Imperial College London DEPARTMENT OF LIFE SCIENCES

THE BIOLOGY OF THE LILY BEETLE, *Lilioceris lilii* (Scopoli) (COLEOPTERA: CHRYSOMELIDAE)

by

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An extract from 'Impact, host range and chemical ecology of the lily beetle, *Lilioceris lilii*', a thesis submitted for the degree of Doctor of Philosophy of Imperial College London

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THE BIOLOGY OF THE LILY BEETLE, *Lilioceris lilii* (Scopoli) (COLEOPTERA: CHRYSOMELIDAE)

The lily beetle, *Lilioceris lilii* (Scopoli) is a bright red leaf beetle (Chrysomelidae: Criocerinae) which has become a pest of lilies (*Lilium*: Liliaceae) in the UK and parts of North America (Salisbury 2003b, Casagrande and Kenis 2004). This review outlines the biology and distribution of *L. lilii*, gives current management practices and discusses avenues of research which could improve management prospects for the beetle.



Figure 1.1. Lilioceris lilii adult.

1.1. DESCRIPTION

Adult *L. lilii* are typical of the criocerine form (Labeyrie 1963), being approximately 8 mm long, bright red with a black head and legs (Figure 1.1). *Lilioceris lilii* is one of 142 described *Lilioceris* species, the largest concentration of which occurs in China (Berti and Rapilly 1976). Two other species of *Lilioceris* occur in Central Europe, the Onion beetle *L. merdigera* (L.) and *L. tibialis* (Villa). *Lilioceris merdigera* is similar in appearance to *L. lilii* but has a red head and legs (with the exception of joints and tarsi, Berti and Rapilly 1976). *Lilioceris merdigera* F. is a synonym of *L. lilii* (Scop.) (Fowler 1890), which can lead to confusion in some older publications; for example Stephens (1839) refers to *Crioceris merdigera* L. although the beetle described feeds on *Lilium* and is black with red thorax and elytra, and so is clearly *L. lilii* (Scop.). *Lilioceris tibialis* is found on wild *Lilium* in the Alps and is distinguished from *L. lilii* by its red tibiae (Berti and Rapilly 1976). In this review the assumption has been made that references to *L.* (*Crioceris*) *lilii* or *merdigera* feeding on *Lilium* or *Fritillaria* refer to the lily beetle and

those concerning a pest of *Allium* spp., *L. merdigera*. Some difficulty remains with articles referring to *Lilioceris* on other plant genera (see section 1.3). Adult *L. lilii* can fly (Cox 2001) but additional literature on this behaviour has not been encountered.

The eggs of *L. lilii* are approximately 1.0 x 0.5 mm (Figure 1.2). Immediately after oviposition they are bright orange and covered in a orange-red sticky layer, which aids adherence to the leaf surface; as they mature the eggs darken (Reinecke 1910, Müller and Rosenberger 2006).



Figure 1.2. Lilioceris lilii eggs on a Lilium leaf.

Lilioceris Iilii larvae (Figure 1.3) are a rather humped eruciform type, dirty orange-red with a dark head and legs, and when mature they are 8 to 10 mm in length (Fox Wilson 1942). The abdomen has regulary disposed dark areas each with two bristles and first instar larvae have an egg bursting spine laterally on the first abdominal segment (Cox 1994). The larvae are normally covered in their own mucilaginous excreta derived from a dorsally situated anal opening (Balachowsky and Mensil 1936), which is distributed over the dorsal surface of the larva using abdominal bristles (Emmel 1936). The four larval instars can be identified by the size of the head capsule (Livingston 1996).

Pupation occurs in the soil beneath the host plant where a 'silken' cocoon incorporating soil particles is constructed (Nolte 1939). The pupa is orange-red and glabrous with a densely microspiculate abdominal cuticle, Cox (1996) gives a detailed description.



Figure 1.3. Lilioceris lilii larvae on Lilium regale.

1.2. LIFE CYCLE

Adult *L. lilii* have been recorded in every month of the year (Cox 2001) and it is this stage that overwinters among plant debris, in soil and similar hibernacula but not necessarily near host plants (Fox Wilson 1942, Haye and Kenis 2004). Adults have been observed on hosts from early spring (Lataste 1931, Haye and Kenis 2004), but may continue to emerge until June (Halstead 1989). Mating behaviour is not well studied, however adults appear to detect one another over long distances and approach each other whilst oscillating their antennae which may indicate the presence of a pheromone (Emmel 1936). A preoviposition period of two weeks following diapause occurs under laboratory conditions (Haye and Kenis 2004). In the field gravid females and eggs have been observed from late March (Cox 2001). Mating may occur before each oviposition (Nolte 1939) which can occur until September (Haye and Kenis 2004). Females can produce 200 to 367 eggs in one season (Lataste 1932, Fox Wilson 1942). It was thought adults could produce eggs in a second season (Lataste 1932) but this has been shown to be untrue (Haye and Kenis 2004).

