

Ecology of *Leptocoris* Hahn (Hemiptera: Rhopalidae) soapberry bugs in Australia

Scott P Carroll,^{1,2*} Jenella E Loye,^{1,2} Hugh Dingle,^{1,2} Michael Mathieson³ and Myron P Zalucki²

¹Department of Entomology, University of California, Davis, CA 95616, USA.

²Department of Zoology and Entomology, University of Queensland, St. Lucia, Qld 4072, Australia.

³Environmental Protection Agency, Wildlife Ecology Unit, 80 Meiers Road, Indooroopilly, Qld 4068, Australia.

Abstract

Soapberry bugs are worldwide seed predators of plants in the family Sapindaceae. Australian sapinds are diverse and widespread, consisting of about 200 native trees and shrubs. This flora also includes two introduced environmental weeds, plus cultivated lychee (*Litchi chinensis* Sonn.), longan (*Dimocarpus longan* Lour.) and rambutan (*Nephelium lappaceum* L.). Accordingly, Australian soapberry bugs may be significant in ecology, conservation and agriculture. Here we provide the first account of their ecology. We find five species of *Leptocoris* Hahn in Australia, and list sapinds that do and do not serve as reproductive hosts. From museum and field records we map the continental distributions of the insects and primary hosts. Frequency of occupation varies among host species, and the number of hosts varies among the insects. In addition, differences in body size and beak length are related to host use. For example, the long-beaked *Leptocoris tagalicus* Burmeister is highly polyphagous in eastern rainforests, where it occurs on at least 10 native and non-native hosts. It aggregates on hosts with immature fruit and commences feeding before fruits dehisce. Most of its continental range, however, matches that of a single dryland tree, *Atalaya hemiglauca* F. Muell., which has comparatively unprotected seeds. The taxon includes a smaller and shorter-beaked form that is closely associated with *Atalaya*, and appears to be taxonomically distinct. The other widespread soapberry bug is the endemic *Leptocoris mitellatus* Bergroth. It too is short-beaked, and colonises hosts phenologically later than *L. tagalicus*, as seeds become more accessible in open capsules. Continentally its distribution is more southerly and corresponds mainly to that of *Alectryon oleifolius* Desf. Among all host species, the non-native environmental weeds *Cardiospermum* L. and *Koelreuteria* Laxm. are most consistently attacked, principally by *L. tagalicus*. These recent host shifts have biocontrol implications. In contrast, the sapinds planted as fruit crops appear to be less frequently used at present and mainly by the longer-beaked species.

Key words *Alectryon*, *Atalaya*, *Cardiospermum*, diet breadth, *Koelreuteria*, *Leptocoris*, plant–insect interactions, soapberry bug.

INTRODUCTION

The rhopalid genus *Leptocoris* Hahn consists of approximately 40 species of medium to large hemipterans occurring in tropical and subtropical regions of the eastern hemisphere (Göllner-Scheidung 1983). It is one of the three genera comprising the subfamily Serinethinae; the remaining two are *Boisea* Kirkaldy with two species each in Africa and North America, and *Jadera* Stål with 17 species in North and South America (Göllner-Scheidung 1983). These insects are seed predators dependent on plants of the Sapindales, especially the Sapindaceae or ‘Soapberry’ family (Schaefer & Chopra 1982; Carroll & Loye 1987). Hence we introduce the term ‘soapberry bugs’ as a common name for that subfamily. They are

often brightly coloured and may form aggregations numbering in the thousands to perhaps millions (Carroll & Loye 1987).

One soapberry bug, *Jadera haematoloma* H.-S., is known for its rapid adaptation to host plants recently introduced into its North American range (e.g. Carroll *et al.* 2001, 2003a). This evolution has occurred in 50 years or less and involves a complex set of traits. These traits include: (i) the length of the mouthparts (labium), termed ‘beak length’; (ii) preference for the introduced hosts over the former native hosts; (iii) higher fitness on the new hosts relative to the old; and (iv) changes in flight morph frequency as influenced by host distribution and fruiting phenology. Likewise, in eastern Australia, some of the same host taxa (*Cardiospermum* L., *Koelreuteria* Laxm.) are horticultural introductions that have become serious environmental weeds (Batianoff & Butler 2002, 2003; Carroll *et al.* in press). These invasive species have been colonised by at least one of the native soapberry bugs (*L.*

*Author to whom correspondence should be addressed (email: spcarroll@ucdavis.edu).

tagalicus Burmeister). Populations of that bug are undergoing rapid evolution in beak length in response to fruit size of the new hosts (Carroll *et al.* 2005). A long-term goal of our research is to document the extent to which Australian soapberry bugs are colonising and adapting to *Cardiospermum* and *Koelreuteria* and potentially paralleling the evolution of similar bugs in North America. Any such host range expansion may contribute to the insects' capacity to control these weedy genera. At the same time, colonisation of sapinds grown as fruit crops (lychee and its relatives) by soapberry bugs could damage production.

Gross (1960) reviewed the species of *Leptocoris* Hahn of the Indo-Pacific and Australian regions. He treated three species in Australia: the endemic *L. mitellatus* Bergroth and the widespread *L. tagalicus* Burmeister and *L. rufomarginatus* F. A fourth species, *L. vicinus* Dallas from Darwin (Northern Territory) was included with the others in the catalogue of Australian Heteroptera: Pentatomorpha by Cassis and Gross (2002). In this paper, we add a fifth resident species to the list, *L. isolatus* Distant in tropical Queensland, which is the first record of this species for Australia.

Despite the fact that *Leptocoris* is frequently collected and often noted for its abundance on planted sapinds, little is known about its basic ecology in Australia or anywhere else. In this paper, we provide the first detailed account of the plants used by Australian *Leptocoris* for juvenile development and reproduction. We map the insects' distributions and examine the relationship between the geographical ranges of the principal hosts and the bugs that exploit them. We make basic morphological comparisons within and among the insect species that may relate to host use. Finally we compare the extent to which the species have colonised the invasive *Cardiospermum* and *Koelreuteria*, as well as horticultural crops.

METHODS

Museum collections

During 2001–2004 we examined all *Leptocoris* specimens held in the following collections: the Australian Museum (Sydney), the Australian National Insect Collection (Canberra), the Queensland Museum (Brisbane), the University of Queensland Insect Collection (Brisbane), the South Australia Museum (Adelaide), the Western Australia Museum (Perth), Museum Victoria (Melbourne), Museum and Art Gallery of the Northern Territory (Darwin), Department of Business, Industry and Resource Development (Darwin), CSIRO-Mareeba (Queensland) and CSIRO-Long Pocket (Queensland).

We sexed specimens and recorded label data. Identifications were made with reference to the descriptions and illustrations of Gross (1960). For each individual we measured maximum pronotum width, body length (clypeus to distal tips of the folded wings) and beak (labial) length, using handheld Mitutoyo 500–133 digital calipers with a 0.01 mm measurement increment. Label data on plant associations were rare;

when present we assumed that they were accurate, but we discounted records not on sapinds (mainly *Eucalyptus* and *Acacia*) as host records, because to our knowledge no species of Serinethine rhopalid has ever been well documented as feeding on the seeds of plants other than Sapindaceae for juvenile development and reproduction.

