well complement other biological control agents such as *Longitarsus* species that are susceptible to flooding events (Potter et al., 2007) and fill an important biological control ecological niche in the control of *J. vulgaris* in Australia and New Zealand. This study shows that *P. isodactyla* can significantly reduce *J. vulgaris* field populations and reproductive capacity that should result in ongoing agricultural benefits through increased production and reduced reliance on chemical control methods. It should also result in environmental benefits through reduced competition to indigenous forb species that currently overlap distributions with *J. vulgaris*. *P. isodactyla* is now widely established in both Australia and New Zealand and beginning to produce substantial impacts on *J. vulgaris* populations.

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Table 1. No Choice Tests - Host Specificity Results for *P. isodactyla*

Scientific Name	Common Name	No. of larvae (whole plants 10/pot)	No of larvae (Petri-dish 1/Petri-dish)	% Survival to adult instar *
ASTERACEAE				
Senecioneae				
<i>Jacobaea vulgaris</i>	Ragwort	550	110	55
<i>Jacobaea maritima</i>	Dusty Miller	80	60	1.3
<i>Senecio madagascariensis</i>	Fireweed	120		5.8
<i>Senecio lautus maritimus</i>	Coastal Groundsel	80		3.8
<i>Senecio lautus lanceolatus</i>	Fireweed	80		1.3
<i>Senecio lautus dissectifolius</i>		80		1.3
<i>Senecio lautus alpinus</i>	Alpine Groundsel	80		1.3
<i>Arrhenechthites mixta</i>	Purple fireweed	80		1.3
<i>Emilia sonchifolia</i>	Purple Sow Thistle	80		1.3
<i>Senecio hispidulus</i>	Hill Fireweed	120	50	4th
<i>Senecio odoratus</i>	Scented Groundsel	80		4th
<i>Senecio macrocarpus</i>	Fluffy Groundsel	180	50	3rd
<i>Senecio linearifolius</i>	Fireweed	80	24	3rd
<i>Senecio quadridentatus</i>	Cotton Groundsel	180	160	2nd
<i>Senecio squarrosus</i>	Leafy Groundsel	80		2nd
<i>Senecio vellioides</i>	Squarrose Fireweed	80		None
<i>Senecio pterophorus</i>	African Daisy	45	50	None
<i>Senecio glomeratus</i>	Annual Fireweed	80	60	None
<i>Senecio biserratus</i>	Jagged Fireweed	80		None
<i>Senecio vulgaris</i>	Common Groundsel	80		None
<i>Senecio vagus</i>	Saw Groundsel	80		None
<i>Euryops pectinatus</i>	Golden Euryops	80		None
<i>Euryops abrotanifolius</i>	Paris Daisy	80		None
<i>Bedfordia arborescens</i>	Blanket Leaf	80		None
Astereae				
<i>Callistephus chinensis</i>	Chinese Aster	190		0.5
<i>Aster alpinus</i>	Alpine Aster		60	None
<i>Olearia lirata</i>	Snow Daisy Bush	80		None
<i>Bellis</i> sp.	Daisy		20	None
Tageteae				
<i>Flaveria australasica</i>	Speedyweed	80		2nd
<i>Tagetes</i> sp.	French Marigold		60	None
Cynareae				
<i>Cynara scolymus</i>	Globe artichoke	80		3rd
<i>Carthamus tinctorius</i>	Safflower		50	None
Gnaphalieae				
<i>Cassinia aculeata</i>	Dogwood	80		None

