Prey specialization in ladybirds: *Iberorhyzobius rondensis*, a potential biological control of *Matsucoccus feytaudi*

Tese apresentada para obtenção do grau de Doutor em Engenharia Florestal e dos Recursos Naturais

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Ao meu Pai.

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Abstract

Iberorhyzobius rondensis (Eizaguirre) (Coleoptera: Coccinellidae) is a recently described species, unique in its genus, endemic to the Iberian Peninsula. The beetle feeds on egg masses of the pine bast scale *Matsucoccus feytaudi* Ducasse (Hemiptera: Matsucoccidae) and is strongly attracted to the prey's sexual pheromone. *M. feytaudi* is endemic to Western Europe and North Africa and invasive in Southeastern Europe. Its sole host is *Pinus pinaster*. Here we evaluate the potential of *I. rondensis* as a biological control agent of *M. feytaudi*. Several characteristics of the beetle were assessed: prey and habitat range, life traits, phenology, phylogeography, phylogeny and predatory efficacy. Our results revealed that *I. rondensis* is highly specialized, depending on *M. feytaudi* to complete its development, and it only occurs on *P. pinaster* trees. Phylogeography matches the one of the prey evidencing a co-evolutionary history. The phylogenetic study validates the genus. A review on the prey specialization of 186 ladybird species was performed. Several traits were found to be related with prey specialization, mainly habitat specialization and host specialization of the prey. *I. rondensis* emerges as a rare case of prey specialization among ladybirds. All results support *I. rondensis* as an appropriate candidate for biological control of *M. feytaudi*.

Key-words: Coccidophagous, Coccoidea, biocontrol, coccinellid, prey-predator.

Resumo

Iberorhyzobius rondensis (Eizaguirre) (Coleoptera: Coccinellidae) é uma espécie descrita recentemente, única no seu género, e endémica na Península Ibérica. Alimenta-se de ovos da cochonilha *Matsucoccus feytaudi* Ducasse (Hemiptera: Matsucoccidae), e é atraída pela feromona sexual desta presa. Esta cochonilha tem como único hospedeiro *Pinus pinaster* , é endémica na Europa Ocidental e Norte de África e invasora no Sudeste da Europa. Neste trabalho avaliámos o potencial de *I. rondensis* como agente de controlo biológico de *M. feytaudi*. Para tal, examinaram-se várias características biológicas, ecológicas e genéticas da joaninha. Os nossos resultados demonstraram que *I. rondensis* é muito especializado tanto a nível da presa (*M. feytaudi*), como do habitat (*P. pinaster*). A sua filogeografia revelou uma história de co-evolução com *M. feytaudi*. A filogenia validou a diferenciação do género *Iberorhyzobius*. Realizámos uma revisão bibliográfica sobre a especialização alimentar em 186 espécies de joaninhas, em que se verificou que as características biológicas estão relacionadas com o grau de especialização alimentar. A especialização ao nível do habitat e a especialização da presa são características principais. *I.rondensis* é um caso único de especialização entre as demais joaninhas. Os nossos resultados revelaram que *I.rondensis* é um candidato apropriado para o controlo biológico de *M. feytaudi*.

Palavras-chave: Coccidófago,Coccoidea, controlo biológico, joaninha, predador-presa

I. Introduction

1.1. Importance of the Coccinellidae

Taxonomy and Phylogeny

Coccinellidae (Coleoptera) is the largest family of the Cerylonid Series CS, including almost 500 genera and 6000 species (Hodek & Honěk, 1996; Seago *et al.*, 2011). The CS series is an artificial group of families within the superfamily Cucujoidea, suborder Polyphaga (Robertson *et al.*, 2008), and it includes the families Cerylonidae, Discolomidae, Alexiidae, Corylophidae, Endomychidae, Lathridiidae and Coccinellidae.

From the 19th century up to the present day, several different systems were proposed to classify the Coccinellidae into subfamilies and tribes (Iperti, 1999). Sasaji (1968) proposed a modern system for classifying all coccinellids based on the comparative morphology of larvae and adults. The author divided Coccinellidae into six subfamilies, which are still broadly recognizable today: Sticholotinae, Scymninae, Chilocorinae, Coccidulinae, Coccinellinae, and Epilachninae (Kovář, 1996). More recent systems were proposed by Chazeau *et al.* (1989), Fürsch (1990), and Kovář (1996). Kovář (1996), elevated the tribe Ortaliini to the subfamily Ortaliinae. This system has been widely used in the past years, but recent phylogenetic analysis has led to the conclusion that it is inadequate (Seago *et al.*, 2011).

Within the CS series the Coccinellidae are a monophyletic clade, but many subfamilies on the group are polyphyletic and paraphyletic (Robertson *et al.*, 2008). The Sticholotidinae are considered the most ancient coccinellid subfamily (Robertson *et al.*, 2008). The subfamilies Coccinellinae and Epilachninae are considered monophyletic (Giorgi *et al.*, 2009) and the subfamilies Chilocorinae, Scymninae and Coccidulinae paraphyletic (Robertson *et al.*, 2008; Giorgi *et al.*, 2009).

Seago *et al.* (2011) performed a major Bayesian analysis based on morphological and multi-locus molecular data for the Coccinellidae. He concluded that coccinellidae classification should suffer a major revision, given the paraphyly and polyphyly of the different subfamilies. He proposed the division of the Coccinellidae into two subfamilies, following the phylogeny suggested by Ślipiński (2007): the Microweisinae Leng and the Coccinellinae Latreille.

A phylogenetic revision of many tribes and genus is still called for in order to clarify their taxonomic relationship. As an example, relevant to the present study, the genus *Rhyzobius* Stephens (Coccidulinae) which includes both Palearctic and Australian species, displays clear polyphyly in molecular studies (Magro *et al.*, 2009; Seago *et al.*, 2011), and therefore should be revised. In chapter 5 we will address, in particular, the phylogenetic position of the new genus *Iberorhyziobius* in relation to other Coccidulinae.

Feeding preferences and evolution

Three types of feeding regimes are present within the Coccinellidae: predation (zoophagy), plant feeding (phytophagy) and fungus feeding (mycophagy). Most Coccinellidae (90%) are predators, feeding on the suborder Sternorrhyncha (Iperti, 1999; Giorgi *et al.*, 2009; Seago *et al.*, 2011). Since most members of the CS are mycophagous, it is believed that the Coccinellidae made a transition from mycophagy to predation. It is suggested that the preference for Sternorrhyncha in ladybirds started with fungus feeding, because of the sooty mold that normally grows on these hemipterans' honeydew (Sutherland & Parrella, 2009; Seago *et al.*, 2011). The first shift from mycophagy to predation occurred in species which started to feed on armored scale insects (Coccoidea: Diaspididae), and then to other soft body Sternorrhyncha (Seago *et al.*, 2011). Coccidophagy is thus considered the ancestral condition of predator ladybirds (Giorgi *et al.*, 2009). Later shifts to Aleyrodoidea, Acari and Formicidae were direct transitions from coccidophagy (Giorgi *et al.*, 2009; Seago *et al.*, 2011). Aphidophagy evolved at least three times during the ladybirds' expansion, and it implied the development of particular traits (Magro *et al.*, 2009). Given the mutualistic interactions between ants and many aphids and scale insects, Seago *et al.* (2011) considers that the ant-specific defensive adaptations were crucial for the Coccinellidae diversification. Secondary shifts to mycophagy and phytophagy are also considered to have occurred directly from coccidophagy (Giorgi *et al.*, 2009). Sloggett & Majerus (2000) consider that prey is the driving force in ladybird specialization. Indeed, prey shifts are considered rather frequent among ladybirds due to long periods when essential prey is scarce and the beetles must feed on alternative prey to survive.

Within coccinellids, each taxonomic group is associated with a group of prey: the Sticholotini feed on Coccoidea, the Serangini on Aleyrodidae. The Scyminini and Hyperaspini feed mostly on aphids, the Stethorini feed on mites and spider mites, the Aspiridimerini on aphids. The Chilocorinae and Coccidulinae prey mostly on coccids, except for the tribe Platynaspini. The Coccinellidae are mostly aphidophagous, except for some genus which feed on coccids and the tribe Psylloborini which is mycophagous. The subfamily Epilachninae is phytophagous. Psyllids are consumed preferentially by the tribe Ortaliini (Hodek & Honěk, 1996; Hodek & Honěk, 2009).

In addition, some species of coccinellids attack other orders of insects such as Thysanoptera, Lepidoptera, Coleoptera, Hymenoptera and Diptera (Evans, 2009). This generalist behavior is mostly common amongst the aphidophagous species, since those are more prone to suffer starvation in periods of scarcity of their main prey (Dixon, 2000; Sloggett & Majerus, 2000). Species with Coleoptera as their main prey usually comprise large, highly polyphagous individuals (Dixon & Hemptinne, 2001). Cannibalism is also common among some species, especially when food shortage occurs (Hodek & Honěk, 1996; Obrycki & Kring, 1998). The predator status of most ladybirds justifies its importance as regulators of many potential insect pests of agricultural and forest ecosystems (Iperti, 1999).

Prey and Habitat Specialization

Ladybird predators present variable degrees of prey specialization. Although certain taxonomic groups are associated with a certain type of prey, different feeding ranges may be found in a given group. Within the Coccidulini Mulsant, for instance, we find that *Rodatus major* Blackburn is a monophagous species, feeding only on *Monophlebulus pilosior* (Maskell), while *Rhyzobius lophanthae* (Blaisdell) is oligophagous, feeding on a large range of coccid species (Hodek & Honěk, 1996). Often, congeneric species display different degrees of feeding specialization (Osawa & Ohashi, 2008).

However, one must be cautious when considering the feeding range of a given ladybird. Not all the food the beetle ingests can be classified as its “typical food”. We need to distinguish between *essential* and *alternative* food/prey (Hodek & Honěk, 1996). Essential food is any that allows for pre-imaginal development with low mortality and high oviposition, while alternative food serves as a source of energy and allows for the ladybird's sustenance, but not its reproduction. Many ladybird species rely on non-prey-food, such as nectar, pollen, plant, fruit and fungi, which sustain the beetles during food scarcity (Lundgren, 2009). Further, several studies have demonstrated that a mixed diet containing the essential prey may result in better performance and fitness of the ladybirds than a diet of essential food alone (Evans *et al.*, 1999).

Sometimes the habitat restricts the prey range of the ladybirds (Hodek & Honěk, 1996; Sloggett & Majerus, 2000). Coccinellids have very different habitat requirements, ranging from stenotopic to eurytopic species (Hodek & Honěk, 1996). They may be restricted to a single plant type, such as *Anatis mali* (Say) on coniferous trees (Berthiaume *et al.*, 2000); to a type of vegetation, such as *Coccinella hieroglyphica* L. on peat bogs with *Calluna vulgaris* (Hippa *et al.*, 1978); or to a kind of habitat strata, such as *Adalia bipunctata* (L.) on trees and bushes (Omkar & Pervez, 2005). Some species are cosmopolitan and found almost everywhere, such as *Coccinella septempunctata* L. (Omkar & Pervez, 2002). The habitat suitability may be defined based on its degree of attractiveness for adults, the quantity of larvae present, and its richness on nutritional resources (Iperti, 1999). However, the most important criteria to identify a habitat as suitable is whether the species breeds in it (Hodek & Honěk, 1996). Since larvae have very low mobility, adults choose the habitat, and with that decision also choose the prey (Hodek & Honěk, 1996; Dixon, 2000). Furthermore, if a species breeds in a specific habitat, this means that its essential prey is present in enough density to sustain the neonate larvae (Evans & Dixon, 1986). Given the relevance of habitat specialization, as related with prey specialization in predacious ladybirds, this topic will be analyzed in the case study presented in chapter 2.

Thus, a habitat's suitability for a given species is intimately linked with the presence in it of the latter's essential prey. When a coccinellid shifts prey or incorporates a novel prey in its diet, it may start to breed on the new prey's habitat. In a laboratory study with *A. bipunctata*, Rana *et al.* (2002) demonstrated that adaptation to alternative prey may be a very quick process. Further generations of the ladybird may remain on the novel habitat, feeding on the new prey, which may eventually lead to a process of parapatric speciation.

Resource competition may also play an important rule on habitat restriction. It is often the case that species with similar food requirements occupy different niches, thus avoiding competition, such as in congeners with different habitat requirements like *A. bipunctata* (Omkar & Pervez, 2005) and *Adalia decempunctata* (L.) (Dixon, 1959); or *C. septempunctata* (Omkar & Pervez, 2002) and *Coccinella magnifica* Redtenbacher (Sloggett *et al.*, 2002).

Further, the specific prey characteristics will condition the life history evolution of the predators (Dixon, 2000). For instance, aphids are ephemeral resources, available in the form of large scattered colonies, and coccids are stable resources, with smaller colonies aggregated in space (Borges *et al.*, 2006). These differences may justify why, in general, aphidophagous species have faster development rate, higher fecundity and shorter longevity than coccidophagous species (Borges *et al.*, 2011; Borges *et al.*, 2013). Different patterns of prey specialization, such as those related with body size, can also be observed in other coccinellid species: mites are the prey of the smallest species of coccinellids, and chrysomelids and lepidopterous larvae the prey of the larger species (Dixon & Hemptinne, 2001). Some geographical patterns also emerge from ladybirds' prey specialization: aphidophagous species from tribes Coccinellini, Hippodamiini, Cheilomenini and Scymnini are more common in the temperate zones of Europe and North America, were aphids are common; coccidophagous ladybirds (Chilocorini, Scymnini, Hyperaspini, Coccidulini and Noviini), are more common in the tropical regions of central and South Africa, South America, India and China, where most coccid species are present (Iperti, 1999; Dixon, 2000).

Despite the diversity of habitat and prey preference among ladybirds, this group occupies most terrestrial regions of the globe, including tundra, forest, grassland and agroecosystems. Further, some species periodically show movements from meadows to forests or from valleys to mountains (Iperti, 1999). This widespread distribution of ladybirds on most land ecosystems makes these species highly noticeable as well as key elements of many ecosystems (Iperti, 1999; Sloggett, 2005).

Diapause and Reproduction

Coccinellids are holometabolous insects, with four larval instars. Duration of a complete life cycle lasts from 2 weeks up to 2 months depending on the thermal conditions and feeding guild of the ladybird species (Iperti, 1999). Usually adults only mate and reproduce after feeding on their essential prey, which also assures prey availability for neonate larvae (Hodek & Honěk, 1996).

Since prey is the main limiting factor for ladybird reproduction (Hodek & Honěk, 1996; Dixon, 2000), adults tend to synchronize their life-cycle with that of their prey (Evans & Dixon, 1986; Dixon, 2000; Sloggett & Majerus, 2000). Life cycle synchronization may be achieved through dormancy, migration or reproductive diapause (Hodek & Honěk, 1996).

Most ladybird species show reproductive diapause (Hodek, 2012). This diapause may be facultative, when it is induced or interrupted by environmental signals or food availability, or obligatory, when dependent on genetic factors (Hodek, 2002; Hodek, 2012). Sometimes, individuals from different populations within the same species may present different types of diapause, as happens with *C. septempunctata* (Hodek & Okuda, 1993).

Voltinism usually depends on the climate of the region (Iperti, 1999). For example, in temperate climates, predaceous coccinellids generally reproduce in spring, when prey is abundant, and diapause during summer and winter, but in tropical regions coccinellids may never diapause (Iperti, 1999). In the case of very specialized predators, however, voltinism depends on, and coincides with, that of the prey (e.g. Soares *et al.*, 1999; Cheah & McClure, 2000; Santos *et al.*, 2010). Variations in voltinism and its relationship with prey voltinism have thus become relevant topics in ladybird investigation, and are of special interest for the model system studied in the present work (chapter 3).

Biological control and risk assessment

Ladybirds are one of the most widely used groups of predators in biological control, with several species being sold worldwide. They are used in the control of whiteflies, scale insects, aphids and psyllids (Evans, 2009; Roy & Migeon, 2010). They are even the icon of biological control in many organizations and projects. In a survey conducted in *Google Images* using the key words “biological control”, ladybirds were present in 16 images out of the first 50 hits.

The first great success in biological control was achieved in 1889 with the release of the ladybird *Rodolia cardinalis* (Mulsant), imported from Australia to California for the control of *Icerya purchasi* Maskell in citrus orchards (Dixon, 2000). This led to the so-called "Ladybird fantasy period", in which several attempts to use ladybirds as biological control agents were made, most of which failed – only 10% of the species introduced in this period were successfully established (Obrycki & Kring, 1998). More recently, it was also proven in the worst possible way that some ladybird species may negatively impact some systems: the introduction of *Harmonia axyridis* (Pallas) in Europe and North America had disastrous ecological and economic consequences (Roy & Migeon, 2010).

Risk assessment studies of potential biological control agents are thus absolutely needed before their release in a novel range. Risk assessment studies consist on the evaluation of certain characteristics of the potential biocontrol agents. Knowledge of such characteristics will avoid the misuse of certain species for biocontrol, avoid the risk of ecological impacts, and maximize the effectiveness of those biocontrol agents (Van Lenteren *et al.*, 2006; Barratt *et al.*, 2010).

Dixon (2000) proposed a list of attributes which make up a good biological control agent: specificity, attack rate, conversion efficiency, relative growth rate, fecundity and generation time ratio. Specificity is no doubt one of the first requisites to be met by any biological control agent (McEvoy, 1996). A high degree of specialization towards a given prey will ensure a strong link to, and maximal impact on, the target, as well as minimal impact on non-target organisms (Obrycki & Kring, 1998; Obrycki *et al.*, 2011). Successful cases of biological control by ladybirds usually happen with more specialized species, such as *R. cardinalis* and *Hyperaspis pantherina* Fürsch, and cases of unsuccessful and high non-target impact are linked with more polyphagous species such as *H. axyridis* and *Cryptolaemus montrouzieri* Mulsant (Dixon, 2000; Roy & Migeon, 2010). Within the coccidophagous group, ladybirds feeding on the Margarodidae bast scale are more specific and have a higher success rate than any of the other remaining coccidophagous species.

Another important attribute for a biocontrol agent is generation time ratio, i.e. the number of generations of the prey within the time of a single generation of the predator (Dixon *et al.*, 1997); this ratio is linked with the rate of development of that predator. In order to control its prey, the predator should develop at a similar or slightly higher rate than it (Dixon *et al.*, 2000).

The importance of these two characteristics - specificity and generation time ratio - may be well exemplified with the two groups of ladybirds most widely used in biocontrol: the aphidophagous and the coccidophagous. Coccidophagous ladybirds are usually more specialized than aphidophagous; and their rate of development is usually faster than that of their prey, which is not the case with aphidophagous (Dixon *et al.*, 1997; Borges *et al.*, 2013). This explains why coccidophagous ladybirds are considered much better biocontrol agents than aphidophagous (Obrycki & Kring, 1998; Iperti, 1999; Obrycki *et al.*, 2009). To date, of 155 attempts to control aphids by ladybirds, only one was a substantial success, while in the case of coccids, of 613 attempts, 53 were successful (Dixon, 2000).

1.2. *Iberorhyzobius rondensis* and *Matsucoccus feytaudi*

Matsucoccus feytaudi Ducasse is a bast scale insect, belonging to the family Matsucoccidae (Hemiptera: Sternorrhyncha: Coccoidea). The oldest known scale insect fossils are the Matsucoccidae, with 40 millions years. They include two genera, the genus *Matsucoccus* with 33 extant and 6 fossil species, and the fossil genus *Eomatsucoccus,* with 4 species (Foldi, 2004).

The Matsucoccidae only inhabit the northern hemisphere, and feed exclusively on *Pinus* species. Usually, each species of *Matsucoccus* is related with a single species or section of pines (Riom & Gerbinot, 1977a). Some *Matsucoccus* are very serious pests of natural pine forests and plantations, particularly in the USA, China and the Mediterranean basin (Foldi, 2004). Outbreaks of this pest cause serious damage which results in needle drop, shortened needles, weakened crowns, chlorosis in mature trees, and deformation or death in young trees (Foldi, 2004). Several coccinelids are known as predators of *Matsucoccus* spp. *H. axyridis* (Coccinellidae) was used to control *Matsucoccus massonianae* Young & Hu in China (Wang, 1982); *Matsucoccus matsumurae* Kuwana in Japan (McClure, 1986) and *Matsucoccus resinosae* Bean & Godwin in the US (Foldi, 2004). *Ballia obscurosignata* Liu and *Mulsantia picta* (Randall) are also efficient predators of *M. matsumurae* in Japan (McClure *et al*., 1983).

In Italy, several ladybirds were observed to feed on *M. feytaudi*: *Scymnus suturalis* Thunberg, *Scymnus interruptus* Goeze, *Oenopia conglobata* (L.), *Oenopia lyncea* (Olivier) and *Rhyzobius chrysomeloides* (Herbst); only the latter one, however , seemed to have some impact on the bast scale level (Covassi *et al*., 1991). *O. conglobata* and *Adalia decempunctata* (L.) are known to prey on *Matsucoccus josephi* Bodenheimer (Bodenheimer & Neumark, 1955).

The maritime pine bast scale *M. feytaudi* Ducasse, collected from *Pinus pinaster* Aiton trees in Southwestern France, was first identified as *M. matsumurae* in 1938, by Ducasse. Later, in 1942, Feytaudi recognized it as a different species and renamed it as *M. feytaudi* Ducasse. *M. feytaudi* lives in the bark crevices of the pine tree, beneath the bark. It is a highly specialized sap-sucker insect, feeding only on *P. pinaster*. The only other *Matsucoccus* species naturally occurring in Europe is *Matsucoccus pini* (Green) feeding on *Pinus nigra* Arnold and *Pinus sylvestris* (L.) (Foldi, 2004).

In *M. feytaudi*, as in all other bast scales, the female presents a neotenic form, while the male goes through complete development. The female goes through three stages, two as a larva (L1, L2) and one as an adult, and the male five, four as an immature (L1, L2, pro-nymph and nymph) and one as an adult. L1 is the mobile stage, with a dispersal phase followed by a phase where the insect fixes itself in the tree crown or trunk. L2 is legless and fixed to the bark (Riom & Gerbinot, 1977a, 1977b; Foldi, 2004).

M. feytaudi is a univoltine species. In Southeastern Europe, the adults appear in February-April to mate and lay eggs. Stage L1 appears in April and L2 in August. Pro-nymphs emerge in December-January (Riom & Gerbinot, 1977a). In Portugal, however, males are present all year round, and the existence of two overlapping generations has been proposed by Branco *et al.* (2001).

The pine bast scale is endemic to the Iberian Peninsula and to North Africa. Mitochondrial data has shown three distinct lineages occurring in different geographical areas: Western and Central Iberian Peninsula; the Andalusia region; and the Atlas Mountains (Burban *et al.*, 1999). The native range of this insect is restricted to the Southwestern part of the Mediterranean basin and Morocco. This corresponds to the refuge areas of *P. pinaster* during the last glaciation (Burban & Petit, 2003), where the maritime pine bast scale is thought to have evolved in close association with its host

(Burban *et al.*, 1999). It becomes than pertinent to evaluate how the phylogeograhy of the predator matches the one of the prey. This will be analyzed in chapter 4.

In its native range *M. feytaudi* is regulated by several natural enemies, which respond to its sex pheromone, such as several *Elatophilus* Reuter (Hemiptera: Anthocoridae), *Hemerobius stigma* Stephens (Neuroptera: Hemerobiidae), *Aplocnemus raymondi* Deville, *Aplocnemus brevis* Rosenhauer (Coleoptera: Dasytidae), *Malachiomimus pectinatus* (Kiesenwetter) (Coleoptera: Malachiidae) and *Iberorhyzobius rondensis* (Eizaguirre) (Coleoptera: Coccinellidae) (Mendel *et al.*, 2004, Branco *et al.*, 2006, Branco *et al.*, 2011, Rodrigo *et al.*, 2013).

During the 20th century, *M. feytaudi* became invasive in several areas of Southeastern Europe, causing severe damage to pine populations (Covassi *et al.*, 1991; Riom & Tacon, 1994; Jactel *et al.*, 1996; Jactel & Menassieu, 2005; Marziali *et al.*, 2011). The insect was first introduced in Southeastern France, from where it expanded its range to north Italy. A later entry into Corsica (1994) occurred from populations coming from north Italy and mostly Southeastern France (Kerdelhué *et al.*, 2014). In 2008, 2000 km^2 of stands were already affected. In Corsica the maritime pine bast scale is now spreading at a rate of 2km/year (Jactel *et al.*, 2012).

Since the bast scale spends most of its life cycle hidden under the bark, control with insecticides or mass trapping is not viable. Methods such as tree cutting or selection of certain genetic types of trees are also rather difficult, at least on the Corsica Island (Jactel *et al.*, 2012). The release of natural enemies of *M. feytaudi* in its invaded range has been therefore envisaged as a possible solution for its biocontrol (Jactel & Menassieu, 2005).

Certain natural enemies of the bast scale are present in invaded areas of Corsica, Italy and France, namely, *Elatophilus nigricornis* (Zetterstedt), predator of *M. pini*, and the generalist beetle *R. chrysomeloides* (Toccafondi *et al.*, 1991; Fabre *et al.*, 2000). Yet, none of them have proven effective enough to slow the spread of the invasive scale.

In Corsica, inundative releases of *E. nigricornis* (normally found on *P. nigra laricio* stands) were made on *P. pinaster* stands in 2011 and 2012 (Jactel *et al.*, 2012). The insects, however, have not yet established on those *P. pinaster* stands. Therefore, another option for the control of *M. feytaudi* in Corsica is the ladybird *I. rondensis*, native from the region of origin of *M. feytaudi* (Jactel *et al.*, 2012).

I. rondensis is a very recently described ladybird species (Eizaguirre, 2004; Raimundo *et al.*, 2006). In the years of 1927, 1934 and in 1967 four exemplars were collected in Vigo (coll. G. C. Champion), Sierra de Gredos (C. Koch &, PCCC), and Ronda (coll. M. E. Baechus & B. Levey). Those exemplars are property of the British Museum of Natural History, London (2 ♀) and the Museo Civico di Storia Naturale di Milano (2 ♀), but were never identified due to absence of males.

In 1997, Eizaguirre found some specimens of *I. rondensis* on conifer trees, probably *P. pinaster*, in the region of Sierra de Ronda, and described them as *Coccidula rondensis.*

In 2000 the ladybird was found in Portugal in *P. pinaster* trees, attracted by the sexual pheromone of *M. feytaudi* (Branco *et al.*, 2006; Branco *et al.*, 2011). The beetle was first considered to belong to the genus *Rhyzobius* (Branco *et al.*, 2006). Later Raimundo *et al.* (2006), using optical and SEM images and comparing several morphological traits, concluded that, although the beetle was a Coccidulini, it neither belonged to the genus *Rhyzobius* nor to the genus *Coccidula* Gyll. Thus, a new genus, *Iberorhyzobius* Raimundo & Canepary was created for the ladybird beetle.

The Coccidulini (subfamily Coccidulinae) comprise 23 genera, and most of them, especially the genus *Rhyzobius*, are tropical species (Tomaszewska, 2010). In the Iberian Peninsula there are only four endemic species of Coccidulini (Eizaguirre, 2004) besides *I. rondensis*: *Rhyzobius litura* (Fabricius), *R. chrysomeloides*, *Coccidula scutellata* (Herbst), and *Coccidula rufa* (Herbst). *R. litura* and *R. chrysomeloides* are abundant species, found in several Mediterranean ecosystems, feeding on aphids and coccids (Raimundo & Alves, 1986; Ricci, 1986; Covassi *et al.*, 1991; Santos *et al.*, 2009). *C. rufa* and *C. scutellata* are rare species, usually found in aquatic plants on humid areas, and they are considered aphidophagous (Raimundo & Alves, 1986).

So far, little is known about the biology of *I. rondensis*. Larvae of the beetle were observed feeding on egg masses of *M. feytaudi* Ducasse, and are known to respond to the sex pheromone of *M. feytaudi* females (Branco *et al.*, 2006). The beetle has only been collected on maritime pines in Portugal and Spain (Eizaguirre, 2004; Raimundo *et* *al.*, 2006), despite focused search for natural enemies of *M. feytaudi* in Italy (Covassi *et al.*, 1991), southern France and Corsica (Branco *et al.*, 2011).

1.3. Objectives

The main objective of this study is to understand basic aspects of the ecology and biology of *I. rondensis*, which will contribute to its risk assessment as a potential biocontrol agent of the pine bast scale. Secondly, given the importance of prey specialization for a biocontrol agent, particularly on the case of ladybirds, we perform a major review on prey specialization of ladybirds.

So, the specific objectives of this work, addressed in different chapters, are to:

1. Determine the phylogenetic position of *I. rondensis* within the tribe Coccidulini and validate its taxonomic position as a unique genus.
2. Determine the habitat specialization of *I. rondensis*, by surveying the main host pines of *Matsucoccus* in Iberian Peninsula.
3. Determine the ladybird’s prey range and compare prey suitability, by measuring development, RGR, survival and prey choice tendencies.
4. Determine several of the beetle’s life traits, such as pre-imaginal development, adult longevity and fecundity. Understand reproductive mechanisms and mating behavior of the ladybirds, and how they relate with the prey’s life cycle.
5. Evaluate the predator’s efficacy through measurement of its prey consumption.
6. Understand the phylogeography of the beetle in the Iberian Peninsula, and how it relates to that of its prey, *M. feytaudi*, and its host plant, *P. pinaster*.
7. Understand several life traits and characteristics related to prey specialization in ladybirds.

1.4. References

Barratt, B., Howarth, F., Withers, T., Kean, J. & Ridley, G. (2010) Progress in risk assessment for classical biological control. *Biological Control* **52**, 245-254.

Berthiaume, R., Hébert, C. & Cloutier, C. (2000) Predation on *Mindarus abietinus* infesting balsam fir grown as Christmas trees: the impact of coccinellid larval predation with emphasis on *Anatis mali*. *Biocontrol* **45**, 425-438.

Borges, I., Soares, A.O. & Hemptinne, J.L. (2006) Abundance and spatial distribution of aphids and scales select for different life histories in their ladybird beetle predators. *Journal of Applied Entomology* **130**, 461-464.

Borges, I., Hemptinne, J.L. & Soares, A.O. (2013) Contrasting population growth parameters of the aphidophagous *Scymnus nubilus* and the coccidophagous *Nephus reunioni*. *BioControl* **58**, 351-357.

Borges, I., Soares, A.O., Magro, A. & Hemptinne, J.-L. (2011) Prey availability in time and space is a driving force in life history evolution of predatory insects. *Evolutionary Ecology* **25**, 1307-1319.

Branco, M., van Halder, I., Franco, J.C., Constantin, R. & Jactel, H. (2011) Prey sex pheromone as kairomone for a new group of predators (Coleoptera: Dasytidae, Aplocnemus spp.) of pine bast scales. *Bullettin of Entomological Research* **101**, 667-674.

Branco, M., Brito, O., Jactel, H., Mendel, Z., Franco, J. & Pellizzari, G. (2001) Seasonal history of the Maritime Pine Bast Scale *Matsucoccus feytaudi* Ducasse (Hemiptera: Matsucoccidae) in Portugal. *Bollettino di Zoologia Agraria e di Bachicoltura* **33**, 319-329

Branco, M., Franco, J.C., Dunkelblum, E., Assael, F., Protasov, A., Ofer, D. & Mendel, Z. (2006) A common mode of attraction of larvae and adults of insect predators to the sex pheromone of their prey (Hemiptera: Matsucoccidae). *Bulletin of Entomological Research* **96**, 179-185.

Bodenheimer, F.S. & Neumark, S. (1955). *The Israeli pine Matsucoccus* (Matsucoccus josephi n. sp.). Kiryath Sepher, Jerusalem.

Burban, C. & Petit, R.J. (2003) Phylogeography of maritime pine inferred with organelle markers having contrasted inheritance. *Molecular Ecology* **12**, 1487-1495.

Burban, C., Petit, R.J., Carcreff, E. & Jactel, H. (1999) Rangewide variation of the maritime pine bast scale *Matsucoccus feytaudi* Duc. (Homoptera: Matsucoccidae) in relation to the genetic structure of its host. *Molecular Ecology* **8**, 1593-1602.

Chazeau, J., Fürsch, H. & Sasaji, H. (1989) Taxonomy of coccinellids. *Coccinella* **1**, 6-8.

Cheah, C.A.J. & McClure, M.S. (2000) Seasonal synchrony of life cycles between the exotic predator, *Pseudoscymnus tsugae* (Coleoptera: Coccinellidae) and its prey, the hemlock woolly adelgid *Adelges tsugae* (Homoptera: Adelgidae). *Agricultural and Forest Entomology* **2**, 241-251.

Covassi, M., Binazzi, A. & Toccafondi, P. (1991) Studies on the entomophagous predators of a scale of the genus *Matsucoccus* Cock. in Italy. I. Faunistical-ecological notes on species observed in pine forests in Liguria and Tuscany. *Redia* **74**, 575-597.

Dixon, A., Hemptinne, J.-L. & Kindlmann, P. (1997) Effectiveness of ladybirds as biological control agents: patterns and processes. *Entomophaga* **42**, 71-83.

Dixon, A.F.G. (1959) An experimental study of the searching behavior of the predtory coccinellid beetle *Adalia decempunctata* (I). *Journal of Animal Ecology* **28**, 259-281.

Dixon, A.F.G. (2000) *Insect Predator-Prey Dynamics: Ladybird Beetles and Biological Control*. New York, USA, Cambridge University Press.

Dixon, A.F.G. & Hemptinne, J.L. (2001) Body size distribution in predatory ladybird beetles reflects that of their prey. *Ecology* **82**, 1847-1856.

Eizaguirre, S. (2004) Revisión de la tribu Coccidulini en la Península Ibérica (Coleoptera: Coccinellidae). *Estudios del Museo de Ciencias Naturales de Álava* **18-19**, 153-170.

Evans, E.W. (2009) Lady beetles as predators of insects other than Hemiptera. *Biological Control* **51**, 255-267.

Evans, E.W. & Dixon, A. (1986) Cues for oviposition by ladybird beetles (Coccinellidae): response to aphids. *The Journal of Animal Ecology* **55**, 1027-1034.

Evans, E.W., Stevenson, A.T. & Richards, D.R. (1999) Essential versus alternative foods of insect predators: benefits of a mixed diet. *Oecologia* **121**, 107-112.

Fabre, J.-P., Menassieu, P., Foing, J.-J. & Chalon, A. (2000) Biology and ecology of *Elatophilus nigricornis* Zetterstedt (Hemiptera Anthocoridae) predator of

Matsucoccus feytaudi Ducasse (Homoptera Matsucoccidae) in the South-East of France. *Annals of Forest Science* **57**, 777-792.

Foldi, A.I. (2004) The Matsucoccidae in the Mediterranean basin with a world list of species (Hemiptera: Sternorrhyncha: Coccoidea). *Annales de la Société Entomologique de France* **40**, 145-168.

Fürsch, H. (1990) Taxonomy of Coccinellids. *Coccinella* **2**, 7-18.

Giorgi, J.A., Vandenberg, N.J., McHugh, J.V., Forrester, J.A., Ślipiński, A., Miller, K.B., Shapiro, L.R. & Whiting, M.F. (2009) The evolution of food preferences in Coccinellidae. *Biological Control* **51**, 215-231.

Hippa, H., Koponen, S. & Laine, T. (1978) On the feeding biology of *Coccinella hieroglyphica* L. (Col., Coccinellidae). *Reports from the Kevo Subarctic Research Station* **14**, 18-20.

Hodek, I. (2002) Controversial aspects of diapause development. *European Journal of Entomology* **99**, 163-174.

Hodek, I. (2012) Adult diapause in Coleoptera. *Psyche: A Journal of Entomology* **2012**, 1-10.

Hodek, I. & Okuda, T. (1993) A weak tendency to "obligatory" diapause in *Coccinella septempunctata* from southern Spain. *Entomophaga* **38**, 139-142.

Hodek, I. & Honěk, A. (1996) *Ecology of Coccinellidae*. Dordrecht, The Netherlands, Kluwer Academic Publishers.

Hodek, I. & Honěk, A. (2009) Scale insects, mealybugs, whiteflies and psyllids (Hemiptera, Sternorrhyncha) as prey of ladybirds. *Biological Control* **51**, 232-243.

Iperti, G. (1999) Biodiversity of predaceous coccinellidae in relation to bioindication and economic importance. *Agriculture, Ecosystems & Environment* **74**, 323-342.

Jactel, H., Ménassieu, P. & Burban, C. (1996) Découverte en Corse de *Matsucoccus feytaudi* Duc (Homoptera: Margarodidae), cochenille du pin maritime. *Annals of Forest Science* **53**, 145-152.

Jactel, H. & Menassieu, P. (2005) La cochenille du pin maritime *Matsuccocus feytaudi*: nouvelles données épidémiologiques et perspectives de lutte. *Forêt Méditerranéenne* **1**, 37-46.

Jactel H., Barbaro, L., Vetillard, F., Nezan, J., Charbonnier, Y., Terraube, J., Halder, I.v., Rigot, T., Roques, A., Tavares, C. & Branco, M. (2012) Rapport final: *Lutte biologique contre la cochenille du pin maritime,* Matsucoccus feytaudi, *en Corse.* Bordeaux, INRA.

Kerdelhué, C., Boivin, T. & Burban, C. (2014) Contrasted invasion processes imprint the genetic structure of an invasive scale insect across southern Europe. *Heredity*, 1–11.

Kovář, I. (1996) Phylogeny pp. 19-31 in Hodek, I. & Honěk, A. (Ed.) *Ecology of Coccinellidae*. Dordrecht, The Netherlands, Kluwer Academic Publishers.

Lundgren, J.G. (2009) Nutritional aspects of non-prey foods in the life histories of predaceous Coccinellidae. *Biological Control* **51**, 294-305.

Magro, A., Lecompte, E., Magne, F., Hemptinne, J.L. & Crouau-Roy, B. (2009) Phylogeny of ladybirds (Coleoptera: Coccinellidae): are the subfamilies monophyletic? *Molecular Phylogenetics and Evolution* **54**, 833-848.

Marziali, L., Marianelli, L., Bagnoli, M. & Roversi, P.F. (2011) Spatial analysis for pest management in Tuscany. *Silva Lusitana* **19**, 134-140.

McClure, M.S., Dahlsten, D.L., DeBarr, G.L. & Hedden, R.L. (1983) World Forestry: Control of Pine Bast Scale in China. *Journal of Forestry* **81**, 440-478.

McClure, M.S. (1986) Role of Predators in Regulation of Endemic Populations of *Matsucoccus matsumurae* (Homoptera: Margarodidae) in Japan. *Environmental Entomology* **15**, 976-983.

McEvoy, P.B. (1996) Host specificity and biological pest control. *BioScience* **46**, 401-405.

Mendel, Z., Assael, F. & Dunkelblum, E. (2004) Kairomonal attraction of predatory bugs (Heteroptera: Anthocoridae) and brown lacewings (Neuroptera: Hemerobiidae) to sex pheromones of *Matsucoccus* species (Hemiptera: Matsucoccidae). *Biological Control* **30**, 134-140.

Obrycki, J.J. & Kring, T.J. (1998) Predaceous Coccinellidae in biological control. *Annual Review of Entomology* **43**, 295-321.

Obrycki, J.J., Harwood, J.D., Kring, T.J. & O'Neil, R.J. (2009) Aphidophagy by Coccinellidae: application of biological control in agroecosystems. *Biological Control* **51**, 244-254.

Obrycki, J.J., Maurice, M.J., Tauber, C.A. & Ruberson, J.R. (2011) Prey Specialization in Insect Predators in Radcliffe E.B., Hutchison, W.D. & Cancelado R.E. (Eds.) *Radcliffe's IPM World Textbook.* University of Minnesota, St. Paul, MN. Available online at http://ipmworld.umn.edu.

Omkar & Pervez, A. (2002) Ecology of aphidophagous ladybird beetle, *Coccinella septempunctata* (Coleoptera: Coccinellidae): a review. *Journal of Aphidology* **16**, 175-201.

Omkar & Pervez, A. (2005) Ecology of two-spotted ladybird, *Adalia bipunctata*: a review. *Journal of Applied Entomology* **129**, 465-474.

Osawa, N. & Ohashi, K. (2008) Sympatric coexistence of sibling species *Harmonia yedoensis* and *H. axyridis* (Coleoptera: Coccinellidae) and the roles of maternal investment through egg and sibling cannibalism. *European Journal of Entomology* **105**, 445–454.

Raimundo, A., Canepari, C., Mendel, Z., Branco, M. & Franco, C. (2006) *Iberorhyzobius* Raimundo & Canepari gen. nov., for *Coccidula rondensis* Eizaguirre (Coleoptera: Coccinellidae). *Zootaxa* **1312**, 49-58.

Raimundo, A. & Alves, M.L.G. (1986) Revisão dos Coccinelídeos de Portugal. *Universidade de Évora, Évora.*

Rana, J.S., Dixon, A.F.G. & Jarošík, V. (2002) Costs and benefits of prey specialization in a generalist insect predator. *Journal of Animal Ecology* **71**, 15-22.

Ricci, C. (1986) Seasonal food preferences and behavior of *Rhyzobius litura*. pp. 119–123 in Hodek, I. (Ed.) *Ecology of Aphidophaga*. Dordrecht, The Netherlands, Academia, Prague & Dr. W. Junk.

Riom, J. & Gerbinot, B. (1977a) Étude biologique et écologique de la cochenille du pin maritime *Matsucoccus feytaudi* Ducasse, 1942 (Coccoidea, Margarodidae, Xylococcinae) dans le Sud-Est de la France. I - Biologie générale et phénologie. *Annales de Zoologie, Écologie Animale* **9**, 11-50.

Riom, J. & Gerbinot, B. (1977b) Étude biologique et écologique de la cochenille du pin maritime *Matsucoccus feytaudi* Ducasse, 1942 (Coccoidea, Margarodidae, Xylococcinae) dans le Sud-Est de la France. III - Structure des populations sur l'arbre. *Annales de Zoologie, Écologie Animale* **9**, 709-732.

Riom J. & Tacon F. (1994). Le dépérissement du pin maritime dans le sudest de la France au cours des années 1960-70: le rôle de la cochenille *Matsucoccus feytaudi* Duc. (Coccoidea, Margarodidae). – Revue Forestière Française **46**, 437-445.

Robertson, J.A., Whiting, M.F. & McHugh, J.V. (2008) Searching for natural lineages within the Cerylonid Series (Coleoptera: Cucujoidea). *Molecular Phylogenetics and Evolution* **46**, 193-205.

Rodrigo, E., Catala-Oltra, M., Perez-Laorga, E. & Baena, M. (2013) Monitoring of *Matsucoccus feytaudi* (Hemiptera: Matsucoccidae) and its natural enemies in Spain using sticky tapes and pheromone traps. *European Journal of Entomology* **110**, 301-310.

Roy, H. & Migeon, A. (2010) Ladybeetles (Coccinellidae) Chapter 8.4. *BioRisk: Biodiversity & Ecosystem Risk Assessment* **4**, 293–313

Santos, S.A.P., Pereira, J.A., Raimundo, A., Torres, L.M. & Nogueira, A.J.A. (2010) Seasonal synchrony between *Saissetia oleae* and coccinellid species in Portuguese olive groves in different management systems. *Bulletin of Insectology* **63**, 51-57.

Santos, S.A.P., Pereira, J.A., Conceição Rodrigues, M., Torres, L.M., Pereira, A.M.N. & Nogueira, A.J.A. (2009) Identification of predator-prey relationships between coccinellids and *Saissetia oleae* (Hemiptera: Coccidae), in olive groves, using an enzyme-linked immunosorbent assay. *Journal of Pest Science* **82**, 101-108.

Sasaji, H. (1968) Phylogeny of the family Coccinellidae (Coleoptera). *Etizenia* **35**, 1-37.

Seago, A.E., Giorgi, J.A., Li, J. & Ślipiński , A. (2011) Phylogeny, classification and evolution of ladybird beetles (Coleoptera: Coccinellidae) based on simultaneous analysis of molecular and morphological data. *Molecular Phylogenetics and Evolution* **60**, 137-151.

Ślipiński, A. (2007) *Australian Ladybird Beetles (Coleoptera: Coccinellidae) Their biology and classification*. Canberra, Australia, Australian Biological Resources Study.

Sloggett, J.J. (2005) Are we studying too few taxa? Insights from aphidophagous ladybird beetles (Coleoptera: Coccinellidae). *European Journal of Entomology* **102**, 391-398.

Sloggett, J.J. & Majerus, M.E.N. (2000) Habitat preferences and diet in the predatory Coccinellidae (Coleoptera): an evolutionary perspective. *Biological Journal of the Linnean Society* **70**, 63-88.

Sloggett, J.J., Volkl, W., Schulze, W., van der Schulenberg, J.H. & Majerus, M.E.N. (2002) The ant-associations and diet of the ladybird *Coccinella magnifica* (Coleoptera: Coccinellidae). *European Journal of Entomology* **99**, 565-569.

Soares, A.O., Elias, R.B. & Schanderl, H. (1999) Population dynamics of *Icerya purchasi* Maskell (Hom; Margarodidae) and *Rodolia cardinalis* Mulsant (Col; Coccinellidae) in two citrus orchards of Sao Miguel island (Azores). *Boletín de Sanidad Vegetal, Plagas* **25**, 459-467.

Sutherland, A.M. & Parrella, M.P. (2009) Mycophagy in Coccinellidae: review and synthesis. *Biological Control* **51**, 284-293.

Toccafondi, P., Covassi, M. & Pennacchio, F. (1991) Studies on the entomophagous predators of scale insects of the genus Matsucoccus Cock. in Italy. II Bio-ethological notes on *Rhyzobius chrysomeloides* (Herbst) in pine forests of Liguria (Coleoptera: Coccinellidae). *Redia* **74**, 599-620.

Tomaszewska, W. (2010) *Rhyzobius (Coleoptera: Coccinellidae): A Revision of the World Species*. Warszawska, Poland, Warszawska Drukarnia Naukowa.

Van Lenteren, J., Bale, J., Bigler, F., Hokkanen, H. & Loomans, A. (2006) Assessing risks of releasing exotic biological control agents of arthropod pests. *Annual Review of Entomology* **51**, 609-634.

Wang, L.Y. (1982) Control of *Matsucoccus massonianae* Young et Hu (Hom.: Margarodidae) by *Leis axyridis* (Pallas). *Natural Enemies of Insects* **4**, 37-39.

II. A case of ecological specialization in ladybirds: *Iberorhyzobius rondensis* (Coleoptera: Coccinellidae), potential biocontrol agent of *Matsucoccus feytaudi* (Hemiptera: Matsucoccidae)

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2.1. Abstract

Specialization is an important atribute of a biological control agent. The maritime pine bast scale, *Matsucoccus feytaudi* (Hemiptera Matsucoccidae), is an invasive species in Southeastern France and the North of Italy. *Iberorhyzobius rondensis* (Coleoptera: Coccinellidae), is a recently described ladybird species. Both adults and larvae are predaceous, feeding on egg masses of *M. feytaudi,* and are strongly attracted to *M. feytaudi'*s sex pheromone.

To evaluate the potential of *I. rondensis* as a biocontrol agent of the scale, we studied its niche breadth and prey range with emphasis on pine forests and hemipterans as tested prey. In this study *I. rondensis* was found to achieve complete development only when fed on *M. feytaudi* egg masses (92.9% survival) and an artificial prey: eggs of *Ephestia kuehniella* (27.6% survival). From the 2nd instar onwards complete development could be achieved using other prey species, although larvae had significantly higher mortality and slower development. In choice tests *M. feytaudi* was the preferred prey. Surveys of the ladybird populations in the Iberian Peninsula revealed that it was found exclusively on *Pinus pinaster,* the sole host of *M. feytaudi*. The unusual specialization of *I. rondensis,* among other predaceous ladybirds, makes it an appropriate candidate for classical biological control of *M. feytaudi.*

Keywords: diet breadth, habitat specialization, predator-prey, coccidophagous

2.2. Introduction

Specialization is considered one critical criterion for classifying predator or parasitoid species as candidates for biological control, given that risk to non-target species, apparent competition and competitive exclusion are expected to be minimal in specialized organisms (Dixon, 2000; Van Lenteren et al., 2006).

Furthermore, specialized predators are expected to display higher efficacy than generalist predators as the former usually have higher prey searching ability and voracity (Dixon, 2000). Still, dietary specialization of predators is often conditioned to the availability of prey in time and space (Hodek & Honěk, 1996; Abrams & Ginzburg, 2000). Specialized predators are usually restricted to the prey's habitat, and their life cycles are often synchronized (Dixon, 2000; Sloggett & Majerus, 2000).

Processes of ecological specialization in insects have been well studied in herbivorous species, with special attention paid to herbivore–plant interactions and associated co-evolutionary processes (Thompson, 1995; Funk *et al.,* 2002; Scriber 2010). Specialization in parasites, parasitoids and predators has also been regularly studied from an evolutionary perspective and for practical biological control purposes (Bristow, 1988; Strand & Obrycki, 1996; Wiegmann et al., 1996; Dixon, 2000; Diehl *et al.*, 2013). Studies on the specialization of arthropod predators cover a large range of orders such as Coleoptera, Diptera, Hemiptera and Araneae (e.g. Pekár, 2004; Short & Bergh, 2004; Jackson *et al*., 2010; Jałoszyński & Olszanowski, 2013; Vieira *et al.*, 2013).

Within Coleoptera, the species studied most often are Coccinellidae (Obrycki & Kring, 1998). Predaceous ladybirds show variable degrees of specialization, and have been widely used in biological control programs (Dixon, 2000). An example of the importance played by specialization in the suitability of a biological control is the contrast between the two species *Harmonia axyridis* (Pallas) and *Rodolia cardinalis* (Mulsant). The first of the two is a generalist predator which has been released to control aphids in Europe and North America, with negative impacts on native fauna, whereas the second species, coccidophagous, has provided highly targeted control of *Icerya purchasi* Maskell (Hemiptera: Monophlebidae) in California and Europe (Caltagirone & Doutt, 1989; Koch & Galvan, 2008; Katsanis *et al*., 2013).

In this study we considered the predaceous ladybird *Iberorhyzobius rondensis* (Eizaguirre) (subfamily Coccidulinae) as a potential biological control agent of the pine bast scale *Matsucoccus feytaudi* Ducasse (Hemiptera: Matsucoccidae). *Matsucoccus feytaudi* is an extremely specialized scale insect which only feeds on maritime pine, *Pinus pinaster* Aiton. The native area of this insect species is restricted to the southwestern part of the Mediterranean basin. This corresponds to the refuge areas of *Pinus pinaster* during the last glaciation (Burban & Petit, 2003), where the bast scale is thought to have evolved in close association with its host (Burban *et al*., 1999). The only other *Matsucoccus* species naturally occurring in Europe is *Matsucoccus pini* (Green) feeding on *Pinus nigra* JF Arnold and *Pinus sylvestris* L. (Foldi, 2004). The distribution of *P. pinaster* has changed in the last two centuries, with afforestation of large areas especially in Southwestern France, Corsica and Italy. During the 20th century *M. feytaudi* expanded its range to the Southeastern of France and later also to the North of Italy and to Corsica, becoming a major pest of maritime pine in those areas (Covassi *et al*., 1991; Jactel *et al*., 1996). In this context, the predaceous ladybird *I. rondensis*, if confirmed as a specialized predator, could be proposed as a good candidate for the classical biological control of *M. feytaudi* in invaded areas.

Iberorhyzobius rondensis is a recently discovered coccidophagous ladybird species (Raimundo *et al*., 2006) and very little is known about its biology. To date this species has been collected only on maritime pines in Portugal and Spain (Eizaguirre, 2004; Raimundo *et al*., 2006), despite focused search for natural enemies of *M. feytaudi* in Italy (Covassi *et al*., 1991), South of France and Corsica (Branco *et al*., 2011). The new genus *Iberorhyzobius* is assumed to be closely related to *Rhyzobius*, based on morphological similarities (Raimundo *et al*., 2006). The larvae of *I. rondensis* have been observed feeding on egg masses of *M. feytaudi* and found to respond to the sex pheromone of the scale insect (Branco *et al*., 2006). Considering these characteristics, we hypothesized that *I. rondensis* is a specialized predator of *M. feytaudi*.

Two main mechanisms have been proposed to explain ecological specialization in ladybirds: diet specialization and habitat specialization. The two are often linked and ladybirds, as with other predators, are usually restricted to the habitat of their main prey (Sloggett & Majerus, 2000). Therefore, given that specialized predators are expected to have a narrow range of hosts and habitats (stenotopic), the main objectives of this study were to determine: i) the habitat specialization of *I. rondensis*, ii) its diet breadth by analyzing its development and survival on different prey species and iii) its host preference with choice tests. In addition, we tested the possibility of rearing the predator with an artificial diet (sterilized eggs of *Ephestia kuehniella* Zeller).

2.3. Material and Methods

Habitat preference of I. rondensis

We tested whether *I. rondensis* occurs only on *P. pinaster* trees or whether it is also present on other native pine species that are hosts of *M. pini* (Foldi, 2004). Plots of three native pine species were surveyed (*P. pinaster*, *P. sylvestris* and *P. nigra*) within six regions of the Iberian Peninsula, where they naturally co-occur (Fig. 1). Two other Iberian regions, where only *P. pinaster* occurs, were also sampled. In each region at least three plots of each pine species were sampled. Distance between sampled plots was, whenever possible, less than 10 km and never more than 50 km. Lures were made of rubber dispensers impregnated with 200 µg of female *M. feytaudi* sex pheromone, pinned to the tree trunk (N = 50 trees per sample area), 1 m above ground level, after smoothing the bark surface to create an arena (Branco *et al.*, 2006). Baited arenas were monitored for 1 h, in March, April and May 2006 to 2012, which corresponds to *I. rondensis* larval activity and male *M. feytaudi* flight, both of which are attracted to the lures. Plots of *P. sylvestris* and *P. nigra* were only sampled from the end of April through the beginning of May, when the flight periods of males *M. pini* and *M. feytaudi* overlap (Foldi, 2004).

Because the data did not satisfy the assumptions of normality and homoscedasticity, differences in the abundance of *I. rondensis* between regions were analyzed with the non-parametric Kruskal-Wallis test followed by the Mann-Whitney test to compare each pair of regions. Pearson’s correlation coefficient was then calculated to assess the relationship between *M. feytaudi* and *I. rondensis* abundances.

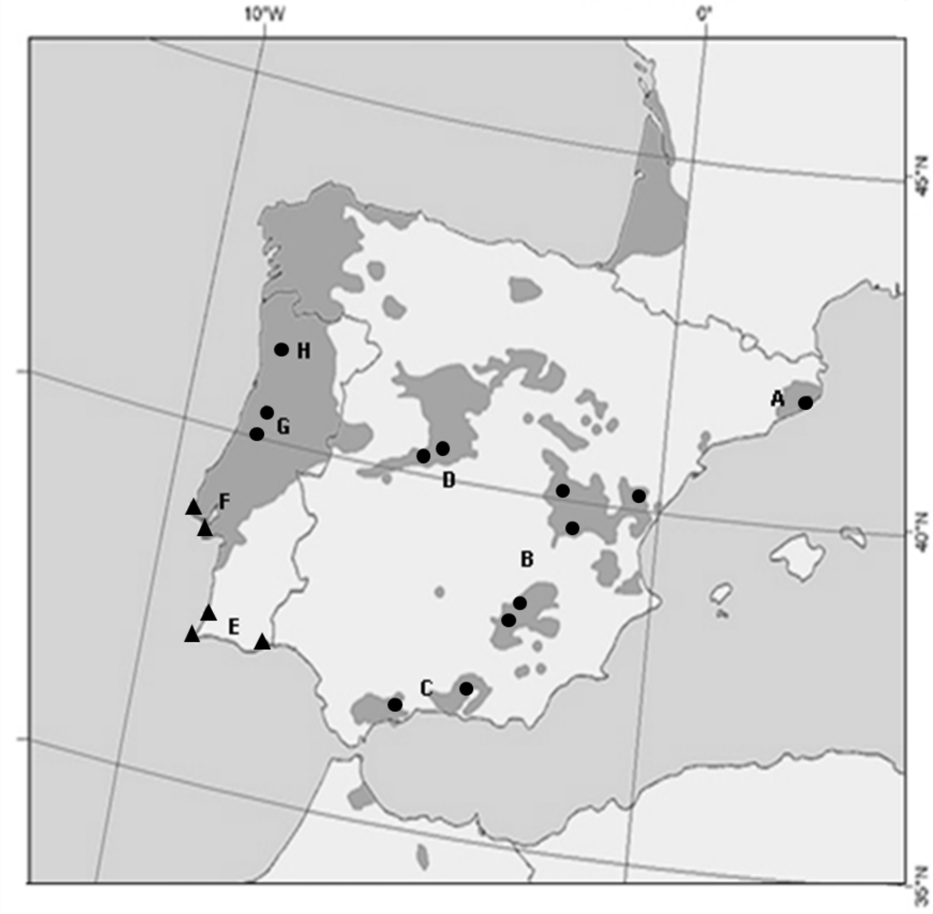

Fig. 1. Distribution map of Maritime pine (*Pinus pinaster*) - EUFORGEN 2009, www.euforgen.org - with the sampled sites in the Iberian Peninsula. A –Catalonia, B - Valencia region C – Andalusia, D – Madrid region, E – South Portugal, F – Setúbal/Sintra, G – Central Portugal, H – North Portugal. Triangles represent sampled sites with only *P. pinaster* and circles sampled sites with all three pine species (*P. pinaster*, *Pinus nigra* and *Pinus sylvestris*).

Diet preference of I. rondensis

Potential prey species of *I. rondensis* were selected using the centrifugal phylogenetic method (Van Lenteren *et al.*, 2006), starting with close relatives of the target prey and continuing with species from more distant taxa e.g. subfamilies and families within the same order. We tested the target prey (*M. feytaudi*) and its congeneric *Matsucoccus josephi* Bodenheimer & Harpaz, which is native from the East Mediterranean region and only inhabits *Pinus halepensis* Mill and *Pinus brutia* Ten.

Some species from the Monophlebidae family, which is phylogenetically very close to the Matsucoccidae, were tested as well: *Palaeococcus fuscipennis* (Burmeister), a scale insect which also feeds on *P. pinaster* trees; and *I. purchasi* and *Gueriniella serratulae* (Fabricius), which feed on several hosts (Ben-Dov *et al.*, 2001). Different families sharing the same pine habitat as the target prey were tested: an Aphididae, *Cinara maritimae* (Dufour) and an Adelgidae, *Pineus pini* (Macquart). From the family Pseudococcidae, we tested *Planococcus citri* (Risso), which feeds on *Citrus* trees. Finally, sterilized eggs of *Ephestia kuehniella* (Lepidoptera: Pyralidae) were used in order to check whether ladybirds could be reared on artificial food (Table 1).

These diets were tested with second, third and fourth instar larvae of *I. rondensis* collected from *P. pinaster* plots in 2006, 2009 and 2010, using sex pheromone lures of *M. feytaudi*, as described above. In the laboratory, larvae were weighed and their body length measured in order to determine their instar. Each larva was put into an individual plastic vial for feeding tests. In 2011 and 2012, neonate larvae were reared under room conditions, from eggs laid by adults in the laboratory.

Prey preference in choice tests

Paired choice tests were performed allowing *I. rondensis* larvae to choose between *M. feytaudi* eggs, *M. josephi* eggs (n = 20), *C. maritimae* nymphs (n = 48), *P. citri* eggs (n = 118), *P. pini* eggs (n = 63) and *E. kuehniella sterilized eggs* (n = 34). Tests were performed in Petri dishes of 10 cm in diameter, with a layer of filter paper, under natural conditions of light and a temperature of 22 ±2ºC. Food items were placed at maximum distance opposite each other, and their position was switched for each replicate. Larvae were starved 48 hours before trials. Assays were monitored for up to 2 hours and the test was considered finished when the larva selected one of the food items and began to eat it. Choice tests were performed with the 3rd and 4th instar larvae collected in the field in Portugal, in March and April 2009 and 2010, with the exception of the test between *M. feytaudi* and *M. josephi* which was performed with 1st instar larvae in 2011. This was because these trials with *M. josephi* were done in Israel (as *M. josephi* is not present in Europe), where the number of *I. rondensis* larvae was limited; none were available in the 3rd and 4th instar to be used for the choice test. A chi-square analysis was performed to test for differences in prey choice.

Table 1. List of selected prey according to the centrifugal phylogenetic method (Van Lenteren *et al*., 2006) to test host range of *Iberorhyzobius rondensis* larvae.

Selected Preys	Order	Family	Origin
Matsucoccus feytaudi egg masses	Hemiptera	Matsucoccidae	*Pinus pinaster* at Forest Unit INRA Bordeaux, France
Matsucoccus josephi egg masses	Hemiptera	Matsucoccidae	*Pinus halepensis* in Eshtao'l forest, Judean Hills, Israel.
Palaeococcus fuscipennis eggs	Hemiptera	Monophlebidae	*Pinus pinaster* at Forest Unit INRA Bordeaux, France
Icerya purchasi eggs	Hemiptera	Monophlebidae	*Citrus sinensis* trees at the Agronomy Institute Lisbon, Portugal
Planococcus citri eggs	Hemiptera	Pseudococcidae	Laboratory rearing on potato sprouts Agronomy Institute - Lisbon, Portugal
Gueriniella serratulae eggs	Hemiptera	Monophlebidae	*Molinia caerulea* Linnaeus at the Forest Unit of INRA Bordeaux, France
Pineus pini egg masses	Hemiptera	Adelgidae	Young potted *Pinus pinaster* trees at Agronomy Institute - Lisbon, Portugal
Cinara maritimae nymphs	Hemiptera	Aphididae	
Sterilized eggs of *Ephestia kuehniella*	Lepidoptera	Pyralidae	Koppert France S.A.R.L., Cavaillon and Koppert España S.L., Almería.

Survival of I. rondensis

Iberorhyzobius rondensis larval survival was analyzed for different feeding regimes. Larvae were reared in small tubes, with cotton as a lid. Feeding trials were performed for the entire life cycle, from the 1st instar larvae to the adult stage, starting from neonate larvae obtained in the laboratory (Table 2) and also separately for each of the 2nd, 3rd and 4th instar for larvae collected in the forest (Table 3). *M. feytaudi* eggs are difficult to obtain and not enough were found to feed all larvae from the 1st instar onwards; therefore larvae of later instars were obtained from the field. The number of larvae and food items available dictated the number of replicates for each regime. Also, 2nd and 3rd instar larvae were further pooled together because the number of 2nd instars captured in the field was very low. For 1st instars, experiments started when neonate larvae hatched. All larvae were reared in separate plastic test vials at 22ºC, 14:10 L:D (ratio of light to dark), and 60% Relative Humidity. A small piece of cardboard was provided to allow them to hide, and the prey was exposed on a piece of paper. Individuals were checked and fresh food was added every two days, so that larvae were never limited by their food supply. Survival until adulthood was monitored for each individual and then analyzed with the Kaplan-Meier estimator, followed by a Log-Rank test based on *I. rondensis* larval stage. Pairwise comparisons of diet effects were also computed using the Log-Rank test. No statistical analysis was performed for the *P. fuscipennis* diet given the low number of replicates.

Growth rate

Performance under each regime was further evaluated by the Relative Growth Rate (*RGR*), calculated for each individual as used by Matsuki & MacLean Jr. (1994):

$$RGR = \frac{(\ln(Wf) - \ln(Wi))}{(Df - Di)} \quad eqn(1)$$

with *Wf* the fresh weight at the final day of the test, *Wi* the fresh weight at the first day, *Df* the final day of the test and *Di* the first day of the test.

Larvae were checked every day and food was added every two days. Larvae were weighed every week, on the same day, and their instar stage was recorded by exuviae observation. Final weight (*Wf*) was measured after adult emergence or otherwise we used the weight of the last day before the larva died. *RGR* was calculated for each instar and diet, i.e. *C. maritimae* nymphs, eggs of *I. purchasi*, *M. feytaudi*, *P. citri*, *E. kuehniella* plus a control with “No food”. For the 1st instar, RGR was calculated only for the diets with *M. feytaudi* and *E. kuehniella* eggs due to the high mortality of neonate larvae on other prey regimes. In the 3rd instar the “No food” RGR was not calculated due to a lack of replicates. One–way analysis of variance (ANOVA) was used to test for differences in mean RGR between diets for each larval stage. It was followed by a multiple comparisons Tukey’s test to identify significant differences between diets. Normality and homogeneity of variances were assessed, prior to all analyses, using the Kolmogorov-Smirnov one sample and Levene’s tests, respectively. For t-tests, the number of degrees of freedom was corrected whenever equal variance was not assumed.

Table 2. Number (n) and survival (%) of *Iberorhyzobius rondensis* larvae reared in the laboratory from neonate to adult on different prey regimes: egg masses of *Matsucoccus feytaudi*, *Matsucoccus josephi*, *Gueriniella serratulae*, *Pineus pini*, *Planococcus citri* and *Palaeococcus fuscipennis*, eggs of *Ephestia kuehniella* and nymphs of *Cinara maritimae*. Within the 1st instar, results with the same letters were not significantly different ($P < 0.05$). With subsequent instars differences were not significant due to high survival rates.

* Since n = 5, this diet was not statistically analyzed; all individuals were dead in 7 days.

	1st instar		2nd instar		3rd instar		4th instar	
	n	Surv. (%)	n	Surv.(%)	n	Surv. (%)	n	Surv. (%)
Matsucoccus feytaudi	42	92.9^{a}	41	95.1	40	97.5	40	97.5
Matsucoccus josephi	-	-	15	86.7	13	100	13	100
Ephestia kuehniella	29	27.6^{b}	10	80	8	100	8	100
Cinara maritimae	14	0^{c}	-	-	-	-	-	-
Gueriniella serratulae	13	0^{c}	-	-	-	-	-	-
Pineus pini	16	0^{c}	-	-	-	-	-	-
Planococcus citri	17	0^{c}	-	-	-	-	-	-
Palaeococcus fuscipennis	5	0*	-	-	-	-	-	-

Pre-imaginal development

Development time from neonate until adulthood was recorded with two diets: *E. kuehniella* eggs and *M. feytaudi* eggs. The duration of each instar was recorded at each molt by exuviae observation. Independent sample t-tests were performed to compare the effect of the two feeding regimes on development time for each larval stage separately. Levene's test was used to test for equality of variances.

All statistics were performed with SPSS version 20.

Table 3. Number (n) and survival (%) of larvae collected in the forest and reared in the laboratory from 2nd, 3rd or 4th instar to adult with different prey regimes: egg masses of *Matsucoccus feytaudi*, *Gueriniella serratulae*, *Pineus pini* and *Planococcus citri*; *Icerya purchasi* and *Matsucoccus feytaudi*; nymphs of *Cinara maritimae* and control (No food). Within each instar, results with the same letters are not significantly different ($P < 0.05$).

	2nd/3rd instar		4th instar	
	n	Survival (%)	n	Survival (%)
Matsucoccus feytaudi	49	91.5^{a}	76	97.4^{a}
Cinara maritimae	37	70.3^{b}	26	100^{a}
Gueriniella serratulae	-	-	16	100^{a}
Pineus pini	-	-	12	91.7^{ab}
Planococcus citri	55	29.1^{c}	43	95.3^{a}
Icerya purchasi	53	5.7^{d}	17	70.6^{b}
No food	13	0^{d}	7	85.7^{ab}

2.4. Results

Habitat preference of I. rondensis

Larvae of *I. rondensis* were only found on *P. pinaster* (Table 4); none were observed on *P. nigra* or *P. sylvestris*, although males of *Matsucoccus* sp. were observed in several of these plots – presumably *M. pini*, which typically reproduces on these two pine species (Foldi, 2004). *Matsucoccus feytaudi* and *I. rondensis* were found in *P. pinaster* from all examined regions except Catalonia.

Pooling of data at regional level showed that most regions presented a low density of *I. rondensis* larvae per maritime pine tree, but with significant differences (Kruskal-Wallis test $\chi_7^2 = 549.19$; $P < 0.001$) in density between regions. Pairwise comparison of regions where the ladybird was found showed that larval density (mean larvae per tree ± standard error) was lowest in Valencia (0.01 ± 0.006) followed by Southern Portugal (Algarve) (0.16 ± 0.036). In the other extreme, Madrid and Setúbal/Sintra had the highest densities (0.62 ± 0.071 and 1.59 ± 0.111, respectively). A density-dependent relationship was found between the total number of larvae of *I.*

rondensis and the total number of *M. feytaudi* males observed in each region (*r* = 0.889; n = 8; *P* = 0.003).

Table 4. Total number of *Iberorhyzobius rondensis* and *Matsucoccus sp*. males sampled in selected regions of Spain and Portugal, on different pine species (*Pinus pinaster, Pinus nigra* and *Pinus sylvestris*).

Species	Country	Region	Number of plots	Sampled trees per stand	Number of *I.rondensis* larvae	Percentage of plots with presence of *I. rondensis*	Number of *Matsucoccus* sp. adult males
P. nigra	Spain	Catalonia	3	45	0	0	0
		Valence	3	50	0	0	1
		Andalusia	3	45	0	0	528
		Madrid	3	46	0	0	6
	Portugal	Centre	3	40	0	0	23
		North	3	40	0	0	0
P. pinaster	Spain	Catalonia	7	50	0	0	1
		Valence	21	18	4	9.5	8
		Andalusia	7	35	64	57.1	491
		Madrid	6	50	187	83.3	24
	Portugal	South	8	22	31	62.5	14
		Setúbal/Sintra	44	43	1539	88.6	1001
		Centre	7	30	51	85.7	45
		North	5	30	47	80	1
P. sylvestris	Spain	Catalonia	3	45	0	0	0
		Valence	3	45	0	0	2
		Andalusia	3	45	0	0	4
		Madrid	3	46	0	0	0
	Portugal	Centre	3	40	0	0	23
		North	6	45	0	0	0

Prey preference in choice-tests

In paired choice tests (df = 1), *M. feytaudi* eggs were preferred by *I. rondensis* larvae to *E. kuehniella* eggs, *M. josephi* eggs, *C. maritimae* nymphs and *P. citri* eggs but not to *P. pini* eggs (Fig. 2). Larvae did not make a choice in 60% of trials.