For *L. tagalicus*, we divided specimens into two forms based on differences in body size, and to a lesser extent, colouration. The 'interior' form was much smaller with more orange or red, and occurred mainly to the west of longitude 150.5°W. The larger 'coastal' form was usually darker in colour and occurred mainly to the east of longitude 152.5°W except in northernmost Northern Territory. These geographically based designations, noted from museum specimens, are best regarded as tentative, as our field results described here suggest that host associations more meaningfully predict the distributions of the two morphs.

Field studies

Field populations were located by searching for fruiting sapinds. Main field periods were November 2001–January 2002 and November 2003–April 2004, and August 2004. In Queensland, the two major road transects were: (i) in November 2003, the Bruce Highway between Brisbane and Cairns, continuing north via Mareeba and Daintree–Cooktown to Iron Range National Park near the northern tip of the Cape York Peninsula; and (ii) in December 2003 Atherton to Charters Towers, Emerald, Roma, and thence to Brisbane. Additional Queensland field surveys focused on wet and dry rainforest, plus woodland, within a 200 km radius of Brisbane at sites indicated by botanists. In New South Wales, most sampling was by watershed on both eastern and western slopes in the Northern Rivers district between Ballina and the Queensland Border. In Northern Territory, sampling was west from Alice Springs to Glenn Helen (January 2001), and east and south of Darwin (April 2004). Surveys for *Cardiospermum* and *Koelreuteria* in Western Australia were in the vicinity of Perth in December 2000.

Sapinds in the field were scored on the presence and absence of fruit, the size, maturity and condition of any fruit crop, and the presence, age, reproductive condition and behaviour of soapberry bugs. Host plants were those on which seed feeding and reproduction (mating, presence of nymphs) were observed. We have included as hosts some species for which we have only one or a few records because it seems sensible to be inclusive at this early stage in our knowledge of *Leptocoris*. Plants were identified with reference to Reynolds (1985) and in consultation with botanists of the Queensland Herbarium in Brisbane. Field insects were measured and classified in the same manner as museum specimens. In addition, a subset of individual adults collected in the Brisbane region were weighed alive in the laboratory within 24 h of collection with a Mettler Toledo analytical balance (0.1 mg measurement increment).

At one field site (Sherwood Forest Park, Brisbane), we conducted more detailed observations on colonisation phenol-

ogy and host use. Here we estimated insect numbers either by counting individuals on the ground under the trees, on the trunks and branches, and in the canopy, or when quiescent, by counting the number of individuals in 10 clusters (in foliage) and then counting the number of clusters. Quiescent bugs were those suspended motionless beneath foliage. Feeding bugs were those with beaks inserted into host fruits. Mating bugs were those in copula. Such behavioural samples were instantaneous (i.e. as encountered rather than of focal individuals), and so give estimates of the percentage of individuals engaged in a particular activity at one point in time. Comparatively few bugs were in the tops of trees and so we consider our counts and estimates to be reasonably complete. However, we regard the resulting values to be rough estimates and report them as such.

Mapping

Distribution maps for host plant species were generated using ESRI ArcGIS (version 8.3) software by adapting data from the Australian Virtual Herbarium. Insect distributions were plotted, using the same ESRI spatial package, from locality data obtained from museum collections and field observations. When locale data lacked coordinates (most instances), we estimated latitude and longitude with the 'Place Name Search' of Geoscience Australia at the website <http://www.ga.gov.au/map/names/>.

Analyses

For morphological measurements of insects, we computed descriptive statistics and compared means (Wilcoxon rank-sum testing) with SAS JMP statistical software (version 5.0.1.2 for Macintosh).

RESULTS

Body size and beak length

While conforming to a general body plan, species vary considerably in body size and markings. Based on maximum pronotum width (as an indicator of overall body size), four size classes were present among the six species and forms (Table 1). A roughly similar pattern appeared for body length.

Leptocoris tagalicus exists in two forms, with its 'interior' form being the smallest of all Australian soapberry bugs, scarcely half the live weight of the 'coastal' form. At the other extreme is *L. rufomarginatus*, which averages three times the live weight of interior *L. tagalicus*. Compared with the other species, *L. rufomarginatus* was long-winged and narrow-bodied. *Leptocoris mitellatus* is the heaviest and broadest-bodied for its length. For all species, males averaged about 20% smaller in linear dimensions and 30% lighter in weight than did females.

Beak length was not as closely related to the two linear body size dimensions as these latter were to one another. Three beak length classes were statistically distinguishable (Table 1). Beak length was relatively the longest in coastal *L. tagalicus*, averaging almost 54% of body length, while it was 50% or less in all other cases.

Relation to sapinds and geographical range

Leptocoris bugs are widespread in Australia, with *L. tagalicus* and *L. mitellatus* occurring in most regions of the continent (Fig. 1). *Leptocoris rufomarginatus* is relatively restricted to the far eastern and northern moist subtropics and tropics, *L. isolatus* to the eastern moist tropics and *L. vicinus* to the vicinity of Darwin.

Our field observations showed that *Leptocoris* species differed substantially in the number of host plant species with which they associate (Table 2). *Leptocoris tagalicus* was the most polyphagous, occurring on at least 10 species of sapinds. All observations for native hosts (species of *Alectryon* Gaertner, *Allophylus* L., *Atalaya* Blume, *Elattostachys* (Blume) Radlk.) as well as for the introduced *Cardiospermum* and *Koelreuteria* are breeding records. In contrast, observations for soapberry bugs on cultivated lychee (*Litchi chinensis* Sonn.), longan (*Dimocarpus longan* Lour.) and rambutan (*Nephelium lappaceum* L.) are from museum records and none directly indicated seed predation or reproduction.

On a continental scale, the distribution of the two forms of *L. tagalicus* accord well with those of their host plants (Fig. 2). The 'coastal form', which is associated with dry and wet rainforest hosts, occurs within their range in the east. The range of the interior form follows that of Whitewood (*Atalaya hemiglauca* F. Muell.) across the northern half of the continent.