Eggs are laid in linear groups of 2-16 on the ventral leaf surface parallel to the leaf veins (Emmel 1936, Müller and Rosenberger 2006). Eclosion occurs after 4-10 days (Balachowsky and Mensil 1936, Haye and Kenis 2004), although incubation times of three weeks have been noted (Cox 2001).

Hatchling larvae feed together on the ventral epidermis of the leaf, leaving the dorsal epidermis intact. Later instars consume the entire leaf, usually from the margin and move upwards to undamaged leaves as foliage is devoured (Nolte 1939, Haye and

Kenis 2004). Larvae will also feed on flowers, seed capsules and the epidermis of the stem and after heavy attacks only the desiccated stem remains (Fox Wilson 1942, Brown 1946). Larvae feed for 10-24 days before entering the soil and constructing silken cocoons at a depth of 3 to 4 cm (Reinecke 1910, Haye and Kenis 2004). Pupation takes place in the cocoon after a mean of 8.9 days at 22 °C and the entire subterranean phase lasts a mean of 20.2 days at 22 °C (Haye and Kenis 2004).

New generation adults are said to occur from mid May to October, but may be most numerous in July (Balachowsky and Mensil 1936, Cox 2001). However, it is not clear how these authors distinguished 'new' adults from those that had previously overwintered. A rigorous study indicates that the first new adults emerge in July (Haye and Kenis 2004). It has been suggested that new adults produce a second generation and that three generations are possible in a year (Lataste 1932, Balachowsky and Mensil 1936), but observations (Fox Wilson 1942, Halstead 1989) and laboratory rearing (Haye and Kenis 2004) indicate that diapause is obligatory before copulation and oviposition.

Much of the available works on the life cycle of *L. lilii* are based on observations made during the early part of the 20^{th} century and the information provided is often unsubstantiated and contradicted in later publications (Halstead 1989, Cox 2001, Haye and Kenis 2004). Several early misconceptions on *L. lilii* life cycle are still widely reported in pest control literature including references to two generations a year (e.g. Alford 1995). It is clear that additional work is required to clarify the phenology of *L. lilii* under UK field conditions.

1.3. HOST RANGE

At least one life stage of *L. lilii* has been reported on 23 plant genera (Table 1.1). However, a distinction should be made between the plants on which the adults have been observed or are able to feed and those on which eggs are laid and development can be completed. Adult *L. lilii* are often observed on plants with no damage occurring (e.g. *Hemerocallis*), or damage has been wrongly attributed to *L. lilii*. Fox Wilson (1942) shows a photograph of *Polygonatum* apparently damaged by *L. lilii*, but is more likely to have been caused by slugs or snails (A. Halstead, pers. com, 2004). Additional inaccuracies may have occurred due to confusion with *L. merdigera* (section 1.1), whose hosts include *Convallaria, Allium* and *Polygonatum* (Labeyrie 1963). In non-choice laboratory tests, adult *L. lilii* will feed on 13 plant genera. However, with the exception of a single larva (out of 45) surviving to adult on *Streptopus amplexifolius* (L.) (Ernst et al. 2007), complete development has only been observed on *Lilium* and

Fritillaria (Tables 1.1, 1.3). Assuming the plants in the above reports are representative of the genera, most of the hosts listed in the literature can be rejected. Only *Lilium* and *Fritillaria* should be considered true hosts, with *Cardiocrinum* included as larvae and extensive damage have been observed on this genus by several authors (Table 1.3).

Table 1.1. Plant genera on which *Lilioceris lilii* has been observed.

O = Observed (no feeding damage noted); Y = Will feed; N = No feeding damage in non-choice tests (Livingston 1996, Scarborough 2002, Ernst et al. 2007, pers. obs); ? = No observation. *In non-choice tests one larva out of 45 completed development to adult (Ernst et al. 2007).

Plant family	Genus	Adult	Larva	Additional reference(s)
Amaryllidaceae	Narcissus	Y	?	Livingston (1996)
Alstroemeriaceae	Alstromeria	Y	Ν	Coghill (1946)
Campanulaceae	Campanula	Ν	Ν	Casagrande and
				Livingston (1995)
Convallariaceae	Convallaria	Y	Ν	Reinecke (1910)
	Maiamthemum	Y	?	LeSage (1983)
	Polygonatum	Y	Ν	Temperé (1926), Fox
				Wilson (1942)
	Streptopus	Y	N*	
	Tricyrtis	Y	?	RHS data
Hostaceae	Hosta	Y	?	
Hemerocallidaceae	Hemerocallis	0/ N	Ν	Cox (2001)
Hyacinthaceae	Muscari	Y	?	
Iridaceae	Crocus	Y	?	
	Iris	Y	?	Cox (2001)
Liliaceae	Cardiocrinum	Y	Y	See Table 1.3
	Fritillaria	Y	Y	See Table 1.3
	Lilium	Y	Y	See Table 1.3
	Medeola	Y	Ν	
	Nomocharis	Y	Y	Fox Wilson (1943)
	Smilax	Y	?	
	Tulipa	Y	?	
Melanthiaceae	Trillium	Y	Ν	
Solanaceae	Nicotiana	0/ N	?	Cox (2001)
	Solanum	Y	Ν	Temperé (1926)