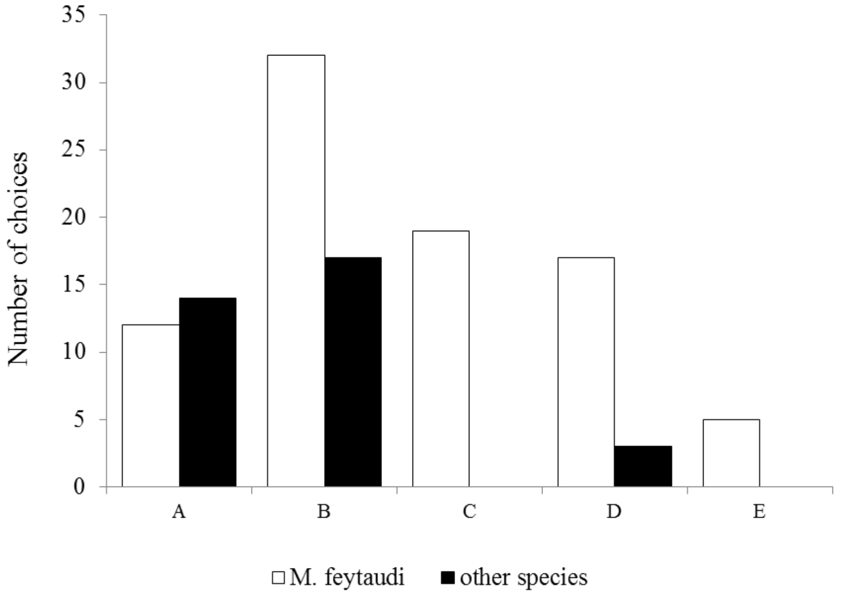

Fig. 2. Results of choice-tests between different prey regimes with larvae of *Iberorhyzobius rondensis*. All tested pairs presented significant differences P < 0.05 excepted pair A. Paired choices: A) *Matsucoccus feytaudi* eggs vs. *Pineus pini* eggs (n = 63, χ^2 = 0.19, P = 0.660), B) *M. feytaudi* eggs vs. *Planococcus citri* eggs (n = 118, χ^2 = 4.61, P = 0.032), C) *M. feytaudi* eggs vs. *Cinara maritimae* nymphs (n = 48, χ^2 = 19.05, P < 0.001), D) *M. feytaudi* eggs vs. *Matsucoccus josephi* eggs (n = 20, χ^2 = 9.85, P = 0.002) and E) *M. feytaudi* eggs vs. *Ephestia kuehniella* eggs (n = 34, χ^2 = 4.33, P = 0.037). All tested larvae were 3rd or 4th instar larvae, except for *M. feytaudi* vs. *M. josephi* for which we had 1st instar larvae.

Survival of I. rondensis

Neonate larvae reached adulthood only when fed *M. feytaudi* or *E. kuehniella* eggs, but *M. josephi* eggs were not tested with 1st instars (Table 2). The survival rate of first instars significantly differed between prey species (χ_6^2 = 102.18; *P* < 0.001). It was highest (92.9%) with *M. feytaudi* eggs, significantly lower (27.6%) with *E. kuehniella* eggs (*P* < 0.001) and null with all other food regimes (Table 2). Survival of 2nd instars was also higher on *M. feytaudi* (95.1%) than on *E. kuehniella* (80%) and *M. josephi* (86.7%) but the differences were not significant (χ_2^2 = 2.4551; *P* = 0.293). For 3rd and 4th instars, survival was around 100% with the 3 prey items with no significant differences between them (χ_2^2 = 0.52; *P* = 0.769).

For 2nd and 3rd instar larvae collected in the forest, the survival rate also differed between preys ($\chi_4^2 = 102.417$, $P < 0.001$). It was highest when larvae were reared on the *M. feytaudi* eggs diet (91.5%), followed by the *C. maritimae* nymphs diet (70.3%). Only a small percentage of individuals survived until adulthood on other regimes and none of the 2nd and 3rd instar larvae survived with the control “No food” regime (Table 3). For the 4th instar larvae collected in the forest, survival was relatively high for all regimes (>70%, Table 3), although significant differences between regimes were still found ($\chi_6^2 = 23.151$, $P < 0.001$). Larvae fed with eggs of *M. feytaudi* again exhibited a high survival rate (97.4%). It is worth noting that these larvae were probably close to pupation, which may explain the high survival rate (85.7%) of the “No food” regime.

Growth rate

The mean RGR varied significantly between prey for the 1st, 2nd, 3rd and 4th instars respectively: ($F_{(1,19)} = 14.33$; $P = 0.001$), ($F_{(5,73)}=60.98$; $P < 0.001$), ($F_{(4,128)}= 22.72$; $P <0.001$), ($F_{(5,68)}=4.55$; $P < 0.001$). For all instars, larvae fed with *M. feytaudi* showed higher RGR than larvae fed on other diets, with the only exception being the 3rd instar fed with *E. kuehniella* (Table 5). This diet provided the second best food, although displaying high variability. The RGR coefficient of variance (CV%) was 8.5 and 41.8 for first instar larvae fed with *M. feytaudi* and *E.kuehniella* respectively. In all other diets, with the exception of *C. maritimae* in the 2nd instar and *I. purchasi* in the 2nd and 3rd instar, larvae showed decrease in their weight which was highest with the “No food” diet (Table 5).

Pre-imaginal development

Development time averaged 10 days longer for *I. rondensis* larvae fed *E. kuehniella* eggs rather than *M. feytaudi* eggs (Table 5). The difference was significant for the 1st ($t_{9.19} = 2.32$, $P = 0.045$), 2nd ($t_{7.32} = 4.23$, $P = 0.004$) and 3rd instars ($t_{45} = 5.43$, $P < 0.001$). No significant differences were found between the two diets for the 4th instar ($t_{45} = -0.90$, $P = 0.371$) and the pupal stage ($t_{45} = -0.21$, $P = 0.837$).

Table 5. Relative Growth Rate (RGR) and development time (DT) in days (mean ± standard error) of *Iberorhyzobius rondensis* instars fed with different prey regimes. Within each instar, values followed by the same letters are not significantly different ($P<0.05$).

Instar	Prey	N	RGR	Development Time
1st instar	*Matsucoccus feytaudi*	15	0.528±0.0116^{a}	8.4±0.35^{a}
	Ephestia kuehniella	5	0.187±0.0349^{b}	10.8±1.30^{b}
2nd instar	*Matsucoccus feytaudi*	23	0.179±0.0017^{a}	4.0±0.13^{a}
	Ephestia kuehniella	7	0.095±0.0058^{b}	7.8±0.98^{b}
	Icerya purchasi	11	0.04±0.0036^{bc}	_
	Cinara maritimae	2	0.018±0.0203^{bd}	_
	Planococcus citri	24	-0.01±0.0017^{d}	_
	No food	7	-0.04±0.0058^{d}	_
3rd instar	*Matsucoccus feytaudi*	24	0.083±0.0016^{a}	5.7±0.24^{a}
	Ephestia kuehniella	6	0.092±0.0075^{a}	8.9±0.74^{b}
	Icerya purchasi	37	0.005±0.0012^{b}	_
	Cinara maritimae	26	-0.002±0.0017^{b}	_
	Planococcus citri	28	-0.009±0.0017^{b}	_
4th instar	*Matsucoccus feytaudi*	18	0.003±0.0007^{a}	14.3±0.23^{a}
	Ephestia kuehniella	4	-0.009±0.0032^{ab}	13.9±0.55^{a}
	Icerya purchasi	11	-0.013±0.0012^{b}	_
	Cinara maritimae	14	-0.014±0.0009^{b}	_
	Planococcus citri	18	-0.014±0.0007^{b}	_
	No food	4	-0.024±0.0031^{b}	_
	Matsucoccus feytaudi	18	-	9.4±.23^{a}
	Ephestia kuehniella	4	-	9.3±0.49^{a}

2.5. Discussion

So far no detailed information on the biology and host range for the recently described ladybird species *I. rondensis* was available (Raimundo *et al.*, 2006). The present findings support the hypothesis that *I. rondensis* is specialized on *M. feytaudi* as indicated by its habitat, prey choice, survival and development rate on different prey species. On the Iberian Peninsula, *I. rondensis* was found only on *P. pinaster* trees, even when other pine species co-occurred. We thus reject the hypothesis that it is likely to naturally prey on *M. pini* which can only reproduce on *P. sylvestris* and *P. nigra*. As for the majority of coccinellids, if neonate larvae can only feed on a specific prey, adult females are most likely to lay eggs in the vicinity of that prey (Ferran & Dixon, 1993; Dixon, 2000).

Full development of *I. rondensis* was only achieved with two prey items, *M. feytaudi*'s eggs and sterilized eggs of *E. kuehniella*. However, survival was much lower for 1st instar larvae fed with eggs of the moth *E. kuehniella* compared to those fed with *M. feytaudi* egg masses. Survival on this artificial food is not unusual since other ladybirds such as *Cryptolaemus montrouzieri* Mulsant (Hodek & Honěk, 2009) have been successfully reared on *E. kuehniella* eggs, which they would never normally find in their natural habitat (Hodek & Honěk, 1996). After the 2nd instar, larval survival increased considerably on alternative prey items. For the 4th instar, survival was almost 100% with all tested prey. This trend suggests a broadening of diet breadth as larvae grow, which may imply the use of alternative food sources towards the end of the developmental season, when *M. feytaudi* egg masses become scarce. Even when left without food, about 85.7% of the 4th instar larvae were able to pupate. As observed by Hodek & Honěk (1996) larvae of ladybirds can complete their development when a certain weight is achieved, although this may be delayed by nutritional deficiency and adults may emerge smaller. Thus it can be hypothesized that, in the absence of *M. feytaudi*, late instars of *I. rondensis* can survive and complete their development on alternative prey occurring in the same habitat, such as *C. maritimae* or *P. pini*.

In two-choice tests a consistent preference of *M. feytaudi* over the other tested prey was observed except for *P. pini* egg masses. Like *M. feytaudi*, females of *P. pini* lay egg masses in cottony ovisacs in tree trunks and twigs. It is possible that *P. pini* is an alternative food prey for 3rd and 4th instar larvae when there is a lack of *M. feytaudi*. By contrast, *C. maritimae*, also occurring on *P. pinaster* trees, is highly mobile, able to defend itself or escape and is a myrmecophilous species, which makes it an improbable prey for *I. rondensis*. *Matsucoccus feytaudi* was preferred to *M. josephi*, the only other tested species of the *Matsucoccus* genus. However, this prey was only tested with 1st instar larvae in the two-choice test, and thus we cannot conclude about its use by older instars.

RGR was highest when *I. rondensis* larvae were reared on *M. feytaudi* eggs for all instars except for the 3rd, for which RGR was approximately the same as with *E. kuehniella* eggs. When larvae were reared on other prey, RGR was in most cases null or even negative, demonstrating a detrimental effect. The lower suitability of other prey is also indicated by the higher variability of RGR with other prey regimes, particularly *E. kuehniella*, compared to *M. feytaudi*. Interestingly, when fed with *I. purchasi* egg masses, 2nd and 3rd instar larvae had a positive RGR but survival was extremely low (5.7%). Apparently, the larvae were able to convert assimilated food into biomass but died, possibly due to some toxic effect. Also, neonate larvae were observed to feed voraciously when *P. citri* eggs were offered, but would die a few days later, without gaining weight and unable to complete molting. These results suggest physiological adaptations of *I. rondensis* to *M. feytaudi*. According to the trade-off specialization theory it is expected that a specialist will perform poorly (development and survival) on other kinds of prey, even if the different prey are taxonomically similar (Ferran & Dixon, 1993). This was observed in a large number of studies. *Coccinella septempunctata* L. is known to feed on *Aphis sambuci* L. although this is a highly unsuitable prey (Hodek & Honěk, 1996). Nine aphid species were tested as prey for the aphidophagous *Calvia quatuordecimguttata* L. but only 6 were “essential” food, and 3 were unsuitable causing 100% mortality in fed larvae (Kalushkov & Hodek, 2001). The specialist *Rodolia cardinalis* was tested on 16 prey species before its introduction in Galapagos and it was only able to complete its life cycle with one, *Margarodes similis* Morrison which, like the target prey *Icerya purchasi*, belongs to the family Monophebidae (Causton *et al.,* 2004). According to Hodek & Honěk (1996) most cases of unsuitable prey concern herbivores that derive chemical protection from their toxic plants (e.g. Mendel *et al.*, 1992).

Iberorhyzobius rondensis distribution overlaps with that of its prey in the Iberian Peninsula where the late found refuge during the last ice age (Burban *et al.*, 1999). Apparently, the ladybird did not follow its prey when the latter expanded its range to new pine forest areas in southern France and northern Italy. Densities of *I. rondensis* were generally low, as are densities of *M. feytaudi,* in its native geographical distribution (Riom & Gerbinot, 1977). Yet, differences could be observed from one region to another. *Iberorhyzobius rondensis* showed the highest abundance in one particular region (Setúbal/Sintra) where *M. feytaudi* was also reported to be particularly abundant (Branco, pers. comm.). In agreement with a density-dependent relationship, a significant and positive correlation was found between the number of ladybird larvae and the number of *M. feytaudi* males caught per region. This result suggests a numerical response of the predator to the density of its prey populations (Abrams & Ginzburg, 2000).

Additional evidence of *I. rondensis* specialization is its foraging behavior. Other coccinellids are known to be attracted to the odor of their prey, e.g. *H. axyridis* to *Aphis citricola* van der Goot (Obata, 1986), *Cryptolaemus montrouzieri* to mealybugs (Heidari & Copland, 1992), *Chilocorus nigritus* F. to *Abgrallaspis cyanophylli* Signoret in conjunction with the host plant (Ponsonby & Copland, 1995) and *Hippodamia convergens* Guérin-Méneville which responds positively to (E)-b-farnesene, the alarm pheromone released by aphids (Acar *et al.*, 2001). In the case of *I. rondensis* it is the species-specific sex pheromone of *M. feytaudi* which acts as kairomone for *I. rondensis* larvae. Using these olfactory cues, ladybirds are able to find the prey on a pine tree within a short period of time which greatly reduces their foraging time (Branco *et al.*, 2006).

The results of this study suggest that *M. feytaudi* is the optimal prey for *I. rondensis*: the highest survival of larvae was achieved when fed with egg masses of *M. feytaudi* and in choice tests *M. feytaudi* was consistently preferred over other prey items. These results, together with its restriction to *P. pinaster* forest habitat, lead us to suggest that *I. rondensis* is specialized on *M. feytaudi.* Due to logistic constraints, we were unable to test the full development of *I. rondensis* on *M. josephi* egg masses. However, this scale species does not occur in the natural range of *I. rondensis.* In contrast, it would be interesting to test the possibility of development on *M. pini* since this prey species can be found in the natural habitat of the ladybird.

Rhyzobius, which is considered the ladybird genus closest *to Iberorhyzobius*, appears to be more generalist in terms of prey and habitat. Two *Rhyzobius* species are native to Europe, *Rhyzobius chrysomeloides* (Herbst) and *Rhyzobius litura* (Fabricius); both are polyphagous species feeding on Aphididae and Coccidae, present in several Mediterranean forest ecosystems and arable lands (Ricci, 1986; Toccafondi et al., 1991). Three species are from Australasian origin, *Rhyzobius lophanthae* (Blaisdell), *Rhyzobius forestieri* (Mulsant) and *Rhyzobius ventralis* (Erichson). The latter is monophagous and stenotopic, feeding only on the genus *Eriococcus* (Hemiptera: Coccoidea) and present mostly on *Eucalyptus* species (Pope, 1981). *R. forestieri* is oligophagous, feeding on several Coccidae species and present on different tree species such as *Casuarina* spp., *Citrus* spp., *Acacia* spp., etc. (Richards, 1981). *R. lophanthae* is polyphagous, feeding on Diaspididae and Pseudococcidae and is present in many different ecosystems, having been introduced in many areas around the world for biological control (Stathas, 2000). Furthermore, in general specificity does not appear to be characteristic of the taxonomic group Coccidulinae, but rather more of the coccidophagous guild: e.g. *Coelophora quadrivittata* Fauvel, *Hyperaspis egregia* Fürsch, *Hyperaspis pantherina* Fürsch, *Rodatus major* Blackburn, *Scymnus mediterraneus* Iablokoff-Khnzorian, *Rodolia cardinalis* (Chazeau, 1981; Richards, 1985; Ragab, 1995; Ackonor & Mordjifa, 1999; Fowler, 2004). Some exceptions are *Diomus thoracicus* Fabricius which is myrmecophagous with a parasitic mode of living (Vantaux *et al*., 2010) and *Anisolemnia dilatata* (Fabricius) which feeds on the woolly aphids *Ceratovacuna silvestrii* Takahashi on bamboo plants (Majumder & Agarwala, 2013).

The fact that late instars of *I. rondensis* can feed on other prey is also common to other specialized predators. Even the successful biological control agent *R. cardinalis* can at least partially develop on the eggs of *P. fuscipennis* in its natural environment (Mendel *et al*., 1998). The ability of *I. rondensis* to feed and develop on *E. kuehniella* eggs is of interest since it might allow mass rearing under laboratory conditions. Nevertheless, we need to consider that at least for the first instar of *I. rondensis*, *M. feytaudi* egg masses will be needed, as the survival rate was very low in our experiments with *E. kuehniella* eggs.

From an applied perspective, our findings suggest that *I. rondensis* may be a potential and safe biological control agent of *M. feytaudi* due to its high level of specialization at both the dietary and habitat level. In particular, acclimation of *I. rondensis* could be envisaged in recently colonized areas of Corsica and Northern Italy where the invasive scale is still spreading and causing important forest damage. However, further studies are needed to estimate the predation effectiveness of *I. rondensis* before deciding on its introduction.

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2.7. References

Abrams, P.A. & Ginzburg, L.R. (2000) The nature of predation: prey dependent, ratio dependent or neither? *Trends in Ecology & Evolution* **15**, 337-341.

Acar, E.B., Medina, J.C., Lee, M.L. & Booth, G.M. (2001) Olfactory behavior of convergent lady beetles (Coleoptera: Coccinellidae) to alarm pheromone of green peach aphid (Hemiptera: Aphididae). *The Canadian Entomologist* **133**, 389-397.

Ackonor, J. & Mordjifa, D. (1999) Parasitism and predation in *Planococcoides njalensis* (Laing) (Homoptera: Pseudococcidae) on cacao in Ghana. *Tropical agriculture* **76**, 269-274.

Ben-Dov, Y., Miller, D.R. & Gibson, G.A.P. (2001) ScaleNet, Catalogue Query Results. 13 June 2013. http://www.sel.barc.usda.gov/scalenet/scalenet.htm.

Branco, M., Franco, J.C., Dunkelblum, E., Assael, F., Protasov, A., Ofer, D. & Mendel, Z. (2006) A common mode of attraction of larvae and adults of insect predators to the sex pheromone of their prey (Hemiptera: Matsucoccidae). *Bulletin of Entomological Research* **96**, 179-185.

Branco, M., van Halder, I., Franco, J.C., Constantin, R. & Jactel, H. (2011) Prey sex pheromone as kairomone for a new group of predators (Coleoptera: Dasytidae, Aplocnemus spp.) of pine bast scales. *Bulletin of Entomological Research* **101**, 667-674.

Bristow, C.M. (1988) What makes a predator specialize? *Tree* **3**, 1-2.

Burban, C., Petit, R.J., Carcreff, E. & Jactel, H. (1999) Rangewide variation of the maritime pine bast scale *Matsucoccus feytaudi* Duc. (Homoptera: Matsucoccidae) in relation to the genetic structure of its host. *Molecular Ecology* **8**, 1593-1602.

Burban, C. & Petit, R.J. (2003) Phylogeography of maritime pine inferred with organelle markers having contrasted inheritance. *Molecular Ecology* **12**, 1487-1495.

Caltagirone, L. & Doutt, R. (1989) The history of the vedalia beetle importation to California and its impact on the development of biological control. *Annual Review of Entomology* **34**, 1-16.

Causton, C.E., Lincango, M.P. & Poulsom, T.G.A. (2004) Feeding range studies of *Rodolia cardinalis* (Mulsant), a candidate biological control agent of *Icerya purchasi* Maskell in the Galapagos islands. *Biological Control* **29**, 315-325.

Chazeau, J. (1981) Biology of *Coelophora quadrivittata* (Col.: Coccinellidae), predator of *Coccus viridis* (Hom.: Coccidae) in New-Caledonia. *Entomophaga* **26**, 301-312.

Covassi, M., Binazzi, A. & Toccafondi, P. (1991) Studies on the entomophagous predators of a scale of the genus *Matsucoccus* Cock. in Italy. I. Faunistical-ecological notes on species observed in pine forests in Liguria and Tuscany. *Redia* **74**, 575-597.

Diehl, E., Sereda, E., Wolters, V. & Birkhofer, K. (2013) Effects of predator specialization, host plant and climate on biological control of aphids by natural enemies: a meta-analysis. *Journal of Applied Ecology* **50**, 262-270.

Dixon, A.F.G. (2000) *Insect predator-prey dynamics: ladybird beetles and biological control*. New York, USA, Cambridge University Press.

Eizaguirre, S. (2004) Revisión de la tribu Coccidulini en la Península Ibérica (Coleoptera: Coccinellidae) *Estudios del Museo de Ciencias Naturales de Álava* **18-19**, 153-170.

Ferran, A. & Dixon, A.F.G. (1993) Foraging behaviour of ladybird larvae (Coleoptera: Coccinellidae). *European Journal of Entomology* **90**, 383-402.

Foldi, A.I. (2004) The Matsucoccidae in the Mediterranean basin with a world list of species (Hemiptera: Sternorrhyncha: Coccoidea). *Annales de la Société entomologique de France* **40**, 145-168.

Fowler, S.V. (2004) Biological control of an exotic scale, *Orthezia insignis* Browne (Homoptera: Ortheziidae), saves the endemic gumwood tree, *Commidendrum robustum* (Roxb.) DC. (Asteraceae) on the island of St. Helena. *Biological Control* **29**, 367-374.

Funk, D.J., Filchak, K.E. & Feder, J.L. (2002) Herbivorous Insects: Model Systems for the Comparative Study of Speciation Ecology. *Genetica* **116**, 251-267.

Heidari, M. & Copland, M. (1992) Host finding by *Cryptolaemus montrouzieri* (Col., Coccinellidae) a predator of mealybugs (Hom., Pseudococcidae). *Entomophaga* **37**, 621-625.

Hodek, I.& Honěk, A. (1996) *Ecology of Coccinellidae*. Dordrecht, The Netherlands, Kluwer Academic Publishers.

Hodek, I. & Honěk, A. (2009) Scale insects, mealybugs, whiteflies and psyllids (Hemiptera, Sternorrhyncha) as prey of ladybirds. *Biological Control* **51**, 232-243.

Jackson, R.R., Salm, K. & Nelson, X.J. (2010) Specialized prey selection behavior of two East African assassin bugs, *Scipinnia repax* and *Nagusta* sp. that prey on social jumping spiders. *Journal of Insect Science* **10**, 1-19.

Jactel, H., Ménassieu, P. & Burban, C. (1996) Découverte en Corse de *Matsucoccus feytaudi* Duc (Homoptera: Margarodidae), cochenille du pin maritime. *Annals of Forest Science* **53**, 145-152.

Jałoszyński, P.& Olszanowski, Z. (2013) Specialized feeding of *Euconnus pubicollis* (Coleoptera: Staphylinidae: Scydmaeninae) on oribatid mites: Prey preferences and hunting behaviour. *European Journal of Entomol*ogy **110**, 339-353.

Kalushkov, P. & Hodek, I. (2001) New essential aphid prey for *Anatis ocellata* and *Calvia quatuordecimguttata* (Coleoptera: Coccinellidae). *Biocontrol Science and Technology* **11**, 35-39.

Katsanis, A., Babendreier, D., Nentwig, W. & Kenis, M. (2013) Intraguild predation between the invasive ladybird *Harmonia axyridis* and non-target European coccinellid species. *BioControl* **58**, 73-83.

Koch, R. & Galvan, T. (2008) Bad side of a good beetle: the North American experience with *Harmonia axyridis* pp. 23-35 in Roy, H. & Wajnberg. E (Eds.)

From Biological Control to Invasion: the Ladybird Harmonia axyridis as a Model Species. Springer Netherlands.

Majumder, J. & Agarwala, B. (2013) Biology and Population Dynamics of Giant Ladybird Predator *Anisolemnia dilatata* (F.) (Coleoptera: Coccinellidae): A Specialized Predator of Woolly Aphids of Bamboo Plants in Northeast India. *World Journal of Zoology* **8**, 55-61.

Matsuki, M. & MacLean Jr, S.F. (1994) Effects of different leaf traits on growth rates of insect herbivores on willows. *Oecologia* **100**, 141-152.

Mendel, Z., Assael, F., Zeidan, S. & Zehavi, A. (1998) Classical Biological Control of *Palaeococcus fuscipennis* (Burmeister) (Homoptera: Margarodidae) in Israel. *Biological Control* **12**, 151-157.

Mendel, Z., Blumberg, D., Zehavi, A. & Weissenberg, M. (1992) Some polyphagous Homoptera gain protection from their natural enemies by feeding on the toxic plants *Spartium junceum* and *Erythrina corallodendrum* (Leguminosae). *Chemoecology* **3**, 118-124.

Obata, S. (1986) Mechanisms of prey finding in the aphidophagous ladybird beetle, *Harmonia axyridis* [Coleoptera: Coccinellidae]. *Entomophaga* **31**, 303-311.

Obrycki, J.J. & Kring, T.J. (1998) Predaceous Coccinellidae in biological control. *Annual Review of Entomology* **43**, 295-321.

Pekár, S. (2004) Predatory behavior of two european ant-eating spiders (Araneae, Zodariidae) *Journal of Arachnology* **32**, 31-41.

Ponsonby, D. & Copland, M. (1995) Olfactory responses by the scale insect predator *Chilocorus nigritus* (F.) (Coleoptera: Coccinellidae). *Biocontrol Science and Technology* **5**, 83-94.

Pope, R.D. (1981) 'Rhyzobius ventralis' (Coleoptera: Coccinellidae), its constituent species, and their taxonomy and historical roles in biological control. *Bulletin of Entomological Research* **71**, 19-32.

Ragab, M.E. (1995) Adaptation of *Rodolia cardinalis* (Mulsant) (Col., Coccinellidae) to *Icerya aegyptiaca* (Douglas) (Hom., Margarodidae) as compared with *Icerya purchasi* Mask. *Journal of Applied Entomology* **119**, 621-623.

Raimundo, A., Canepari, C., Mendel, Z., Branco, M. & Franco, C. (2006) *Iberorhyzobius* Raimundo & Canepari gen. nov., for *Coccidula rondensis* Eizaguirre (Coleoptera: Coccinellidae). *Zootaxa* **1312**, 49-58.

Ricci, C. (1986) Seasonal food preferences and behavior of *Rhyzobius litura*. pp. 119-123 in Hodek, I (Ed.) *Ecology of Aphidophaga*. Dordrecht, The Netherlands. Academia, Prague & Dr. W. Junk.

Richards, A.M. (1981) *Rhyzobius ventralis* (Erichson) and R. *forestieri* (Mulsant) (Coleoptera: Coccinellidae), their biology and value for scale insect control. *Bulletin of Entomological Research* **71**, 33-46.

Richards, A.M. (1985) Biology and defensive adaptations in *Rodatus major* (Coleoptera: Coccinellidae) and its prey, *Monophlebulus pilosior* (Hemiptera: Margarodidae). *Journal of Zoology* **205**, 287-295.

Riom, J. & Gerbinot, B. (1977) Étude biologique et écologique de la cochenille du pin maritime *Matsucoccus feytaudi* Ducasse, 1942 (Coccoidea, Margarodidae, Xylococcinae) dans le Sud-Est de la France. 1. Biologie générale et phénologie. *Annales de Zoologie, Écologie Animale* **9**, 11-50.

Scriber, J.M. (2010) Integrating ancient patterns and current dynamics of insect–plant interactions: Taxonomic and geographic variation in herbivore specialization. **17**, 471-507.

Short, B.D. & Bergh, J.C. (2004) Feeding and egg distribution studies of *Heringia calcarata* (Diptera: Syrphidae), a specialized predator of woolly apple aphid (Homoptera: Eriosomatidae) in Virginia Apple Orchards. *Journal of Economic Entomology* **97**, 813-819.

Sloggett, J.J. & Majerus, M.E.N. (2000) Habitat preferences and diet in the predatory Coccinellidae (Coleoptera): an evolutionary perspective. *Biological Journal of the Linnean Society* **70**, 63-88.

Stathas, G.J. (2000) *Rhyzobius lophanthae* prey consumption and fecundity. *Phytoparasitica* **28**, 203-211.

Strand, M.R. & Obrycki, J.J. (1996) Host specificity of insect parasitoids and predators. *BioScience* **46**, 422-429.

Thompson, A.J.J.N. (1995) Trade-offs and the evolution of host specialization. *Evolutionary Ecology* **9**, 82-92.

Toccafondi, P., Covassi, M. & Pennacchio, F. (1991) Studies on the entomophagous predators of scale insects of the genus *Matsucoccus* Cock. in Italy. II Bio-ethological notes on *Rhyzobius chrysomeloides* (Herbst) in pine forests of Liguria (Coleoptera: Coccinellidae). *Redia* **74**, 599-620.

Van Lenteren, J., Bale, J., Bigler, F., Hokkanen, H. & Loomans, A. (2006) Assessing risks of releasing exotic biological control agents of arthropod pests. *Annual Review of. Entomology* **51**, 609-634.

Vantaux, A., Roux, O., Magro, A., Ghomsi, N.T., Gordon, R.D., Dejean, A. & Orivel, J. (2010) Host-Specific Myrmecophily and Myrmecophagy in the Tropical Coccinellid *Diomus thoracicus* in French Guiana. *Biotropica* **42**, 622-629.

Vieira, L., Salom, S., Montgomery, M. & Kok, L. (2013) Field-cage evaluation of the survival, feeding and reproduction of *Laricobius osakensis* (Coleoptera: Derodontidae), a predator of *Adelges tsugae* (Hemiptera: Adelgidae). *Biological Control* **66**, 195-203.

Wiegmann, B., Mitter, C. & Farrell, B. (1996) Diversification of Carnivorous Parasitic Insects: Extraordinary Radiation or Specialized Dead End? *The American Naturalist* **142**, 737-754

III. Reproductive synchronization of a ladybird with its prey: evidence for prey specialization on a predator of *Matsucoccus feytaudi*

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Manuela Branco

3.1. Abstract

1. The pine bast scale *Matsucoccus feytaudi* is an invasive pest of maritime pine forests in Southeastern Europe. *Iberorhyzobius rondensis* is a potential candidate for biological control of this pest. In this study we evaluated prey specialization as mediated by reproductive activity of the predator. We further studied fecundity and prey consumption of the beetle.

2. In laboratory, *I. rondensis* displayed a reproductive diapause of 5-6 months which was unaffected by the factors tested: temperature, photoperiod and diet. After diapause, oviposition was initiated with consumption of *M. feytaudi* eggs or *Ephestia kuehniella* eggs. Female fecundity was higher when ladybirds were fed on *M. feytaudi* eggs and increased with mating frequency.

3. In the field, *I. rondensis* larvae were mainly observed in the 2 months period following the flight peak of *M. feytaudi.*

4. At 25ºC, pre-imaginal development was completed in 39 days. Each larva ate around 2000 *M. feytaudi* eggs during its development.

5. An obligatory reproductive diapause resulting in seasonal synchrony with the prey is reported for this species. This trait reinforces the existence of prey-specialization in this species. It thus supports *I. rondensis* as a promising biological control agent for *M. feytaudi.*

Keywords: bast scale, biological control, coccidophagous, diapause, Coccinellidae, prey-predator

3.2. Introduction

The maritime pine bast scale *Matsucoccus feytaudi* Ducasse (Hemiptera: Matsucoccidae) is a univoltine and highly specialized sap sucker insect, feeding exclusively on the tree trunk of maritime pine, *Pinus pinaster* Aiton (Foldi, 2004). The species is endemic to South Western Europe and North Africa (Burban *et al.*, 1999). In the second half of the 20th century it became an invasive pest in Southeastern France, Corsica and Italy, where it has to this date caused important damage, triggering dieback of large areas of maritime pine forest (Covassi & Binazzi, 1992; Jactel *et al.*, 1996; Jactel & Menassieu, 2005). In its native range *M. feytaudi* is regulated by several natural enemies, which respond to its sex pheromone, such as several *Elatophilus sp.* Reuter (Hemiptera: Anthocoridae), *Hemerobius stigma* Stephens (Neuroptera: Hemerobiidae), *Aplocnemus raymondi* Deville, *A. brevis* Rosenhauer (Coleoptera: Dasytidae), *Malachiomimus pectinatus* (Kiesenwetter) (Coleoptera: Malachiidae) and *Iberorhyzobius rondensis* (Eizaguierre) (Coleoptera: Coccinellidae) (Mendel *et al.*, 2004; Branco *et al*., 2006; Branco *et al*., 2011; Rodrigo *et al.*, 2013). In the invaded range of the bast scale, *E. nigricornis* (Fabre *et al.*, 2000; Foldi, 2004), *H. stigma* and *Rhyzobius chrysomeloides* (Herbst) (Toccafondi *et al.*, 1991) prey on *M. feytaudi*, but were unable to reduce its densities to acceptable levels (Schvester & Fabre, 2001).

Iberorhyzobius rondensis is a recently described coccinellid predator from the Iberian Peninsula (Raimundo, 2006). Tavares *et al*. (2014) reported extreme prey and habitat specialization for this beetle and the possibility of using it for biological control of *M. feytaudi.* Coccinellidae, and especially coccidophagous ladybirds, have often been successfully used as biological control agents (Dixon, 2000). Still, research on prey specificity and predation efficacy is essential to minimize ecological and environmental impacts, and maximize effectiveness of the biological control (Van Lenteren *et al*., 2006; Barratt *et al.*, 2010). Predation efficacy greatly relies on prey and predator's life cycle synchronization (Van Lenteren *et al*., 2006). This synchronization is particularly relevant for specialized predators (e.g., Cheah & McClure, 2000; Lu and Montgomery, 2001; Santos *et al*., 2010). In ladybirds, it is often achieved through dormancy, migration or reproductive diapause (Hodek & Honěk, 1996; Dixon *et al*., 1997). Through this synchronization, adult's ladybirds match their oviposition with prey availability, since the larvae's essential prey is usually the same for adults' reproduction (Hodek & Honek, 1996; Dixon, 2000).

Based on the above facts, and given *I. rondensis'* degree of specialization, and previous field observations (Branco *et al*., 2006; Tavares *et al.*, 2014), we hypothesized that: (1) this predator has a univoltine life cycle synchronized with that of *M. feytaudi*; and (2) its oviposition is elicited by preying on *M. feytaudi* egg masses. In order to test hypothesis (1), we determined i) duration of pre-imaginal development; ii) adult longevity; and iii) seasonal field activity. To test hypothesis (2), we determined i) the effect of diet, temperature and photoperiod on the reproductive activity of the beetle. Also, as additional indicators of predator efficacy, we tested i) fecundity of *I. rondensis*, ii) prey consumption by larvae, and iii) mating behavior. These are traits which should always be determined in a risk assessment study for a potential biological control agent (Van Lenteren *et al.,* 2006).

3.3. Materials and Methods

Iberorhyzobius rondensis development and survival

Egg development

Eggs of *I. rondensis,* 24-48 hours old, were put in glass Petri dishes and left in a climate chamber at different temperatures: 4ºC, 11ºC, 13.5ºC, 18ºC, 20ºC, 22ºC, 25ºC, 28ºC and 30ºC. Five to 10 Petri dishes (i.e. replicates), each with 5 to 10 eggs were used for each treatment. Eggs were checked every day until they hatched or deteriorated. Development time, i.e. number of days until hatching (D), and survival was registered. Since at 4ºC hatching never occurred, we tested moving the eggs to 22°C after 2 and 3 months.

A quadratic model was used to fit development time to temperature. Temperatures of 4ºC and 30ºC where excluded for this model because they caused very high mortality (>97%). Distribution of residuals was checked for normality with a Kolmogorov-Smirnov test. The lower theoretical temperature threshold (i.e., base temperature Ts) was derived from the linear function ($Y = a + bT$) where Y is the development rate, T is temperature, a and b are parameters estimated by the model,

$Ts = -\frac{a}{b}$ (Damos & Savopoulou-Soultani, 2012). The linear model is only adequate over a range of favorable temperatures (Damos & Savopoulou-Soultani, 2012), so only temperatures corresponding to a survival rate higher than 75% were used for the linear model, in this case 11ºC to 25ºC.

Pre-imaginal development

Complete development of larvae (n = 27) from egg hatching until adulthood was determined at 22ºC, 14:10 L:D (ratio of light to dark) and 60% relative humidity. We used 22ºC because it is the mean temperature observed in March-April, when larvae are found in the field in the studied region (Setúbal, Portugal) (Tavares *et al*., 2014). Eggs were obtained from adults reared in the laboratory. Larvae were fed *ad libitum* with *M. feytaudi* eggs masses and reared in separate plastic test vials. Larvae were checked every other day, when fresh surplus food was added. Duration of each instar was recorded by exuviae observation. Weight of larvae was determined once for each instar, at beginning of the stage using a laboratory precision scale (Shimdzu, Aux 220).

Pre-imaginal egg consumption

Daily consumption of *M. feytaudi* eggs was determined from hatching until pupation for *I. rondensis* larvae (n=10) reared in the laboratory, under a 14:10 L:D at 22ºC and 60% relative humidity. Every day a quantified number of fresh eggs of *M. feytaudi* was offered and the number of non-consumed eggs was counted. Eggs were always supplied *ad libitum*. Daily egg consumption was calculated as the mean number of eggs consumed per day and per larva for each instar. Differences in mean daily consumption between instars were determined with a one-way ANOVA, followed by a post-hoc Tukey test. Normality of residuals and homogeneity of variances were assessed with Kolmogorof-Smirnov and Levene tests, respectively.

Adult survival and sex ratio

In 2008, 2010 and 2011, survival of 155 adults, 75 females and 80 males, was determined in the laboratory, under natural light conditions and room temperatures (22ºC ± 5ºC). Adults were either obtained from late instar larvae captured with *M. feytaudi* pheromone lures in the field, or reared in the laboratory from the egg stage and fed with *M. feytaudi* eggs. Adults were reared in boxes, with 5 to 7 individuals per box, and fed with a mixture of *M. feytaudi* eggs, *Ephestia kuehniella* (Zeller) eggs, pollen and 50% honey-water solution. After their death all individuals were dissected in order to confirm their sex. Survival of both sexes was analyzed with the Kaplan-Meier curve, followed by a Log-Rank test.

In 2011 and 2012 the sex ratio was determined for 52 adults reared from eggs obtained in the laboratory and 300 adults collected at the larval stage in the field. A chi-square analysis was used to test if the sex ratio was different from 1:1.

Weight of two weeks old adults (n = 53), males and females, was also determined and a *t*-test was used to test for differences between sexes.

Reproductive activity and fecundity

Reproductive activity and fecundity were observed by a set of trials. For that, adults were reared in the laboratory from the 3rd and 4th instar larvae collected in the field in 2009, 2010, 2011 and 2012. Larvae were fed with a mixture of *M. feytaudi* and *E. kuehniella* eggs until pupation (Tavares *et al*., 2014). Egg masses of *M. feytaudi* were collected on *P. pinaster* trees at the Experimental Forest Unit of INRA, Bordeaux, France in February-March, and stored in the freezer. Sterilized eggs masses of *E. kuehniella* were bought from Koppert España S.L.

Immediately after adults' emergence, beetles were sexed, by observation of female and male abdomen according to Stathas *et al*. (2002). All adults were dissected after the trials to confirm their sexes.

Observations on the reproductive activity

Since the reproductive activity of this species was completely unknown, a preliminary study was conducted from 2008 to 2011 to characterize its seasonal oviposition pattern and fecundity. Observations were conducted under a continuous supply of food mixture consisting of *M. feytaudi* and *E. kuehniella* eggs, supplemented with pollen and a honey-water solution. Since the quantity of *M. feytaudi* egg masses collected in the field was insufficient to feed the adults all year, we needed to complement it with other food items. *E. kuehniella* eggs, pollen and honey were chosen because, the first are well accepted by larvae (Tavares *et al*., 2014) and the second and third are a common complement in many ladybirds diets (Hodek & Honěk, 1996; Hodek & Honěk, 2009).

Two to eight couples were put in rearing boxes (9.5 × 9.5 × 7.5 cm) and kept under a 14:10 L:D at 22ºC and 66% relative humidity, during 6 months, after which they were left at room temperatures (15–25ºC) and natural photoperiod. The length of the pre-oviposition period and fecundity were determined for 67 females. The eggs laid by *I. rondensis* females were counted and removed every second day during the entire adult life. Fecundity was calculated as the total number of eggs laid per box, divided by the total number of females alive at each egg count.

Influence of diet, temperature and photoperiod on reproductive diapause length

The preliminary observations, described above, suggested that the beetles had a pre-reproductive diapause. Therefore, an experiment was carried out in 2012, to test the effects of diet and photoperiod on reproductive diapause break. Adults were separated, 5 females and 4 males per box. Three types of diet were tested, always complemented with pollen and honey-water solution (control): A) *M. feytaudi* egg masses, an egg batch c.a. 350 eggs, was added to each box once a week due to the scarcity of this feeding resource; B) Eggs of *E. kuehniella*; and C) Control. Two photoperiods were tested for each of the three diets: 16:8 L:D and 8:16 L:D, at 22ºC (Table 1a). Data were treated with a two-way ANOVA and assumptions of normality of residuals and homogeneity of variances were verified.

A second experiment was designed to test for the combined influence of temperature and photoperiod on the length of the reproductive diapause (Table 1b). Adults were kept in separated boxes as described above and fed with *M. feytaudi* egg masses, pollen and honey-water solution. Three treatments were compared: (1) natural day light and temperature conditions, (2) a long day length followed by a shorter day length with decreasing temperatures and (3) a short day length followed by a longer day length with constant temperatures (Table 1b). One-way ANOVA was performed in order to detect differences between the three treatments.

Influence of diet on fecundity

Female fecundity was compared between three groups under different diets in three consecutive periods (Table 2). Diet of the groups was complemented with pollen and honey-water solution (control) and differentiated as follow: During period (i) from 1 October to 9 November 2012, Group A was fed with egg masses of *M. feytaudi*, Group B was fed with eggs of *E. kuehniella*, and Group C was control. During period

(ii) from 9 November 2012 to 9 May 2013, beetles of group A were no longer fed with *M. feytaudi* due to the scarcity of this food item; groups B and C were kept on the same diet provided during period (i). During period (iii) from 9 May to 16 July 2013, Group A and C were given egg masses of *M. feytaudi* while Group B remained on the same diet (Table 2). Rearing boxes were left at room temperatures (20-25ºC) and natural photoperiod. Independent sample t-tests were used to test for differences in fecundity between diets for each period.

Table 1. Effect of diet, photoperiod and temperature on the length of reproductive diapause in *Iberorhyzobius rondensis*. a) Trial 1: Influence of different diets and photoperiods, all diets contained pollen and honey-water solution (control) and differed as follow: A1, A2: Eggs masses of *Matsucoccus feytaudi*, B1, B2: *Ephestia kuehniella* eggs and C1, C2: control. b) Trial 2: Influence of photoperiod and temperature (D1, D2, and D3). Beetles were fed with the same diet as A1 and A2.

Treatment	Photoperiod L:D	Temperature	Number of boxes	Days until oviposition (±SE)
a) Trial 1				
A1	16:8	22ºC	3	151.7 ± 4.05
A2	8:16	22ºC	2	141.5 ± 12.50
B1	16:8	22ºC	5	165.8 ± 6.62
B2	8:16	22ºC	5	165.4 ± 2.68
C1	16:8	22ºC	5	_
C2	8:16	22ºC	5	_
b) Trial 2				
D1	Natural[1]	23ºC – 30ºC[1]	3	173.3 ± 20.59
D2	16:8[2] - 8:16[3]	22ºC[2] -14ºC[3]	3	138.33 ± 6.17
D3	8:16[2] - 16:8[3]	22ºC[1]	3*	150.5 ± 6.50

[1] 10 July to 25 Sept, natural photoperiod ranged from L15:D9 to L13:D11; [2] 10 July to 10Aug; [3] 11Aug to 25Sept.

Table 2. Effect of diet on fecundity (eggs/female/week) in *Iberorhyzobius rondensis*. Periods: (i) 1/10/12 - 9/11/12, (ii) 9/11/12 - 9/5/13 and (iii) 9/5/13 – 16/7/13.
All the groups were given pollen + honey-water solution and differentiated as following: Group A was fed with egg-masses of *Matsucoccus feytaudi* during period (i) and (iii), but not during period (ii). Group B was always fed with *Ephestia kuehniella* eggs. Group C was fed with egg-masses of *Matsucoccus feytaudi* only during period (iii). Beetles were left at natural photoperiod and room temperature (22ºC).

Group	Number of boxes	Period (i)	Period (ii)	Period (iii)
A	8	17.4 ± 9.42[a]	4.2 ± 1.23[b]	7.5 ± 2.14[a]
B	10	6.1 ± 2.14 [b]	22.1 ± 3.24[a]	5.3 ± 1.13[a]
C	10	0 ± 00	0 ± 00	0.14 ± 0.08

[a,b] Different letters correspond to significant differences within the same column·

Reproductive behavior

In 2012 and 2013 one year old mature ladybirds were separated in three different groups to test for polygamy*:* (1) two males with one female, (2) two females with one male and (3) one female with one male. Beetles were fed with a mixture of *M. feytaudi* egg masses, *E. kuehniella* eggs, pollen and honey-water solution.

Individuals were marked with different colors and observed during 5 months, three times a week and three times a day for 10 minutes in the following intervals: 9h-12h, 12h-14h and 14h-17h. The number of matings and eggs laid was recorded. All beetles were dissected after death to confirm their sex.

The influence of the sex-ratio on mating and fecundity was tested with one way ANOVA. A Pearson’s correlation test was performed to determine the effect of mating frequency on fecundity.

Field seasonality and synchronization with the prey life cycle

Synchronization of *I. rondensis* and *M. feytaudi* life cycles was investigated in two maritime pine stands, located in Sintra and Setúbal, Portugal, c.a. 70 km distant. Monitoring was done once a month, during 24 months at Setúbal and 18 months at Sintra. Insects were detected using lures baited with *M. feytaudi* sex pheromone which attracts *M. feytaudi* males as well as several other natural enemies of *M. feytaudi* (Branco *et al*., 2006; Branco *et al*., 2011). In each stand 30 trees were baited with a dispenser of *M. feytaudi* sex pheromone, 200 µg (synthesized at the UPMC, INRA-Versailles). The lure was placed on the trunk, at 1.30m height, in the center of an arena where the bark was smoothed. Observations were conducted during 1 hour. Total number of *I. rondensis*, both larvae and adults and *M. feytaudi* males were recorded per tree. Sampling was done when air temperature was above 15ºC (on average 19.6ºC ± 0.79) to guarantee sufficient activity of insects and diffusion of pheromone. *M. feytaudi* males live for a short period of 2-3 days, thus the presence of males accurately reveals male emergence and reproductive activity (Riom & Gerbinot, 1977; Foldi, 2004). Sampling could not be done in November and December 2012 at Sintra, and August 2011, December 2011, November 2012 and January 2013 at Setúbal due to adverse weather conditions.

In order to test life cycle synchronization of *M. feytaudi* and *I. rondensis*, a lag-correlation between monthly abundance of each species was performed for each region separately. Lagged correlation refers to the correlation between two time series shifted in time relative to one another. Lag correlation occurs when one series has a delayed response to the other series, or a differential delayed response to a common stimulus that affects both series (Brockwell & Davis, 2002). We analyzed lag-correlation between *M. feytaudi* and *I. rondensis* densities, at lag intervals ranging from 0 to 12 months. All analyses were performed in SPSS 20.

3.4. Results

Iberorhyzobius rondensis development and survival

Egg development

A quadratic model was fitted to egg development time $y = 0.24x^2 - 11.13x + 139.19$ ($r^2 = 0.889$, F = 167.84, df = 42, $P < 0.001$) (Fig.1A). The optimal temperature for egg development was 25ºC, with a development time of 8.6 ± 0.5 days (Fig. 1A). All eggs died if left at 4ºC for three months (n = 45) (Fig.1B) but showed at least 89% survival if removed from this temperature after two months (n = 87). Mortality was 97% at 30ºC (Fig.1B).

Temperature threshold for development was estimated to be 8.4ºC, from the linear model ($r^2 = 0.878$, F = 265.42, df = 37, P < 0.001). The number of degree days for egg development was then estimated as 142.8.

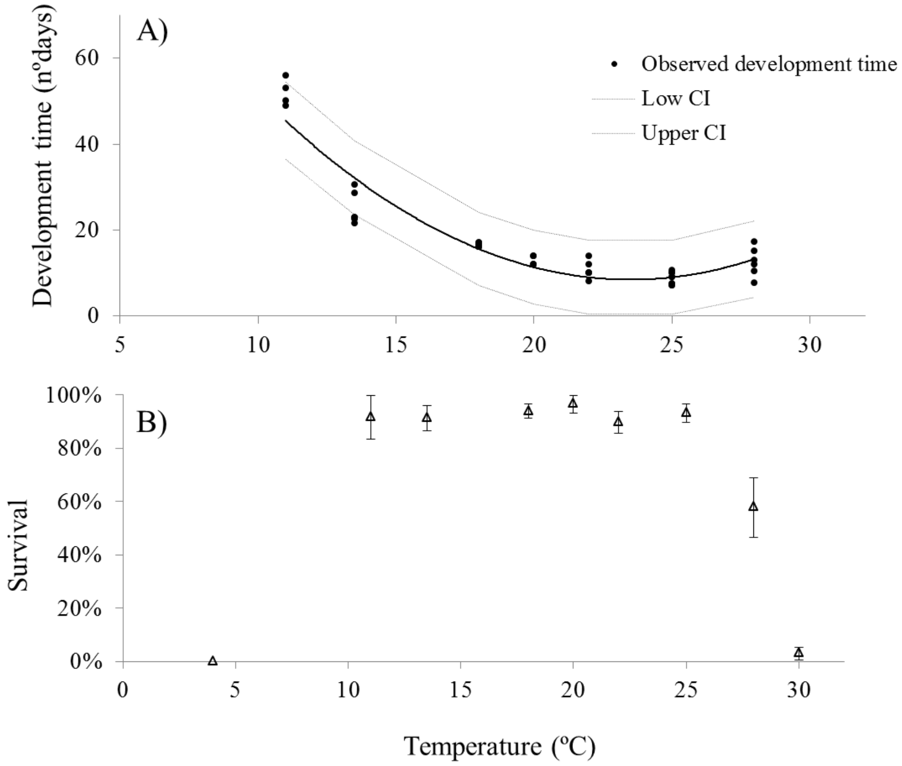

Fig. 1. (A) Development time (days) of *Iberorhyzobius rondensis* eggs (black dots) and corresponding quadratic model and (B) Survival (%) at 4ºC (more than 3 months); 11ºC, 13.5ºC, 18ºC, 20ºC, 22ºC, 28ºC and 30ºC (represented by white triangles).

Pre-imaginal development

Complete development from egg to adult took 39.1 ± 0.19 days at 22°C. Larvae gained in weight very quickly, especially after the 2nd instar (Table 3). Survival was relatively high for all life stages (90% to 100%).

Pre-imaginal egg consumption

Significant differences were found in *M. feytaudi* egg consumption by different larval instars ($F_{(3,40)} = 19.99$, P < 0.001). In particular, consumption by first instar larvae differed considerably from all the other instars. On average 1st instars ate 18.9 ± 1.28 eggs per day, 2nd instars 64.6 ± 10.04, 3rd instars 82.7 ± 5.25 and 4th instars 83.9 ±

7.41. During their entire development larvae consumed on average 1851.6 ± 98.34 eggs of *M. feytaudi* which is equivalent to 5 to 7 egg masses of *M. feytaudi* (Foldi, 2004).

Table 3. Development time of *Iberorhyzobius rondensis*, from egg hatching until adulthood with the mean weight of larvae and recently emerged adults of *I. rondensis*. Larvae were reared at 22ºC, 14:10 L:D and 60% RH, fed *ad libitum* with egg masses of *Matsucoccus feytaudi.*

Stage	n (development)	Mean number of days ± SE	Range (days)	Survival (%)	n (weight)	Mean weight (mg) ± SE
Egg	70	10.6 ± 0.72	8 - 12	91%	-	-
1st Instar	27	6.7 ± 0.15	6 - 8	92%	16	0.032 ± 0.004
2nd Instar	25	4.0 ± 0.14	3 - 5	100%	25	0.642 ± 0.047
3rd Instar	25	5.8 ± 0.16	5 - 7	100%	24	2.175 ± 0.120
4th Instar	25	11.1 ± 0.09	11 - 12	100%	25	4.183 ± 0.202
Pre-pupa	25	3.0 ± 0.04	2 - 3	100%	-	-
Pupa	25	8.5 ± 0.16	7 - 9	100%	-	-
Adult Female	-	-	-	-	27	2.270 ± 0.078
Adult Male	-	-	-	-	26	2.000 ± 0.104
Total (egg to adult)	27	39.1 ± 0.19	37 - 40	92%	-	-

Adult survival and sex ratio

Adult ladybirds lived on average 288.3 ± 11.8 days (ca. 10 months) when fed *ad libitum* in the laboratory. A maximum longevity of 690 days (almost two years) was observed for 3 individuals. Females had on average a longer longevity (319.8 ± 18.40 days) than males (245.4 ± 14.67 days) (Log-Rank Chi-square test = 8.58, P < 0.003).

Of the 300 adults collected in the field with pheromone lures, 165 were females and 150 were males, and of the 52 adults reared from the egg stage in the laboratory, 29 were females and 23 were males. The sex ratio did not significantly differ from 1:1 in neither of the cases: ($\chi_1^2 = 3.00$, $P = 0.08$ and $\chi_1^2 = 0.69$, $P = 0.404$). Adult females (2.3 ± 0.08 mg) were significantly heavier than males (2.0 ± 0.1mg) (n = 53, t = 2.085, P = 0.042).

Reproductive activity and fecundity

Observations on the reproductive activity

Mean pre-oviposition period was observed to last 161.5 ± 14.5 days, varying from 71 to 220 days per box. Total fecundity was 73.0 ± 10.1 eggs per female, ranging from 23 to 135 eggs. The oviposition period could last up to 10 months and if food was available females could continue to oviposit until death.

Influence of diet, temperature and photoperiod on reproductive diapause length

Beetles fed only with pollen and honey-water solution (group C) never laid eggs. Thus, the two-way ANOVA was only performed for beetles of group A and B. Ladybirds fed with eggs of *M. feytaudi* or *E. kuehniella* started laying eggs almost at the same time, about five months after emergence (Table 1a). Length of reproductive diapause was independent of the tested factors: photoperiod ($F_{(1,11)} = 0.173$, $P = 0.685$), diet ($F_{(1,11)} = 2.243$, $P = 0.162$) or their interaction ($F_{(1,11)} = 0.148$, $P = 0.708$) (Table 1a).

On the second experiment (Table 1b), length of reproductive diapause was similar for all photoperiods and temperatures tested ($F_{(2,5)} = 1.654$, $P = 0.281$).

Influence of diet on fecundity

Ladybirds fed with eggs of *M. feytaudi* (group A) or *E. kuehniella* (group B) laid eggs from November 2012 until July-August 2013 (day 376), but fertility differed between periods (i), (ii) and (iii) (Table 2). Ladybirds fed only with pollen and honey-water solution never laid any eggs (group C, periods i and ii). In period (iii) during which some eggs of *M. feytaudi* were provided to group C, a unique oviposition event in one box was observed. Group C was thus excluded from statistic tests on fecundity.

Independent sample *t*-tests showed that fecundity differed significantly between groups A and B (Table 2) during period (i) ($t_{11.9} = 2.367$, $P = 0.034$) and (ii) ($t_{24.2} = -4.121$, $P < 0.001$). During period (i) fecundity was higher for group A fed with *M. feytaudi* eggs than for group B fed with *E. kuehniella* eggs. In period (ii) fecundity was higher for group B fed with *E. kuehniella* eggs than for group A fed only with pollen and honey-water solution (although previously fed with *M. feytaudi* eggs). No significant differences between group A and B were observed during period (iii) when *M. feytaudi* eggs were again supplied to group A ($t_{22} = -0.859$, $P = 0.399$) (Table 2).

Reproductive behavior

Of the 381 observations made during 5 months only 66 mating events were recorded, out of which 35 were from a single couple in a single box in group B. Nevertheless, polygamy (polyandry and polygyny) was observed in almost all boxes where three individuals were placed (groups A and B) (Table 4). No significant differences were found on fecundity between the different groups (F = 0.038, df = 25, *P* = 0.962) and no significant differences were found between groups on mating frequencies (F = 1.764, df = 15, P = 0.205), but a significant correlation was found between mating frequency and fecundity (r = 0.852, n = 19, *P* < 0.0001). Egg laying stopped in boxes where males died.

Table 4. Mating frequency and fecundity (eggs/female/day) of *Iberorhyzobius rondensis* females in relation with the sex ratio. Group A) 2 females (F1, F2) and 1 male (M1); Group B) 1 female (F1) and 2 males (M1, M2); Group C) 1 female and 1 Male.

Groups	Number of boxes	Matings couple 1	Matings couple 2	Number of boxes with observed mating	Fecundity (eggs/female/day)
A) F1, F2, M1	5	3	4	1	0.223 ± 0.055
B) F1, M1, M2	6	42	8	6	0.249 ± 0.078
C) F1, M1	6	9	-	4	0.228 ± 0.048

Field seasonality and synchronization with prey life cycle

Iberorhyzobius rondensis larvae were only observed in the field in the period February-May, after the main flight peak of *M. feytaudi* (Fig. 2). Most observed larvae were at the 3rd and 4th instar. Adults of *I. rondensis* were scarcely observed throughout the year. A total of 12 adults were observed in Setúbal (2 in May, 4 in June, 2 in July, 2 in October) and 6 adults in Sintra (3 in April, 1 in June, 1 in July and 1 in January).

In Setúbal a significant lag-correlation with a lag of 2 months was found between densities of *M. feytaudi* males and of *I. rondensis* larvae (*r* = 0.82 ± 0.209, *P* < 0.05). No significant lag-correlation was found in Sintra.

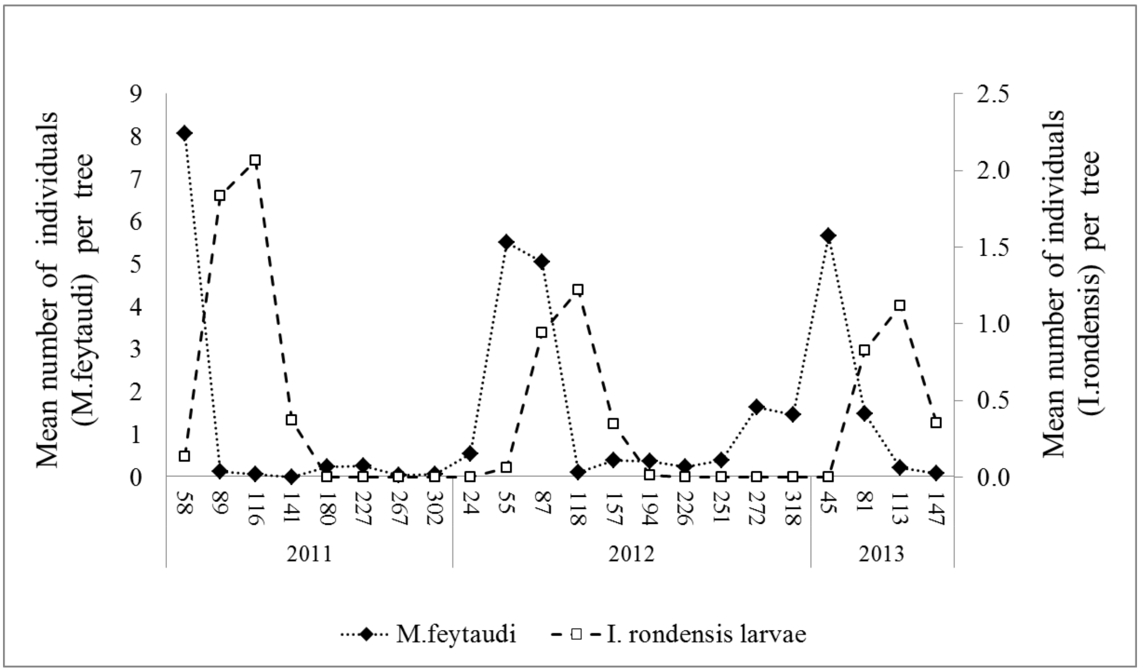

Fig. 2. Phenology of *Matsucoccus feytaudi* males and *Iberorhyzobius rondensis* larvae in Setúbal, Portugal in 2011, 2012 and 2013. The number of individuals per tree is presented as moving average between each sampled day, and Julian days are given for each year.

3.5. Discussion

Requirements for reproduction and fecundity

In the present study we found evidence for a long reproductive diapause, of 5-6 month, in *I. rondensis*. During this period oviposition was not induced by exposure of adult beetles to different combinations of photoperiods, temperatures or diets. Thus, we suggest this diapause to be obligatory, and mostly driven by genetic factors (Koštál, 2006). Obligatory reproductive diapause in predator species usually allows synchronization with prey availability (Danks, 2002).This mechanism was observed on a few other ladybird species, namely *Coccinella septempunctata* L. (Hodek & Okuda, 1993) and *Hippodamia undecimnotata* Schneider (Katsoyannos *et al.*, 2005).

In our study, when the beetle's reproductive diapause ended, provision of *M. feytaudi* eggs or *E. kuehniella* eggs was essential to start and maintain reproductive activity. Beetles fed only with pollen and the honey-water solution never oviposited.

Therefore, it is very unlikely that, in the field, *I. rondensis* starts oviposition before finding *M. feytaudi* eggs. In specialized ladybirds, gonadal development usually requires essential food, which is also the one needed for larval development (Hodek & Honěk, 1996).When individuals were provided with *M. feytaudi* egg masses only one year after emergence, fecundity was extremely low. This suggests that one year-old beetles were already in senescence (Dixon, 2000) and that a provision of protein so late in life did not allow for optimal gonadal development.

Iberorhyzobius rondensis was also capable of reproducing when fed on *E. kuehniella* eggs. This diet is usually used for development and reproduction of ladybird species in artificial laboratorial conditions, due to its high acceptance and nutritional value (De Clercq *et al*., 2005; Berkvens *et al*., 2008). However, more eggs were laid by *I. rondensis* females when fed with egg-masses of the natural prey, *M. feytaudi*, than with the eggs of *E. kuehniella.* A low fecundity (73 ± 10.1 eggs per female) was found with a mixed *E. kuehniella* + *M. feytaudi* diet. This low fecundity may be further related with *I. rondensis*'s voltinism. Multivoltine species usually have a high fecundity, up to 1000 eggs/female (Hodek & Honěk, 1996). In contrast, univoltine species, such as *Scymnus sinuanodulus* Yu & Yao (Lu & Montgomery, 2001), show a lower fecundity in comparison to its multivoltine congeners.

Mating and oviposition were observed with polygamous groups of *I. rondensis* in laboratory conditions. Polygamy is quite common in Coccinellidae and usually increases fecundity (Hodek & Ceryngier, 2000). In our study such was not observed, but mating frequency was found to be correlated with fecundity. Also, although females have a spermatheca (Raimundo *et al*., 2006), it was observed that oviposition stopped after males died. *I. rondensis* females may thus require a constant supply of sperm to fertilize new eggs, as observed in other species of insects (Hosken & Stockley, 2003).

Life cycle synchronization with Matsucoccus feytaudi

In two years of field surveys, larvae of *I. rondensis* were only observed in February-May, with a peak in April, two months after the flight peak of *M. feytaudi*. The association between the number of *I. rondensis* larvae and *M. feytaudi* males with a two months lag-time provides further evidence of life cycle synchronization between the two species. Several specialized ladybird species present a life cycle synchronization with their prey: e.g. *Sasajiscymnus tsugae* (Sasaji and McClure) with *Adelges tsugae* (Annand) (Cheah & McClure, 2000), *Rodolia cardinalis* (Mulsant) with *Icerya purchasi* Maskell (Soares *et al*., 1999) and *Aiolocaria hexaspilota* (Hope) with *Gastrolina depressa* Baly (Chang *et al.*, 1992).

Based on our findings, we predict that *I. rondensis* starts its reproduction between December and February at low temperatures. In laboratory, *I. rondensis* was observed to lay eggs at 10-12ºC, but at this temperature egg hatching takes about 50 days. Below 8ºC embryonic development is arrested, although eggs may still survive at 4ºC for about two months. Thus, even if some eggs are laid too early in winter, egg hatching will only occur around February, when *M. feytaudi* reproduction peaks (Branco *et al.*, 2001; Foldi, 2004).

After oviposition starts it can continue for some months as long as prey is available. Since at 22-25ºC *I. rondensis* eggs take less than 9 days to hatch, availability of *M. feytaudi* eggs to neonate larvae is guaranteed until March-April. *M. feytaudi* stops laying eggs in late April, early May, which justifies the absence of larvae in the field after late May.

At temperatures above 28-30ºC, egg mortality increases steeply. This evidences the evolution of a reproductive obligatory diapause in the summer, when temperatures above 30ºC are frequent in this region. Such a period corresponds to the aestivation of second instar larvae of *M. feytaudi* (Foldi, 2004). Beetles may be able to feed on pollen and honeydews to survive this period.

Pre-imaginal egg consumption

During its pre-imaginal development, a single *I. rondensis* larva can eat around 2000 eggs, which corresponds to 5-7 egg batches of *M. feytaudi*. This is an average value compared to those found for other ladybirds successfully used as biological control agents for scale insects; e.g. 3500 eggs for *Cryptolaemus montrouzieri* Mulsant (Mani & Krishnamoorthy, 1990), 8500 eggs for *Exochomus quadripustulatus* L. (Sengonca & Arnold, 2003), 600 eggs for *Pullus mediterraneus* Fabr. (Ba M'hamed & Chemseddine, 2001) and 950 eggs for *Chilocorus bipustulatus* L. (Santos *et al*., 2009).

Conclusions

Specialization in ladybirds is often food-driven and partly achieved by an adaptation to the seasonality of the prey's abundance, which allows the predator oviposition to match with the prey availability (Sloggett & Majerus, 2000).

The life history traits of *I. rondensis* indicate synchronization with the prey's life-cycle, notably through a long reproductive diapause, linked with the evolution of prey-specialization. Although fecundity is not very high in this species (ca. 70 eggs/female), each larva can eat almost 2000 eggs of *M. feytaudi* during its lifetime which is similar to those observed on other successful biological control agents. All together, these traits make *I. rondensis* a good candidate for biological control of *M. feytaudi*.

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3.7. References

Ba M'Hamed, T. & Chemseddine, M. (2001) Assessment of temperature effects on the development and fecundity of *Pullus mediterraneus* (Col., Coccinellidae) and consumption of *Saissetia oleae* eggs (Hom., Coccoida). *Journal of Applied Entomology* **125**, 527-531.

Barratt, B., Howarth, F., Withers, T., Kean, J. & Ridley, G. (2010) Progress in risk assessment for classical biological control. *Biological Control* **52**, 245-254.

Berkvens, N., Bonte, J., Berkvens, D., Tirry L. & De Clercq, P. (2008) Influence of diet and photoperiod on development and reproduction of European populations of *Harmonia axyridis* (Pallas) (Coleoptera : Coccinellidae). *Biocontrol* **53**, 211-221.

Branco, M., Brito, O., Jactel, H., Mendel, Z., Franco, J. & Pellizzari, G. (2001) Seasonal history of the Maritime Pine Bast Scale *Matsucoccus feytaudi* Ducasse (Hemiptera: Matsucoccidae) in Portugal. *Bollettino di Zoologia Agraria e Bachicoltura* **33**, 319-329.

Branco, M., Franco, J., Dunkelblum, E., Assael, F., Protasov, A., Ofer, D. & Mendel, Z. (2006) A common mode of attraction of larvae and adults of insect predators to the sex pheromone of their prey (Hemiptera: Matsucoccidae). *Bulletin of Entomological Research* **96**, 179-186.

Branco, M., van Halder, I., Franco, J., Constantin, R. & Jactel H. (2011) Prey sex pheromone as kairomone for a new group of predators (Coleoptera: Dasytidae, *Aplocnemus* spp.) of pine bast scales. *Bulletin of Entomological Research* **101**, 667-674.

Brockwell, P.J. & Davis, R.A. (2002) *Introduction to time series and forecasting*. Taylor & Francis, US.

Burban, C., Petit, R.J., Carcreff, E. & Jactel, H. (1999) Rangewide variation of the maritime pine bast scale *Matsucoccus feytaudi* Duc. (Homoptera: Matsucoccidae) in relation to the genetic structure of its host. *Molecular Ecology* **8**, 1593-1602.

Chang, K-S, Morimoto, N. & Nakasuji, F. (1992) A Study of the Relationship between Population Density and Mortality for the Walnut Leaf Beetle, *Gastrolina depressa*. *Chinese Journal of Entomology* **12**, 201-212.

Cheah, C.A.J. & McClure, M.S. (2000) Seasonal synchrony of life cycles between the exotic predator, *Pseudoscymnus tsugae* (Coleoptera: Coccinellidae) and its prey, the hemlock woolly adelgid *Adelges tsugae* (Homoptera: Adelgidae*). Agricultural and Forest Entomology* **2**, 241-251.

Covassi, M. & Binazzi, A. (1992) Primi focolai di *Matsucoccus feytaudi* Duc. nella Liguria orientale (Homoptera: Margarodidae). *Redia* **75**, 453-466.

Damos, P. & Savopoulou-Soultani, M. (2012) Temperature-Driven Models for Insect Development and Vital Thermal Requirements. *Psyche* **2012**,1-13.

Danks, H.V. (2002) The range of insect dormancy responses. *European Journal of Entomology* **99**, 127-142.

De Clercq, P., Bonte, M., Van Speybroeck, K., Bolckmans, K. & Deforce, K. (2005) Development and reproduction of *Adalia bipunctata* (Coleoptera : Coccinellidae) on eggs of *Ephestia kuehniella* (Lepidoptera: Phycitidae) and pollen. *Pest Management Science* **61**, 1129-1132.

Dixon, A., Hemptinne, J-L. & Kindlmann, P. (1997) Effectiveness of ladybirds as biological control agents: patterns and processes. *Entomophaga* **42**, 71-83.

Dixon, A. (2000) *Insect predator-prey dynamics: ladybird beetles and biological control*. Cambridge University Press, USA.

Fabre, J-P., Menassieu, P., Foing, J-J. & Chalon, A. (2000) Biology and ecology of *Elatophilus nigricornis* Zetterstedt (Hemiptera Anthocoridae) predator of *Matsucoccus feytaudi* Ducasse (Homoptera Matsucoccidae) in the South-East of France. *Annals of Forest Science* **57**, 777-792.

Foldi, A.I. (2004) The Matsucoccidae in the Mediterranean basin with a world list of species (Hemiptera: Sternorrhyncha: Coccoidea). *Annales de la Société Entomologique de France* **40**, 145-168.

Hodek, I. & Ceryngier, P. (2000) Sexual activity in Coccinellidae (Coleoptera): a review. *European Journal of Entomology* **97**, 449-456.

Hodek, I. & Honěk, A. (1996) *Ecology of Coccinellidae*. Dordrecht, The Netherlands, Kluwer Academic Publishers, Netherlands.

Hodek, I. & Honěk, A. (2009) Scale insects, mealybugs, whiteflies and psyllids (Hemiptera, Sternorrhyncha) as prey of ladybirds. *Biological Control* **51**, 232-243.

Hodek, I. & Okuda, T. (1993) A weak tendency to obligatory diapause in *Coccinella septempunctata* from southern Spain. *Entomophaga* **38**, 139-142.

Hosken, D.J. & Stockley, P. (2003) Benefits of Polyandry: A Life History Perspective pp. 173-194 in Macintyre, R. & Clegg, M. (Eds.) *Evolucionary Biology*. Springer, US.

Jactel, H., Ménassieu, P. & Burban, C. (1996) Découverte en Corse de *Matsucoccus feytaudi* Duc (Homoptera: Margarodidae), cochenille du pin maritime. *Annals of Forest Science* **53**,145-152.

Jactel, H. & Ménassieu, P. (2005) La cochenille du pin maritime *Matsuccocus feytaudi*: nouvelles données épidémiologiques et perspectives de lutte. *Forêt Méditerranéenne* **26**, 37-46.

