Review

Cryptolaemus montrouzieri (Mulsant) (Coccinellidae: Scymninae): a review of biology, ecology, and use in biological control with particular reference to potential impact on non-target organisms

Moses T.K. Kairo[1]*, Oulimathe Paraiso[2], Ram Das Gautam[3] and Dorothy D. Peterkin[4]

Address: [1] School of Agricultural and Natural Sciences, University of Maryland, Eastern Shore, Suite 3055, Richard A. Hazel Hall, Princess Anne, MD 21853, USA. [2] Florida Department of Agriculture and Consumer Services, Division of Plant Industry, Gainesville, FL, USA. [3] Indian Agricultural Research Institute, New Delhi, India. [4] CABI, Gordon Street, Curepe, Trinidad and Tobago, West Indies.

***Correspondence:** Moses Kairo. E-mail: mkairo@umes.edu

Received: 6 July 2012
Accepted: 19 November 2012

doi: 10.1079/PAVSNNR20138005

The electronic version of this article is the definitive one. It is located here: http://www.cabi.org/cabreviews

Abstract

Over the years, *Cryptolaemus montrouzieri* Mulsant (Coleoptera: Coccinellidae) has been used in both classical and augmentative biological control programmes. The ladybird is also considered important in certain conservation biological control programmes. This paper provides a critical review of the literature pertaining to its biology, ecology and use, with a particular emphasis on potential impact on non-target organisms. *C. montrouzieri* has many of the attributes of an effective natural enemy, including a rapid development rate, high reproductive potential, good adaptation to a range of tropical and subtropical climates, high prey consumption rates by both adults and larvae and ease of rearing. The coccinellid has been introduced into at least 64 countries/territories to control more than 16 pest species. *C. montrouzieri* is a polyphagous predator that exploits hosts in at least eight hemipteran families. It is noteworthy that it has adapted to feed on new insect families in some new localities where it has been introduced. Although the wide host range has allowed its use against a variety of pest species, it is also a good indicator of the potential to feed on non-target species. In view of the continued interest to utilize the predator in new non-native localities, questions have arisen regarding its potential to cause negative impacts, especially against non-target organisms. Given the wide recorded host range, it seems unnecessary to conduct additional host range tests as significant decisions can be made based on the available information. Thus, when the available data are interpreted based on a centrifugal process, it is apparent that the ladybird has a potentially very broad host range. Therefore, even without additional studies, it would be reasonable to assume that the ladybird has the potential to extend its host range in unpredictable ways. Clearly, the beetle would provide a good model for conducting post-release studies, especially where the predator has been established for a long time. Such studies would not only provide insight into the impact of introducing generalist non-native coccinellid predators but also help to increase our understanding of the mechanisms limiting host range.

Keywords: *Cryptolaemus montrouzieri*, Coccinellidae, Biological control, Biology, Ecology, Host range, Host specificity, Pseudococcidae, Hemiptera

Introduction

Cryptolaemus montrouzieri Mulsant (Coleoptera: Coccinellidae) is arguably one of the most widely used biological control agents. The first introduction of this ladybird for biological control dates back to 1891 when Albert Koebele brought it into California for control of *Planococcus citri* Risso [1]. Since then, the beetle has been introduced into many countries around the world. Most recently, it was introduced in parts of the Caribbean and

Central and South America for control of the hibiscus mealybug, *Maconellicoccus hirsutus* Green [2–5]. The ladybird is also used in augmentation programmes against several pests around the world [6–12]. Its use has not been without controversy and one important area where concerns have been raised has to do with its host range and potential impact on non-target organisms. Such concerns are, however, not limited to *C. montrouzieri* alone as indeed, recent years have seen increased general interest and concerns regarding the potential negative impact of introduced biological control agents [30–32]. Despite these concerns, the importance of biological control for the management of both native and non-native pests cannot be overstated. It is therefore vital that strategies for the mitigation of risks associated with biological control introductions are developed. This has been the topic of several international meetings, most notably the one organized by the IOBC during 1999 [33].

The ratification in 1996 of an internationally accepted code of conduct outlining guidelines for the introduction and release of natural enemies [34] was a significant step. This third international standard for phytosanitary measures (ISPM # 3) was later revised to include beneficial organisms [35]. One of the requirements of the standard is that prior to the introduction of a prospective biological control agent, a critical assessment of the host range and risks of introduction should be carried out. This information is typically summarized in a dossier, which is meant to assist importing countries make an informed decision on whether or not to introduce a particular agent. Indeed, the idea for the present paper originated from preparation of such a dossier on *C. montrouzieri* [36, 37].

While standard methods for assessing the host range for weed biological control agents have been well established, a similar approach for natural enemies of arthropod pests has been difficult to implement. Recent years have seen considerable interest in the development of a framework including methods and decision-making mechanisms that can be used to assess natural enemies of arthropod pests [38–41]. This paper provides a critical appraisal of the available information on the biology, ecology and use of the organism in biological control. Particular attention is given to host range and potential impact on non-target organisms. It is anticipated that, in addition to providing key information, this article will highlight gaps in knowledge on the use of this ladybird and similar species. In particular, it provides a basis for the future assessment of species for which there is a considerable amount of information.

Taxonomy, Origin and Distribution

C. montrouzieri was first described by Mulsant [42] and the genus was later reviewed by Cockrell [43] and Korschefsky [44]. A more recent revision of the genus recognized two subspecies, *C. montrouzieri* and the less common *C. montrouzieri simplex* Blackburn [45]. *C. montrouzieri* can be separated from all other known species of the genus by coloration; it is the only species with dark tibiae. *C. montrouzieri* is native to the Australasian Zoogeographic Region. However, it now has a world-wide distribution, having been introduced into at least 64 countries in North and South America, the Caribbean, Africa, Asia, Oceania and Europe (Table 2 and Figure 1). There is little information available on the natural spread of *C. montrouzieri* into new countries adjacent to those where it was introduced. However, this would seem likely which suggests that the distribution may be even wider.