Lilioceris lilii has been observed on 57 hybrid Lilium, 30 Lilium, one Cardiocrinum and five Fritillaria species. Within Lilium the beetle has been observed on species and hybrids from all major taxonomic groups and hybrid divisions, with the exception of division III (Tables 1.2, 1.3, 1.4). Casual observation is the source for much of the information on these hosts: Fox Wilson (1943) and Halstead (1990) use data provided by Royal Horticultural Society (RHS) members and the largest contributions to the list were made at the RHS Garden Wisley between 2000 and 2003 by casual observation (Cox 2001, pers. obs). This type of data can indicate which plants are hosts for L. lilii, particularly if larvae are present, but cannot give any indication of resistance. C. Conjin (pers. com, 2000) recorded percentage foliar damage in laboratory and field trials to determine differences in the susceptibility of several Lilium, and concluded that some cultivars are less susceptible to attack than others, although all *Lilium* could be attacked by adult *L. lilii* (Table 1.4). In other studies eggs were laid on L. henryi and L. speciosum but these did not hatch or larva died soon after ecdysis and it was concluded that these lilies were less susceptible to attack than Oriental hybrids and L. lancifolium (Livingston 1996); larval survival has been found to be lower on L. 'Black Beauty' than on L. 'Oriental Pink' and Asiatic Hybrids (Casagrande and Tewksbury 2007a). However, other authors have recorded larvae on these plants but give no indication of survival (Table 1.3). There are approximately 100 Lilium species and more than 8000 hybrids (McRae 1998), three Cardiocrinum species (Synge 1980) and at least 100 species of *Fritillaria* (Pratt and Jefferson-Brown 1997). It is clear that additional work and a more systematic approach is required to assess the resistance of any Lilium or Fritillaria to L. lilii.

S	pecies groups	Hybrid divisions	
1	martagon	I	Asiatic hybrids
2	American	П	Martagon hybrids
3	candidum	Ш	Euro-Caucasian hybrids
4	Oriental	IV	American hybrids
5	Asian	V	Longiflorum hybrids
6	Trumpet	VI	Trumpet and Aurelian hybrids
7	dauricum	VII	Oriental hybrids
		VIII	Other hybrids
		IX	Species and cultivars of species

 Table 1.2. Lily species groups and hybrid divisions after Comber (1949) and the
 lily register (Leslie 1982, Matthews 2007)

Table 1.3. Part 1 of 3. Observations made on the presence of *Lilioceris Iilii* on *Lilium, Fritillaria* and *Cardiocrinum.* * see Table 1.2. 1 = Beitrag (1932), 2 = Barton (1941), 3 = Fox Wilson (1943), 4 = Coghill (1946), 5 = Southgate (1959), 6 = Livingston (1996), 7 = Cox (2001), 8 = Anderson and Bell (2002), 9 = Salisbury (2003b), 10 = pers. obs. (1999-2004), 11 = Haye and Kenis (2004), 12 = Ernst et al. (2007).

Species/Variety	Group*	Adults	Eggs/ Larvae
Cardiocrinum giganteum (Wallich)	n/a	4, 9, 11	8, 11
Fritillaria imperialis L.	n/a	8, 9, 11	9, 9
F. meleagris L.	n/a	8, 9	8, 9
<i>F. pontica</i> Wahlenberg	n/a	8	-
F. pyrenaica L.	n/a	8	-
Lilium hansonii Moore	1	9, 10	9, 10
L. martagon L.	1	1	1, 7, 9, 10, 11
<i>L. tsingtauense</i> Gilg	1	10	9, 10
L. occidentale Purdy	2	9	9
<i>L. pardalinum</i> Kellogg	2	4, 7, 9, 10	7, 9, 10
L. philadelphicum	2	12	12
L. superbum L.	2	9, 10	9, 10
L. bulbiferum L.	3	11	11
L. candidum L.	3	2, 4, 5, 9	5, 9, 10
L. monadelphum Bieberstein	3	9	9
L. pomponium L.	3	9	9
<i>L. pyrenaicum</i> Gouan	3	9	-
<i>L. auratum</i> Lindley	4	5, 7	5
<i>L. rubellum</i> Baker	4	10	9, 10
L. speciosum Thunberg	4	6, 10	9, 10
L. concolor Salisbury	5		10
<i>L. davidii</i> Elwes	5	7, 9, 10	9, 10
<i>L. duchartrei</i> Farnchet	5	9	9, 10
<i>L. henryi</i> Baker	5	4, 5, 6, 9, 10	4, 5, 9, 10
L. lancifolium Thunberg	5	3, 5, 6, 7, 9, 10	3, 5, 6, 9,
<i>L. leichtlinii</i> Hooker	5	10	10
<i>L. nepalense</i> Don	5	9	9
L. pumilum de Candole	5	5	5
L. formosanum Wallace	6	9, 10	9, 10