Katsoyannos, P., Kontodimas, D.C. & Stathas, G. (2005) Summer diapause and winter quiescence of *Hippodamia (Semiadalia) undecimnotata* (Coleoptera: Coccinellidae) in central Greece. *European Journal of Entomology* **102**, 453.

Koštál, V. (2006) Eco-physiological phases of insect diapause. *Journal of Insect Physiology,* **52** 113-127.

Lu, W. & Montgomery, M.E. (2001) Oviposition, development, and feeding of *Scymnus* (*Neopullus*) *sinuanodulus* (Coleoptera: Coccinellidae): a predator of *Adelges tsugae* (Homoptera: Adelgidae). *Annals of the Entomological Society of America* **94**, 64-70.

Mani, M. & Krishnamoorthy, A. (1990) Evaluation of the exotic predator *Cryptolaemus montrouzieri* Muls. (Coccinellidae, Coleoptera) in the suppression of green shield scale, *Chloropulvinaria psidii* (Maskell) (Coccidae, Hemiptera) on guava. *Entomon* **15**, 45-48.

Mendel, Z., Assael, F. & Dunkelblum, E. (2004) Kairomonal attraction of predatory bugs (Heteroptera: Anthocoridae) and brown lacewings (Neuroptera: Hemerobiidae) to sex pheromones of *Matsucoccus* species (Hemiptera: Matsucoccidae). *Biological Control* **30**, 134-140.

Raimundo, A., Canepari, C., Mendel, Z., Branco, M. & Franco, C. (2006) *Iberorhyzobius* Raimundo & Canepari gen. nov., for *Coccidula rondensis* Eizaguirre (Coleoptera: Coccinellidae). Zootaxa **1312**, 49-58.

Riom, J. & Gerbinot, B. (1977) Étude biologique et écologique de la cochenille du pin maritime *Matsucoccus feytaudi* Ducasse, 1942 (Coccoidea, Margarodidae, Xylococcinae) dans le Sud-Est de la France. 1. Biologie générale et phénologie. *Annales de Zoologie Écologie Animale* **9**,11-50.

Rodrigo, E., Catala-Oltra, M., Perez-Laorga, E. & Baena, M. (2013) Monitoring of *Matsucoccus feytaudi* (Hemiptera: Matsucoccidae) and its natural enemies in Spain using sticky traps and pheromone traps. *European Journal of Entomology* **110**, 301-310.

Santos, S.A., Pereira, J., Torres, L. & Nogueira, A. (2009) Voracity of coccinellid species on different phenological stages of the olive pest *Saissetia oleae* (Homoptera, Coccidae). *Applied Ecology and Environmental Research* **7**, 359-365.

Santos, S.A., Pereira, J., Torres, L. & Nogueira, A. (2010) Seasonal synchrony between *Saissetia oleae* and coccinellid species in Portuguese olive groves in different management systems. *Bulletin of Insectology* **63**, 51-57.

Schvester, D. & Fabre, J-P. (2001) Le dépérissement du pin maritime des Maures et de l'Estérel provoqué par *Matsucoccus feytaudi* Ducasse (Homoptera, Matsucoccidae), connaissances acquises de 1964 à 1990. II. Dynamique des populations de la Cochenille et ses facteurs. *Forêt méditerranéenne* **22**, 303-317.

Sengonca, C. & Arnold, C. (2003) Development, predation and reproduction by *Exochomus quadripustulatus* L. (Coleoptera: Coccinellidae) as predator of *Pulvinaria regalis* Canard (Homoptera : Coccidae) and its coincidence with the prey in the field. *Journal of Plant Diseases and Protection* **110**, 250-262.

Sloggett, J. & Majerus, M. (2000) Habitat preferences and diet in the predatory Coccinellidae (Coleoptera): an evolutionary perspective. *Biological Journal of the Linnean Society* **70**, 63-88.

Soares, A., Elias, R. & Schanderl, H. (1999) Population dynamics of *Icerya purchasi* Maskell (Hom; Margarodidae) and *Rodolia cardinalis* Mulsant (Col; Coccinellidae) in two citrus orchards of São Miguel Island (Azores). *Boletín de Sanidad Vegetal Plagas* **25**, 459-467.

Stathas, G.J., Eliopoulos, P.A., Kontodimas, D.C. & Siamos, D.T. (2002) Adult morphology and life cycle under constant temperatures of the predator *Rhyzobius lophanthae* Blaisdell (Col., Coccinellidae). *Anzeiger für Schädlingskunde* **75**,105-109.

Tavares, C., Jactel, H., van Halder, I., Mendel, Z. & Branco, M. (2014). A case of ecological specialization in ladybirds: *Iberorhyzobius rondensis* (Coleoptera: Coccinellidae), potential biocontrol agent of *Matsucoccus feytaudi* (Hemiptera: Matsucoccidae). *Bulletin of Entomological Research* **104**, 367-375.

Toccafondi, P., Covassi, M. & Pennacchio, F. (1991) Studies on the predator complex of Matsucoccus Cock. occurring in Italy. II. Bio-ethological notes on *Rhyzobius chrysomeloides* (Herbst) in the pine woods of Liguria (Coleoptera: Coccinellidae). *Redia* **74**, 599-620.

Van Lenteren, J., Bale, J., Bigler, F., Hokkanen, H. & Loomans, A. (2006) Assessing risks of releasing exotic biological control agents of arthropod pests. *Annual Review of Entomology* **51**, 609-634.

IV. Phylogeography of the ladybird *Iberorhyzobius rondensis*, a potential biological control agent of the invasive pine bast scale *Matsucoccus feytaudi*

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4.1. Abstract

Understanding the genetic structure of natural enemies is an important step to develop efficient biocontrol programs. The ladybird beetle *Iberorhyzobius rondensis* (Coleoptera: Coccinellidae) from the Iberian Peninsula, is a specialized predator of the invasive maritime pine bast scale *Matsucoccus feytaudi* (Hemiptera: Matsucoccidae), and it is a potential biological control agent for that insect. *M. feytaudi* is specialized on *Pinus pinaster*. The beetle is also restricted to this habitat. Genetic structure of *I. rondensis* populations was analysed with the barcode region (COI). It revealed two main refugia areas for the beetle in Iberian Peninsula. Comparative phylogeography of the three trophic levels, plant-herbivore-predator is discussed. Similar population structure was found for the prey and to some extent for the pine. Indications are given on where to collect the beetles for their use in biocontrol of *M. feytaudi*, in order to obtain the highest genetic diversity and match with the origin of the invasive prey.

Key-words: invasive species; mtDNA; *Pinus pinaster*; Matsucoccidae; Coccinellidae

4.2. Introduction

Invasive alien species presently constitute a major worldwide threat to biodiversity on the planet (Shea & Chesson, 2002) and can generate severe ecological and economic impacts (Perrings *et al.*, 2002; Kenis *et al*., 2009). The lack of natural enemies of exotic species in the invaded region is considered one of the main causes of their establishment, spread and impact (Sax *et al*., 2007). By introducing natural enemies, such as predators and parasitoids, from the native region of the pest in its invaded area, classical biological control programmes try to achieve a self-regulatory control of the pest (Hoelmer & Kirk, 2005).

Molecular markers are increasingly being used in biological control studies to identify the target pest species and its natural enemies (Hoelmer & Kirk, 2005; Gariepy *et al*., 2007). In addition, molecular data is also being used to determine the areas of origin of invasive species (Valade *et al*., 2009; Lees *et al*., 2011) and to search for natural enemies in the native region (Hernandez-Lopez *et al*., 2011; Gebiola *et al*., 2013). It is expected that natural enemies, which came from the areas of origin of the pest, are more specific and efficient, as a result of long periods of co-evolution (Roderick & Navajas, 2003; Hufbauer & Roderick, 2005).

The maritime pine bast scale, *Matsucoccus feytaudi* Ducasse (Homoptera: Matsucoccidae) is a recently invasive species in the South eastern part of France, Corsica and Italy (Covassi *et al*., 1991; Jactel *et al*., 1996). It is a highly specialized sap-sucker insect, feeding exclusively on the tree trunk of maritime pine, *Pinus pinaster* Aiton (Pinales: Pinaceae) (Foldi, 2004). The bast scale is endemic to the Iberian Peninsula and North Africa, and mitochondrial data has shown three distinct lineages occurring in different geographical areas: Western and Central Iberian Peninsula; Andalusia region and the Atlas Mountains (Burban *et al.*, 1999). In its native range *M. feytaudi* has several natural predators, some specialized on this prey; including, *Elatophilus crassicornis* Reuter (Heteroptera: Anthocoridae), *Hemerobius stigma* Stephens (Neuroptera: Hemerobiidae), *Aplocnemus brevis* Rosenhauer (Coleoptera: Dasytidae) and *Iberorhyzobius rondensis* (Eizaguirre) (Coleoptera: Coccinellidae) (Mendel *et al*., 2004; Branco *et al*., 2006a). In the invaded range, other natural enemies are present; e.g. *Elatophilus nigricornis* (Zetterstedt), predator of *Matsucoccus pini* (Green), and the generalist beetle *Rhyzobius chrysomeloides* (Herbst) (Covassi *et al*., 1991; Fabre *et al.*, 2000), but none of them have proved effective enough to slow the spread of the invasive scale insect. The release of native natural enemies of *M. feytaudi* in its invaded range has been therefore envisaged as a possible solution for biocontrol (Jactel & Menassieu, 2005).

Iberorhyzobius rondensis is a recently discovered species (Raimundo *et al.*, 2006), from the Iberian Peninsula (Tavares *et al.*, 2014). This ladybird is highly specialized on the pine bast scale. It occurs only in pine woodlands of *Pinus pinaster*, the habitat of its prey (Tavares *et al.*, 2014) and cannot complete its life cycle without egg-masses of *M. feytaudi* as feeding resources. The beetles are highly attracted to the sex pheromone of the prey *M. feytaudi*, especially the larval instars (Branco *et al.*, 2006b). Therefore *I. rondensis* is regarded as a potential biocontrol agent against *M. feytaudi*.

According to Smith et al. (2011) the extent to which co-distributed species share a common biogeographic history depends on the strength and specificity of their ecological relationships. Thus, it is expected that specialized natural enemies display similar phylogeographic patterns to that of their host or prey (Barbosa *et al.*, 2012). Most of the studies on the genetic structure of the third trophic level are focused on parasitoids (e.g. Lozier *et al.*, 2008; Hernandez-Lopez *et al.*, 2011; Nadel *et al.*, 2012; Gebiola *et al.*, 2013) but only few studies have addressed predators (e.g. Coll *et al.*, 1994; Omondi *et al.*, 2011). Given the high degree of prey and habitat specialization of the ladybird beetle *I. rondensis* (Tavares *et al.*, 2014), and the strict species-specific association between *M. feytaudi* and *P. pinaster* (Burban & Petit, 2003), the phylogeographic pattern of the predator in the Iberian Peninsula is expected to match that of its prey and prey’s host plant.

Mitochondrial DNA has been widely used in phylogeographic studies due to extensive intraspecific polymorphism, rapid mutation rate, maternal inheritance and absence of recombination (Avise, 2000). Mitochondrial genes have recently been used in several genetic studies of ladybird beetles (e.g. Brown *et al.*, 2008; Gregory *et al.*, 2003; Greenstone *et al.*, 2011; Kim *et al.*, 2012).

In this study we used DNA sequence data to reconstruct the phylogeography of *I. rondensis* in the Iberian Peninsula and to compare it with that of its prey, *M. feytaudi*, and host plant, *P. pinaster*. Our main objective was to provide information to allow decision making for the biocontrol of the bast scale, and especially for the selection of areas from which the predators should be collected for rearing and release (Roderick & Navajas, 2003; Lozier *et al*., 2008).

Our results show that *I. rondensis* has a similar phylogeographic pattern to that of its prey. In addition, we identify areas as sources for ladybird specimens to be potentially used in biocontrol programs.

4.3. Material and Methods

Insect sampling

Twelve locations were sampled from 6 different regions of the Iberian Peninsula (Table 1).

In each location at least three different stands of *P. pinaster*, and 30 to 50 trees per stand were surveyed. Beetles were attracted with a rubber dispenser impregnated with 200 µg of the female sex pheromone of *M. feytaudi* (UPMC, INRA-Versailles, France). The lure was pinned to the trunk 1 m above the ground level where the bark surface had been smoothed to produce an 'arena' which allowed for the detection of *I. rondensis* larvae. The arena was monitored for 1 hour since the larvae respond quickly to the kairomone (Branco *et al*., 2006a; Branco *et al.,* 2006b). Only one beetle per tree was collected in order to prevent the collection of siblings, and immediately killed and stored in 98% alcohol. Sampling was carried out in 2010 - 2012, in the months of March, April and May, which corresponds to the peak period of *I. rondensis* larval activity (Tavares *et al*., 2014).

A total of 104 ladybird beetles were collected (all larvae except for three adults). Due to its geographical proximity and low number of individuals, Sierra d'Espada and Cova de l' Aigua were grouped together. Similarly, the three locations in Algarve were grouped in a single population (Table 1). Usually individuals from the same populations were no more than 130 km apart, except in Sintra and Setúbal (two localities separated by a large estuary).

Table 1. Sampled regions and locations, with the different populations and corresponding geographic coordinates. Nucleotide (π) and haplotype (Hd) diversity and standard deviation (SD), for each population, sampled for COI. Haplotype richness was calculated with the rarefaction method.

Regions	**Locations**	**Populations**	**Geographic coordinates (Lat, Long)**	**Samples**	**Haplotypes**	**Haplotype richness**	**(Hd+SD)**	**(π+SD)**	**Haplotype distribution**
North of Portugal	Lousã	1	40.07, -8.22	16	4	2.0 ± 0.60	0.62 ± 0.096	0.07 ± 0.0419	H1 (9), H3 (5), H4 (1), H5 (1)
	Vila Real	1	41.28, -7.86	16	4	1.6 ± 0.62	0.35 ± 0.148	0.016 ± 0.0133	H3 (1), H11 (1), H26 (13), H27 (1)
Center of Portugal	Setúbal	1	38.57, -9.14	12	2	1.8 ± 0.40	0.53 ± 0.08	0.04 ± 0.0269	H2 (7), H3 (5)
	Sintra	1	38.80, -9.45	11	5	2.4 ± 0.60	0.76 ± 0.107	0.065 ± 0.0402	H1 (1), H2 (1), H10 (3), H19 (5), H20 (1)
South Portugal (Algarve)	Vila Real St. Ant.	1	37.18, -7.41	5	2	1.7 ± 0.46	0.47 ± 0.132	0.062 ± 0.0391	H1 (1), H2 (4)
	Vila Bispo		37.08, -8.92	4					H1 (1), H2 (3)
	Odeceixe		37.38, -8.78	1					H1 (1)
Central System	Sierra de Gredos	1	40.38, -4.58	17	13	2.9 ± 0.32	0.96 ± 0.033	0.039 ± 0.0256	H6 (1), H7 (1), H8 (2), H9 (1), H10 (2), H11 (3), H12 (1), H13 (1), H14 (1), H15 (1), H16 (1), H17 (1), H18 (1)
Iberian System	Sierra d'Espadá	1	40.01, -0.38	2	4	3.0 ± 0.00	1.00 ± 0.177	0.132 ± 0.0939	H11 (1), H21 (1)
	Cova de l'Aigua	1	38.86, -0.11	2					H22 (1), H23 (1)
Betic System	Ronda	1	36.58, -5.19	3	2	2.0 ± 0.00	0.67 ± 0.314	0.126 ± 0.1018	H24 (1), H25 (1)
	Sierra Nevada	1	37.08, -3.52	15	6	2.5 ± 0.56	0.83 ± 0.064	0.07 ± 0.0422	H28 (4), H29 (5), H30 (2), H31 (2), H32 (1), H33 (1)

Molecular procedures

Genetic variation of *I. rondensis* was examined by amplifying the barcode fragment (658 bp) of the mitochondrial gene, cytochrome oxidase c subunit 1 (COI) (Hebert & Gregory, 2005). The whole genomic DNA was extracted from the abdomen of individual specimens preserved in alcohol, using a Nucleospin®Tissue XS Kit (Macherey-Nagel, Düren, Germany). DNA was amplified with the COI primers LCO1490 and HCO2198 (Folmer *et al.*, 1994). Reactions were performed in 25 µl volumes containing 2 µl of DNA template (concentration around 30ng/µl), 1x PCR Buffer without $MgCl_2$ (Sigma, Saint Louis, MS, USA), 2.5 mM MgCl2, 400 µM of each dNTP, 1 U REDTaq Genomic DNA polymerase (Sigma, Saint Louis, MS, USA), and 1µM each of the forward and reverse primers. PCR was carried out using a 2720 Thermal Cycler (Applied Biosystems, Foster City, California, USA) with the following settings: 5 min at 94°C; followed by five cycles of 30 s at 94°C, 40 s at 47°C, and 1 min at 72°C; followed by a further 40 cycles of 30 s at 94°C, 40 s at 52°C, and 1 min at 72°C; and a final extension of 5 min at 72°C. Successful amplification was confirmed by agarose gel electrophoresis and PCR products were subsequently cleaned by using a Nucleospin® Gel and PCR Clean-up Kit (Macherey-Nagel, Düren, Germany). PCR fragments were then sequenced in both directions using the ABI Prism® BigDye® Terminator v3.1 Cycle Sequencing Kit (Applied Biosystems, Foster City, California, USA). Sequencing reactions were purified by ethanol precipitation, loaded on a 3500 Genetic Analyzer (Applied Biosystems, Foster City, California, USA) and analyzed with Sequencing Analysis v5.4 software. Sequences were aligned by ClustalW Multiple alignment in BioEdit 7.0.9.0 (Hall, 1999) and primers sequences were removed from the analysis. Ambiguities were edited by eye. COI sequences were translated by using the EMBOSS-Transeq website (http://www.ebi.ac.uk/Tools/emboss/transeq/index.html) to confirm the absence of nuclear pseudogenes (Song *et al.*, 2008). All sequences have been deposited in GenBank (KJ637343 - KJ637446). DNA barcodes have been deposited in the Published Projects section of the Barcode of Life Data systems (BOLD) project code: IBERH (www.barcodinglife.org). Information on specimen vouchers (field data and GPS coordinates) and sequences (nucleotide composition, trace files) can be found in this project. The *Iberorhyzobius rondensis* dataset is registered under DOI number dx.doi.org/10.5883/DS-RONDEN.

Data analyses

Because the number of beetles studied differed between the different populations, a rarefaction method was used to compare the haplotype diversity across populations using the Rarefaction Calculator (http://www.biology.ualberta.ca/jbrzusto/rarefact.php) (Kalinowski, 2004). A correlation between number of samples and haplotypes was calculated. Haplotype (Hd) and nucleotide diversity (π) were estimated for each population (Table 1) with Arlequin 3.5 (Excoffier & Lischer, 2010). A parsimony haplotype network with 95% support (Templeton *et al.*, 1992) was constructed using TCS version 1.21 (Clement *et al*., 2000). Loops were removed, following the criteria suggested by Crandall and Templeton (1993): i) rare haplotypes are more likely to be found at the tip and more common haplotypes at interior nodes; ii) a singleton is more likely to be connected to haplotypes from the same population than to haplotypes from different populations. The genetic diversity of the different populations was visualized by plotting genetic data as pie charts on a map with *P. pinaster* and *M. feytaudi* distributions using ArcGIS 2012 (ESRI, 2011). Genetic structure was studied with a Spatial Analysis of Molecular Variance, which is based on a simulated annealing procedure that aims to maximize the proportion of total genetic variance due to differences between groups of populations (SAMOVA 1.0 (Dupanloup *et al*., 2002)). The program was run for 10 000 iterations for k = 2 to 7 (groups of populations) from each of 100 random initial conditions. Analyses were repeated 3 times for consistency. The genetic differentiation among groups was computed as genetic molecular distance between DNA sequences using pairwise differences. A Mantel test with 1000 permutations was performed to test if the genetic structure of the population follows isolation by distance model (Slatkin, 1993) using pairwise Fst values and straight-line geographical distances in km estimated by using Google Maps Distance Calculator. Neutrality tests Tajima's D test (Tajima, 1989) and Fu's Fs (Fu, 1997) test were used to test for selective neutrality and population equilibrium, with 1000 simulations. Since some populations had a very low number of sampled individuals, they were enclosed by geographic proximity and the neutrality tests were applied to these groups: Portugal (Vila Real, Lousã, Sintra, Setúbal, Algarve); Central System (Sierra de Gredos) and Betic System + Iberian System (Sierra Nevada, Sierra Ronda, Sierra d'Espadá and Cova de l'Aigua).

4.4. Results

A total of 33 different haplotypes were obtained, with 20 unique haplotypes (Table 1, Fig. 1). The highest haplotype diversity was observed in Sierra de Gredos, Sierra Nevada and the Iberian System, although in this last region only 4 individuals were sampled (Table 1). These results were confirmed after the rarefaction analysis. Haplotype diversity was not correlated with sampling effort ($r = 0.526$, $n = 9$, $P = 0.156$). The highest nucleotide diversity was found in the Betic system group (Ronda, Sierra Nevada), the Iberian System and Lousã (Table 1).

In the spatial analysis of molecular variance (SAMOVA) differentiation was maximized between four groups of populations and minimized between populations within these four groups ($\varphi_{CT} = 0.466$, $P = 0.013$) (Fig. 2). Parsimony network analysis separated populations in two main distinct groups: I) Western and Central Iberia (Portugal and Central System), and II) Eastern Iberia (Betic and Iberian Systems) (Fig. 1b). The ancestral haplotype, defined by the parsimony network analysis as H8, is originary from Sierra de Gredos populations, with two individuals represented. The haplotype H11 ($n = 5$), may also be considered an ancestral haplotype and it is shared between Sierra de Gredos (Central System), Sierra d'Espadá (Iberian System) and North Portugal. Only another haplotype is shared between Sierra de Gredos and Portugal (center): H10 ($n = 2$). The populations from Central System, Iberian System and Betic System are well separated. However haplotypes from Sierra de Ronda are split between Group I and II, respectively, H24 ($n = 2$) and H25 ($n = 1$) (Fig.1). The most shared haplotypes are found in Portugal: H1 ($n = 13$), H2 ($n = 15$), H3 ($n = 11$) and H26 ($n = 13$).

The Mantel test revealed a significant correlation between geographic distance and pairwise Fst ($r = 0.512$, $P = 0.011$). Values of Tajima's D test and Fu's Fs were negative for the Betic System and Sierra de Gredos ($D = -0.68$, $Fs = -1.013$ and $D = -2.06$, $Fs = -11.13$) but were only significant ($P < 0.05$) for Sierra de Gredos. Positive and non-significant values of Tajima's and Fu's F test were found for Portugal populations ($D = 0.6075$, $Fs = 1.11$).

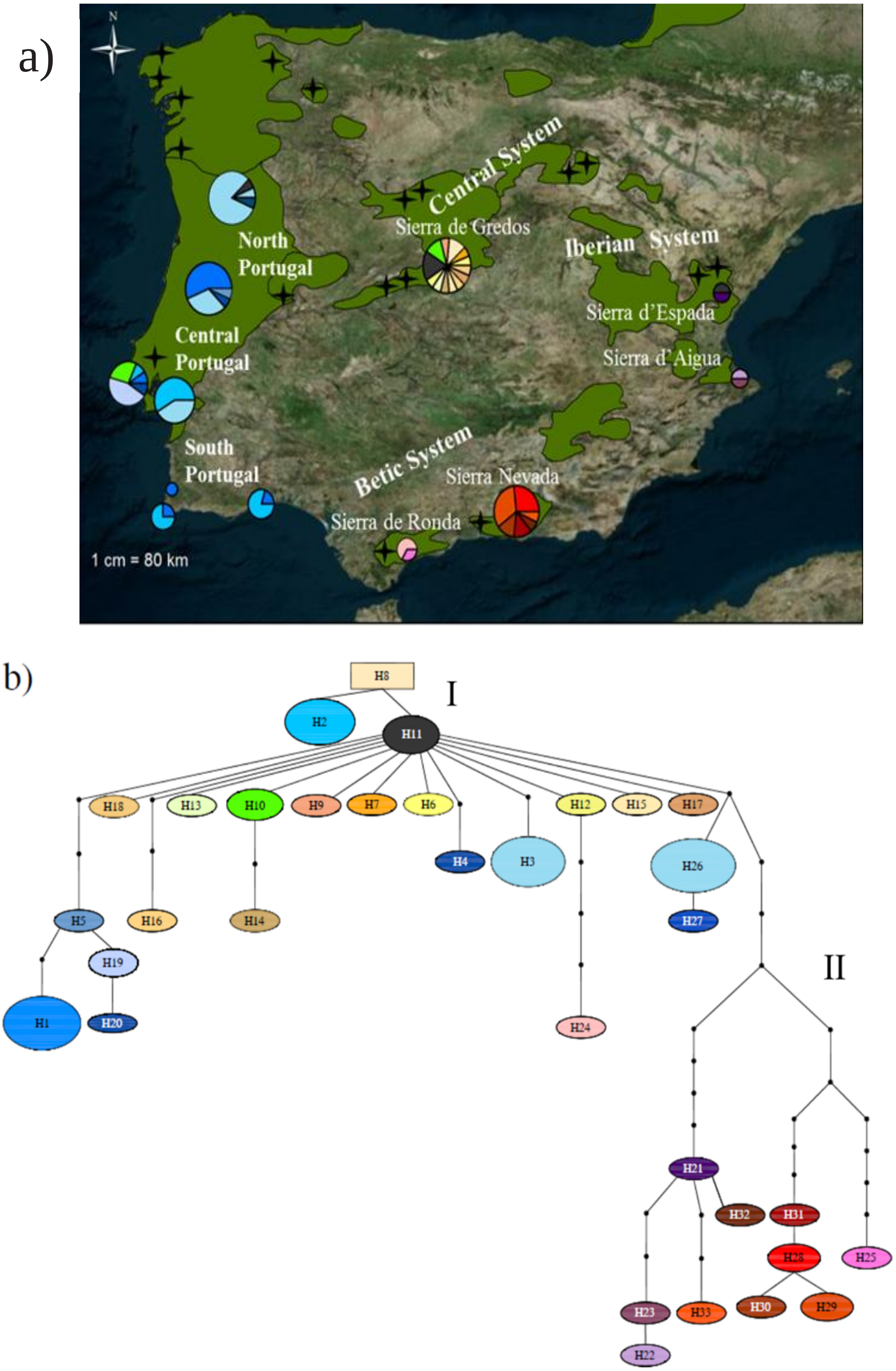
a)
N
Central System
Sierra de Gredos
Iberian System
Sierra d'Espada
Sierra d'Aigua
North Portugal
Central Portugal
South Portugal
Betic System
Sierra Nevada
Sierra de Ronda
1 cm = 80 km
b)
I
II
H8
H2
H11
H18
H13
H10
H9
H7
H6
H12
H15
H17
H4
H3
H26
H27
H5
H16
H14
H19
H1
H20
H24
H21
H32
H31
H28
H25
H23
H33
H30
H29
H22

Fig. 1. Geographical distribution of mtDNA haplotypes of 104 *Iberorhyzobius rondensis specimens*. Tones of red and rose correspond to the Betic Sytem, tones of violet to the Iberian System, tones of yellow to the Central System and tones of blue to Portugal. Group I; Western and Central Iberian comprising Atlantic Coast (Portugal), Sierra de Gredos and partially Sierra de Ronda and Group II: Eastern Iberian comprising Sierra Ronda, Sierra Nevada and Iberian System. **a)** Haplotype distribution of the 33 haplotypes found among the 6 regions sampled in the Iberian Peninsula. Size of pies is correlated with number of sampled individuals. Green layer corresponds to the *Pinus pinaster* distribution on Iberian Peninsula, black stars present the known distribution of *Matsucoccus feytaudi* populations (Burban *et al*., 1999*)*; **b)** COI statistical parsimony network (95%) of *Iberorhyzobius rondensis*. Haplotypes frequencies are represented by the size of the circles. Each line corresponds to a mutational step. Black dots represent possible haplotypes.

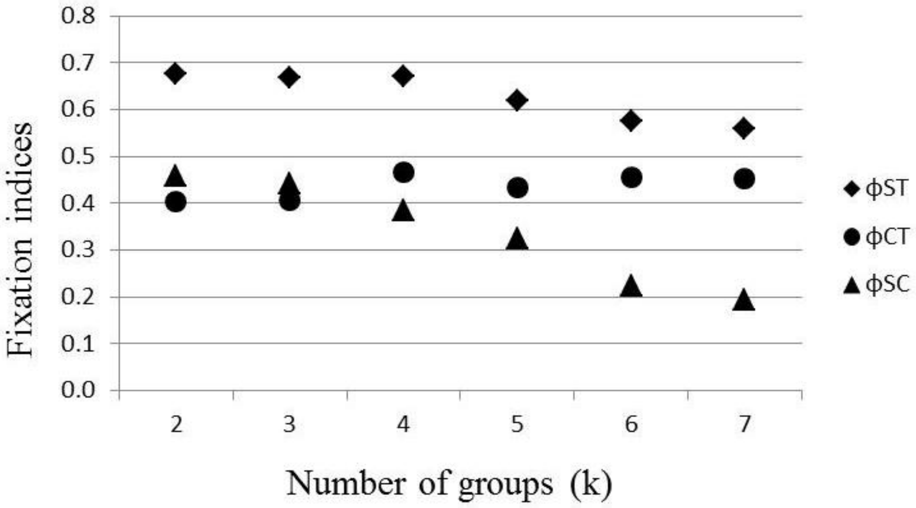

Fig. 2. Population structure results from both molecular datasets. Values of fixation indices (φ_{CT} = among groups differentiation; φ_{SC} = among populations within groups differentiation; φ_{ST} = total differentiation among populations) obtained by SAMOVA from a predefined number of groups (K) ranging from 2 to 7.

4.5. Discussion

Phylogeography of Iberorhyzobius rondensis

The mitochondrial DNA revealed geographically structured populations for *I. rondensis*. Also, a relatively high number of haplotypes (33) was found compared with other studies of ladybird species using COI (Greenstone *et al*., 2011; Kobayashi *et al*., 2011; Zakharov & Shaikevich, 2013). COI haplotype diversity varies greatly among coccinellid species: e.g. 15 haplotypes were found in 127 individuals of *Adalia bipunctata* (L.), an eurytopic predator, whereas 44 haplotypes were found in 70 individuals of *Henosepilachna pustulosa* (Kôno), a stenotopic and phytophagous species (Kobayashi *et al*., 2011; Zakharov & Shaikevich, 2013).

The highest genetic diversity was found in Sierra de Gredos and Sierra Nevada, where most of the unique haplotypes occur. A high genetic diversity was also found for the Iberian System, but that is probably due to the low number of samples (Table 1). Parsimony haplotype network shows two main groups separated by a high number of mutational steps: Western and Central Iberia and Eastern Iberia. Only one haplotype (H11) is shared between both groups. In addition, SAMOVA analysis, using geographical information, structured the populations in four groups due to the high number of unique haplotypes.

Independent refugia may explain this phylogeographic structure. For instance, Sierra de Ronda, together with Sierra Nevada are part of the Betic System, which is considered an important glacial refugium for several species (Gómez & Lunt 2007), with a high level of endemism (González-Martínez *et al.,* 2007). This may explain the presence of so many unique haplotypes in this region. However, since a low number of individuals were collected from Ronda and the Central System, interpretation on its phylogeography must be addressed with caution. Another important refugium is Central System, to which belongs Sierra de Gredos (Gómez & Lunt, 2007). This refugium is supported by the high polymorphism and genetic diversity of *I. rondensis* populations found on those areas.

Haplotypes from Portugal present a low genetic diversity and are closely related with the ones from Sierra de Gredos. Usually populations in the more recently colonized areas exhibit lower genetic diversity following rapid expansion of refugial populations leading to series of bottlenecks (Hewitt, 1996). Thus, we hypothesize that

Sierra de Gredos populations expanded their range to the Atlantic coast (Portugal). This is also supported by the demographic results: negative values of Tajima's D and Fu's F tests indicate population expansion in Sierra de Gredos (Fu, 1997; Tajima, 1989). Another hypothesis is that the restricted group of haplotypes in the Atlantic area may be evidence that this region acted as a refugium. This has been suggested for other Mediterranean species, such as *Tomicus destruens* (Vasconcelos *et al*., 2006), which also feeds on *P. pinaster* trees.

The Mantel test revealed isolation by distance. The fragmentation of *P. pinaster* forests could have prevented the spread of the beetles explaining this result. Indeed, until recent historical times, *P. pinaster* remained restricted to specific areas in the Iberian Peninsula, which would probably reflect the post-glacial refugia areas (Bucci *et al*., 2007). During the twentieth century large areas were planted with this pine species especially in the Northwest and the Center of Iberia accounting for its present distribution (Figueiral, 1995). Thus, the phylogeographic structure of *I. rondensis* populations could reflect the isolation of ancient *P. pinaster* natural forests, despite the recent afforestation programs. Still, the shared haplotypes H11 and H10 evidence some gene flow. A low capacity of dispersal of the beetle could also explain the isolation by distance pattern. Studies on the flight performances of this ladybird beetle would help to test this hypothesis.

Comparative phylogeography of the tritrophic interaction

Matsucoccus feytaudi phylogeography has been studied using RFLP fragments of COI + COII and cytB + 12S rDNA, and 22 mitotypes were found (Burban *et al*., 1999). Although the genetic markers used were partly different, the predator *I. rondensis* shows a remarkably similar phylogeographical pattern with that of its prey *M. feytaudi* (Burban *et al*., 1999) and that of the prey's host, *P. pinaster* (Carrión *et al*., 2000; Salvador *et al*., 2000; Burban & Petit, 2003; Bucci *et al*., 2007; González-Martínez *et al*., 2007) (Fig. 3). A comparison across the phylogeography of the three trophic levels highlights some common patterns:

i) *Western and Central Iberian Peninsula* group*:* It includes the populations of *I. rondensis* from Sierra de Gredos and Portugal (Fig. 3c), which match the group of *M. feytaudi* found in Portugal and the Central System (Burban *et al*., 1999) (Fig 3b). This lineage presents high polymorphism and is considered a center of origin for the bast scale. The *M. feytaudi* group present in Portugal was considered less polymorphic than the one of Central System which suggested an expansion to Portugal (Burban *et al.*, 1999). However for *P. pinaster*, the Central System is considered a zone of admixture of divergent lineages from different refugia (Carrión *et al.*, 2000; Salvador *et al.*, 2000; Bucci *et al.*, 2007) (Fig. 2a). Bucci *et al.* (2007) suggested that Portugal is an Atlantic refugium for *Pinus pinaster*.

ii) *Eastern Iberian Peninsula group.* The *M. feytaudi* group in this area is constituted by populations from Málaga and Granada (Fig. 3b), which correspond to the Sierra de Ronda and Sierra Nevada populations of *I. rondensis* (Fig. 3c). No genetic information is available for populations of *M. feytaudi* from the Iberian System. The Betic System is also considered a refugium for *P. pinaster* (Fig 3a), supported by several authors (Salvador *et al.*, 2000; Burban & Petit, 2003; Bucci *et al.*, 2007; González-Martínez *et al.*, 2007). Carrión *et al.* (2000) suggested that Sierra de Ronda and Sierra Nevada were different refugia areas of *P. pinaster*, which may explain the differences found between the two *I. rondensis* populations from these two mountain ranges. The Iberian System is considered another refugium of *P. pinaster* (Carrión *et al.*, 2000; Salvador *et al.*, 2000), from where populations migrated to the center and south of Iberia (Fig.2a). It is possible that the Iberian System, may also have been a refugial area for *I. rondensis*, given the polymorphism and distribution of the haplotypes found (Fig.1).

In conclusion, the three trophic-linked species, *P. pinaster*, *M. feytaudi* and *I. rondensis*, share, to some extent, the same phylogeographic pattern in the Iberian Peninsula. In particular, the phylogeography of the predator is well explained by the one of the prey, which agrees with our hypothesis of prey-predator phylogeographic match. There is a clear cleavage between south-eastern of Spain and the rest of Iberian Peninsula. The Betic system was a shared refugium for the 3 species.

Since we only used a fragment of the mtDNA, this pattern should be confirmed with nuclear markers. Further, it would be quite interesting to see whether the ladybird beetle is present in the Atlas region (Morocco), where a different lineage of *M. feytaudi* and *P. pinaster* occurs (Burban *et al.*, 1999; Burban & Petit, 2003).

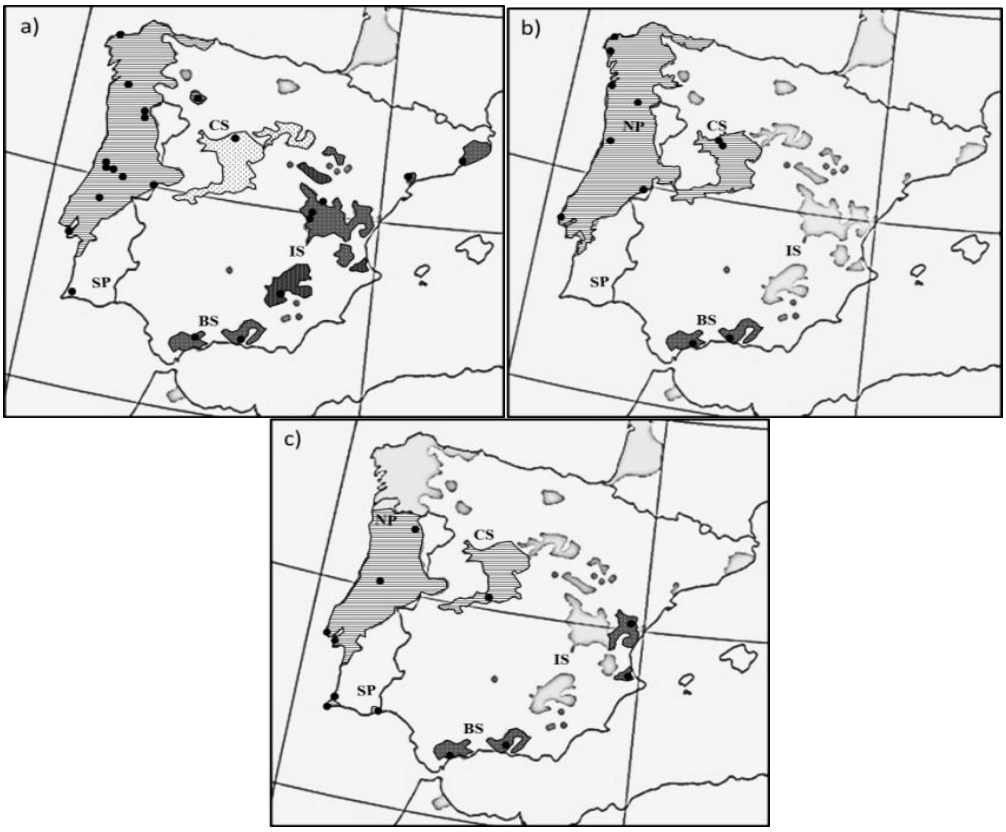

Fig. 3. Distribution maps of maritime pine (*Pinus pinaster*) - EUFORGEN 2009, www.euforgen.org - with the main genetic groups of the 3 trophic system: *Pinus pinaster – Matsucoccus feytaudi – Iberorhyzobius rondensis*.

a) *Pinus pinaster* (Bucci *et al*., 2007); two main genetic groups with admixture in Central Spain based on 16 spatially interpolated haplotype frequencies from five chloroplast microsatellites, Western (horizontal lines) and Central Iberian (light pattern) and Eastern (dark pattern).

b) Distribution of *Matsucoccus feytaudi* mitotypes with RFLP fragments of COI + COII and cytB+ 12S rDNA (Burban *et al*., 1999), focusing on two phylogeographic lineages, Western and Central Iberian (horizontal lines) and Southern Iberian (dark pattern).

c) *Iberorhyzobius rondensis* distribution with the 2 major genetic lineages based on mtDNA: Western and Central Iberian (horizontal lines) and Eastern (dark pattern). The greyish area corresponds to the natural distribution of maritime pine in Iberian Peninsula. Black dots correspond to sampled areas. Regions: NP-North of Portugal; SP-South of Portugal; CS-Central System; BS – Betic System; IB-Iberian System.

Implications for biological control

Matsucoccus feytaudi has expanded to France, Italy and Corsica, and these populations present only a few haplotypes, which originated from the Western and Central part of Iberia (Burban *et al*., 1999). Apparently the predator beetle has not yet followed its prey's expansion. Hence, when considering the use of *I. rondensis* for biocontrol of *M. feytaudi* in its new range, two important points should be taken into consideration: i) laboratory rearing colonies to be used in biocontrol should have a high genetic diversity (Roderick & Navajas, 2003; Hufbauer & Roderick, 2005), and ii) the ladybirds to be used in biocontrol in the invaded areas should be collected in the same native areas as their invasive prey (Hoelmer & Kirk, 2005). Because most haplotypes of *M. feytaudi* in the invaded regions are coming from the Central System and western of Iberian Peninsula (Burban *et al*., 1999), it would be advisable to use *I. rondensis* beetles collected from those areas. This would allow the capture of a high genetic diversity, and match *I. rondensis* haplotypes with the ones of *M. feytaudi* from the same region.

4.6. References

Avise, J.C. (2000) *Phylogeography: The History and Formation of Species*. Harvard University Press, Cambridge, Massachusetts.

Barbosa, A.M., Thode, G., Real, R., Feliu, C. & Vargas, J.M. (2012) Phylogeographic Triangulation: Using Predator-Prey-Parasite Interactions to Infer Population History from Partial Genetic Information. *PloS ONE* **11**, 1-5.

Branco, M., Franco, J.C., Dunkelblum, E., Assael, F., Protasov, A., Ofer, D. & Mendel, Z. (2006a) A common mode of attraction of larvae and adults of insect predators to the sex pheromone of their prey (Hemiptera: Matsucoccidae). *Bullettin of Entomological Research* **96**,179-185.

Branco, M., Lettere, M., Franco, J.C., Binazzi, A. & Jactel, H. (2006b) Kairomonal Response of Predators to Three Pine Bast Scale Sex Pheromones. *Journal of Chemical Ecology* **32**, 1577-1586.

Brown, P., Adriaens, T., Bathon, H., Cuppen, J., Goldarazena, A, Hägg, T., Kenis, M., Klausnitzer, B., Kovář, I. & Loomans, A. (2008) *Harmonia axyridis* in Europe: spread and distribution of a non-native coccinellid. *BioControl* **53**, 5-21.

Bucci, G., González-Martínez, S.C., Le Provost, G., Plomion, C., Ribeiro, M.M., Sebastiani, F., Alía, R. & Vendramin, G.G. (2007) Range-wide phylogeography and gene zones in *Pinus pinaster* Ait. revealed by chloroplast microsatellite markers. *Molecular Ecology* **16**, 2137-2153.

Burban, C. & Petit, R.J. (2003) Phylogeography of maritime pine inferred with organelle markers having contrasted inheritance. *Molecular Ecology* **12,**1487-1495.

Burban, C., Petit, R.J., Carcreff, E. & Jactel, H. (1999) Rangewide variation of the maritime pine bast scale *Matsucoccus feytaudi* Duc. (Homoptera: Matsucoccidae) in relation to the genetic structure of its host. *Molecular Ecology* **8**, 1593-1602.

Carrión, J.S., Navarro, C., Navarro, J. & Munuera, M. (2000) The distribution of cluster pine (*Pinus pinaster*) in Spain as derived from palaeoecological data: relationships with phytosociological classification. *The Holocene* **10**, 243-252.

Clement, M., Posada, D. & Crandall, K.A. (2000) TCS: a computer program to estimate gene genealogies. *Molecular Ecology* **9**, 1657-1659.

Coll, M., de Mendoza, G. & Roderick, G.K. (1994) Population structure of a predatory beetle: the importance of gene flow for intertrophic level interactions. *Heredity* **72,** 228-236.

Covassi, M., Binazzi, A. & Toccafondi, P. (1991) Studies on the entomophagous predators of a scale of the genus *Matsucoccus* Cock. in Italy. I. Faunistical-ecological notes on species observed in pine forests in Liguria and Tuscany. *Redia* **74**, 575-597.

Crandall, K.A. & Templeton, A.R. (1993) Empirical tests of some predictions from coalescent theory with applications to intraspecific phylogeny reconstruction. *Genetics* **134**, 959-969.

Dupanloup, I., Schneider, S. & Excoffier, L. (2002) A simulated annealing approach to define the genetic structure of populations. *Molecular Ecology* **11**, 2571-2581.

ESRI (2011) ArcGIS Desktop: Release 10. Redlands, CA: Environmental Systems Research Institute.

EUFORGEN (2009) Distribution map of maritime pine (*Pinus pinaster*). Available online at www.euforgen.org.

Excoffier, L. & Lischer, H.E.. (2010) Arlequin suite ver 3.5: a new series of programs to perform population genetics analyses under Linux and Windows. *Molecular Ecology Resource* **10**, 564-567

Fabre, J-P., Menassieu, P., Foing, J-J. &. Chalon, A. (2000) Biology and ecology of *Elatophilus nigricornis* Zetterstedt (Hemiptera Anthocoridae) predator of *Matsucoccus feytaudi* Ducasse (Homoptera Matsucoccidae) in the South-East of France. *Annals of Forest Science* **57**, 777-792.

Figueiral, I. (1995) Charcoal analysis and the history of *Pinus pinaster* (cluster pine) in Portugal. *Review of Palaeobotany and Palynology* **89**, 441-454.

Foldi, I. (2004) The Matsucoccidae in the Mediterranean basin with a world list of species (Hemiptera: Sternorrhyncha: Coccoidea). *Annales de la Société Entomologique de France* **40**, 145-168.

Folmer, O., Black, M., Hoeh, W., Lutz, R. & Vrijenhoek, R. (1994) DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. *Molecular Marine Biology and Biotechnology* **3**, 294-299.

Fu, Y-X (1997) Statistical Tests of Neutrality of Mutations Against Population Growth, Hitchhiking and Background Selection. *Genetics* **147**, 915-925.

Gariepy, T.D., Kuhlmann, U., Gillott, C. & Erlandson, M. (2007) Parasitoids, predators and PCR: the use of diagnostic molecular markers in biological control of Arthropods. *Journal of Applied Entomology* **131**, 225-240.

Gebiola, M., Lopez-Vaamonde, C., Nappo, A. & Bernardo, U. (2013) Did the parasitoid *Pnigalio mediterraneus* (Hymenoptera: Eulophidae) track the invasion of the horse chestnut leafminer? *Biological Invasions* **16**, 843-857.

Gómez, A. & Lunt, D. (2007) Refugia within Refugia: Patterns of Phylogeographic Concordance in the Iberian Peninsula pp. 155-188 in Weiss, S. & Ferrand, N. (Eds.) *Phylogeography of Southern European Refugia*. Springer, Dordrecht, The Netherlands.

González-Martínez, S., Gómez, A., Carrión, J., Agúndez, D., Alía, R. & Gil, L. (2007) Spatial genetic structure of an explicit glacial refugium of maritime pine (*Pinus pinaster* Aiton) in southeastern Spain pp. 257-269 in Weiss, S. & Ferrand, N. (Eds.) *Phylogeography of Southern European Refugia*. Springer, Dordrecht, The Netherlands.

Greenstone, M.H., Vandenberg, N.J. & Hu, J.H. (2011) Barcode haplotype variation in north American agroecosystem lady beetles (Coleoptera: Coccinellidae). *Molecular Ecology Resource* **11**, 629-637.

Gregory, T.R., Nedvěd, O. & Adamowicz, S.J. (2003) C-value estimates for 31 species of ladybird beetles (Coleoptera: Coccinellidae). *Hereditas* **139**, 121-127.

Hall, T.A. (1999) BioEdit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. *Nucleic Acids Symposium Series* **41**, 95-98.

Hebert, P.D.N. & Gregory, T.R. (2005) The Promise of DNA Barcoding for Taxonomy. *Systematic Biology* **54**, 852-859.

Hernandez-Lopez, A., Rougerie, R., Augustin, S., Lees, D., Tomov, R., Kenis, M., Cota, E., Kullaj, E., Hansson, C., Grabenweger, G., Roques, A. & Lopez-Vaamonde, C. (2011) Host tracking or cryptic adaptation? Phylogeography of *Pediobius saulius* (Hymenoptera, Eulophidae), a parasitoid of the highly invasive horse chestnut leafminer. *Evolutionary Applications* **5**, 256-269.

Hewitt, G.M. (1996) Some genetic consequences of ice ages, and their role in divergence and speciation. *Biological Journal of the Linnean Society* **58**, 247-276.

Hoelmer, K.A. & Kirk, A.A. (2005) Selecting arthropod biological control agents against arthropod pests: Can the science be improved to decrease the risk of releasing ineffective agents? *Biological Control* **34**, 255-264.

Hufbauer, R.A. & Roderick, G.K. (2005) Microevolution in biological control: Mechanisms, patterns, and processes. *Biological Control* **35**, 227-239.

Jactel, H. & Menassieu, P. (2005) La cochenille du pin maritime *Matsuccocus feytaudi*: nouvelles données épidémiologiques et perspectives de lutte. *Forêt Méditerranée* **26**, 37-46.

Jactel, H., Ménassieu, P. & Burban, C. (1996) Découverte en Corse de *Matsucoccus feytaudi* Duc (Homoptera: Margarodidae), cochenille du pin maritime. *Annals of Forest Science* **53**, 145-152.

Kalinowski, S. (2004) Counting Alleles with Rarefaction: Private Alleles and Hierarchical Sampling Designs. *Conservation Genetics* **5**, 539-543.

Kenis, M., Auger-Rozenberg, M-A., Roques, A., Timms, L., Péré, C., Cock, M.W., Settele, J., Augustin, S. & Lopez-Vaamonde, C. (2009) Ecological effects of invasive alien insects. *Biological Invasions* **1**, 21-45.

Kim, M.J., Wan, X. & Kim, I. (2012) Complete mitochondrial genome of the seven-spotted lady beetle, *Coccinella septempunctata* (Coleoptera: Coccinellidae). *Mitochondrial DNA* **23**, 179-181.

Kobayashi , N., Kumagai, M., Minegishi, D., Tamura, K., Aotsuka, T. & Katakura, H. (2011) Molecular population genetics of a host-associated sibling species complex of phytophagous ladybird beetles (Coleoptera: Coccinellidae:

Epilachninae). *Journal of Zoological Systematics and Evolutionary Research* **49**, 16-24.

Lees, D.C., Lack, H.W., Rougerie, R., Hernandez-Lopez, A., Raus, T., Avtzis, N.D., Augustin, S. & Lopez-Vaamonde, C. (2011) Tracking origins of invasive herbivores through herbaria and archival DNA: the case of the horse-chestnut leaf miner. *Frontiers in Ecology and the Environment* **9**, 322-328.

Lozier, J.D., Roderick, G.K. & Mills, N.J. (2008) Evolutionarily significant units in natural enemies: Identifying regional populations of *Aphidius transcaspicus* (Hymenoptera: Braconidae) for use in biological control of mealy plum aphid. *Biological Control* **46**, 532-541.

Nadel, R.L., Wingfield, M.J., Scholes, M., Lawson, S., Noack, A., Neser, S. & Slippers, B. (2012) Mitochondrial DNA diversity of *Cleruchoides noackae* (Hymenoptera: Mymaridae): a potential biological control agent for *Thaumastocoris peregrinus* (Hemiptera: Thaumastocoridae). *BioControl* **57**, 397-404.

Omondi, B., Van den Berg, J., Masiga, D. & Schulthess, F. (2011) Phylogeographic structure of *Teretrius nigrescens* (Coleoptera: Histeridae) predator of the invasive post harvest pest *Prostephanus truncatus* (Coleoptera: Bostrichidae). *Bullettin of Entomological Research* **101**, 521-532.

Perrings, C., Williamson, M., Barbier, E.B., Delfino, D., Dalmazzone, S., Shogren, J., Simmons, P. & Watkinson, A. (2002) Biological invasion risks and the public good: an economic perspective. *Conservation ecology* **6**, 1.

Raimundo, A., Canepari, C., Mendel, Z., Branco, M. & Franco, C. (2006) *Iberorhyzobius* Raimundo & Canepari gen. nov., for *Coccidula rondensis* Eizaguirre (Coleoptera: Coccinellidae). *Zootaxa* **1312**, 49-58.

Roderick, G.K. & Navajas, M. (2003) Genes in new environments: genetics and evolution in biological control. *Nature Reviews Genetics* **4**, 889-899.

Salvador, L., Alía, R., Agúndez, D. & Gil, L. (2000) Genetic variation and migration pathways of maritime pine (*Pinus pinaster* Ait) in the Iberian peninsula. *Theoretical and Applied Genetics* **100**, 89-95.

Sax, D.F., Stachowicz, J.J., Brown, J.H., Bruno, J.F., Dawson, M.N., Gaines, S.D., Grosberg, R.K., Hastings, A., Holt, R.D., Mayfield, M.M., O'Connor, M.I. & Rice, W.R. (2007) Ecological and evolutionary insights from species invasions. *Trends Ecology Evolution* **22**, 465-471.

Shea, K. & Chesson, P. (2002) Community ecology theory as a framework for biological invasions. *Trends on Ecology and Evolution* **17**, 170-176.

Slatkin, M. (1993) Isolation by distance in equilibrium and non-equilibrium populations. *Evolution* **47**, 264-279.

Smith, C.I., Tank, S., Godsoe, W., Levenick, J., Strand, E., Esque, T. & Pellmyr, O. (2011) Comparative phylogeography of a coevolved community: concerted population expansions in Joshua trees and four yucca moths. *PloS ONE* **6**, 1-18.

Song, H., Buhay, J.E., Whiting, M.F. & Crandall, K.A. (2008) Many species in one: DNA barcoding overestimates the number of species when nuclear mitochondrial pseudogenes are coamplified. *Proceedings of the National Academy of Sciences USA* **105**, 13486-13491.

Tajima, F. (1989) Statistical method for testing the neutral mutation hypothesis by DNA polymorphism. *Genetics* **123**, 585-595.

Tavares, C., Jactel, H., van Halder, I., Mendel, Z. & Branco, M. (2014) A case of ecological specialization in ladybirds: *Iberorhyzobius rondensis* (Coleoptera: Coccinellidae), potential biocontrol of *Matsucoccus feytaudi* (Hemiptera: Matsucoccidae). *Bullettin of Entomological Research* **104**, 367-375.

Templeton, A.R., Crandall, K.A. &Sing, C.F. (1992) A cladistic analysis of phenotypic associations with haplotypes inferred from restriction endonuclease mapping and DNA sequence data. III. Cladogram estimation. *Genetics* **132**, 619-633.

Valade, R., Kenis, M., Hernandez-Lopez, A., Augustin, S., Mari Mena, N., Magnoux, E., Rougerie, R., Lakatos, F., Roques, A. & Lopez-Vaamonde, C. (2009) Mitochondrial and microsatellite DNA markers reveal a Balkan origin for the highly invasive horse-chestnut leaf miner *Cameraria ohridella* (Lepidoptera, Gracillariidae). *Molecular Ecology* **18**, 3458-3470.

Vasconcelos, T., Horn, A., Lieutier, F., Branco, M. & Kerdelhué, C. (2006) Distribution and population genetic structure of the Mediterranean pine shoot beetle *Tomicus destruens* in the Iberian Peninsula and Southern France. *Agriculture and Forest Entomology* **8**, 103-111.

Zakharov, I. & Shaikevich, E. (2013) Comparative study of mtDNA in species of the genus *Adalia* (Coleoptera: Cocinellidae) and origin of ancient mitochondrial haplotypes in the gene pool of *Adalia bipunctata*. *European Journal of Entomology* **110**, 427–433.

V.Validation of the genus *Iberorhyzobius* using molecular methods

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5.1. Abstract

Iberorhyzobius rondensis (Eizaguirre) is a recently discovered species from the tribe Coccidulini, which was exclusively found on the Iberian Peninsula. The species was first classified as *Coccidula rondensis*. Yet, its unique morphological characters led to the proposal of a new genus *Iberorhyzobius,* with a single species. The genus and species were so far described based on morphological traits. Here we propose to determine its phylogenetic position in the tribe Coccidulini and validate the new genus based on molecular data. Specimens of *I. rondensis* and others ladybirds from the tribe Coccidulini, Chilocorini and Scyminini were collected in the field. DNA of the beetles was analyzed using COI and 18S markers. A phylogenetic tree was reconstructed based on maximum likelihood estimates, also using genetic sequences from GenBank. We found that the *I. rondensis* group formed a distinct well supported clade, validating the genus. Monophyly of the other genera is well supported except for *Rhyzobius* which emerges as a polyphyletic genus. The interrelationships among genus remain unresolved. We discuss these results and suggest that further works should address the phylogeny of the group.

Key-words: Coccidulini, Rhyzobius, phylogeny

5.2. Introduction

Iberorhyzobius rondensis (Eizaguirre) is a recently discovered species (Eizaguirre, 2004; Raimundo *et al.*, 2006), restricted to the Iberian Peninsula (Tavares *et al.*, 2014). It is a monophagous species preying specifically in the pine bast scale *Matsucoccus feytaudi* Ducasse, and it is only present on its habitat, *Pinus pinaster* Aiton (Branco *et al.*, 2006; Tavares *et al.*, 2014). It has recently been suggested as a possible biological control agent, in Southeastern France and also Northern Italy and Corsica, to where the bast scale has spread causing important damage to the *P. pinaster* forest (Jactel *et al.*, 1996).

Iberorhyzobius rondensis was first described by Eizaguirre, 2004 as *Coccidulla rondensis*. Specimens were found on conifers (probably *P. pinaster*) in the region of Ronda. In separate studies the ladybird was found in Portugal in *P. pinaster* trees, attracted by the sexual pheromone of *M. feytaudi* (Branco *et al.*, 2006; Branco *et al.*, 2011). The species was first considered to belong to the genus *Rhyzobius* Stephens (Branco *et al.*, 2006). A few specimens of this species, collected in Spain by different collectors, from 1927 to 1967, were present on the British Museum of Natural History, London (2 ♀) and Museo Civico di Storia Naturale di Milano (2 ♀). Identification has not been previoulsy attempted due to the unavaibility of males. Raimundo and co-authors (2006) using optical and SEM images and several morphological traits concluded, that although the beetle was clearly from the tribe Coccidulini Mulsant, it neither belonged to the genus *Rhyzobius*, nor to the genus *Coccidula* Gyll. Thus the new genus *Iberorhyzobius* Raimundo & Canepari was created for this ladybird beetle.

The Coccidulini, belonging to the subfamily Coccidulinae, comprise 23 genera, and most of them, especially the genus *Rhyzobius* are tropical (Tomaszewska, 2010). In Iberian Peninsula there were only four endemic species of Coccidulini (Eizaguirre, 2004): *Rhyzobius litura* (Fabricius), *Rhyzobius chrysomeloides* (Herbst), *Coccidula scutellata* (Herbst), and *Coccidula rufa* (Herbst). Recent phylogenetic studies on the phylogeny of ladybirds have included some species of the tribe Coccidulini, such as the genus *Rhyzobius*, *Coccidula* and *Rodolia* (Giorgi *et al.*, 2009; Magro *et al.*, 2009; Seago *et al.*, 2011). It emerged that the tribe is polyphyletic.

The main aim of this study is to determine the phylogenetic position of *I. rondensis* within the tribe Coccidulini and test its taxonomic position as a unique genus.

5.3. Material and Methods

Insect sampling

Samples of adult species belonging to the tribes Scyminini (Scymininae), Coccidulini (Coccidulinae), Platynaspini (Chilochorinae) and Chilochorini (Chilochorinae) were field-collected mainly in Portugal, Spain and France (Table 1). Beetles were captured with a sweeping net by beating branches, except for *I. rondensis* larvae individuals which were collected with the prey's pheromone traps as described in Branco *et al.*, (2006). They were then preserved in 96% ethanol. Beetles collected in the field were identified with taxonomic identification keys (Raimundo & Alves, 1986). Eight DNA sequences (18S and COI), available in Genbank, taken from Magro *et al.*, (2009) were added to our sample (Table 1). For each species we tried to sequence at least two specimens. Taxonomy of coccinellids as suggested by Kovář (1996) was used.

Molecular procedures

Genetic variation of the beetles was examined by amplifying the barcode fragment of the mitochondrial gene, cytochrome oxidase c subunit 1 (COI) (Hebert & Gregory, 2005) and the nuclear gene 18S rDNA, as used in the phylogeny of many ladybirds (Magro *et al.*, 2009; Seago *et al.*, 2011).

The whole genomic DNA was extracted from the abdomen of individual specimens preserved in alcohol, using a Nucleospin®Tissue XS Kit (Macherey-Nagel, Düren, Germany). DNA was amplified with primers LCO1490 and HCO2198 (Folmer *et al*., 1994) for COI, and with the primers 18S-H17F and 18S-H35R (Heraty *et al.*, 2004). Reactions and PCR were carried out as described in Tavares et al. 2014 (chapter 4).

Table 1. List of species used to contruct the phylogenetic tree.

Tribe	Species	Total	Origin	Collection	ID (COI)	Id (18S)
Coccidulini	*Rhyzobius litura*	2	Paleartic	Center Portugal		
	Rhyzobius chrysomeloides	1	Australasia	Center Portugal		
		1		(Magro *et al.*, 2009)	GU073964*	GU073723*
	Iberorhyzobius rondensis	1	Iberian Peninsula	South Portugal		
		1		South Spain (Ronda)		
		1		Eastern Spain (Valencia)		
	Coccidula rufa	1	Paleartic	Center France		
	Rodolia cardinalis	2	Australasia	South Portugal		
	Rhyzobius lophanthae	1	Australasia	Center Portugal		
		1		Greece		
Chilocorini	*Chilocorus bipustulatus*	1	Paleartic	Center Portugal		
	Chilocorus renipustulatus	1	Paleartic	(Magro *et al.*, 2009)	GU073961*	GU073720*
	Exochomus childreni	1	Nearctic	Center Portugal		
	Exochomus quadripustulatus	1	Paleartic	Center Portugal		
Platynaspini	*Platynaspis luteorubra*	2	Paleartic	Center Portugal		
				(Magro *et al.*, 2009)	GU073963*	GU073722*
Coccinellini	*Adalia bipunctata*	1	Paleartic	(Magro *et al.*, 2009)	GU073919*	GU073675*

Data analyses

A total of 1320 base pairs were amplified. Sequences were aligned by ClustalW Multiple alignment in BioEdit 7.0.9.0 (Hall, 1999) and primer sequences were removed from the analysis. Ambiguities were edited by visual observation. Matrices of COI and 18S were concatenated.

A phylogenetic tree was built, using, whenever possible at least 2 specimens per species, on MEGA 6.04 (Kumar *et al.*, 1994). The phylogenetic reconstruction was done with a maximum likelihood analysis with the Tamura-Nei model (Tamura & Nei, 1993) at uniform rates. One thousand bootstrap replicates were performed to assess the statistical support of the nodes in the phylogenetic tree (Hall, 2013).

5.4. Results and Discussion

Sequences with 1320 bp sequences were obtained from 8 genera and 12 species of Coccinellidae.

Two major clades, well supported, separate the Chilocorini and Coccinellini from the tribes Coccidulini, Scymnini and Platysnipini (Fig. 1). The Chilocorini are represented by the genus *Chilocorus* Leach and *Exochomus* Redtenb. Only the monophyly of the tribe Chilocorini is well supported in our analysis. They form a single distinct clade from the tribe Platynaspidi, which agrees with the results of Giorgi *et al.*, 2009, Magro *et al.*, 2009, Seago *et al.*, 2011. The other clades present low values of bootstrap, which do not support the monophyly of the different tribes, Platynaspidi, Scyminini and Coccidulini.

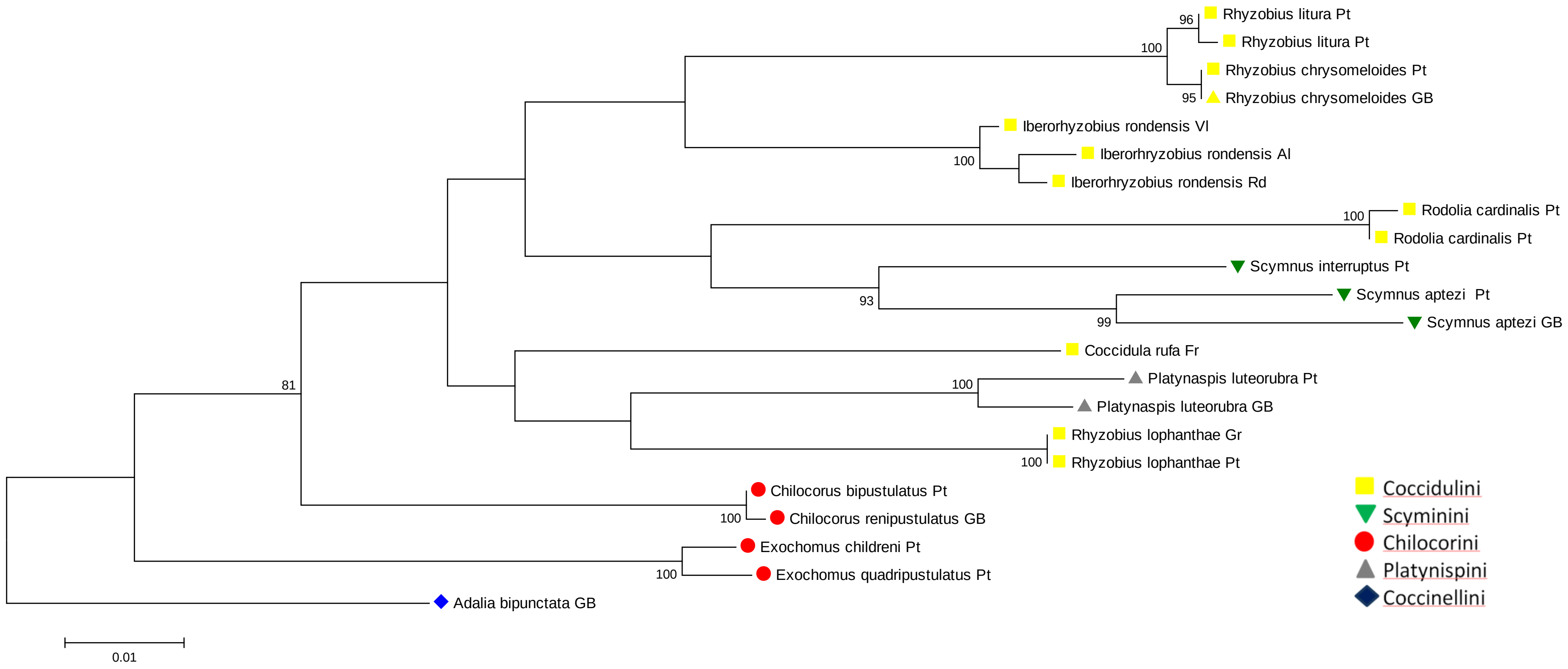

Fig. 1. Phylogenetic tree from the ML analysis derived from 1319 base pairs from the COI (553 bp) and 18S (766) with branch lengths drawn to scale. Bootstrap values (1000 replicates) above 70 are indicated on branches (>70%). Abreviations: Pt – Portugal, GB – GeneBank; Vl – Valencia, Al – Algarve (South Portugal), Rd – Ronda, Fr –France, Gr – Greece. Colors indicate the different tribes.

The remaining tribes are mostly from the tribe Coccidulini and Scyminini. These tribes are considered polyphyletic (Magro *et al.*, 2009; Seago *et al.*, 2011), which is reflected in our results (Fig. 1). Interesting, Seago *et al.*, 2011 in a phylogenetic analysis of ladybirds, considered that the tribe Coccidulini should incorporate the Scyminini, since those also form an unresolved polyphyletic group. In that perspective the proximity of *Rodolia* Mulsant to *Scymnus* Kugelann may be explained.

However, the lower clades, at the genus level are well-supported except for *Rhyzobius* (Fig.1). *Rhyzobius* is the only genus which appears separate in our results. *R. litura* and *R. chrysomeloides* make a strong clade, but *Rhyzobius lophanthae* (Blaisdell) is part of another clade. This corroborates the hypothesis of polyphyly of the genus *Rhyzobius*, with both the Old World and the Australian species separated (Seago *et al.*, 2011).

The *I. rondensis* group forms a well-supported clade, well separated from all the other genera. Although it appears in the same major clade as the Old-World *Rhyzobius*, it is not possible to affirm that those are its closer relatives, since the bootstrap value is rather low. However, it is possible to validate *Iberorhyzobius* as an independent genus, well separated from the other genus of the Coccidulini.

This separation is also reflected in its unique ecological requirements, which are different from the other species of Coccidulini found in Iberian Peninsula. *R. litura* and *R. chrysomeloides* are abundant species, found in several Mediterranean ecosystems, feeding on aphids and coccids (Raimundo & Alves, 1986; Ricci, 1986; Covassi *et al.*, 1991; Santos *et al.*, 2009). *C. rufa* is an aphidophagous species, present in aquatic plants on humid areas (Majerus, 1994) and *C. scutellata* is a rare species also present in humid areas (Raimundo & Alves, 1986).

Our work further reflects the need for more phylogenetic studies addressing the tribe Coccidulini, and especially the genus *Rhyzobius*. The use of more molecular markers should be considered. Also, more species from the tribe Coccidulini should be incorporated on the analysis.

5.5. References

Branco, M., Lettere, M., Franco, J.C., Binazzi, A. & Jactel, H. (2006) Kairomonal Response of Predators to Three Pine Bast Scale Sex Pheromones. *Journal of Chemical Ecology* **32**, 1577-1586.

Branco, M., van Halder, I., Franco, J.C., Constantin, R. & Jactel, H. (2011) Prey sex pheromone as kairomone for a new group of predators (Coleoptera: Dasytidae, Aplocnemus spp.) of pine bast scales. *Bulletin of Entomological Research* **101**, 667-674.

Covassi, M., Binazzi, A. & Toccafondi, P. (1991) Studies on the entomophagous predators of a scale of the genus *Matsucoccus* Cock. in Italy. I. Faunistical-ecological notes on species observed in pine forests in Liguria and Tuscany. *Redia* **74**, 575-597.

Eizaguirre, S. (2004) Revisión de la tribu Coccidulini en la Península Ibérica (Coleoptera: Coccinellidae) *Estudios del Museo de Ciencias Naturales de Álava* **18-19**, 153-170.

Folmer, O., Black, M., Hoeh, W., Lutz, R. & Vrijenhoek, R. (1994) DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. *Molecular Marine Biology and Biotechnology* **3**, 294-299.

Kovář, I. (1996) Phylogeny pp. 19–31in Hodek, I., Honěk, A. (Eds.), *Ecology of Coccinellidae*. Dordrecht, The Netherlands, Kluwer Academic Publishers.

Giorgi, J.A.,Vandenberg, N.J., McHugh, J.V., Forrester, J.A., Ślipiński, A., Miller, K.B., Shapiro, L.R. & Whiting, M.F. (2009) The evolution of food preferences in Coccinellidae. *Biological Control* **51**, 215-231.

Hall, T.A. (1999) BioEdit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. *Nucleic Acids Symposium Series* **41**, 95-98.

Hall, B.G. (2013) Building phylogenetic trees from molecular data with MEGA. *Molecular Biology and Evolution* **30**, 1229-1235.

Heraty, J., Hawks, D., Kostecki, J.S. & Carmichael, A. (2004) Phylogeny and behaviour of the Gollumiellinae, a new subfamily of the ant-parasitic Eucharitidae (Hymenoptera: Chalcidoidea). *Systematic Entomology* **29**, 544-559.