Developmental and Reproductive Biology

The biology of *C. montrouzieri* has been widely reported [5, 11, 15, 17, 20, 105, 127–133]. Based on these reports, the salient biological features are summarized in Table 1 and a brief discussion is provided below. Under laboratory conditions ranging from 25 to 29°C and 58–64% RH, development from egg to adult is completed in 27–30 days. Adults spend about a day in the pupal case before emergence. A sex ratio of 1 : 1 is common and adults have a pre-mating period of 5–7 days. Females mate repeatedly throughout their life and may receive spermatozoa from 3 to 4 males at a time. Frequent multiple matings help keep the population of *C. montrouzieri* genetically diversified [134]. The pre-oviposition period ranges from 10 to 16 days. Adult longevity ranges between 50 and 110 days under controlled temperature (25–30°C). The average fecundity of *C. montrouzieri* is 211 eggs per female, although a maximum fecundity of 500 eggs per female has been reported.

Prey Location

Adult *C. montrouzieri* locate their prey using visual and chemical stimuli [92]. Larvae perceive prey only when there is actual physical contact. The wax secretions and honeydew produced by host mealybugs act as attractants as well as oviposition stimulants for *C. montrouzieri* [135, 136]. Studies have also shown that oviposition may be suppressed by an oviposition deterring pheromone associated with the waxy filaments produced by conspecific larvae [137].

Feeding Patterns and Predatory Potential

Both larvae and adults are voracious feeders, which prey on all stages of the mealybug hosts. Predation rates are higher for adult females than for males [138]. Each larva can consume 900–1500 *M. hirsutus* eggs or 300 nymphs or 30 adults during its development [105]. Mani and Thontadaraya [15] report an average consumption of

Table 1 Developmental periods of *Cryptolaemus montrouzieri* reared on selected hosts

Host	Temperature (C°)	Relative humidity (%)	Developmental stage (days)							References
			Egg incubation time	Larval	Prepupal	Pupal	Male longevity	Female longevity	Total developmental time	
Pseudococcidae										
M. hirsutus Green	20		6.2	26.9	17.7	14.3	109.00	122.40	65.10	[13]
M. hirsutus	20	75	8.35	33.26	3.25	11.94	307.70–390	231.05–295.99		[14]
M. hirsutus	24–28	58–64	4.10	22.80	2.15	8.50	55.90	61.40	29.15	[15]
M. hirsutus			4.78	23.9	2.80	2.96	72.38	77.44	39.86 ± 0.43	[16]
M. hirsutus			5–6	11–15	3–4	7–8			26–33	[17]
M. hirsutus	25		6.1	18.8	11.1	10.7			46.70	[13]
M. hirsutus	25	75	4.43	20.71	1.75	6.58	155.35–258.33	212.21–364.50		[14]
M. hirsutus	25–31	65–72	3–7	19–33	2–3	6–10	69.70	74.70	30–53	[11]
M. hirsutus	25.2		5.9–6	17.7–19.1	9.6–10.4	8.4–8.7			42.70–43.10	[13]
M. hirsutus	27.2		3.5	11.9	7.2	6			28.60	[13]
M. hirsutus	27.4		3.2	12.1	7	5.5			27.80	[13]
M. hirsutus	27.5		3.3	11.6	7.1	6.1			28.10	[13]
M. hirsutus	28	55 ± 5	3–5	12–15		5–7	60–110	200–500	20–27	[18]
M. hirsutus	28		3	11.5	7	6.2			27.90	[13]
M. hirsutus	28.9		3	10.5	6.8	5.9			26.20	[13]
M. hirsutus	29.5		2.4	10.1	6.4	6.6			25.50	[13]
M. hirsutus	30		3	10.3	5.5	6.2	81.70	94.80	25.20	[13]
M. hirsutus	30	75	3.90	16.02	1.46	5.96	103.51–77.57	161.50–129.56		[14]
M. hirsutus	35	75	4.20	15.13	1.41	5.29	68.75–48	90.53–80.60		[14]
Phenacoccus madeirensis Green	17 ± 2	37 ± 5	11.07	22.13	15.2	12.3			59.98	[19]
P. madeirensis	20 ± 2	40 ± 5	7.09	10.77	7.65	11.87			37.38	[19, 20]
P. madeirensis	27 ± 2	50 ± 5	6	8.3	5.7	9.5			29.50	[21]
P. madeirensis	28 ± 1	80 ± 5	5	7.36	4.98	9.35			26.69	[19]
P. madeirensis	28 ± 2	44 ± 5	5.12	9.43	5.41	9.72			29.68	[19, 22]
Phenacoccus solenopsis Tinsley	27 ± 2	65 ± 5	5.5	10.6	4.2	10.8	86.60	97.80	31.10 ± 0.60	[23]
P. solenopsis			4.88	25.72	8.08	8.28	78.44	80.49	42.08 ± 0.38	[16]
Planococcus citri	27 ± 1	65 ± 5	4.00	13.00	2.45	7.80		125.33	52.35 ± 1.3	[24]
P. citri	27 ± 2	50 ± 5	6	8.13	3.09	9.36			26.36 ± 0.15	[21]
P. citri	27 ± 2	60–70	4.25	20.25	2.00	8.50	100.10	104.50		[25]
P. citri	29.4–32.1	65–71	4.00	12.42	2.17	7.50			26.09	[26]
Coccidae										
Chloropulvinaria psidii (Maskell)	25–27	50–60		17.60						[27]
Chloropulvinaria polygonata Cockerell	25–28	60–75		13.92						[28]
Dactylopiidae										
Doctylopious tomentasus	29.4–32.1	65–71	4.23	17.67	2.44	8.17			32.51	[26]
Aleyrodidae										
Aleurodicus disperses Russell	25 ± 5	60–70		17.2						[29]
Pyralidae										
Ephestia kuehniella Zeller	27 ± 2	60–70	4.17	16.74	1.36	8.00	109.70	111.50		[25]
Aphididae										
Schizaphis graminium (Rondani)	27 ± 2	60–70	4.11	20.14	2.00	7.95	46.30	45.30		[25]