Species/ variety	Grou	p* Adults	Eggs/ Larvae
L. leucanthum Baker	6	9, 10	9, 10
L. sulphureum Baker	6	9	-
L. dauricum Ker-Gawler	7	5	-
L. 'Amber Gold'	I	9	9
L. 'Butter Pixie'	I	9, 10	9, 10
L. 'Connecticut King'	I	6, 8	6
L. 'Enchantment'	I	6, 7, 9, 10	6, 9, 10
L. 'George Soper'	I	10	-
L. 'Karen North'	I	10	9, 10
L. 'Karmen'	I	10	10
L. 'King Pete'	Ι	9	-
L. 'Ladykiller'	I	9, 10	-
L. 'Marie North'	I	9	-
L. 'Matchless'	I	10	-
L. 'Mont Blanc'	I	6	6
L. 'Montreaux'	I	6	6
L. 'Nutmegger'	I	10	10
L. 'Orange Pixie'	I	-	9
L. 'Orange Triumph'	I	10	10
L. 'Pandora'	I	-	9, 10
L. 'Peggy North'	I	9	9
L. 'Pink Tiger'	I	9	9
L. 'Prins Constatjn'	I	9	4, 5
L. 'Red Lion'	I	9	-
L. 'Rosemary North'	I	9, 10	9, 10
L. 'Santorin'	I	9, 10	9, 10
L. 'Vanguard'	I	9	9
L. 'Yellow Blaze'	I	9, 10	9, 10
L. x hollandicum	Ι	10	10
L. 'Brocade'	II	9, 10	9, 10
L. 'Mrs R.O. Backhouse'	II	9	9, 10
L. x dalhansonii	II	9	9, 10
L. 'Afterglow'	IV	9	9

 Table 1.3. Part 2 of 3. Observations made on the presence of Lilioceris lilii on

 Lilium, Fritillaria and Cardiocrinum. * see Table 1.2.

Species/ variety	Group*	Adults	Eggs/ Larvae
L. 'Kirschroter Tänzer'	IV	-	10
L. Bellingham Group	IV	9, 10	9, 10
L. San Gabrial Group	IV	9, 10	9, 10
L. 'Casa Rosa'	V	6	6
L. 'Bright Star'	VI	9, 10	9, 10
L. 'Green Magic'	VI	9	9
L. 'Moonlight'	VI	9	10
L. Pink Perfection Group	VI	9	9, 10
L. 'Thunderbolt'	VI	-	9, 10
L. 'Vico Queen'	VI	10	10
L. Golden Splendor Group	VI	9, 10	9, 10
L. 'Arthur Grove'	VII	9, 10	9, 10
L. 'Cover Girl'	VII	9	9
L. 'Mona Lisa'	VII	6	6
L. 'Showbiz'	VII	9, 10	10
L. 'Star Gazer'	VII	6, 7	6, 7
L. Everest Group	VII	-	9
L. 'Smoky Mountain'	VIII	9	9

Table 1.3. Part 3 of 3. Observations made on the presence of Lilioceris lilii onLilium, Fritillaria and Cardiocrinum. * see Table 1.2.

Table 1.4. Lilies investigated for resistance to Lilioceris Iilii (after C. Conjin, pers.com 2000). * see Table 1.2.

Most resistant	Group*	Most susceptible	Group*
L. henryi	5	L. auratum	4
L. 'Black Beauty'	VII	L. 'Acapulco'	VII
<i>L.</i> 'Donau'	VII	L. 'African Queen'	VI
L. 'Lollypop'	Ι	L. 'Berlin'	VII
L. 'Reinesse'	I	L. 'Casa Blanca'	VII
		L. 'Grand Cru'	I

1.4. WORLDWIDE DISTRIBUTION

Lilioceris Iilii can be found almost anywhere Iilies grow (natural or cultivated) in the northern hemisphere and is the most widely distributed of the *Lilioceris* species (Nolte 1939, Berti and Rapilly 1976, Cox 2001, Gold 2003, Figure 1.4.). The origin of *L. Iilii* is unclear: It has been speculated that the beetle originated in China, but records from China are sparse and a centre of origin there is now considered unlikely (Lu and Casagrande 1998, Yu et al. 2001). *Lilioceris Iilii* is an established alien in the UK (Fox Wilson 1942) and North America (Brown 1946, Casagrande and Livingston 1995)

In North America, *L. lilii* was established in Montreal, Canada, by 1945 (Brown 1946). The beetle remained restricted to Montreal Island until 1978, then in 1981 it was reported from Ottawa and by 2002 had been reported across the Canadian provinces of Québec, Ontario, Nova Scotia, Manitoba and New Brunswick (LeSage 1984, Casagrande and Kenis 2004). *Lilioceris lilii* was first reported in the USA from Cambridge, Massachusetts in 1992 (Casagrande and Livingston 1995). *Lilioceris lilii* spread rapidly, in 1995 occurring over 50 miles from the original infestation and by 2007 being firmly established in seven states in north-eastern USA (Casagrande and Kenis 2004, Casagrande and Tewksbury 2007b). It is thought that *L. lilii* could become much more widely distributed in North America, based on its Eurasian distribution and the establishment of other Criocerinae of European origin (Haye and Kenis 2000, Gold et al. 2001).