Hebert, P.D.N. & Gregory, T.R. (2005) The Promise of DNA Barcoding for Taxonomy. *Systematic Biology* **54**, 852-859.

Jactel, H., Ménassieu, P. & Burban, C. (1996) Découverte en Corse de *Matsucoccus feytaudi* Duc (Homoptera: Margarodidae), cochenille du pin maritime. *Annals of Forest Science* **53**, 145-152.

Kumar, S.,Tamura, K. & Nei, M. (1994) MEGA: molecular evolutionary genetics analysis software for microcomputers. *Computer applications in the biosciences: CABIOS* **10**, 189-191.

Magro, A., Lecompte, E., Magne, F., Hemptinne, J.L. & Crouau-Roy, B. (2009) Phylogeny of ladybirds (Coleoptera: Coccinellidae): are the subfamilies monophyletic? *Molecular Phylogenetics and Evolution* **54**, 833-848.

Majerus, M. (1994) *The New Naturalist- Ladybirds*. HarperCollins Academic, London.

Raimundo, A., Canepari, C., Mendel, Z., Branco, M. & Franco, C. (2006) *Iberorhyzobius* Raimundo & Canepari gen. nov., for *Coccidula rondensis* Eizaguirre (Coleoptera: Coccinellidae). *Zootaxa* **1312**, 49-58.

Raimundo, A. A. C. & Alves, M. L. G. (1986) Revisão dos Coccinelídeos de Portugal. *Universidade de Évora, Évora.*

Ricci, C. (1986) Seasonal food preferences and behavior of *Rhyzobius litura* pp. 119-123 in Hodek, I. (Ed.) *Ecology of Aphidophaga.* Dordrecht, The Netherlands, Kluwer Academic Publishers.

Santos, S.A.P., Pereira, J.A., Rodrigues, C. M., Torres, L. M., Pereira, A.M.N. & Nogueira, A.J.A. (2009) Identification of predator-prey relationships between coccinellids and *Saissetia oleae* (Hemiptera: Coccidae), in olive groves, using an enzyme-linked immunosorbent assay. *Journal of Pest Science* **82**, 101-108.

Seago, A.E., Giorgi, J.A., Li, J. & Ślipiński, A. (2011) Phylogeny, classification and evolution of ladybird beetles (Coleoptera: Coccinellidae) based on simultaneous analysis of molecular and morphological data. *Molecular Phylogenetics and Evolution* **60**, 137-151.

Tavares, C., Jactel, H.,van Halder, I., Mendel, Z. & Branco, M. (2014) A case of ecological specialization in ladybirds: *Iberorhyzobius rondensis* (Coleoptera: Coccinellidae), potential biocontrol agent of *Matsucoccus feytaudi* (Hemiptera: Matsucoccidae). *Bulletin of Entomological Research* **104**, 367-375.

Tamura, K. & Nei, M. (**1993**). Estimation of the number of nucleotide substitutions in the control region of mitochondrial DNA in humans and chimpanzees. *Molecular Biology and Evolution* **10**, 512-526.

Tomaszewska, W (2010) *Rhyzobius* Stephens 1829 (Coleoptera, Coccinellidae), a Revision of the World Species. Fauna Mundi 2. Natura optima fux Foundation, Warszawa, Poland, Warszawska Drukarnia Naukowa.

VI. A systematic review of prey specialization in ladybirds

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6.1. Abstract

Ladybirds are important predators widely used in biological control programs. In this work we test some hypothesis related with specialization in predacious ladybirds by using a systematic review. With data retrieved from 186 species, we analyzed association between prey specialization and several life and ecological traits (body length, fecundity, voltinism, use of chemical cues), taxonomy, and habitat and plant specialization of the prey. We further analyzed the relation between biological control success and specialization of the predator. Quantitative data analyses by chi-square tests, one-ways ANOVA or logistic regression models were used to relate variables. Prey specialization of predacious ladybirds was found related with habitat specialization: Although some specialized ladybirds feed on specialized prey, most of the specialized ladybirds feed on generalist preys. The degree of specialization was found to be conservative within feeding guilds: ladybirds feeding on scale insects were more specialized than those feeding on aphids. Consequently specialization was also conservative within taxonomic close species, which in general feed on similar types of prey. The prey's characteristics are a possible major driver of the ladybird's prey specialization. Ladybird's traits are relevant predictors of their degree of specialization. Polyphagous species are usually bigger and more fecund than oligophagous and monophagous species. Univoltinism is more common in monophagous species and multivoltinism in polyphagous ones. No association was found between prey specialization and biological control success. Yet, most of the reported cases in biological control refer to oligophagous species. These results are thorough discuss in an evolutionary and an applicable context. The results also evidence the need for further knowledge on some aspects of understanding ladybirds prey specialization, in particular in the use of chemical cues.

6.2. Introduction

Ladybirds (Coleoptera, Coccinellidae) represent one of the most studied and paradigmatic group of insect predators. About 90% of the 6000 species of ladybirds known worldwide are predators, and mostly feed on sap sucking insects, such as scale insects, aphids, whiteflies and psyllids (Hemiptera, Sternorrhyncha) (Iperti, 1999; Seago *et al.*, 2011). The remaining species are phytophagous or mycophagous (e.g., Epilachnini and *Psyllobora* spp.) (Iperti, 1999; Dixon, 2000). Ladybirds originate from an ancestral mycophagous clade within the Cerylonid and predation is a recent condition (Seago *et al.*, 2011). Since ladybirds mostly prey on Sternorrhyncha producing honeydew, it has been suggested that the preference for this group of prey started with feeding on the fungi associated with honeydew (Magro *et al.*, 2009; Seago *et al.*, 2011). Another important contribution to the adaptative radiation on ladybirds was the origin of ant-specific larval defense mechanisms, such as waxy exudates and dorsal defensive glands. Because many Sternorrhyncha are ant-guarded, this allowed ladybirds to exploit a series of different species (Seago, 2011). Among predatory ladybirds, coccidophagy is considered an ancestral condition, and aphidophagy a derived one (Giorgi *et al.*, 2009). Phylogenetic studies support the hypothesis that aphidophagy appeared several times during ladybirds' radiation (Magro *et al.*, 2009). Predation on mites, whiteflies and psyllids is considered a direct transition from coccidophagy (Magro *et al.*, 2009; Seago *et al.*, 2011). A high degree of variation of prey taxa is found among tribes within Coccinellidae (Iperti, 1999; Giorgi *et al.*, 2009; Magro *et al.*, 2009): most of the Coccinellini, Platynaspidini, Aspidimerini and some Coccidulini prey on aphids, whilst Sticholotidini, Chilocorini, and Coccidulini mostly prey on scale insects, and Serangiini prey on whiteflies. All *Stethorus* (Coccidulini) prey on tetranychid mites.

Although ladybirds are in general considered highly specialized predators, there are large differences in dietary range among species, from strict monophagy, such as in *Iberorhyzobius rondensis* (Eizaguirre) (Tavares *et al.*, 2014), to extreme polyphagy, e.g., *Coleomegilla maculata* (De Geer) (Roger *et al.*, 2000). Even congeneric species can present differences in their level of prey and habitat specialization (Hodek & Honěk, 1996; Sloggett & Majerus, 2000). Given their different levels of prey specialization and feeding guilds, ladybirds are considered very good models for the study of ecological specialization in predatory insects (Sloggett, 2008a). Several studies have been conducted on this family addressing the relation between prey specialization and ladybird size (e.g. Dixon & Hemptinne, 2001; Sloggett, 2008b), habitat specialization (Sloggett & Majerus, 2000; Sloggett, 2008a), feeding guilds (Hodek & Honěk, 1996; Evans, 2009; Hodek & Honek, 2009), phylogeny (e.g., Giorgi *et al.*, 2009; Magro *et al.*, 2009; Seago *et al.*, 2011) and life history traits (e.g., Rana *et al.*, 2002; Kajita *et al.*, 2009; Ferrer *et al.*, 2010; Borges *et al.*, 2011).

Prey range expansion and prey shifts in predatory ladybirds are considered frequent and mainly due to food scarcity. Since the abundance of sap sucking insects is usually seasonal, the lack of preferable prey on some periods often leads ladybirds to search for alternative prey in order to survive (Sloggett & Majerus, 2000). This allows them to exploit new trophic niches (Giorgi *et al.*, 2009). Since Sternorrhyncha are usually found on certain habitats, if a ladybird shifts onto a new prey species, it may remain restricted to that prey's habitat. The ladybird may then start breeding within that habitat, and larvae may be eventually forced to feed on that prey, thus leading to both prey and habitat range expansion or shift. A study with *Adalia bipunctata* (L.) (Rana *et al.*, 2002) demonstrated that adaptation to alternative prey may be a very fast process. Since ladybirds can quickly incorporate novel prey into their diet when the main prey is scarce, this process may ultimately lead ladybirds species to move from a specialist strategy to a generalist one, according to the hypothesis of the specialist –> generalist evolutionary process (Futuyma & Moreno, 1988; Schluter, 2001). On the other hand, prey defense mechanisms (such as chemical, morphological, behavioral defenses) may trigger prey specialization, due to trade-offs which will allow a poor performance on alternative prey species (Rana *et al.*, 2002). Other studies have shown that ladybirds have the capacity to feed on a larger number of prey species than those they find in their specific habitat, such as in the case of *Harmonia yedoensis* Takizawa and *Coccinella hieroglyphica* (L.) (e.g. Hippa *et al.*, 1978; 1984; Noriyuki & Osawa, 2012). These may have conserved traits belonging to a more generalist ancestral (Sloggett & Majerus, 2000), according to the hypothesis that specialization is derived from a generalist ancestor (Futuyma & Moreno, 1988). A process of specialization linked with shifts in habitat and diet further supports the hypothesis of parapatric, or possibly sympatric, speciation in the Coccinellidae. Resource competition further plays an important role in ladybird specialization. Several cases show that close species of coccinellid have well separated niches, either through habitat (e.g., Honěk, 1985; Nedved, 1999), food (e.g., Noriyuki & Osawa, 2012), or both (Ferrer *et al.*, 2010), which might result from divergent selection under interspecific competition.

Ladybirds have been widely used in biological control of different sap sucking pest insects and a few species, such as *Cryptolaemus montrouzieri* Mulsant are commercially available for augmentative release (Evans, 2009; Roy & Migeon, 2010). Prey specificity of predators is an important requisite in biological control (McEvoy, 1996). Theoretically, a high degree of prey specialization will ensure a maximal impact on the target prey (van Lenteren *et al*., 2006). A high degree of specialization will also reduce the impact on non-target organisms. The fact that ladybirds are considered specialized predators justifies their extensive use in biological control programs (Hodek & Honěk, 1996; Obrycki & Kring, 1998; Iperti, 1999; Dixon, 2000). Nevertheless as we said, the degree of specialization may greatly vary among ladybirds, even in congeneric species, with possible implications on their success and safe use as biological control organisms. Cases of success have been usually associated with more specialized species, such as *Rodolia cardinalis* (Mulsant), whereas unsuccessful cases, with high non-target impact are linked to more generalist species, such as *Harmonia axyridis* (Pallas) (Dixon, 2000; Roy & Migeon, 2010). Regarding feeding guilds, coccidophagous species are known to be the most successful in biological control, although most studies have been devoted to aphidophagous (Dixon, 2000).

In this work we review some of the main factors considered important for coccinellids specialization. Based on data collected from 186 species we also conduct a quantitative analysis to investigate the links between ecological and life traits and the degree of specialization. In particularly, we test the following four hypothesis for ladybirds: i) prey specialization is associated with habitat specialization; ii) the degree of prey specialization is associated with the diet breadth of the prey; iii) prey specialization is linked to different life traits such as size; fecundity, voltinism and chemical cues used for prey recognition; iv) prey specialization is conservative within the genus or the tribe.

Finally, we further test if the success of ladybirds as biological control agents is associated with prey specialization

6.3. Material & Methods

Literature review and classification

In a first step, we conducted a literature review on CABI Abstracts, ISI Web of Knowledge and Google Scholar (first 100 results), for the period of 1900 until February 2014, using as keywords the genera of coccinellids retrieved from Hodek & Honěk, (1996) and Hodek & Honek, (2009). In a second step, we carried out a bibliographic search for each ladybird species found in the first stage of the review, considering all the publications related with prey, habitat, life traits, host plants of prey, and biological control. University websites containing information on coccinellids were also searched (González, 2006, 2007; Poorani, 2013; Shelton, 2014; VanDyk, 2014). Mycophagous, phytophagous and pollinivorous coccinellid species were ignored for the review, since we were only interested in predatory species. The retrieved coccinellid species were organized in subfamilies and tribes according to the system proposed by Seago *et al.*, (2011).

A list of ladybird species and the corresponding taxonomic information, habitat, biogeographic distribution (Neartic, Neotropical, Palearctic, Afrotropical, Oriental, Australasian and Indo-Malaysian), prey species, ecological traits, and their use and success as biological control agents was then organized (Annex 1). The following ecological traits were considered: i) degree of prey specialization; ii) habitat specialization; iii) feeding guild; iv) trophic level specialization; v) size (body length); vi) fecundity; vii) voltinism; and viii) use of chemical cues in prey location.

The degree of prey specialization of each coccinellid species was defined according to its essential prey, i.e. prey species allowing successful pre-imaginal development and reproduction (Hodek & Honěk, 1996). Prey species were retrieved from as many publications as possible reporting on laboratory experiments, gut dissections or field observations. Since no consensual prey specialization classification exists (Hodek &

Honek, 1996; Strand & Obrycki, 1996) we classified ladybirds in three groups: (1) monophagous, if feeding on a single prey species or genus; (2) oligophagous, if feeding on prey species from the same family or superfamily; or (3) polyphagous, if feeding on a range of prey species belonging to different families or superfamilies.

The degree of habitat specialization was defined based on two categories (Hodek & Honěk, 1996): (1) stenotopic species, i.e. restricted to a single habitat and breeding in that same habitat, which might be a single plant family (e.g., Pinaceae), a type of vegetation (e.g., reed beds), or the herbaceous stratum of a certain habitat; or (2) eurytopic species, which can be found in different habitats. In order to classify the different types of habitat, the IUCN Habitats Classification was used (IUCN, 2011)

The classification of ladybirds feeding guilds was based on the taxa of their essential prey: Aphidoidea, Coccoidea, Aleyrodoidea, Acari, and “other prey” when feeding on other taxa (e.g., Coleoptera, Lepidoptera), or “several prey”, when feeding on prey species of different orders (e.g., Hemiptera and Acari).

Dietary specialization across the tri-trophic system (predator – herbivore – plant) was used as proposed by Vet & Dicke (1992). The specialization of the predator/prey was classified as: (1) specialist, when feeding in a single family of prey/plants; or (2) generalist, when feeding in more than one family of prey/plants. The following groups were considered: SS – Both predator and prey are specialists; GS – Predator generalist, prey specialist; SG – Predator specialist, prey generalist; GG –Predator and prey are generalists. The degree of the prey specialization was based on their host plants, which were searched on specific databases (Gillett-Kaufman, 1996; Ben-Dov, 2001; Percy, 2002; Migeron & Dorkeld, 2006-2013; Blackman & Eastop, 2014; Ouvrard, 2014; Ouvrard & Martin, 2014)

Ladybirds described as biological control agents were separated into two groups, according to their type of use: i) biological control in the native range – usually through augmentative releases; or ii) biological control in an introduced range – the so called classical biological control. Two categories were further considered to classify their effectiveness as biological control agent: 1) successful, when able to reduce the target pest density; or 2) unsuccessful, if unable to reduce the target pest or if not even established in the new environment. Impacts on non-target species were not considered.

Data analysis

Chi-square analyses were used to test association between variables. The following questions were addressed: i) Are the predators' prey specialization and habitat specialization associated? ii) Species within the same taxonomic level (considering tribe and genus) tend to display the same level of prey specialization? iii) Is the level of prey specialization conservative within each ladybird's feeding guild? iv) Is there an association between the degree of the prey specialization of the predator and the degree of the host' specialization of the prey? When the chi-square test did not fulfill the assumptions of "No more than 20% of the expected counts are less than 5" (Yates, 1999), we performed a test of goodness-of-fit with 100 000 Monte Carlo simulations (McDonald, 2009)

One-way ANOVAs were performed to test if quantitative life traits (body length and fecundity) were related with the prey specialization. Outliers, considered as cases that fall more than 1.5 box lengths from the lower or upper hinge of the box-plot (interquartile) (IBM, 2011), were removed from the analysis. The Tukey's test was used to compare means among factor levels. Normality and homogeneity of variances were assessed, prior to all analyses, using the Kolmogorof-Sminorff one sample and Levene's tests, respectively.

Binary logistic regressions were used to test if the binary categorical life trait variable voltinism (monovoltine vs. multivoltine) was dependent on the predators' prey specialization. A binary logistic regression was also used to test if the success of biological control (response variable) was dependent on the predators' prey specialization. This was done independently for both classical biological control and for the augmentative releases in the native range.

6.4. Results

Prey specialization in relation to habitat and taxonomic groups

From the review, a total of 186 predatory ladybird species were retrieved and classified according to their prey and habitat specialization (Annex 1). Seventy two species belong to the tribe Coccinellini, 68 to Coccidulini, and 21 to Chilocorini. The remaining 25 species belong to the tribes Cryptognathini, Diomini, Hyperaspini, Microweiseini, Serangiini and Sticholotidini. The majority of species are from the Palearctic (54), Nearctic (33) and Indo-Malayan (41) regions. Coccinellini and Coccidulini were equally abundant in the Paleartic, Coccinellini was most abundant in the Neartic and Indo-Malayan regions and Cociidulini in the Neotropic, Australasian and Afrotropic regions. More Coccidulini species than Coccinellini were found in the tropical regions. Most of the ladybird species retrieved in the review were oligophagous (129 out of 186), followed by polyphagous (35) and monophagous (22).

Habitat and prey specialization were significantly associated ($\chi^2 = 11.36$; df = 2; $P = 0.003$) (Fig. 1). The majority of the monophagous species were stenotopic (17 out of 22), whereas the majority of the polyphagous species were eurytopic (24 out of 35). Almost as many species were found to be stenotopic (91) as eurytopic (95).

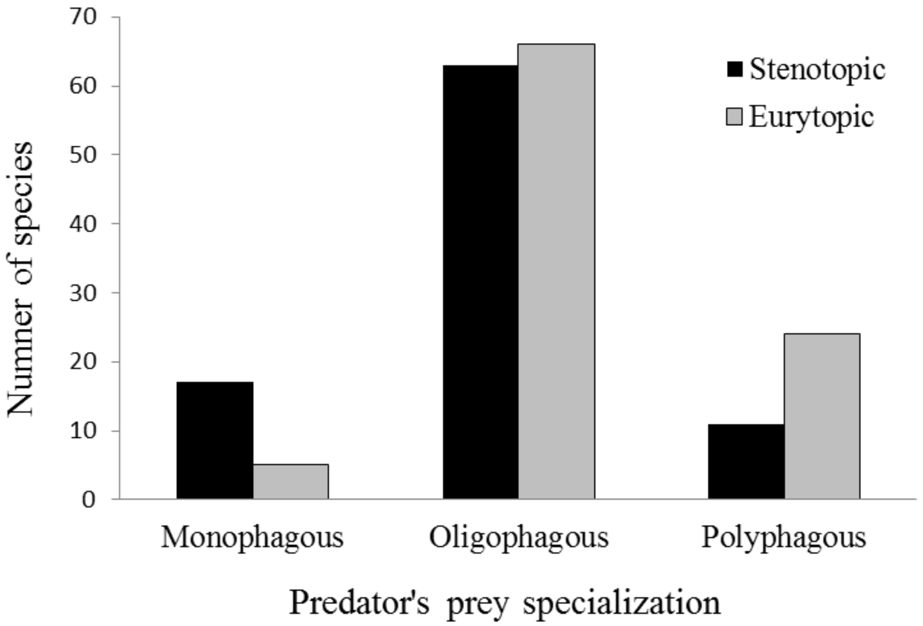

Fig. 1. Classification of 186 ladybird species, according to prey (monophagous, oligophagous and polyphagous) and habitat specialization (stenotopic and eurytopic).

Species within the same genus ($\chi^2 = 42.011$; df = 1; $P < 0.001$) and within the same family ($\chi^2 = 16.19$; df = 1; P< 0.001) tend to display the same level of prey specialization.

Since the aphidophagous and coccidophagous guilds of ladybirds constituted about 62% of all retrieved species, chi-square analysis on prey specialization and feeding guild were only performed for these groups. Monophagous species were significantly more common among coccidophagous than among aphidophagous ladybirds ($\chi^2 = 9.66$ df = 1; $P = 0.002$) (Fig. 2). Polyphagous species were not used in the analysis since they feed in more than one order.

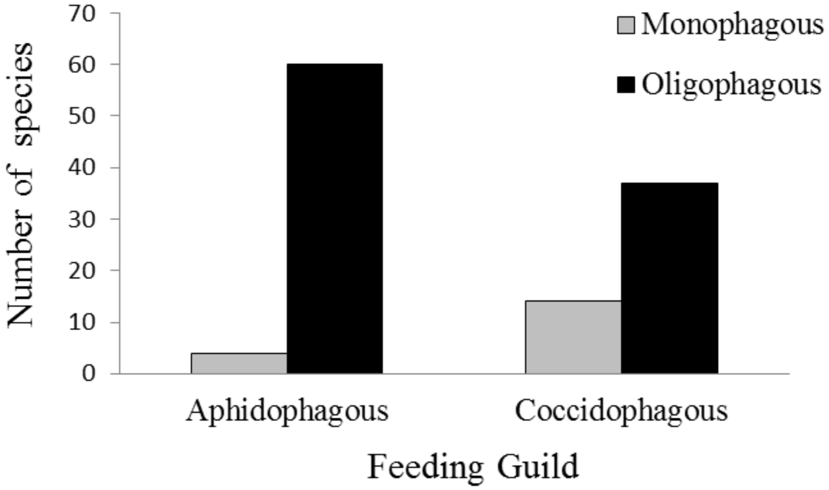

Fig. 2. Association of 186 ladybird species, according to prey specialization (monophagous, oligophagous and opolyphagous) and their feeding guild (aphidophagous or coccidophagous).

Prey specialization of the ladybirds in relation to life traits

Information on body length (L) was retrieved for 152 species. Body length varied from a minimum of 0.85 mm for *Stethorus punctum* (LeConte) to a maximum of 12 mm for *Synonycha grandi*s (Thunberg) and was on average (±SE) 3.8 ± 2.2 mm. Three outliers were removed: *S. grandi*s, *Anisolemnia dilatata* (Fab.) and *Harmonia eucharis* (Mulsant). Significant differences were found on the body size of ladybirds among prey specialization levels ($F_{2,149} = 3.84$; $P = 0.025$). Polyphagous species (n = 33, L = 4.03 ± 0.317) were significantly larger than oligophagous species (n = 102, L = 3.42 ± 0.188) (Fig. 3). Nevertheless, oligophagous and monophagous species (n = 17; L = 3.29 ± 0.347) had similar body sizes (Fig. 3).

Fecundity (E) was retrieved for 93 species of ladybirds. On average females produce 500.2 ± 39 eggs. Maximum fecundity was found for *Oenopia conglobata* (L.), with 1435 eggs/female. The minimum was observed for *Diomus terminatus* (Say) with 42 eggs/female. Two outliers were excluded: *Synona melanaria* (Mulsant) (1075 eggs/female) and *Coccinella septempunctata* L. (1428 eggs/female). Significant differences were found among the three levels of prey specialization ($F_{2,88} = 3.84$, $P = 0.025$). Monophagous species had a significantly lower fecundity (n = 10, E = 281.4 ± 87.70) than polyphagous species (n = 22, E = 637.67 ± 86.47). Oligophagous were not significantly different (n = 61, E = 471.43 ± 46.45) (Fig. 3)

Voltinism was retrieved for 72 ladybird species; 44 out of 49, i.e. 90% of the oligopaghous species, were multivoltine and 12 out of 15, i.e. 80% of the polyphagous species were also multivoltine. In contrast, 5 out of 8, i.e. 60% of the monophagous species were monovoltine. Voltinism was significantly influenced by the degree of prey specialization: ($\chi^2 = 8.35$; df = 2; $P = 0.015$) (Fig. 4). Polyphagous ladybirds are 11.67 times more probable to be multivoltine in comparison with monophagous species. For oligophagous species the same probability is 6.67 higher in comparison with monophagous ones.

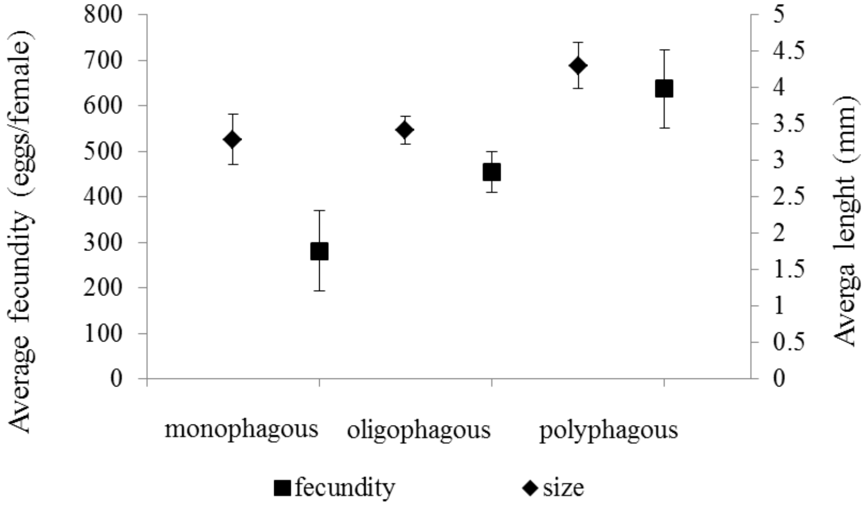

Fig. 3. Mean (± SE) body length (n = 152 species) and fecundity (eggs/female, n= 93 species) of predatory ladybirds, according to their prey specialization (monophagous, oligophagous and polyphagous).

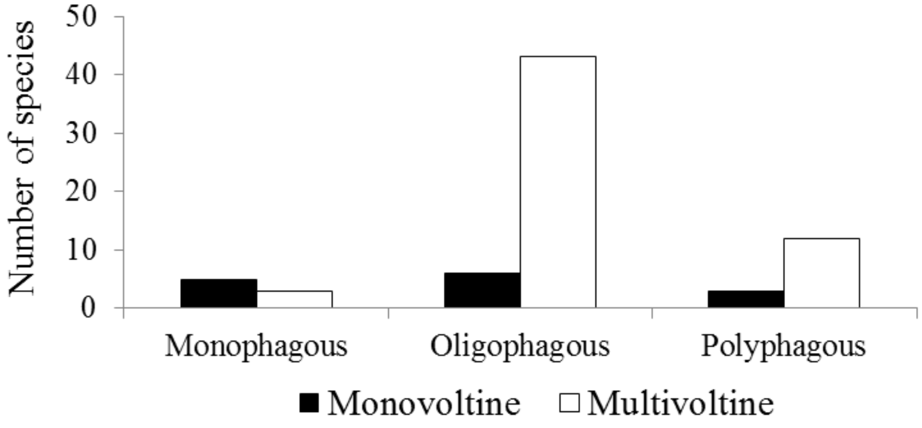

Fig. 4. Association of 72 ladybird species, according to prey specialization (monophagous, oligophagous and polyphagous) and their type of voltinism (monovoltine and multivoltine).

The use of chemical cues by predatory ladybirds was only found for 19 species (Table 1). Most of the species were either polyphagous or oligophagous, and mostly respond to volatiles of the plant attacked by the prey. A single case of attraction to the sexual pheromone of the prey was reported in a monophagous ladybird, *I. rondensis*. The aphid alarm pheromone (b-farnesene) was reported as attractant to ladybirds in four cases, all belonging to the tribe Coccinellini, including polyphagous and oligophagous species.-

Prey specialization of the ladybirds in relation to host plant specialization of the prey

When considering the three-trophic level classification, we found that most of the species fall into category SG (110 out of 186, 59%), with specialized predators preying on generalist preys, followed by category GG (53 out of 186, 28%) where both predator and prey are generalists. Only 2 species out of 186, 1% belong to category GS (*Brumoides septentrionis* (Leng) and *Aphidecta obliterata* (L.), corresponding to generalist predators and specialized prey. Category SS, where both predator and prey are specialists, was represented by 21 ladybird species out of 186, 11.3% (Fig. 5).

A strong and positive association ($\chi^2 = 9.529$; df = 2; $P = 0.009$) was found between prey specialization of ladybirds and host plant specialization of the prey, using a Chi-square test with 100 000 Monte Carlo simulations. Six monophagous species were found to prey on specialist preys and 16 in generalists. Seventeen oligophagous species were found to prey on specialist preys and 112 in generalists. All the 35 polyphagous species prey on generalist species.

Table 1. Chemical cues used to detect prey for 18 species of Coccinellidae.

Species	**Feeding guild**	**Prey specialization**	**Chemical cue type**	**Compound**	**Reference**
Adalia bipunctata	Aphidoidea	oligophagous	aphids' alarm pheromone	(E)-b-farnesene	Omkar & Pervez, 2005
Aiolocaria hexaspilota	Chrysomelidae	oligophagous	prey attacked plants	plant volatiles	Yoneya *et al.*, 2009
Anatis ocellata	Aphidoidea	oligophagous	pine volatiles	plant volatiles	Sloggett, 2008a
Chilocorus nigritus	Coccoidea	oligophagous	prey attacked plants	Prey odour + plant volatiles	Ponsonby & Copland, 1995
Chilocorus rubidus	Coccoidea	oligophagous	prey attacked plants	plant volatiles	Yang , 2009
Coccinella magnifica	Aphidoidea	oligophagous	ant trail pheromones	ant pheromones	Godeau *et al.*, 2009
Coccinella septempunctata	Aphidoidea	oligophagous	prey attacked plants	plant volatiles	Zhu & Park, 2005
Coccinella undecimpunctata	Hemiptera	polyphagous	aphids' alarm pheromone	(E)-b-farnesene	Khidr *et al.*, 2011
Cryptolaemus montrouzieri	Hemiptera	polyphagous	prey odour	-	Heidari & Copland, 1992
Cycloneda sanguinea	Hemiptera	polyphagous	prey attacked plants	plant volatiles	Heit *et al.*, 2005; Sarmento *et al.*, 2007; Heit *et al.*, 2008
Diomus hennesseyi	Coccoidea	oligophagous	prey odour	-	Borowka & Hummel, 1997
Diomus seminulus	Hemiptera	polyphagous	prey attacked plants	plant volatiles	Auad *et al.*, 2013
Hippodamia convergens	Hemiptera Tysanoptera	polyphagous	aphids' alarm pheromone	(E)-b-farnesene	Acar *et al.*, 2001
Harmonia axyridis	Hemiptera Lepidoptera Coleoptera	polyphagous	Aphids' alarm pheromone	(E)-b-farnesene	Verheggen *et al.*, 2007
Eriopis connexa	Hemiptera Acari	polyphagous	prey attacked plants with a conspecific	plant volatiles	Tapia *et al.*, 2010
Exochomus flaviventris	Coccoidea	oligophagous	prey attacked plants	plant volatiles	Le Ru & Makaya-Makosso, 1999
Iberorhyzobius rondensis	Coccoidea	monophagous	odour of the prey	sex pheromone of the prey	Branco *et al.*, 2006
Stethorus gilvifrons	Hemiptera, Acari	polyphagous	prey attacked plants	plant volatiles	Sachin *et al.*, 2008
Stethorus punctillum	Tetranychidae	oligophagous	prey attacked plants	plant volatiles	Lentz *et al.*, 2004

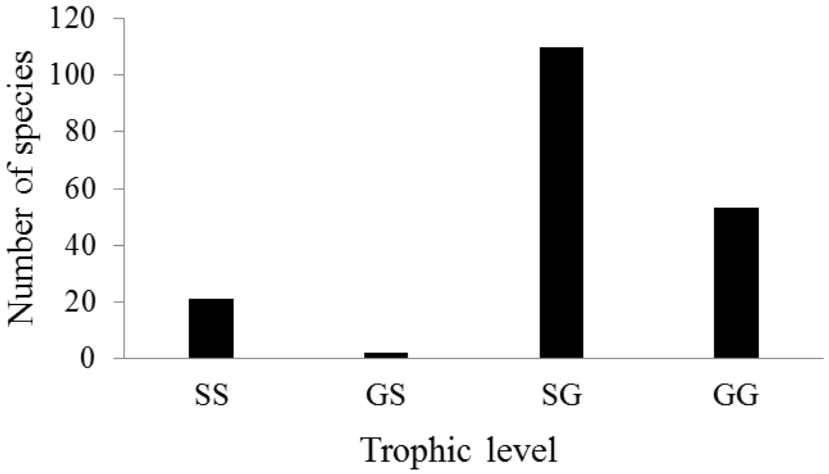

Fig. 5. Distribution of the 186 ladybird species according to the three trophic level classification (SS, GS, SG and GG, see the text for explanation).

Biological control success according to prey specialization of the ladybirds

Forty two cases of classical biological control and 22 cases of biological control on the native range were retrieved (Table 2). More cases were reported for oligophagous (40) and polyphagous (17), than for monophagous species (7). No influence was found of the degree of prey specialization on biological control success, neither for the classical approach ($\chi^2 = 2.419$; df = 2; $P = 0.298$) or for augmentative releases in the native range ($\chi^2 = 0.012$; df = 2; $P = 0.994$) (Fig. 6).

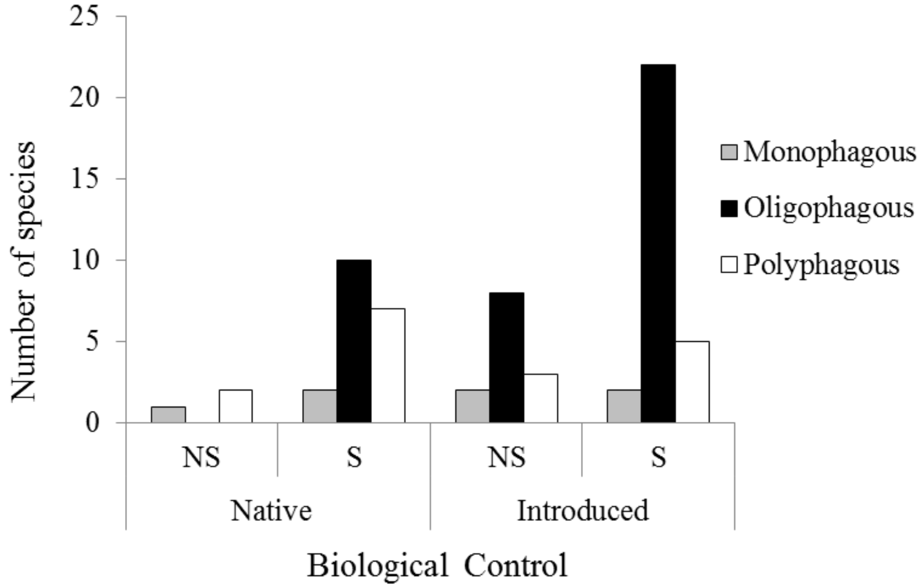

Fig. 6. Success (S) and unsuccess (NS) of 64 biological control cases (native and introduced range) according to prey specialization of the ladybirds (monophagous, oligophagous and polyphagous)

Table 2. Biological control of 58 species: in the native (augmentative releases) or in a novel region (classical biological control). Origin (i.e. native range of the bettle): Af – Afrotropical, Al- Australasian, IM- Indo-Malayan, Nc- Nearctic, Nt-Neotropical, P-Palaeartic; Essential prey: Ac – Acari (Tetranychidae or Eriophyidae), Ad-Adelgidae, Ap-Aphidoidea, Al – Aleyrodoidea, Cc-Coccoidea, Cl – Coleoptera, Hp – Hemiptera, Lp-Lepidoptera, Ps –Psylloidea, Tp-Thripidae; Prey Specialization (PS): mono – monophagous; oli-oligophagous; poly – polyphagous; Biological control success: NS- Non-sucessful, S- Sucessful.

Species	Origin	Prey	PS	Introduced	Native	References
Adalia bipunctata	Pl	Ap	oli	**NS.** Introduced several times with many failed attempts.	-	Omkar & Pervez, 2005.
Adalia tetraspilota	IM	Ap	oli	**NS**. Released to control *Adelges piceae* in USA/Canada but not established.	-	Zilahi-Balogh *et al.*, 2002.
Aphidecta obliterata	Pl	Ap	oli	**S**. The most abundant exotic predator of *Adelges piceae* in British Columbia. It significantly reduced its densities	-	Humble, 1994; Montgomery & Lyon, 1996.
Axinoscymnus cardilobus	Pl	Al	oli	-	**S**. Effective biological control agent of *Bemesia tabaci* in China.	Huang *et al.*, 2006.
Azya orbigera	Nt	Cc	oli	**S.** Together with two other Cocccinellid predators it has contributed to the biological control of *Coccus viridis* in *Plumeria* spp. in Hawaii.	-	Charanasri & Nishida, 1973.
Brumoides suturalis	IM	Hm Lp	poly	-	**S.** Used against first instar nymphs of *Phenacoccus solenopsis* in various crops, ornamental plants and weeds in Pakistan.	Arif *et al.*, 2012; Khuhro *et al.*, 2012.
Calvia quatuordecimguttata	Pl	A Ps	poly	**NS.** Released in deciduous fruit orchards in central Washington for the control of *Cacopsylla pyricola* without apparent	-	Fye, 1981.
Chilocorus baileyi	Al	Cc	oli	-	**S.** Used in inundative releases for control of *Aonidiella orientalis* in papaya orchards. Effective.	Elder & Bell, 1998.
Chilocorus bijugus	IM	Cc	oli	-	**S.** Used for control of *Quadraspidiotus perniciosus* in Himachal Pradesh and Kashmir.	Gupta, 2005.
Chilocorus bipustulatus	Pl	Cc	oli	**S.** Established in oases of the Air Mountain region of Northern Niger, where it controlled adult females of *Parlatoria blanchardi*.	-	Stansly, 1984.

Chilocorus cacti	Nc	Cc	oli	**S**. Released against *Melanaspis glomerata* in sugarcane in Uttar Pradesh, India. It was effective.	-	Misra *et al.*, 1984.
Chilocorus circumdatus	IM	Cc	oli	**S**. Introduced in Australia (Queensland), where it has controlled the *Unaspis citri* in most orchards.	-	Smith *et al.*, 1995.
Chilocorus kuwanae	Pl	Cc	oli	**S**. Introduced on several states in USA, where it is established and successful controls *Unaspis euonymi*.	-	Hendrickson *et al.*, 1991; Van Driesche *et al.*, 1998; Matadha *et al.*. 2003.
Chilocorus nigritus	IM	Cc	oli	**S**. Successful in many biocontrol programmers and introduced in several regions infested with scale pests.	-	Samways, 1984; Samways *et al.*, 1999.
Cleobora mellyi	Al	Ps Cl Lp	poly	**NS**. Introduced in New Zealand from Australia in the 1970s and 1980s to control of *Paropsis charybdi*. It remained restricted to a single region with no significant impact.	**S.** Inundative augmentative releases of adults beetle were made to control populations of *Chrysophtharta bimaculata* in *Eucalyptus nitens*. Effective.	Bain *et al.*, 1984; Baker *et al.*, 2003; Murray *et al.*, 2008; Withers & Berndt, 2010.
Clitostethus arcuatus	Pl	Al	oli	**S**. Introduced in Egipt and California for control of *Siphoninus phillyreae*. Established in some locations where it controlled the pest.	-	Abd-Rabou, 2006.
Coccinella septempunctata	Pl	A	oli	**NS.** Released several times in the USA to control aphis in crops. No success.	-	Obrycki & Kring, 1998.
Coccinella undecimpunctata	Pl	Hm	poly	**S.** Introduced in New Zealand for control of aphids. It is now spread around the country where it is an important predator.	**-**	Hodek & Honěk, 1996.
Coelophora biplagiata	IM	A	oli	**-**	**S.** Used in augmentative releases together with *Synonycha grandis* to reduce aphids on sugarcane on Guangxi, China. Effective.	Deng *et al.*, 1987.

Coleomegilla maculata	Nc	A Cl Lp	poly	-	**S**. Controls *Leptinotarsa decemlineata*. Commercially available in the USA for augmentative releases.	Groden *et al.*, 1990; Hazzard & Ferro, 1991; Hilbeck & Kennedy, 1996.
Cryptognatha nodiceps	Nt	Cc	oli	**S.** It was successful introduced in the Fiji islands in 1928. It has been used in several successfully classical biological control programs, particularly against A*leurodicus destructor.*		Lopez *et al.*, 2004.
Cryptolaemus montrouzieri	Al	Hm	poly	**S.** Used in several biological control programs. It is an effective natural enemy of certain Hemiptera species, mainly mealybugs.	**S**. Used in several augmentative releases with success.	Obrycki & Kring, 1998; Iperti, 1999; Roy & Migeon, 2010; Kairo *et al.*, 2013.
Delphastus catalinae	Nc	Al	oli	**S.** Introduced in Europe for control of *Bemisia tabaci* and *Trialeurodes vaporariorum*. Established and successful in greenhouses.		Kutuk & Yigit, 2007; Legaspi *et al.*, 2008
Diomus pumilio	Al	Hm	poly	**S.** Introduced from Victoria to California to control *Acizzia uncatoides*. Became established with good results.		Pinnock *et al.*, 1978.
Exochomus flavipes	Af	Cc	oli	**-**	**S.** Used to control *Pulvinaria psidii*, on guava trees in Gahrbiya, Egypt in April/ May	Abd-Rabou, 2011.
Exochomus flaviventris	Af	Cc	oli	-	It was also released in cassava plants on Congo to control *Phenacocccus manihoti*. Effective.	Reyd & Leru, 1992.
Exochomus quadripustulatus	Pl	Hm	poly		**S.** Controlled *Pulvinaria regalis* in ornamental trees in Duisburg, Germany; *Adelges cooleyi* in douglas fir and *Heliococcus bohemicus* on vines on South of France, along with *Chrysoperla sp.*.	Moraal & Steingrover, 1991; Arnold & Sengonca, 2003; Sentenac & Kuntzmann, 2013.

Halmus chalybeus	Al	Hm	oli	**S**. Introduced in New Zealand for control of *Ceroplastes destructor* and *C. sinensis.* Effective.	-	Lo & Chapman, 2001.
Harmonia axyridis	Pl	Hm	poly	**S**. Released in North America were it is an effective control of aphids in several crops and orchards. Established in other continents: Africa, S. America and Europe were it is also effective.	-	Roy & Migeon, 2010.
Harmonia conformis	Al	A Cl Ps	poly		**NS**. Inundative releases of the beetle, together with *Cleobora mellyi* were performed to control *Chrysophtharta bimaculata* eggs. The beetle is not very efficacious.	Baker *et al.*, 2003; Coutanceau, 2009
Harmonia dimidiata	IM	Ap	oli	**S.** Introduced in Russia from Vietnam and China for control of aphids in greenhouses. It was very effective.	-	Kuznetsov & Pang, 2002.
Harmonia eucharis	IM	Ap Ad	oli	**NS.** Released against *Adelges piceae* in Canada/USA between 1933 -1969, without becoming established.	-	Zilahi-Balogh *et al.*, 2002.
Hippodamia convergens	Nc	Hm Tp	poly	**NS.** Introduced in Europe for control of aphids, it is not known if its established.	**NS.** Used as biocontrol in North America. Vey ineffective due to adult dispersal.	Roy & Migeon, 2010.
Hyperaspis notata	Nt	Cc	oli	-	**S.** Introduced in Africa for control of *Phenacoccus manihoti* on cassava plant. Effective.	Herren, 1990.
Hyperaspis pantherina	Nt	Cc	mono	**S.** Between 1908 and 1959, the coccinellid was released for the biological control of *Insignorthezia insignis* in Hawaii, 4 African countries and Peru. Substantial control was reported after all the releases.	-	Fowler, 2004.
Micraspis discolor	IM	Hm Ac	poly	-	**S**. Augmentative releases of *M. discolor*, to control *Planococcus citri* populations on Bangladesh. In 3 weeks, they reduced the population of mealybugs.	Islam *et al.*, 2007.

Nephaspis bicolor	Nc	Al	oli	**S.** Introduced in Hawaii, West Africa and Asia for control of *Aleurodicus dispersus*. Control was achieved together with the parasitoid *Encarsia sp*.	-	Lopez & Kairo, 2003; Lopez, 2008.
Nephaspis oculatus	Nt	Al	oli	**S**. Introduced from Honduras, Trinidad, and the West Indies to Hawaii in 1979-1980 where it has become effective in biological control of *Aleurodicus dispersus.*	-	Liu *et al.*, 1997; Liu & Stansly, 2005.
Nephus reunioni	Af	Hm	oli	**S.** Introduced and established in several European countries and Madagascar for control of *Planococcus citri*.	-	Izhevsky & Orlinsky, 1988; Roy & Migeon, 2010.
Olla v-nigrum	Nt	Hm Cl Ac	poly	**S**. Introduction of the beetle to control *Heteropsylla cubana* in Asia and Pacific countries. Effective.	-	Chazeau *et al.*, 1991; Michaud, 2001.
Pharoscymnus flexibilis	IM	Cc	oli		**S.** Introduced into Himachal Pradesh, India, and released in 1983-86 against *Quadraspidiotus perniciosus* on apples. Effective	Rawat *et al.*, 1988; Thakur *et al.*, 1989.
Pharoscymnus horni	IM	Cc	oli	-	**S.** Together with *Chilocorus nigritus* and *Sticholotis madagassa*, *P.horni* was released in sugarcane plantations in Karnataka, for control of *Melanaspis glomerata*.	Ansari *et al.*, 1989.
Propylea quatuordecimpunctata	Pl	A	oli	**NS.** Released several times in Delaware, New Jersey, and Oklahoma, to control native aphid populations. Poor success.	-	Dysart, 1988; Obrycki & Orr, 1990; Obrycki *et al.*, 1993; Day *et al.*, 1994
Rhyzobius lophanthae	Al	Cc	oli	**NS**. Effective classical biocontrol agent of Diaspididae in several countries in USA and Europe.	-	Iperti, 1999; Stathas, 2001; Roy & Migeon, 2010.

Rhyzobius forestieri	Al	Cc	oli	**S.** Introduced in several countries, in Europe and USA for control of coccids. Quite effective. Also established in the coastal areas of California.	-	Richards, 1981; Iperti *et al.*, 1989; Katsoyannos, 1997.
Rhyzobius ventralis	Al	Cc	mono	**NS.** Introduced several times in California but it failed to become established.	**S**. It was released in New Zealand were it is high successful on *Eriococcus coriaceus.*	Pope, 1981; Richards, 1981.
Rodolia cardinalis	Al	Cc	mono	**S.** Introduced into 33countries to control *Icerya purchasi* and has yielded complete control in 26; substantial control in 4 countries and partial control in 2.	-	Caltagirone & Doutt, 1989; Iperti, 1999.
Rodolia iceryae	Af	Cc	mono	**NS.** Several attempts to use *R.iceryae* in biological control of *Icerya purchasi* Maskell in USA and New Zealand failed.	**S.** It was reintroduced into a plantation to control *Icerya pattersoni* populations. Effective.	Kairo & Murphy, 1995.
Rodolia limbata	Pl	Cc	mono	-	**NS.** Released to control *Drosicha corpulenta* on *Populus* sp. It reduced the pest densities, but complete control was not achieved.	Wang *et al.*, 2002; Jia-zhong *et al.*, 2010.
Sasajiscymnus tsugae	Pl	Ap	oli	**S.** *S. tsugae* was release in the USA for control of *Adelges tsuga*. It was established and is effective.	-	Klunk, 2007; Wiggins *et al.*, 2010.
Scymnodes lividigaster	Al	Ap	oli	**NS.** Introduced in Hawaii to control aphids affecting the sugarcane in citrus plantations. It was established but remained on small numbers.	-	Richards, 1980.
Scymnus coccivora	IM	Cc	oli	**S.** Introduced in Trinidad with *Anagyrus kamali* and *Cryptolaemus montrouzieri*. It was established and *M. hirsutus* populations have been reduced below the economic injury level.	**S.** The beetle was released on guava trees in India to control *M. hirsutus.* It reduced the infestation of the pest.	Persad & Khan, 2002.

Scymnus impexus	Pl	Ap	oli	**S**. Introduced to control the balsam wooly adelgid, *Adelges piceae*, in Canada. Effective.	-	Delucchi, 1954; Zilahi-Balogh *et al.*, 2002.
Serangium parcesetosum	IM	Al	oli	**S**. It has been used to control the citrus whitefly, *Dialeurodes citri* in Georgia and *Bemisia tabaci in Europe*. Effective.	-	Yigit & Canhilal, 2005; Roy & Migeon, 2010.
Stethorus gilvifrons	Pl	Ac Al	poly	-	**S.** Released in greenhouses, where it controlled *Tetranychus urticae*.	Ahmad *et al.*, 2010.
Stethorus nigripes	Al	Ac	oli	***NS.*** About 300 and1000 *S. nigripes* were released in California to control mites in 1974 and 1976, but were not established.	-	Obrycki & Kring, 1998.
Stethorus punctillum	Pl	Ac	oli	***S.*** Introduced on several regions of N. America: effective in IPM systems to control spider mites on peppers and cucumbers, but not tomatoes in greenhouses.	-	Raworth, 2001.
Stethorus siphonulus.	IM	Ac	oli	**S.** It was introduced in Fujian China to control *Panonychus citri.* It supressed populations in citrus orchards in Fujian, China.	-	Huang *et al.*, 1988.

6.5. Discussion

Ladybirds prey specialization

Ladybirds are considered a very specialized group of predators (Giorgi *et al.*, 2009). In this study we found that the intermediate level of specialization, oligophagy, is the most common, since the majority of species (69%) showed to be specialized in a family or in a superfamily of prey species. Only 12% of the studied species were monophagous. On the other extreme, 19% species were polyphagous. Since polyphagous ladybirds have larger and more colorful bodies, they are probably more often studied (Sloggett, 2005) and the percentage of species found in our analysis is probably close to the real proportion of polyphagous species. By contrast since specialists (monophagous) ladybirds are usually more discrete species, with specific habitat requirements and present in low densities (Sloggett, 2005) the number of monophagous species retrieved in our research may be underestimated.

Prey Specialization and Habitat

While stenotopic and eurytopic species were equally represented, a strong association between prey specialization and habitat specialization was found. Most of the monophagous species are stenotopic, whereas polyphagous have a tendency to be eurytopic. Therefore, our results based on quantitative analysis support the theory proposed by Sloggett & Majerus, (2000) according to which prey specialization is linked with habitat specialization. Interestingly, oligophagous species were found to be equally distributed between stenotopic and eurytopic groups.

Several hypotheses have been proposed for explaining why specialized predators tend to remain in the same habitat (Sloggett & Majerus, 2000). One of those hypotheses is that specialists can usually feed on lower prey densities (Sloggett & Majerus, 2000). Another is that, reproduction in the habitat of the specific prey is advantageous since neonate larvae will have available food immediately (Evans, 2003). A predator might also prefer a specific habitat to avoid intra guild competition (e.g., Noriyuki & Osawa, 2012). Further, the use of a specific habitat limits the costs of migration, change to less suitable prey and search for appropriate oviposition places (Dixon, 2000).

On the other hand, under food supply uncertainty (in both quantity and location) an habitat generalist strategy is expected to be more favorable (Rana *et al.*, 2002), as it seems the case for several species of aphidophagous ladybirds, since aphids are less predictive resources (Evans, 2009). In such a situation, it is advantageous for ladybirds to breed in different habitats where different prey species are available, even if some of them are not the most suitable feeding resources, such as happens with *C. septempunctata*, *A. bipunctata* and *Propylea quatuordecimpunctata* L. (Sloggett & Majerus, 2000; Fréchette *et al.*, 2006).

Prey specialization and taxonomy

Prey specialization was found to be conservative at the genus and tribe level, which agrees with other studies (Obrycki *et al.*, 2011). Species within the same genus tend to display the same level of prey specialization. For instance all the seven species of *Chilocorus* considered in our analysis were classified as oligophagous, and all the six *Exochomus* species were classified as oligophagous except for *Exochomus childreni* Mulsant. Yet, several other studies describe cases of congeneric species which do not have the same level of prey specialization, such as *H. axyridis* and *H. yedoensis* (Noriyuki & Osawa, 2012) and *A. bipunctata* and *Adalia decempunctata* (L.) (Ferrer *et al.*, 2010). These cases may support the hypothesis that at the least at the genus level, the evolution of the predator’s prey specialization is not dependent on its phylogeny. However caution must be taken since some genus and tribes of ladybirds are paraphyletic and polyphyletic, such as *Rhyzobius* (Seago *et. al*, 2011).

Prey specialization and host plant specialization of the prey

Since taxonomically close ladybird species tend to belong to the same feeding guild (Giorgi *et al.*, 2009; Magro *et al.*, 2009), we hypothesized that the degree of prey specialization on its host plant might lead to the same level of prey specialization within a certain taxonomic group. In fact, high prey specialization in ladybirds was associated with the two main feeding guilds: aphidophagous and coccidophagous. In our review 14 out of 22 monophagous species were found to prey on scale insects, whereas those that feed on aphids were mainly oligophagous or polyphagous. Because aphids are an instable, transitory prey, aphidophagous predators are often forced to switch habitats in search of alternative prey (Hodek & Honěk, 1996). On the contrary, coccids often form sessile and more stable colonies, allowing coccidophagous species to remain longer within the same habitat and feeding on the same prey (Borges *et al.*, 2011; Dixon *et al.*, 2011).

Prey specialization of ladybirds may be also connected to the specific prey traits (Dixon, 2000; Rana *et al.*, 2002). For instance, specialization on coccids might be associated with the defensive traits of the prey, such as hard and waxy cover scales or toxic compounds demanding higher handling time from the predator (Dixon, 2000; Obrycki *et al.*, 2011). A longer prey handling time requires a higher investment which may imply greater specialization (Pyke, 1984). The specialist ladybird *Anatis mali* (Say) searches more efficiently for pioneer aphids *Mindarus abietinus* Koch, which are usually found in very low densities, than the generalist *H. axyridis*. The monophagous ladybird *I. rondensis* finds its prey, the pine bast scale, *Matsucoccus feytaudi* Ducasse, deep into the bark crevices, by detecting the prey sex pheromone (Branco *et al.*, 2006, 2011; Tavares *et al.*, 2014).

A significant and positive association between prey specialization of ladybirds and host plant specialization of their prey was found. This pattern was suggested by other authors (Strand & Obrycki, 1996). Specialized phytophagous insects are usually restricted to specific host plants, and this may have a cascading effect, restricting the predator's habitat (Sloggett & Majerus, 2000). Further, when a predator is confined to a certain habitat, especially in the larval instar, it will often restrict its feeding range to the preys available in that habitat.

Classification on a three trophic level following Steidle & Van Loon (2003) reveals that specialist predators (oligophagous and monophagous) will consume mainly specialist or generalist prey (SS and SG categories, respectively), but generalist predators will only feed on generalist prey (GG category). In our work, only two species were classified as GS - generalist predators which feed only on specialized prey - which supports the hypothesis that this type of trophic interaction is rare in nature (Steidle & Van Loon, 2003). Yet, category SG, corresponding to specialist predators which feed on generalist preys was the most commonly found in the retrieved species of ladybirds, which reflects the idea that ladybirds may switch habitat in search for their preferable prey, such as in some more specialized species of ladybirds (Hodek & Honěk, 1996).

Body Size and Fecundity

In general it is considered that predator size determines the size of the prey it can feed on (Dixon, 2000; Dixon & Hemptinne, 2001). It has been observed that the smallest ladybird species feed on mites, while the largest ones rather feed on caterpillars or beetle larvae (Dixon & Hemptinne, 2001).Yet, this does not elucidate on a possible relationship between predator size and its degree of prey specialization. For aphidophagous ladybird species, Sloggett (2008b) proposed that body size could be a predictor of prey specialization, suggesting a bell shape; with more specialized species having a size closer to the one of their prey, being either small or large, whilst generalists would present intermediate body sizes. We found that body length differed significantly among different levels of prey specialization in the studied species of ladybirds. In particular, polyphagous species were significantly larger than oligophagous and monophagous species. Similar results were obtained by Dixon & Hemptinne (2001) on 503 species. However, we also found that some of the larger species belong to the monophagous and oligophagous groups, such as *S. grandis* and *H. eucharis*. These Asiatic species with large body size prey on aphids (Annex 1) and were considered outliers. In our study the more polyphagous species were found to be more fecund than oligophagous and monophagous species. Although we did not find a correlation between size and fecundity, this is probably the case: larger species are usually more fecund and lay larger eggs than smaller species, which happens even in the same species between different individuals (Hodek & Honěk, 1996; Dixon & Hemptinne, 2001).

Voltinism

A significant association was found between voltinism and the degree of prey specialization in ladybirds. Specialized ladybirds were more frequently univoltine whereas polyphagous species were more frequently multivoltine. Univoltine species are generally from the northeastern regions, and are more likely to reproduce in a single habitat during the whole season, which may eventually lead to specialization (Sloggett & Majerus, 2000). In these climates, breeding seasons are shorter and synchronized with prey abundance (Sloggett, 2008a). Another possibility is that, it is most relevant for specific predators to synchronize their life cycle with the one of their prey. This adaptation might result into univoltinism if the prey also has a single generation per year. For example several *Scymnus* species which prey on univoltine adelgids are univoltine (Lu & Montgomery, 2001). Other specialist ladybirds whose prey is univoltine, such as *I. rondensis* (Tavares *et al*., 2014) and *A. mali* (Berthiaume *et al.*, 2007) are also univoltine.

Chemical cues

Information on the use of chemical cues was only found for 10% of the reviewed species of ladybirds. Since the use of chemical cues is expected to be more common among predators, regardless of dietary specialization (Steidle & Van Loon, 2003; Obrycki *et al.*, 2011),we may conclude that not enough studies have addressed this relevant aspect of ladybird behavior and that chemical ecology of ladybirds is a largely unexplored field of research. Most of the few studies on this issue reported a ladybird response to the prey’s odors but without specifying the involved compounds. Aphid alarm pheromone and volatiles emitted by plants when damaged by phytophagous insects are the most often reported chemical cues (Table 1). In all but one case, these responses were observed with oligophagous and polyphagous species. This outcome is possibly due to a bias in research studies, and not to a lack of chemical cues in highly specialized ladybird species. For example *I. rondensis* was found to respond to the prey’s sex pheromone (Branco *et al.*, 2006; Tavares *et al.*, 2014).

Biological control

Information on biological control use was only found for 61 species (64 cases) out of the 186 reviewed ladybirds, suggesting that this remains an open question (Obrycki & Kring, 1998; Roy & Migeon, 2010). Some species, which are not part of this 61, were referred as having been released for biological control but with no more details. Further, much more information was found on successful than on unsuccessful cases, although we know the percentage of unsuccessful cases to be very high (Iperti, 1999; Dixon, 2000). This may have induced a publication bias.

No association was found between biological control success and the level of prey specialization, neither in the native nor in the introduced range whereas specificity is considered an important attribute for a biological control agent (Dixon, 2000; Obrycki *et al.*, 2011). For classical biological control, a higher number of successful cases were found for oligophagous species, although they were the most commonly used predators (Table 2). However, and surprisingly, a high number of successful cases were also found amongst polyphagous species as already noticed by Symondson *et al.* (2002). Generalist predators may be more able to shift between habitats and then follow their prey (Evans *et al.*, 2011). However, generalist predators may then have a higher impact on non-target species (Roy & Migeon, 2010; Obrycki *et al.*, 2011). Non-target effects were not considered in our analysis due to scarcity of information.

Of the four monophagous species reported for classical biological control, two cases were a complete success: *R. cardinalis* on the control of *Icerya purchasi* Maskell and *Hyperaspis pantherina* Fürsch on the control of *Insignorthezia insignis* (Browne). The two others were unsuccessful: *Rhyzobius ventralis* (Erichson) failed to become established in California and control coccids and *Rodolia iceryae* Janson failed to control *I. purchasi*. In the first case this was due to a low dispersal capacity of the predator. In the second case, the predator was incorrectly chosen, since the target prey *I. purchasi* was outside of the host range of *R. iceryae*. However the number of reported cases is too low to conclude on any effect of prey specialization on classical biocontrol effectiveness.

Most of the reported cases on augmentative releases were successful, especially with oligophagous species. Augmentative releases are known to quickly reduce pests (Obrycki & Kring, 1998), although predators may fail to stay long in the same habitat (Dixon, 2000).

General conclusions

Based on a thorough bibliographic research we classified the degree of prey and habitat specialization for 186 ladybird species, as well as their specific life and ecological traits. First, as predicted by Sloggett & Majerus (2000), our data confirm that prey and habitat specialization are positively correlated. Further, ladybird specialization is linked with the one of their prey. Consequently, different feeding guilds are associated with different levels of prey specialization; e.g. coccidophagous and acararophagous ladybirds are more specific than aphidophagous ladybirds. Because those feeding guilds are often associated with different taxonomic groups (Giorgi *et al.*, 2009), this further justifies a tendency to conserve similar prey specialization among close taxonomic groups.

Ladybird's prey specialization was found to be associated with some specific traits such as fecundity, size and voltinism. Generalists are usually larger, more fecund and multivoltine, whereas specialized species have a tendency for being less fecund, smaller and univoltine.

These outcomes may be of interest when looking for relevant biocontrol agents. In particular they suggest that predatory ladybirds should be selected depending on the target prey characteristics, such as its diet breadth, habitat specialization and voltinism. By contrast in our review we did not find any relationship between the biological control success and a high degree of prey specialization in ladybirds. However monophagous species are poorly studied and their use in biological control is apparently not very common. In some specific cases, their success is complete and their non-target impact is none. Nevertheless further studies are needed to ascertain the importance of prey specialization for the effectiveness of ladybirds as biocontrol agents.

6.6. References

Abd-Rabou, S. (2006) Biological control of the pomegranate whitefly, *Siphoninus phillyreae* (Homoptera: Aleyrodidae: Aleyrodinae) by using the bioagent, *Clitostethus arcuatus* (Coleoptera: Coccinellidae). *Journal of Entomology* **3**, 331-335.

Abd-Rabou, S. (2011) Field efficacy of parasitoid, *Coccophagus scutellaris* (Hymenoptera: Aphelinidae) and the predator, *Exochomus flavipes* (Coleoptera: Coccinellidae) against *Pulvinaria psidii* (Hemiptera: Coccidae) in Egypt. *Journal of Biological Control* **25**, 85-91.

Acar, E., Medina, J., Lee, M. & Booth, G. (2001) Olfactory behavior of convergent lady beetles (Coleoptera: Coccinellidae) to alarm pheromone of green peach aphid (Hemiptera: Aphididae). *The Canadian Entomologist* **133**, 389-397.

Ahmad, M., Mofleh, M. & Haloum, M. (2010) The efficiency of the predator *Stethorus gilvifrons* Mulsant to control the two spotted spider mite *Tetranychus urticae* Koch in greenhouse eggplant. *Arab Journal of Plant Protection* **28**, 169-174.

Ansari, M.A., Pawar, A.D., Murthy, K.R.K. & Ahmed, S.N. (1989) Sugarcane scale, *Melanaspis glomerata* Green and its biocontrol prospects in Karnataka. *Plant Protection Bulletin* **41**, 21-23.

Arif, M.I., Muhammad, R., Shabana, W., Nasir, M. & Abdul, G. (2012) Studies on cotton mealybug, *Phenacoccus solenopsis* (Pseudococcidae: Homoptera), and its natural enemies in Punjab, Pakistan. *International Journal of Agriculture and Biology* **14**, 557-562.

Arnold, C. & Sengonca, C. (2003) Possibilities of biological control of the horse chestnut scale insect, *Pulvinaria regalis* Canard (Homoptera: Coccidae), on ornamental trees by releasing its natural enemies. *Zeitschrift für Pflanzenkrankheiten und Pflanzenschutz* **110**, 591-601.

Auad, A.M., Fonseca, M.G., Monteiro, P.H., Resende, T.T. & Santos, D.R. (2013) Aspects of the biology of the lady beetle *Diomus seminulus* (Coleoptera: Coccinellidae): a potential biocontrol agent against the yellow sugarcane aphid in Brazil. *Annals of the Entomological Society of America* **106**, 243-248.

Bain, J., Singh, P., Ashby, M. & Van Boven, R. (1984) Laboratory rearing of the predatory coccinellid *Cleobora mellyi* for biological control of *Paropsis charybdis* in New Zealand. *Entomophaga* **29**, 237-244.

Baker, S.C., Elek, J.A., Bashford, R., Paterson, S.C., Madden, J. & Battaglia, M. (2003) Inundative release of coccinellid beetles into eucalypt plantations for biological control of chrysomelid leaf beetles. *Agricultural and Forest Entomology* **5**, 97-106.

Ben-Dov, Y., Miller, D.R. & Gibson, G.A.P. (2001) ScaleNet, Life Histories. Available online at http://www.sel.barc.usda.gov/scalenet/lifehist.htm.

Berthiaume, R., Hebert, C. & Cloutier, C. (2007) Comparative use of *Mindarus abietinus* (Homoptera: Aphididae) by two coccinellids (Coleoptera: Coccinellidae), the native *Anatis mali* and the exotic *Harmonia axyridis*, in a Christmas tree plantation. *Environmental Entomology* **36**, 319-328.

Blackman, R. & Eastop, V. (2014) Aphids on World Plants. Available online at http://www.aphidsonworldsplants.info/.

Borges, I., Soares, A.O., Magro, A. & Hemptinne, J.-L. (2011) Prey availability in time and space is a driving force in life history evolution of predatory insects. *Evolutionary Ecology* **25**, 1307-1319.

Borowka, R. & Hummel, H.E. (1997) Olfactometric response of one introduced exotic and two indigenous coccinellid beetle predators of the cassava mealybug in Malawi. *Mitteilungen der Deutschen Gesellschaft für allgemeine und angewandte Entomologie* **11**, 529-532.

Branco, M., Franco, J.C., Dunkelblum, E., Assael, F., Protasov, A., Ofer, D. & Mendel, Z. (2006) A common mode of attraction of larvae and adults of insect predators to the sex pheromone of their prey (Hemiptera: Matsucoccidae). *Bulletin of Entomological Research* **96**, 179-185.

Branco, M., van Halder, I., Franco, J.C., Constantin, R. & Jactel, H. (2011) Prey sex pheromone as kairomone for a new group of predators (Coleoptera: Dasytidae, Aplocnemus spp.) of pine bast scales. *Bulletin of Entomological Research* **101**, 667-674.

Caltagirone, L. & Doutt, R. (1989) The history of the vedalia beetle importation to California and its impact on the development of biological control. *Annual Review of Entomology* **34**, 1-16.

Charanasri, V. & Nishida, T. (1973) Relative abundance of three Coccinellid predators of the green scale, *Coccus viridis* (Green) on Plumeria trees. *Proceedings of the Hawaiian Entomological Society* **22**, 27-32.

Chazeau, J., Bouye, E. & Delarbogne, L.B. (1991) Development and life table of *Olla-V-nigrum* Col., Coccinellidae, a natural enemy of *Heteropsylla cubana* Hom, Psyllidae introduced in New Caledonia. *Entomophaga* **36**, 275-285.

Coutanceau, J. (2009) *Harmonia conformis* (Boisduval, 1835): an Australian coccinellid introduced and acclimatized in France (Col. Coccinellidae). *Bulletin de la Société Entomologique de France* **114,** 110.

Day, W., Prokrym, D., Ellis, D. & Chianese, R. (1994) The known distribution of the predator *Propylea quatuordecimpunctata* (Coleoptera: Coccinellidae) in the United States, and thoughts on the origin of this species and five other exotic lady beetles in eastern North America. *Entomological News* **105**, 244-256.

Delucchi, V. (1954) *Pullus impexus* (Muls.) (Coleoptera, Coccinellidae): A Predator of *Adelges piceae* (Ratz.) (Hemiptera, Adelgidae): with Notes on Its Parasites (European Investigations). Master Thesis, Cambridge University, UK.

Deng, G.R., Yang, H.H. & Jin, M.X. (1987) Augmentation of coccinellid beetles for controlling sugarcane woolly aphid. *Chinese Journal of Biological Control* **3**, 166-168

Dixon, A.F.G. (2000) *Insect predator-prey dynamics: Ladybird Beetles and Biological Control*. p.288. New York, USA, Cambridge University Press.

Dixon, A., Agarwala, B., Hemptinne, J.-L., Honěk, A. & Jarošík, V. (2011) Fast–slow continuum in the life history parameters of ladybirds revisited. *European Journal of Environmental Sciences* **1**, 2336-1964.

Dixon, A.F.G. & Hemptinne, J.L. (2001) Body size distribution in predatory ladybird beetles reflects that of their prey. *Ecology* **82**, 1847-1856.

Dysart, R.J. (1988) The European lady beetle *Propylea quatuordecimpunctata*: new locality records for North America (Coleoptera: Coccinellidae). *Journal of the New York Entomological Society* **96,** 119-121.

Elder, R.J. & Bell, K.L. (1998) Establishment of *Chilocorus* spp. (Coleoptera: Coccinellidae) in a *Carica papaya* L. orchard infested by *Aonidiella orientalis* (Newstead) (Hemiptera: Diaspididae). *Australian Journal of Entomology* **37**, 362-365.

Evans, E., Soares, A. & Yasuda, H. (2011) Invasions by ladybugs, ladybirds, and other predatory beetles. *BioControl* **56**, 597-611.

Evans, E.W. (2003) Searching and reproductive behaviour of female aphidophagous ladybirds (Coleoptera: Coccinellidae): a review. *European Journal of Entomology* **100**, 1-10.

Evans, E.W. (2009) Lady beetles as predators of insects other than Hemiptera. *Biological Control* **51**, 255-267.

Ferrer, A., Dixon, A.F., Gibernau, M. & Hemptinne, J.L. (2010) Ovarian dynamics and specialisation in ladybirds. *Ecological Entomology* **35**, 100-103.

Fowler, S.V. (2004) Biological control of an exotic scale, *Orthezia insignis* Browne (Homoptera : Ortheziidae), saves the endemic gumwood tree, *Commidendrum robustum* (Roxb.) DC. (Asteraceae) on the island of St. Helena. *Biological Control* **29**, 367-374.

Fréchette, B., Dixon, A.F.G., Alauzet, C., Boughenou, N. & Hemptinne, J.-L. (2006) Should aphidophagous ladybirds be reluctant to lay eggs in the presence of unsuitable prey? *Entomologia Experimentalis et Applicata* **118**, 121-127.

Futuyma, D.J. & Moreno, G. (1988) The Evolution of Ecological specialization. *Annual Review of Ecology and Systematics* **19**, 207-233.

Fye, R.E. (1981) Rearing and release of coccinellids for potential control of pear psylla pp. 9 in *Advances in Agricultural Technology*. Agricultural Research Service, United States Department of Agriculture.

Gillett-Kaufman, J.L. (1996) Featured Creatures. Available online at http://entnemdept.ufl.edu/creatures.

Giorgi, J.A., Vandenberg, N.J., McHugh, J.V., Forrester, J.A., Ślipiński, A., Miller, K.B., Shapiro, L.R. & Whiting, M.F. (2009) The evolution of food preferences in Coccinellidae. *Biological Control* **51**, 215-231.