Table 1 Body size and beak length comparisons for females of *Leptocoris* in Australia

Species/form	Pronotum width	Body length	Beak length	Live weight
<i>Leptocoris tagalicus</i> 'interior'	2.89 ± 0.16 (121) a	10.99 ± 0.61 (118) a	5.47 ± 0.30 (121) a	31.9 ± 5.6 (10) a
<i>Leptocoris tagalicus</i> 'coastal'	3.29 ± 0.19 (27) b	13.25 ± 0.85 (27) b	7.11 ± 0.48 (28) b	57.9 ± 8.5 (18) b
<i>Leptocoris mitellatus</i>	3.35 ± 0.29 (229) b	12.41 ± 0.76 (228) c	5.74 ± 0.39 (204) a	79.6 ± 16.4 (12) c
<i>Leptocoris isolatus</i>	3.59 ± 0.28 (11) c	14.25 ± 0.92 (11) d	6.82 ± 0.48 (11) b	–
<i>Leptocoris vicinus</i>	3.71 ± 0.37 (2) c	14.12 ± 0.94 (2) b,d	6.98 ± 0.32 (2) b	–
<i>Leptocoris rufomarginatus</i>	4.64 ± 0.20 (15) d	17.69 ± 0.74 (15) e	8.34 ± 0.40 (14) c	93.1 ± 15.0 (16) d

Values are mean ± SD in mm or mg. Sample sizes are in parentheses. Data are from museum specimens, except for 'Live weight', which is from field-collected individuals. For *L. tagalicus*, 'interior' specimens are principally those from west of longitude 150.5°E and 'coastal' specimens are those to the east of longitude 150.5°E plus a few from far northern Northern Territory. Means joined by letters within columns are not significantly different at $P < 0.05$ in Wilcoxon rank-sum tests

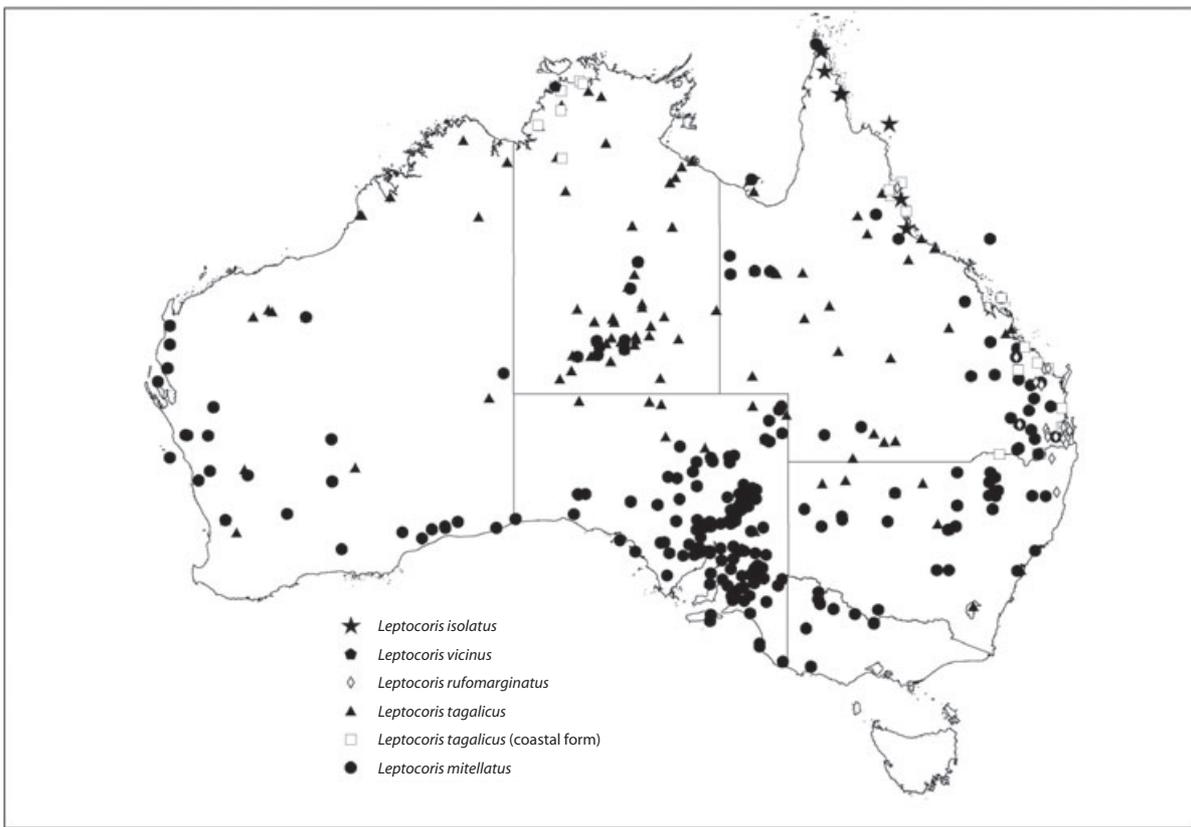


Fig. 1. Australian spatial distributions of *Leptocoris* species.

We found 'interior form' *L. tagalicus* on a majority of fruiting Whitewood inspected around Alice Springs (Northern Territory), as well as in central and southern Queensland (Table 3). In addition, we found it on unusual near-coast populations of Whitewood at dry sites near Marlborough, Queensland (ca. 22°S, 150°W). When we sampled within longitudes rare in the museum collections, and near the zone intermediate between the 'coastal' and 'interior' designations (ca. longitude 152°30' W), we found 'interior' *L. tagalicus* form on the dry rainforest congener Scrub Whitewood (*Atalaya salicifolia* (A. DC.) Blume).

In our field surveys we found the 'coastal' *L. tagalicus* form also occurred in dry rainforests at the intermediate longitudes. However, instead of frequenting *Atalaya*, they were on Scrub Boonaree (*Alectryon diversifolius* F. Muell.) and *Elatostachys xylocarpa* (Cunn. ex F. Muell.) Radlk. in summer, and on *Alectryon connatus* Radlk. in winter. All three of these hosts commonly grow in mixed stands with Scrub Whitewood, and while small numbers (<5%) of each morph occurred on the alternate host genera, we did not observe mixed matings.

In association with the non-native weeds Balloon Vine (*Cardiospermum grandiflorum*) Sw. and Goldenrain Tree (*Koelreuteria elegans*) (Seeman) A.C. Smith, we found coastal form *L. tagalicus* in isolated locales well within the so-called interior region. For example, such a population occurs on the balloon vine along the Macintyre River in Goondiwindi, Queensland, where we also found it on adjacent Boonaree

(*Alectryon oleifolius* Desf.) and *A. hemiglauca* in a botanical garden. On goldenrain tree, coastal form bugs occur at least as far west as Roma, Queensland (ca. 26°44' S, 148°40' W). To sum up these geographical results for *L. tagalicus*, small-bodied 'interior' bugs appear to be a host race associated with trees in the genus *Atalaya*. The much larger 'coastal' form is a rainforest species, and its range may be spreading into interior dryland habitats as it colonises plantings and escapes of the non-native ornamentals.

We found *L. tagalicus* at a majority of the fruiting host sites sampled, but their frequency varied among the host species (Table 3). In contrast to the native hosts, the two introduced host species were occupied in *all* cases. At these hosts, *L. tagalicus* was also much more abundant than any congeners.