Table 2 Introductions of *C. montrouzieri* with approximate dates and results of introduction where known. Unknown Information (?); Establishment failed (-); Temporarily established (+); Permanently established (+ +), Substantial control (+ + +)

Country/Territory	Date(s) introduced	Target pest	Source of *C. montrouzieri*	Result of introduction	References
Central, North and South America					
USA, California	1891–92	*P. citri* Risso	New South Wales, Australia	+ +	[1, 45–47]
USA, Florida	1930–1931	*P. citri*	California	+ +	[1, 48, 49]
Mexico	2004	*M. hirsutus* (Green)	?	+ + +	[50]
Mexico, Nayarit	?	*M. hirsutus*	Australia	+	[51]
Brazil	1971–1973	*Diaspidiotus* sp.	?	?	[52]
Guyana	1997	*M. hirsutus* (Green)	Barbados, USA	+ +	[3]
Chile	1931, 1939, 1975	*Pseudococcus* sp.	?	+ +	[53]
	1931, 1933, 1939	*P. citri*	Far East	–	[54, 55]
Costa Rica	*ca.* 1912	*Pseudococcus* sp.	California, USA	?	[53]
Peru	1932, 1937, 1960, 1965, 1967	*Pseudococcus* sp.	Far East	?	[56]
	?	*P. citri*	?	–	[56]
Belize	1999	*M. hirsutus*	USA	?	[57]
Venezuela	2000	*M. hirsutus*	?	?	[2]
Caribbean and Bermuda					
Bahamas	1932	*P. citri*	India	–	[2–4, 58]
	1961	*Pulvinaria psidii* Maskell	California	–	[2–4, 58]
	1968	*D. brevipes* Cockerell	?	+ +	[2–4, 58]
	?	*Saccharicoccus sacchari* Cockerell	India	–	[59]
	2000	*M. hirsutus*	USA		[2–4]
Barbados	1968–69	*S. sacchari*	Indonesia	?	[58]
	1998	*M. hirsutus*	USA	+ +	[58]
	2000–2003	*M. hirsutus*		+ +	[60]
Bermuda	1926	*Nipaecoccus nipae* Maskell	California	–	[58]
	1951–1955	*P. citri*	California	–	[61, 62]
	1956–57	*Pulvinaria psidii* Maskell	Australia	Established & having observed impact	[58]
	1953, 1955, 1973	*Pseudococcus longispinus* Targioni – Tozzetti	California	+	[58, 61]
British Virgin Islands	1998	*M. hirsutus*	USA, Trinidad	+ +	[3]
Cuba	1917	*P. citri* Risso	California	–	[45, 63]
	1960	*Pseudococcus* spp.	URSS	–	[63]
	2000	*Paracoccus marginatus*	Trinidad	?	[63]
	2001	*M. hirsutus*	?	?	[2, 7, 64]
Dominica	2001	*M. hirsutus*	?	?	[2]
Grenada and Cariacou	1996	*M. hirsutus*	Trinidad, UK, USA	+ +	[2]
Montserrat	1935	*P. citri*	Florida	?	[58]
	1973	*Puto barberi* Cockerell	India	?	[58]
	1998	*M. hirsutus*	Trinidad	?	[2]

Nevis	1997	*M. hirsutus*	USA	+ +	[2]
Puerto Rico	1911–1913	*Nipaecoccus nipae* Maskell	Far East	+ + +	[1, 2, 45]
	1911–1913	*Pulvinaria psidii*	Far East	+ + +	[45]
	1997	*M. hirsutus*	Lesser Antilles	+ +	[4]
St Kitts	1971–1973	*Nipaecoccus nipae*	India	+ +	[58]
	1996	*M. hirsutus*	Trinidad, USA	+ +	[2, 65]
St Lucia	1996	*M. hirsutus*	St Lucia		[2]
St Vincent and the Grenadines	1996	*M. hirsutus*	USA	+ +	[66]
Suriname	2001	*M. hirsutus*			[2]
Trinidad and Tobago	1973	*Puto barberi*	India	?	[58]
	1996	*M. hirsutus*	India	+ +	[2, 67]
US Virgin Islands	1997	*M. hirsutus*	USA	+ +	[2]
Europe					
Cyprus	1954, 1956, 1966	*P. citri*	Far East	+ +	[68, 69]
Greece	1933, 1964, 1965, 1969	*P. citri*	Far East	–	[70, 71]
France	1918, 1974	*P. citri*	California	+	[72–75]
France, Corsica	1970	*P. citri*		+ +	[12]
Italy	1907–1908	*P. citri*	California	+	[12, 69, 70, 76–78]
Poland	1970	Pseudococcidae	USSR	Reintroductions necessary	[79]
Portugal	1929, 1984	Mealybugs	?	+ + +	[69, 80]
Italy, Sardinia	1978	*P. citri*	Far East	Established & having observed impact	[81, 82]
Italy, Sicily	?	*P. citri*	Far East	+ +	[83]
Spain	*ca.* 1926	*P. citri*	California	+	[69, 84]
Sweden	2001	*P. citri*		?	[12]
USSR, Georgian SSR	1932–1933	*P. citri*	Egypt	+	[85–87]
USSR	1970's	Mealybugs	Georgian SSR	+	[87]
Africa/Middle East					
Algeria	*ca.* 1918	Mealybugs	California	–	[88]
Cape Verde	1986–1987	*P. longispinus*	Australia	+ +	[89, 90]
Egypt	1922	*M. hirsutus*	France	+ +	[1]
	1922	*S. sacchari*			[91]
Iran	? pre 1970	*Pseudococcus malvaecarum*	Australia	?	[92]
	1987	*Nipaecoccus filamentosus* Cockerell	Northern Iran	Established & having observed impact	[92]
Israel	1924, 1941, 1958	*P. citri*	France and Egypt	–	[93–95]
	1980	*P. citri*	Spain	+	[94]
	?	*Pseudococcus* sp.	?	–	[94]
Kenya	1924	*P. kenyae* Le Pelly	Uganda	+ +	[96]
	1929–1930	*P. kenyae*	?Australia	+ +	[69]
Mauritius	1938–1939	*D. brevipes*	South Africa	–	[97]
Morocco	*ca.* 1921	Mealybugs	France	?	[98]
St. Helena	1973	*P. citri*	Far East	+ + +	[99]
Saudi Arabia	1972–1973	*P. citri*	Far East	+ + +	[100]
Somalia	1933	*Saccharicoccus sachari Cockerell*	Indonesia	–	[97]
South Africa	1900	*P. citri*	California and Australia	+ + +	[99]
Seychelles	1959–1961	*Pseudococcus longispinus*	California	-	[97]