Godeau, J.F., Hemptinne, J.L., Dixon, A.F.G. & Verhaeghe, J.C. (2009) Reaction of ants to, and feeding biology of, a congeneric myrmecophilous and non-myrmecophilous ladybird. *Journal of Insect Behavior* **22**, 173-185.

González, G. (2006) Los Coccinellidae de Chile. Available online at http://www.coccinellidae.cl.

González, G. (2007) Los Coccinellidae de Perú. Available online at http://www.coccinellidae.cl/paginasWebPeru/Paginas/InicioPeru.php.

Groden, E., Drummon, F.A.; Casafrande, R.A.; Yness, H & Dean, L..(1990) *Coleomegilla maculata* (Coleopera: Coccinellidae): Its Predation upon the Colorado Potato Beetle (Coleoptera: Chrysomelidae) and Its Incidence in Potatoes and Surrounding Crops. *Journal of Economic Entomology* **83**, 1306-1315.

Gupta, P.R. (2005) Biological control of San Jose scale in India - An overview. pp. 427-432 in *Proceedings of the VIIth International Symposium on Temperate Zone Fruits in the Tropics and Subtropics* organized by the *International Society for Horticultural Science*, Nauni, Solan (India), 14 October 2003.

Hazzard, R.V. & Ferro, D.N. (1991) Feeding Responses of Adult *Coleomegilla maculata* (Coleoptera: Coccinellidae) to Eggs of Colorado Potato Beetle (Coleoptera: Chrysomelidae) and Green Peach Aphids (Homoptera: Aphididae). *Environmental Entomology* **20**, 644-651.

Heidari, M. & Copland, M. (1992) Host finding by *Cryptolaemus montrouzieri* (Col., Coccinellidae) a predator of mealybugs (Hom., Pseudococcidae). *Entomophaga* **37**, 621-625.

Heit, G., Castresana, J., Puhl, L. & Mareggiani, G. (2005) Role of volatiles emitted by cultivated and wild Solanaceae in foraging behaviour of coccinellid predators. *Idesia* **23**, 13-19.

Heit, G.E., Cohen, G. & Mareggiani, G. (2008) Impact of odor signals on *Cycloneda sanguinea* (Coleoptera : Coccinellidae) searching behavior. *Ciencia E Investigacion Agraria* **35**, 205-210.

Hendrickson, R.M., Drea, J.J. & Rose, M. (1991) A distribution and establishement program for *Chilocorus-kuwanae* (Silvestri) (Coleoptera, Coccinellidae) in the United-States.*Proceedings of the Entomological Society of Washington* **93**, 197-200.

Herren, H.R. (1990) The use of natural enemies for controlling the cassava pests in Africa Tukuba-gun. p. 23 in *FFTC-NARC International Seminar on 'The use of parasitoids and predators to control agricultural* pests', Japan, Tukuha Science City, Ibaraki-ken, 2-7 October 1989.

Hilbeck, A. & Kennedy, G.G. (1996) Predators feeding on the Colorado potato beetle in insecticide-free plots and insecticide-treated commercial potato fields in eastern North Carolina. *Biological Control* **6**, 273-282.

Hippa, H., Koponen, S. & Laine, T. (1978) On the feeding biology of *Coccinella hieroglyphica* L.(Col., Coccinellidae). *Reports from the Kevo Subarctic Research Station* **14**, 18-20.

Hodek, I. & Honěk, A. (1996) *Ecology of Coccinellidae*. p. 464. Dordrecht, The Netherlands, Kluwer Academic Publishers.

Hodek, I. & Honěk, A. (2009) Scale insects, mealybugs, whiteflies and psyllids (Hemiptera, Sternorrhyncha) as prey of ladybirds. *Biological Control* **51**, 232-243.

Honěk, A. (1985) Habitat preferences of aphidophagous coccinellids [Coleoptera]. *Entomophaga* **30**, 253-264.

Huang, P.K., Luo, X.N. & Song, S.L. (1988) Control of *Panonychus citri* using *Stethorus siphonulus* Kapur in southeastern China. *Acta Phytophylactica Sinica* **15**, 1-6.

Huang, Z., Ren, S.X. & Yao, S.L. (2006) Life history of *Axinoscymnus cardilobus* (Col., Coccinellidae), a predator of *Bemisia tabaci* (Hom., Aleyrodidae). *Journal of Applied Entomology* **130**, 437-441.

Humble, L.M. (1994) Recovery of additional exotic predators of balsam woolly adelgid *Adelges piceae* (Ratzeburg) (Homoptera: Adelgidae), in Brithish Columbia. *The Canadian Entomologist* **126**, 1101-1103

IBM (2011) SPSS Statistics 20 core systems user’s guide.

Iperti, G. (1999) Biodiversity of predaceous coccinellidae in relation to bioindication and economic importance. *Agriculture, Ecosystems & Environment* **74**, 323-342.

Iperti, G., Giuge, L. & Roger, J.P. (1989) The establishment of *Rhyzobius forestieri* (Col., Coccinellidae) on the Island of Porquerolles. *Entomophaga* **34**, 365-372.

Islam, M.R., Islam, K.S., Ahmad, M., Uddin, M.F. & Ahad, M.A. (2007) Biological control of citrus mealybug *Planococcus citri* (Risso) by ladybird beetle, *Menochilus sexmaculatus* F. and *Micrapis discolor* F. in Bangladesh. *Journal of Subtropical Agricultural Research and Development* **5**, 332-335.

IUCN (2011) Habitats Classification Scheme (Version 3.1) in The IUCN Red List of Threatened Species. Version 2013.2. Available online at http://www.iucnredlist.org.

Izhevsky, S. & Orlinsky, A. (1988) Life history of the imported *Scymnus* (*Nephus*) *reunioni* (Coleoptera: Coccinellidae) predator of mealybugs. *Entomophaga* **33**, 101-114.

Jia-zhong, G., Tong-bin, G., HU-cheng, W., Guang-biao, W., Wei, D. & Si-he, Z. (2010) A progress of research on biology and applied technology of *Rodolia limbata* Motschulsky. *Journal of Jiangsu Forestry Science & Technology* **4**, 50-54.

Kairo, M. & Murphy, S. (1995) The life history of *Rodolia iceryae* Janson (Col., Coccinellidae) and the potential for use in innoculative releases against *Icerya pattersoni* Newstead (Hom., Margarodidae) on coffee. *Journal of Applied Entomology* **119**, 487-491.

Kairo, M.T.K., Paraiso, O., Gautam, R.D. & Peterkin, D.D. (2013) *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. *CAB Reviews* **8**, 1-20.

Kajita, Y., Evans, E.W. & Yasuda, H. (2009) Reproductive responses of invasive and native predatory ladybeetles (Coleoptera: Coccinellidae) to varying prey availability. *Environmental Entomology* **38**, 1283-1292.

Katsoyannos, P. (1997) Status and importance of *Rhyzobius forestieri* (Col.: Coccinellidae) on citrus at chios Island, Greece, nine years after its introduction. *Entomophaga* **42**, 387-392.

Khidr, A.A., El-Fatih, M.M., Nada, M.S. & El-Nemaky, I.H. (2011) Comparative evaluation between aphid alarm pheromone and conventional methods for controlling the green peach aphid, *Myzus persicae* Sulz. in pepper fields. *Egyptian Journal of Biological Pest Control* **21**, 45-49.

Khuhro, S.N., Lohar, M.K., Abro, G.H., Talpur, M.A. & Rabdino, K. (2012) Feeding potential of ladybird beetle, *Brumus suturalis* Fabricius (Coleoptera: Coccinellidae) on cotton mealy bug *Phenacoccus solenopsis (*Tinsley) in laboratory and field. Sarhad Jorunal of Agriculture **28**, 259-265.

Klunk, W.M. (2007) *Sasajiscymnus tsugae (Coleoptera: Coccinellidae) as a biological control for hemlock wolly adelgid (Adelges tsugae (Hemiptera: Adelgidae) on eastern hemlock (Tsugae canadensis) and carolina hemlock (T. caroliniana)*. Master Thesis. Clemson University, South Carolina, U.S.

Kutuk, H. & Yigit, A. (2007) Life table of *Delphastus catalinae* (Horn) (Coleoptera : Coccinellidae) on cotton whitefly, *Bemisia tabaci* (Genn.) (Homoptera : Aleyrodidae) as prey. *Journal of Plant Diseases and Protection* **114**, 20-25.

Kuznetsov, V. & Pang, H. (2002) Employment of Chinese Coccinellidae in biological control of aphids in greenhouse in Primorye. *Far Eastern Entomologist* **119**, 1-5.

Le Ru, B. & Makaya-Makosso, J.P. (1999) Importance of semiochemicals in prey habitat location by the coccinellid predator *Exochomus flaviventris* (Coleoptera : coccinellidae). *Annales de la Société Entomologique de France* **35**, 203-205.

Legaspi, J.C., Simmons, A.M. & Legaspi, B.C., Jr. (2008) Life history of *Delphastus catalinae*: A predator of *Bemisia tabaci*. *Journal of Insect Science* **8**, 27-27.

Lentz, C., Petersen, G., Molck, G. & Wyss, U. (2004) Olfactory orientation of the spider mite predator *Stethorus punctillum*. *Mitteilungen der Deutschen Gesellschaft für allgemeine und angewandte Entomologie* **14**, 191-194.

Liu, T., Stansly, P.A., Hoelmer, K.A. & Osborne, L.S. (1997) Life history of *Nephaspis oculatus* (Coleoptera: Coccinellidae), a predator of *Bemisia argentifolii* (Homoptera: Aleyrodidae). *Annals of the Entomological Society of America* **90**, 776-782.

Liu, T.X. & Stansly, P.A. (2005) Timing and release rates for control of *Bemisia tabaci* (Homoptera : Aleyrodidae) by *Nephaspis oculatus* (Coleoptera : Coccinellidae) under confined conditions. *Journal of Entomological Science* **40**, 74-79.

Lo, P.L. & Chapman, R.B. (2001) Predation by *Halmus chalybeus* (Coleoptera: Coccinellidae) on *Ceroplastes destructor* and *C. sinensis* (Hemiptera: Coccidae:

Ceroplastinae) Infesting Citrus in Northland, New Zealand. *Biocontrol Science and Technology* **11**, 57-66.

Lopez, V. & Kairo, M. (2003) Prey range of *Nephaspis bicolor* Gordon (Coleoptera: Coccinellidae), a potential biological control agent of *Aleurodicus dispersus* and other *Aleurodicus spp*.(Homoptera: Aleyrodidae). *International Journal of Pest Management* **49**, 75-88.

Lopez, V., Kairo, M. & Irish, J. (2004) Biology and prey range of *Cryptognatha nodiceps* (Coleoptera: Coccinellidae), a potential biological control agent for the coconut scale, *Aspidiotus destructor* (Hemiptera: Diaspididae). *Biocontrol Science and Technology* **14**, 475-485.

Lopez, V. (2008) Evaluation of *Nephaspis bicolor* gordon (Coleoptera: coccinellidea) as a biological control agent of aleyrodidae (particularly *Aleurodicus* spp.)(Hemiptera: sternorrhyncha).

Lu, W. & Montgomery, M.E. (2001) Oviposition, development, and feeding of *Scymnus* (*Neopullus*) *sinuanodulus* (Coleoptera: Coccinellidae): a predator of *Adelges tsugae* (Homoptera: Adelgidae). *Annals of the Entomological Society of America* **94**, 64-70.

Magro, A., Lecompte, E., Magne, F., Hemptinne, J.L. & Crouau-Roy, B. (2009) Phylogeny of ladybirds (Coleoptera: Coccinellidae): are the subfamilies monophyletic? *Molecular Phylogenetics and Evolution* **54**, 833-848.

Majerus, M. & Fowles, A. (1989) The rediscovery of the 5-spot ladybird beetle (*Coccinella 5-punctata* L.) (Col., Coccinellidae) in Britain. *Entomologist's Monthly Magazine* **125**, 177-181.

Matadha, D., Hamilton, G.C., Hughes, M.G. & Lashomb, J.H. (2003) Distribution of natural enemies of euonymus scale, *Unaspis euonymi* (Comstock) (Homoptera : Diaspididae), in New Jersey. *Environmental Entomology* **32**, 602-607.

McDonald, J.H. (2009) Small numbers in chi-square and G-tests pp. 80-83 in McDonald, J.H. (Ed.) *Handbook of Biological Statistics*. Sparky House Publishing, Baltimore, Maryland.

McEvoy, P.B. (1996) Host specificity and biological pest control. *BioScience,* 401-405.

Michaud, J. (2001) Numerical response of *Olla v-nigrum* (Coleoptera: Coccinellidae) to infestations of Asian citrus psyllid,(Hemiptera: Psyllidae) in Florida. *Florida Entomologist* **84**, 608-612.

Migeron, A. & Dorkeld, F. (2006-2013) Spider Mites Web: a comprehensive database for the Tetranychidae. Avaiable online at http://www.montpellier.inra.fr/CBGP/spmweb.

Misra, M., Pawar, A. & Samujh, R. (1984) Biological control field trials with *Chilocorus cacti* Linnaeus (Coleoptera: Coccinellidae)-an exotic predator of sugarcane scale insect *Melanaspis glomerata* (Green). *Indian Journal of Entomology* **46**, 374-375.

Montgomery, M.E. & Lyon, S.M. (1996) Natural enemies of adelgids in North America: their prospect for biological control of *Adelges tsugae* (Homoptera: Adelgidae). pp. 89-102 in *Proceedings, The First Hemlock Woolly Adelgid Review. U.S. Dep. Agric. Forest Service , 1996.*

Moraal, L.G. & Steingrover, E.G. (1991) Ladybirds for biological control of *Adelges cooleyi*, in gas exchange experiments with Douglas-fir (Coleoptera: Coccinellidae; Homoptera: Adelgidae). *Entomologische Berichten* **51**, 136-138.

Murray, T., Withers, T., Mansfield, S. & Bain, J. (2008) Distribution and current status of natural enemies of *Paropsis charybdis* in New Zealand. *New Zealand Plant Protection* **61**, 185-190.

Nedved, O. (1999) Host complexes of predaceous ladybeetles (Col., Coccinellidae). *Journal of Applied Entomology* **123**, 73-76.

Noriyuki, S. & Osawa, N. (2012) Intrinsic prey suitability in specialist and generalist Harmonia ladybirds: a test of the trade-off hypothesis for food specialization. *Entomologia Experimentalis Et Applicata* **144**, 279-285.

Obrycki, J., Orr, D., Orr, C., Wallendorf, M. & Flanders, R. (1993) Comparative Developmental and Reproductive Biology of Three Populations of *Propylea quatuordecimpunctata* (Coleoptera: Coccinellidae). *Biological Control* **3**, 27-33.

Obrycki, J.J. & Kring, T.J. (1998) Predaceous Coccinellidae in biological control. *Annual Review of Entomology* **43**, 295-321.

Obrycki, J.J. & Orr, C.J. (1990) Suitability of three prey species for Nearctic populations of *Coccinella septempunctata*, *Hippodamia variegata*, and *Propylea quatuordecimpunctata* (Coleoptera: Coccinellidae). *Journal of Economic Entomology* **83**, 1292-1297.

Obrycki, J.J., Maurice J., Tauber, M.J., Tauber, C.A. & Ruberson, J.R. (2011) Prey Specialization in Insect Predators. in *E. B. Radcliffe,W. D. Hutchison & R. E.*

Cancelado (Eds.) Radcliffe's IPM World Textbook. University of Minnesota, St. Paul, MN.

Omkar & Pervez, A. (2005) Ecology of two-spotted ladybird, *Adalia bipunctata*: a review. *Journal of Applied Entomology* **129**, 465-474.

Ouvrard, D. & Martin, J.H. (2014) The White-files (30 May 2014)- Taxonomic checklist of the world’s whiteflies (Insecta: Hemiptera: Aleyrodidae).Available online at http://www.hemiptera-databases.org/whiteflies/

Ouvrard, D. (2014) Psyl'list (30 May 2014) - The World Psylloidea Database. Available online at http://www.hemiptera-databases.com/psyllist.

Percy, D.M. (2002) Psyllids or 'jumping plant lice' (Psylloidea, Hemiptera). Available online at http://www.psyllids.org/.

Persad, A. & Khan, A. (2002) Comparison of life table parameters for *Maconellicoccus hirsutu*s, *Anagyrus kamali, Cryptolaemus montrouzieri* and *Scymnus coccivora*. *Biocontrol* **47**, 137-149.

Pinnock, D., Hagen, K., Cassidy, D., Brand, R., Milstead, J. & Tasson, R. (1978) Integrated pest management in highway landscapes. *California Agriculture* **32**, 33-34.

Ponsonby, D.J. & Copland, M.J.W. (1995) Olfactory responses by the scale insect predator *Chilocorus nigritus* (F) (Coleoptera, Coccinellidae). *Biocontrol Science and Technology* **5**, 83-93.

Poorani, J. (2013) FactSheets on Agriculturally Important Insects. Available online at http://www.nbaii.res.in/Featured_insects/index.php.

Pope, R. (1981) ‘*Rhyzobius ventrails*’(Coleoptera: Coccinellidae), its constituent species, and their taxonomy and historical roles in biological control. *Bulletin of Entomological Research* **71**, 19-32.

Pyke, G.H. (1984) Optimal Foraging Theory: A Critical Review. *Annual Review of Ecology and Systematics* **15**, 523-575.

Rana, J.S., Dixon, A.F.G. & Jarošík, V. (2002) Costs and benefits of prey specialization in a generalist insect predator. *Journal of Animal Ecology* **71**, 15-22.

Rawat, U.S., Thakur, J.N. & Pawar, A.D. (1988) Introduction and establishment of *Chilocorus bijugus* Mulsant and *Pharaoscymnus flexibilis* Mulsant, predatory beetles of San Jose scale at Thanedhar areas in Himachal Pradesh. *Current Science* **57**, 1250-1251.

Raworth, D.A. (2001) Development, larval voracity, and greenhouse releases of *Stethorus punctillum* (Coleoptera : Coccinellidae). *Canadian Entomologist* **133**, 895-895.

Reyd, G. & Leru, B. (1992) Predation by *Hyperaspis raynevali* and *Exochomus flaviventris* larvae (Col. Coccinellidae) on cassava mealybug *Phenacoccus manihoti* (Hom. Pseudococcidae) colonies. Experimental study in the laboratory. *Entomophaga* **37**, 317-325..

Richards, A.M. (1980) Defensive adaptations and behaviour in *Scymnodes lividigaster* (Coleoptera: Coccinellidae). *Journal of Zoology* **192**, 157-168.

Richards, A.M. (1981) *Rhyzobius ventralis* (Erichson) and *R. forestieri* (Mulsant) (Coleoptera: Coccinellidae), their biology and value for scale insect control. *Bulletin of Entomological Research* **71**, 33-46.

Roger, C., Coderre, D. & Boivin, G. (2000) Differential prey utilization by the generalist predator *Coleomegilla maculata lengi* according to prey size and species. *Entomologia Experimentalis Et Applicata* **94**, 3-13.

Roy, H. & Migeon, A. (2010) Ladybeetles (Coccinellidae) Chapter 8.4. *BioRisk: Biodiversity & Ecosystem Risk Assessment* **4**, 293–313.

Sachin, James, P., Babu, A., Perumalsamy, K., Muraleedharan, N. & Selvasundaram, R. (2008) Red spider mite, *Oligonychus coffeae* (Nietner) induced plant volatiles from tea leaves, an invitation to its predators. *Journal of Plantation Crops* **36**, 425-429.

Samways, M. (1984) Biology and economic value of the scale predator, *Chilocorus nigritus* (F.) (Coccinellidae). *Biocontrol News and Information* **5**, 91-105.

Samways, M.J., Osborn, R., Hastings, H. & Hattingh, V. (1999) Global climate change and accuracy of prediction of species' geographical ranges: establishment success of introduced ladybirds (Coccinellidae, Chilocorus spp.) worldwide. *Journal of Biogeography* **26**, 795-812.

Sarmento, R.A., Venzon, M., Pallini, A., Oliveira, E.E. & Janssen, A. (2007) Use of odours by *Cycloneda sanguinea* to assess patch quality. *Entomologia Experimentalis Et Applicata* **124**, 313-318.

Schluter, D. (2001) Ecology and the origin of species. *Trends in Ecology & Evolution* **16**, 372-380.

Seago, A.E., Giorgi, J.A., Li, J. & Slipiński, A. (2011) Phylogeny, classification and evolution of ladybird beetles (Coleoptera: Coccinellidae) based on simultaneous analysis of molecular and morphological data. *Molecular Phylogenetics and Evolution* **60**, 137-151.

Sentenac, G. & Kuntzmann, P. (2013) Biological control against *Heliococcus bohemicus* (Pseudococcidae) involving two predators, *Chrysoperla* sp. and *Exochomus quadripustulatus*. *IOBC/WPRS Bulletin* **85**, 3-12.

Shelton, A. (2014) *Biological Control: A Guide to Natural Enemies in North America*. Available online at http://www.biocontrol.entomology.cornell.edu/

Sloggett, J.J. (2005) Are we studying too few taxa? Insights from aphidophagous ladybird beetles (Coleoptera: Coccinellidae). *European Journal of Entomology* **102**, 391–398.

Sloggett, J.J. (2008b) Weighty matters: Body size, diet and specialization in aphidophagous ladybird beetles (Coleoptera: Coccinellidae). *European Journal of Entomology* **105**, 381-389.

Sloggett, J.J. (2008a) Habitat and dietary specificity in aphidophagous ladybirds (Coleoptera: Coccinellidae): Explaining specialization. *Procedings of the Netherlands Entomological Society Meeting* **19**, 95-113.

Sloggett, J.J. & Majerus, M.E.N. (2000) Habitat preferences and diet in the predatory Coccinellidae (Coleoptera): an evolutionary perspective. *Biological Journal of the Linnean Society* **70**, 63-88.

Smith, D., Papacek, D. & Smith, N. (1995) Biological control of citrus snow scale, *Unaspis citri* (Comstock) (Homoptera: Diaspididae) in south-east Queensland, Australia. *Israel Journal of Entomology* **29**, 253-260.

Stansly, P.A. (1984) Introduction and evaluation of *Chilocorus bipustulatus* (Col.: Coccinellidae) for control of *Parlatoria blanchardi* (Hom.: Diaspididae) in date groves of Niger. *Entomophaga* **29**, 29-39.

Stathas, G. (2001) Studies on morphology and biology of immature stages of the predator *Rhyzobius lophanthae* Blaisdell (Col.: Coccinellidae). *Anzeiger für Schädlingskunde* **74**, 113-116.

Steidle, J.L.M. & Van Loon, J.J.A. (2003) Dietary specialization and infochemical use in carnivorous arthropods: testing a concept. *Entomologia Experimentalis Et Applicata* **108**, 133-148.

Strand, M.R. & Obrycki, J.J. (1996) Host specificity of insect parasitoids and predators. *BioScience* **46**, 422-429.

Symondson, W.O.C., Sunderland, K.D. & Greenstone, M.H. (2002) Can generalist predators be effective biocontrol agents? *Annual Review of Entomology* **47**, 561-594.

Tapia, D.H., Morales, F. & Grez, A.A. (2010) Olfactory cues mediating prey-searching behaviour in interacting aphidophagous predators: are semiochemicals key factors in predator-facilitation? *Entomologia Experimentalis Et Applicata* **137**, 28-35.

Tavares, C., Jactel, H., van Halder, I., Mendel, Z. & Branco, M. (2014) A case of ecological specialization in ladybirds: *Iberorhyzobius rondensis* (Coleoptera: Coccinellidae), potential biocontrol agent of *Matsucoccus feytaudi* (Hemiptera: Matsucoccidae). *Bulletin of Entomological Research* **104**, 367-375.

Thakur, J.N., Rawat, U.S. & Pawar, A.D. (1989) Investigations on the occurrence of natural enemies of San Jose scale, *Quadraspidiotus perniciosus* Comstock (Hemiptera: Coccidae) in Jammu & Kashmir and Himachal Pradesh. *Entomon* **14**, 143-146.

Van Driesche, R., Idoine, K., Rose, M. & Bryan, M. (1998) Evaluation of the effectiveness of *Chilocorus kuwanae* (Coleoptera: Coccinellidae) in suppressing Euonymus scale (Homoptera: Diaspididae). *Biological Control* **12**, 56-65.

VanDyk, J. (2041) *BugGuide*. Available online at BugGuide.net.

Van Lenteren, J. C., Bale, J., Bigler, F., Hokkanen, H. M. T., & Loomans, A. J. M. (2006). Assessing risks of releasing exotic biological control agents of arthropod pests. Annual Review of Entomology, **51**, 609-634.

Verheggen, F., Fagel, Q., Heuskin, S., Lognay, G., Francis, F. & Haubruge, E. (2007) Electrophysiological and Behavioral Responses of the Multicolored Asian Lady Beetle, *Harmonia axyridis* Pallas, to sesquiterpene Semiochemicals. *Journal of Chemical Ecology* **33**, 2148-2155.

Vet, L.E.M. & Dicke, M. (1992) Ecology of infochemical use by natural enemies in a tritrophic context. *Annual Review of Entomology* **37**, 141-172.

Wang, X., Gao, C., Zhang, J., Yang, D. & Wang, Z. (2002) Study on the forest application techniques of *Rodolia limbata*. *Acta Universitatis Agriculturalis Boreali-occidentalis* **30**, 59-61.

Wiggins, G., Hakeem, A., Follum, R., Rhea, R., Lambdin, P.L. & Grant, J.F. (2010) Seasonality of established populations of *Sasajiscymnus tsugae* on eastern hemlock in the southern Appalachians. pp. 203–205 in the *Fifth Symposium on*

Hemlock Woolly Adelgid in the Eastern United States, 17–19 August 2010, U.S. Department of Agriculture, Forest Service, Asheville, NC.

Withers, T. & Berndt, L. (2010) Southern ladybird gets a second chance. *New Zealand Tree Grower* **31**, 37-38.

Yang, H. (2009) Orientation response of *Chilocorus rubidus* hope to prey and host plant volatiles. *Chinese Journal of Biological Control* **25**, 304-308.

Yates, D., Moore, Moore, D., McCabe, G. (1999). *The Practice of Statistics* (3rd Ed.), New York, USA, W.H. Freeman. Available onlie at http://bcs.whfreeman.com/tps3e/

Yigit, A. & Canhilal, R. (2005) Establishment and dispersal of *Serangium parcesetosum* Sicard (Coleoptera, Coccinellidae), a predatory beetle of citrus whitefly, *Dialeurodes citri* Ashm. (Homoptera, Aleyrodidae) in the East Mediterranean region of Turkey. *Zeitschrift Fur Pflanzenkrankheiten Und Pflanzenschutz-Journal of Plant Diseases and Protection* **112**, 268-275.

Yoneya, K., Kugimiya, S. & Takabayashi, J. (2009) Can herbivore-induced plant volatiles inform predatory insects about the most suitable stage of its prey? *Physiological Entomology* **34**, 379-386.

Zhu, J. & Park, K.C. (2005) Methyl salicylate, a soybean aphid-induced plant volatile attractive to the predator *Coccinella septempunctata*. *Journal of Chemical Ecol*ogy **31**, 1733-1746.

Zilahi-Balogh, G., Kok, L.T., Salom, S.M., Onken, B., Reardon, R. & Lashomb, J. (2002) A review of world-wide biological control efforts for the family Adelgidae. pp. 129-140 in *Proceedings of the Symposium on the Hemlock Woolly Adelgid in Eastern North America*. USDA Forest Service Forest Health Protection, East Brunswick, NJ.

Annex 1. List of the 186 species of ladybirds reviwed..

Species	Origin	Prey	3 trophic-level	Prey specialization	Habitat type	Habitat Specialization	References
Adalia bipunctata	Pl	*46 species of Aphididae*	**C**	oligophagous	Trees and bushes in temperate deciduous forests.	stenotopic	Kalushkov, 1994, 1998; Hodek & Honěk, 1996, Vanhaelen, 2002; Ozder, 2003; De Clercq *et al.*, 2005; Bonte, 2010.
Adalia conglomerata	Pl	*Adelges sp., Pineus sp.*	**A**	oligophagous	Pinacea in temperate coniferous forests.	stenotopic	Hodek & Honěk, 1996; GuoYue, 1999; Yu, 2000.
Adalia decempunctata	Pl	Several Aphididae, *Matsucoccus josephi*	**D**	polyphagous	Trees (e.g. *Castanea sativa, Citrus spp., Juglans regia, Quercu*s spp.) in temperate deciduous forests and arable land.	stenotopic	Hodek & Honěk, 1996; Stork *et al.*, 2001.
Adalia fasciatopunctata	Pl	*Callaphis juglandis* *Dysaphis pyri* *Hyalopterus pruni*	**C**	oligophagous	Mainly shrubs and trees. (e.g. *Prunus spp., Rosa spp.*) in temperate shrublands and arable land.	stenotopic	Atlihan, 1995; Erol & Atlihan, 1995; Ulgenturk & Toros, 1999; Yaşar & Ozger, 2005a; Atlıhan *et al.*, 2010.
Adalia flavomaculata	Af	*Schizaphis graminum*	**A**	monophagous	Mainly crops (e.g. *Raphanus sativus, Sorghum spp., Triticum spp.*) in arable land.	stenotopic	Brown, 1972; Mitchels & Bateman, 1986; Hodek & Honěk, 1996.
Adalia tetraspilota	IM	*Aphis pomi* *Myzus persicae*	**C**	oligophagous	Mainly trees and bushes in temperate deciduous forests.	stenotopic	Khan & Mir, 2008; Joshi, 2012.
Aiolocaria mirabilis	Pl	*Chrysomela sp.* *Gastrolina depressa*	**C**	oligophagous	Mainly decidous trees (e.g. *Alnus spp.*, Betulaceae, *Juglans spp., Populus spp.*) in temperate deciduous forests.	stenotopic	Phaloura &Tarlok, 1992; Chang *et al*, 1993; Yan Shuqin, 1994; Hodek & Honěk, 1996

Anatis labiculata	Nc	*Aphis sp.* *Lymantria dispar*	**D**	polyphagous	Mainly trees in temperate forests.	stenotopic	Watson, 1976; Cook & Webb, 1995.
Anatis mali	Nc	*Acyrthosiphon pisum Cinara sp.* *Mindarus abietinus* *Rhopalosiphum maidis*	**A**	oligophagous	Mainly Pinaceae (e.g. *Abies spp.*, *Picea spp.*) in temperate coniferous forests.	stenotopic	Smith, 1966; Houseweart & Lawrence, 1986; Hodek & Honěk, 1996; Berthiaume *et al.*, 2000, 2007.
Anatis ocellata	Pl	*several Aphididae*	**C**	oligophagous	Mainly Pinaceae in temperate coniferous forests.	stenotopic	Czechowska, 1995; Hodek & Honěk, 1996; Kalushkov & Hodek, 2001.
Anegleis cardoni	IM	*Aphis craccivora* *Aphis gossypii* *Brevicoryne brassicae* *Centrococcus insolitus* *Hyadaphis coriandri* *Lipaphis erysimi* *Myzus persicae* *Rhopalosiphum maidis* *Uroleucon compositae*	**D**	polyphagous	Arable land (orchards - e.g. *Citrus spp.;* crops - e.g. *Helianthus spp.; Triticum spp.*). Plantations (e.g. *Brassica spp.*, *Saccharum spp.*, *Solanum spp.*; rice fields; ornamental plants - e.g. *Dodonea viscosa*, *Canthium didymum*, *Lantana spp.*, *Pterolobium indicum*).	eurytopic	Shama, 2000; Omkar *et al.*, 2009, 2011; Omkar & Gyanendra, 2013.
Anisolemnia dilatata	IM	*Ceratovacuna indica* *Ceratovacuna lanigera* *Ceratovacuna silvestrii* *Pseudoregma bambusicola* *Pseudoregma bucktoni*	**A**	oligophagous	Mainly Poaceae (e.g. *Phyllostachys spp.*, *Saccharum spp.*) in tropical moist lowland forest and arable land.	stenotopic	Liu, 1933; Hodek & Honěk, 1996; Kazmi & Husen, 1999; Majumder & Agarwala, 2013; Majumder *et al.*, 2013.
Anisolemnia tetrasticta	Af	*Libyaspis sp.*	**C**	monophagous	Tropical moist lowland forest.	stenotopic	Dejean *et al.*, 2002.
Anisosticta novemdecimpunctata	Pl	*Hyalopterus pruni*	**C**	monophagous	Reed beds in bogs, marshes, swamps, fens, and peatlands.	stenotopic	Halima-Kamel, 1993; Sem’yanov, 2006; Sloggett & Lorenz, 2008; Slogget *et al.*, 2008.

Aphidecta obliterata	Pl	*Adelges cooleyi* *Adelges nusslini* *Adelges piceae* *Adelges tsugae* *Elatobium abietinum* *Pineus pini*	**B**	oligophagous	Mainly Pinaceae (*Abies spp., Larix spp., Tsuga spp.*) in temperate coniferous forests.	stenotopic	Smith, 1958; Wylie, 1958; Witter, 1969; Parry, 1992; Montgomery & Lyon, 1995; Hodek & Honěk, 1996; Oliver *et al.*, 2006; Timms *et al.*, 2008.
Axinoscymnus cardilobus	Pl	*Bemisia tabaci* *Aleyrodidae*	**C**	oligophagous	Plantations (e.g. *Codiaeum variegatum*, *Solanum melonena*). Temperate forest on the Dinghu Mountains, Guangdong, China.	eurytopic	Huang *et al.*, 2003, 2006.
Axinoscymnus puttarudriahi	IM	*Aleurodicus dispersus* *Aleurocanthus spp.* *Bemisia tabaci*	**C**	oligophagous	Arable land (crops - e.g. *Gossypium spp.*; orchards - e.g. *Punica spp.*). Plantations (e.g. *Bauhinia purpurea*, *Cassia siamea*, *Psidium spp.).*	eurytopic	Aishwariya *et al.*, 2007; Karnataka, 2007.
Azya luteipes	Nt	*Coccus viridis*	**C**	monophagous	Arable land (crops - e.g.; orchards - e.g. *Citrus spp.).* Plantations (e.g. *Coffea spp.*, *Ilex paraguariensis*).	eurytopic	Nais & Busoli, 2012.
Azya orbigera	Nt	*Asterolecanium pustulans* *Coccus viridis* *Protopulvinaria pyriformis* *Parasaissetia nigra*	**C**	oligophagous	Plantations (e.g. *Coffea spp.*, *Plumeria spp.*). Marine coastal habitats (e.g. *Pluchea indica*).	eurytopic	Charanasri & Nishida, 1973; González, 2007; Liere & Perfect, 2008.
Brumoides septentrionis	Nc	*Chionaspis heterophyllae* *Matsucoccus gallicolus*	**B**	oligophagous	Mainly Pinaceae in coniferous forests.	stenotopic	Wheeler Jr., 2003.

Brumoides suturalis	IM	*Aleurolobus barodensis* *Aphis affinis* *Aphis craccivora* *Bemisia tabaci* *Dialeurodes citri* *Ferrisia virgata* *Lipaphis erysimi* *Maconellicoccus hirsutus* *Myzus persicae* *Phenacoccus solani* *Phenacoccus solenopsis* *Phthorimaea operculella* *Planococcus minor*	**D**	polyphagous	Plantations (e.g. *Cocos spp., Vigna radiata*). Arable land (orchards - e.g. *Citrus spp.; Malus spp;* crops - e.g. *Gossypium spp.*). Irrigated land (rice fields).	eurytopic	Misra *et al.*, 1980; Hodek & Honěk, 1996; Chandrababu *et al.*, 1999; Zulfiqar *et al.*, 1999; Khuhro *et al.*, 2012; Mahadev *et al.*, 2012.
Calvia punctata	IM	*Acyrthosiphon gossypii* *Aphis craccivora* *Aphis pomi* *Chromaphis juglandicola* *Myzus persicae*	**C**	oligophagous	Mainly deciduous trees and vegetation (e.g. *Juglans spp.*) in temperate deciduous forests.	stenotopic	Booth, 1997; Khan *et al.*, 2007; Khan & Mir, 2008.
Calvia quatuordecimguttata	Pl	*Aphis farinosa* *Aphis pomi* *Cacopsylla pyri* *Cavariella konoi* *Chaitophorus tremulae* *Chionaspis salicis* *Eucallipterus tiliae* *Euceraphis betulae* *Euceraphis punctipennis* *Macrosiphoniella artemisiae* *Psylla alni* *Psylla mali* *Schizaphis graminum*	**D**	polyphagous	Mainly deciduous trees (e.g. *Acer spp., Alnus glutinosa, Betula spp., Citrus spp., Fagus spp., Malus spp., Prunus spp., Quercus spp., Sorbus aucuparia*) in temperate deciduous forests and orchards (arable land).	stenotopic	Sem'yanov, 1980; 1996; Hodek & Honěk, 1996; Palmeri,1996; Kalushkov & Hodek, 2001.
Calvia quindecimguttata	Pl	*Melasoma aenea*	**C**	monophagous	In marshy habitats, trees and bushes near water (e.g. *Alnus glutinosa)* in bogs, marshes, swamps.	stenotopic	Hodek & Honěk, 1996; Florek *et al.*, 2011.

Ceratomegilla notata	Pl	*Acyrthosiphon pisum* *Aphis fabae* *Cavariella theobaldi* *Megoura viciae* *Rhopalosiphum maidis* *Rhopalosiphum padi* *Therioaphis luteola* *Uroleucon cichorii* *Uroleucon jaceae*	**C**	oligophagous	In several perennial plants (e.g. Compositae, Umbelliferae, Poacea) in Alpine wetlands.	stenotopic	Ricci & Ponti, 2005.
Ceratomegilla undecimnotata	Pl	*Aphis fabae* *Aphis gossypii* *Myzus persicae* *Toxoptera aurantii*	**C**	oligophagous	Arable land (Crops - e.g. *Helianthus spp.*). Plantations (e.g. *Beta vulgaris*, *Solanum tuberosum*). Pasturelands (e.g. *Medicago sativa)*	eurytopic	Ettifouri & Ferran, 1992; Katsoyannos *et al.*, 1997, 2005.
Cheilomenes lunata	Af	*Aphis craccivora* *Aphis gossypii* *Diuraphis noxia* *Metopolophium dirhodum* *Rhopalosiphum padi* *Sitobion avenae* *Sitobion graminum*	**C**	oligophagous	Arable land (Orchards - e.g. *Citrus spp.*) Plantations (e.g. *Vigna spp.*). Dry savanna (grassland savanna). Irrigated land (rice fields).	eurytopic	Ofuya, 1995; Woin *et al.*, 2000; Magagula & Samways, 2001; Munyuli *et al.*, 2006; Nyaanga *et al.*, 2012.
Cheilomenes sexmaculata	IM	*Acyrthosiphon pisum* *Aphis spp.* *Aulacorthum solani* *Hyperomyzus lactucae* *Lipaphis erysimi* *Myzus persicae* *Rhopalosiphum maidis* *Sitobion akebiae* *Sitobion ibarae* *Uroleucon compositae*	**C**	oligophagous	Permanent Freshwater Marshes/Pools (e.g. *Crotalaria juncea*, rice fields). Arable land (Orchards – e.g. *Citrus spp.*, crops - *Gossypium spp.*, *Glycine spp.*). Plantations (e.g. *Psidium spp.*, *Saccharum spp.*).	eurytopic	Hukusima & Kouyama, 1974; Behura & Parida, 1979; Chaudhary *et al.*, 1983; Hussein, 1991; Varma *et al.*, 1993; Sugiura & Takada, 1998; Bind, 1998, 2007; Agarwala *et al.*, 2001; Joshi *et al.*, 2008.
Cheilomenes vicina	Af	*Aphis craccivora* *Aphis fabae* *Aphis gossypii* *Diuraphis noxia* *Melanaphis sacchari*	**C**	oligophagous	Arable land (Crops - e.g. *Phaseolus vulgaris*, *Zea mays* and rice fields).	stenotopic	Ofuya, 1986, 1990; Mrosso *et al.*, 2013

Chilocorus baileyi	Al	*Aonidiella aurantii* *Aonidiella orientalis* *Aspidiotus nerii*	**C**	oligophagous	Mainly trees (e.g. *Carica papaya*, *Citrus spp.*, *Mangifera indica*) in tropical plantations.	stenotopic	Elder & Bell, 1998; Slipinski & Giorgi, 2006.
Chilocorus bijugus	IM	*Aonidiella aurantii* *Comstockaspis perniciosa* *Diaspidiotus prunorum* *Ericerus pela* *Lepidosaphes afganensis* *Lopholeucaspis japonica* *Metaceronema japonica* *Parlatoria ziziphi*	**D**	oligophagous	Mainly deciduous trees (e.g. *Ligustrum* woods, *Morus spp.*, Rosaceae, Rutaceae, *Salix spp.*, and orchards (e.g. *Citrus spp.*, *Malus spp.*, *Olea spp.*, *Prunus spp.*) in temperate deciduous forest and arable land.	stenotopic	Ahmed & Ghani, 1966; Shunxiang *et al.*, 1990; Rawat *et al.*, 1992; Rawat & Pawar, 1993; Jiao *et al.*, 1997; Farooq-Ahmad *et al.*, 1999; Ren *et al.*, 2001; Gupta & Inderjit, 2007.
Chilocorus bipustulatus	Pl	*Aonidiella aurantii* *Aspidiotus nerii* *Chionaspis salicis* *Coccus hesperidum* *Parlatoria blanchardi* *Protopulvinaria pyriformis* *Pseudaulacaspis pentagona* *Pulvinaria psidii* *Saissetia oleae* *Unaspis yanonensis*	**D**	oligophagous	Arable land (Orchards - e.g. *Citrus spp.*). Plantations (e.g. Arecaceae). Rural gardens; Temperate deciduous forests (e.g. *Laurus spp.*, *Salix spp.*).	eurytopic	Rosen & Gerson, 1965; Kehat, 1968a; Kaufmann, 1977; Hodek & Honěk, 1996; Uygun & Elekcioglu, 1998; Santos *et al.*, 2009; Stathas *et al.*, 2009; Karatay & Karaca, 2013.
Chilocorus cacti	Nc	*Acutaspis agavis* *Aulacaspis yasumatsui* *Comstockiella sabalis* *Dactylopius opuntiae* *Melanaspis glomerata*	**D**	oligophagous	Arable land (orchards - e.g. *Citrus spp.*). Plantations (e.g. Arecaceae, *Persea americana*). Tropical dry-shrubland (Arecaceaes, cycads, *Opuntia ficus-indica*, *Agave tequilana*). Pasturelands (pastural system of *Leucaena leucocephala*).	eurytopic	Pluke *et al.*, 2005; Cave, 2006; Salas-Araiza *et al.*, 2008; Vanegas-Rico *et al.*, 2010; Flores *et al.*, 2013.

Chilocorus circumdatus	IM	*Aonidiella aurantii* *Aonidiella orientalis* *Aspidiotus nerii* *Aulacaspis rosarum* *Chrysomphalus aonidum* *Coccus viridis* *Comstockaspis perniciosa* *Unaspis citri*	**D**	oligophagous	Arable land (Orchards – e.g. *Citrus spp.*); Plantations (e.g. *Camellia sinensis*, *Coffea spp.*, *Morus alba*, *Piper spp.*).	eurytopic	Das *et al.*, 1988; Houston, 1991; Mani & Krishnamoorthy, 1996; Chen, 1998.
Chilocorus hauseri	IM	*Aonidiella aurantii* *Aonidiella orientalis* *Chrysomphalus aonidum*	**C**	oligophagous	On trees (e.g. *Morus alba, Citrus spp.*) on arable land.	stenotopic	Khan *et al.*, 2007.
Chilocorus kuwanae	Pl	*Chionaspis alnus* *Chionaspis salicis* *Chrysomphalus bifasciculatus* *Unaspis yanonensis* *Unaspis euonymi*	**C**	oligophagous	Mostly on deciduous trees (e.g. *Euonymus japonicas*, *E. europeus*, *Malus spp.*, *Populus spp.*) on arable land and temperate deciduous forest.	stenotopic	Nohara, 1962; Nalepa *et al.*, 1992; Yang *et al.*, 1997; Van Driesche *et al.*, 1998a; 1998b.
Chilocorus nigritus	IM	*Abgrallaspis cyanophylli* *Acutaspis umbonifera* *Aonidiella aurantii* *Aspidiotus sp. (several)* *Asterolecanium miliaris* *Aulacaspis tubercularis* *Ceroplastes actiniformis* *Chrysomphalus aonidum* *Coccus sp. (several)* *Comstockaspis perniciosa* *Hemiberlesia lataniae* *Lepidosaphes beckii* *Melanaspis glomerata* *Parlatoria blanchardi* *Phoenicococcus marlatti* *Pinnaspis buxi* *Pseudococcus citriculus* *Pseudaulacaspis pentagona* *Saissetia coffeae* *Vinsonia stellifera*	**D**	oligophagous	Plantations (e.g. Arecaceae, *Coffea spp.*, *Cocos spp.*, *Mangifera indica*, *Phyllostachys spp.*, *Saccharum spp.*). Arable land (Orchards - e.g. *Citrus spp.*).	eurytopic	Samways, 1984; Samways & Wilson, 1988; Muralidharan,1994; Hodek & Honěk, 1996; Ponsonby & Copland, 2000, 2007;Omkar & Pervez, 2003.

Chilocorus rubidus	IM	*Comstockaspis perniciosa* *Didesmococcus koreanus* *Eulecanium caraganae* *Ericerus pela* *Pseudaulacaspis pentagona* *Physokermes jezoens*	**C**	oligophagous	Mainly on deciduous trees (e.g. *Prunus spp.*, *Quercus aliena*) in arable land and temperate deciduous forests.	stenotopic	Qi, 1989; Liu, 1993; Sakuratani & Ito, 1995; Hodek & Honěk, 1996; Huang *et al.*, 2002, 2007 ; Chen *et al.*, 2003; Liu & He, 2009.
Chilocorus stigma	Nc	*Chionaspis heterophyllae* *Chionaspis pinifoliae* *Cryptococcus fagisuga* *Chrysomphalus aonidum* *Fiorinia externa*	**C**	oligophagous	Mainly trees (e.g. *Citrus spp.*, *Pinus sylvestris)* in arable land and coniferous forests.	stenotopic	Mayer & Allen, 1982; Lamp *et al.*, 1994; Colunga-Garcia *et al.*, 1997; Cooper & Cranshaw, 1999; Lynch *et al.*, 2006.
Cleobora mellyi	Al	*Bactericera cockerelli* *Chrysophtharta bimaculata* *Ctenarytaina thysanura* *Paropsis charybdis* *Psylla acaciaebaileyanae*	**D**	polyphagous	Dry savannas (e.g. *Acacia spp.*, *Eucalyptus spp.*).	stenotopic	Alma, 1980; Bain *et al.*,1984; Mensah & Madden, 1994; Bashford, 1999; Berndt *et al.*, 2010; Pugh, 2013.
Clitostethus arcuatus	Pl	*Aleurothrixus floccosus* *Aleurotrachelus jelinekii* *Aleyrodes proletella* *Bemisia tabaci* *Dialeurodes citri* *Metaleurodicus cardini* *Siphoninus phillyreae* *Trialeurodes vaporariorum*	**C**	oligophagous	Temperate forests: woodlands and shrubs. Arable land (orchards - e.g. *Citrus spp.*, *Oleae spp.*, *Punica spp.*). Plantations (e.g. *Brassica spp.*, *Meconopsis cambrica*).	eurytopic	Abraham *et al.*, 1973; Agekyan, 1977; Loi, 1978; Mesbah, 2000; Hassan, 2001; Tavadjoh *et al.*, 2010; Yazdani & Zarabi, 2010; Brown & Whitehead 2012.
Coccinella hieroglyphica	Nc	*Galerucella sagittariae* *Lochmaea suturalis*	**A**	oligophagous	Peat bogs with *Calluna vulgaris*.	stenotopic	Hippa *et al.*, 1978, 1984; Scandrett & Gimingham, 1991; Hodek & Honěk, 1996; Stenlokk, 2004.
Coccinella magnifica	Pl	*Acyrthosiphon pisum* *Aphis sp.* (several*)* *Cinara sp.* (several) *Elatobium abietinum* *Schizolachnus pineti* *Sitobion fragariae*	**C**	oligophagous	Near ant (*Formica rufa* group) nests in temperate forests.	stenotopic	Majerus, 1989; Sloggett *et al.*, 1998; Sloggett & Majerus, 2000a; Sloggett *et al.*, 2002; Sloggett & Majerus, 2003.

Coccinella novemnotata	Nc	*Aphis fabae* *Aphis punicae* *Brevicoryne brassicae* *Rhopalosiphum padi*	**C**	oligophagous	Arable land (orchards - e.g. *Malus spp.*, *Prunus spp.*; crops - e.g. *Triticum spp.*, *Zea mays*)	stenotopic	McMullen, 1967a, 1967b; ElHag & Zaitoon, 1996.
Coccinella septempunctata	Pl	*Acyrthosiphon pisum* *Aphis sp* (several) *Brevicoryne brassicae* *Ceratovacuna lanigera* *Diuraphis noxia* *Hyalopterus pruni* *Hyperomyzus lactucae* *Lipaphis erysimi* *Macrosiphoniella artemisiae* *Macrosiphum avenae* *Megoura viciae* *Metopolophium dirhodum* *Microlophium carnosum* *Myzus persicae* *Rhopalosiphum spp.* *Schizaphis graminum* *Sitobion avenae* *Uroleucon spp. (2 sp)*	**C**	oligophagous	Temperate grasslands. Arable land (crops, orchards). Plantations. Rural gardens. Temperate forests.	eurytopic	Hodek & Honěk, 1996; Kawauchi, 1997; Omkar & Pervez, 2002; Kalushkov & Hodek, 2004.
Coccinella transversalis	IM	*Acyrthosiphon kondoi* *Acyrthosiphon pisum* *Aphis craccivora* *Aphis fabae* *Aphis gossypii* *Aphis nerii* *Lipaphis erysimi* *Myzus persicae* *Therioaphis trifolii* *Toxoptera aurantii* *Uroleucon carthami* *Uroleucon compositae*	**C**	oligophagous	Arable land (crops - e.g. *Gossypium spp.*, *Helianthus spp.*, *Sorghum spp.*, *Triticum spp.*, *Zea mays*.). Plantations (e.g. *Brassica spp.*, *Vigna spp.*).	eurytopic	Srivastava *et al*, 1987; Hodek & Honěk, 1996; Malik *et al.*, 1998; George, 2000; James, 2001; Omkar & James, 2004; Omkar *et al.*, 2005b; Mishra *et al.*, 2011, 2012; Navodita *et al.*, 2011; Bista & Omkar, 2013.

Coccinella transversoguttata	Nc	*Acyrthosiphon pisum* *Aphis pomi* *Eriosoma lanigerum* *Myzus persicae* *Phorodon humuli* *Schizaphis graminum* *Sitobion avenae*	**C**	oligophagous	Arable land (crops - e.g. *Raphanus sativus, Triticum spp., Zea mays*); orchards (*Prunus spp.*). Temperate coniferous forests (e.g. *Pinus sylvestris*). Temperate shrublands (e.g. *Juniperus virginiana)*. Pasturelands (e.g. *Medicago sativa*)	eurytopic	Obrycki & Tauber, 1981; Hodek & Honěk, 1996; Zhang, 1997; Evans *et al.*, 1999; Hesler *et al.*, 2009; Kajita *et al.*, 2009; Davidson & Evans, 2010
Coccinella trifasciata	Nc	*Macrosiphum albifrons* *Macrosiphum euphorbiae* *Macrosiphum pseudorosae* *Myzus persicae*	**C**	oligophagous	Pasturelands (e.g. .*Cirsium spp, Lupine spp., Phleum pratense, Trifolium spp., Vicia spp.*). Arable land (e.g. *Avena spp., Hordeum spp.*) Temperate shrubland (e.g. *Alnus spp., Cornus sericea, Prunus spp., Rosa spp., Rubus spp., Solidago spp.*)	eurytopic	Ives, 1981; Marriot *et al.*, 2009; Finlayson *et al.*, 2010.
Coccinella undecimpunctata	Pl	*Acyrthosiphon pisum* *Agonoscena pistaciae* *Aleyrodes proletella* *Aphis craccivora* *Aphis fabae* *Aphis gossypii* *Aphis pomi* *Bemisia tabaci* *Brevicoryne brassicae* *Diuraphis calamagrostis* *Laingia psammae* *Lipaphis erysimi* *Macrosiphoniella sanborni* *Metapolophium dirhodum* *Myzus persicae* *Phenacoccus solenopsis* *Rhopalosiphum padi* *Sitobion avenae* *Therioaphis trifolii*	**D**	polyphagous	Seasonal/Intermittent Freshwater Marshes/Pool - near the seashore grassy communities, in *Tripleurospermum maritium.* Plantations (e.g. *Beta vulgaris, Brassica spp., Nicotiana spp., Saccharum spp., Vigna spp.*). Arable land (crops - e.g. *Gossypium spp., Triticum spp., Zea mays*; orchards - e.g. *Malus spp.*). Pasturelands (e.g. *Medicago sativa*).	eurytopic	Ibrahim, 1955; Singh & Malhotra, 1979; Obrycki & Tauber, 1981; ElHag & Zaitoon, 1996; Hodek & Honěk, 1996; Karaman *et al.*, 1998; Mari *et al.*, 2004; Ali *et al.*, 2005; Cabral *et al.*, 2006, 2009; Solangi *et al.*, 2007; Asifa *et al.*, 2013.

Coelophora biplagiata	IM	*Aphis craccivora* *Aphis gossypii* *Ceratovacuna lanigera* *Rhopalosiphum maidis*	**C**	oligophagous	Perenneal plants - mainly Poaceae and Fabaceae (e.g. *Phaseolus spp.*, *Saccharum spp.*, *Vigna spp.*) in plantations.	stenotopic	Omkar *et al.*, 2005a; Saurabh *et al.*, 2007.
Coelophora bissellata	IM	*Aphis craccivora* *Aphis fabae* *Aphis gossypii* *Cervaphis rappardi* *Rhopalosiphum maidis* *Toxoptera aurantii* *Toxoptera odinae*	**C**	oligophagous	Arable land (e.g. *Argemone spp.*, *Oryza glaberrima*). Plantations (e.g. *Santalum spp.*, *Saccharum spp.*, *Vigna spp.*). Tropical moist montane forest (Arecaceae, *Picea spp.*, *Pterolobium indicum*, *Tarenna asiatica*).	eurytopic	Poorani, 2013.
Coelophora inaequalis	Al	*Aphis craccivora* *Aphis gossypii* *Aphis spiraecola* *Toxoptera aurantii* *Toxoptera citricidus*	**C**	oligophagous	Arable land (orchards - e.g. *Citrus spp.*; crops - e.g. *Capsicum annuum*). Grasslands (near crops) (e.g. *Carex lenticularis*, *Eleusine indica*).	eurytopic	Houston, 1988; Mora, 1993; Michaud, 2000; Wang & Tsai, 2001.
Coelophora quadrivittata	Al	*Coccus viridis*	**C**	monophagous	Mainly ornamental plants (e.g. *Plumeria spp.*) in Tropical Montane Forest. Rain forest.	stenotopic	Chazeau, 1981; Houston, 1988.
Coelophora saucia	Al	*Aphis craccivora* *Aphis glycines* *Aphis pomi* *Ceratovacuna lanigera* *Lipaphis erysimi*	**C**	oligophagous	Subtropical/ Tropical Moist Lowland Forest (Tropical evergreen forest). Arable land (horticultural and ornamental crops).	eurytopic	Dai, 1990; Poorani, 2004; Omkar *et al.*, 2010; Devikarani *et al.*, 2013.

Coleomegilla maculata	Nc	*Acyrthosiphon pisum* *Aphis glycines* *Aphis gossypii* *Pieris rapae* *Galerucella calmariensis* *Helicoverpa zea* *Hypera postica* *Hyphantria cunea eggs* *Leptinotarsa decemlineata eggs* *Myzus lythri* *Myzus persicae* *Ostrinia nubilalis* *Rhopalosiphum maidis* *Schizaphis graminum* *Spodoptera frugiperda*	**D**	polyphagous	Arable land (crops - e.g. *Anethum graveolens*, *Coriandrum sativum*, *Fagopyrum esculentum*, *Glycine spp.*, *Gossypium spp.*, *Phaseolus spp.*, *Triticum spp.*, *Zea mays*,). Plantations (e.g. Cucurbitaceae*; Solanum tuberosum*); Temperate shrubland (e.g. *Juniperus virginiana*).	eurytopic	Arallah & Newsom, 1966; Groden *et al.*, 1990; Giles *et al.*, 1994; Hilbeck & Kennedy, 1996; Hodek & Honěk, 1996; Munyaneza & Obrycki, 1997; Roger *et al.*, 2000; Rondon *et al.*, 2006; Silva, 2009; Silva *et al.*, 2010b.
Cryptognatha nodiceps	Nt	*Aonidiella orientalis* *Aspidiotus destructor* *Parlagena bennetti* *Coccus viridis*	**D**	oligophagous	Plantations (e.g. *Cocos spp.*, *Musa spp.*, *Persea spp.*, *Piper methysticum*, *Theobroma cacao*)	stenotopic	Lopez *et al.*, 2004.
Cryptolaemus montrouzieri	Al	*Aleyrodidae (6 species)* *Aphididae (1 sp)* *Coccidae (18 species)* *Eriococcidae (1 sp)* *Pseudococcidae (23 species)* *Margarodidae (1 sp)*	**D**	polyphagous	Arable land (orchards - e.g., *Citrus spp.*, *Malus spp.*). Plantations (*Alpinia purpurata*, *Coffea spp.*, *Carica papaya*, *Crossandra undulifolia*, *Decalepis hamiltonii*, *Mangifera indica*, *Manilkara zapota*, *Morus alba*, *Passiflora spp.*, *Psidium spp.*, *Solanum tuberosum*, ornamental plants - e.g. *Acalypha spp.).*	eurytopic	Ghorpade, 1981; Bhat *et al.*, 1983; Satyanarayanamurthy & Lakshmi, 1986; Fand *et al.*, 2010; Attia *et al.*, 2011a, 2011b; Naser *et al.* 2011; Rashid *et al.*, 2012; Deokar *et al.*, 2013; Gore *et al.*, 2013a, 2013b, Kairo *et al.*, 2013; Kakde & Patel, 2013.

Curinus coeruleus	Nc	*Aleurodicus dispersus* *Aphis craccivora* *Ceratovacuna lanigera* *Coccidohystrix insolita* *Diaphorina citri* *Diaspis echinocacti* *Dysmicoccus neobrevipes* *Ferrisia virgata* *Heteropsylla cubana* *Rhopalosiphum maidis* *Nipaecoccus nipae*	**D**	polyphagous	Arable land (crops - e.g. *Gliricidia sepium*, *Phaseolus vulgaris*,orchards - e.g. *Citrus spp.*). Plantations (e.g. Arecaceae, *Psidium guajava*).	eurytopic	Villacarlos & Robin, 1992; Doungsa-ard & Osatapan, 1997; Jalali & Singh, Joshi *et al.*, 2001; Michaud, 2002; Yang *et al.*, 2006; Soemargono *et al.*, 2008; Nawanich *et al.*; 2013; Poorani, 2013.
Cycloneda ancoralis	Nt	*Aphis debilicornis* *Aphis gossypii* *Diuraphis noxia* *Lipaphis erysimi*	**C**	oligophagous	Pastureland (e.g. *Cirsium vulgare, Medicago sativa*). Arable land (orchards - e.g. *Malus pumila*).	eurytopic	Elliott *et al.*, 1994.
Cycloneda sanguinea	Nt	*Aleurocanthus woglumi* *Aphis craccivora* *Aphis fabae* *Aphis gossypii* *Aphis spiraecola* *Bemisia tabaci* *Cinara atlantica* *Cinara pinivora* *Diaphorina citri* *Heteropsylla cubana* *Hyadaphis foeniculi* *Lipaphis pseudobrassicae* *Macrosiphum euphorbiae* *Myzus persicae* *Megoura viciae* *Toxoptera citricidus*	**D**	polyphagous	Arable land (orchards - e.g. *Citrus spp.*, *Prunus persica*; crops - e.g. *Lens spp.*). Plantations (e.g. *Solanum lycopersicum)* Temperate coniferous forests (e.g. *Pinus spp.*). Pasturelands (e.g. *Medicago sativa*).	eurytopic	Husband, 1972; Santos & Pinto, 1981; Michaud, 2000; Isikber & Copland, 2001; 2002; Cardoso & Lazzari, 2003a; 2003b; Boica Jr. *et al.* 2004, Oliveira *et al.*, 2004; 2006; Resende *et al.*, 2006; Isikber, 2008.

Delphastus catalinae	Nc	*Aleurotuberculatus takahashii* *Bemisia tabaci* *Singhiella simplex*	**C**	oligophagous	Plantations (e.g. *Ageratum spp., Brassica spp., Carica papaya, Nicotiana spp., Solanum tuberosum, Vigna poinsettia*). Arable land - Horticultural crops.	eurytopic	Fu *et al*., 1999; Simmons & Legaspi, 2004; Guershon & Gerling, 2006; Legaspi *et al*., 2007; Kutuk & Yigit, 2007; Simmons *et al*., 2008; 2012.
Delphastus pallidus	Nc	*Aleurocanthus woglumi* *Bemisia tabaci* *Dialeurodes citri* *Dialeurodes citrifolii*	**C**	oligophagous	Mainly trees (e.g. *Citrus spp., Morinda citrifolia*) in arable land.	stenotopic	Hodek & Honěk, 1996; Brito *et al*., 2007.
Delphastus pusillus	Nc	*Aleurocanthus woglumi* *Aleurothrixus floccosus* *Aleurotrachelus socialis* *Bemisia tabaci* *Dialeurodes citrifolli* *Trialeurodes vaporariorum* *Paraleyrodes citri* *Trialeurodes abutilonea* *Trialeurodes variabilis*	**C**	oligophagous	Plantations (e.g. *Brassica oleracea, Hibiscus spp., Lycopersicon esculentum, Vigna unguiculata*). Arable land (crops - e.g. *Gossypium spp.*).	eurytopic	Hoelmer *et al*., 1993; Heinz & Parrella, 1994; Liu & Stansly, 1996; Vieira & Correa, 2001; Hagler *et al*., 2004; Gonzalez *et al*., 2005; 2006; Garcia *et al*., 2007.
Diomus austrinus	Nc	*Phenacoccus madeirensis* *Planococcus citri*	**C**	oligophagous	Plantations (e.g. *Carica papaya*, *Saccharum spp.* and ornamental plants).	stenotopic	Chong *et al*., 2005; Cave, 2006.
Diomus flavifrons	Al	*Planococcus citri*	**C**	monophagous	On trees (orchards - e.g. *Citrus spp.*) in arable land.	stenotopic	Meyerdirk, 1983.
Diomus hennesseyi	IM	*Phenacoccus manihoti* *Phenacoccus madeirensis* *Planococcus citri*	**C**	oligophagous	Perennial plants in Plantations (e.g. *Manihot esculenta*).	stenotopic	Kiyindou, 1990; Kanika-Kiamfu *et al*., 1992; Kiyindou *et al*., 1992; Neuenschwander & Ajuonu, 1995.
Diomus pumilio	Al	*Acizzia uncatoides* *Adelges piceae* *Bemisia tabaci* *Pineus laevis* *Saissetia oleae*	**D**	polyphagous	Dry Savanna. Arable land (orchards - e.g. *Malus spp.*).	eurytopic	Pinnock *et al*., 1978; Zilahi-Balogh *et al*., 2002.

Diomus seminulus	Nt	*Planococcus citri* *Sipha flava*	**D**	polyphagous	Arable land (orchards - e.g. *Prunus spp.*; crops - e.g. *Triticum spp.*). Plantations (e.g. Arecaceae, *Saccharum spp.*).	eurytopic	Gonzalez *et al.*, 2012*;* Auad *et al.*, 2013.
Diomus terminatus	Nc	*Aphis craccivora* *Aphis gossypii* *Aphis nerii* *Rhopalosiphum maidis* *Rhopalosiphum padi* *Melanaphis sacchari* *Myzus persicae* *Sipha flava*	**C**	oligophagous	Perennial herbs - mainly Fabaceae and Poaceae (e.g. *Lablab purpureus, Phaseolus spp., Saccharum spp., Zea mays*) in arable land.	stenotopic	Hall, 2001; Hentz & Nuessly, 2002; Majken, 2003; Tifft *et al.*, 2006; Akbar *et al.*, 2009.
Diomus thoracicus	Nt	*Wasmannia auropunctata*	**C**	monophagous	Near ant (*Wasmannia auropunctata*) nests in Tropical Rainforest.	stenotopic	Vantaux *et al.*, 2010.
Eriopis connexa	Nt	*Acyrthosiphon pisum* *Aphis gossypii* *Cinara atlantica* *Diuraphis noxia* *Diatraea saccharalis* eggs *Lipaphis erysimi* *Lipaphis pseudobrassicae* *Macrosiphum euphorbiae* *Myzocallis coryli* *Myzus persicae* *Rhopalosiphum maidis* *Schizaphis graminum* *Spodoptera frugiperda* *Tetranychus evansi*	**D**	polyphagous	Arable land (orchards - e.g. *Corylus spp., Malus spp., Prunus spp.*; crops - e.g. *Glycine spp., Gossypium spp., Hordeum vulgare*); Pasturelands (e.g. *Medicago sativa*); Plantations (ornamental plants – e.g. *Nicotiana spp.; Vitis spp.).*	eurytopic	Ogas, 1970; Cividanes *et al.*, 1987; Demoraes *et al.*, 1991; Bertolaccini *et al.*, 1994; Aguilera & Pacheco, 1995; Obrycki & Kring, 1998; Bado *et al.*, 2002; Oliveira *et al.*, 2004; Navarrete & Landa, 2006; Gomez & Polania, 2006; Sarmento *et al.*, 2007; Gomez & Polania, 2009; Silva *et al.*, 2009, 2010a; 2013a, 2013b; Gomez *et al.*, 2013; Spindola *et al.*, 2013.
Exochomus childreni	Nc	*Aulacaspis yasumatsui* *Chrysomphalus aonidum* *Diaphorina citri* *Haliaspis nakaharai* *Lepidosaphes beckii* *Pseudaulacaspis pentagona*	**D**	polyphagous	Arable land (orchards - e.g. *Citrus sp.*). Subtropical/Tropical swamp forests. Urban gardens.	eurytopic	Michaud & Olsen, 2004; Villanueva *et al.*, 2004; Cave, 2006; Mehrnejad *et al.*, 2011.

Exochomus flavipes	Nt	*Dactylopius opuntiae* *Ferrisia virgata* *Matsucoccus josephi* *Phenacoccus manihoti* *Pulvinaria floccifera* *Pulvinaria mesembryanthemi* *Pulvinaria psidii* *Saissetia oleae*	**D**	oligophagous	Arable land (crops - e.g. *Gossypium spp.*; orchards - e.g. *Malus spp., Olea spp.*) Plantations (e.g. Arecaceae, *Opuntia spp., Persea spp., Psidium spp., Vigna unguiculata*)	eurytopic	Geyer, 1947; Dirorimwe, 1996; Shaaban *et al.*, 2003; Abd-Rabou & Badary, 2004; Pour & Shakarami, 2012.
Exochomus flaviventris	Af	*Phenacoccus manihoti* *Planococcus citri*	**C**	oligophagous	Plantations (e.g. *Manihot esculenta*). Tropical moist montane forest.	eurytopic	Fabres & Kiyindou, 1985; 1990b; Reyd & Leru, 1992; Kanika-Kiamfu *et al.*, 1992, 1993, 1994.
Exochomus nigromaculatus	Af	*Aphis craccivora* *Aphis nerii* *Diuraphis noxia* *Hyalopterus pruni* *Phloeomyzus passerinii*	**C**	oligophagous	Arable lands (crops - eg *Triticum spp.*; orchards - e.g. *Pistacia spp.*). Plantations (e.g. Arecaceae**).** Pasturelands (e.g. *Medicago sativa*). Mediterranean-type shrubby vegetation (e.g. *Juniperus spp., Populus spp., Ulmus glabra*).	eurytopic	Kasap & Yaşar, 1996; Ghahhari & Hatami, 2000; Atlhan & Ozgokce, 2002; Nazari *et al.*, 2006; Goncalves *et al.*, 2007; Basar & Yaşar, 2011.
Exochomus pubescens	Pl	*Aphis pomi* *Brachycaudus schwartzi* *Eriosoma lanigerum* *Myzus persicae*	**C**	oligophagous	Pasturelands (e.g. *Medicago sativa*). Plantations (e.g. Arecaceae).	eurytopic	Saharaoui *et al.*, 2001; 2010; Efil *et al.*, 2010; Pour & Shakarami, 2011; 2012.

Exochomus quadripustulatus	Pl	*Acyrthosiphon pisum* *Aonidiella aurantii* *Aonidiella citrina* *Aphis fabae* *Aphis pisum* *Aphis pomi* *Ceroplastes sinensis* *Chionaspis salicis* *Coccus pseudomagnoliarum* *Comstockaspis perniciosa* *Dysaphis devecta* *Dysaphis plantaginea* *Eriosoma lanigerum* *Eulecanium ciliatum* *Lepidosaphes ulmi* *Myzus persicae* *Nemolecanium graniformis* *Phenacoccus aceris* *Physokermes piceae* *Planococcus citri* *Planococcus vovae* *Pseudochermes fraxini* *Pseudococcus cryptus* *Pulvinaria regalis* *Saissetia coffeae* *Saissetia oleae* *Sphaerolecanium prunastri* *Unaspis euonymi*	**D**	polyphagous	Only trees (*Piceae spp.*, *Pseudotsuga menziesii*, *Ulmus spp.*, *Quercus spp.*, *Prunus spp.*) in temperate forests and arable land.	stenotopic	Bogya, 1996; Lotfalizadeh *et al.*, 2000; Mols, 2000; Farnoosh, 2003; Sengonca & Arnold, 2003; Aslan & Uygun, 2005; Bayram, 2008; Bayram, 2009; Ozturk & Ulusoy, 2009; Demirozer *et al.*, 2011; Farooq-Ahmad, 2012.
Halmus chalybeus	Al	*Ceroplastes destructor* *Ceroplastes sinensis* *Coccus viridis* *Saissetia oleae* *Pulvinaria spp.*	**C**	oligophagous	Arable land (orchards - e.g. *Citrus spp.*, *Prunus spp.*). Bogs, marshes, swamps.	eurytopic	Nishida, 1975; Lo, 2000; Lo & Chapman, 2001; Young, 2003; Jamieson *et al.*, 2005; Sheppard *et al.*, 2005.