The other common and geographically widespread soapberry bug, *L. mitellatus*, is capable of producing aggregations of thousands of adults and juveniles in stands of fruiting *A. oleifolius* and on *Alectryon subcinereus* (A. Gray) Radlk. It is patchy on *A. oleifolius*, little sampled on *A. subcinereus* and typically rare on other host species (Tables 2,3). The body of its continental distribution corresponds to that of the three subspecies of *A. oleifolius* (Fig. 3). In many areas of southern and west-central Australia, *A. oleifolius* is the only sapind present other than *Dodonea* Miller spp. (which appear not to be hosts). Geographically, the insect tracks this host to remote corners of the plant's range, a geographical concordance suggesting this sole endemic *Leptocoris* is very closely associated with *A. oleifolius*. Note, however, that we did record it breed-

Table 2 Host plants of soapberry bugs in Australia

Soapberry bug	Host plant
<i>Leptocoris tagalicus</i> Coastal form	<i>Alectryon connatus</i>
	<i>Alectryon coriaceus</i> (Benth.) Radlk.
	<i>Alectryon diversifolius</i>
	<i>Alectryon oleifolius</i>
	<i>Alectryon subcinereus</i>
	<i>Alectryon subdentatus</i> (F. Muell. ex Benth) Radlk.
	<i>Alectryon tomentosus</i>
	<i>Allophylus cobbe</i>
	<i>Elattostachys xylocarpa</i>
	<i>Cardiospermum grandiflorum</i> †
	<i>Dimocarpus longan</i> †
	<i>Koelreuteria elegans</i> †
	<i>Litchi chinensis</i> †
	Interior form
<i>Atalaya salicifolia</i>	
<i>Leptocoris mitellatus</i>	<i>Alectryon oleifolius</i>
	<i>Alectryon subcinereus</i>
	<i>Atalaya hemiglauca</i>
	<i>Elattostachys xylocarpa</i>
	<i>Koelreuteria elegans</i> †‡
<i>Leptocoris rufomarginatus</i>	<i>Alectryon diversifolius</i>
	<i>Alectryon tomentosus</i>
	<i>Allophylus cobbe</i>
	<i>Elattostachys xylocarpa</i>
<i>Leptocoris isolatus</i>	<i>Allophylus cobbe</i> §
	<i>Litchi chinensis</i> †
	<i>Nephelium lappaceum</i> †
<i>Leptocoris vicinus</i>	<i>Schleichera oleosa</i> †

†Introduced species. ‡*L. mitellatus* was reproductive on *K. elegans* at one of only four occupied sites. §Postulated; see Discussion section.

ing on *A. subcinereus* and *A. tomentosus* (F. Muell) Radlk. to the east of the range of *A. oleifolius*, as well. *Alectryon tropicus* S. Reyn. should be investigated as a possible host for *L. mitellatus* in the drier areas on and adjacent to the Atherton Tablelands from which specimens in the CSIRO Mareeba collections were taken.

Like the coastal form of *L. tagalicus*, *L. rufomarginatus* is mainly restricted to subtropical and tropical moist forest habitats of the eastern and northern coastal margins of the continent (Fig. 1, Table 2). In the east it ranges from northern New South Wales (ca. 30°S at Dorrig National Park) northward to Cairns (17°S). In the Northern Territory we found a single female feeding on *Allophylus cobbe* (L.) Blume. In museum collections we located a total of 44 specimens (females + males), far fewer than for *L. tagalicus* or *L. mitellatus* (332 and 373 adults, respectively). In no instances did we find it occupying introduced hosts. We found it more often, but without higher incidence, on *A. tomentosus* than on *A. diversifolius*, *E. xylocarpa* or *A. cobbe* (Table 3).

Leptocoris isolatus occurs in far north-eastern Queensland (Fig. 1). Just 23 specimens are in museum collections, representing eight collection events. We made no field observations of this species. Wildland collections were in the Cape York Peninsula, principally in eastern near-coast locales. Farther to the south, but still in tropical north Queensland, were two

collections, one on rambutan at Miriwinni, and another on lychee at Ingham. These collections on the planted fruit crops appear to be geographical range extensions, although we have no evidence of seed predation or breeding on those plants.

Leptocoris vicinus appears restricted within Australia to the tropical Northern Territory. All known specimens (two females and five males) were taken in a single collection by Gross in Darwin in 1961 (South Australian Museum). In the field we have found it breeding on seeds of the introduced ornamental tree *Schleichera oleosa* Lour. near Darwin.

Beyond the species in the nine genera listed in Table 2, we sampled for soapberry bugs at fruiting plants of an additional 17 species of sapinds in 11 genera in New South Wales, Northern Territory and Queensland, including four species of *Dodonea*. No soapberry bugs were observed on these species (Table 4). The number of plants inspected ranges from one to 55 depending on the species. In addition to the need for further sampling at many of these species, the final 13 genera of Australian sapinds also remain to be sampled while in fruit.

Phenological and behavioural contrasts

During field studies from November 2003 to April 2004, notable contrasts were observed in host use biology among *L. tagalicus*, *L. rufomarginatus* and *L. mitellatus* co-occurring on *A. tomentosus*, *A. diversifolius* and *E. xylocarpa*. Because foraging ecology has not been described for this genus, we provide a concise record here. Observations at a planting of three large *A. tomentosus* at one intensively studied site in Brisbane were typical of that observed at several others and are summarised here. At that site, flowering was completed and development of many thousands of fruit had commenced by early November. At that time, thousands of inactive adult *L. tagalicus* were present in clusters beneath leaflets (Table 5). Adults removed to the laboratory and given ripe seeds of *K. elegans* fed within 5 min, and mated within 1 h.

This pattern of quiescence and clustering in the field continued until early January, after which clustering gradually diminished, bugs became active on developing fruits, and there was some feeding and mating. However, the number of individuals declined precipitously throughout January and February, with little evidence of successful reproduction. By early March, 28 (33%) of 84 adults surveyed on the ground were dead. Adult numbers continued to decline into late March, when renewed quiescence was observed, and about 200 young nymphs were counted beneath the trees.

Leptocoris rufomarginatus joined *L. tagalicus* at the site in January. In contrast to *L. tagalicus*, mating took place in the absence of feeding. As seeds approached maturity, feeding became more common in instantaneous samples, and eggs were laid on the undersides of leaves. Advanced nymphs identified in early March suggest that oviposition first took place in late January. However, like *L. tagalicus*, the number of adults declined during February. In early March, we determined that less than 10% of seeds were actually filled and viable, perhaps explaining these declines. (Similar scant viability was observed at the same time at other *A. tomentosus*

Fig. 2. Australian distribution of *Leptocoris tagalicus* and major host species. The hosts *Alectryon tomentosus*, *Elattostachys xylocarpa*, *Allophylus cobbe* are combined (hatching); of those three species, only *A. cobbe* occurs in Northern Territory, and *E. xylocarpa* is restricted to relatively more inland areas (dry rainforest) in southern Queensland and adjacent northern New South Wales.