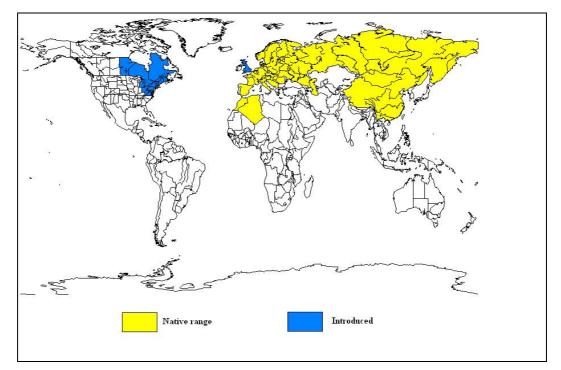


Figure 1.4. Worldwide distribution of Lilioceris lilii.

1.5. DISTRIBUTION IN THE UK

Before 1900, *L. lilii* was recorded from London, Swansea and Chatterden, Kent and considered very rare (Stephens 1839, Turner 1895), subsequently it was not reported in the UK for another 44 years. In 1939 "numbers" of *L. lilii* were recorded at Chobham, Surrey (Barton 1940, Fox Wilson 1942), in 1940 a single adult *L. lilii* was recorded in Carlisle (Richards 1943), in 1945 infestations were reported in Liverpool (Anon 1954) and at a nursery in Flintshire; the Flintshire infestation may have originated with bulbs imported from Holland and was probably destroyed by applications of DDT (Coghill 1946). The lack of records from Carlisle, Liverpool and Flintshire between the 1940s and 1989 indicates a failure to establish in these areas at that time (Halstead 1989).

In addition to Chobham, by 1943 L. lilii had been reported from two sites in Surrey and one in Middlesex (Fox Wilson 1943). By 1959 L. lilii was widespread in Surrey and occurred in the surrounding areas of Hampshire and Berkshire (Southgate 1959). The continued presence of *L. lilii* in Chobham and its apparent spread outwards from the town indicates that this was probably the site of establishment in the UK (Halstead 1990, Salisbury 2003b). By the late 1970s L. lilii was established in four south-eastern counties adjoining Surrey (Salisbury 2003b). During the 1980s the range of L. lilii extended to most counties in south-east England, although virtually all records fell within a 40 km radius of Chobham (Halstead 1989). By 2000, L. lilii was present in almost every county in southern England and reported as far north as Cheshire and Lincolnshire (Cox 2001). Lilioceris lilii was reported from Scotland (Glasgow) and Northern Ireland (Belfast) in 2002, in both cases it is likely to have been present for at least a year before being reported (Anderson and Bell 2002). Lilioceris lilii continues to survive and appears to be spreading in Scotland and Northern Ireland (RHS data). The distribution of *L. lilii* in England and Wales continues to expand: by the end of 2006 L. lilii had been recorded in almost every English county and was becoming widespread in Wales (Figure 1.5).

1.6. GENERALIST PREDATORS

Nolte (1939) observed a *L. lilii* larva killed by a nymph of the Brassica shield bug, *Eurydema oleracea* (L.) (Hemiptera: Pentatomidae). A lacewing (Neuroptera) larva and Anthocorid nymph (Hemiptera) have been observed feeding on *L. lilii* larvae (A. Salisbury, unpublished). Simple non-choice tests with carabid beetles (*Abax parallelepipedus* (Pill. & Mitt.), *Carabus nemoralis* Müll. and *Nebria brevicollis* (F.)) have been carried out (pers. obs). Adult *L. lilii* were not consumed in these tests but a low level of egg predation was observed with *A. parallelepipedus*.

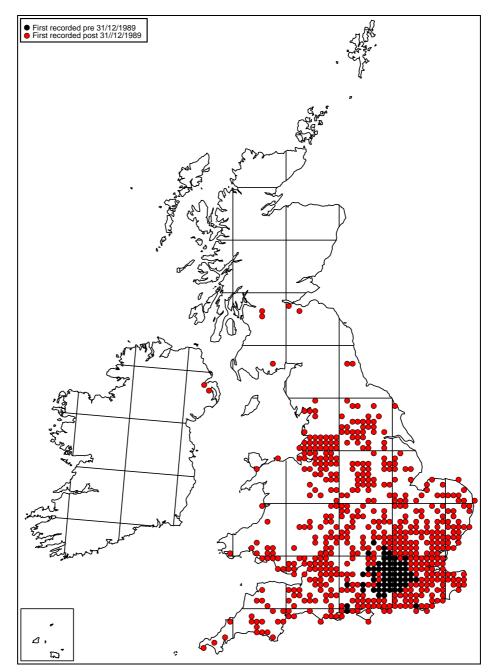


Figure 1.5. Post 1939 10 km dot distribution map of *Lilioceris Iilii* from records held by the RHS (at October 2007). Produced using DMAP[©].