Harmonia axyridis	Pl	several Aphididae several Coccidae Several Psyllidae eggs and larvae of many other insects, including other coccinellids and lepidopterans	**D**	polyphagous	Forests. Arable land (crops and orchards). Rural gardens. Urban areas. Wetlands (e.g. riparian zones). Shrublands (e.g. heathland).	eurytopic	Koch, 2003; Brown *et al.*, 2008; Chen *et al.*, 2012.
Harmonia conformis	Al	*Acizzia jucunda* *Acyrthosiphon pisum* *Aphis durantae* *Bactericera cockerelli* *Cacopsylla pyricola* *Chrysophtharta bimaculata* *Ctenarytaina thysanura* *Macrosiphum rosae* *Myzus persicae* *Schizaphis graminum*	**D**	polyphagous	Dry savanna (e.g. *Acacia spp.*, *Eucalyptus spp.*). Tropical Moist Lowland Forests (in e.g. *Boronia megastigma*, *Syzygium paniculatum*).	eurytopic	Hales, 1979; Elliott & Little, 1980; Baker *et al.*, 2003; Coutanceau, 2009; Larsen *et al.*, 2011.
Harmonia dimidiata	IM	*Aphis gossypii* *Brevicoryne brassicae* *Cervaphis quercus* *Eriosoma lanigerum* *Macrosiphum rosae* *Myzus persicae* *Schizaphis graminum* *Tuberculatus nervatus*	**C**	oligophagous	Mainly trees and shrubs: (e.g. *Abies amabilis*, *Euonymus spp.*, *Malus spp.*, *Prunus spp.*, *Quercus spp.*, *Rosa spp.*, *Salix spp.*) in arable land and temperate deciduous forests.	stenotopic	Saharia, 1980; Fye, 1981; Chakrabarti *et al.*, 1988; Gillani *et al.*, 2007; Sharmila *et al.*, 2010; Poorani, 2013; Yu *et al.*, 2013.

Harmonia eucharis	IM	*Aphis sp.* (4 sp) *Brachycaudus helichrysi* *Brevicoryne brassicae* *Cervaphis quercus* *Cervaphis rappardi* *Adelges knucheli* *Adelges piceae* *Eriosoma lanigerum* *Eulecanium tiliae* *Hyalopterus pruni* *Macrosiphoniella pseudoartemisiae* *Mollitrichosiphum montanum* *Myzus persicae* *Myzus varians* *Phorodon cannabis* *Rhopalosiphum nymphaeae* *Tuberculatus indicus*	**D**	oligophagous	Mainly trees (e.g. *Alnus nitida*, *Juglans regia*, *Malus spp.*, *Pinus spp.*, *Prunus spp.*, *Quercus incana*) in subtropical/Tropical moist montane forests and arable land.	stenotopic	Ghosh *et al.*, 1976; Phaloura & Singh, 1993; Chakrabarti *et al.*, 1995, 2012; Singh *et al.*, 2012.
Harmonia octomaculata	IM	*Aphis craccivora* *Aphis gossypii* *Brevicoryne brassicae* *Ceratovacuna lanigera* *Myzus persicae* *Nephotettix nigropictus* *Nephotettix virescens* *Nilaparvata lugens* *Peregrinus maidis* *Phenacoccus solenopsis*	**D**	polyphagous	Plantations (e.g. *Brassica spp.*, *Nicotiana spp.*, *Saccharum spp.*). Arable land (crops - e.g. *Zea mays*). Irrigated land (rice ecosystem). Tropical moist montane forests (e.g. *Quercus spp.*)	eurytopic	Wiryadiputra *et al.*, 1987; Peter, 1988; Singh, 1999; Kumar & Prabhuraj, 2006; Suja & Beevi, 2007; Tank *et al.*, 2007; Lokeshwari *et al.*, 2010.
Harmonia quadripunctata	Pl	*Aphis pomi* *Cinara sp.*	**C**	oligophagous	Trees and shrubs in temperate forests.	stenotopic	Vandenberg, 1990; Hoebeke & Wheeler, 1996; Antonucci, 2005.
Harmonia sedecimnotata	IM	*Myzus persicae* *Mollitrichosiphum alni* *Sitotroga cerealella*	**D**	polyphagous	Arable land (crops - e.g. *Zea mays*). Dry savanna (e.g. *Acacia auriculiformis*).	eurytopic	Phaloura & Singh, 1993; Sem’yanov & Vaghina, 2003; Sem’yanov, 2007, 2008.

Harmonia yedoensis	Pl	*Acyrthosiphon pisum Cinara pini* *Eulachnus thunbergii* *Lachnus tropicalis*	**A**	oligophagous	Coniferous trees (*e.g. Pinus densiflora*) in temperate forests.	stenotopic	Osawa & Ohashi, 2008; Noriyuki *et al.*, 2011; Noriyuki & Osawa, 2012; Suzuki *et al.*, 2013.
Hippodamia convergens	Nc	*Acyrthosiphon pisum* *Aphis gossypii* *Aphis spiraecola* *Bemisia tabaci* *Cinara atlantica* *Cinara pinivora* *Diaphorina citri* *Myzus persicae* *Schizaphis graminum* *Phorodon humuli* *Toxoptera citricidus* *Thrips tabaci* *Therioaphis maculata* *Rhopalosiphum padi* *Sitobion avenae*	**D**	polyphagous	Arable fields (crops - e.g., *Gossypium spp.*, *Triticum spp.*, orchards - e.g. *Citrus spp.*, *Malus spp.*). Pastureland (e.g. *Medicago sativa*). Temperate coniferous forests (e.g. *Pinus spp.*). Temperate grasslands.	eurytopic	Andow, 1990; Giles *et al.*, 1994; Cardoso & Lázzari, 2003a; Boica Jr. *et al*. 2004; Ehler, 2007; Zarpas *et al.*, 2007; El-Heneidy *et al.*, 2008; Phoofolo *et al.*, 2008; Jackson *et al.*, 2009; Conway & Kring, 2010; Arif *et al.*, 2011; Elliott *et al.*, 2011, 2012, 2013; Qureshi & Stansly, 2011; Diepenbrock & Finke, 2013.
Hippodamia parenthesis	Nc	*Acyrthosiphon pisum* *Schizaphis graminum*	**C**	oligophagous	Arable land (orchards - e.g. *Malus spp.*, *Prunus spp.*; crops - e.g. *Zea mays*). Rural gardens. Temperate grasslands.	eurytopic	Andow, 1990; Kieckhefer & Elliott, 1990; Orr & Obrycki, 1990; Kieckhefer *et al.*, 1992; Giles *et al.*, 1994; Wright & Vries, 2000; Kriz *et al.*, 2006.
Hippodamia quinquesignata	Nc	*Acyrthosiphon pisum* *Chromaphis juglandicola* *Diuraphis noxia*	**C**	oligophagous	Arable land (orchards - e.g. *Juglans regia*; crops - e.g. *Triticum spp.*). Plantations (ornamental plants). Rocky areas (hibernation). Pasturelands (e.g. *Medicago sativa).*	eurytopic	Harper & Lilly, 1982; Evans & Toler, 2007.
Hippodamia sinuata	Nc	*Rhopalosiphum maidis* *Schizaphis graminum*	**A**	oligophagous	Mainly Poaceae (e.g. *Sorghum* sp, *Medicago sativa*) in temperate grasslands, pasturelands and marshes.	stenotopic	Kring *et al.*, 1985; Michels & Behle, 1991.

Hippodamia tredecimpunctata	Nc	*Acyrthosiphon kondoi* *Acyrthosiphon pisum Aphis gossypii* *Aphis fabae* *Diuraphis noxia* *Myzus persicae* *Rhopalosiphum padi* *Schizaphis graminum* *Sitobion avenae*	**C**	oligophagous	Arable Land (Crops - e.g.; orchards - e.g. *Prunus spp.*). Plantations (glasshouse production of vegetables; e.g. *Solanum tuberosum*). Pasturelands (e.g. *Cirsium palustre*, *Medicago sativa*)	eurytopic	Storch & Vaundell, 1972; Kieckhefer & Elliott, 1990; Speight, 1990; Gruber *et al.*, 1991; Michels & Flanders, 1992; Kauffman & LaRoche, 1994; Elliott *et al.*, 1998; Hafez, 2001; Ren, 2007.
Hippodamia variegata	Pl	*Acyrthosiphon malvae* *Aphis spp.(5 sp)* *Brachycaudus spp. (2 sp)* *Brachyunguis harmalae* *Brevicoryne brassicae* *Diuraphis noxia* *Drosicha stebbingi* *Dysaphis crataegi* *Eriosoma lanigerum* *Hayhurstia atriplicis* *Hyalopterus pruni* *Hyperomyzus carduellinus* *Lipaphis sp.* (2 sp) *Liosomaphis himalayensis* *Macrosiphoniella artemisiae* *Macrosiphum sp.* (2 sp) *Myzus spp.* (2 sp) *Rhopalosiphum spp.* (2 sp) *Sitobion spp.* (3 sp) *Toxoptera aurantii*	**C**	oligophagous	Arable land (crops - e.g. *Triticum spp.*, *Zea mays*; orchards - e.g. *Malus spp.*, *Pistacia spp.*). Temperate forests (Conifers - e.g. *Abies alba*). Plantations (e.g. *Brassica spp.*).	eurytopic	Michels & Bateman, 1986; El Habi *et al.*, 2000; Franzmann, 2002; Kontodimas & Stathas, 2005; Jafari *et al.*, 2008; Jalali *et al.*, 2009; Farhadi *et al.*, 2010, 2011; Heimoana, 2011; Sarhan *et al.*, 2011; Golizadeh & Jafari-Behi, 2012; Dehkordi & Sahragard, 2013.
Hyperaspis lateralis	Nc	*Nipaecoccus aurilanatus* *Planococcus citri* *Pseudococcus calceolariae* *Pseudococcus maritimus* *Pseudococcus sequoia*	**C**	oligophagous	Arable land (orchards - e.g. *Citrus spp.*, *Malus spp.*). Temperate forests.	eurytopic	McKenzie, 1932; Grasswitz & Burts, 1995; VanDyk, 2014.

Hyperaspis maindroni	IM	*Aphis spp. (4 sp)* *Antonina graminis* *Coccidohystrix insolita* *Ferrisia virgata* *Melanaphis sacchari* *Maconellicoccus hirsutus* *Nipaecoccus viridis* *Paracoccus marginatus* *Phenacoccus solenopsis* *Planococcus citri* *Planococcus lilacinus* *Nipaecoccus viridis* *Rastrococcus iceryoides* *Saccharicoccus sacchari*	**D**	polyphagous	Plantations (e.g. *Carica papaya, Cocos spp.*, *Psidium spp.*, *Saccharum spp.*). Arable land (crops – e.g. *Gossypium spp.*). Seasonal/Intermittent freshwater marshes/pools.	eurytopic	Weng & Huang, 1988; Pervez, 2004a; Fand *et al.*, 2010; Arif *et al.*, 2012; Poorani, 2013.
Hyperaspis notata	Nt	*Ferrisia virgata* *Phenacoccus herreni* *Phenacoccus manihoti* *Phenacoccus madeirensis*	**C**	oligophagous	Plantations (e.g. *Manihot esculenta*). Arable land (orchards - e.g. *Citrus spp.*). Tropical forest in Colombian highlands.	eurytopic	Carrejo *et al.*, 1991; Sullivan *et al.*, 1991; Neuenschwander & Ajuonu, 1995; Dreyer, 1995, Dreyer *et al.*, 1997a, 1997b; 1997c.
Hyperaspis paludicola	Nc	*Miscanthicoccus miscanthi*	**A**	monophagous	Shrub dominated wetlands - swampy meadows of pinelands.	stenotopic	Gordon & Davidson, 2008; Wheeler Jr., 2013.
Hyperaspis pantherina	Nt	*Insignorthezia insignis*	**C**	monophagous	Mainly trees (e.g. *Commidendrum robustum*, *Jacaranda spp.*, *Lantana spp.)* in tropical moist lowland forests.	stenotopic	Booth *et al.*, 1995; Felix *et al.*, 2004; Fowler, 2004.
Hyperaspis raynevali	Nt	*Planococcus citri* *Phenacoccus herreni* *Phenacoccus manihoti*	**C**	oligophagous	Plantations (e.g. *Manihot esculenta*).	stenotopic	She *et al.*, 1984; Kiyindou, 1989; Reyd *et al.*, 1991; Kanika-Kiamfu *et al.*, 1992; Reyd & Ru, 1992.
Hyperaspis senegalensis	Af	*Ferrisia virgata* *Phenacoccus manihoti* *Pseudococcus citri*	**C**	oligophagous	Plantations (e.g. *Coffea spp.*, *Manihot esculenta*). Arable land (orchards - e.g. *Citrus spp.*).	eurytopic	Fabres & Kiyindou, 1985; Fabres *et al.*, 1989; Kiyindou *et al.*, 1990a; 1990b.
Hyperaspis venustulus	Nc	*Dysmicoccus dennoi* *Trionymus clandestinis*	**C**	oligophagous	Marshes, swamps (e.g. *Andropogon tenuispatheus, Spartina cynosuroides*).	stenotopic	Wheeler Jr., 2010.
Iberorhyzobius rondensis	Pl	*Matsucocccus feytaudi*	**A**	monophagous	*Pinus pinaster* in Temperate forests.	stenotopic	Tavares *et al.*, 2014.

Micraspis discolor	IM	*Aphis spp (4sp)* *Drone honey bee powder* *Myzus persicae* *Nephotettix virescens* *Nilaparvata lugens* *Oligonychus coffeae* *Toxoptera aurantii* *Rhopalosiphum maidis* *Sogatella furcifera*	**D**	polyphagous	Plantations (e.g. *Saccharum spp.*). Arable land (e.g. crops - *Gossypium spp.*, *Zea mays*; orchards - e.g. *Citrus spp.*). Permanent Freshwater Marshes/Pools -Irrigated land (rice).	eurytopic	Choudhuri & Agarwala; 1990; Hannan *et al.*, 1998; Afsana & Islam, 2001a, 2001b; Omkar & Ahmad, 2001; Rai *et al.*, 2002; Omkar, 2006; Islam *et al.*, 2007; Chowdhury *et al.*, 2008; Rekha *et al.*, 2009; Rattanapun, 2012.
Microweisea misella	Nc	*Chionaspis heterophyllae* *Chionaspis pinifoliae* *Diaspidiotus ancyclus* *Comstockaspis perniciosa* *Fiorinia theae* *Lepidosaphes beckii* *Melanaspis obscura* *Pseudaonidia duplex*	**C**	oligophagous	Temperate coniferous forests and shrublands (e.g. *Pinus sylvestris*).	stenotopic	Fondren & McCullough, 2005; Gordon & Davidson, 2008.
Mulsantina hudsonica	Nc	*Cinara confinis* *Mindarus abietinus*	**A**	oligophagous	Pinaceae (e.g. *Abies spp.*, *Picea spp.*) in Temperate coniferous forests.	stenotopic	Varty, 1969; Marriot *et al.*, 2009.
Mulsantina picta	Nc	*Adelges tsugae* *Eulachnus rileyi* *Myzocallis coryli* *Schizolachnus piniradiatae*	**D**	oligophagous	Mainly trees (e.g. *Abies spp.*, *Malus spp.*, *Picea spp.*) in temperate coniferous forests and arable land.	stenotopic	Beato, 1979; Kohler *et al.*, 2008; Sloggett *et al.*, 2008.
Myrrha octodecimguttata	Pl	*Cinara sp.* *Schizolachnus pineti*	**A**	oligophagous	Trees, mainly coniferous (e.g. *Pinus sylvestris*) in temperate forests.	stenotopic	Perez *et al.*, 1992; Sloggett & Majerus, 2000b; Sloggett, 2008; Rittner & Nir, 2013; Ulgenturk *et al.*, 2013.
Myzia oblongoguttata	Pl	*Cinara sp.* *Schizolachnus pineti*	**A**	oligophagous	Coniferous trees (e.g. *Picea spp.*) in temperate forests.	stenotopic	Sloggett *et al.*, 1999; Sloggett & Majerus, 2000b.
Nephaspis bicolor	Nc	*Aleurodicus cocois* *Aleurodicus maritimus* *Aleurothrixus floccosus*	**C**	oligophagous	Plantations.	stenotopic	Lopez &Kairo, 2003; Lopez, 2008.

Nephaspis oculatus	Nt	*Aleurocanthus woglumi* *Aleurodicus dispersus* *Aleurothrixus floccosus* *Bemisia argentifolii* *Bemisia tabaci* *Dialeurodes citri* *Dialeurodes citrifolii* *Orchamoplatus mammaeferus* *Paraleyrodes citri* *Pealius kelloggi* *Tripteroides floridensis* *Trialeurodes vaporariorum*	**C**	oligophagous	Plantations (e.g. *Carica papaya*, *Mangifera indica, Musa spp.*). Arable land (orchards - e.g. *Citrus spp.*).	eurytopic	Liu & Stansly, 1996, 1999; Liu *et al.*, 1997; Valenciaga *et al.*, 1999; Ren *et al.*, 2002.
Nephus bilucernarius	Nt	*Dysmicoccus brevipes* *Dysmicoccus neobrevipes*	**C**	oligophagous	Maily trees (e.g. *Malus spp.*, *Pinus spp.*) in plantations and arable land (orchards).	stenotopic	Gonzalez-Hernandez *et al.*, 1999a; 1999b.
Nephus bisignatus	Pl	*Dysmicoccus brevipes* *Nipaecoccus vastator* *Planococcus citri* *Planococcus ficus* *Planococcus vovae*	**C**	oligophagous	Plantations (e.g. Arecaceae, *Morus alba*, *Vitis spp.*). Arable land (crops - e.g. *Triticum spp.*, *Zea mays*; orchards - *e.g. Citrus spp.*). Mediterranean type shrubby vegetation.	eurytopic	Kehat, 1967b, Kontodimas, 1997, Marzo, 2001; Kontodimas *et al.*, 2007.
Nephus includens	Pl	*Planococcus citri* *Planococcus ficus* *Pseudococcus cryptus*	**C**	oligophagous	Arable land (orchards - e.g. *Citrus spp.*).	stenotopic	Canhilal, 1995, Kontodimas *et al.*, 2004, 2007, Bayoumy, 2011, Milonas *et al.*, 2011.
Nephus regularis	IM	*Coccidohystrix insolita* *Ferrisia virgata* *Maconellicoccus hirsutus* *Phenacoccus solani* *Phenacoccus solenopsis* *Planococcus minor* *Pseudococcus filamentosus* *Saccharicoccus sacchari*	**C**	oligophagous	Arable land (crops - e.g. *Gossypium spp.*). Plantations (e.g. *Bauhinia purpurea*, *Mangifera indica, Psidium spp.*).	eurytopic	Rawat & Modi, 1969; Gautam *et al.*, 2007; Fand *et al.*, 2010; Poorani, 2013.

Nephus reunioni	Af	*Planococcus citri* *Planococcus ficus* *Pseudococcus affinis* *Pseudococcus viburni*	**C**	oligophagous	Arable land (orchards - e.g. *Citrus spp.*) Plantations (e.g. *Coffea arabica, Passiflora caerulea*).	eurytopic	Orlinsky & Izhevsky, 1987, Izhevsky & Orlinsky 1988; Heidari, 1999; Borges *et al.*, 2013.
Oenopia conglobata	Pl	*Acizzia jamatonica* *Agonoscena pistaciae* *Aphis gossypii* *Brachycaudus helichrysi* *Ceroplastes rusci* *Chaitophorus populeti* *Chaitophorus leucomelas* *Diuraphis noxia* *Dysaphis devecta* *Eulecanium ciliatum* *Hyalopterus pruni* *Matsucoccus josephi* *Myzus persicae* *Pterochloroides persicae* *Rhopalosiphum padi* *Sitobion avenae*	**D**	polyphagous	Trees (e.g. *Pistacia vera, Populus spp., Prunus* spp., *Quercus spp.*) in arable land and temperate forests.	stenotopic	Ulgenturk & Toros, 1999; Mehrnejad & Jalali, 2004; Sadeghi *et al.*, 2004; Ghadam *et al.*, 2005; Yaşar & Özger, 2005b; Goncalves *et al.*, 2007; Hassani *et al.*, 2009; Yanik *et al.*, 2011.
Oenopia oncina	IM	*Aphis craccivora* *Aphis gossypii* *Brachycaudus cardui* *Macrosiphum sp.* *Myzus persicae*	**C**	oligophagous	Arable land (orchards - e.g. *Prunus spp.*; perennial herbs). Pasturelands (perennial plants - e.g. *Medicago sativa*).	eurytopic	Aslan & Uygun, 2005; Pour & Shakarami, 2011, 2012.

Olla v-nigrum	Nt	*Aphis pomi* *Aphis spiraecola* *Cacopsylla pyricola* *Chromaphis juglandicola* *Diaphorina citri* *Diaprepes abbreviatus* drone honeybee powder *Heteropsylla cubana* *Ephestia kuehniella* *Monellia caryella* *Panonychus citri* *Sarucallis kahawaluokalani* *Toxoptera citricidus* *Trialeurodes abutilonea* *Monelliopsis californica* *Monelliopsis caryae* *Phorodon humuli*	**D**	polyphagous	Pasturelands (e.g. *Leucaena leucocephala, Medicago sativa*). Arable land (orchards - e.g. *Carya illinoensis, Citrus spp., Prunus spp.*; crops - e.g. *Gossypium spp.*). Urban areas (ornamental trees - e.g. *Caesalpinia pluviosa, Tipuana tipu*).	eurytopic	Chazeau *et al.*, 1991; Bado & Rodriguez, 1997; Kato *et al.*, 1999; Stuart *et al.*, 2002, Vanderberg, 2004a, Silva *et al.*, 2013c.
Paranaemia vittigera	Nc	*Acyrthosiphon pisum* *Cavariella theobaldi* *Diuraphis noxia* *Macrosiphum weberi* *Megoura viciae* *Rhopalosiphum maidis* *Sitobion avenae* *Therioaphis luteola* *Uroleucon cichorii* *Uroleucon jaceae*	**C**	oligophagous	Alpine ecosystems. Crops - e.g. *Avena spp., Trifolium spp., Zea mays*) in alpine wetlands.	stenotopic	Mendivil-Portillo *et al.*, 1984; Marriott *et al.*, 2009.
Pentilia egena	Nt	*Aspidiotus nerii* *Chrysomphalus aonidum* *Chrysomphalus ficus* *Parlatoria cinerea* *Parlatoria pergandii* *Parlatoria ziziphi* *Selenaspidus articulatus* *Unaspis citri*	**C**	oligophagous	Arable land (orchards - e.g. *Citrus spp)* and other herbs (e.g. *Myrtus communis*).	stenotopic	De Bortoli *et al.*, 2001; Guerreiro *et al.*, 2003; Azeredo *et al.*, 2004.

Pharoscymnus flexibilis	IM	*Comstockaspis perniciosa* Diaspididae (several)	**C**	oligophagous	Arable land (orchards - e.g. *Citrus spp.*, *Malus spp.*). Plantations (e.g. Arecaceae, *Mangifera indica*). Tropical montane forest (e.g. *Pinus spp.*).	eurytopic	Rawat *et al.*, 1988; Thakur *et al.*, 1989; Sharma *et al.*, 1990; Irshad, 2001.
Pharoscymnus horni	IM	*Aspidiotus destructor* *Hemiberlesia lataniae* *Andaspis leucophleae* *Aulacaspis tubercularis* *Chrysomphalus aonidum* *Chrysomphalus bifasciculatus* *Coccus viridis* *Diaspis echinocacti* *Duplaspidiotus tesseratus* *Hemiberlesia lataniae* *Lepidosaphes beckii* *Lepidosaphes piperis* *Melanaspis glomerata* *Parlatoria blanchardii* *Phoenicococcus marlatti* *Octaspidiotus tamarindi*	**D**	oligophagous	Plantations (e.g. *Mangifera indica*, *Saccharum* spp.). Tropical dry shrubland (e.g. Cactaceae, *Rosa spp.*, *Thevetia neriifolia*).	eurytopic	Das & Gope, 1984; Murlidharan, 1993; Selvakumaran *et al.*, 1996; Omkar & Ahmad, 2000; Poorani, 2013.
Pharoscymnus numidicus	Nt	*Asterolicanium phoenicis* *Parlatoria blanchardi* *Spodoptera litura (eggs)*	**D**	oligophagous	Plantations (e.g. Arecaceae). Arable land (orchards - e.g. *Prunus spp.*).	eurytopic	Pope, 1961; Kehat, 1967a; 1968b.
Phrynocaria astrolabiana	Al	*Hyperomyzus carduellinus* *Hyperomyzus lactucae* *Pulvinaria spp.*	**D**	polyphagous	Arable land (orchards - e.g. *Ficus spp.).*	stenotopic	Houston, 1988.
Phrynocaria congener	Al	*Bemisia tabaci* *Lecanium spp.* *Myzus persicae Pulvinaria spp.*	**D**	polyphagous	Arable land (orchards - *Citrus spp., Olea spp.*).	stenotopic	Houston, 1988; Chen *et al.*, 1997; Wu *et al.*, 2010.
Phrynocaria gratiosa	Al	*Coccus viridis Hyperomyzus carduellinus Hyperomyzus lactucae* *Parasaissetia nigra*	**D**	polyphagous	Only trees (e.g. *Acacia spp.*, *Citrus spp.)* in arable land and dry savanna).	stenotopic	Houston, 1988.

Propylea quatuordecimpunctata	Pl	*Acyrthosiphon pisum* *Aphis craccivora* *Aphis fabae* *Aphis glycines* *Brachycaudus helichrysi* *Diuraphis noxia* *Eucallipterus tiliae* *Euceraphis betulae* *Metopolophium dirhodum* *Myzus persicae* *Phorodon humuli* *Pterocallis alni* *Rhopalosiphum maidis* *Schizaphis graminum* *Sitobion avenae* *Uroleucon cirsii* *Uroleucon jacae*	**C**	oligophagous	Temperate forests (e.g. *Fagus spp.*, *Pyrus spp.*, *Quercus spp.*, *Tilia spp.*). Arable land (crops - e.g. *Avena spp.*, *Faba spp.*, *Triticum spp.*).	eurytopic	Dysart, 1988; Obrycki & Orr, 1990; Day *et al.*, 1994; Kalushkov & Hodek, 2005; Kontodimas *et al.*, 2008; Finlayson *et al.*, 2010; Omkar, 2011.
Propylea dissecta	IM	*Aphis affinis* *Aphis craccivora* *Aphis gossypii* *Aphis nerii* *Lipaphis erysimi* *Myzus persicae* *Rhopalosiphum maidis* *Uroleucon compositae*	**C**	oligophagous	Arable land (crops - e.g. *Gossypium spp.)* Tropical Moist Montane forests (e.g. *Cedrus deodara, Ilex spp., Quercus floribunda, Quercus oblongata, Rhododendron arboreum*).	eurytopic	Mishra & Omkar, 2004; Omkar & Ahmad, 2004, 2010; Pervez, 2004b; Geetanjali *et al.*, 2011, 2012; Omkar, 2011.

Propylea japonica	Pl	*Acyrthosiphon pisum* *Aphis craccivora* *Aphis gossypii* *Bemisia tabaci nymphs* *Chaitophorus populeti* *Hyperomyzus lactucae* *Macrosiphum albifrons* *Megoura viciae* *Myzus persicae* *Rhopalosiphum maidis* *Trialeurodes vaporariorum* *Sitobion avenae* *Sitobion ibarae* *Uroleucon formosanus*	**D**	polyphagous	Arable land (crops - e.g. *Gossypium spp.*, *Zea mays*). Plantations (e.g. *Cucumis sativus*, *Cucurbita pepo, Solanum spp.*). Irrigated land (rice). Temperate deciduous forests (e.g. *Acer spp.*, *Rosa multiflora*). Temperate grasslands.	eurytopic	Song *et al.*, 1988; Kawauchi, 1997; Guo & Wan, 2001; Huang *et al.*, 2001; Chi & Yang, 2003; Zhang *et al.*, 2007, 2012; Tang *et al.*, 2013.
Rhyzobius lophanthae	Al	*Aonidiella aurantii* *Aulacaspis yasumatsui* *Aspidiotus nerii* *Carulaspis juniperi* *Chrysomphalus aonidum* *Chrysomphalus ficus* *Comstockaspis perniciosa* *Fiorinia externa* *Heiniberlesia lataniae* *Parlatoria pergandii* *Pseudaulacaspis pentagona*	**C**	oligophagous	Dry savanna (e.g. *Acacia spp.*). Arable land (orchards - e.g. *Citrus spp.*, *Olea spp.*, *Prunus spp.*). Temperate forests (e.g. *Pinus spp.*, *Quercus spp.*). Plantations (e.g. *Vitis spp.)*	eurytopic	Honda & Luck, 1995; Karaca *et al.*, 1999; Stathas, 2000, 2001; Abu-Alloush, 2005.
Rhyzobius chrysomeloides	Pl	*Adelges piceae* *Ceroplastes japonicus* *Eulachnus mediterraneus* *Lichtensia viburni* *Matsucoccus feytaudi* *Matsucoccus pini* *Myzus persicae* *Pemphigus bursarius* *Pineus pini* *Rhopalosiphum padi* *Saissetia oleae* *Schizolachnus pineti*	**D**	polyphagous	Temperate forests and Mediterranean shrublands. Arable land (several crops and orchards).	eurytopic	Raimundo 1986; Covassi, 1991; Toccafondi *et al.*, 1991, Winiarska, 1996.

Rhyzobius forestieri	Al	*Aonidiella aurantii* *Ceroplastes destructor* *Ceroplastes japonicus* *Ceroplastes rubens* *Coccus hesperidum* *Coccus longulus* *Coccus pseudomagnoliarum* *Coccus viridis* *Cryptes baccatus* *Eriococcus casuarinae* *Eriococcus mancus* *Icerya purchasi* *Monophlebulus sp.* *Orchamoplatus citri* *Parthenolecanium fletcheri* *Parthenolecanium persicae* *Planococcus citri* *Protopulvinaria mangiferae* *Saisseta oleae*	**D**	oligophagous	Arable land (orchards - e.g. *Citrus spp.*). Plantations (e.g. *Cucurbitacea*e). Dry savanna (*Acacia spp.*, *Casuarina spp.*).	eurytopic	Richards, 1981; Iperti, 1985; Iperti *et al.*, 1989; Kim & Morimoto, 1995; Katsoyannos, 1997; Canovai & Raspi, 1999.
Rhyzobius litura	Pl	*Aphis fabae* *Metopolophium dirhodum* *Sitobion avenae* *Sitobion fragariae* *Uroleucon cirsii* *Uroleucon jaceae*	**C**	oligophagous	Temperate forests and Mediterranean shrublands. Arable land (several crops and orchards).	eurytopic	Raimundo 1986; Schembri, 1993.
Rhyzobius ventralis	Al	*Eriococcus coriaceus* *Eriococcus sp.*	**C**	monophagous	Trees in dry savanna (e.g. *Acacia spp.*, *Eucalyptus spp.*).	stenotopic	Pope, 1981; Richards, 1981.
Rodatus major	Al	*Monophlebulus pilosior*	**A**	monophagous	*Lophostemon conferta* in dry savanna.	stenotopic	Richards, 1985.
Rodolia amabilis	IM	*Icerya aegyptiaca* *Icerya purchasi* *Icerya seychellarum*	**C**	monophagous	Plantations (e.g. *Mangifera indica*, *Psidium spp.*, *Populus spp.*, *Saccharum spp.*). Arable land (orchards - e.g. *Citrus spp.*, *Ficus spp.*).	eurytopic	Kairo & Murphy, 1995a; Poorani, 2013.

Rodolia cardinalis	Al	*Icerya aegyptiaca* *Icerya purchasi* *Icerya seychellarum*	**C**	monophagous	Dry savanna. Arable land (orchards - e.g. *Citrus spp.*). Plantations (e.g. *Vaccinium spp.*).	eurytopic	Chessman & Dumestre, 1930; Loia, 1992; Ragab, 1995; Mendel *et al.*, 1998; Causton *et al.*, 2004; Salisbury & Booth, 2004.
Rodolia fumida	IM	*Drosicha stebbingi* *Icerya pilosa* *Perissopneumon ferox* *Perissopneumon tamarindus*	**C**	monophagous	Plantations (e.g. *Mangifera indica, Psidium spp, Saccharum spp.*); Arable land (Orchards – e.g. *Citrus spp.*).	eurytopic	Rasheed *et al.*, 1986; Mukhtar *et al.*, 2001.
Rodolia iceryae	Af	*Icerya pattersoni* *Icerya seychellarum*	**C**	monophagous	Plantations (e.g. *Coffea spp.*).	stenotopic	Mendel & Blumberg, 1991; Kairo & Murphy, 1995b.
Rodolia limbata	Pl	*Drosicha corpulenta*	**C**	monophagous	On decidous trees (*Castanea sativa; Populus spp.*) in temperate forests.	stenotopic	Kairo & Murphy, 1995b.
Sasajiscymnus quinquepunctatus	IM	*Paracoccus marginatus*	**C**	monophagous	Plantations (e.g. *Mangifera indica*). Arable land - Orchards (e.g. *Citrus spp.*).	eurytopic	Vandenberg, 2004b; Saengyot & Burikam, 2011, 2012.
Sasajiscymnus tsugae	Pl	*Adelges piceae* *Adelges tsugae* *Pineus strobi*	**A**	oligophagous	*Tsuga spp.* trees in temperate coniferous forests.	stenotopic	Sasaji & McClure, 1997; Cheah & McClure, 1998, 2000, Butin *et al.*, 2004, Cheah *et al.*, 2005, Klunk, 2007, Wiggins *et al.*, 2010, Cheah, 2011.
Scymnodes lividigaster	Al	*Aphis citricidus* *Aphis eugeniae* *Aphis gossypii* *Toxoptera aurantiae*	**C**	oligophagous	Arable land (orchards - e.g. *Citrus spp.).* Tropical moist montane forests (e.g. *Glochidion ferdinandi*).	eurytopic	Anderson, 1980; 1981a, 1981b, 1982; Richards, 1980; Pope & Lawrence, 1990.
Scymnus apetzi	Pl	*Aphis gossypii* *Eriosoma lanuginosum* *Eriosoma ulmi* *Hyalopterus pruni* *Myzus persicae* *Tetraneura ulmi* *Toxoptera aurantii*	**C**	oligophagous	Only trees. Temperate deciduous forests (e.g. *Castanea sativa, Ulmus spp.*). Arable land (orchards - e.g. *Citrus spp., Prunus spp.*).	stenotopic	Raimundo 1986; Atlhan & Kaydan, 2002, Santos *et al.*, 2012.

Scymnus camptodromus	Pl	*Adelges cooleyi* *Adelges laricis* *Adelges tsugae* *Pineus strobi*	**A**	oligophagous	Pinaceae.	stenotopic	Lu & Montgomery, 2000; Keena *et al.*, 2012.
Scymnus castaneus	IM	*Aphis craccivora* *Aphis gossypii* *Aphis nerii* *Aphis punicae* *Melanaphis sacchari* *Rhopalosiphum maidis* *Schoutedenia emblica*	**C**	oligophagous	Plantations (e.g. *Psidium spp.*, *Vigna spp.*). Arable land (crops - e.g. *Gossypium spp.*, *Phaseolus spp.*). Tropical Forests (e.g. *Spathodea campanulata*).	eurytopic	Mani & Krishnamoorthy, 1995; Baskaran *et al.*, 2009.
Scymnus coccivora	IM	*Ferrisia virgata* *Maconellicoccus hirsutus* *Planococcus citri* *Planococcus lilacinus* *Phenacoccus solenopsis*	**C**	oligophagous	Plantations (e.g. *Psidium spp.*, *Sechium edule*, *Vitis spp.*, *Ziziphus mauritiana*). Arable land (orchards - e.g. *Citrus spp.*, *Punica spp.*; crops - e.g. *Gossypium spp.*). Wetlands such as permanent rivers (e.g. *Eichhornia crassipes*).	eurytopic	Padmaja *et al.*, 1995; Anand & Ayub, 2002; Baskaran *et al.*, 2006, 2007; Fand, 2010.
Scymnus frontalis	Pl	*Aphis craccivora* *Aphis glycines* *Acyrthosiphon pisum* *Diuraphis noxia* *Myzus persicae* *Schizaphis graminum* *Sitobion avenae*	**C**	oligophagous	Mainly perennial plants (e.g. *Hordeum vulgare*, *Medicago sativa*, *Triticum spp.*) in arable land, temperate grasslands and pasturelands.	stenotopic	Fursch, 1990; Naranjo *et al.*, 1990; Gibson *et al.*, 1992; Wang *et al.*, 2010.
Scymnus impexus	Pl	*Adelges nordmanniana* *Adelges piceae* *Adelges tsugae*	**A**	oligophagous	Pinaceae (e.g. *Pinus spp.*, *Pseudotsuga spp.*) in temperate forests.	stenotopic	Delucchia, 1954; Clarke & Brown, 1961.

Scymnus interruptus	Pl	*Aphis craccivora* *Aphis gossypii* *Icerya aegyptiaca* *Maconellicoccus hirsutus* *Planococcus citri* *Planococcus vovae* *Rhopalosiphum maidis* *Rhopalosiphum padi* *Saissetia oleae* *Schizaphis graminum* *Sitobion avenae*	**D**	polyphagous	Arable land (orchards - e.g. *Castanea sativa, Citrus spp., Olea spp., Punica granatum*; crops - e.g. *Zea mays*). Temperate deciduous forests (e.g. *Juniperus spp., Quercus spp.*).	eurytopic	Raimundo, 1986; Canovai, 1996; Boddi *et al.*, 2005; Mesbah *et al.*, 2008; Santos *et al.*, 2009.
Scymnus latemaculatus	IM	*Aphis craccivora* *Aphis nerii* *Aphis punicae* *Aphis rumicis* *Aphis spiraecola* *Myzus persicae* *Nipaecoccus viridis* *Rhopalosiphum maidis*	**C**	oligophagous	Arable land (crops - e.g. *Gossypium spp.*; orchards - e.g. *Punica granatum*). Plantations (e.g. *Nicotiana spp., Vigna spp.*).	eurytopic	Rahman, 1993; Mani & Krishnamoorthy, 1995.
Scymnus mediterraneus	Pl	*Aphis sp.* *Saissetia oleae*	**D**	polyphagous	Mainly trees (e.g. *Acacia spp., Citrus spp., Olea spp., Pinus spp., Prunus spp.)* in arable land and temperate forests.	stenotopic	Raimundo 1986; M'Hamed & Chemseddine, 1996; Ba M'Hamed & Chemseddine, 2001.
Scymnus nigrinus	Pl	*Eulachnus agilis* *Pineus pini* *Schizolachnus pineti*	**A**	oligophagous	*Pinus spp* in temperate coniferous forests.	stenotopic	Vohland, 1996; Nevdved, 1999.
Scymnus ningshanensis	Pl	*Adelges tsugae*	**A**	monophagous	*Tsuga spp.* in temperate coniferous forests.	stenotopic	Butin *et al.*, , 2002, 2003a ; 2004; Montgomery *et al.*, 2002.
Scymnus nubes	Nc	*Aphis gossypii* *Aphis rumicis* *Chromaphis juglandicola* *Myzus persicae* *Myzaphis rosarum* *Rhopalosiphum maidis* *Rhopalosiphum padi* *Wahlgreniella nervata*	**C**	oligophagous	Mainly Poaceae (crops - e.g. *Gossypium spp., Zea mays*) in arable lands.	stenotopic	Davidson, 1923.

Scymnus nubilus	IM	*Aleurolobus barodensis* *Aleurolobus dispersus* *Aphis craccivora* *Aphis gossypii* *Aphis nerii* *Coccidohystrix insolita* *Contarinia sorghicola* *Maconellicoccus hirsutus* *Neomaskellia andropogonis* *Nipaecoccus viridis* *Rhopalosiphum nymphaeae* *Rhopalosiphum padi* *Therioaphis trifolii*	**D**	polyphagous	Arable land (crops - e.g. *Gossypium spp.*, *Sorghum spp.*, *Zea mays*). Plantations (e.g. *Morus alba*, *Musa spp.*, *Psidium spp.*, *Santalum album*). Pasturelands (e.g. *Medicago sativa*).	eurytopic	Johnson, 1972; Kumar & Chakraborty, 1997; Borges *et al.*, 2013.
Scymnus sinuanodulus	Pl	*Adelges tsugae*	**A**	monophagous	*Tsuga spp.* in temperate coniferous forests.	stenotopic	Lu & Montgomery, 2000; 2001; Lu *et al.*, 2002.
Scymnus subvillosus	Pl	*Aphis gossypii* *Aphis sambuci* *Brachycaudus amygdalinus* *Brachycaudus helichrysi* *Dysaphis devecta* *Hyalopterus pruni* *Myzus persicae* *Toxoptera aurantii*	**C**	oligophagous	Mainly trees (e.g. Arecaceae, *Citrus spp.*, *Oleae spp.*, *Prunus spp.*, *Quercus spp.*, *Sambucus spp.*) in temperate deciduous forests, arable land and plantations.	stenotopic	Atlhan & Kaydan, 2002; Tezcan & Uygun, 2003; Atlihan & Chi, 2008; Atlıhan & Güldal, 2009; Milek *et al.*, 2009; Santos *et al.*, 2010, 2012.
Scymnus suturalis	Pl	*Adelges tsugae* *Pineus strobi*	**A**	oligophagous	Pinaceae (e.g. *Pinus spp.*, *Tsuga spp.*) in temperate coniferous forests.	stenotopic	McNamara, 1992; Lyon & Montgomery, 2010.
Scymnus syriacus	Pl	*Aphis craccivora* *Aphis fabae* *Aphis gossypi* *Aphis nerii* *Aphis punicae* *Aphis spiraecola* *Hyalopterus pruni* *Macrosiphum rosae*	**C**	oligophagous	Plantations (e.g. Arecaceae, *Psidium spp.*). Ornamental plants (e.g. *Hibiscus spp.*, *Jasminum spp.*). Arable land (orchards -e.g. *Citrus spp.*, *Pistacia spp.*, *Prunus spp.*; crops - e.g. *Gossypium spp.*).	eurytopic	Emami *et al.*, 2000; Allawi, 2006; Soroushmehr *et al.*, 2008; Sabaghi *et al.*, 2011a, 2011b.

Serangium parcesetosum	IM	*Aleurolobus barodensis* *Aleurocanthus arecae* *Aleurocanthus woglumi* *Aleurodicus dispersus* *Aleurothrixus floccosus* *Bemisia argentifolii* *Bemisia tabaci* *Dialeurodes citri* *Paraleyrodes minei* *Trialeurodes ricini* *Trialeurodes vaporariorum*	**C**	oligophagous	Plantations (e.g. *Brassica spp.*, *Cocos spp.*, *Psidium spp.*, *Solanum lycopersicum*). Arable land (orchards - e.g. *Citrus spp.*).	eurytopic	Kapadia & Puri, 1992; Legaspi *et al.*, 1996; Patel *et al.*, 1996; Kapadia & Butani, 1997; Ellis *et al.*, 2001; Al-Zyoud & Sengonca, 2004; Sengonca *et al.*, 2004, Al-Zyoud *et al.*, 2005; Yigit & Canhilal, 2005; Aboud *et al.*, 2006; Al-Zyoud *et al.*, 2007, Kutuk *et al.*, 2008.
Sospita vigintiguttata	Pl	*Aphis sp.* *Psyllidae*	**D**	polyphagous	On *Alnus glutinosa* , in terrestrial reed bed in Seasonal Freshwater Marshes.	stenotopic	Palmeri, 1996; Floreck *et al.*, 2011.
Stethorus aethiops	Af	*Mononychellus tanajoa* *Tetranychus lombardinii* *Tetranychus neocaledonicus* *Tetranychus urticae*	**C**	oligophagous	Plantations (e.g. *Manihot esculenta*).	stenotopic	Fursch, 2006.
Stethorus bifidus	Al	*Bryobia spp.* *Eotetranychus sexmaculatus* *Panonychus ulmi* *Tetranychus lambi* *Tetranychus lintearius* *Tetranychus urticae*	**C**	oligophagous	Arable land (orchards - e.g. *Malus spp.*). Dry Savanna (shrubs - e.g. *Ulex spp.*).	eurytopic	Houston, 1990; Peterson, 1993; Jamieson *et al.*, 2005.
Stethorus chengi	Pl	*Panonychus citri* *Tetranychus urticae* *Tetranychus truncatus*	**C**	oligophagous	Plantations (e.g. *Artocarpus altilis, Jatropha curkas*; *Quisqualis indica*). Arable land (orchards - e.g. *Prunus spp.*).	eurytopic	Cheng *et al.*, 1993; Wenlong & Longshu, 1993; Chen *et al.*, 1994.
Stethorus comoriensis	Af	*Eutetranychus africanus* *Oligonychus coffeae* *Tetranychus neocaledonicus*	**C**	oligophagous	Plantations (e.g. *Artocarpus altilis, Jatropha curkas*; *Quisqualis indica*). Arable land (orchards – e.g. *Prunus spp.*).	eurytopic	Chazeau, 1971.
Stethorus darwini	Nt	*Mononychellus caribbeanae* *Panonychus ulmi* *Tetranychus evansi*	**C**	oligophagous	Plantations (e.g. *Manihot esculenta*, *Lycopersicum esculentum*). Arable land orchards - e.g. *Malus spp.*).	eurytopic	Chazeau, 1983b; Lorenzato, 1988.

Stethorus exspectatus	Af	*Oligonychus sp.* *Panonychus sp.* *Tetranychus fijiensis* *Tetranychus lambi*	**C**	oligophagous	Plantations (e.g. *Cocos spp.*, *Manihot esculenta*). Arable land (crops).	eurytopic	Chazeau, 1983a.
Stethorus exsultabilis	Af	*Oligonychus sp.* *Panonychus sp.* *Tetranychus fijiensis* *Tetranychus lambi*	**C**	oligophagous	Plantations (e.g. *Cocos spp.*, *Manihot esculenta*; ornamental plants - e.g. *Lagerstroemia indica*).	stenotopic	Chazeau, 1983b.
Stethorus fenestralis	Al	*Tetranychus kanzawai* *Tetranychus lambi* *Tetranychus urticae*	**C**	oligophagous	Plantations (e.g. *Carica papaya*, Cucurbitaceae, *Manihot esculenta*, *Morus alba*, *Musa spp.*, *Ricinus communis*; ornamental plants - e.g. *Convolvulus spp.*).	stenotopic	Houston, 1980.
Stethorus gilvifrons	Pl	*Bemisia tabaci* *Eutetranychus hirsti* *Eutetranychus orientalis* *Panonychus citri* *Panonychus ulmi* *Oligonychus afrasiaticus* *Oligonychus coffeae* *Oligonychus sacchari* *Tetranychus cinnabarinus (eggs)* *Tetranychus turkestani* *Tetranychus urticae (eggs)*	**D**	polyphagous	Arable land (orchards - e.g. *Ficus spp.*, *Malus spp.*, *Prunus spp.*; crops - *Phaseolus spp.*). Plantations (*Camellia sinensis*, *Cucumis sativus*, *Fragaria spp.*, *Mangifera indica;* *Ricinus communis*, *Solanum melongena*).	eurytopic	Ahmed, 1989; Haji-Zadeh, 1994; Mridul, 2002; Al-Duhawi, 2006; Kheradpir, 2006; Sohrabi & Shishehbor, 2007; Taghizadeh, 2008; Gencer, 2009; Ahmad, 2010; Kandasamy, 2010; Imani, 2011; Osman, 2011; Latifian, 2012.
Stethorus histrio	Nt	*Eutetranychus orientalis* *Oligonychus thelytokus* *Oligonychus vitis* *Oligonychus yothersi* *Panonychus citri* *Panonychus ulmi* *Tetranychus kanzawai* *Tetranychus lintearius* *Tetranychus neocaledonicus* *Tetranychus urticae*	**C**	oligophagous	Plantations (e.g. *Camellia sinensis*, *Carica papaya*). Arable land (crops - e.g. *Phaseolus spp.*, *Zea mays*; orchards - e.g. *Citrus spp.*, *Malus spp.*). Temperate forests (coniferous - e.g. *Pinus spp.*; ornamental deciduous trees - e.g. *Cercis canadensis*).	eurytopic	Alves, 2009.

Stethorus japonicus	Pl	*Amphitetranychus viennensis* *Panonychus citri* *Panonychus mori* *Tetranychus kanzawai* *Tetranychus viennensis* *Tetranychus urticae*	***C***	*oligophagous*	Arable land (orchards - *e.g. Citrus spp., Malus spp.).* Plantations (e.g. *Camellia sinensis, Vitis spp.;* ornamental plants - e.g. *Hydrangea spp.*).	eurytopic	Kishimoto, 2002, 2003, 2008; Mori, 2005.
Stethorus jejunus	Af	*Mononychellus tanajoa* *Tetranychus lombardinii* *Tetranychus neocaledonicus* *Tetranychus urticae*	***C***	*oligophagous*	Plantations (e.g. *Manihot esculenta*).	stenotopic	Fursch, 2006.
Stethorus keralicus	IM	*Raoiella indica* *Raoiella macfarlanei*	***C***	*oligophagous*	Plantations (e.g. Arecaceae, *Cocos spp., Syzygium jambas*).	stenotopic	Kapur, 1961; Daniel, 1976; Rangaswamy, 1976; Nageshchandra, 1983.
Stethorus madecassus	IM	*Eotetranychus limoni* *Eotetranychus sambiranensis* *Tetranychus neocaledonicus* *Oligonychus coffea*	***D***	*oligophagous*	Arable land (Crops - *e.g. Gossypium spp.*). Plantations (e.g. *Persea spp.*).	eurytopic	Kapur, 1961; Blommers,1975; Daniel, 1976; Rangaswamy, 1976; Nageshchandra, 1983.
Stethorus nigripes	Al	*Oligonychus pratensis* *Panonychus citri* *Panonychus ulmi* *Tetranychus lambi* *Tetranychus pacificus* *Tetranychus urticae*	***C***	*oligophagous*	Arable land (crops - e.g. *Zea mays*; orchards - *e.g. Citrus spp., Prunus spp.*).	*stenotopic*	Hoy, 1982; Bailey, 1986; Gordon, 1993; Pollock, 2002; Yoder, 2003.
Stethorus pauperculus	IM	*Oligonychus pratensis* *Tetranychus lambi* *Tetranychus pacificus* *Tetranychus urticae*	***D***	*oligophagous*	Plantations (*e.g. Manihot esculenta, Musa spp.*).	*stenotopic*	Puttaswamy, 1977; Jianlin, 1990; Rattanatip, 2008; Zhang *et al.*, 2010.

Stethorus punctillum	Pl	*Eotetranychus buxi* *Eotetranychus carpini* *Eotetranychus tiliarium* *Metatetranychus ulmi* *Oligonychus afrasiaticus* *Oligonychus bicolor* *Oligonychus ilicis* *Oligonychus ununguis* *Panonychus citri* *Panonychus ulmi* *Tetranychus bioculatus* *Tetranychus cinnabarinus* *Tetranychus mcdanieli* *Tetranychus ludeni* *Tetranychus turkestani* *Tetranychus urticae* *Tetranychus viennensis*	***D***	*oligophagous*	Arable land - orchards, tree plantations, gardens, and crop fields. Plantations - greenhouses, interiorscapes, nurseries.	eurytopic	Putman,1955; Pasqualini & Antropoli,1994; Espinha, 1995; Yang *et al*., 1996; Gu *et al*.,1996; Kasap, 2003; Arbabi, 2008; Idder, 2008; Gorzka *et al*. 2009.
Stethorus punctum	Nc	*Panonychus ulmi* *Tetranychus mcdanieli* *Tetranychus pacificus* *Tetranychus tumidus* *Tetranchys urticae*	***C***	*oligophagous*	Arable land (orchards - e.g. *Malus spp.*). Plantations (e.g. *Fragaria spp., Musa spp., Vitis spp.*).	eurytopic	Colburn, 1970, 1971; Emel'yanov *et al*., 1988; Houck, 1986; Congdon, 1993; Hull, 1997; Kishimoto, 2011.
Stethorus siphonulus	IM	*Oligonychus exsiccator* *Panonychus citri* *Tetranychus cinnabarinus* *Tetranychus piercei* *Tetranychus tumidus* *Tetranychus urticae*	***C***	*oligophagous*	Plantations (e.g. *Anona spp., Carica papaya, Morus alba, Saccharum spp.*; ornamental plants - e.g. *Calotropis gigantea, Codiaeum variegatum*). Arable land (orchards - e.g. *Citrus spp.*).	eurytopic	Raros, 1974; Huang, 1988; Taili, 1989; Jian *et al.*, 1999.
Stethorus tridens	Nt	*Panonychus citri* *Tetranychus cinnabarinus* *Tetranychus evansi* *Tetranychus urticae*	***C***	*oligophagous*	Plantations (e.g. *Manihot esculenta, Solanum spp.*). Arable land (orchards - e.g. *Citrus spp.*).	eurytopic	Fiaboe *et al*., 2007; Guanilo & Martinez, 2007; Britto, 2009.

Stethorus utilis	Nc	*Eutetranychus banksi* *Eotetranychus hicoriae* *Eotetranychus sexmaculatus* *Mononychellus caribbeanae* *Mononychellus tanajoa* *Oligonychus pratensis* *Tetranychus citri* *Tetranychus urticae*	***D***	*oligophagous*	Plantations (e.g. *Carya spp.*, *Citrus spp.*, *Cocos spp.*, *Manihot esculenta*,). Arable land (orchards - e.g. *Citrus spp.;* crops - *Sorghum spp*.).	*eurytopic*	Muma, 1955; Pena *et al*., 2009.
Stethorus vagans	Al	*Bryobia praetiosa* *Oligonychus exsiccator* *Oligonychus thelytokus* *Panonychus ulmi* *Polyphagotarsonemus latus* *Tetranychus lambi* *Tetranychus marianae* *Tetranychus neocaledonicus* *Tetranychus urticae*	***D***	*oligophagous*	Plantations (*e.g. Cocos spp., Manihot esculenta, Carya papaya, Saccharum spp.).* Arable land (orchards - *Citrus spp., Malus spp.;* crops - *Phaseolus spp.*). Forests (*e.g. Pinus spp.).*	*eurytopic*	Houston, 1980; Khan, 2000; Inamullah et al. 2007.
Sticholotis marginalis	IM	*Aonidiella orientalis* *Comstockaspis perniciosa* *Leucaspis coniferarum*	**D**	oligophagous	Plantations (*Solanum nigrum*); Temperate Coniferous forests (e.g. *Pinus spp.).*	eurytopic	Ahmad & Ghani, 1971; Thakur, 1989; Rajesh, 2011.
Synona melanaria	Al	*Coptosoma ostensum*	**C**	monophagous	Crops (e.g. Fabaceae).	stenotopic	Shama, 1998; Dejean, 2002; Rachappa, 2002; Poorani, 2008.
Synonycha grandis	IM	*Ceratovacuna lanigera* *Ceratovacuna silvestrii* *Pseudoregma alexandri* *Pseudoregma bambusicola* *Pseudoregma bucktoni* *Tuberculatus indicus*	**A**	oligophagous	Mostly in Poaceae (e.g. *Phyllostachys spp.*) in Tropical Moist Lowland Forest. Plantations (e.g. *Abelmoschus esculentus, Lablab purpureus, Saccharum spp.*) in plantations.	stenotopic	Arakaki, 1992; Wenlong, 1992; Li *et al*., 2001; Vidya, 2004; Poorani, 2013.

References – annex 1.

Abd-Rabou, S. & Badary, H. (2004) Survey and abundance of natural enemies of the cottony camellia scale, *Pulvinaria floccifera* (Westwood) (Homoptera: Coccidae) in Egypt. *Annals of Agricultural Science, Moshtohor* **42**, 831-838.

Aboud, R., Ahmed, M. & Kaf, N.A. (2006) Evaluation of the efficiency of the coccinelllid *Serangium parcesetosum* Sicard (Coleoptera: Coccinellidae) for controlling *Bemisia tabaci* Genn. (Homoptera: Aleyrodidae). *Arab Journal of Plant Protection* **24**, 107-111.

Abraham, C., Mathew, K. & Das, N. (1973) New record of *Coccinella arcuata* Fabricius (Col.: Coccinellidae) as a predator of *Nilaparvata lugens* Stål in Kerala. *Agricultural Research Journal of Kerala* **11**, 75.

Abu-Alloush, A.H. (2005) Biological study on *Rhyzobius lophanthae* Blaisdell (Coleoptera: Coccinellidae), a predator of scale insect *Aspidiotus hederae* (Homoptera: Diaspididae). Master’s Thesis, University of Jordan.

Afsana, N. & Islam, Z. (2001a) Effects of the ladybird beetle *Micraspis discolor* on yield components and grain yield of rice. *International Rice Research Notes* **26**, 43-44.

Afsana, N. & Islam, Z. (2001b) Predation potential of *Micraspis discolor* Fabricius (Coleoptera: Coccinellidae) on rice leafhopper and planthopper. *Bangladesh Journal of Entomology* **11**, 67-74.

Agarwala, B.K., Bardhanroy, P., Yasuda, H. & Takizawa, T. (2001) Prey consumption and oviposition of the aphidophagous predator *Menochilus sexmaculatus* (Coleoptera: Coccinellidae) in relation to prey density and adult size. *Environmental Entomology* **30**, 1182-1187.

Agekyan, N. (1977) *Clitostethus arcuatus* Rossi (Coleoptera, Coccinellidae) – a predator of citrus whitefly in Adzharia. *Entomologicheskoe Obozrenie* **56**, 31-33.

Aguilera, P. A. & Pacheco, V.C. (1995) Determination of predators of the hazelnut aphid, *Myzocallis coryli* (Goeze) (Homoptera: Aphididae) in the IX region of Chile. *Revista Chilena de Entomología* **22**, 17-19.

Ahmad, P. & Omkar (2010) Prey-dependent life attributes of an aphidophagous ladybird beetle, *Propylea dissecta* (Coleoptera: Coccinellidae). *Biocontrol Science and Technology* **14**, 385-396.

Ahmad, R. & Ghani, M. (1966) Biology of *Chilocorus infernalis* Muls. (Col.: Coccinellidae). *Technical bulletin of the Commonwealth Institute of Biological Control* **7**, 101-106.

Ahmad, R. & Ghani, M. (1971) The biology of *Sticholotis marginalis* Kapur (Col.: Coccinellidae). *Technical Bulletin of the Commonwealth Institute of Biological Control* **14**, 91-95.

Aishwariya, K.K., Manjunatha, M. & Naik, M.I. (2007) Seasonal incidence of spiralling whitefly *Aleurodicus dispersus* Russell and its natural enemies in relation to weather in Shimoga. *Karnataka Journal of Agricultural Sciences* **20**, 146-148.

Akbar, W., Carlton, C. & Reagan, T.E. (2009) Life cycle and larval morphology of *Diomus terminatus* (Coleoptera: Coccinellidae) and its potential as a biological control agent of *Melanaphis sacchari* (Hemiptera: Aphididae). *Annals of the Entomological Society of America* **102**, 96-103.

Al-Duhawi, S.S., Ali, A.A. & Sameer, S.H. (2006) The predation efficacy of the predators *Stethorus glivifrons* (Muls.) and *Scolothrips sexmaculatus* (Perg.) on tobacco whitefly *Bemisia tabaci* (Gen.) which attacks cotton plants. *Arab Journal of Plant Protection* **24**, 112-117.

Ali, S.S., Sheikh, S.A., Rizwana, H., Baloch, G.M., Kaleri, A.N., Ahmed, S.S. & Shereen, N. (2005) Predatory potential of 11-spotted ladybird beetle on cotton aphid under laboratory conditions. *Industrial Cottons* **2**, 161-165.

Allawi, T.F. (2006) Biological and ecological studies on *Scymnus syriacus* and *Scymnus levaillanti* (Coleoptera: Coccinellidae). *European Journal of Entomology* **103**, 501-503.

Alma, P. (1980) Observations on some coccinellids in New Zealand and their significance to the biological control of *Paropsis charybdis* (Coleoptera: Chrysomelidae). *New Zealand Entomologist* **7**, 164-165.

Alves, L.F.A. & Oliveira, D.G. (2009) *Parastethorus histrio* (Chazeau) (Coleoptera: Coccinellidae) predator of the red mite *Oligonychus yothersi* (McGregor) (Acari: Tetranychidae), on Paraguay tea (*Ilex paraguariensis* A.St.Hil.) in Brazil. *Revista Brasileira de Biociencias* **7**, 229-230.

Al-Zyoud, F. & Sengonca, C. (2004) Prey consumption preferences of *Serangium parcesetosum* Sicard (Col., Coccinelidae) for different prey stages, species and parasitized prey. *Journal of Pest Science* **77**, 197-204.

Al-Zyoud, F. (2007) Prey species preference of the predator *Serangium parcesetosum* Sicard (Col., Coccinellidae) and its interaction with another natural enemy. *Pakistan Journal of Biological Sciences* **10**, 2159-2165.

Al-Zyoud, F., Blaeser, P. & Sengonca, C. (2005) Investigations on the biology and prey consumption of the *predator Serangium parcesetosum* Sicard (Col., Coccinellidae) by feeding on *Trialeurodes vaporariorum* Westwood (Hom.: Aleyrodidae) as prey. *Journal of Plant Disease and Protection* **112**, 485-496.

Al-Zyoud, F., Sengonca, C. & Al-Abbadi, S. (2007) Evaluation of *Serangium parcesetosum* (Col.: Coccinellidae) for biological control of *Bemisia tabaci* under greenhouse conditions. *Journal of Pest Science* 80, 85-92.

Anand, P.& Ayub, K. (2002) Comparison of life table parameters for *Maconellicoccus hirsutus*, *Anagyrus kamali*, *Cryptolaemus montrouzieri* and *Scymnus coccivora*. *Biocontrol* **47**, 137-149.

Anderson, J. (1980) Biology and distribution of *Scymnodes lividigaster* (Mulsant) and *Leptothea galbula* (Mulsant), Australian ladybirds (Coleoptera: Coccinellidae). *Proceedings of the Linnean Society of New South Wales*, **105**: 1-15.

Anderson, J. (1982) Seasonal Habitat Utilization and Food of the Ladybirds *Scymnodes Lividigaster* (Mulsant) and *Leptothea Galbula* (Mulsant) (Coleoptera: Coccinellidae). *Australian Journal of Zoology* **30**, 59-70.

Anderson, J.M.E. (1981a) Seasonal analysis of fat content, live weight, dry weight and water content of the aphidophagous *Scymnodes lividigaster* and mycophagous *Leptothea galbula* (Mulsant) (Coleoptera, Coccinellidae). *Australian Journal of Zoology* **29**, 679-689.

Anderson, J.M.E. (1981b) Sex-ratios of adult *Scymnodes lividigaster* and *Leptothea galbula* Col, Coccinellidae, sampled in the field. *Entomophaga* **26**, 39-45.

Andow, D.A. (1990) Characterization of predation on egg masses of *Ostrinia nubilalis* (Lepidoptera: Pyralidae). *Annals of the Entomological Society of America* **83**, 482-486.

Antonucci, C. (2005) *Acizzia jamatonica* – an insect harmful to *Albizia julibrissin*. *Sherwood Foreste ed Alberi Oggi* **116**, 45-46.

Arakaki, N. (1992) Feeding behaviour of the ladybeetle, *Pseudoscymnus kurohime*. *Journal of Ethology* **10**, 7-13.

Arallah, Y. & Newsom, L.D. (1966) Ecological and nutritional studies on *Coleomegilla maculata* De Geer (Coleoptera: Coccinellidae). I. The development of an artificial diet and a laboratory rearing technique. *Journal of Economic Entomology* **59**, 1173-1178.

Arbabi, M. & Singh, J. (2008) Biology of *Stethorus punctillum*, a potential predator of *Tetranychus ludeni*. *Tunisian Journal of Plant Protection* **3**, 95-100.

Arif, M., Gogi, M.D., Abid, A.M., Muhammad, I., Shahid, M.R., Sabir, H. & Muhammad, A. (2011) Predatory potential of some native coccinellid predators against *Phenacoccus solenopsis*, Tinsely (Pseudococcidae: Hemiptera). *Pakistan Entomologist* **33**, 97-103.

Arif, M., Muhammad, R., Shabana, W., Nasir, M. & Abdul, G. (2012) Studies on cotton mealybug, *Phenacoccus solenopsis* (Pseudococcidae: Homoptera), and its natural enemies in Punjab, Pakistan. *International Journal of Agriculture and Biology* **14**, 557-562.

Asifa, H., Muhammad, S., Haider, K., Saghir, A., Mussarat, H., Wajid, N., Muhammad, A., Hammad, H. & Shuaib, F. (2013) Life history and predatory potential of eleven spotted beetle (*Coccinella undecimpunctata* Linnaeus) on cotton mealybug (*Phenacoccus solenopsis* Tinsley). *African Journal of Agricultural Research* **8**, 6142-6148.

Aslan, M.M. & Uygun, N. (2005) The aphidophagus coccinellid (Coleoptera: Coccinellidae) species in Kahramanmaras, Turkey. *Turkish Journal of Zoology* **29**, 1-8.

Atlıhan, R. & Chi, H. (2008) Temperature-Dependent Development and Demography of *Scymnus subvillosus* (Coleoptera: Coccinellidae) reared on *Hyalopterus pruni* (Homoptera: Aphididae). *Journal of Economic Entomology* **101**, 325-333.

Atlıhan, R. & Güldal, H. (2009) Prey density-dependent feeding activity and life history of *Scymnus subvillosus*. *Phytoparasitica* **37**, 35-41.

Atlıhan, R. & Kaydan, M.B. (2002) Development, survival and reproduction of three coccinellids feeding on *Hyalopterus pruni* (Geoffer) (Homoptera: Aphididae). *Turkish Journal of Agriculture and Forestry* **26**, 119-124.

Atlıhan, R. & Ozgokce, M.S. (2002) Development, fecundity and prey consumption of *Exochomus nigromaculatus* feeding on *Hyalopterus pruni*. *Phytoparasitica* **30**, 443-450.

Atlıhan, R. (1995) Studies on the biology of *Adalia fasciatopunctata revelierei* Mulsant Coleoptera: Coccinellidae feeding on some aphid species Homoptera: Aphididae, Callaphididae. *Turkiye Entomoloji Dergisi* **19**, 277-286.

Atlıhan, R., Kaydan, M.B., Yarımbatman, A. & Okut, H. (2010) Functional response of the coccinellid predator *Adalia fasciatopunctata revelierei* to walnut aphid (*Callaphis juglandis*). *Phytoparasitica* **38**, 23-29.

Attia, A.R., Afifi, A.I., El Arnaouty, S.A. & Abd Alla, A.E. (2011a) Feeding potential of the predator, *Cryptolaemus montrouzieri* Mulsant on eggs, nymphs and adults of *Planococcus citri* and *Ephestia kuehniella* eggs. *Egyptian Journal of Biological Pest Control* **21**, 291-296.

Attia, A.R., El-Arnaouty, S.A., Afifi, A.I. & Abd Alla, A.E. (2011b) Development and fecundity of the coccinellid predator, *Cryptolaemus montrouzieri* Mulsant on different types of preys. *Egyptian Journal of Biological Pest Control* **21**, 283-289.

Auad, A.M., Fonseca, M.G., Monteiro, P.H., Resende, T.T. & Santos, D.R. (2013) Aspects of the biology of the lady beetle *Diomus seminulus* (Coleoptera: Coccinellidae): a potential biocontrol agent against the yellow sugarcane aphid in Brazil. *Annals of the Entomological Society of America* **106**, 243-248.

Azeredo, E.H.D., W.C. Rodrigues & P.C.R. Cassino (2004) Occurrence of *Selenaspidus articulatus* (Morgan) (Hemiptera, Diaspididae) and of the predator *Pentilia egena* (Mulsant) (Coleoptera, Coccinelidae) on *Myrtus communis* L.(Myrtaceae), in Pinheiral County, Rio de Janeiro, Brazil. *Revista Brasileira de Entomologia* **48**, 569-576.

Babu, A. (1999) Influence of prey species on feeding preference, post-embryonic development and reproduction of *Coccinella transversalis* F. (Coccinellidae: Coleoptera). *Entomon* **24**, 221-228.

Bado, S.G. & Rodriguez, S.M. (1997) Aspects of morphology, biology and diet of *Olla v-nigrum* (Mulsant) (Coleoptera: Coccinellidae) in Buenos Aires (Argentina). *Boletin de Sanidad Vegetal, Plagas* **23**, 201-207.

Bado, S.G., Rodriguez, S.M. & Folcia, A.M. (2002) Variation in abundance of aphids (Homoptera: Aphididae) and predatory ladybirds (Coleoptera: Coccinellidae) in a barley cultivar at different practices of use of fertilizers. *Idesia* **20**, 35-42.

Bailey, P. & Caon, G. (1986) Predation on the 2-spotted mite, *Tetranychus urticae* Koch (Acarina, Tetranychidae) by *Haplothrips nigripes* Bagball (Thysanoptera, Phlaeothripidae) and *Stethorus nigripes* Kapur (Coleoptera, Coccinellidae) on seed lucerne crops in South-Austraulia. *Australian Journal of Zoology* **34**, 515-525.

Bain, J., Singh, P., Ashby, M.D. & Boven, R.J. (1984) Laboratory rearing of the predatory coccinellid *Cleobora mellyi* (Col.: Coccinellidae) for biological control of *Paropsis charybdis* (Col.: Chrysomelidae) in New Zealand. *Entomophaga* **29**, 237-244.

Baker, S.C., Elek, J.A., Bashford, R., Paterson, S.C., Madden, J. & Battaglia, M. (2003) Inundative release of coccinellid beetles into eucalypt plantations for biological control of chrysomelid leaf beetles. *Agricultural and Forest Entomology* **5**, 97-106.

Basar, M.K. & Yasar, B. (2011) Determination of Ladybird species (Coleoptera: Coccinellidae) on fruit trees in Isparta, Turkey. *Turkiye Entomoloji Dergisi* **35**, 519-534.

Bashford, R. (1999) Predation by ladybird beetles (coccinellids) on immature stages of the Eucalyptus leaf beetle *Chrysophtharta bimaculata* (Olivier). *Tasforest-Hobart* **11**, 77-86.

Baskaran, R.K.M., Mahendhiran, G. & Suresh, K. (2006) Life table of *Scymnus coccivora* Ayyar (Coccinellidae: Coleoptera) on two mealybugs. *Journal of Entomological Research* **30**, 295-299.

Baskaran, R.K.M., Mahendhiran, G. & Suresh, K. (2007) Field evaluation of *Scymnus coccivora* Ayyar for the management of guava mealybug, *Maconellicoccus hirsutus* Green. *Journal of Entomological Research* **31**, 137-140.

Baskaran, R.K.M., Sasikumar, S., Rajavel, D.S. & Suresh, K. (2009) Studies on population fluctuation of guava aphid, *Aphis gossypii* Glover (Hemiptera: Aphididae) and its predators. *Journal of Entomological Research* **33**, 247-255.

Bayoumy, M.H. (2011) Foraging behavior of the coccinellid *Nephus includens* (Coleoptera: Coccinellidae) in response to *Aphis gossypii* (Hemiptera: Aphididae) with particular emphasis on larval parasitism. *Environmental Entomology* **40**, 835-843.

Bayram, S. (2008) Predator species belong to families of Coccinellidae (Coleoptera), Chrysopidae and Hemerobiidae (Neuroptera) of gall-making aphids on elm (*Ulmus glabra* Mill.) in Ankara. *Tarim Bilimleri Dergisi* **14**, 386-393.

Bayram, S. (2009) Predator species of Coccinellidae (Coleoptera) of *Dysaphis devecta* Walk. (Homoptera, Aphididae), Rosy Leaf-curling aphid on apple in Ankara. *Tarim Bilimleri Dergisi-Journal of Agricultural Sciences* **15**, 53-57.

Beato, D. T. (1979) *Biología, morfología y comportamiento alimenticio de Mulsantina picta minor (Casey) (Coleoptera: coccinellidae).* Ph.D. Thesis. Colegio de Postgraduados, Escuela Nacional de Agricultura: Mexico.

Behura, B. & Parida, G. (1979) Observation on the life history of *Menochilus sexmaculatus* (Fabr.) (Coleoptera, Coccinellidae). Sup 1, p. 31 in *Symposium on Recent Trends Aphidology Studies,* Bhubaneswar (India).