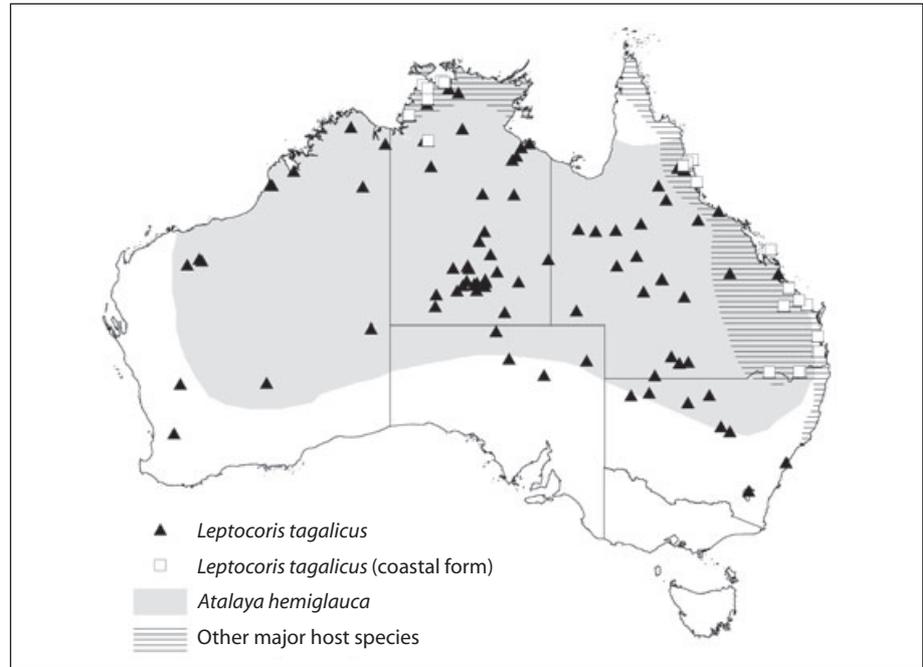


Table 3 Frequency of occurrence of three *Leptocoris* species within and among fruiting plants of the host species

Host species	No. of sites	<i>Leptocoris tagalicus</i>	<i>Leptocoris mitellatus</i>	<i>Leptocoris rufomarginatus</i>	No. of plants	<i>Leptocoris tagalicus</i>	<i>Leptocoris mitellatus</i>	<i>Leptocoris rufomarginatus</i>
<i>Alectryon connatus</i>	4	4	3	2	4	4	3	2
<i>Alectryon coriaceus</i>	1	1	0	0	1	1	0	0
<i>Alectryon diversifolius</i>	2	2	0	1	10	8	4	1
<i>Alectryon oleifolius</i>	3	1	2	0	20	1	4	0
<i>Alectryon subcinereus</i>	1	0	1	0	1	0	1	0
<i>Alectryon subdentatus</i>	1	1	0	0	1	1	0	0
<i>Alectryon tomentosus</i>	18	17	3	5	28	25	5	5
<i>Allophylus cobbe</i>	1	1	0	1	1	1	0	1
<i>Atalaya hemiglauca</i>	22	14	0	0	157	35	0	0
<i>Atalaya salicifolia</i>	3	2	0	0	4	3	0	0
<i>Elattostachys xylocarpa</i>	3	2	1	1	11	6	1	1
<i>Cardiospermum grandiflorum</i> †	25	25	1	0	–	–	–	–
<i>Koeleruteria elegans</i>	17	17	4	9	37	37	4	0

†Individual plants were not readily distinguishable at *C. grandiflorum* sites.

and *A. diversifolius* sites.) Of 12 adults on the ground, 11 (92%) were dead. While adults continued to be scarce through March, essentially all juveniles approaching maturity were of this species.

Leptocoris mitellatus arrived at the site only as seeds neared maturity. No quiescence was observed and feeding and mating quickly became relatively common, and adults of this species outnumbered those of the other two within 2 weeks. In contrast to the other species, the majority of individuals were found on the ground. Of these, only three (1.6%) of 190 were dead. By late March adult number had declined in this species as well, but several hundred nymphs were present, principally younger instars.

Finally, on the non-indigenous environmental weeds *C. grandiflorum* and *K. elegans*, *L. tagalicus* was virtually the exclusive seed predator (Table 3). In most of our observations it is the only species on these hosts. A second species sometimes present was *L. mitellatus*, but even when observed, it is

outnumbered on the order of 100 to one by its congener. Based on data collected between March 2003 and June 2004, bugs are on balloon vine throughout the year and usually in numbers that are higher on vines with a greater number of developing pods. Numbers of bugs, however, rarely exceed a few tens or hundreds of individuals on any given vine, in contrast to thousands of nymphs and adults found on goldenrain trees in the autumn and early winter. Lower numbers on balloon vine are consistent with the generally lower number of fruits present compared with goldenrain trees (Carroll *et al.* 2003b).

As is the case with bugs on native hosts, populations on *K. elegans* are seasonally coordinated with fruit and hence seed production. Goldenrain trees flower in late summer and early autumn (Carroll *et al.* 2003b), and in south-east Queensland the peak of flowering occurs in March. Fruits set soon after and mature into late May and early June. Individuals of (mostly) *L. tagalicus* appear in small numbers once fruit has