1.7. PARASITOIDS

It was not until 1996 that four hymenopteran larval parasitoids, one hyperparasitoid, one egg parasitoid and some generalist tachinid (Diptera) parasitoids of *L. lilii* were confirmed (Table 1.5). Despite extensive surveillance, parasitoids of adult *L. lilii* have not been found (Haye and Kenis 2004). Combined, the parasitoids infect 25% to 94% of *L. lilii* larvae in mainland Europe (Haye and Kenis 2000, Kenis et al. 2002a, Haye and Kenis 2004). None of the larval parasitoid kills *L. lilii* larvae before they are mature. All three ichneumonid parasitoids are solitary; superparasitism and

multiparasitism occur frequently but only one larva completes development (Casagrande and Kenis 2004). The dominant parasitoid in most of Northern and Western Europe (including the UK) is *Lemophagus errabundus* (Figures 1.6 and 1.7), *Diaparsis jucundus* is dominant in Southern Europe and *Tetrastichus setifer* (Figures 1.8 and 1.9) in Germany (Haye and Kenis 2000, 2004). The parasitoids are distributed temporally: *T. setifer* infects larvae throughout the summer; *L. errabundus* is an early season parasitoid; the other species occur mainly in July (Kenis et al. 2002a, Haye and Kenis 2004). There is some evidence that habitat can affect the distribution of the parasitoids: *D. jucundus* has a lower rate of parasitism in *L. lilii* populations on cultivated lilies (50%) compared to *L. lilii* populations on natural *Lilium martagon* L. (up to 90%) (Haye and Kenis 2004).

The first confirmed report of *T. setifer* in the UK was from East Kent in 1997 (Cox 2001). This species has since been recorded from South Essex, Surrey, Sussex, Kent, Middlesex, Suffolk, Cambridge and East Yorkshire (Cox 2001, Salisbury 2003a, RHS data, Figure 1.11). *Tetrastichus setifer* may therefore be as widely distributed as its host as it is present in areas where *L. lilii* has only recently become established (section 1.5). *Lemophagus errabundus* was reared from *L. lilii* larvae collected from Essex in 1998, and has been recorded in Surrey, Sussex and Middlesex (Salisbury 2003a, RHS data, Figure 1.11). The hyperparasitoid *Mesochorus lilioceriphilus* (Figure 1.10) has been recorded in Surrey from *L. lilii* larvae collected in June (Salisbury 2004). None of the parasitoids can be native to the UK as they are specific to the genus *Lilioceris* (Gold et al. 2001, Kenis et al. 2002a): *L. lilii* is the only representative of the genus in the UK and is an established alien (section 1.5).

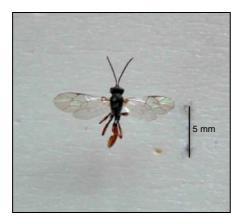




Figure 1.6. Lemophagus errabundusFigure 1.7.Larva ofLemophagusfemale.errabundus.





Figure 1.8. Tetrastichus setifer female. Figure 1.9. Tetrastichus setifer larvae

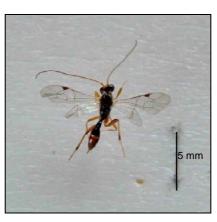


Figure 1.10. Mesochorus lilioceriphilus female.

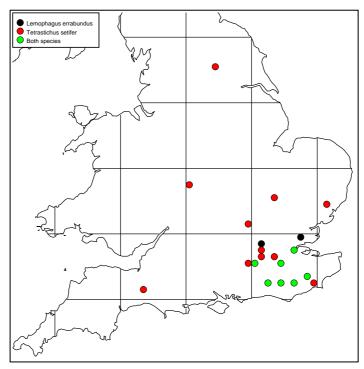


Figure 1.11. Distribution of *Lilioceris Iilii* parasitoids in England (at October 2007). Produced using DMAP[©].

Table 1.5. Characteristics of larval parasitoids and hyperparasitoid of *Liliocerislilii* (after Haye and Kenis 2000, Gold et al. 2001, Kenis et al. 2001, Kenis et al.2002a, Gold 2003, Haye and Kenis 2004).