Berndt, L., Withers, T. & Gresham, B. (2010) Southern ladybird (*Cleobora mellyi*) is now well established in New Zealand. *New Zealand Plant Protection* **63**, 282.

Berthiaume, R., Hébert, C. & Cloutier, C. (2000) Predation on *Mindarus abietinus* infesting balsam fir grown as Christmas trees: the impact of coccinellid larval predation with emphasis on *Anatis mali*. *Biocontrol* **45**, 425-438.

Berthiaume, R., Hébert, C. & Cloutier, C. (2007) Comparative use of *Mindarus abietinus* (Homoptera: Aphididae) by two Coccinellids (Coleoptera: Coccinellidae), the Native *Anatis mali* and the Exotic *Harmonia axyridis*, in a Christmas Tree plantation. *Environmental Entomology* **36**, 319-328.

Bertolaccini, I., Salto, C., Imwinkelried, J. & Lubatti, P. (1994) Influence of larval food level on the fecundity and fertility of *Eriopis connexa* Guerin (Coleoptera, Coccinellidae). *Revista de Investigaciones Agropecuarias* **25**, 159-166.

Bhat, P.K., Chacko, M., Sreedharan, K. & Ram, V. (1983) Biology of the ladybird beetle, *Cryptolaemus montrouzieri* Mulsant, a predator of mealybugs. pp. 221-226 in Ram, V. (Ed) *Proceedings of the Second Annual Symposium on Plantation Crops. Plant protection (entomology, microbiology, nematology, plant pathology and rodentology). PLACROSYM II 1979 PLACROSYM Standing Committee*, Kerala (India).

Bind, R. (1998) Bioecology and behaviour of a ladybird beetle, *Cheilomenes* (= *Menochilus*) *sexmaculata* (Fabricius) (Coleoptera: Coccinellidae), Ph.D. Thesis. University of Lucknow, Lucknow (India).

Bind, R.B. (2007) Reproductive behaviour of a generalist aphidophagous ladybird beetle *Cheilomenes sexmaculata* (Coleoptera: Coccinellidae). *International Journal of Tropical Insect Science* **27**, 78-84.

Bista, M. & Omkar (2013) Effects of body size and prey quality on the reproductive attributes of two aphidophagous Coccinellidae (Coleoptera) species. *Canadian Entomologist* **145**, 566-576.

Blommers, L. & Gutierrez, J. (1975) Les tétranyques vivant sur agrumes et avocatiers dans la région de Tamatave (Madagascar-est) et quelques-uns de leurs prédateurs. *Fruits* **30**, 191-200.

Boddi, G., Rodas, N.C., Canovai, R. & Petacchi, **R.** (2005) Survey of populations and the role played by coccinellids in ornamental cut foliage crops. *Frustula Entomologica* **28**, 58-67.

Bogya, S. (1996) The role of conifer ladybird (*Exochomus quadripustulatus* L.) in controlling the populations of woolly apple aphid (*Eriosoma lanigerum* Hausm.). *Novenyvedelem* **32**, 407-410.

Boica Junior, A.L., Santos, T.M.d. & Kuranishi, A.K. (2004) Larval development and predatory capacity of Cycloneda sanguinea (L.) and *Hippodamia convergens* Guerin-Men. fed on *Aphis gossypii* Glover on cotton cultivars. *Acta Scientiarum Agronomy* **26**, 239-244.

Bonte, M., Samih, M.A. & De Clercq, P. (2010) Development and reproduction of *Adalia bipunctata* on factitious and artificial foods. Biocontrol **55**, 485-491.

Booth, R.G. (1997) A review of the species of *Calvia* (Coleoptera: Coccinellidae) from the Indian subcontinent, with descriptions of two new species. *Journal of Natural History* **31**, 917-934.

Booth, R.G., Cross, A.E., Fowler, S.V. & Shaw, R.H. (1995) The biology and taxonomy of *Hyperaspis pantherina* (Coleoptera: Coccinellidae) and the classical biological control of its prey, *Orthezia insignis* (Homoptera: Ortheziidae). *Bulletin of Entomological Research* **85**, 307-314.

Borges, I., J.L. Hemptinne & A.O. Soares (2013) Contrasting population growth parameters of the aphidophagous *Scymnus nubilus* and the coccidophagous *Nephus reunioni*. *Biocontrol* **58**, 351-357.

Britto, E.P.J.,Gondim, M.G.C., Jr.,Torres, J.B.,Fiaboe, K.K.M., Moraes, G.J. & Knapp, M. (2009) Predation and reproductive output of the ladybird beetle *Stethorus tridens* preying on tomato red spider mite *Tetranychus evansi*. *Biocontrol* **54**, 363-368.

Brown, A. & Whitehead, P. (2012) *Clitostethus arcuatus* (Rossi, 1794) (Col., Coccinellidae) breeding in the Kidderminster area of Worcestershire: overwintering strategies and breeding biology. *Worcestershire Record* **33**, 20-22.

Brown, H.D. (1972) On the biology of *Lioadalia flavomaculara* (Deg.) (Col.: Coccinellidae), a predator of the wheat aphid (*Schizaphis graminum* (Rond.) in South Africa. *Bulletin of Entomological Research* **61**, 673-679.

Brown, P., Adriaens, T., Bathon, H., Cuppen, J., Goldarazena, A., Hägg, T., Kenis, M., Klausnitzer, B., Kovář, I. & Loomans, A. (2008) *Harmonia axyridis* in Europe: spread and distribution of a non-native coccinellid. *Biocontrol* **53**, 5-21.

Butin, E., Havill, N., Elkinton, J. & Montgomery, M. (2004) Feeding preference of three lady beetle predators of the hemlock woolly adelgid (Homoptera: Adelgidae). *Journal of Economic Entomology* **97**, 1635-1641.

Butin, E., J. Elkinton, N. Havill, and M. E. Montgomery (2003b) Comparative impact of Scymnus ningshanensis and Pseudoscymnus tsugae (Coleoptera: Coccinellidae) on the hemlock woolly adelgid, p. 14. In: Fosbroke, S. L. C. and K. W. Gottschalk (eds.). Proceedings of the USDA

Interagency Research Forum on Gypsy Moth and other Invasive Species 2002, January 15-18, 2002. Annapolis, Maryland, USA.

Butin, E., Montgomery, M., Havill, N. & Elkinton, J. (2002) Pre-release host range assessment for classical biological controls: experience with predators for the hemlock woolly adelgid. pp. 205-213. In Onken, B., Reardon, R. & Lashomb, J. (Eds.) *Proceedings: Hemlock Woolly Adelgid in the Eastern United States Symposium* organized by the *USDA Forest Service and New Jersey Agricultural Experiment Station*, East Brunswick, New Jersey, February 5-7, 2002.

Cabral, S., Soares, A.O. & Garcia, P. (2009) Predation by *Coccinella undecimpunctata* L. (Coleoptera: Coccinellidae) on *Myzus persicae* Sulzer (Homoptera: Aphididae): Effect of prey density. *Biological Control* **50**, 25-29.

Cabral, S., Soares, A.O., Moura, R. & Garcia, P. (2006) Suitability of *Aphis fabae*, *Myzus persicae* (Homoptera: Aphididae) and *Aleyrodes proletella* (Homoptera: Aleyrodidae) as prey for *Coccinella undecimpunctata* (Coleoptera: Coccinellidae). *Biological Control* **39**, 434-440.

Canhilal, R. (1995) Effects of different temperatures on biological characteristics of *Nephus includens* Kirsch (Col.: Coccinellidae). *Zirai Mucadele Arastrma Yllg* **30**, 29-30.

Canovai, R. & Raspi, A. (1999) First occurrence of *Rhyzobius forestieri*, an active predator of the coccid *Ceroplastes japonicus* in Tuscany. *Informatore Fitopatologico* **49**, 41-43.

Canovai, R. (1996) Ecological and morphological remarks on *Scymnus interruptus* (Goeze) and *Scymnus femoralis* (Gyllenhal) (Coleoptera Coccinellidae) in a Tuscan biotope. *Frustula Entomologica* **19**, 139-145.

Cardoso, J.T. & Lazzari, S.M.N. (2003a) Comparative biology of *Cycloneda sanguinea* (Linnaeus, 1763) and *Hippodamia convergens* Guerin-Meneville, 1842 (Coleoptera, Coccinellidae) focusing on the control of *Cinara* spp. (Hemiptera, Aphididae). *Revista Brasileira de Entomologia* **47**, 443-446.

Cardoso, J.T. & Lázzari, S.M.N. (2003b) Consumption of *Cinara* spp. (Hemiptera, Aphididae) by *Cycloneda sanguinea* (Linnaeus, 1763) and *Hippodamia convergens* Guérin-Méneville, 1842 (Coleoptera, Coccinellidae). *Revista Brasileira de Entomologia* **47**, 559-562.

Carrejo, G.N.S., Bellotti, A.C. & Gonzalez, O. R. (1991) Evaluation of some determining factors in the efficiency of *Cleothera notata* (Col: Coccinellidae) as predator of the cassava mealybug *Phenacoccus herreni* (Hom: Pseudococcidae). *Revista Colombiana de Entomología* **17**, 21-27.

Causton, C.E., M.P. Lincango & T.G. Poulsom (2004) Feeding range studies of *Rodolia cardinalis* (Mulsant), a candidate biological control agent of *Icerya purchasi* Maskell in the Galápagos islands. *Biological Control* **29**, 315-325.

Cave, R.D. (2006) Biological control agents of the cycad aulacaspis scale, *Aulacaspis yasumatsui*. pp. 422-424 in *Proceedings of the 119th Annual Meeting of the Florida State Horticultural Society*, Florida, U.S.A.

Chakrabarti, S., Debnath, N. & Ghosh, D. (1995) Bioecology of *Harmonia eucharis* (Mulsant) (Coleoptera: Coccinellidae). An aphidophagous predator in Western Himalayas. *Entomon* **20**, 191-196.

Chakrabarti, S., Ghosh, D. & Debnath, N. (1988) Developmental rate and larval voracity in *Harmonia(Leis) dimidiata* (Col., Coccinellidae), a predator of *Eriosoma lanigerum* (Hom., Aphididae) in western Himalaya. *Acta Entomologica Bohemoslov.* **85**, 335-339.

Chakrabarti, S., Sarkar, S. & Debnath, M. (2012) Diversity, bioecology and biosystematics of aphidophagous predators of eastern Himalaya and Northeast India. *Biodiversitat and Naturausstattung im Himalaya* **IV**, 129-147.

Chandrababu, A., Gautam, R.D. & Garg, A.K. (1999) Biology of ladybird beetle, *Brumoides suturalis* (Fabricius) on aphid and mealybugs. *Annals of Plant Protection Sciences* 7, 13-18.

Chang, K.S., Morimoto, N. & Nakasuji, F. (1993) The functional response of a coccinellid beetle, *Aiolocaria hexaspilota* to its prey, the walnut leaf beetle (*Gastrolina depressa*). *Chinese Journal of Entomology* **13**, 187-193.

Charanasri, V. & Nishida, T. (1973) Relative abundance of three Coccinellid predators of the green scale, *Coccus viridis* (Green) on Plumeria trees. *Proceedings of the Hawaiian Entomological Society* **22**, 27-32.

Chaudhary, D., David, B. & Singh, D. (1983) Studies on the host preference of *Cheilomenus sexmaculata* (Fabr.) (Coleoptera: Coccinellidae) on the different aphid hosts. *Comparative physiology and ecology* **8**, 289-290.

Chazeau, J. (1971) *Stethorus comoriensis*, nouvelle espèce de Coccinellidae de l'archipel des Comores. *Bulletin de la Société Entomologique de France*, **76**, 60-63.

Chazeau, J. (1981) Biology of *Coelophora quadrivittata* (Col, Coccinellidae), predator of *Coccus viridis* (Hom, Coccidae) In New Caledonia. *Entomophaga* **26**, 301-311.

Chazeau, J. (1983a) Two predators of Tetranychidae in New Guinea – *Stethorus exspectatus* n-sp and *Stethorus exsultabilis* n-sp Col, Coccinellidae. *Entomophaga* **28**, 373-378.

Chazeau, J. (1983b) The biogeography of Coccinellidae in the Pacific area. *GeoJournal* **7**, 527-532.

Chazeau, J., Bouye, E. & Delarbogne, L.B. (1991) Developmente and life table of *Olla-v-nigrum* Col, Coccinellidae, a natural enemy of *Heteropsylla cubana* Hom., Psyllidae introduced in New Caledonia. *Entomophaga* **36**, 275-285.

Cheah, C. (2011) Sasajisymnus (=Pseudoscymnus) tsugae, a ladybeetle from Japan. pp. 43–52 in Onken, B. & Reardon, R. (Eds.), *Third Symposium on Hemlock Woolly Adelgid in the Eastern United States* organized by the *USDA Forest Service*, February 1-3, 2005.

Cheah, C., Mayer, M., Palmer, D., Scudder, T. & Chianese, R. (2005) Assessments of biological control of hemlock woolly adelgid with *Sasajiscymnus tsugae* in Connecticut and New Jersey. pp. 116-130 in Onken, B. & Reardon, R. (Eds.) *Third Symposium on Hemlock Woolly Adelgid in the Eastern United States* organized by the *USDA Forest Service*, Ashville, U.S.A., Feb. 1-3, 2005.

Cheah, C.A.J. & McClure, M.S. (2000) Seasonal synchrony of life cycles between the exotic predator, *Pseudoscymnus tsugae* (Coleoptera: Coccinellidae) and its prey, the hemlock woolly adelgid *Adelges tsugae* (Homoptera: Adelgidae). *Agricultural and Forest Entomology* **2**, 241-251.

Cheah, C.A.-J.& McClure, M.S. (1998) Life history and development of *Pseudoscymnus tsugae* (Coleoptera: Coccinellidae), a new predator of the hemlock woolly adelgid (Homoptera: Adelgidae). *Environmental Entomology* **27**, 1531-1536.

Chen, D. (1998) Study on bionomics of fourladybird beetles preying on *Aulacaspis roarum*. *Wuyi Science Journal* **14**, 106-111.

Chen, G., Tao, M., Yang, B. & Chen, F. (2003) Study on the population dynamics of *Chilocorus rubidus* Hope and its predacious function. *Journal of Yunnan Agricultural University* **18**, 136-139.

Chen, J., Qin, Q.J., Liu, S. & He, Y.Z. (2012) Effect of Six Diets on Development and Fecundity of *Harmonia axyridis* (Pallas) (Coleoptera: Coccinellidae). *African Entomology* **20**, 85-90.

Chen, S., Lin, G., Yan, Z., Wong, S., Chen, S., Huang, Q. & Zhang, H. (1997) A study on *Pseudophacopteron canarium* in Fujian province. *Acta Phytophylacica Sinica* **24**, 209-214.

Chen, W.L., Zhao, Z.M., Li, L.S. & Wei, Q.C. (1994) Predation of three natural enemies in citrus orchard on citrus red mite (*Panonychus citri* McGregor). *Journal of Shanghai Agricultural College* **12**, 9-15.

Cheng, W.L., Li, L.S., Zai, Z.M. & Zhu, W.B. (1993) Predation behavior of *Stethorus chengi* Sasaji on patchily distributed prey. *Journal of Shanghai Agricultural College* **11**, 209-213.

Chessman, A. & Dumestre, J. (1930) The feeding Rate of the Australian Lady Beetle, *Rodolia cardinalis*. *Journal of Agricultural Research* **41**, 197-203.

Chi, H. & T.-C. Yang (2003) Two-sex life table and predation rate of *Propylaea japonica* Thunberg (Coleoptera: Coccinellidae) fed on *Myzus persicae* (Sulzer) (Homoptera: Aphididae). *Environmental Entomology* **32**, 327-333.

Chong, J.-H., Oetting, R.D. & Osborne, L.S. (2005) Development of *Diomus austrinus* Gordon (Coleoptera: Coccinellidae) on two mealybug prey species at five constant temperatures. *Biological Control* **33**, 39-48.

Choudhuri, M.S. & Agarwala, B.K. (1990) Rearing *Micraspis discolor* (Coccinellidae) by feeding drone honey bee powder. *Journal of Aphidology* **4,** 1-2.

Chowdhury, S.P., Ahad, M.A., Amin, M.R. & Hasan, M.S. (2008) Biology of ladybird beetle *Micraspis discolors* (Fab.) (Coccinellidae: Coleoptera). *International Journal of Sustainable Crop Production* **3**, 39-44.

Cividanes, F.J., Silvestre, L.H. & Thomazini, M.J. (1987) Population survey of insects on wheat crop. *Semina* **8**, 14-16.

Clark, R.C. & Brown, N.R. (1961) Studies of predators of the balsam woolly aphid *Adelges piceae* (Ratz.) (Homoptera: Adelgidae) IX. *Pullus impexus* (Muls.) (Coleoptera: Coccinellidae), an introduced predator in eastern Canada. *Canadian Entomologist,* **93**, 1162–1168.

Colburn, R & Asquith., D. (1971) Observations on the morphology and biology of the ladybird beetle *Stethorus punctum*. *Annals of the Entomological Society of America* **64**, 1217-1221.

Colburn, R. & Asquith, D. (1970) A cage used to study finding of a host by ladybird beetles, *Stethorus punctum*. *Journal of Economic Entomology* **63**, 1376-1377.

Colunga-Garcia, M., Gage, S.H. & Landis, D.A. (1997) Response of an assemblage of Coccinellidae (Coleoptera) to a diverse agricultural landscape. *Environmental Entomology* **26**, 797-804.

Congdon, B.D.,Shanks, C.H. & Antonelli, A.L. (1993) Population Interaction Between *Stethorus punctum picipes* (Coleoptera: Coccinellidae) and *Tetranychus urticae* (Acari: Tetranychidae) in Red Raspberries at Low Predator and Prey Densities. *Environmental Entomology* **22**, 1302-1307.

Conway, H.E. & Kring, T.J. (2010) Coccinellids associated with the cotton aphid (Homoptera: Aphididae) in northeast Arkansas cotton. *Journal of Entomological Science* **45**, 129-139.

Cook, S. & Webb, R. (1995) Predation of early instar gypsy moth larvae by a generalist predator, *Anatis labiculata* (Say) (Coleoptera: Coccinellidae). *Journal of Entomological Science* **30**, 258–261.

Cooper, D.D. & Cranshaw, W.S. (1999) The natural enemy complex associated with pine needle scale, *Chionaspis pinifoliae* (Fitch) (Homoptera: Diaspididae), in north central Colorado. *Journal of the Kansas Entomological Society* **72**, 131-133.

Coutanceau, J. (2009) *Harmonia conformis* (Boisduval, 1835): an Australian coccinellid introduced and acclimatized in France (Col. Coccinellidae). *Bulletin de la Société Entomologique de France* **114**, 110.

Covassi, M., Binazzi, A. & Toccafondi, P. (1991) Studies on the entomophagous predators of a scale of the genus *Matsucoccus* Cock. in Italy. I. Faunistical-ecological notes on species observed in pine forests in Liguria and Tuscany. *Redia* **74**, 575-597.

Czechowska, W. (1995) Neuropteroidea and Coccinellidae (Coleoptera) of pine canopies of the pine forests in the Berezinsky Biosphere Reserve in Byelorussia. *Fragmenta Faunistica* **38**, 159-163.

Dai, Z.Y. (1990) Seasonal occurrence of *Coelophora saucia* (Col.: Coccinellidae) and its predation rate on aphids. *Chinese Journal of Biological Control*, **6**, 113-115.

Das, S.& Gope (**B.** 1984) More about a less known predator: *Pharoscymnus horni* (Weise), a predator of *Chrysomphalus ficus* Ashm. *Two and a bud* **31**, 46-47.

Das, S., Borthakur, M. & Gope, B. (1988) Bio-ecological studies on *Chilocorus circumdatus* Sch. an efficient predator of black scale, *Chrysomphalus aonidium* (= *C. ficus*) Ashm. *Two and a bud* **35**, 15-18.

Davidson, L.N. & Evans, E.W. (2010) Frass analysis of diets of aphidophagous lady beetles (Coleoptera: Coccinellidae) in Utah alfalfa fields. *Environmental Entomology* **39**, 576-582.

Davidson, W. (1923) Biology of *Scymnus nubes* Casey (Coleoptera; Coccinellidae). *Transactions of the American Entomological Society* **49**, 155-163.

Day, W., Prokrym, D., Ellis, D. & Chianese, **R.** (1994) The known distribution of the predator *Propylea quatuordecimpunctata* (Coleoptera: Coccinellidae) in the United States, and thoughts on the origin of this species and five other exotic lady beetles in eastern North America. *Entomological News* **105**, 244-256.

De Bortoli, S.A., S.R. Benvenga, S. Gravena & J. Ednilson Miranda (2001) Biologia de *Pentilia egena* Mulsant (Coleoptera: Coccinellidae) e predaçao sobre *Chrysomphalus ficus* Ashmead (Homoptera: Diaspididae). *Boletín de Sanidad Vegetal. Plagas* **27**, 337-343.

Dehkordi, S.D. & Sahragard, A. (2013) Functional response of *Hippodamia variegata* (Coleoptera: Coccinellidae) to different densities of *Aphis gossypii* (Hemiptera: Aphididae) in an open patch design. *Journal of Agricultural Science and Technology* **15**, 651-659.

Dejean, A., Orivel, J. & Gibernau, M. (2002) Specialized predation on plataspid heteropterans in a coccinellid beetle: adaptive behavior and responses of prey attended or not by ants. *Behavioral Ecology* **13**, 154–159.

Delucchia, V. (1954) Pullus impexus *(Muls.) (Coleoptera, Coccinellidae), a Predator of* Adelges piceae *(Ratz.) (Hemiptera, Adelgidae)*, with notes on its Parasites. Ph. D. Thesis. Swiss Federal Institute of Technology, Zurich.

Demirozer, O., Karaca, I. & Karsavuran, Y. (2011) Population fluctuations of some important pests and natural enemies found in Oil-bearing rose (*Rosa damascena* Miller) production areas in Isparta province (Turkey). *Turkiye Entomoloji Dergisi* **35**, 539-558.

Demoraes, R.R., Loeck, A.E. & Belarmino, L.C. (1991) Natural enemies of *Rachiplusia-nu* (Guenee, 1852) and *Pseudoplusia-includens* (Walker, 1857) (Lepidoptera, Noctuidae) on soybean in Rio Grande do Sul. *Pesquisa Agropecuaria Brasileira* **26**, 57-64.

Deokar, M.D., Shetgar, S.S., Sonkamble, M.M. & Gade, R.S. (2013) Biology and consumption capacity of *Cryptolaemus montrouzieri* Mulsant on *Maconellicoccus hirsutus* (Green). *Journal of Entomological Research* **37**, 61-66.

Devikarani, K., Bhola, R.K. & Singh, T.K. (2013) Effect of prey densities on the larval development of a ladybird beetle, *Coelophora saucia* (Mulsant). *Indian Journal of Entomology* **75**, 15-18.

Diepenbrock, L.M. & Finke, D.L. (2013) Refuge for native lady beetles (Coccinellidae) in perennial grassland habitats. *Insect Conservation and Diversity* **6**, 671-679.

Dirorimwe, W. (1996) A study on some predatory coccinellids (Coleoptera: Coccinellidae) found in cotton fields in Zimbabwe. *Zimbabwe Journal of Agricultural Research* **34**, 145-152.

Doungsa-ard, C. & Osatapan, P. (1997) Biological control of leucaena psyllid, *Heteropsylla cubana* crawford (Homoptera: Psyllidae) in the Northern Region of Thailand. *Wichai lae songsoem wichakan kaset* **15**, 1-15.

Dreyer, B. S., Neuenschwander, P., Bouyjou, B., Baumgartner, J. & Dorn, S. (1997c) Biology of *Hyperaspis notata* Mulsant (Coleoptera, Coccinellidae), an introduced predator of the cassava mealybug in Africa: Life tables at different temperatures. *Entomologia Experimentalis et Applicata* **84**, 85-92.

Dreyer, B.S. (1995) Biology and feeding behaviour of the coccinellid *Hyperaspis notata* in relation to its prey, the cassava mealybug, *Phenacoccus manihoti*. Ph. D. Thesis, Swiss Federal Institute of Techonology, Zurich, Switzerland.

Dreyer, B.S., Neuenschwander, P., Baumgartner, J. & Dorn, S. (1997a) Trophic influences on survival, development and reproduction of *Hyperaspis notata* (Col., Coccinellidae). *Journal of Applied Entomology* **121**, 249-256.

Dreyer, B.S., Neuenschwander, P., Bouyjou, B., Baumgartner, J. & Dorn, S. (1997b) The influence of temperature on the life table of *Hyperaspis notata*. *Entomologia Experimentalis Et Applicata* **84**, 85-92.

Dysart, R.J. (1988) The European lady beetle *Propylea quatuordecimpunctata*: new locality records for North America (Coleoptera: Coccinellidae). *Journal of the New York Entomological Society* **96**, 119-121.

Efil, L., Bayram, A., Ayaz, T. & Senal, D. (2010) Coccinellidae species and their population changes in alfalfa field of Akcakale country of Sanlurfa province and a new record, *Exochomus pubescens* Kuster for Turkey. *Bitki Koruma Bülteni* **50**, 101-109.

Ehler, L.E. (2007) Impact of native predators and parasites on *Spodoptera exigua*, an introduced pest of alfalfa hay in northern California. *Biocontrol* **52**, 323-338.

El Habi, M., Sekkat, A., El Jadd, L. & Boumezzough, A. (2000) Biology of *Hippodamia variegata* Goeze (Col., Coccinellidae) and its suitability against *Aphis gossypii* Glov (Hom., Aphididae) on cucumber under greenhouse conditions. *Journal of Applied Entomology,* **124**, 365-374.

Elder, R.J. & Bell, K.L. (1998) Establishment of *Chilocorus* spp. (Coleoptera : Coccinellidae) in a *Carica papaya* L. orchard infested by *Aonidiella orientalis* (Newstead) (Hemiptera : Diaspididae). *Australian Journal of Entomology* **37**, 362-365.

ElHag, E.T.A. & Zaitoon, A.A. (1996) Biological parameters for four coccinellid species in Central Saudi Arabia. *Biological Control* **7**, 316-319.

El-Heneidy, A.H., Hafez, A.A., Shalaby, F.F. & El-Din, I.A.B. (2008) Comparative biological aspects of the two coccinellid species, *Coccinella undecimpunctata* L. and *Hippodamia convergens* Guer. under laboratory conditions. *Egyptian Journal of Biological Pest Control* **18**, 51-59.

Elliott, H. & Little, D.d. (1980) Laboratory studies on predation of *Chrysophtharta bimaculata* (Olivier) (Coleoptera: Chrysomelidae) eggs by the coccinellids *Cleobora mellyi* Mulsant and *Harmonia conformis* (Boisduval). *General and Applied Entomology* **12**, 33-36.

Elliott, N.C., French, B., Michels Jr, G. & Reed, D. (1994) Influence of four aphid prey species on development, survival, and adult size of *Cycloneda ancoralis*. *The Southwestern entomologist* **19**, 57-61.

Elliott, N.C., Kieckhefer, R.W. & Phoofolo, M.W. (2011) Functional response of *Hippodamia convergens* to *Sitobion avenae* on wheat plants in the laboratory. *Southwestern Entomologist* **36**, 423-431.

Elliott, N.C., Kieckhefer, R.W. & Phoofolo, M.W. (2012) Foraging by *Hippodamia convergens* for the Aphid *Sitobion avenae* on Wheat Plants Growing in Greenhouse Plots. *Southwestern Entomologist* **37**, 467-473.

Elliott, N.C., Kieckhefer, R.W. & Phoofolo, M.W. (2013) Prey foraging movements by *Hippodamia convergens* in wheat are influenced by hunger and aphids. *Southwestern Entomologist* **38**, 163-171.

Elliott, N.C., Kieckhefer, R.W., French, B.W. & Lee, J.H. (1998) A comparison of size, sex ratio, and dispersal in three coccinellids. *Southwestern Entomologist* **23**, 137-145.

Ellis, D., McAvoy, R., Ayyash, L.A., Flanagan, M. & Ciomperlik, M. (2001) Evaluation of *Serangium parcesetosum* (Coleoptera: Coccinellidae) for biological control of silverleaf whitefly, *Bemisia argentifolii* (Homoptera: Aleyrodidae), on poinsettia. *Florida Entomologist* **84**, 215-221.

Emami, M.S., Sahragard, A. & Haji-Zadeh. J. (2000) Studies on functional response of *Scymnus syriacus* to different densities of Aphis spiraecola. *Applied Entomology and Phytopathology* **67**, 42-50.

Emel'yanov, V.A.,Simonishvili, R.A. & Sungulia, M.A. (1988) The punctated *Stethorus* - a specialized acariphage of the citrus red hairy mite. Subtropicheskie Kul'tury **3**, 146-147.

Erol, T. & Atlihan, R. (1995) Studies on the biology of *Adalia fasciatopunctata revelierei* (Mulsant) (Coleoptera: Coccinellidae) feeding on some aphid species (Homoptera: Aphididae, Callaphididae). *Turkiye Entomoloji Dergisi* **19**, 277-286.

Espinha, I.G. & Torres, L.M. (1995) Study of the role of *Stethorus punctillum* (Weise) in the control of *Panonychus ul*mi (Koch) on apple, in the region of Vila Real (northeast Portugal). Boletin de Sanidad Vegetal, Plagas **21**, 337-347.

Ettifouri, M. & Ferran, A. (1992) Effect of a prior feeding period and of fasting on the occurrence of intensive searching for prey by *Semiadalia undecimnotata*. *Entomologia Experimentalis Et Applicata* **65**, 101-111.

Evans, E.W. & Toler, T.R. (2007) Aggregation of polyphagous predators in response to multiple prey: ladybirds (Coleoptera: Coccinellidae) foraging in alfalfa. *Population Ecology* **49**, 29-36.

Evans, E.W., Stevenson, A.T. & Richards, D.R. (1999) Essential versus alternative foods of insect predators: benefits of a mixed diet. *Oecologia* **121**, 107-112.

Fabres, G. & Kiyindou, A. (1985) Comparison of the biotic potential of two coccinellids (*Exochomus flaviventris* and *Hyperaspis senegalensis hottentotta*, Col. Coccinellidae), predators of *Phenacoccus manihoti* (Hom. Pseudococcidae) in the Congo. *Acta Oecologica, Oecologia Applicata* **6**, 339-348.

Fabres, G., Nenon, J.P., Kiyindou, A. & Biassangama, A. (1989) Reflections on the acclimatization of exotic entomophages for the regulation of populations of the cassava mealybug in the Congo. *Bulletin de la Societé Zoologique de France* **114**, 43-48.

Fand, B.B., Gautam, R.D. & Suroshe, S.S. (2010) Comparative biology of four coccinellid predators of solenopsis mealybug, *Phenacoccus solenopsis* Tinsley (Hemiptera: Pseudococcidae). *Journal of Biological Control* **24**, 35-41.

Farhadi, R., Allahyari, H. & Chi, H. (2011) Life table and predation capacity of *Hippodamia variegata* (Coleoptera: Coccinellidae) feeding on *Aphis fabae* (Hemiptera: Aphididae). *Biological Control* **59**, 83-89.

Farhadi, R., Allahyari, H. & Juliano, S.A. (2010) Functional Response of Larval and Adult Stages of *Hippodamia variegata* (Coleoptera: Coccinellidae) to Different Densities of *Aphis fabae* (Hemiptera: Aphididae). *Environmental Entomology* **39**, 1586-1592.

Farnoosh, Y. (2003) Some coccinellid scale and aphid predators (Coleoptera, subfamily, Chilocorinae) prevalent in north east, Khorasan Province of Iran. *Arab Journal of Plant Protection* **21**, 60-62.

Farooq-Ahmad, K. (2012) Development and growth of *Exochomus quadripustulatus* (Coleoptera: Coccinellidae): a predator of mussel scale *Lepidosaphes ulmi* (Homoptera: Diaspididae) on apple. *Pakistan Journal of Zoology* **44**, 1021-1029.

Farooq-Ahmad, K., Inam-Ullah, M. & Mustafa, S. (1999) Spatial Distribution and Phenology of Adult *Chilocorus infernalis* (Mulsant) (Coccinellidae: Coleoptera) on Apple Trees in Kashmir-Pakistan. *Sarhad Journal of Agriculture* **15**, 343-346.

Felix, A.P., Vasconcelos, J., Brazão, C.I., Aguiar, A.M.F. & Rocha, P. (2004) Bio-ecological aspects of *Hyperaspis pantherina* Fursch (Coleoptera: Coccinellidae) a predator of the Lantana Bug, *Orthezia insignis* Browne (Homoptera: Ortheziidae). *Boletin de Sanidad Vegetal, Plagas* **30**, 347-354.

Fiaboe, K.K.M., Gondim Junior, M.G.C., Moraes, G.J.d., Ogol, C.K.P.O. & Knapp, M. (2007) Bionomics of the acarophagous ladybird beetle *Stethorus tridens* fed *Tetranychus evansi*. *Journal of Applied Entomology* **131**, 355-361.

Finlayson, C., Alyokhin, A., Gross S. & Porter, E. (2010) Differential consumption of four aphid species by four lady beetle species. *Journal of Insect Science* **10**, 1-10.

Florek, K., J. Tragarz & P. Ceryngier (2011) Species composition and diets of ladybird beetles (Coleoptera: Coccinellidae) associated with black alder (*Alnus glutinosa* (L.) Gaertner) in a marshy forest. *Aphids and Other Hemipterous Insects* 17, 165-174.

Flores, A., Olvera, H., Rodriguez, S. & Barranco, J. (2013) Predation Potential of *Chilocorus cacti* (Coleoptera: Coccinellidae) to the Prickly Pear Cacti Pest *Dactylopius opuntiae* (Hemiptera: Dactylopiidae). *Neotropical Entomology* **42**, 407-411.

Fondren, K.M. & McCullough, D.G. (2005) Phenology, natural enemies, and efficacy of horticultural oil for control of *Chionaspis heterophyllae* (Homoptera: Diaspididae) on Christmas tree plantations. *Journal of Economic Entomology* **98**, 1603-1613.

Fowler, S.V. (2004) Biological control of an exotic scale, *Orthezia insignis* Browne (Homoptera: Ortheziidae), saves the endemic gumwood tree, *Commidendrum robustum* (Roxb.) DC. (Asteraceae) on the island of St. Helena. *Biological Control* **29**, 367-374.

Franzmann, B.A. (2002) *Hippodamia variegata* (Goeze) (Coleoptera: Coccinellidae), a predacious ladybird new in Australia. *Australian Journal of Entomology* **41**, 375-377.

Fursch, H. (1990) The African species of the *Scymnus frontalis* group (Coleoptera, Coccinellidae). *Entomologica Fennica* **1**, 163-170.

Fursch, H. (2006) The afrotropical species of *Stethorus* Weise, 1885 (Coleoptera: Coccinellidae, Scymninae). *Entomologische Zeitschrift mit Insekten Borse* **116**, 261-268.

Fye, R.E. (1981) Rearing and release of coccinellids for potential control of pear psylla. *Advances in Agricultural Technology, Agricultural Research Service, United States Department of Agriculture* **20**, 1-9.

Garcia, J., Benitez, E.R. & Lopez-Avila, A. (2007) Population density effect of *Trialeurodes vaporariorum* (Hemiptera: Aleyrodidae) on the efficiency of the predator *Delphastus pusillus* (Coleoptera: Ciccinellidae). *Revista Corpoica Ciencia y Tecnologia Agropecuarias* **8**, 17-21.

Gautam, R.D., Usha, S., Sudhida, G., Khan, M.A. & Gautam, C.P.N. (2007) Studies on Solanum mealy bug, *Phenacoccus solani* Ferris (Hemiptera: Pseudococcidae), its parasitoid and predator complex, reproductive potential and utilization as laboratory prey for rearing the ladybird and green lacewing predators. *Journal of Entomological Research* **31**, 259-264.

Geetanjali, M., Bhupendram K., Mohd, S., Deepanti, S. & Omkar (2011) Evaluation of four co-occurring ladybirds for use as biocontrol agents of the pea aphid, *Acyrthosiphon pisum* (Homoptera: Aphididae). *Biocontrol Science and Technology* **21**, 991-997.

Geetanjali, M., Omkar, Bhupendra, K. & Garima, **P.** (2012) Stage and age-specific predation in four aphidophagous ladybird beetles. *Biocontrol Science and Technology* **22**, 463-476.

George, P. (2000) Prey preference of a ladybird beetle, *Coccinella transversalis* Fab.(Coleoptera: Coccinellidae). *Insect Environment* **6**, 124-125.

Geyer, J. (1947) A study of the biology and ecology of *Exochomus flavipes* Thunb.(Coccinellidae, Coleoptera). Part II. *Journal of the Entomological Society of South Africa* **10**, 64-108.

Ghadam, Z.M.H., Sadeghi, S.E., Sendi, J.J. & Hajizadeh, J. (2005) Biological investigation of *Oenopia conglobata* a predator of the poplar aphid *Chaitophorus populeti* in laboratory conditions. *Iranian Journal of Forest and Range Protection Research* **2**, 119-132.

Ghahhari, H. & Hatami, B. (2000) Study on natural enemies of whiteflies (Homoptera: Aleyrodidae) in Isfahan Province. *Journal of Entomological Society of Iran* **20**, 1-24.

Ghorpade, K. (1981) *Cryptolaemus montrousieri* (Coleoptera: Coccinellidae) breeding on aphids. *Colemania* **1**, 59.

Ghosh, A., Lahiri, A. & Biswas, S. (1976) Preliminary observation on the development of a predaceous ladybird beetle *Ballia eucharis* Mulsant (Coleoptera: Coccinellidae). *Newsletter, Zoological Survey of India* **2**, 129-130.

Gibson, R.L., Elliott, N.C. & Schaefer, **P.** (1992) Life history and development of *Scymnus frontalis* (Fabricius) (Coleoptera: Coccinellidae) on four species of aphid. *Journal of the Kansas Entomological Society* **65**, 410-415.

Giles, K.L., Obrycki, J.J. & Degooyer, T.A. (1994) Prevalence of Predators Associated with *Acyrthosiphon pisum* (Homoptera: Aphididae) and *Hypera postica* Gyllenhal (Coleoptera: Curculionidae) during growth of the first crop of alfalfa. *Biological Control* **4**, 170-177.

Gillani, W., Matin, M. & Rafi, M. (2007) Bionomics of tropical coccinellid beetle *Harmonia (Leis) dimidiata* (F) (Coleoptera: Coccinellidae) under laboratory conditions. *Pakistan Journal of Agricultural Research* **20**, 79-83.

Golizadeh, A. & Jafari-Behi, V. (2012) Biological traits and life table parameters of variegated lady beetle, *Hippodamia variegata* (Coleoptera: Coccinellidae) on three aphid species. *Applied Entomology and Zoology* **47**, 199-205.

Gomez, D.W. & Polania, I.Z.d. (2006) Feeding preference of *Eriopis connexa connexa* (Germar) (Coleoptera: Coccinellidae). *Revista U.D.C.A. Revista U.D.C.A. Actualidad & Divulgacion Cientifica* **9,** 1.

Gomez, D.W. & Polania, I.Z.d. (2009) Life table of the predatory beetle *Eriopis connexa connexa* (Germar) (Coleoptera: Coccinellidae). *Revista U.D.C.A. Actualidad & Divulgacion Cientifica* **12**, 147-155.

Gomez, D.W., Arevalo, H. & Polania, I.Z.d. (2013) Influence of three aphid species used as prey on some biological aspects of the predator *Eriopis connexa*. *Open Journal of Animal Sciences* **3**, 193-199.

Goncalves, M.F., Santos, S.A.P., Raimundo, A., Pereira, J.A. & Torres, L.M. (2007) Coccinellids associated with olive groves in north-eastern Portugal. *Bulletin OILB/SROP* **30**, 211.

Gonzalez F, G., Lopez Bermudez, R. & Kondo, T. (2012) First report of *Delphastus quinculus* Gordon and *Diomus seminulus* (Mulsant) (Coleoptera: Coccinellidae) feeding on eggs and first-instar nymphs of *Crypticerya multicicatrices* Kondo and Unruh (Hemiptera: Monophlebidae). *Insecta Mundi* **0268**, 1-6.

Gonzalez, J.G., Benitez, E.R. & Lopez-Avila, A. (2005) Life table of *Delphastus pusillus* (Coleoptera: Coccinellidae) on the whitefly *Trialeurodes vaporariorum* (Hemiptera: Aleyrodidae). *Revista Colombiana de Entomología* **31**, 155-160.

Gonzalez, J.G., Benitez, E.R. & Lopez-Avila, A. (2006) Effect of density of the whitefly predator *Delphastus pusillus* (Le Conte) (Coleoptera: Coccinellidae) on its searching efficiency. *Revista Colombiana de Entomología* **32**, 10-17.

Gonzalez-Hernandez, H., Johnson, M.W. & Reimer, N.J. (1999b) Impact of *Pheidole megacephala* (F.) (Hymenoptera: Formicidae) on the biological control of *Dysmicoccus brevipes* (Cockerell) (Homoptera: Pseudococcidae). *Biological Control* 15, 145-152.

Gonzalez-Hernandez, H., Reimer, N.J. & Johnson, M.W. (1999a) Survey of the natural enemies of *Dysmicoccus* mealybugs on pineapple in Hawaii. *Biocontrol* **44**, 47-58.

Gordon, R. & Davidson, J. (2008) A new prey record and range extension for *Hyperaspis paludicola* Schwarz and a new prey record for *Microweisea misella* (LeConte) (Coleoptera: Coccinellidae). *Insecta Mundi **43**, 1-2.*

Gordon, R.D. (1993) *Stethorus nigripes* Kapur new to North America, and a new synonym in *Stethorus* Weise (Coleoptera: Coccinellidae). *Southwestern Entomologist*, **18**, 67-68.

Gore, A.B., Shetgar, S.S. & Deokar, M.D. (2013a) Growth and development of Cryptolaemus montrouzieri (Mulsant) on *Phenacoccus solenopsis* (Tinsley). *Journal of Entomological Research* **37**, 239-242.

Gore, A.B., Shetgar, S.S. & Deokar, M.D. (2013b) Predatory potential of *Cryptolaemus montrouzieri* mulsant on *Phenacoccus solenopsis* Tinsley. *Indian Journal of Entomology* **75**, 282-284.

Gorzka, D.,Olszak, R.W. & Holdaj, M. (2009) Effectiveness of ladybird beetles (*Stethorus punctillum*) in reduction of red spider mite (*Panonychus ulmi*) population. *Progress in Plant Protection* **49**, 1953-1955.

Grasswitz, T.R. & Burts, E.C. (1995) Effect of native natural enemies on the population dynamics of the grape mealybug, *Pseudococcus maritimus* (Hom: Pseudococcidae), in apple and pear orchards. *Entomophaga* **40**, 105-117.

Groden, E., Drummon, F.A., Casagrande, R.A., Yness, H. & Dean, L. (1990) *Coleomegilla maculata* (Coleopera: Coccinellidae): Its Predation upon the Colorado Potato Beetle (Coleoptera: Chrysomelidae) and Its Incidence in Potatoes and Surrounding Crops. *Journal of Economic Entomology* **83**, 1306-1315.

Gruber, F., Poprawski, T.J. & Rey, E. (1991) Survey for natural enemies of *Diuraphis noxia* (Mordvilko) in Eurasia. *Bulletin SROP* **14**, 102-109.

Gu, Y., Zhang, Y. & Zhang, Z. (1996) Study on the predation of *Stethorus punctillum* Weise to *Tetranychus urticae* (Koch). *Natural Enemies of Insects* **18**, 163-166.

Guanilo, A.D. & Martinez, N. (2007) Predators associated to *Panonychus citri* McGregor (Acari: Tetranychidae) in the central coast of Peru. *Ecologia Aplicada* **6**, 117-129.

Guerreiro, J.C., Busoli, A.C. & Filho, E.B. (2003) Oviposition and predation of *Pentilia egena* Mulsant (Coleoptera: Coccinellidae) in response to temperature. *Scientia Agricola* **60**, 587-589.

Guershon, M. & Gerling, D. (2006) Effects of plant and prey characteristics on the predatory behavior of *Delphastus catalinae*. *Entomologia Experimentalis Et Applicata* **121**, 15-21.

Guo, J.& Wan, F. (2001) Effect of three diets on development and fecundity of the ladybeetles *Harmonia axyridis* and *Propylaea japonica*. *Chinese Journal of Biological Control* **17**, 116-120.

GuoYue, Y. (1999) Lady beetles (Coleoptera: Coccinellidae) from *Pinus armandii* Franchet infested with *Pineus* sp. *Entomotaxonomia* **21**, 281-287.

Gupta, P., Inderjit, S. (2007) Growth, development and feeding potential of grubs of *Chilocorus infernalis* Mulsant (Coleoptera: Coccinellidae) on the San Jose scale, *Quadraspidiotus perniciosus* (Comstock). *Journal of Biological Control* **21**, 119-124.

Hafez, A.A. (2001) Functional response, and some biological parameters of *Hippodamia tredecimpunctata* Goet. (Coleoptera: Coccinellidae). *Egyptian Journal of Biological Pest Control* **11**, 31-38.

Hagler, J.R., Jackson, C.G., Isaacs, R. & Machtley, S.A. (2004) Foraging behavior and prey interactions by a guild of predators on various lifestages of *Bemisia tabaci*. *Journal of Insect Science* **4**, 1.

Hales, D. (1979) Population dynamics of *Harmonia conformis* (Boisel.) (Coleoptera: Coccinellidae) on Accacia. *General & Applied Entomology.* **11**, 3-8.

Halima-Kamel, M. B. B. & Hamouda, M. H. B. (1993) Aphids from protected crops and their enemies in Tunisia., *Tropicultura* **11**, 50-53.

Hall, D.G. (2001) Notes on the yellow sugarcane aphid *Sipha flava* (Homoptera:Aphididae) and the lady beetle *Diomus terminatus* (Coleoptera:Coccinellidae) in Florida. *Journal American Society of Sugar Cane Technologists* **21**, 21-29.

Hallborg, H.M. (2003) Biology and Rearing of *Diomus terminatus* (Coleoptera: Coccinellidae) on *Rhopalosiphum maidis* (Homoptera: Aphididae) and artificial diet. Master's Thesis. University of Florida, U.S.A.

Hannan, A.K.M., Ahmad, M. & Taleb, M.A. (1998) Influence of different foods on the biology of *Micraspis discolor* (Fabricius) (Coleoptera: Coccinellidae). *Bangladesh Journal of Entomology* **8**, 69-80.

Harper, A.M. & Lilly, C.E. (1982) Aggregations and winter survival in southern Alberta of *Hippodamia quinquesignata* (Coleoptera, Coccinellidae), a predator of the pea aphid (Homoptera, Aphididae). *Canadian Entomologist* **114**, 303-309.

Hassan, M.A. (2001) Biology and efficiency of *Clitostethus arcuatus* (Rossi) (Coleoptera: Coccinellidae) as a predator of *Bemisia tabaci* (Genn.) (Homoptera: Aleyrodidae). *Egyptian Journal of Biological Pest Control* **11**, 95-100.

Hassani, M., Mehrnejad, M. & Ostovan, H. (2009) Some biological and predation characteristics of *Oenopia conglobata contaminata* (Col.: Coccinellidae) on the common pistachio psylla in laboratory conditions. *Iranian Journal of Forest and Range Protection Research* **6**, 110-117.

Heidari, M. (1999) Influence of host-plant physical defences on the searching behaviour and efficacy of two coccinellid predators of the obscure mealybug, *Pseudococcus viburni* (Signoret). *Entomologica* **33**, 397-402.

Heimoana, V. (2011) The potential of *Hippodamia variegata* (Coleoptera, Coccinellidae) and *Micromus tasmaniae* (Neuroptera: Hemerobiidae) as biological control agents for arthropod pests in Brassica crops. PhD Thesis. School of Agricultural and Wine Sciences, Charles Sturt University, Australia.

Heinz, K.M. & Parrella, M.P. (1994) Biological Control of *Bemisia argentifolii* (Homoptera: Aleyrodidae) Infesting *Euphorbia pulcherrima*: Evaluations of Releases of *Encarsia luteola* (Hympenoptera: Aphelinidae) and *Delphastus pusillus* (Coleoptera: Coccinellidae). *Environmental Entomology* **23**, 1346-1353.

Hentz, M.G. & Nuessly, G.S. (2002) Morphology and biology of *Diomus terminatus* (Coleoptera: Coccinellidae), a predator of *Sipha flava* (Homoptera: Aphidae). *Florida Entomologist* **85**, 276-278.

Hesler, L.S., Catangui, M.A., Losey, J.E., Helbig, J.B. & Mesman, A. (2009) Recent records of *Adalia bipunctata* (L.), *Coccinella transversoguttata richardsoni* Brown, and *Coccinella novemnotata* Herbst (Coleoptera: Coccinellidae) from South Dakota and Nebraska. *Coleopterists Bulletin* **63**, 475-484.

Hilbeck, A. & Kennedy, G.G. (1996) Predators feeding on the Colorado potato beetle in insecticide-free plots and insecticide-treated commercial potato fields in eastern North Carolina. *Biological Control* **6**, 273-282.

Hippa, H., Koponen, S. & Laine, T. (1978) On the feeding biology of *Coccinella hieroglyphica* L.(Col., Coccinellidae). *Reports from the Kevo Subarctic Research Station* **14**, 18-20.

Hippa, H., Koponen, S. & Roine, R. (1984) Larval growth of *Coccinella hieroglyphica* (Col., Coccinellidae) fed on aphids and preimaginal stages of *Galerucella sagittariae* (Col., Chrysomelidae). *Reports from the Kevo Subarctic Research Station* **19**, 67-70.

Hodek, I. & Honěk, A. (1996) Ecology of Coccinellidae. P. 464. Dordrecht, The Netherlands, Kluwer Academic Publishing.

Hoebeke, E.R. & Wheeler, A.G. Jr. (1996) Adventive lady beetles (Coleoptera: Coccinellidae) in the Canadian maritime provinces, with new eastern U.S. records of *Harmonia quadripunctata*. *Entomological News* **107**, 281-290.

Hoelmer, K.A., Osborne, L.S. & Yokomi, R.K. (1993) Reproduction and Feeding Behavior of *Delphastus pusillus* (Coleoptera: Coccinellidae), a Predator of *Bemisia tabaci* (Homoptera: Aleyrodidae). *Journal of Economic Entomology* **86**, 322-329.

Honda, J.Y. & Luck, R.F. (1995) Scale morphology effects on feeding behavior and biological control potential of *Rhyzobius lophanthae* (Coleoptera: Coccinellidae). *Annals of the Entomological Society of America* **88**, 441-450.

Houseweart, M.W. & Lawrence, R.K. (1986) *Anatis mali* (Say), a coccinellid predator of spruce budworm, *Choristoneura fumiferana* (Clemens), egg masses. CFRU Research Note. *College of Forest Resources, University of Maine*, (16): 6.

Houston, K. (1980) A revision of the Australian species of *Stethorus* Weise (Coleoptera: Coccinellidae). *Australian Journal of Entomology* **19**, 81-91.

Houston, K.J. (1988) Larvae of *Coelophora inaequalis* (F.), *Phrynocaria gratiosa* (Mulsant) and *P. astrolabiana* (Weise) (Coleoptera: Coccinellidae) with notes on their relationships and prey records. *Australian Journal of Entomology* **27**, 199-211.

Houston, K.J. (1990) The New Zealand species of *Stethorus* Weise (Coleoptera: Coccinellidae). *New Zealand Journal of Zoology* **17**, 271-278.

Houston, K.J. (1991) *Chilocorus circumdatus* Gyllenhal newly established in Australia and additional records for *Coccinella undecimpunctata* L. (Coleoptera: Coccinellidae). *Journal of the Australian Entomological Society* **30**, 341-342.

Huang, B., Chen, Q., Li, Z., Qiu S., Zhao, J., & Fu, J. (2001) The predatory functional response and searching efficiency of *Propylaea japonica* (Thunberg) on *Myzus persicae* (Sulzer). *Wuyi Science Journal* **17**, 39-43.

Huang, B., Wang, B. & Yu, B. (2002) Bionomics of *Chilocorus rubidus*. *Entomological Knowledge* **39**, 126-129.

Huang, B., Zou, Y., Bi, S. & Fan, T. (2007) Dynamics and spatial pattern of *Didesmococcus koreanus* Broch population in a plum orchard. *Journal of China Agricultural University* **12**, 39-44.

Huang, Z., Ren, S.-X. & Yao, S.-L. (2003) Morphological and life habit of *Axinoscymnus cardilobus*. *Entomological Knowledge* **5**, 450-452.

Huang, Z., Ren, S.X. & Yao, S.L. (2006) Life history of *Axinoscymnus cardilobus* (Col., Coccinellidae), a predator of *Bemisia tabaci* (Hom., Aleyrodidae). *Journal of Applied Entomology* **130**, 437-441.

Hukusima, S. & Kouyama, S. (1974) Life histories and food habits of *Menochilus sexmaculatus* Fabricius (Coleoptera: Coccinellidae). *Research Bulletin of the Faculty of Agriculture-Gifu University,* **36**, 19-29.

Husband, R.W. (1972) A new genus and species of mite (Acarina: Podapolipidae) associated with the coccinellid *Cycloneda sanguinea*. *Annals of the Entomological Society of America* **65**, 1099-1104.

Hussein, M. (1991) *Menochilus sexmaculatus* Fabr.(Coleoptera: Coccinellidae): its biology, prey requirement and artificial diets. *Journal of Plant Protection in the Tropics*, **83:iv**, 153-160.

Ibrahim, M. (1955) Studies of *Coccinella undecimpunctata aegyptiaca* Rche II. Biology and Lifehistory (Coleoptera: Coccinellidae). *Bulletin of the Entomological Society of Egypt* **39**, 395-423.

Idder, M.A.,Doumandji-Mitiche, B. & Pintureau, B. (2013) Biological control in Algerian palm groves. *Acta Horticulturae* **994**, 347-354.

Imani, Z. & Shishehbor, P. (2011) Functional response of *Stethorus gilvifrons* (Col.: Coccinellidae) to different densities of *Eutetranychus orientalis* (Acari: Tetranychidae) in laboratory. *Journal of Entomological Society of Iran* **31**, 29-40.

Iperti, G. (1985) Preliminary phenological data before establishment of *Rhyzobius forestieri* (Muls.)(Coleoptera, Coccinellidae) in olive-trees near Antibes (Southern France). pp. 451-456 in *Proceedings of the Integrated Pest Control in Olive: CEC/FAO/ IOBC International Joint Meeting*, Pisa (Italy), April 3-6,1984.

Iperti, G., Giuge, L. & Roger, J.P. (1989) The establishment of *Rhyzobius forestieri* (Col., Coccinellidae) on the Island of Porquerolles. *Entomophaga* **34**, 365-372.

Irshad, M. (2001) Distribution, hosts, ecology and biotic potentials of coccinellids of Pakistan. *Pakistan Journal of Biological Sciences* **4**, 1259-1263.

Isikber, A.A. & Copland, M.J.W. (2001) Food consumption and utilisation by larvae of two coccinellid predators, *Scymnus levaillanti* and *Cycloneda sanguinea*, on cotton aphid, *Aphis gossypii*. *Biocontrol* **46**, 455-467.

Isikber, A.A. & Copland, M.J.W. (2002) Effects of various aphid foods on *Cycloneda sanguinea*. *Entomologia Experimentalis Et Applicata* **102**, 93-97.

Isikber, A.A. (2008) Feeding and foraging behaviour in two coccinellid predators: *Scymnus levaillanti* Muls. and *Cycloneda sanguinea* L. *Turkish Journal of Agriculture and Forestry* **32**, 391-400.

Islam, M.R., Islam, K.S., Ahmad, M., Uddin, M.F. & Ahad, M.A. (2007) Biological control of citrus mealybug *Planococcus citri* (Risso) by lady bird beetle, *Menochilus sexmaculatus* F. and *Micrapis discolor* F. in Bangladesh. *Journal of Subtropical Agricultural Research and Development* **5**, 332-335.

Ives, P.M. (1981) Feeding and egg production of two species of Coccinellis in the laboratory. *The Canadian Entomologist* **113**, 999-1005.

Izhevsky, S. &. Orlinsky, A. (1988) Life history of the imported *Scymnus* (*Nephus*) reunioni (Coleoptera: Coccinellidae) predator of mealybugs. *Entomophaga* **1**, 101-114

Jackson, D., Gonzalez, G., Jackson, T. & Rothmann, S. (2009) *Hippodamia convergens* (Coleoptera: Coccinellidae) aggregations in the Maule region, Chile. *Revista Chilena de Entomología* **35**, 89-94.

Jafari, R., Kamali, K. & Ostovan, H. (2008) Biology of *Hippodamia variegata* (Col.: Coccinellidae) in laboratory conditions. *Journal of Plant Protection Research* **51**, 190-194.

Jalali, M.A., Tirry, L. & De Clercq, P. (2009) Effects of food and temperature on development, fecundity and life-table parameters of *Adalia bipunctata* (Coleoptera: Coccinellidae). *Journal of Applied Entomology* **133**, 615-625.

Jalali, S.K. & Singh, S.P. (1992) Biology and feeding potential of *Curinus coeruleus* (Mulsant) and *Chrysoperla carnea* (Stephens) on subabul psyllid, *Heteropsylla cubana* Crawford. *Journal of Insect Science* **5**, 89-90.

James, B. (2001) *Contribution on certain aspects of bioecology and behaviour of a ladybeetle,* Coccinella transversalis *Fabricius (Coccinellidae: Coleoptera)*. PhD Thesis. University of Lucknow, India.

Jamieson, L., Charles, J., Stevens, P., McKenna, C. & Bawden, R. (2005) Natural enemies of citrus red mite (*Panonychus citri*) in citrus orchards. *New Zealand Plant Protection* **58**, 299.

Jian, H.; Xiaonan, L.; Axing, H.; Bangkan, H.; Yidi, X.; Desheng, Y. & Xiyuan, C. (1999) The establishment of natural population base of *Stethorus siphonulus* Kapur (Coleoptera: Coccinellidae). *Entomological Journal of East China* **82**, 30-35.

Jianwei, Fu, J., Huang, B. & Liu, J.Y.X. (1999) Studies on characters and biology of *Delphastus catalinae* (Horn)(Coleoptera: Coccinellidae) introduced. Entomological Journal of East China **1**, 017.

Jiao, Y., Chen, Y. & Ye, S. (1997) A study on *Chilocorus bijugus* Mulsant (Coccinellidae, Coleoptera). Forest Research-Chinese Academy of Forestry **10**, 328-331.

Johnson, J. (1972) Biology of *Scymnus nubilus* Muls.(Coccinellidae: Coleoptera) an insect predator. *Agricultural Research Journal of Kerala* **10**, 183-185.

Joshi, P. (2012) Predation of *Adalia tetraspilota* (Hope)(Coleoptera: Coccinellidae) on Green Peach Aphid (*Myzus persicae*. Sulzer). *Entomology, Ornithology & Herpetology* **1**, 1-2.

Joshi, P., Sharma, P.K. & Goel, S. (2008) Feeding performance of *Cheilomenes sexmaculata* (Fabr.) on mustard aphid, *Lipaphis erysimi* (Kalt.) and cotton aphid, *Aphis gossypii* (Glover). pp. 269-273in

Uttar Pradesh Zoological Society (Eds) *Procedings of the 8th, Symposium on Emerging trends of researches in insect pest management and environmental safety, Volume I*., Haridwar, India, 24-26 September 2008.

Joshi, S., Ballal, C. & Rao, N. (2001) An alternative host for rearing the exotic leucaena psyllid predator, *Curinus coeruleus* (Mulsant)(Coleoptera: Coccinellidae). *Entomon-Trivandrum-* **26**, 86-92.

Kairo, M. & Murphy, S. (1995a) The life history of *Rodolia iceryae* Janson (Col., Coccinellidae) and the potential for use in innoculative releases against *Icerya pattersoni* Newstead (Hom., Margarodidae) on coffee. *Journal of Applied Entomology* **119**, 487-491.

Kairo, M.T.K. & Murphy, S.T. (1995b) The life history of *Rodolia iceryae* Janson (Col., Coccinellidae) and the potential for use in innoculative releases against *Icerya pattersoni* Newstead (Hom., Margarodidae) on coffee. *Journal of Applied Entomology* **119**, 487-491.

Kairo, M.T.K., Paraiso, O., Gautam, R.D. & Peterkin, D.D. (2013) *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. *CAB Reviews* **8**, 1-20.

Kajita, Y.e.-m.y.k.u.e., Evans, E.W. & Yasuda, H. (2009) Reproductive responses of invasive and native predatory lady beetles (Coleoptera: Coccinellidae) to varying prey availability. *Environmental Entomology* **38**, 1283-1292.

Kakde, A.M. & Patel, V.N. (2013) Studies on feeding potential of *Cryptolaemus montrouzieri* Mulsant on *Phenacoccus solenopsis* Tinsley. *Journal of Cotton Research and Development* **27**, 310-312.

Kalushkov, P. & Hodek, I. (2001a) New Essential Aphid Prey for *Anatis ocellata* and *Calvia quatuordecimguttata* (Coleoptera: Coccinellidae). *Biocontrol Science and Technology* **11**, 35-39.

Kalushkov, P. & Hodek, I. (2005) The effects of six species of aphids on some life history parameters of the ladybird *Propylea quatuordecimpunctata* (Coleoptera: Coccinellidae). *European Journal of Entomology* **102**, 449-452.

Kalushkov, P. (1998) Ten aphid species (Sternorrhyncha: Aphididae) as prey for *Adalia bipunctata* (Coleoptera: Coccinellidae). *European Journal of Entomology* **95**, 343-349.

Kalushkov, P.K. (1994) Longevity, fecundity and development of *Adalia bipunctata* (L) (Col, Coccinellidae) when reared on 3 aphid diet. *Anzeiger Fur Schadlingskunde Pflanzenschutz Umweltschutz* **67,** 6-7.

Kandasamy, P., Rajagopal, S., Amsalingam, R., Rahman, V.J. & Muraleedharan, N.N. (2010) Life table and predatory efficiency of *Stethorus gilvifrons* (Coleoptera: Coccinellidae), an important predator of the red spider mite, *Oligonychus coffeae* (Acari: Tetranychidae), infesting tea. *Experimental and Applied Acarology* **50**, 141-150.

Kanika-Kiamfu, J., Brun, J. & Iperti, G. (1994) Development of *Exochomus flaviventris* Mader (Coleoptera, Coccinellidae) at variable temperatures and with a substitute food. *Journal of African Zoology* **108**, 569-583.

Kanika-Kiamfu, J., Iperti, G. & Brun, J. (1993) Study of food consumption of *Exochomus flaviventris* (Col. Coccinellidae), predator of *Phenacoccus manihoti* (Hom.: Pseudococcidae). *Entomophaga* **38**, 291-298.

Kanika-Kiamfu, J., Kiyindou, A., Brun, J. & Iperti, G. (1992) Comparison of the biological potential of 3 coccinellid predators of the cassava mealybug *Phenacoccus manihoti*. *Entomophaga* **37**, 277-282.

Kapadia, M.N. & Butani, **P.G.** (1997) Record of *Serangium parcesetosum* Sicard, a predator of sugarcane whitefly in south Saurashtra (Gujarat). *Indian Sugar* **47**, 503-504.

Kapadia, M.N. & Puri, S.N. (1992) Biology of *Serangium parcesetosum* as a predator of cotton whitefly. *Journal of Maharashtra Agricultural Universities* **17**, 162-163.

Kapur, A. (1961) A new species of *Stethorus* Weise (Coleoptera-Coccinellidae), feeding on arecanut palm mites in Kerala, southern India. *Entomophaga* **6**, 35-38.

Karaca, I., Senal, D., Colkesen, T. & Ozgokce, M.S. (1999) Observations on the oleander scale, *Aspidiotus nerii* Bouche (Hemiptera: Diaspididae) and its natural enemies on blueleaf wattle in Adana Province, Turkey. *Entomologica* **33**, 407-412.

Karaman, G., Makady, M., Ali, F. & Hamouda, S. (1998) Effect of feeding the ladybeetle *Coccinella undecimpunctata aegyptiaca* Reiche on different aphid species on fecundity and longevity of the adults stage. *Arab Journal of Plant Protection* **16**, 3-6.

Karnataka (2007) Seasonal Incidence of Spiralling Whitefly *Aleurodicus dispersus* Russell and its Natural Enemies in Relation to Weather in Shimoga. *Journal of Agricultural Sciences* **20**, 146 - 148.

Kasap, I. & Yasar, B. (1996) Studies on the life table of *Exochomus nigromaculatus* Goeze (Col.: Coccinellidae) feeding on *Hyalopterus pruni* (Geoffr.)(Hom.: Aphididae) and *Chaitophorus leucomelas* Koch (Hom.: Chaitophoridae). *Procedings of the Turkish National Congress on Entomology* **3**, 675-681.

Kato, C.M., Auad, A.M. & Bueno, V.H.P. (1999) Aspectos biológicos e etológicos de *Olla v-nigrum* (Mulsant, 1866)(Coleoptera: Coccinellidae) sobre *Psylla* sp.(Homoptera: Psyllidae). *Ciência e Agrotecnologia* **23**, 19-23.

Katsoyannos, P. (1997) Status and importance of *Rhyzobius forestieri* (Col.: Coccinellidae) on citrus at Chios Island, Greece, nine years after its introduction. *Entomophaga* **42**, 387-392.

Katsoyannos, P., Kontodimas, D.C. & Stathas, G. (2005) Summer diapause and winter quiescence of *Hippodamia (Semiadalia) undecimnotata* (Coleoptera: Coccinellidae) in central Greece. *European Journal of Entomology* **102**, 453-457.

Katsoyannos, P., Kontodimas, D.C. & Stathas, G.J. (1997) Phenology of *Hippodamia undecimnotata* (Col.: Coccinellidae) in Greece. *Entomophaga* **42**, 283-293.

Kauffman, W.C. & LaRoche, S.L. (1994) Searching activities by coccinellids on rolled wheat leaves infested by the russian wheat aphid. *Biological Control* **4**, 290-297.

Kaufmann, T. (1977) Binomics of *Chilocorus bipustulatus* (Coleoptera, Coccinellidae) and its future for biological control of date palm scale, *Parlatoria blanchardi*, (Homoptera-Coccidae) in Niger, W. Africa. *Environmental Entomology* **6**, 559-562.

Kawauchi, S. (1997) Life histories of *Coccinella septempunctata brucki*, *Propylea japonica* and *Scymnus hoffmanni* (Col., Coccinellidae) in Japan. *Entomophaga* **42**, 41-47.

Kazmi, S. & Husen, A. (1999) Record of *Anisolemnia (Caria) dialatata* FAB.(Coleoptera: Coccinellidae) as a predator on *Oregma bambusa* Bukton (Homoptera: Aphididae) infesting bamboo. *Annals of Forestry* **7**, 299-300.

Keena, M.A., Trotter, R.T., Cheah, C. & Montgomery, M.E. (2012) Effects of temperature and photoperiod on the aestivo-hibernal egg diapause of *Scymnus camptodromus* (Coleoptera: Coccinellidae). *Environmental Entomology* **41**, 1662-1671.

Kehat, M. (1967a) Studies on the biology and ecology of *Pharoscymnus numidicus* (Coccinellidae), an important predator of the date palm scale *Parlatoria blanchardi*. *Annales de la Société Entomologique de France* **3**, 1053-1069.

Kehat, M. (1967b) Survey and distribution of common lady beetles [Col. Coccinellidae] on data palm trees in Israel. *Entomophaga* **12**, 119-125.

Kehat, M. (1968a) Phenology of *Pharoscymnus* spp. and *Chilocorus bipustulatus* L. (Coccinellidae) in date palm plantations in Israel. *Annales Des Epiphyties* **19**, 605-614.

Kehat, M. (1968b) The feeding behavior of *Pharoscymnus numidicus* (Coccinellidae), predator of the date palm scale *Parlatoria blanchardi*. *Entomologia Experimentalis et Applicata* **11**, 30-42.

Khan, A. & Mir, R. (2008) Functional response of four predaceous coccinellids, *Adalia tetraspilota* (Hope), *Coccinella septempunctata* L., *Calvia punctata* (Mulsant) and *Hippodamia variegata* (Goeze) feeding on the green apple aphid, *Aphis pomi* De Geer (Homoptera: Aphididae). *Journal of Biological Control* **22**, 291-298.

Khan, I. (2000) Aspects of the biology of the ladybird beetle *Stethorus vagans* (Blackburn)(Coleoptera: Coccinellidae). PhD Thesis. University of Western Sydney, Hawkesbury, Australia.

Khan, I., Din, S., Khalil, S.K. & Rafi, M.A. (2007) Survey of predatory coccinellids (Coleoptera: Coccinellidae) in the Chitral District, Pakistan. *Insect Science* **7**, 1-6.

Khan, I., Din, S., Khalil, S.K. & Rafi, M.A. (2007) Survey of predatory Coccinellids (Coleoptera : Coccinellidae) in the Chitral District, Pakistan. *Journal of Insect Science* **7**, 1-7.

Kheradpir, N., Khalghani, J., Ostovan, H. & Rezapanah, M.R. (2006) Feeding rate of *Stethorus gilvifrons* on *Tetranychus urticae* in three greenhouse cucumber cultivars with different resistance levels. *Bulletin OILB/SROP* **29**, 139-143.

Khuhro, S.N., Lohar, M.K., Abro, G.H., Talpur, M.A. & Rabdino, K. (2012) Feeding potential of lady bird beetle, *Brumus suturalis* Fabricius (Coleoptera: Coccinellidae) on cotton mealy bug *Phenacoccus solenopsis* (Tinsley) in laboratory and field. *Sarhad Jorunal of Agriculture* **28**, 259-265.

Kieckhefer, R.W. & Elliott, N.C. (1990) A 13-year survey of the aphidophagous Coccinellidae in maize fields in eastern South Dakota. *Canadian Entomologist* **122**, 579-581.

Kieckhefer, R.W., Elliott, N.C. & Beck, D.A. (1992) Aphidophagous coccinellids in alfalfa, small grains, and maize in eastern South Dakota. *Great Lakes Entomologist* **25**, 15-23.

Kim, J. & Morimoto, K. (1995) Biological studies on *Rhyzobius forestieri* (Mulsant) (Coleoptera: Coccinellidae). *Science Bulletin of the Faculty of Agriculture, Kyushu University* **50**, 45-50.

Kishimoto, H. & Adachi, I. (2008) Predation and oviposition by predatory *Stethorus japonicus*, *Oligota kashmirica benefica*, and *Scolothrips takahashii* in egg patches of various spider mite species. *Entomologia Experimentalis Et Applicata* **128**, 294-302.

Kishimoto, H. (2002) Species composition and seasonal occurrence of spider mites (Acari: Tetranychidae) and their predators in Japanese pear orchards with different agrochemical spraying programs. *Applied Entomology and Zoology* **37**, 603-615.

Kishimoto, H. (2003) Development and oviposition of predacious insects, *Stethorus japonicus* (Coleoptera: Coccinellidae), *Oligota kashmirica benefica* (Coleoptera: Staphylinidae), and *Scolothrips takahashii* (Thysanoptera: Thripidae) reared on different spider mite species (Acari: Tetranychidae). *Applied Entomology and Zoology* **38**, 15-21.

Kishimoto, H., Maeda, T., Wright, L.C. & James, D.G. (2011) Identification of prey consumed by *Stethorus punctum picipes* (Casey) (Cleoptera: Coccinellidae) in tree fruit and vines in Washington State, USA. *International Journal of Acarology* **37**, 216-220.