Scientific Name	Common Name	No. of larvae (whole plants 10/pot)	No of larvae (Petri-dish 1/Petri-dish)	% Survival to adult instar *
<i>Gnaphalium pensylvanicum</i>	Wandering Cudweed	80		None
<i>Helichrysum luteoalbum</i>	Jersey Cudweed		50	None
<i>Ozothamnus ferrugineus</i>	Tree Everlasting	80		None
Calenduleae				
<i>Calendula</i> sp.	Marigold		60	None
Anthemideae				
<i>Chrysanthemum</i> sp.	Chrysanthemum		60	None
Cichorieae				
<i>Hieracium</i> sp.	Hawkweed		60	None
<i>Lactuca sativa</i>	Lettuce		60	None
<i>Cichorium intybus</i>	Common Chicory		60	None
Coreopsidae				
<i>Dahlia</i> sp.	Dahlia		60	None
Heliantheae				
<i>Helianthus annuus</i>	Sunflower		60	None
<i>Zinnia</i> sp.	Zinnia		60	None
ARALIACEAE				
<i>Astrotricha ledifolia</i>	Common Star-hair	80		None
GENTIANACEAE				
<i>Pelargonium australe</i>	Austral Stork's bill	80		None
<i>Gentianella diemensis</i>	Ben Lomond	80		None
SCROPHULARIACEAE				
<i>Derwentia perfoliata</i>	Austral Storksbill	80		None
<i>Antirrhinum majus</i>	Snapdragon		60	None
CARICACEAE				
<i>Carica papaya</i>	Pawpaw		60	None
FABACEAE				
<i>Acacia melanoxylon</i>	Black Wattle		60	None
<i>Acacia molissima</i>	Sydney Wattle		60	None
<i>Glycine hispida</i>	Soybean		60	None
<i>Medicago littoralis</i>	Coastal Medick		60	none
<i>Trifolium subterraneum</i>	Subterranean Clover		60	None
<i>Arachis hypogaea</i>	Peanut		60	None
GERANIACEAE				
<i>Geranium</i> sp.	Geranium		60	None
LAMIACEAE				
<i>Mentha</i> sp	Mint		60	None
<i>Salvia officinalis</i>	Common Sage		60	None

Scientific Name	Common Name	No. of larvae (whole plants 10/pot)	No of larvae (Petri-dish 1/Petri-dish)	% Survival to adult instar *
MALVACEAE				
<i>Gossypium hirsutum</i>	Upland Cotton		60	None
MUSACEAE				
<i>Musa sapientum</i>	Banana		60	None
MYRTACEAE				
<i>Eucalyptus grandis</i>	Flooded Gum		60	None
<i>Eucalyptus globulus</i>	Blue Gum		60	None
PINACEAE				
<i>Pinus radiata</i>	Radiata Pine		60	None
PROTEACEAE				
<i>Macadamia tetraphylla</i>	Macadamia		60	None
ROSACEAE				
<i>Rosa</i> sp.	Rose		60	None
<i>Rubus</i> L. sp	Berries		60	None
VITACEAE				
<i>Vitis vinifera</i>	Grape vine	80		None
POACEAE				
<i>Oryza sativa</i>	Rice		60	None
<i>Phalaris aquatica</i>	Phalaris		60	None
<i>Saccharum officinarum</i>	Sugar		60	None
<i>Sorghum bicolor</i>	Sorghum		60	None

* Last instar stage observed

Table 2. Generation trial. Survival and impacts of *P. isodactyla* on Australian native *Senecio* species and *J. vulgaris*.

Taxon	No. of Plants	<i>P. isodactyla</i> inoculation rate	<i>P. isodactyla</i> emergence		% Plant survival
			Total	Per Plant	
First Generation (F1)					
<i>J. vulgaris</i>	20	34	173	8.65	0
<i>S. lautus lanceolatus</i>	66	141	58*	0.88	27.3
<i>S. linearifolius</i>	20	34	0	0	100
<i>A. mixta</i>	20	40	2	0.1	100
Second Generation (F2)					
<i>J. vulgaris</i>	8	12*	28	3.5	0
<i>S. lautus lanceolatus</i>	8	21*	0	0	87.5
<i>S. lautus maritimus</i>	8	20*	0	0	37.5**

* All 2nd generation trials used moths from *S. lautus lanceolatus* F1 generation.