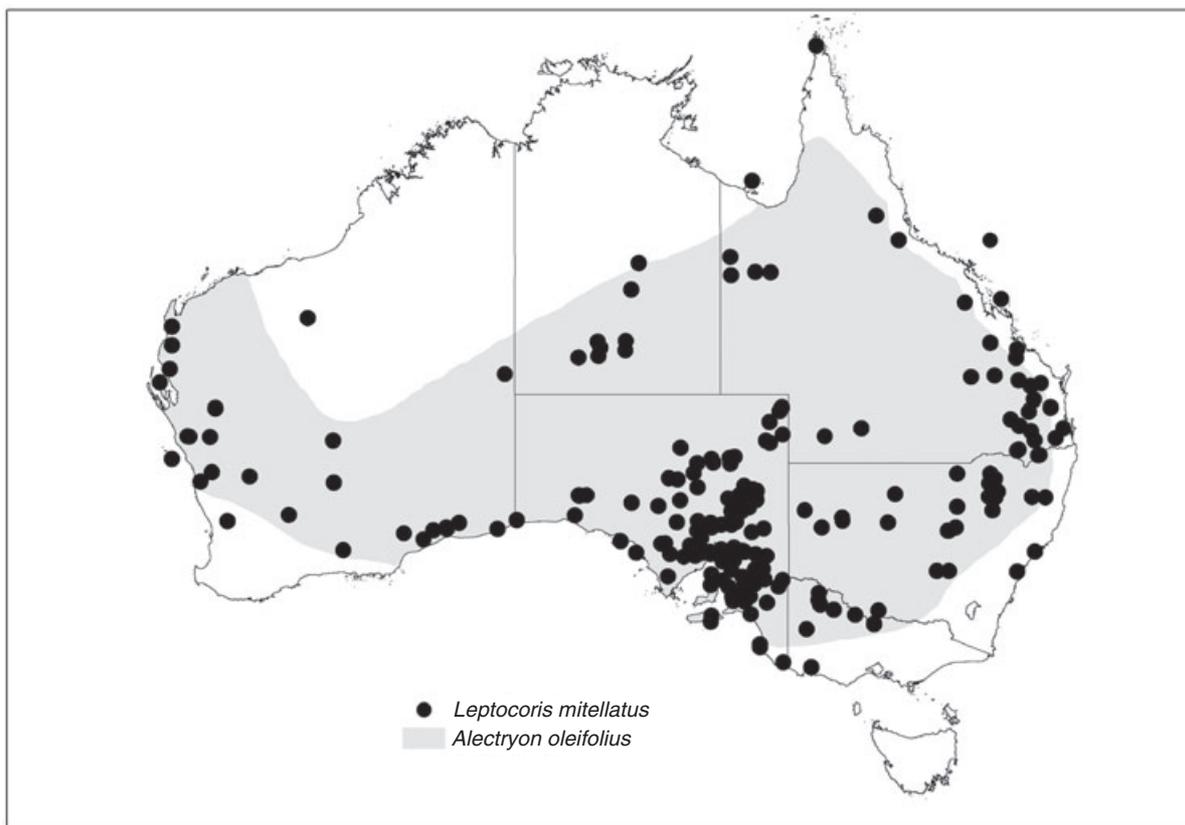


Fig. 3. Spatial distributions of *Leptocoris mitellatus* and *Alectryon oleifolius*.

Table 4 Australian sapinds with mature fruits on which we did not find *Leptocoris*

Plant species	Region sampled	No. of sites	No. of individuals	Status
<i>Arytera divaricata</i> F. Muell.	NE Qld	2	4	Wild
<i>Cupaniopsis anacardioides</i> A. Rich.	SE Qld, NE NSW	10	35	Wild & cultivated
<i>Cupaniopsis parviflora</i> Bailey	SE Qld	1	1	Wild
<i>Diploglottis australis</i> (G. Don) Radlk.	SE Qld, NE NSW	3	14	Wild
<i>Dodonea</i> spp.	NT	7	25	Wild
<i>Dodonea filifolia</i> Hook.	SE Qld	2	25	Wild
<i>Dodonea macrossani</i> F. Muell. & Scortech	SE Qld	10	55	Wild
<i>Dodonea triangularis</i> Lindley	SE Qld	5	25	Wild
<i>Guioa acutifolia</i> Radlk.	NE Qld	2	7	Wild
<i>Harpullia alata</i> F. Muell.	NE NSW	1	1	Wild
<i>Harpullia pendula</i> Planchton ex F. Muell.	S-C Qld, NE NSW	12	40	Wild & cultivated
<i>Harpullia ramiflora</i> Radlk.	NE Qld	2	6	Wild
<i>Jagera pseudorhus</i> (A. Rich.) Radlk.	SE, NE Qld	6	11	Wild & cultivated
<i>Lepiderema largiflorens</i> S. Reyn.	SE Qld	1	1	Cultivated
<i>Lepidopetalum xylocarpum</i> Radlk.	NE Qld	3	13	Wild
<i>Sarcopteryx martyana</i> (F. Muell.) Radlk.	SE Qld	1	1	Cultivated
<i>Toechima daemelianum</i> (F. Muell.) Radlk.	NE Qld	2	2	Wild

NE, north-eastern; NSW, New South Wales; NT, Northern Territory; Qld, Queensland; S-C, south-central, SE, south-east.

set and are observed feeding and mating. By June large numbers of nymphs are present on the ground beneath trees and are feeding on the seeds from dehisced fruits. The new generation of adults appears shortly after. By mid-July most fruits have dehisced and dropped off the trees, and bugs have become less evident. Bugs apparently leave the areas around

trees and gather near walls and buildings exposed to the sun and may be observed basking through much of the spring. They are reproductively inactive at this time. We speculate that later in the spring a portion of these bugs move to other hosts such as *A. tomentosus* (see above) where they produce the generation that returns to the exotic hosts in March and April.

Table 5 Phenology of adult number, behaviour and reproduction of three *Leptocoris* species in an aggregation on *Alectryon tomentosus* in Brisbane in late 2003 and early 2004

Date	Fruit	<i>Leptocoris tagalicus</i>	<i>Leptocoris rufomarginatus</i>	<i>Leptocoris mitellatus</i>
10 November	Nascent	4000, quiescent	Absent	Absent
10 December	4 mm	4000, quiescent	Absent	Absent
23 December	5 mm	4000, quiescent	Absent	Absent
03 January	6 mm	4000, quiescent	Absent	Absent
27 January	8 mm immature	4000, 20% active, <1% feeding, 0 mating	100, 2% mating	Absent
31 January	9 mm immature	3250, 20% active, <1% feeding, 0 mating	150, 5% feeding, mating	Absent
14 February	9 mm immature	1000, 70% active, 2% feeding, mating	100, 5% feeding, eggs	10
27 February	9 mm mature	300, 70% active, 5% feeding, mating	50, 5% feeding, eggs	150, 10% mating
03 March	1% open, 8% viable	250, 100% active, 10% feeding, mating	50, 15% feeding, nymphs	300, 15% mating
25 March	3% open, 5% viable	100, 75% active, early instars	25, advanced instars	200, early instars

DISCUSSION

Leptocoris soapberry bugs are distributed through most of the Australian continent. Two species, *L. tagalicus* and *L. mitellatus*, are particularly widespread, and correspond (away from the eastern coastal wet and dry rainforests) to the distributions of two sapindaceous trees, Whitewood (*A. hemiglauca*) and Boonaree (*A. oleifolius*), respectively. Differences in the distributions of these two plants help to explain the observation by Gross (1960) that *L. tagalicus* is principally distributed in the northern half of Australia, while *L. mitellatus* is mainly in the southern half. However, outlying collections visible on our maps suggest that individuals may sometimes fly long distances from the ranges of their hosts. Whether colonies occasionally establish at remote sites, on other host species, is unknown. Most records of *L. mitellatus* on their less frequented hosts refer to individuals collected in the midst of large aggregations of *L. tagalicus*, raising the possibility that attraction to congeners may result in visits to plants that are not readily adopted as hosts. Note also that we regard the report by Kumar (1966) of *L. mitellatus* on Wilga (*Geijera parviflora* Lindley, Rutaceae) as a misidentification of the superficially similar, commonly co-occurring true host, *A. oleifolius*.

In the case of *L. tagalicus*, the continentally 'interior' bugs are morphologically distinct from the more coastal populations, which feed on the seeds of a variety of rainforest species. Gross (1960) noted this longitudinal distinction as well, based on his study of museum specimens, and suggested that the inland form be regarded as a separate race. Our field collections of this race on *A. hemiglauca* at inland sites around Alice Springs (Northern Territory) and between Charters Towers and Roma (Queensland) are consistent with Gross' observation. In addition, we found this small race on *A. hemiglauca* near the coast in central Queensland, and in dry rainforest near Marburg Queensland on Scrub Boonaree (*A. salicifolia*). These latter records suggest that the racial distinction is host-based rather than purely geographical, in that the so-called interior form becomes coastal where *Atalaya* is coastal. Accordingly, we suggest that these bugs, which are distinctively smaller-bodied, shorter-beaked, and more orange or red, be referred to as the 'Atalaya' race of *L. tagalicus*.