Table 2 (Continued)

Country/Territory	Date(s) introduced	Target pest	Source of *C. montrouzieri*	Result of introduction	References
Sultanate of Oman	1994	*P. citri*	?	+ + +	[101]
	1994	*M. hirsutus*	?	+ + +	[101]
Tanzania	pre-1935	Mealybugs	South Africa	?	[45]
Asia					
Bonin Islands	*ca.* 1935	?	?	?	[45]
China	1950's	Mealybugs	?	+ +	[102]
Hong Kong	1962	*Icerya purchasi* Maskell	Australia	+ + +	[103]
India	1898	Scale insects and mealybugs	Australia	+ +	[104–109]
Indonesia		*P. citri*		–	[103, 110]
Indonesia, Java	1918	*Ferrisia virgata* Cockerell	Hawaii	+ +	[110]
Indonesia, Sulawesi	1928	*Rastrococcus iceryoides* Green	Java	+ +	[110]
Philippines	1928–1931	*Dysmicoccus brevi pes*	Australia	+ +	[103, 110]
	1928	*S. sachari*	Australia	–	[103]
Taiwan	1909	*P. citri* Risso	Far East	+ + +	[111]
	1909	*N. filamentosus*	Far East	+ + +	[111]
West Malaysia	pre-1916	Mealybugs	?	?	[111]
Oceania					
Caroline Island (excl. Palau Island)	1907–1908	*Pseudococcus* sp	Australia	–	[112]
Cook Island	1934	*Pseudococcus* sp.	Australia	?	[113]
	1939	*Pseudococcus* sp.	New Zealand	+ +	[112]
Fiji	*ca.* 1923	Mealybugs	Australia	+ +	[112, 114]
Guam	?	*Nipaecoccus viridis* (Newstead)	?	?	[115]
Guam	1921–1926	*Dysmicoccus boninsis Kuwana*	Australia	–	[103]
Guam, Micronesia	1926	*Pulvinaria psidii*	Hawaii	?	[116]
	1926	*Ferrisia virgata Cockerell*	Hawaii	?	[116]
	1926	*Tylococcus giffardi Ehrhorn*	Hawaii	?	[116]
Hawaii (USA)	1893–1994	*P. citri*	Australia	+ +	[117–119]
Marianas	1911, 1926	*D. brevipes*	Australia	+ +	[120]
		M. hirsutus	California; Egypt	+	[121]
Mariana (Saipan)	1926	Mealybugs	Australia	+ +	[112, 120]
Marshall Islands	1959, 1964	Mealybugs	Asutralia	+ +	[122]
New Hebrides	pre-1915	Mealybugs	Australia	?	[112]
New Zealand	1897–99	Mealybugs	Australia	+ +	[45, 123]
Palau Islands	pre-1940	Mealybugs	Australia	+ +	[124]
		Pseudococcus sp.	Guam	+ +	[112]
Solomon Islands	1915	*Pseudococcus* sp.	Australia	?	[112]
Australia					
Western Australia	1902	Mealybugs	New South Wales, Australia	?	[125]
		P. citri	New South Wales, Australia	+ + +	[126]

Figure 1 World wide distribution of *Cryptolaemus montrouzieri*

881.30 eggs, 259 nymphs or 27.55 adult female *M. hirsutus* or 3330.60 eggs of *P. citri* [139]. A large proportion of the hosts are consumed by the fourth larval instar. The female ladybird must consume at least eight adult *P. citri* for normal egg production to occur [140]. Feeding rate studies have also been undertaken using *Phenacoccus solenopsis* Tinsley, which is native to the USA but has been introduced into other parts of the world [141]. As in studies using other prey hosts, fourth instar larvae and adult ladybirds were the most voracious. In the absence of adequate prey, a high incidence of larval cannibalism usually results, which can reduce adult emergence [142]. This has been cited as a reason for poor persistence of *C. montrouzieri* at low host densities [142], although other studies suggest that cannibalism may be adaptive [143]. Feeding and development of *C. montrouzieri* may be inhibited by the presence of toxins sequestered by prey that are fed on certain species of alkaloid producing plants [94, 144].

Climatic Adaptation

C. montrouzieri is adapted to tropical temperatures. The optimum temperature for development is about 25–30°C and minor fluctuations appear to have little effect on development [145, 146]. *C. montrouzieri* was unable to complete development between 0 and 17°C [13, 147]. Panis and Brun [71] and Codling [148] reported that a minimum temperature of 21°C was needed for the predator to feed and lay eggs. The coccinellid is unable to persist and control target mealybugs effectively below 20°C, and populations often die out during the winter in temperate countries [71, 84, 147–149]. However, Bartlett [46] was able to select cold tolerant biotypes of *C. montrouzieri* which may persist in colder climates. It is not clear how widely such biotypes have been used in practical biological control.