** Also found infested with the native moth, *Nyctemera amica* (White).

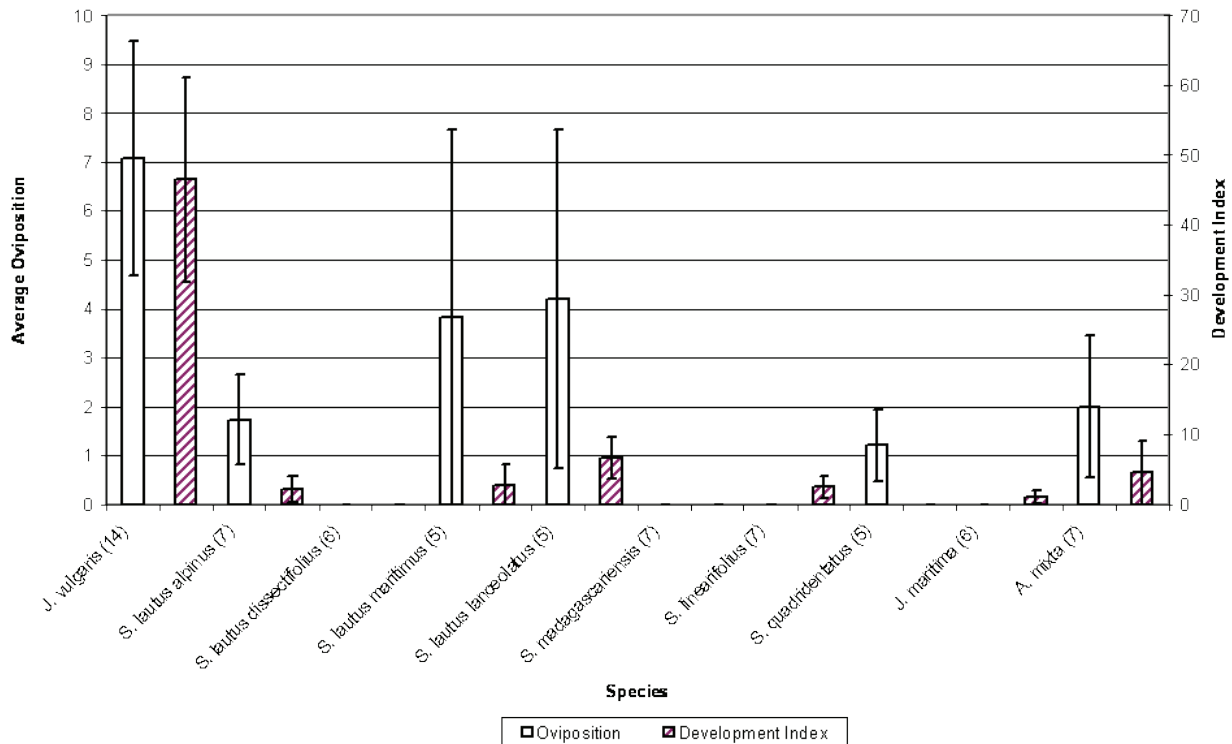


Figure 1. Average oviposition and development index for host specificity latin square choice tests for *P. isodactyla*. Numbers in parenthesis represent number of replications.

Development Index = ((I1x1)+(I2x2)+(I3x3)+(I4x4)+(Px5)+(Ax6))/n Where:

DI = development index: I1, I2, I3, I4, P, A equal number of first, second, third and fourth Instar larvae, pupae (not including emerged cases) and adults respectively found in dissected plants of each separate test taxon in all tests. n=number of test plants.

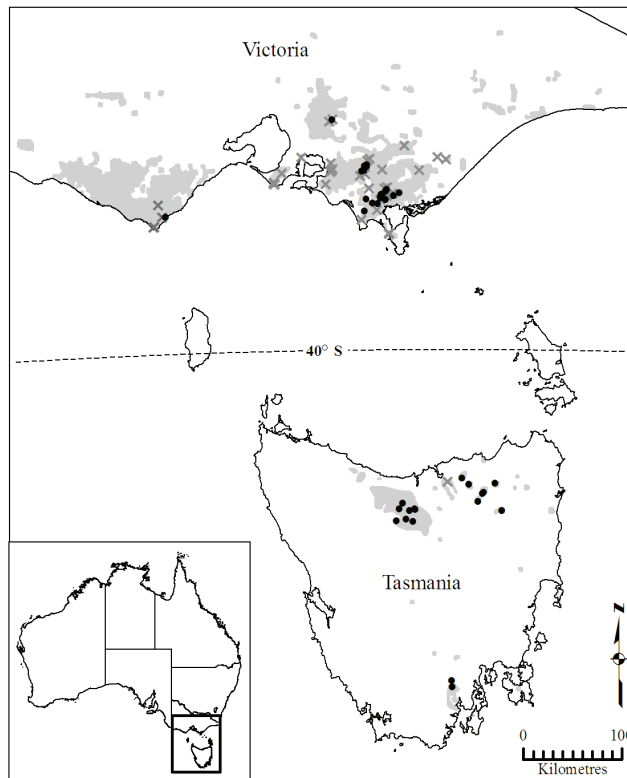


Figure 2. Distribution of *J. vulgaris* in Australia (grey).

• *P. isodactyla* found, X *P. isodactyla* not found.