This diversity of hosts used by the other form of *L. tagalicus* makes a plant-based designation more challenging. Certainly various species of *Alectryon* are used and it is possible that all members of the genus are hosts, but this speculation remains to be verified. Information about the systematics of the Sapindaceae might permit inferences about the likely full host array based on intergeneric relations. That there may be additional differentiation among populations on other native hosts is strongly implied by the evolution of long-beaked bugs on balloon vine (which has large, inflated pods) in historical time (Carroll *et al.* 2005). Any differences in host preference, or differential host effects on development and reproduction, would be subtler and will require additional experimental study. In addition, the colonisation of the non-native *C. grandiflorum* and *K. elegans* appears to be drawing coastal *L. tagalicus* out of its rainforest habitats and into drier, more westerly sites in Queensland along river courses and in plantings, respectively. In late 2000 we found it absent from large stands of *C. grandiflorum* to the south in the Bellinger River Valley (New South Wales, ca. 153°W, 31°S), and this location may give the general current limit for the spread of the insect to the south on this host. In Western Australia, around Perth, we were unable to find *C. grandiflorum* at known locales that have been subject to recent weed control activities (S.P. Carroll *et al.* per. obs. 2001). *Koelreuteria elegans* appears not to have been planted there. Hence we have no evidence that *Leptocoris* has colonised these hosts in that region.

The geographical range of *L. rufomarginatus* mapped from museum specimens accords well with those of the three eastern plant species on which we observed it seed-feeding (*A. diversifolius*, *A. tomentosus* and *E. xylocarpa*). Other potential host species that should be examined are those occurring in similar dry and wet rainforest habitats, including *A. subcinereus* and *Elattostachys nervosa*. Our Northern Territory field record on *A. cobbe* is of a female that differed in dorsal coloration from the east coast conspecifics. Intriguingly, this individual had a bright orange dorsal margin to the pronotum and lateral folded wings, a colour pattern we have observed in specimens collected in Indonesia and other tropical areas to the north, but never in eastern Australia. This record may suggest an independent colonisation of the continent, perhaps from Indonesia.

The speculation that Australian *L. isolatus* are associated with the sapind *A. cobbe* is based on the report by Braekman *et al.* (1982) of its occurrence on this plant in New Guinea. Our recognition of the plant's presence in tropical Australia, immediately to the south of New Guinea, led to our prediction that the bug too would be present. Museum specimens confirmed that prediction, and the distribution of wildland collections within tropical north Queensland matches that of *A. cobbe*. Only the collections on the horticultural sapinds are to the south of that range. In our single field trip to far north Queensland, however, we were not successful in locating fruiting *A. cobbe*. Nor did we find the insect on fruiting *Arytera* Blume, *Guioa* Cav., *Harpullia* Roxb., *Jagera* Blume, *Lepidopetalum* Blume or *Toechima* Radlk in that region. Gross (1960) reports two separate collections of this insect on *Allophylus* on different atolls of the Marshall Islands.

Leptocoris vicinus is rare in collections, but appears established in the Darwin region on the introduced ornamental *S. oleosa*, which is native to southern Asia. The possibility that this insect was introduced with this plant (perhaps in the adhesive egg stage) should be considered. Gross's original collections of 1960 were made at the Darwin Botanical Garden (host unrecorded). We did not observe it on native sapinds in the region (*A. cobbe*, *Atalaya variifolia* and *A. salicifolia*). In addition, *Cardiospermum halicacabum* is widespread in northern Northern Territory and Western Australia. Generally regarded as a pantropical weed (e.g. Reynolds 1985), others have suggested that it is native to this area (Cowie & Finlayson 1986). Accordingly, it should be examined as another possible indigenous host for *L. vicinus* and for other *Leptocoris* in the region as well. Observations are lacking for this host when fruiting.

Among the three species that we studied in the field, we found substantial differences in biology even within a single site and host. We surveyed behaviour and phenology at an *A. tomentosus* site over a 5-month period during which seeds were ripening. For at least 3 months, large numbers of *L. tagalicus* adults were present in a quiescent state. We do not know whether these individuals matured *in situ* or flew in from other sites. (However, we did witness the colonisation of other hosts and sites by flying individuals of this species during our study.) As seeds neared maturity, bugs were able to access them by feeding through the capsule walls with their comparatively long beaks. Nonetheless, most seeds were destroyed internally by other agencies (perhaps fungal attack), and little reproduction occurred before most of these individuals had departed or died. Most of the population decline took place before the seeds had matured, and we suspect (but do not know) that it resulted from emigration.

Leptocoris rufomarginatus adults began to arrive at least 2 months later, and much closer to the time of fruit ripening. It too used its long beak to access seeds in still closed fruits, and it reproduced more successfully than *L. tagalicus* during this period. Adult *L. mitellatus* arrived even later, as fruits were beginning to dehisce. Their shorter beaks were adequate for feeding on seeds so exposed; they also fed on smaller, apparently aborted fruits beneath the trees. The contrasts among the

species in the timing of colonisation as it related to host phenology, and in beak length as it related to fruit dehiscence, is intriguing. These patterns were observed on three host species at five sites. To examine their generality, additional studies should be conducted at other seasons, sites and years. In addition, the possibility that individuals or generations of the polyphagous species move among host species, including those that fruit during different seasons, remains wholly unexplored.

It is interesting that the most polyphagous of the Australian soapberry bugs, the coastal form of *L. tagalicus*, is also the one that has colonised the two naturalised sapinds, *C. grandiflorum* and *K. elegans*. This insect is broadly distributed outside Australia, ranging from Indonesia and the Philippines east to Tahiti, wherein it is principally represented by the larger morph (Gross 1960). Across this range it likely utilises a great variety of sapinds. *Cardiospermum grandiflorum*, although now a widespread weed, is native to South and Central America. *Koelreuteria elegans* is native to Taiwan and Fiji; its congeners are more temperate. Accordingly, both hosts are probably relatively new to *L. tagalicus*, and its adoption of these hosts in Australia is probably novel from the standpoint of its ancestral lineage that originally colonised (or arose in) Australia.

Leptocoris tagalicus, in its coastal form, occurred more regularly on fruiting individuals of the environmental weeds than it did on most of the native hosts. This difference may stem from chance high attraction, adaptations that increase attraction, or better survival and reproduction on these invaders. Enhanced attraction is predicted if the probability of finding food and reproducing are relatively high on these hosts. Notably, we did not detect other seed predators on these two plants, such that competition above the genus level may be absent. In addition, the introduced plants might lack defences to this specific predator that the natives possess. Sapinds are known to vary substantially in the chemistry of their defensive cyanogenic lipids (e.g. Siegler & Kawahara 1976).