Natural Enemies

C. montrouzieri is attacked by several natural enemies including parasitoids, pathogens and predators. These include a *Homalotylus* spp. (Hymenoptera: Encyrtidae) from the former USSR, *Aminellus* spp. (Hymenoptera: Encyrtidae) and *Cowperia indica* Kerrich (Hymenoptera: Encyrtidae) from India [85, 150, 151]. In Iran, *Metastenus concinnus Walker* (Hymenoptera: Pteromalidae) has been recovered from *C. montrouzieri* preying on citrus mealybug [152]. In laboratory tests, *C. montrouzieri* was susceptible to *Beauveria bassiana* (Bals.-Criv.) Vuill. [153]. This fungus is also recorded as a pathogen of at least 61 other coccinellid species [154]. Vertebrate predators, including lizards, are reported to have annihilated populations of *C. montrouzieri* in Bermuda [61]. In Trinidad, six insectivorous bird species (blue-grey tanager, parson, great kiskadee, yellow oriole, carpenter bird and blue crowned mot-mot) were observed to feed occasionally on high populations of the larvae and adults of *C. montrouzieri* [155]. Although extensive studies have not yet been conducted, no protozoan parasites have been recorded attacking *C. montrouzieri.* However, several temperate species of predatory coccinellids and at least three species of phytophagous coccinellids are known to be parasitized by protozoa, the most important of these are *Nosema coccinellae* Lipa and *Gregarina coccinellae* Lipa [154, 156, 157]. The discovery of these parasites was a direct result of surveys conducted with the specific objective of searching for diseases of selected species of coccinellid that are pests. Therefore, it is reasonable to suppose that protozoan parasite of *C. montrouzieri* may exist, but no specific efforts to search for them have been reported. Ants may also be considered indirect natural enemies of the coccinellid through interference. This is a common behaviour for many honeydew-feeding ant species that protect hemipteran honeydew producers. They are known to disrupt feeding and/or remove smaller coccinellid larvae [158, 159]. Some ant species which have been reported as antagonistic to *C. montrouzieri* include: *Iridomyrmex humilis* Mayr. in France [160], *Pheidole megacephala* F., *Iridomyrmex* sp. and *Crematogaster* sp. in Australia [161].

Use in Biological Control

C. montrouzieri has been introduced into at least 64 countries/territories for control of a range of mealybugs and scale insects (Table 2 and Figure 1). In some of these countries, it is also used extensively for augmentative releases, for instance in citrus orchards in the Mediterranean, the former USSR and USA [86, 87]. In India, it is used in coffee plantations, fruit orchards and vineyards [87, 105, 162, 163]. In South Africa, it is used against mealybugs in citrus [164].

In India, maximum control of *M. hirsutus* on grape was attained 6–8 weeks after initial release of 1000–1500 (10 per vine) ladybirds per hectare [105, 165]. In the Black Sea area of the former USSR, 5000 ladybirds per hectare were used with good results in tea plantations to control *Chloropulvinaria floccifera* Westwood [166]. *Chloropulvinaria aurantii* Cockerell was controlled in citrus plantations in Azerbaijan when 5000 *C. montrouzieri* were released in 3 ha of orchards [167]. Similar results were obtained for *P. citri* on citrus in Italy [168]. Repeated releases of the predator controlled mealybug pests on ornamental plants in European glasshouses [71]. In New Delhi, 2–3 larvae and adults of *C. montrouzieri* per tobacco plant controlled the mealybug, *Ferrisia virgata* (Cockerell) successfully within 1 month under glasshouse conditions [169]. In many instances, periodic releases were necessary since the predator was unable to survive the winter or persist at low prey densities [170, 171]. Most recently, the coccinellid has been introduced/re-introduced into several Caribbean and Latin American countries for control of *M. hirsutus* [2, 3].

Generally, *C. montrouzieri* has been regarded as an outstanding biological control success [171]. Of the 83 documented introductions (Table 2), substantial control of the target pest was achieved in 14 cases. The predator became permanently established in 37 cases; it afforded partial control in three instances and became temporarily established on 10 occasions; re-introduction was necessary on one occasion and; in 19 (22.9 % of introductions) instances, *C. montrouzieri* failed to control the target pest, even when large numbers of the predator were released. For example, *C. montrouzieri* had little effect on *Eriococcus coriaceus* Maskell, attacking eucalyptus trees in New Zealand [123]. The ladybirds were, however, common in unsprayed fields in the warmer Northern areas of New Zealand. The recent use of *C. montrouzieri* in the Caribbean and Central and South America for control of *M. hirsutus* was very successful [2, 3].

Reasons cited for failure include the negative effects of pesticides, which have been well documented [172–175], and the inability to reach concealed hosts such as *Dysmicoccus brevipes* Cockerell on pineapple, and *D. boninsis* (Kuwana) and *Saccharicoccus sacchari* Cockerell on sugarcane [103, 176]. The size of field populations of the host exerts a profound influence on the persistence of the predator. *C. montrouzieri* operates well at high host densities [1]. Interestingly, the predator has been recovered in Trinidad and other islands in the Caribbean even at low population density of *M. hirsutus* [18]. Inadequate prey numbers can interfere with egg production and oviposition as well as development [139, 177] and can lead to cannibalism [17]. Rao *et al.* [103] reported that the predator disappeared during the rainy season because of the scarcity of its host and was active only when adequate numbers of hosts were present. As discussed in the section on ecology, poor adaptation to climate is another reason for failure. Other factors that may influence the effectiveness of the coccinellid include host plant characteristics and interference or predation by other organisms [171].