*Times of larval infestation	**Under laboratory conditions

Taxonomy	European distribution	Life cycle*	Specificity**			
Hymenoptera: Ichneumonidae						
Lemophagus errabundus	Widespread, UK	Univoltine,	Lilioceris spp.			
(Grav.)		Solitary. May -				
		June.				
Lemophagus pulcher	Widespread (not UK)	Multivoltine. July -	Criocerinae			
(Szepligeti)		August				
Diaparsis jucundus	Widespread (not UK)	Univoltine. July.	Lilioceris spp.			
(Holmgren)						
Mesochorus lilioceriphilus	Widespread, UK	Solitary	Lemophagus			
Schwenke			spp.			
Eulophidae						
Tetrastichus setifer	Widespread, UK	Univoltine. May-	Lilioceris spp.			
Thomson		August.				
		Gregarious				
Mymaridae						
Anaphes sp.	France, Switzerland	Egg parasitoid.	Unknown			
(undescribed)		Multivoltine,	alternate			
		gregarious	hosts			
Diptera: Tachinidae						
Meigenia species	Widespread (three		Generalists			
	species in UK)					

1.8. DEFENCE

Both adults and larvae of *L. lilii* contain carotenoid pigments sequestered and modified from host plants (Mummery and Valadon 1974) and the red colour of the adults is assumed to be aposematic (Jolivet and Verma 2002). Adult *L. lilii* produce phenylanine derivatives as defensive compounds from glands on their pronotum and elytra (Pasteels et al. 1994). Like most adult Criocerinae, *L. lilii* stridulates by contracting and extending its abdomen, causing a 'file and scraper' located on the abdomen and elytra respectively to move against one another (Emmel 1936); this can produce 200 chirps/min with amplitude maxima of 1-1.3k Hz or 6k Hz (Schmitt and Traude 1990). It

has been suggested that this stridulation is a defensive behaviour (Emmel 1936, Schmitt and Traude 1990). However, it is also possible that *L. lilii* uses sound as communication between conspecifics as may be the case with the Orchid beetle *Stethopachys formosa* Balay (Criocerinae), which will stridulate without any noticeable disturbing stimulus (Schmitt 1994). Adult beetles show a feigned death (thanatosis) defence when disturbed, falling to the ground and remaining motionless, often landing on their dorsal side leaving their black ventral side exposed increasing the effectiveness of the defence (Livingston 1996).

It has been suggested that the excrement cover of L. lilii larvae provides thermal protection and predator avoidance (Reinecke 1910, Nolte 1939) and the faecal shield reduces predation by the earwig Forficula auricularia L. (Schaffner and Kenis 1999). It may be the case that such coverings are multifunctional, acting as thermoregulation and reduction of desiccation (reviewed in Olmstead 1994). Whilst defensive secretions and coverings can provide protection against generalist predators, specialists can exploit them. Schaffner and Müller (2001) investigated the foraging behaviour of the L. lilii parasitoid Lemophagus pulcher. In static four-chamber olfactometers and contact bioassays, L. pulcher adults moved towards larvae with or without faecal shields, to faecal shields alone, to lily leaves with larval damage and to the defensive secretion produced by larvae. In contact bioassays, L. pulcher females showed ovipositor probing of shields, (in the presence or absence of larvae), and dummies coated with shield extract, suggesting that the shield plays a primary role in short-range host location and host acceptance, and that the stimulus is chemical. Initial work with L. pulcher, D. jucunda and T. setifer indicate that these species have similar responses and that in T. setifer volatiles emitted by L. lilii larvae, shields and damaged plants have a synergistic effect (Scarborough 2002).

1.9. PEST STATUS

Lilioceris Iilii is a pest in the UK, North America and the Netherlands where it is a problem for amateur gardeners, as well as in public parks and gardens, but there is also a risk to the native *Lilium* of North America and the native *Fritillaria meleagris* of England (Sutton 2004, Ernst et al. 2007, C. Conjin pers. com. 2000). Gold (2003) considers *L. Iilii* to have potential to threaten lily production in the USA, an industry worth \$65 million. *Lilioceris Iilii* occurs in commercial lily fields in France and Switzerland but rarely causes significant damage in established lily fields, possibly due to high levels of parasitism (Kenis et al. 2001, Casagrande and Gold 2002).

In the UK RHS data indicates the rise of *L. lilii* as a problem to the gardener since 1967 (Figure 1.12). A mean of four *L. lilii* enquiries per year (0.5% of total pest

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enquiries) were received during the 1970s; in the 1980s the mean rose to 26.7 (1.8% of total), in the 1990s rising to 76.1 (3.0%); in the new millennium (up to December 2006) the figure is 101 (3.2%). No information is available on the problems the beetle causes the professional horticulturalist in the UK, and an assessment of this risk needed to be carried out (see Chapter 2).

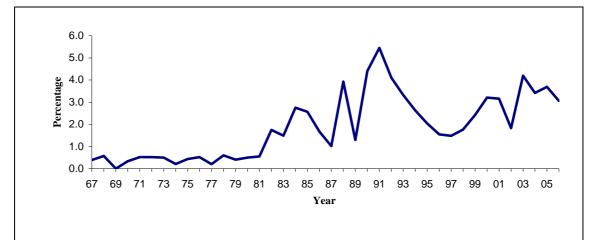


Figure 1.12. *Lilioceris Iilii* enquiries as a proportion of all pest enquiries received by the RHS (1967 to 2006).