Our study of *L. tagalicus* populations on the two non-native host plants demonstrates recent adaptive evolution. Balloon vine has large inflated fruit capsules that protect predispersal seeds from bugs with short beaks. Bugs on this host have longer beaks than do those on all other hosts (Carroll *et al.* 2005). *Koelreuteria elegans*, in contrast, has flat uninflated pods, and those bugs have shorter beaks (S.P. Carroll *et al.* unpubl. data 2004). Both patterns suggest a degree of host-specific adaptation. We are currently testing for differences in preference and performance among host-associated populations of *L. tagalicus*. In laboratory experiments we found that adults reared from populations on balloon vine were substantially more efficient in attacking seeds within the inflated capsules than were those reared from nearby, shorter-beaked populations on native *A. tomentosus* (Carroll *et al.* 2005).

Because seed predation may influence host population biology, the presence of *Leptocoris* as a seed predator on at least nine species of sapinds indicates that the insects may be ecologically significant in a variety of plant communities. Its presence on an additional six species of introduced sapinds indicates further importance in conservation and economic

contexts. In particular, the reliable presence of *L. tagalicus* on these declared environmental weeds over large portions of their ranges suggests that this insect may assist in control efforts by reducing the production of viable seeds.

In tropical fruit horticulture, Waite and Hwang (2002) report damage to lychee crops by seed-feeding *L. tagalicus* and *L. ruformarginatus*, and we found museum records from longan and rambutan in addition. *Leptocoris tagalicus* in particular shows considerable flexibility in host choice, and is probably now increasing in overall population size as a result of plant introductions. Entomologists and growers should monitor for geographical and host range expansions of all members of the genus onto sapindaceae horticultural crops. Additional study of species interactions and differences among them in host use will further illuminate evolutionary and ecological aspects of their population biology, behaviour, morphology and physiology, as well as their potential economic significance.

ACKNOWLEDGEMENTS

This work represents the combined efforts of a great many. For assistance with plants, we thank L. Jessup, W. McDonald, G. Batianoff and P. Forster of the Queensland Herbarium, B. Hyland (CSIRO Atherton), J. Hauser, M. Bennett, D. Ambler, R. Whyte, S. Legge and the Brisbane Rainforest Action and Information Network. For help with insects, we thank T. Armijo-Prewitt, T. Weir (Australian National Insect Collection), G. Cassis (Australian Museum), G. Monteith (Queensland Museum), G. Daniels, M. Schneider and A. O'Toole (University of Queensland), J. Donaldson (CSIRO Long Pocket), J. Forrest (South Australia Museum), B. Hanich (Western Australian Museum), K. Walker (Museum Victoria), G. Brown (Department Business, Industry and Resource Development, Darwin), G. Dally (Museum and Art Gallery of Northern Territory, Darwin), R. Storey (CSIRO-Mareeba), and T. Schuh (American Museum of Natural History). Many of those listed also provided generous hospitality during fieldwork. Institutional support was provided by the School of Integrative Biology, University of Queensland. Financial support was provided by the Australian-American Fulbright Commission in the form of a Senior Scholarship to S.P.C.

Finally, we would be remiss were we not to acknowledge the great degree to which we have depended on the pioneering research of Sally Reynolds (Queensland Herbarium) on Australian sapinds and Gordon Gross (South Australian Museum) on Australian *Leptocoris* throughout the course of our work.

REFERENCES

- Batianoff GW & Butler DW. 2002. Assessment of invasive naturalised plants in south-east Queensland. *Plant Protection Quarterly* **17**, 27–34.
- Batianoff GW & Butler DW. 2003. Impact assessment and analysis of sixty-six priority invasive weeds in south-east Queensland. *Plant Protection Quarterly* **18**, 11–17.
- Braekman JC, Daoze D & Pasteels JM. 1982. Cyanogenic and other glucosides in a Neo-Guinean Bug *Leptocoris isolatus*: possible precursors in its host-plant. *Biochemical Systematics and Ecology* **10**, 355–364.
- Carroll SP, Dingle H & Famula TR. 2003a. Rapid appearance of epistasis during adaptive divergence following colonization. *Proceedings of the Royal Society of London B* **270** (Suppl.), S80–S83.
- Carroll SP, Dingle H, Famula TR & Fox CW. 2001. Genetic architecture of adaptive differentiation in evolving host races of the soapberry bug, *Jadera haematoloma*. *Genetica* **112–113**, 257–272.
- Carroll SP & Loye JE. 1987. Specialization of *Jadera* species (Hemiptera: Rhopalidae) on seeds of the Sapindaceae, and coevolution of defense and attack. *Annals of the Entomological Society of America* **80**, 373–378.
- Carroll SP, Loye JE, Dingle H, Mathieson M, Famula T & Zalucki M. 2005. And the beak shall inherit—evolution in response to invasion. *Ecology Letters* **8**, 944–951.
- Carroll SP, Mathieson M & Loye JE. In press. Invasion history and ecology of the environmental weed Balloon Vine, *Cardiospermum grandiflorum* Swartz, in Australia. *Plant Protection Quarterly*.
- Carroll SP, Marler M, Winchell R & Dingle H. 2003b. Evolution of cryptic flight morph and life history differences during host race radiation in the soapberry bug, *Jadera haematoloma* Herrich-Schaefer (Hemiptera: Rhopalidae). *Annals of the Entomological Society of America* **96**, 135–143.
- Cassis G & Gross GF. 2002. *Zoological Catalogue of Australia 27.3B, Hemiptera: Heteroptera (Pentatomomorpha)*. CSIRO Publishing, Canberra, Australia.
- Cowie ID & Finlayson CM. 1986. *Plants of the Alligator Rivers Region Northern Territories*. Government Publishing Service Canberra, Canberra, Australian.
- Göllner-Scheidung U. 1983. General-Katalog der Familie Rhopalidae (Heteroptera). *Mitteilungen aus dem Zoologischen Museum* **59**, 37–189.
- Gross GF. 1960. A revision of the genus *Leptocoris* Hahn (Heteroptera: Coreidae: Rhopalinae) from the Indo-Pacific and Australian Regions. *Records of the Australian Museum* **13**, 403–451.
- Kumar R. 1966. Studies on the biology, immature stages, and relative growth of some Australian Bugs of the superfamily Coreoidea (Hemiptera: Heteroptera). *Australian Journal of Zoology* **14**, 895–991.
- Reynolds ST. 1985. Sapindaceae. In: *Flora of Australia* 25 (ed. AS George), pp. 4–164. Government Publishing Service Canberra, Canberra, Australian.
- Schaefer CW & Chopra NP. 1982. Cladistic analysis of the Rhopalidae, with a list of food plants. *Annals of the Entomological Society of America* **75**, 224–233.
- Siegler DS & Kawahara W. 1976. New reports of cyanolipids from sapindaceous plants. *Biochemical Systematics and Ecology* **4**, 263–265.
- Waite JK & Hwang JS. 2002. Pests of litchi and longan. In: *Tropical Fruit Pests and Pollinators: Biology, Economic Importance, Natural Enemies and Control* (eds JE Pena, JL Sharp & M Wysoki), pp. 331–360. CAB International Oxford, Oxford, UK.

Accepted for publication 11 April 2005.