Rearing Methods

One of the reasons *C. montrouzieri* has been so widely used is the fact that it is easy to rear. Indeed, rearing systems range from very simple systems producing a few thousand, to large systems producing several million beetles a year [13, 105, 142, 145, 155, 178–180]. Mealybug hosts, primarily *P. citri* or *M. hirsutus*, are reared on bleached (etiolated) potato sprouts or pumpkin fruits. *P. citri* is thought to be better suited as a host because it has a shorter developmental period and higher fecundity [105]. Commercial insectaries in California still employ

Table 3 Hosts of *C. montrouzieri* which will support its reproduction and development

Order/Family/Species	References
Order Hemiptera	
Pseudococcidae	
Dysmicoccus brevipes Cockerell	[150]
Ferrisia virgata Cockerell	[9, 43, 169]
M. Maconellicoccus hirsutus Green	[182, 183]
Nipaecoccus filamentosus Cockerell	[184, 185]
Nipaecoccus nipae Maskell	[1, 171]
Nipaecoccus viridis Newstead	[9, 171, 186]
Paracoccus marginatus Williams Granara de Willink	[187]
Planococcus citri Risso	[24, 26]
Planococcus kenyae Le Pelley	[104, 171]
Planococcus lilacinus Cockerell	[150]
Planococcus pacificus Cox	[104]
Planococcus ficus Signoret	[188, 189]
Phenacoccus solenopsis Tinsley	[141]
Pseudococcus calceolariae Maskell	[171, 190, 191]
Pseudococcus comstocki Kuwana	[46, 192]
Pseudococcus fragilis Brain	[97]
Pseudococcus longispinus Targioni-Tozzetti	[75, 171, 191]
Pseudococcus obscurus Essig	[97]
Pseudococcus virbuni Signoret	[1, 193]
Puto barberi Cockerell	[194]
Rastrococcus iceryoides Green	[97]
Rastrococcus invadens Williams	[195]
Trabutina mannipara (Hemprich & Ehrenberg)	[196]
Coccidae	
Coccus viridis Green	[104, 172, 197]
Chloropulvinaria aurantii Cockerell	[198]
Chloropulvinaria floccifera Westwood	[198]
Chloropulvinaria polygonata	[28]
Pulvinaria psii Maskell	[28]
Chloropulvinaria psidii Maskell	[199]
Dactylopius confusus Cockerell	[97, 200]
Dactylopius opuntiae Cockerell	[97]
Dactylopius tomentosus Lamarck	[182]
Dactylopius indicus Green	[201]
Drepanococcus chiton Green	[202, 203]
Lichtensia viburni Signoret	[202, 203]
Neopulvinaria imeretina Khadzhibeili	[193]
Philephedra tuberculosa Nakahara & Gill	[204]
Pulvinaria hydrangeae Steinweden	[202, 203]
Pulvinaria mesembryanthemi Vallot	[205, 206]
Saissetia coffeae Walker	[1, 207]
Saissetia oleae Olivier	[1, 208]
Eriococcidae	
Eriococcus araucariae Maskell	[150]
Magarodidae	
Icerya purchasi Maskell	[201]
Order Hemiptera	
Aleyrodidae	
Aleurothrixus floccosus Maskell	[82]
Aleurodicus cocois Curtis	
Aleurodicus maritimus Hempel	[29, 209]
Aleurodicus pulvinatus Maskell	[29, 209]
Aleurodicus dispersus Russel	[29, 209]
Aleurodicus mirabilis Cockerell	[29, 209]
Aphididae	
Aphis gossypii Glover	[210, 211]
Aphis nerii Boyer de Fonscolombe	[150]
Myzus persicae Sulzer	[212]
Order Lepidoptera Gelechiidae	
Eggs of *Sitotroga cerealella* Olivier	[213]

methods described by Fisher [178] for mass production of *C. montrouzieri*. *P. citri* are reared in the dark on bleached potato sprouts, stacked in trays in an open room. Crawlers are transferred onto sprouts with branches of *Pittosporum undulatum Ventenant* (Apiales: Pittosporaceae) and allowed to develop for 20–25 days, after which adult ladybirds are introduced. Newly emerged adult coccinellids, which are attracted to light, are collected by opening screened windows and scooping them off the mesh using a broad scoop that narrows into a funnel connected to a plastic tube. The tube is calibrated to allow for easy volumetric measurement (100 ladybirds per tube). Several million *C. montrouzieri* can be produced yearly using these methods (Libby Oulette, personal communication).

For smaller-scale cultures, Kishore *et al*. [142] found that the best yields were obtained when pumpkins were placed on a plastic stand in wooden, glass-topped cages. Pumpkins were infested with a minimum of 50 gravid female *M. hirsutus* and the resulting 20-day-old colony exposed to 10 ovipositing female *C. montrouzieri* for 10 days. An average of 250 ladybirds was obtained per pumpkin 50–55 days after initial infestation with mealybugs. Gautam *et al*. [67] also described methods for rearing *C. montrouzieri* at $28 \pm 10^{\circ}$C and 55 ± 5% RH using *M. hirsutus* reared on pumpkins, or batches of sprouted potatoes. *C. montrouzieri* was also reared in the laboratory on eggs of the Angoumois grain moth, *Sitotroga cerealella* (Olivier). When using *S. cerealella* as a host, it was found necessary to provide empty mealybug ovisacs in order to induce oviposition [181].

Host Range and Potential Impact on Non-Target Organisms

C. montrouzieri has been used extensively in biological control efforts for a wide range of pests and thus, there is considerable field and laboratory data on its host range. A detailed review of the literature was carried out. Therefore, the hosts of *C. montrouzieri* were categorized into two main groups (Tables 3 and 4):

- The host supports reproduction and development.
- The host are fed upon but reproduction and development of *C. montrouzieri* are not confirmed.

The two categories correspond to Hodek's [225] classification of essential and alternative food, respectively. The other category suggested by Hodek and Honek [226], comprising rejected or toxic prey was not considered. In order to deduce which hosts would support reproduction and development as opposed to feeding only, literature records were categorized on the basis of whether: (i) immature stages (larvae and pupae) were recorded on a particular host, (ii) developmental data and/or reports of sustained field populations, particularly

Table 4 Hosts of *C. montrouzieri* which are fed upon and have not been demonstrated to support reproduction and development