1.10. MANAGEMENT IN THE UK

Management of *L. lilii* currently relies on hand-picking or the use of pesticides (Alford 1995). These measures often need to be repeated throughout the growing season due to the long period of activity of *L. lilii*. The excrement-covered larvae, and the adult behaviour of dropping to the ground when disturbed, in addition to the time consumed can make hand-picking undesirable (RHS 2007). In 2007, three synthetic insecticide foliar sprays were available to the amateur gardener to control beetle pests on ornamental plants in the UK: bifenthrin, thiacloprid and imidacloprid. These active ingredients are broad spectrum and not suitable for use on plants in flower.

Two insecticides tested in the USA (active ingredients imidacloprid and azadirachtin), were found to repel adults but not cause adult mortality (Livingston 1996), adding weight to the conclusion of LeSage (1992) that no insecticide at present can completely eradicate the adults or larvae of *L. lilii*.

1.11. BIOLOGICAL CONTROL

The complex of specific parasitoids of *L. lilii* is similar to that found on other Criocerinae, such as the cereal leaf beetle (*Oulema melanopus* (L.)), an established alien pest in North America (Casagrande and Kenis 2004). Since introduction, three

parasitoids of *O. melanopus* have become widespread in the USA and are important in its control (Barbosa et al. 1994). This success led a team at the University of Rhode Island and CABI Bioscience to instigate a classical biological control programme against *L. lilii* in the USA (Gold et al. 2001, Gold 2003).

Following host testing, a licence was granted to release T. setifer in Massachusetts during 1999 to 2003 (Haye and Kenis 2000, Gold 2003, Tewksbury et al. 2005). Three thousand female T. setifer were released in trial plots: initially up to 60% parasitism was recorded, but low winter survival was observed, as the bark mulch used on the plots was unsuitable for the overwintering parasitoids (Casagrande and Gold 2002). Tetrastichus setifer has now been released in four New England States, is established and beginning to spread from the sites of introduction, parasitism rates of between 37% and 100% had been observed by 2007 and declines in L. lilii have been seen as a result (Kenis et al. 2002b, Tewksbury et al. 2005, Casagrande and Tewksbury 2007a). Releases of *L. errabundus* and *D. jucunda* occurred from 2004 to 2006; L. errabundus is established at its release sites in Rhode Island and Maine, where parasitism rates of 13% to 90% have been observed and it appears to be spreading from its release sites; D. jucunda has not yet become established although additional releases are planned (Casagrande and Tewksbury 2007b). By using a single parasitoid species, early or late host larvae may evade parasitism and so it is believed that the release of these additional species of parasitoid in the USA will result in a high degree of parasitism over the entire season (Casagrande and Gold 2002).

It has been suggested that it is a complex of three or more parasitoid species that reduce *L. lilii* populations to an acceptable level in mainland Europe and that in the UK *L. lilii* may be managed by the introduction of an additional parasitoid (Casagrande and Gold 2002, Kenis et al. 2002a). However, the introduction of non-indigenous species into the UK requires extensive quarantine testing in a registered UK laboratory to satisfy a plethora of government advisory bodies before a release licence can be granted (sections 14 and 16 of the UK Wildlife and Countryside Act 1981; HMSO). Such data collection can take many years, the cost of quarantine facilities can be prohibitive and it is still possible that a licence will not be granted. In the event that a licence is granted, there is no guarantee that the addition of a further parasitoid will control *L. lilii*.

Preliminary laboratory tests have been conducted with a commercial formulation of *Bacillus thuringiensis* var. san diego (Bonide Colorado Potato Beetle Beater), however this gave only 30% larval mortality, in comparison with 100% mortality with conventional insecticides (Livingston 1996).

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1.12. CONCLUSIONS

It is clear that there is still much to be learned about *L. lilii*. Inaccuracies from the early literature on *L. lilii* life cycle are still repeated in pest management literature and its phenology is not thoroughly understood. The beetle's host range, in particular the preferences it may have for different *Lilium* or *Fritillaria* has shown potential in the search for resistant varieties but rigorous investigation is lacking. *Lilioceris lilii* has shown considerable range expansion in the UK since its establishment in 1939, and it is likely that the beetle will become more widespread. Whilst there is some knowledge of the extent of the problem for the amateur gardener little is known of the problem faced by the professional horticulturalist and this required further investigation.

Current management options for *L. lilii* are unsatisfactory. In the USA biological control with parasitoids is being attempted, yet despite two parasitoids being present in the UK, *L. lilii* continues to be a problem and the deliberate introduction of further natural enemies to the UK is unlikely. A different pest management approach would be to manipulate *L. lilii* by use of semiochemicals (see review Pickett et al. 1997). Despite the wealth of literature concerning other chrysomelid leaf beetles (see chapter 4), Southgate's (1959) statement that "it is obvious that smell plays a large part in the location of these insects with their food-plant" and the observations of Emmel (1936) that some mating behaviour could be chemically-mediated, very little is known about the chemical ecology of *L. lilii*.

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