Family/Species	Reference
Pseudococcidae	
Dysmicoccus boninsis Kuwana	[214]
Dysmicoccus brevipes (Cockerell)	[214]
Nipaecoccus aurilanatus Maskell	[215]
Phenacoccus gossypii Townsend & Cockerell	[1, 171]
Phenacoccus graminicola Leonardo	[216]
Phenacoccus insolitus Green	[201]
Planococcus krauhniae Kuwana	[217]
Planococcus mali Ezzat & McConnell	[218]
Planococcus vitis Neidielski	[217]
Planococcus maritimus Ehrhom	[217]
Pseudococcus crotonis Green	[217]
Saccharicoccus sacchari Cockerell	[217]
Trionymus insularis Ehrhom	[217]
Coccidae	
Coccus hesperidum Linnaeus	[1]
Coccus pseudomagnoliarum Kuwana	[1]
Dactylopius tomentosus Lamark	[217]
Pulvinaria cellulosa Green	[201]
Pulvinaria icerya Guerin	[217]
Pulvinaria maxima Green	[201]
Pulvinaria psidii Maskell	[214]
Pulvinaria vitis Linnaeus	[193]
Saccharipulvinaria iceryi Signoret	[201]
Diaspididae	
Aonidiella aurantii Maskell	[201]
Aspidiotus destructor Signoret	[219]
Chrysomphalus pinnulifer Maskell	[217]
Selenaspidus articulatus Morgan	[219]
Unaspis citri Comstock	[219]
Ortheziidae	
Orthezia insignis Browne	[220]
Orthezia annae Cockerell	[221]
Aphididae	
Aphis spiraecola Patch	[36]
Sipha sp.	[36]
Aleyrodidae	
Aleurocanthus floccosus (Maskell)	[222]
Aleurocanthus spiniferus (Quaintance)	[222]
Aleurocanthus woglumi Ashby	[222]
Aleurodicus dispersus Russell	[222]
Lipaleyrodes sp.	[222]
Order Hemiptera Triozidae	
Bactericera cockerelli (Sulc.)	[223]
Order Coleoptera Coccinellidae	
Cryptolaemus montrouzieri	[36, 193]
Scymnus coccivora (Ayyar)	[37]
Order Hymenoptera Encyrtidae	
Anagyrus kamali Moursi	[36]
Leptomastix dactylopii Howard	[224]

where the ladybird was used as a biological control agent or recoveries were made. While, this approach provided a basis for categorization, it was not foolproof and there may well be hosts categorized as only accepted hosts, yet in actual fact they may support development and reproduction.

Hosts which support reproduction and development

C. montrouzieri was recorded as being able to feed, develop and reproduce on 49 species in six families of the order Hemiptera (Tables 3 and 4). This included 23 species of Pseudococcidae, 18 of Coccidae, one of Eriococcidae, one of Margarodidae and six of Aleyrodidae. In addition, the coccinellid was reared on *Aphis nerii* Boyer de Fonscolombe (Hemiptera: Aphididae) and eggs of *S. cerealella* (Olivier) (Lepidoptera: Gelechidae). However, in these instances, oviposition was induced by the presence of empty pseudococcid ovisacs [144, 181]. The data suggest that the ladybird specializes on attacking sedentary Hemipteran hosts. However, host suitability in terms of supporting reproduction and development is not family or genus specific. While there is a dearth of information on relative suitability of different species, there is evidence to suggest that some hosts are more suitable than others. For instance, Baskaran *et al.* [26] found that the ladybird developed faster on *P. citri* compared with *Dactylopius tomentosus* (Lamarck) (Hemiptera: Dactylopiidae).

Hosts which are fed on but do not support reproduction and development

C. montrouzieri appears capable of feeding on a wide range of insects (Table 4). This includes at least 35 species in 8 families and 3 orders as follows: 13 Pseudococcidae, 9 Coccidae, 5 Diaspidae, 2 each of Ortheziidae and Aphididae, 5 Aleyrodidae, 2 each of Coccinellidae and Encyrtidae. Although the coccinellid has been reared on *A. nerii* and *S. cerealella*, these hosts appear unsuitable for supporting reproduction and development under natural conditions. While *C. montrouzieri* can be cannibalistic and also feed on *Scymnus coccivora* (Olivier) larvae and encyrtid parasitoid pupae, these cannot be considered as natural hosts. Furthermore, there are no records of coccinellids which specialize on feeding on other coccinellids or on parasitoids.

Interaction with parasitoids and other natural enemies

In many situations, where *C. montrouzieri* is used for classical biological control, it is often introduced together with other natural enemies, particularly parasitoids. For instance, in the programme against *M. hirsutus*, it was used together with at least two other parasitoids. The interactions between *C. montrouzieri* and such parasitoids can therefore have significant implications on overall performance. Therefore, it is important to know if the predator can avoid feeding on parasitized hosts. *C. montrouzieri* has been shown to feed indiscriminately on both parasitized and unparasitized hosts in no-choice situations [227]. Peterkin *et al.* [36, 37] also found that when adult ladybirds were given a choice between pupae of *Anagyrus kamali* Moursi (Hymenoptera: Encyrtidae) and unparasitized *M. hirsutus*, they fed preferentially on the mealybugs. In preference studies with adults and fourth instar larvae of *C. montrouzieri,* Chong and Oetting [224], showed that the ladybird strongly discriminated against *P. citri* parasitized by *Leptomastix dactylopii* Howard (Hymenoptera: Encyrtidae), especially where the parasitoid was highly developed (mummy stage). This would suggest that there is some degree of host discrimination. Although no data are available to show whether *C. montrouzieri* can discriminate between unparasitized mealybugs and those containing a developing larval parasitoid, studies on other coccinellid species suggest that this is possible, particularly when the parasitoid larva is at an advanced stage of development. For instance, adult *Delphastus pusillus* (LeConte) (Coleoptera: Coccinellidae) avoided feeding on *Bemisia tabaci* (Gennadius) (Hemiptera: Aleyrodoidea) containing developing *Encarsia* spp. at an advanced stage of development. Similar results were also obtained in tests with another coccinellid, *Nephaspis bicolor* Gordon, a predator of *Aleurodicus* spp. [228]. In general, coccinellid larvae display a very limited degree of host discrimination. Indeed, conspecific cannibalism is quite common. However, host discrimination is expected to be more important in ladybird adults as this is the stage that seeks out new mealybug colonies for oviposition. A few studies have been carried out to show possible consequences of the interaction between *C. montrouzieri* and other coccinellids. Thus, Peterkin *et al.* [36] showed that both larvae and adult *C. montrouzieri* are capable of feeding on larvae of *S. coccivora* when no other food is available. There is little information on what actually happens in the field, but recent studies are beginning to shed some light on this important subject [229].

Potential risks associated with introduction of C. montrouzieri

C. montrouzieri has evolved as a predator feeding primarily on phytophagous Hemiptera. It poses no risk of attacking crops or natural vegetation. *C. montrouzieri* has a broad host range (Tables 3 and 4). Although it was recorded feeding on lepidopteran eggs in the laboratory and occasionally on aphids, its natural hosts are sedentary Hemiptera and includes species in several families (Pseudococcidae, Coccidae, Diaspidiae, Eriococcidae, Ortheziidae, Magarodidae and Aleyrodidae). Within these families, it appears likely that the host range may be wider than what is currently known. Furthermore, it is likely that species from other hemipteran families could be exploited by the coccinellid. Thus, it can be expected that, when introduced into new localities, *C. montrouzieri* will feed on some non-target hosts, possibly reducing populations of some species. It could be argued that in view of the observations that the coccinellid is not effective at low prey densities (presumably because of lower searching capability), its impact on non-target species is likely to be reduced. This is because most indigenous non-target species are likely to occur in low density populations which might be difficult for the ladybird to locate. When they do occur, it is likely that potential negative impacts will be more prominent in small island systems where extinctions can be expected to occur more easily [230].

C. montrouzieri has the potential to interfere with biological control of weeds. For example, in South Africa, the predator was reported to prey on *Dactylopius* sp., an agent introduced for control of the exotic weed *Opuntia megacantha* Salm-Dyck [231]. In this case, the plants were treated with pesticides that killed the predators but left the scales unharmed before sufficient control of *O. megacantha* was obtained [231].

There is also a risk that the coccinellid might displace natural enemies of other indigenous or exotic insects which are utilized as hosts. This aspect has been poorly studied, although Bennett [232] and Harris [233] cite examples which suggest that native natural enemies can be displaced over much of their range by introduced species. This could have negative consequences as illustrated in the establishment of an exotic generalist predator, *Coccinella septempunctata* L. on the native coccinellid fauna of South Dakota [234–236]. Prior to the establishment of *C. septempunctata*, seven indigenous coccinellid species were present on lucerne, maize and small grains; one of these, *Adalia bipunctata* L. occurred only on maize. Their abundance was severely reduced without significant reduction in pest populations, with the level of reduction of one species being 20–32 times lower following the establishment of the exotic ladybird [143].

Another important concern is the possibility that *C. montrouzieri* might interfere with the functioning of natural enemies of other phytophagous pests which it preys upon. This could be through interference or competition. Dixon [229] reviewed this topic from a perspective of coccinellids used in the biological control of aphids. In simple cage studies on the interactions between a coccinellid predator, *Cycloneda sanguinea* L. and *Aphidius floridaensis* Smith, a parasitoid of the aphid *Dactynotus* sp., parasitoids reduced aphid populations more effectively in the absence of predators. The coccinellid disrupted oviposition of the parasitoid and fed on parasitized aphids [237]. In laboratory studies, *C. montrouzieri* has been shown to be capable of feeding on both healthy and parasitized citrus mealybugs in no-choice tests and it may consume parasitized mealybugs in the field [227]. However, it is noteworthy that *C. montrouzieri* is often recorded occurring together with parasitoids in the field [180, 238, 239]. In addition, we are not aware of situations where new pests have arisen as a direct result of the presence of *C. montrouzieri.* With over 100 years of successful use, there is strong evidence that *C. montrouzieri* does not interfere with the functioning of other natural enemies. In protected agriculture, *C. montrouzieri* appears to complement parasitoids, resulting in more sustainable pest suppression [238]. In previous mealybug biological control programmes, introduction of a parasitoid has been recommended if the predator was not successful or required repeated releases [1, 105, 240]. Experiences from the control of *M. hirsutus* in Trinidad and Tobago, Grenada and St. Kitts indicate that in the field *C. montrouzieri* and *A. kamali* co-exist [2, 3].

As with other coccinelids, the possibility of *C. montrouzieri* attacking humans and domestic animals is minimal, as it is specifically adapted to feeding on insects. However, some temperate Coccinellidae, are reported to occasionally bite strongly into human skin. This occurred in Britain during the population explosion of *C. septempunctata* in 1976 when millions of ladybirds, having destroyed aphid populations, became a nuisance by biting virtually anything [241]. However, although very large numbers of *C. montrouzieri* developed in Trinidad and Tobago, Grenada, and St. Kitts and Nevis after its initial introduction for biocontrol of *M. hirsutus,* biting of humans was not observed. Hence *C. montrouzieri* is unlikely to pose any risk to humans, livestock or other animals.

While some environmental risks are inherent in any introduction of exotic natural enemies, these must be balanced against the risks of doing nothing. A wide knowledge of the ecosystems into which introductions are being made, and of the specific taxa within them, is important in making such judgements. Efforts should be made to identify local biological resources of special significance so that these are not threatened by the introduced exotic. It is noteworthy that Sands [242] points out that a limited degree of attack on indigenous hosts by an introduced natural enemy may be acceptable, if the benefits gained from controlling a pest outweigh risks of effects on the abundance of indigenous species. In the case of the *M. hirsutus*, the potential damage by the pest was so great and in the absence of alternative control measures, many national programmes in the Caribbean did not consider non-target effects on other Hemiptera as a sufficient high risk to oppose introduction.

Conclusions

C. montrouzieri is an effective natural enemy for biological control of certain species of Hemiptera. However, it has a wide host range, which suggests that the potential to impact non-target organisms is high. There is a paucity of field-level ecological studies on the species, but with its wide distribution, the ladybird would be a good model for comparative retrospective studies on impact on non-target organisms. Such studies would be vital in order to justify further use, and to check that the ladybird does not have a negative impact on the environment.

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