Kiyindou, A. (1989) Temperature threshold for development of three coccinellid predators of cassava mealybug in Congo. *Entomophaga* **34**, 409-415.

Kiyindou, A. (1990) Étude Biologique de *Diomus hennesseyi* Fürsch Coleoptera, Coccinellidae) determination de ses aptitudes predatices pour lutter contre la cochenille du manioc *Phenacoccus manihoti* Mat. Ferr. (Homoptera, Pseudococcidae). Master's Thesis. Nice University, France.

Kiyindou, A., Iperti, G., Ferran, A. & Brun, J. (1992) Influence of temperature and food biomass on the development of a coccinellid, *Diomus hennesseyi* (Coleoptera: Coccinellidae), a predator of *Phenacoccus manihoti* (Homoptera: Pseudococcidae) in intertropical Africa. *Revue de Zoologie Africaine* **106**, 479-488.

Kiyindou, A., Leru, B. & Fabres, G. (1990a) The numerical response of 2 coccinellids preying on the cassava mealybug to changes in the nature and abundance of the preys. *Entomophaga* **35**, 611-620.

Kiyindou, A., Ru, B.l. & Fabres, G. (1990b) The influence of the nature and abundance of prey on the numerical response of two coccinellids preying on the cassava mealybug in Congo. *Entomophaga* **35**, 611-620.

Klunk, W.M. (2007) *Sasajiscymnus tsugae* (Coleoptera: Coccinellidae) as a biological control for hemlock wolly adelgid (Adelges tsugae (Hemiptera: Adelgidae) on eastern hemlock (Tsugae canadensis) and carolina hemlock (T. caroliniana). Master's Thesis. Clemson University, South Carolina, U.S.A.

Koch, R. (2003) The multicolored Asian lady beetle, Harmonia axyridis: a review of its biology, uses in biological control, and non-target impacts. *Journal of Insect Science* **3**, 1-16.

Koch, R.L., Hutchison, W.D., Venette, R.C. & Heimpel, G.E. (2003) Susceptibility of immature monarch butterfly, *Danaus plexippus* (Lepidoptera: Nymphalidae: Danainae), to predation by *Harmonia axyridis* (Coleoptera: Coccinellidae). *Biological Control* **28**, 265-270.

Kohler, G., Stiefel, V., Wallin, K. & Ross, D. (2008) Predators associated with the hemlock woolly adelgid (Hemiptera: Adelgidae) in the Pacific Northwest. *Environmental Entomology* **37**, 494-504.

Kontodimas, D.C. & Stathas, G.J. (2005) Phenology, fecundity and life table parameters of the predator *Hippodamia variegata* reared on *Dysaphis crataegi*. *Biocontrol* **50**, 223-233.

Kontodimas, D.C. (1997) First record of the predatory insect *Nephus bisignatus* (Boheman) (Coleoptera: Coccinellidae) in Greece. *Annales de l'Institut Phytopathologique Benaki* **18**, 61-63.

Kontodimas, D.C., Eliopoulos, P.A., Stathas, G.J. & Economou, L.P. (2004) Comparative temperature-dependent development of *Nephus includens* (Kirsch) and *Nephus bisignatus* (Boheman) (Coleoptera: Coccinellidae) preying on *Planococcus citri* (Risso)(Homoptera: Pseudococcidae): evaluation of a linear and various nonlinear models using specific criteria. *Environmental Entomology* **33**, 1-11.

Kontodimas, D.C., Milonas, P.G., Stathas, G.J., Economou, L.P. & Kavallieratos, N.G. (2007) Life table parameters of the pseudococcid predators *Nephus includens* and *Nephus bisignatus* (Coleoptera: Coccinelidae). *European Journal of Entomology* **104**, 407-415.

Kontodimas, D.C., Milonas, P.G., Stathas, G.J., Papanikolaou, N.E., Skourti, A. & Matsinos, Y.G. (2008) Life table parameters of the aphid predators *Coccinella septempunctata*, *Ceratomegilla undecimnotata* and *Propylea quatuordecimpunctata* (Coleoptera: Coccinellidae). *European Journal of Entomology* **105**, 427-430.

Kring, T.J., Gilstrap, F.E. & Michels, G.J. (1985) Role of Indigenous Coccinellids in Regulating Greenbugs (Homoptera: Aphididae) on Texas Grain Sorghum. *Journal of Economic Entomology* **78**, 269-273.

Kriz, J.C., Danielson, S.D., Brandle, J.R. & Blankenship, E.E. (2006) Relative abundance of exotic and native Coccinellidae (Coleoptera) in Southeast Nebraska alfalfa. *Journal of Entomological Science* **41**, 84-86.

Kumar, L.V. & Prabhuraj, A. (2006) Seasonal incidence of sorghum shoot bug, *Peregrinus maidis* (Ashmead) (Homoptera: Delphacidae) and its natural enemies in Karnataka. *Journal of Plant Protection and Environment* **3**, 95-100.

Kumar, M.V.S. & Chakraborty, N. (1997) Biology of *Scymnus nubilus* Mulsant (Coleoptera: Coccinellidae), a native predator of pink mealy bug, *Maconellicoccus hirsutus* (Green) (Hemiptera: Pseudococcidae). *Journal of Entomological Research* **21**, 329-334.

Kutuk, H. & Yigit, A. (2007) Life table of *Delphastus catalinae* (Horn) (Coleoptera : Coccinellidae) on cotton whitefly, *Bemisia tabaci* (Genn.) (Hornoptera : Aleyrodidae) as prey. *Journal of Plant Diseases and Protection* **114**, 20-25.

Kutuk, H., Alaoglu, O. & Yigit, A. (2008) Evaluation of the lady beetle, *Serangium parcesetosum* for control of *Bemisia tabaci* on greenhouse eggplant in the Mediterranean region. *Biocontrol Science and Technology* **18**, 675-683.

Lamp, W.O., Liewehr, D., Fuentes, C. & Dively, G.P. (1994) First report of the blue alfalfa aphid (Homoptera: Aphididae) in Maryland: natural enemies and biotype. *Journal of the Kansas Entomological Society* **67**, 129-132.

Larsen, N., MacDonald, F., Connolly, P. & Walker, G. (2011) Could *Harmonia conformis* be an important predator of *Bactericera cockerelli*? *New Zealand Plant Protection* **64**, 293.

Legaspi, J.C., Legaspi, B., Meagher, R. & Ciomperlik M. (1996) Evaluation of *Serangium parcesetosum* (Coleoptera: Coccinellidae) as a biological control agent of the silverleaf whitefly (Homoptera: Aleyrodidae). *Environmental Entomology* 25, 1421-1427.

Legaspi, J.C., Legaspi, B.C., Jr., Simmons, A.M. & Soumare, M. (2008b) Life table analysis for immatures and female adults of the predatory beetle, *Delphastus catalinae*, feeding on whiteflies under three constant temperatures. *Journal of Insect Science* **8**, 1-7.

Legaspi, J.C., Simmons, A.M. & Legaspi Jr, B.C. (2006) Prey preference by *Delphastus catalinae* (Coleoptera: Coccinellidae) on *Bemisia argentifolii* (Homoptera: Aleyrodidae): effects of plant species and prey stages. *Florida Entomologist* **89**, 218-222.

Legaspi, J.C., Simmons, A.M. & Legaspi Jr, B.C. (2008a) Life History of *Delphastus catalinae*: a predator of *Bemisia tabaci*. pp. 27 in *Journal of Insect Science* (Eds) *The Fourth International Bemisia Workshop International*, Duck Key, Florida, USA, 3-8 December 2006.

Li, W. Huang,Y., Luo, Z.(2001) Studies on the bionomics and population fluctuations of *Synonycha grandis* (Thunberg)[J]. *Natural Enemies of Insects* 2, 002.

Liere, H. & Perfect, I. (2008) Cheating on a mutualism: Indirect benefits of ant attendance to a coccidophagous coccinellid. *Environmental Entomology* **37**, 143-149.

Liu, C. (1993) A study on the predation of *Chilocorus rubidus* Hope on the Korean lecanium (Didesmococcus koreanus). *Plant Protection* **19**, 13-14.

Liu, C.Y. (1933) Notes on the biology of two giant coccinellids in Kwangsi (*Caria dialatata* Fabr. and *Synonycha grandis* Thunbg.) with special reference to the morphology of *Caria dilatata*. *Yearb. Bureau of Entomology Hangchow* **2**, 205-250.

Liu, J. & He, D. (2009) The community composition and niche of ladybirds in orchard of American apricot and plum. *Chinese Bulletin of Entomology* **46**, 445-449.

Liu, T. & Stansly, P.A. (1996) Morphology of *Nephaspis oculatus* and *Delphastus pusillus* (Coleoptera: Coccinellidae), predators of *Bemisia argentifolii* (Homoptera: Aleyrodidae). *Proceedings of the Entomological Society of Washington* **98**, 292-300.

Liu, T.-X.& Stansly, P.A. (1999) Searching and feeding behavior of *Nephaspis oculatus* and *Delphastus catalinae* (Coleoptera: Coccinellidae), predators of *Bemisia argentifolii* (Homoptera: Aleyrodidae). *Environmental Entomology* **28**, 901-906.

Liu, T.-X., Stansly, P.A., Hoelmer, K.A. & Osborne, L.S. (1997) Life history of *Nephaspis oculatus* (Coleoptera: Coccinellidae), a predator of *Bemisia argentifolii* (Homoptera: Aleyrodidae). *Annals of the Entomological Society of America* **90**, 776-782.

Lo, P.L. & Chapman, R.B. (2001) Predation by *Halmus chalybeus* (Coleoptera: Coccinellidae) on *Ceroplastes destructor* and *C. sinensis* (Hemiptera: Coccidae: Ceroplastinae) Infesting Citrus in Northland, New Zealand. *Biocontrol Science and Technology* **11**, 57-66.

Lo, P.L. (2000) Species and abundance of ladybirds (Coleoptera: Coccinellidae) on citrus orchards in Northland, New Zealand, and a comparison of visual and manual methods of assessment. *New Zealand Entomologist* **23**, 61-65.

Loi, G. (1978) Ecological and behavioural observations on *Clitostethus arcuatus* (Rossi) (Coleoptera Coccinellidae Scymninae), a predator of *Dialeurodes citri* (Ashm.) in Tuscany. *Frustula Entomologica* **1**, 123-145.

Loia, M. (1992) The influence of some factors (temperature and feeding) on the reproduction of *Rodolia cardinalis* (Mulsant) (Coleoptera: Coccinellidae). *Bollettino del Laboratorio di Entomologia Agraria 'Filippo Silvestri'* **49**, 69-84.

Lokeshwari, R.K., Devikarani, K.H. & Singh, T.K. (2010) Seasonal dynamics of *Aphis gossypii* and relative abundance of its coccinellid predators on cucumber. *Indian Journal of Entomology* **72**, 114-116.

Lopez, V. & Kairo, M. (2003) Prey range of *Nephaspis bicolor* Gordon (Coleoptera: Coccinellidae), a potential biological control agent of *Aleurodicus dispersus* and other *Aleurodicus* spp. (Homoptera: Aleyrodidae*). International Journal of Pest Management* **49**, 75-88.

Lopez, V., Kairo, M. & Irish, J. (2004) Biology and prey range of *Cryptognatha nodiceps* (Coleoptera: Coccinellidae), a potential biological control agent for the coconut scale, *Aspidiotus destructor* (Hemiptera: Diaspididae). *Biocontrol Science and Technology* **14**, 475-485.

Lopez, V.F. (2008) Evaluation of *Nephaspis bicolor* Gordon (Coleoptera: coccinellidea) as a biological control agent of Aleyrodidae (particularly Aleurodicus spp.) (Hemiptera: sternorrhyncha). PhD Thesis. University of West Indies, St Augustine, Trinidad and Tobago.

Lorenzato, D. (1988) Biological control of phytophagous mites in apple orchards in Farroupilha, RS. *Agronomia Sulriograndense* **23**, 167-183.

Lotfalizadeh, H., Hatami, B. & Khalaghani, J. (2000) Biology of *Exochomus quadripustulatus* (L.) (Col.: Coccinellidae) on cypress tree mealybug, *Planococcus vovae* (Nasanov) (Hom.: Pseudococcidae) in Shiraz. *Journal of Entomological Society of Iran* **20**, 61-76.

Lu, W. & Montgomery, M.E. (2000) Comparative biology of three *Scymnus* lady beetles (Coleoptera: Coccinellidae): predators of *Adelges tsugae* (Homoptera: Adelgidae) in In: McManus, K.A.; Shields, K.S. & Souto D.R. (Eds.) *Proceedings of the Symposium on Sustainable Management of Hemlock Ecosystems in Eastern North America,* Newtown, U.S.A.

Lu, W. & Montgomery, M.E. (2001) Oviposition, development, and feeding of *Scymnus* (*Neopullus*) *sinuanodulus* (Coleoptera: Coccinellidae): a predator of *Adelges tsugae* (Homoptera: Adelgidae). *Annals of the Entomological Society of America* **94**, 64-70.

Lu, W., Souphanya, P. & Montgomery, M.E. (2002) Descriptions of immature stages of *Scymnus* (*Neopullus*) *sinuanodulus* Yu and Yao (Coleoptera: Coccinellidae) with notes on life history. *The Coleopterists Bulletin* **56**, 127-141.

Lynch, C., Lambdin, P., Grant, J., Reardon, R. & Rhea, R. (2006) Survey for potential predators of the elongate hemlock scale in Tennessee and North Carolina. *Florida Entomologist* **89**, 527-528.

Lyon, S. & Montgomery, M. (2010) *Scymnus* (*Pullus*) *suturalis* Thunberg (Coleoptera: Coccinellidae): New locality records and a report on feeding on hemlock woolly adelgid, *Adelges tsugae* Annand (Homoptera: Adelgidae). *The Coleopterists Bulletin* **49**, 118.

Magagula, C.N. & Samways, M.J. (2001) Maintenance of ladybeetle diversity across a heterogeneous African agricultural/savanna land mosaic. *Biodiversity and Conservation* **10**, 209-222.

Mahadev, B., Geetanjali, M. & Omkar (2012) Influence of crowding and diet on the development and survival of the ladybird *Brumoides suturalis* (Coleoptera: Coccinellidae) reared on two aphid species. *International Journal of Tropical Insect Science* **32**, 64-68.

Majerus, M.E.N. (1989) *Coccinella magnifica* (Redtenbacher): a myrmecophilous ladybird. *British Journal of Entomology and Natural History* **2**, 97-106.

Majumder, J. & Agarwala, B. (2013) Biology and Population Dynamics of Giant Ladybird Predator *Anisolemnia dilatata* (F.) (Coleoptera: Coccinellidae): A Specialized Predator of Woolly Aphids of Bamboo Plants in Northeast India. *World Journal of Zoology* **8**, 55-61.

Majumder, J., Bhattacharjee, P.P. & Agarwala, B.K. (2013) Diversity, Distribution and habitat preference of predatious coccinellids (Coleoptera: Coccinellidae) in Agro and forest habitats of Tripura, Northeast India. *International Journal of Current Research* **5**, 1060-1064.

Malik, Y.P., Bhagwan, D. & Singh, S.V. (1998) Feeding propensity of different coccinellids on mustard aphid, *Lipaphis erysimi*. *Indian Journal of Entomology* **60**, 414-415.

Mani, M. & Krishnamoorthy, A. (1995) Natural enemies of *Siphoninus phillyreae* (Homoptera: Aleurodidae) and *Aphis punicae* (Homoptera: Aphididae) on pomegranate. *Entomon* **20**, 31-34.

Mani, M. & Krishnamoorthy, A. (1996) Discovery of the coccinellid predator *Chilocorus circumdatus* on the green scale *Coccus viridis*. *Entomon* **21**, 295-296.

Mari, J.M., Nizamani, S.M., Lohar, M.K. & Khuhro, R.D. (2004) Biology of *Menochilus sexmaculatus* Fab. and *Coccinella undecimpunctata* L. (Coccinellidae: Coleoptera) on alfalfa aphid *Therioaphis trifolii* Monell. *Journal of Asia Pacific Entomology* **7**, 297-301.

Marriott, S., Giberson, D. & McCorquodale, D. (2009) Changes in the status and geographic ranges of Canadian Lady Beetles (Coccinellinae) and the selection of candidates for risk assessment. *Part 1. Foundation Report*, 1-53.

Marzo, L.d. (2001) A description of *Nephus bisignatus* (Boheman) larvae (Coleoptera Coccinellidae) feeding on *Planococcus vovae* (Nassonov) (Rhynchota Coccoidea Pseudococcidae) in Southern Italy. *Entomologica* **35**, 181-187.

Mayer, M. & Allen, D.C. (1982) *Chilocorus stigma* (Coleoptera: Coccinellidae) and other predators of beech scale in central New York. pp. 89-98 in Proceedings of IUFRO Beech Bark DiseaseWorking Party Conference sponsored by the USDA Forest Service, Northeastern Forest Experiment Station, Hamden, Connecticut, U.S.A, September -8 October 1982

McMullen, R.D. (1967a) The effects of photoperiod, temperature, and food supply on rate of development and diapause in *Coccinella novemnotata*. *Canadian Entomologist* **99**, 578-586.

McMullen, R.D. (1967b) A field study of diapause in *Coccinella novemnotata* (Coleoptera: Coccinellidae). *Canadian Entomologist* **99**, 42-49.

McNamara, J. (1992) The first Canadian records of *Scymnus* (*pullus*) *suturalis* Thunberg (Coleoptera: Coccinellidae). *Coleopterists Bulletin* **46**, 359-360.

Mehrnejad, M. & Jalali, M. (2004) Life history parameters of the coccinellid beetle, *Oenopia conglobata contaminata*, an important predator of the common pistachio psylla, *Agonoscena pistaciae* (Hemiptera: Psylloidea). *Biocontrol Science and Technology* **14**, 701-711.

Mehrnejad, M.R., Jalali, M.A. & Mirzaei, R. (2011) Abundance and biological parameters of psyllophagous coccinellids in pistachio orchards. *Journal of Applied Entomology* **135**, 673-681.

Mendel, Z. & Blumberg, D. (1991) Colonization trials with *Cryptochetum iceryae* and *Rodolia iceryae* for improved biological control of *Icerya purchasi* in Israel. *Biological Control* **1**, 68-74.

Mendel, Z., Assael, F., Zeidan, S. & Zehavi, A. (1998) Classical biological control of *Palaeococcus fuscipennis* (Burmeister) (Homoptera: Margarodidae) in Israel. *Biological Control* **12**, 151-157.

Mendivil-Portillo, N., Bravo-Mojica, H., Carrillo-Sanchez, J.l. (1984) Competition by *Acyrthosiphon pisum* (Harris) (Homoptera: Aphididae) of *Hippodamia convergens* Guerinmeneville and *Paranaemia vittigera* (Mannerheim) (Coleoptera: Coccinellidae). *Agrociencia* **7**, 9-23.

Mensah, R.K. & Madden, J.L. (1994) Conservation of two predator species for biological control of *Chrysophtharta bimaculata* (Col.: Chrysomelidae) in tasmanian forests. *Entomophaga* **39**, 71-83.

Mesbah, A.H. (2000) Development and efficiency of *Clitostethus arcuatus* (Coleoptera, Coccinellidae) predated on *Siphoninus phillyreae* (Hom., Aleurodidae). *Egyptian Journal of Biological Pest Control* **10**, 123-127.

Mesbah, A.H., Marie, S.S. & El-Husseini, M.M. (2008) Biocontrol agents of three lepidopterous insect pests on some crops during summer season at Khafr-Elshikh Governorate. *Egyptian Journal of Biological Pest Control* **18**, 171-176.

Meyerdirk, D. (1983) Biology of *Diomus flavifrons* (Blackburn) (Coleoptera: Coccinellidae), a citrus mealybug predator. *Environmental Entomology* **12**, 1275-1277.

Michaud, J.P. & Olsen, L.E. (2004) Suitability of Asian citrus psyllid, *Diaphorina citri*, as prey for ladybeetles. *Biocontrol* **49**, 417-431.

Michaud, J.P. (2000) Development and reproduction of ladybeetles (Coleoptera : Coccinellidae) on the citrus aphids *Aphis spiraecola* patch and *Toxoptera citricida* (Kirkaldy) (Homoptera : Aphididae). *Biological Control* **18**, 287-297.

Michaud, J.P. (2002) Biological control of Asian citrus psyllid, *Diaphorina citri* (Hemiptera : Psyllidae) in Florida: A preliminary report. *Entomological News* **113**, 216-222.

Michels Jr, G. & Behle, R. (1991) Effects of Two Prey Species on the Development of *Hippodamia sinuata* (Coleoptera: Coccinellidae) Larvae at Constant Temperatures. *Journal of Economic Entomology* **84**, 1480-1484.

Michels, G.J. & Bateman, A.C. (1986) Larval biology of two imported predators of the greenbug (Homoptera: Aphididae), *Hippodamia variegata* Goetz and *Adalia flavomaculata* Degeer (Coleoptera: Coccinellidae), under constant temperatures. *Southwestern Entomologist* **11**, 23-30.

Michels, G.J. & Flanders, R.V. (1992) Larval development, aphid consumption and oviposition for 5 imported coccinellids at constant temperature on russian wheat aphids and greenbugs. *Southwestern Entomologist* **17**, 233-243.

Milek, T.M., Simala, M. & Jelovcan, S. (2009) Ladybirds (Coleoptera: Coccinellidae) as the predators of the scale insects (Hemiptera: Coccoidea) in Croatia. *Glasilo Biljne Zastite* **9**, 163-173.

Milonas, P.G., Kontodimas, D.C. & Martinou, A.F. (2011) A predator's functional response: influence of prey species and size. *Biological Control* **59**, 141-146.

Mishra, G. &Omkar (2004) Diel rhythmicity of certain life events of a ladybird, *Propylea dissecta* (Mulsant). *Biological Rhythm Research* **35**, 269-276.

Mishra, G., Kumar, B., Shahid, M., Singh, D. & Omkar (2011) Evaluation of four co-occurring ladybirds for use as biocontrol agents of the pea aphid, *Acyrthosiphon pisum* (Homoptera: Aphididae). *Biocontrol Science and Technology* **21**, 991-997.

Mishra, G., Omkar, Kumar, B. & Pandey, G. (2012) Stage and age-specific predation in four aphidophagous ladybird beetles. *Biocontrol Science and Technology* **22**, 463-476.

Misra, M.P.P., Pawar, A.D. (1980) Biocontrol trials against the sugarcane scale insect, *Melanaspis glomerata* (Green) in eastern Uttar Pradesh pp.71-73 in Sithanantham, S. & Solayappan, A.R. (Eds.) *Biological control of sugarcane pests in India.*

Mitchels, G. & Bateman, A. (1986) Larval biology of two imported predators of the greenbug, *Hippodamia variegata* (Goeze) and *Adalia flavomaculata* Degeer, under constant temperatures. *Southwestern Entomologist* **11**, 23-30.

Mols, P.J.M. (2000) Simulation approach of the role of the pine ladybird (*Exochomus quadripustulatus* L). and the earwig (*Forficula auricularia* L). in controlling the woolly apple aphid (*Eriosoma lanigerum* Haussmann). *Proceedings of the Section Experimental and Applied Entomology of the Netherlands Entomological Society* **11**, 129-134.

Montgomery, M., Wang, H., Yao, D., Lu, W. Havill, N. & Li, G. (2002) Biology of *Scymnus ningshanensis* (Coleoptera: Coccinellidae): a predator of *Adelges tsugae* (Homoptera: Adelgidae). pp. 181-188 in *Proceedings of the Hemlock Woolly Adelgid in the Eastern United States Symposium*, East Brunswick, New Jersey, U.S.A., 5-7 February 2002.

Montgomery, M.E. & Lyon, S.M. (1995) Natural enemies of adelgids in North America: their prospect for biological control of Adelges tsugae (Homoptera: Adelgidae). pp. 89-102 *in Proceedings of the First Hemlock Woolly Adelgid Review*, U.S. Department of Agriculture, Forest Service, Northeastern Center for Forest Health Research, U.S.A, 1995.

Mora, J. (1993) Life history and voracity of *Coelophora inaequalis* (Fabricus) (Coccinellidae: Coleoptera) on *Aphis craccivora* (Aphididae: Homoptera). *in Proceedings of the 24 Annual Scientific Meeting of the Pest Management Council* of the Philippines, Cebu City (Philippines), 4-7 May 1993.

Mrosso, F., Mwatawala, M. & Rwegasira, G. (2013) Functional Responses of *Cheilomenes propingua*, *C. lunata* and *C. sulphurea* (Coleoptera: Coccinellidae) to Predation on *Aphis gossypii* (Homoptera: Aphididae) in Eastern Tanzania. *Journal of Entomology* **10**, 1812-5670.

Mukhtar, A., Ahmad, M.J., Shama, A. & Mishra, R.K. (2001) First record of coccinellid beetles (Coleoptera: Coccinellidae) on poplar, *Populus deltoides* from North India. *Indian Forester* **127**, 891-897.

Munyaneza, J. & Obrycki, J.J. (1997) Functional Response of *Coleomegilla maculata* (Coleoptera: Coccinellidae) to Colorado Potato Beetle Eggs (Coleoptera: Chrysomelidae). *Biological Control* **8**, 215-224.

Munyuli, M.B.T., Kyamanywa, S. & Luther, G.C. (2006) Feeding behavior of ladybeetles on *Aphis craccivora* Koch (Homoptera: Aphididae) in Eastern and Central Africa. *Indus Journal of Biological Sciences* **3**, 578-585.

Muralidharan, C.M. (1994) Biology and feeding potential of black beetle (*Chilocorus nigritus*), a predator on date palm scale (*Parlatoria blanchardii*). *Indian Journal of Agricultural Sciences* **64**, 270-271.

Murlidharan, C.M. (1993) Scale insects of date palm (*Phoenix dactylifera*) and their natural enemies in the date groves of Kachchh (Gujarat). *Plant Protection Bulletin* **45**, 31-33.

Nageshchandra, B. & ChannaBasavanna, G. (1983) *Stethorus keralicus* (Coleoptera: Coccinellidae) feeding on *Raoiella macfarlanei* infesting roseapple. *Acarology Newsletter* **13,** 3**.**

Nais, J. & Busoli, A.C. (2012) Morphological, behavioral and biological aspects of *Azya luteipes* Mulsant fed on *Coccus viridis* (Green). *Scientia Agricola* **69**, 81-83.

Nalepa, C., Bambara, S. & Burroughs, A. (1992) Pollen and nectar feeding by *Chilocorus kuwanae* (Silvestri) (Coleoptera: Coccinellidae). *Proceedings of the Entomological Society of Washington* **94**, 596-597.

Naranjo, S.E., Gibson, R.L. & Walgenbach, D.D. (1990) Development, survival, and reproduction of *Scymnus frontalis* (Coleoptera: Coccinellidae), an imported predator of Russian wheat aphid, at four fluctuating temperatures. *Annals of the Entomological Society of America* **83**, 527-531.

Naser, K.S.A., Al-Humiari, A.A., Elsherif, M.E. & Atif, J.Y.M. (2011) Comparative Biology and Larval Predatory Potential of the Predator, *Cryptolaemus montrouzieri* (Mulsant) when Reared on Certain Mealy Bug Species. *Egyptian Journal of Biological Pest Control* **21**, 257-260.

Navarrete, A.A.B. & Landa, E.Y. (2006) The genus *Eriopis* Mulsant, 1850 (Coleoptera, Coccinellidae) in southern Peru. *Boletin de la S.E.A.* **38**, 167-172.

Navodita, M., Pervez, A., Kumar, A. & Ramteke, P. (2011) Duration of development and survival of larvae of *Coccinella transversalis* fed on essential and alternative foods. *European Journal of Environmental Sciences* **1**, 2336-1964.

Nawanich, S., Fudsiri, S. & Chongrattanameteekul, W. (2013) Predatory efficiency study of *Curinus coeruleus* Mulsant on *Rhopalosiphum maidis* (Fitch) and *Phenacoccus manihoti* Matile-Ferrero Bangkok, Kasetsart University in *Proceedings of the 51st Kasetsart University Annual Conference*, Bangkok, Thailand, 5-7 February 2013.

Nazari, A., Sahragard, A. & Haji-Zadeh, J. (2006) Study on food consumption of *Exochomus nigromaculatus* Goeze (Coleoptera: Coccinellidae), and effect of temperature on larval food consumption. *Journal of Agricultural Sciences Islamic Azad University* **12**, 35-41.

Nedved, O. (1999) Host complexes of predaceous ladybeetles (Col., Coccinellidae). *Journal of Applied Entomology* **123**, 73-76.

Neuenschwander, P. & Ajuonu, O. (1995) Measuring host finding capacity and arrestment of natural enemies of the cassava mealybug, *Phenacoccus manihoti*, in the field. *Entomologia Experimentalis Et Applicata* **77**, 47-55.

Nohara, K. (1962) Studies on the life history and predatory behaviour of *Chilocorus kuwanae* Silvestri (Coleoptera, Coccinellidae). *Science bulletin of the Faculty of Agriculture, Kyushu University* **20**, 29-32.

Noriyuki, S. & Osawa, N. (2012) Intrinsic prey suitability in specialist and generalist *Harmonia lad*ybirds: a test of the trade-off hypothesis for food specialization. *Entomologia Experimentalis Et Applicata* **144**, 279-285.

Noriyuki, S., Osawa, N. & Nishida, T. (2011) Prey capture performance in hatchlings of two sibling *Harmonia* ladybird species in relation to maternal investment through sibling cannibalism. *Ecological Entomology* **36**, 282-289.

Nyaanga, J.G., Kamau, A.W., Pathak, R.S. & Tuey, R.K. (2012) The effect of different cereal aphid species on the performance of two coccinellid predators. *Journal of Entomology* **9**, 41-49.

Obrycki, J.J. & Kring, T.J. (1998) Predaceous Coccinellidae in biological control. *Annual Review of Entomology* **43**, 295-321.

Obrycki, J.J. & Orr, C.J. (1990) Suitability of three prey species for Nearctic populations of *Coccinella septempunctata*, *Hippodamia variegata*, and *Propylea quatuordecimpunctata* (Coleoptera: Coccinellidae). *Journal of Economic Entomology* **83**, 1292-1297.

Obrycki, J.J. & Tauber, M.J. (1981) Phenology of three coccinellid species: thermal requirements for development. *Annals of the Entomological Society of America* **74**, 31-36.

Ofuya, T. (1986) Predation by *Cheilomenes vicina* (Coleoptera: Coccinellidae) on the cowpea aphid, *Aphis craccivora* (Homoptera: Aphididae): Effect of prey stage and density. *Entomophaga* **31**, 331-335.

Ofuya, T. (1990) Observation on the biology of *Cheilomenes vicina* (Mulsant)(Coleoptera: Coccinellidae), a predator of the cowpea aphid, *Aphis craccivora* Koch (Homoptera: Aphididae) in Nigeria. *Nigerian Journal of Science* **24**, 171-173.

Ofuya, T.I. (1995) Studies on the capability of *Cheilomenes lunata* (Fabricius) (Coleoptera: Coccinellidae) to prey on the cowpea aphid, *Aphis craccivora* Koch (Homoptera: Aphididae) in Nigeria. *Agriculture, Ecosystems & Environment* **52**, 35-38.

Ogas, F. M. (1970) Biology and morphology of *Eriopis connexa* Germar 1824 and of *Adalia bipunctata* Linnaeus 1758 (Coleoptera). *Publicaciones del Centro de Estudios Entomológicos* **10,** 43-56.

Oliveira, E.E., Oliveira, C.L., Sarmento, R.,d.A. Fadini, M.A.M. & Moreira, R. L. (2006) Aspectos biológicos do predador *Cycloneda sanguinea* (Linnaeus, 1763) (Coleoptera: Coccinellidae) alimentado com *Tetranychus evansi* (Baker e Pritchard, 1960) (Acari: Tetranychidae) e *Macrosiphum euphorbiae* (Thomas, 1878) (Homoptera: Aphididae). *Bioscience journal* **21**, 33-39.

Oliveira, N.C.d., Wilcken, C.F. & Matos, C.A.O.d. (2004a) Biological cycle and predation of three coccinellid species (Coleoptera, Coccinellidae) on giant conifer aphid *Cinara atlantica* (Wilson) (Hemiptera, Aphididae). *Revista Brasileira de Entomologia* **48**, 529-533.

Oliver, T.H., Timms, J.E.L., Taylor, A. & Leather, S.R. (2006) Oviposition responses to patch quality in the larch ladybird *Aphidecta obliterata* (Coleoptera : Coccinellidae): effects of aphid density, and con- and heterospecific tracks. *Bulletin of Entomological Research* **96**, 25-34.

Omkar & Pervez A. (2002) Ecology of aphidophagous ladybird beetle, *Coccinella septempunctata* (Coleoptera: Coccinellidae): a review. *Journal of Aphidology* **16**, 175-201.

Omkar & Gyanendra, K. (2013) Responses of an aphidophagous ladybird beetle, *Anegleis cardoni*, to varying densities of *Aphis gossypii*. *Journal of Insect Science* **13**, 1-12.

Omkar & James, B.E. (2004) Influence of prey species on immature survival, development, predation and reproduction of *Coccinella transversalis* Fabricius (Col., Coccinellidae). *Journal of Applied Entomology* **128**, 150-157.

Omkar & Pervez A. (2001) Prey preference of a ladybeetle, *Micraspis discolor* (Fabricius). *Entomon* **26**, 195-197.

Omkar & Pervez, A (2011a) Ecology of aphidophagous ladybird *Propylea* species: a review. *Journal of Asia Pacific Entomology* **14**, 357-365.

Omkar & Pervez, A. (2000) New record of coccinellids from Uttar Pradesh II. *Journal of Advanced Zoology* **21**, 43-47.

Omkar & Pervez, A. (2003) Ecology and Biocontrol potential of a scale-predator, *Chilocorus nigritus*. *Biocontrol Science and Technology* **13**, 379-390.

Omkar & Pervez, A. (2004) Comparative demographics of a generalist predatory ladybird on five aphid prey: a laboratory study. *Entomologia Sinica* **11**, 211-218.

Omkar (2006) Suitability of different foods for a generalist ladybird, *Micraspis discolor* (Coleoptera: Coccinellidae). *International Journal of Tropical Insect Science* **26**, 35-40.

Omkar, Gyanendra, K. & Jyotsna, S. (2009) Performance of a predatory ladybird beetle, *Anegleis cardoni* (Coleoptera: Coccinellidae) on three aphid species. *European Journal of Entomology* **106**, 565-572.

Omkar, Gyanendra, K. & Jyotsna, S. (2011b) Monotypic prey-mediated development, survival and life table attributes of a ladybird beetle *Anegleis cardoni* (Coleoptera: Coccinellidae) on different aphid species. *International Journal of Tropical Insect Science* **31**, 162-173.

Omkar, Mishra, G., Srivastava, S., Gupta, A.K. & Singh, S.K. (2005b) Reproductive performance of four aphidophagous ladybirds on cowpea aphid, *Aphis craccivora* Koch. *Journal of Applied Entomology* **129**, 217-220.

Omkar, Pervez, A. & Singh, S.K. (2005a) Development and immature survival of two aphidophagous ladybirds, Coelophora biplagiata and Micraspis discolor. *Insect Science* **12**, 375-379.

Omkar, Singh, S.K. & Mishra, G. (2010) Multiple matings affect the reproductive performance of the aphidophagous ladybird beetle, *Coelophora saucia* (Coleoptera: Coccinellidae). *European Journal of Entomology* **107**, 177-182.

Orlinsky, A.D. &. Izhevsky, S.S (1987) The life history of *Nephus reunioni* (Coleoptera, Coccinellidae) an introduced predator of mealybugs. *Zoologichesky Zhurnal* **66**, 701-707.

Orr, C.J. & Obrycki, J.J. (1990) Thermal and dietary requirements for development of *Hippodamia parenthesis* (Coleoptera: Coccinellidae). *Environmental Entomology* **19**, 1523-1527.

Osawa, N. & Ohashi, K. (2008) Sympatric coexistence of sibling species *Harmonia yedoensis* and *H. axyridis* (Coleoptera: Coccinellidae) and the roles of maternal investment through egg and sibling cannibalism. *European Journal of Entomology* **105**, 445-454.

Ozturk, N. & Ulusoy, M.R. (2009) Pests and natural enemies determined in pomegranate orchards in Turkey. *Acta Horticulturae* **818**, 277-284.

Padmaja, C., Babu, T.R., Reddy, D. & Sriramulu, M. (1995) Biology and predation potential of *Scymnus coccivora* Aiyar (Coleoptera: Coccinellidae) on mealybugs. *Journal of Entomological Research* **19**, 79-81.

Palmeri, V., Russ, O.A., Longo, S. (1996.) On food preferences of *Calvia quatuordecimguttata* and *Sospita vigintigutt*ata (Coleoptera Coccinellidae) in alder woods of southern Italy. pp. 528 in *Procedings of the XX International Congress of Entomology,* Firenze, Italy, 15-31 August 1996,

Parry, W.H. (1992) A comparison of *Aphidecta obliteratae* (L.) (Col., Coccinellidae) populations feeding on *Elatobium abietinum* (Walker) and on *Adelges cooleyi* (Gillette). *Journal of Applied Entomology* **114**, 280-288.

Pasqualini, E. & Antropoli, A. (1994) *Stethorus punctillum*. Informatore Fitopatologico **44**, 33-36.

Patel, C.B., Rai, A.B., Pastagia, J.J., Patel, H.M. & Patel, M.B. (1996) Biology and predator potential of *Serangium parcesetosum* Sci. (Coleoptera: Coccinellidae), of sugarcane whitefly (*Aleurolobus barodensis* Mask.). *Gujarat Agricultural University Research Journal* **22**, 56-60.

Pena, J.E., Rodrigues, J.C.V., Roda, A., Carrillo, D. & Osborne, L.S. (2009) Predator-prey dynamics and strategies for control of the red palm mite (*Raoiella indica*) (Acari: Tenuipalpidae) in areas of invasion in the Neotropics. IOBC/WPRS Bulletin **50**, 69-79.

Perez, N.E., Morales, E.J.T. & Nafria, J.M.N. (1992) Coccinellid (Col.: Coccinellidae) predators of aphids (Hom.: Aphididae) on cultivated plants in Leon. *Boletin de Sanidad Vegetal, Plagas* **18**, 765-775.

Pervez, A. (2004a) Functional and numerical responses of *Propylea dissecta* (Col., Coccinellidae). *Journal of Applied Entomology* **128**, 140-146.

Pervez, A. (2004b) Predaceous Coccinellids in India: Predator-Prey Catalogue (Coleoptera: Coccinellidae). *Oriental Insects* **38**, 27-61.

Peter, C. (1988) New records of natural enemies associated with the brown planthopper, *Nilaparvata lugens* (Stal). *Current Science* **57**, 1087-1088.

Peterson, P.G. (1993) *The potential ability of* Stethorus bifidus *(Kapur) to regulate populations of* Tetranychus lintearius *(Dufour).* Master's Thesis. Massey University, Tennent Dr, New Zealand.

Peterson, P.G., McGregor, P.G. & Springett, B.P. (2000) Density dependent prey-feeding time of *Stethorus bifidus* (Coleoptera: Coccinellidae) on *Tetranychus lintearius* (Acari : Tetranychidae). *New Zealand Journal of Zoology* **27**, 41-44.

Phaloura, S.P.S. & Singh, T. (1993) Biological observations on three species of aphidophagous coccinellids of genus *Harmonia* Mulsant. *Journal of Insect Science* **6**, 246-249.

Phaloura, S.P.S. & Tarlok, S. (1992) Biological observations on *Aiolocaria hexaspilota* (Hope) (Coleoptera: Coccinellidae) - a predator on the immature stages of a chrysomelid (Coleoptera) - *Chrysomela chlorian* Maulik. *Journal of Ecobiology* **4**, 33-37.

Phoofolo, M.W., Giles, K.L. & Elliott, N.C. (2008) Larval life history responses to food deprivation in three species of predatory lady beetles (Coleoptera : Coccinellidae). *Environmental Entomology* **37**, 315-322.

Pinnock, D., Hagen, K., Cassidy, D., Brand, R., Milstead, J. & Tasson, R. (1978) Integrated pest management in highway landscapes. *California Agriculture* **32**, 33-34.

Pluke, R.W.H., Escribano, A., Michaud, J.P. & Stansly, P.A. (2005) Potential impact of lady beetles on *Diaphorina citri* (Homoptera : Psyllidae) in Puerto Rico. *Florida Entomologist* **88**, 123-128.

Ponsonby, D.J. & Copland, M.J.W. (2000) Maximum feeding potential of larvae and adults of the scale insect predator, *Chilocorus nigritus* with a new method of estimating food intake. *Biocontrol* **45**, 295-310.

Ponsonby, D.J. & Copland, M.J.W. (2007) Aspects of prey relations in the coccidophagous ladybird *Chilocorus nigritus* relevant to its use as a biological control agent of scale insects in temperate glasshouses. *Biocontrol* **52**, 629-640.

Poorani, J. (2004) An annotated checklist of the Coccinellidae (Coleoptera) of the Indian subregion. *Oriental Insects* **38**, 1-90.

Poorani, J. (2013) *FactSheets on Agriculturally Important Insects*. National Bureau of Agriculturally Important Insects. Available online at http://www.nbaii.res.in/Featured_insects/index.php.

Poorani, J., Ślipiński, S.A. & Booth, R. (2008) revision of the genus *Synona* Pope (Coleoptera: Coccinellidae, Coccinellini). *Annales Zoologici* **58**, 350–362.

Pope, R. (1981) 'Rhyzobius ventrails'(Coleoptera: Coccinellidae), its constituent species, and their taxonomy and historical roles in biological control. *Bulletin of Entomological Research* **71**, 19-32.

Pope, R.D. & Lawrence, J.F. (1990) A review of Scymnodes Blackburn, with the description of a new Australian species and its larva (Coleoptera: Coccinellidae). *Systematic Entomology* **15**, 241-252.

Pope, R.D. (1961) A review of the Pharini (Coleoptera : Coccinellidae). *Journal of Natural History* **4**, 627-640.

Pour, A.A. & Shakarami, J. (2011) Study of ladybirds (Col:Coccinellidae) in Khorramabad district and the first report of *Hyperaspis quadrimaculata* (Redtenbacher 1844) for Iranian fauna. *Life Science Journal-Acta Zhengzhou University Overseas Edition* **8**, 488-495.

Pour, A.A. & Shakarami, J. (2012) Recognition of ladybird fauna (Col.: Coccinellidae) in the Alfalfa fields of Khorramabad. *JAPS, Journal of Animal and Plant Sciences* **22**, 939-943.

Pugh, A.R. (2013) *The potential of* Cleobora mellyi *(southern ladybird) as a biological control agent of the invasive tomato-potato psyllid (*Bactericera cockerelli*) on potatoes.* Master's Thesis. Lincoln University, UK.

Putman, W.L. (1955) Bionomics of *Stethorus punctillum* Weise (Coleoptera: Coccinellidae) in Ontario. *The Canadian Entomologist* **87**, 9-33.

Puttaswamy & Channabasavanna, G.P. (1977) Biology of *Stethorus pauperculus* Weise (Coleoptera – Coccinellidae), a predator of mites. *Mysore Journal of Agricultural Sciences* **11**, 81-89.

Qi, Q.L. (1989) Study on the bionomics of *Physokermes jezoensis* Siraiwa and its control. *Insect Knowledge* **26**, 23-24.

Qureshi, J.A. & Stansly, P.A. (2011) Three Homopteran Pests of Citrus as Prey for the Convergent Lady Beetle: Suitability and Preference. *Environmental Entomology* **40**, 1503-1510.

Rachappa, V., Rajendra, H., Kulkarni, K.A. & Patil, R.K. (2002) Biology and feeding potential of *Synia melanaria* Mulsant on *Coptosoma ostensum* Distant. *Myforest* **38**, 145-150.

Ragab, M. (1995) Adaptation of *Rodolia cardinalis* (Mulsant)(Col., Coccinellidae) to *Icerya aegyptiaca* (Douglas)(Hom., Margrodidae) as compared with *Icerya purchasi* Mask. *Journal of Applied Entomology* **119**, 621-623.

Rahman, M.J. (1993) A new report of lady beetle *Scymnus latemaculatus* Mots. (Coleoptera: Coccinellidae) from Bangladesh. *Bangladesh Journal of Entomology* **3**, 89-90.

Rai, M.K., Ramamurthy, V.V. & Singh, P.K. (2002) Bionomics of the coccinellid predator *Micraspis discolor* (Fabricius). *Shashpa* **9**, 121-125.

Raimundo, A.A.C. & Alves, M.L.G. (1986) *Revisão dos Coccinelídeos de Portugal*. Évora, Universidade de Évora.

Rajesh, S., Anil, S., Meenu, S. & Sharma, K.C. (2011) Seasonal abundance of some coccinellid predators associated with *Aphis fabae scopoli* infesting *Solanum nigrum* in the mid hill region of Himachal Pradesh. *Journal of Insect Science* **24**, 166-169.

Rangaswamy, H. (1976) *Stethorus keralicus* Kapur,(Coleoptera: Coccinellidae)-a predator of arecanut palm mite. *Current Research* **5**, 27-28.

Raros, E.S. & Haramoto, F.H. (1974) Biology of *Stethorus siphonulus* Kapur (Coccinellidae: Coleoptera), a predator of spider mites, in Hawaii *in Proceedings of the Hawaiian Entomological Society* **21**, 457-465.

Rasheed, S., Mahmood, R. & Mohyuddin, A.I. (1986) Notes on biology and population trends of *Sumnius renardi* Weise and *Rodolia fumida* Muls. (Coleoptera: Coccinellidae) and their potential as biocontrol agents of *Drosicha stebbingi* Green (Homoptera: Margarodidae). *Proceedings of Pakistan Congress of Zoology* **6**, 137-142.

Rashid, M.M.U., Khattak, M.K., Abdullah, K., Amir, M., Tariq, M. & Nawaz, S. (2012) Feeding potential of *Chrysoperla carnea* and *Cryptolaemus montrouzieri* on cotton mealybug, *Phenacoccus solenopsis*. *JAPS, Journal of Animal and Plant Sciences* **22**, 639-643.

Rattanapun, W. (2012) Biology and potentiality in biological control of *Micraspis discolor* (Fabricius) (Coleoptera: Coccinellidae). *Communications in agricultural and applied biological sciences* **77**, 541-548.

Rattanatip (2008) Comparative biology and life table of *Stethorus pauperculus* (Weise) and *S. siphonulus* Kapur (Coleoptera: Coccinellidae) fed on *Tetranychus urticae* Koch (Acari: Tetranychidae) in Thailand. *Thai Journal of Agricultural Science* **41**, 117-126.

Rawat R.R. & Pawar, A.D. (1993) Predation potential of coccinellidae *Chilocorus bijugus* Mulsant on the San Jose scale *Quadraspidiotus perniciosus* (Comstock). *Journal Of Advanced Zoology*. **14**, 28-32

Rawat, R.R. & Modi, B.N. (1969) Studies on *Nephus regularis* (Coleoptera-Coccinellidae) as predator of striped mealybug in Madhya Pradesh (India). *Annals of the Entomological Society of America* **62**, 953- 956.

Rawat, U., Sangal, S. & Pawar, A. (1992) Biology of *Chilocorus bijugus* Mulsant (Coleoptera: Coccinellidae), Predator of San Jose scale, *Quadraspidiotus perniciosus* (Comstock). *Biological Control* **6**, 97-100.

Rawat, U.S., Thakur, J.N. & Pawar, **A.D.** (1988) Introduction and establishment of *Chilocorus bijugus* Mulsant and *Pharaoscymnus flexibilis* Mulsant, predatory beetles of San Jose scale at Thanedhar areas in Himachal Pradesh. *Current Science* **57**, 1250-1251.

Rekha, B.S., Ramkumar, J., Kandibane, M., Raguraman, S. & Swamiappan, M. (2009) Diversity of coccinellids in cereals, pulses, vegetables and in weeded and partially weeded rice-cowpea ecosystems in Madurai District of Tamil Nadu. *Madras Agricultural Journal* **96**, 251-264.

Ren, S., Guo, Z., Xiong, J. & He, Y. (2001) Predation of *Chilocorus bijugus* (Col.: Coccinellidae) to *Unaspis yanonensis* (Hom.: Diaspidae). *Acta Ecologica Sinica* **21**, 1602-1606.

Ren, S., Stansly, P.A. & Liu, T.X. (2002) Life history of the whitefly predator *Nephaspis oculatus* (Coleoptera: Coccinellidae) at six constant temperatures. *Biological Control* 23, 262-268.

Ren, S.X., Guo, Z.Z., Xiong, J.W. & He, Y.F. (1990) A life history study of *Chilocorus bijugus* [Col.: Coccinellidae], an important predator of the arrowhead scale in Guizhou [China]. *Chinese Journal of Biological Control (China)* **6,** 71-73.

Ren, Y. (2007) Research on preying function and searching effect of *Hippodamia tredecimpunctata* to *Aphis* sp. *Journal of Jilin Agricultural University* **29**, 616-619.

Resende, A.L.S., Silva, E.E., Silva, V.B., Ribeiro, R.L.D., Guerra, J.G.M. & Aguiar-Menezes, E.L. (2006) First record of *Lipaphis pseudobrassicae* Davis (Hemiptera: Aphididae) and its association with predator insects, parasitoids and ants in kale (Cruciferae) in Brazil. *Neotropical Entomology* **35**, 551-555.

Reyd, G. & Leru, B. (1992) Impact of Predation by Coccinellidae larvae on colonies of the mealybug *Phenacoccus manihoti* in crop lands. *Acta Oecologica-International Journal of Ecology* **13**, 181-191.

Reyd, G. & Ru, B.l. (1992) Predation by *Hyperaspis raynevali* and *Exochomus flaviventris* larvae (Col. Coccinellidae) on cassava mealybug *Phenacoccus manihoti* (Hom. Pseudococcidae) colonies. Experimental study in the laboratory. *Entomophaga* **37**, 317-325.

Reyd, G., Gery, R., Ferran, A., Iperti, G. & Brun, J. (1991) Voracity of *Hyperaspis raynevali* (Col.: Coccinellidae) - a predator of cassava mealybug, *Phenacoccus manihoti* (Hom.: Pseudococcidae). *Entomophaga* **36**, 161-171.

Ricci, C. & Ponti, L. (2005) Seasonal food of *Ceratomegilla notata* (Coleoptera: Coccinellidae) in mountain environments of Northern Italian Alps. *European Journal of Entomology* **102**, 527.

Richards, A.M. (1980) Defensive adaptations and behaviour in *Scymnodes lividigaster* (Coleoptera: Coccinellidae). *Journal of Zoology* **192**, 157-168.

Richards, A.M. (1981) *Rhyzobius ventralis* (Erichson) and *R. forestieri* (Mulsant)(Coleoptera: Coccinellidae), their biology and value for scale insect control. *Bulletin of Entomological Research* **71**, 33-46.

Richards, A.M. (1985) Biology and defensive adaptations in *Rodatus major* (Coleoptera: Coccinellidae) and its prey, *Monophlebulus pilosior* (Hemiptera: Margarodidae). *Journal of Zoology* **205**, 287-295.

Rittner, O.Z. & Nir, A. (2013) First record of *Myrrha octodecimguttata* (Coleoptera: Coccinellidae) and *Epuraea ocularis* (Coleoptera: Nitidulidae) from Israel. *Zootaxa* **3**, 349-350.

Roger, C., Coderre, D. & Boivin, G. (2000) Differential prey utilization by the generalist predator *Coleomegilla maculata lengi* according to prey size and species. *Entomologia Experimentalis Et Applicata* **94**, 3-13.

Rondon, S.I., Price, J.F. & Cantliffe, D.J. (2006) Developmental time, reproduction, and feeding of two subspecies of *Coleomegilla maculata* (Coleoptera: Coccinellidae) in the laboratory. *Florida Entomologist* **89**, 85-88.

Rosen, D. & Gerson, U. (1965) Field studies of *Chilocorus bipustulatus* on citrus Israel. *Annales Des Epiphyties* **16**, 71-76.

Sabaghi, R., Sahragard, A. & Hosseini, R. (2011a) Area dependent searching efficiency of *Scymnus syriacus* (Col.: Coccinellidae) feeding on *Aphis craccivora* (Hem.: Aphididae). *Journal of Entomological Society of Iran* **31**, 1-16.

Sabaghi, R., Sahragard, A. & Hosseini, R. (2011b) Functional and numerical responses of *Scymnus syriacus* Marseul (Coleoptera: Coccinellidae) to the black bean aphid, *Aphis fabae* Scopoli (Hemiptera: Aphididae) under laboratory conditions. *Journal of Plant Protection Research* **51**, 423-428.

Sadeghi, S.E., Mojib, Z., Jalali, J. & Haji, J. (2004) Investigation on the biology of lady beetle *Oenopia conglobata* (L.) on poplar aphid *Chaitophorus leucomelas* (Koch) in laboratory conditions. *Natural Resources* **62**, 20-24.

Saengyot, S. & Burikam, I. (2011) Host plants and natural enemies of papaya mealybug, *Paracoccus marginatus* (Hemiptera: Pseudococcidae) in Thailand. *Thai Journal of Agricultural Science* **44**, 197-205.

Saengyot, S. & Burikam, I. (2012) Development and growth ratio of predaceous coccinellid, *Sasajiscymnus quinquepunctatus* (Weise) on papaya mealybug, *Paracoccus marginatus* Williams & Granara de Willink. *Kasetsart Journal, Natural Sciences* **46**, 418-426.

Saharaoui, L., Biche, M. & Hemptinne, J.L. (2010) Dynamics of ladybird communities (Coleoptera, Coccinellidae) and interactions with their prey on date palms in Biskra (South-East Algeria). *Bulletin de la Société Zoologique de France* **135**, 265-280.

Saharaoui, L., Gourreau, J.M. & Iperti, G. (2001) Bioecological parameters of some aphidophagous coccinellids in Algeria (Coleoptera, Coccinellidae). *Bulletin de la Société Zoologique de France* **126**, 351-373.

Saharia, D. (1980) Some aspects of the biology of coccinellid predators associated with *Aphis craccivora* Koch on cowpea. *Journal of Research, Assam Agricultural University* **1**, 82-89.

Sakuratani, Y. & Ito, F. (1995) Aestivating site of *Chilocorus rubidus* Hope (Coleoptera: Coccinellidae) in Central Japan. *Applied Entomology and Zoology* **30**, 375-376.

Salas-Araiza, M.D., Jones, R.W., Montesinos-Silva, G., Salazar-Solis, E., Parra-Negrete, L.A., Martinez-Jaime, O., Ramirez-Malagon, R. & Flores-Mejia, S. (2008) Population Dynamics of the Agave Scale, *Acutaspis agavis* (Hemiptera: Diaspididae), on *Agave tequilana* var. azul (Agavaceae) in Central Mexico. *Southwestern Entomologist* **33**, 289-298.

Salisbury, A. & Booth, R.G. (2004) *Rodolia cardinalis* (Mulsant), the Vedalia ladybird (Coleoptera: Coccinellidae) feeding on *Icerya purchasi* Maskell, cottony cushion scale (Hemiptera: Margarodidae) in London gardens. *British Journal of Entomology and Natural History* **17**, 103-104.

Samways, M. (1984) Biology and economic value of the scale predator, *Chilocorus nigritus* (F.)(Coccinellidae). *Biocontrol News and Information* **5**, 91-105.

Samways, M.J. & Wilson, S.J. (1988) Aspects of the feeding behavior of *Chilocorus nigritus* (F.) (Col, Coccinellidae) relative to its effectiveness as a biocontrol agent. *Journal of Applied Entomology* **106**, 177-182.

Santos, G.P. & Pinto, A.C.D. (1981) Biology of *Cyclonea sanguinea* and its association with aphids in mango seedlings. *Pesquisa Agropecuaria Brasileira* **16**, 473-476.

Santos, S.A.P., Pereira, J.A., Raimundo, A., Torres, L.M. & Nogueira, A.J.A. (2010) Seasonal synchrony between *Saissetia oleae* and coccinellid species in Portuguese olive groves in different management systems. *Bulletin of Insectology* **63**, 51-57.

Santos, S.A.P., Pereira, J.A., Torres, L.M., & Nogueira, A.J.N. (2009) Voracity of coccinellid species on different phenological stages of the olive pest *Saissetia oleae* (Homoptera, Coccidae). *Applied Ecology and Environmental Research* **7**, 359-365.

Santos, S.A.P., Raimundo, A., Bento, A. & Pereira, J.A. (2012) Species abundance patterns of coccinellid communities associated with olive, chestnut and almond crops in north-eastern Portugal. *Agricultural and Forest Entomology* 14, 376-382.

Sarhan, A., Mandour, N., El-Basha, N.A. & Abdel-Motaal, D.S. (2011) Effect of different preys on immature and adult stages of *Hippodamia variegata* (Goeze)(Coleoptera: Coccinellidae). *Egyptian Journal of Biological Pest Control* **21**, 297-304.

Sarmento, R.A., Pallini, A., Venzon, M., Souza, O.F.F.d., Molina-Rugama, A.J. & Oliveira, C.L.d. (2007) Functional response of the predator *Eriopis connexa* (Coleoptera: Coccinellidae) to different prey types. *Brazilian Archives of Biology and Technology* **50**, 121-126.

Sasaji, H. & McClure, M. (1997) Description and distribution of *Pseudoscymnus tsugae* sp. nov.(Coleoptera: Coccinellidae), an important predator of hemlock woolly adelgid in Japan. *Annals of the Entomological Society of America* **90**, 563-568.

Karatay, Z.S. & Karaca, I. (2013) Temperature-dependent development of *Chilocorus bipustulatus* (L.) (Coleoptera: Coccinellidae) on *Aspidiotus nerii* Bouche (Hemiptera: Diaspididae) under laboratory conditions. *Turkiye Entomoloji Dergisi-Turkish Journal of Entomology* **37**, 185-194.

Satyanarayanamurthy, M. & Narayana, K.L. (1986) Biology of *Cryptolaemus montrouzieri* Muls.(Coleoptera: Coccinellidae), a predatory beetle of mealybugs. *Indian Grape Journal* **2**, 40-52.

Saurabh, S., Saikia, D.K., Badal, B. & Dutta, S.K. (2007) Population fluctuations of sugarcane woolly aphid, *Ceratovacuna lanigera* Zehntner (Homoptera: Aphididae), and its natural enemies in plant and ratoon sugarcane crops in Assam. *Journal of Biological Control* **21**, 241-246.

Scandrett, E. & Gimingham, C.H. (1991) The effect of heather beetle *Lochmaea suturalis* on vegetation in a wet heath in NE Scotland. *Holarctic Ecology* **14**, 24-30.

Schembri, S. (1993) The coccinellid fauna of the Maltese Islands (central Mediterranean): an annotated list (Coleoptera Coccinellidae). *Bollettino della Societa Entomologica Italiana* **125**, 45-52.

Selvakumaran, S., K. Mini & Devasahayam, S. (1996) Natural enemies of two major species of scale insects infesting black pepper (*Piper nigrum* L.) in India. *Pest Management in Horticultural Ecosystems* **2**, 79-83.

Sem'yanov, V.P. & Vaghina, N.P. (2003) Effect of the trophic diapause on fecundity and longevity of a tropical Coccinellid, *Harmonia sedecimnotata* (Fabr.). (Coleoptera, Coccinellidae). *Entomologicheskoe Obozrenie* **82**, 3-5.

Sem'yanov, V.P. (1996) Lady beetles (Coleoptera, Coccinellidae) of Leningrad region orchards (fauna, biology and their role in pest population dynamics) pp. 208-211 in Polesny, F., Muller, W. & Olszak, R. W. Iobc/Wprs (Eds.). *Proceedings of the International Conference on Integrated Fruit Production*, Cedzyna, Poland, 18 August – 29 September, 1995.

Sem'yanov, V.P. (2006) On the change of habitat in aphidophagous coccinellids (Coleoptera, Coccinellidae). *Entomologicheskoe Obozrenie* **85**, 35-38.

Sem'yanov, V.P. (2007) Tropical ladybirds for controlling aphids in greenhouses. *Ochrona Roslin* **52**, 28-32.

Sem'yanov, V.P. (1980) Biology of the coccinellid *Calvia quatuordecimguttata* L. (Coleoptera, Coccinellidae). *Entomologicheskoe Obozrenie* **59**, 757-763

Sem'yanov, V.P. (2008) Coccinellidae against aphids. *Zashchita i Karantin Rastenii* **1**, 30.

Sengonca, C. & Arnold, C. (2003) Development, predation and reproduction by *Exochomus quadripustulatus* L. (Coleoptera: Coccinellidae) as predator of *Pulvinaria regalis* Canard (Homoptera: Coccidae) and its coincidence with the prey in the field. *Zeitschrift für Pflanzenkrankheiten und Pflanzenschutz* **110**, 250-262.

Sengonca, C., F. Al-Zyoud & Blaeser, P. (2004) Life table of the entomophagous ladybird *Serangium parcesetosum* Sicard (Coleoptera : Coccinellidae) by feeding on *Bemisia taba*ci (Genn.) (Homoptera : Aleyrodidae) as prey at two different temperatures and plant species. *Zeitschrift Fur Pflanzenkrankheiten Und Pflanzenschutz-Journal of Plant Diseases and Protection* **111**, 598-609.

Shaaban, A.R., Hafez, A.A. & Badary, H. (2003) Survey and dynamics of natural enemies of the Mediterranean black scale, *Saissetia oleae* (Homoptera: Coccidae) in Egypt. *Egyptian Journal of Agricultural Research* **81**, 113-123.

Shama, A. & Shuja, U. (1998) Bioecology of *Synia melanaria* Mulsant (Coleoptera: Coccinellidae), predating on *Coptosoma ostensum* distant. *Journal of Entomological Research* **22**, 329-336.

Shama, A. (2000) Bioecology of the coccinellid, *Anegleis cardoni* (Weise) (Coleoptera: Coccinellidae), an important predator of aphids, coccids and pseudococcids. *Journal of Entomological Research* **24**, 55-62.

Sharma, D.C., Rawat, U.S. & Pawar, A.D. (1990) Effect of temperature and humidity on the development, longevity and predatory potential of *Pharoscymnus flexibilis* Muls. on San Jose scale. *Journal of Biological Control* **4**, 11-14.

Sharmila, M., Devikarani, K. & Singh, T. (2010) Seasonal incidence and Predatory potential of *Harmonia dimidiate* (Fab.) in relation to *Tuberculatum nervatus* Chakrabarti and Raychaudhuri. *Annals of Plant Protection Sciences* **18**, 340-343.

She, H.N., Odebiyi, J. & Herren, H. (1984) The biology of *Hyperaspis jucunda* (Coleoptera, Coccinellidae), an exotic predator of the cassava mealybug *Phenacoccus manihoti* (Hom: Pseudococcidae) in Southern Nigeria. *Entomophaga* **29**, 87-93.

Sheppard, S.K., Bartlett, H., Memmott, J. & Symondson, W.O.C. (2005) Alien ladybirds invade Hawaiian ecosystems. *Antenna* **29**, 105-110.

Shuqin, Y. (1994) Study on the Biological Characteristics of *Aiolocaria miralilis* (Motschulsky). *Journal of Jilin Agricultural University* **1994**, 01

Silva, R., Cruz, I., Zanuncio, J., Figueiredo, M., Canevari, G., Pereira, A. & Serrão, J. (2013a) Biological aspects of *Eriopis connexa* (Germar)(Coleoptera: Coccinellidae) fed on different insect pests of maize (*Zea mays* L.) and sorghum [*Sorghum bicolor* L.(Moench.)]. *Brazilian Journal of Biology* **73**, 419-424.

Silva, R.B., Cruz, I., Lourdes, Figueiredo, M.L.C., Tavares, W.S., Ferreira C.F. & Redoan, A.C. (2010a) Fecundidade e Fertilidade de *Eriopis connexa* (Germar) (Coleoptera: Coccinellidae) com Ovos de *Diatraea saccharalis* Fabr. (Lepidoptera: Crambidae) in *Proceedings of the XXVIII Congresso Nacional de Milho e Sorgo* organized by the Associação Brasileira de Milho e Sorgo, Goiânia, Brasil 2010.

Silva, R.B., Cruz, I., Zanuncio, J.C., Figueiredo, M.d.L.C., Zanuncio, T.V. & Serrao, J.E. (2013b) *Spodoptera frugiperda* (J.E. Smith) (Lepidoptera: Noctuidae) eggs as alternative food for rearing of lady beetles *Eriopis connexa* (Germar) (Coleoptera: Coccinellidae). *Biological Control* **64**, 101-105.

Silva, R.B., Zanuncio, J.C., Serrão, J.E., Lima, E.R., Figueiredo, M.L.C. & Cruz, I. (2009) Suitability of different artificial diets for development and survival of stages of the predaceous ladybird beetle *Eriopis connexa*. *Phytoparasitica* **37**, 115-123.

Silva, R.B.d., Cruz, I., Figueiredo, M.d.L.C. & Tavares, W.d.S. (2010b) Development of *Coleomegilla maculata* De Geer (Coleoptera: Coccinellidae) with prey and artificial diet. *Revista Brasileira de Milho e Sorgo* **9**, 13-26.

Silva, R.B.D., Cruz, I., Figueiredo, M.D.L.C., Tavares, W.D.S., Serrão, J.E. & Zanuncio, J.C. (2013d) Development and Reproduction of *Olla v-nigrum* (Coleoptera: Coccinellidae) fed *Anagasta kuehniella* (Lepidoptera: Pyralidae) Eggs Supplemented with an Artificial Diet. *Florida Entomologist* **96**, 850-858.

Simmons, A.M. & Legaspi, J.C. (2004) Survival and predation of *Delphastus catalinae* (Coleoptera : Coceinellidae), a predator of whiteflies (Homoptera : Aleyrodidae), after exposure to a range of constant temperatures. *Environmental Entomology* **33**, 839-843.

Simmons, A.M. & Legaspi, J.C. (2007) Ability of *Delphastus catalinae* (Coleoptera: Coccinellidae), a predator of whiteflies (Homoptera: Aleyrodidae), to survive mild winters. *Journal of Entomological Science* **42**, 163-173.

Simmons, A.M., Legaspi, J.C. & Legaspi, B.C. (2008) Responses of *Delphastus catalinae* (Coleoptera : Coccinellidae), a predator of whiteflies (Hemiptera : Aleyrodidae), to relative humidity: Oviposition, hatch, and immature survival. *Annals of the Entomological Society of America* **101**, 378-383.

Simmons, A.M., Legaspi, J.C. & Legaspi, B.C. (2012) Adult survival of *Delphastus catalinae* (Coleoptera: Coccinellidae), a predator of whiteflies (Hemiptera: Aleyrodidae), on diets of whiteflies, honeydew, and honey. *Environmental Entomology* **41**, 669-675.

Singh, R. & Malhotra, R.K. (1979) Some studies on the biology of *Coccinella undecimpunctata memetriesi* Muls. – predator of mustard aphid. *Current Science* **48**, 904-905.

Singh, S.S. (1999) Studies on the occurrence of natural enemies of rice yellow stem borer. *Annals of Agricultural Research* **20**, 125-126.

Singh, T.K., Shah, M.A.S. & Devikarani, K. (2012) Spatial distribution of three species of coccinellid predators on oak plant. *Uttar Pradesh Journal of Zoology* **32**, 171-180.

Ślipiński, A. & Giorgi, J.A. (2006) Revision of the Australian Coccinellidae (Coleoptera). Part 6. Tribe Chilocorini. *Annales Zoologici* **56**, 265-304.

Sloggett, J.J. & Lorenz, M.W. (2008) Egg composition and reproductive investment in aphidophagous ladybird beetles (Coccinellidae: Coccinellini): egg development and interspecific variation. *Physiological Entomology* **33**, 200-208.

Sloggett, J.J. & Majerus, M.E.N. (2000a) Aphid-mediated coexistence of ladybirds (Coleoptera : Coccinellidae) and the wood ant *Formica rufa*: seasonal effects, interspecific variability and the evolution of a coccinellid myrmecophile. *Oikos* **89**, 345-359.

Sloggett, J.J. & Majerus, M.E.N. (2000b) Habitat preferences and diet in the predatory Coccinellidae (Coleoptera): an evolutionary perspective. *Biological Journal of the Linnean Society* **70**, 63-88.

Sloggett, J.J. & Majerus, M.E.N. (2003) Adaptations of *Coccinella magnifica*, a myrmecophilous coccinellid to aggression by wood ants (*Formica rufa* group). II. Larval behaviour, and ladybird oviposition location. *European Journal of Entomology* **100**, 337-344.

Sloggett, J.J. (2008) Habitat and dietary specificity in aphidophagous ladybirds (Coleoptera: Coccinellidae): Explaining specialization. *Procedings of the Netherlands Entomological Society Meeting* **19**, 95-113.

Sloggett, J.J., Manica, A., Day, M.J. & Majerus, M.E.N. (1999) Predation of ladybirds (Coleoptera: Coccinellidae) by wood ants, *Formica rufa* L. (Hymenoptera: Formicidae). *Entomologist's Gazette* **50**, 217-221.

Sloggett, J.J., Volkl, W., Schulze, W., van der Schulenberg, J.H. & Majerus, M.E.N. (2002) The ant-associations and diet of the ladybird *Coccinella magnifica* (Coleoptera : Coccinellidae). *European Journal of Entomology* **99**, 565-569.

Sloggett, J.J., Wood, R.A. & Majerus, M.E.N. (1998) Adaptations of *Coccinella magnifica* Redtenbacher, a myrmecophilous coccinellid, to aggression by wood ants (*Formica rufa* group). I. Adult behavioral adaptation, its ecological context and evolution. *Journal of Insect Behavior* **11**, 889-904.

Sloggett, J.J., Zeilstra, I. & Obrycki, J.J. (2008) Patch residence by aphidophagous ladybird beetles: do specialists stay longer? *Biological Control* **47**, 199-206.

Smith, B.C. (1958) Development, Feeding Habits, and Predator-Prey Relations of Insect Predators of the Balsam Woolly Aphid, "*Adelges piceae*" (Ratz.) (Homoptera: Adelgidae), recently Introduced into Canada. *The Canadian Entomologist* **90**, 441-449

Smith, B.C. (1966) Effects of food quality and age on larval activities of *Anatis mali* Auct. (Coleoptera-Coccinellidae). *Canadian Journal of Zoology* **44**, 251-255.

Soemargono, A., Ibrahim, Y., Ibrahim, R. & Osman, M. (2008) Life table and demographic parameters of the metallic blue ladybeetle, *Curinus coeruleus* Mulsant, fed with the Asian citrus psyllid, *Diaphorina citri* Kuwayama. *Pertanika Journal of Tropical Agriculture Science* **31**, 1-10.

Sohrabi, F. & Shishehbor, P. (2007) Functional and numerical responses of *Stethorus gilvifrons* Mulsant feeding on strawberry spider mite, *Tetranychus turkestani* Ugarov and Nikolski. *Pakistan Journal of Biological Sciences* **10**, 4563-4566.

Solangi, B.K., Lanjar, A.G. & Lohar, M.K. (2007) Biology of 11-spotted beetle *Coccinella undecimpunctata* L. (Coccinellidae: Coleoptera) on mustard aphid *Lipaphis erysimi* Kalt. *Journal of Applied Sciences* **7**, 3086-3090.

Song, H.Y., Wu, L.Y., Guofa, C., Zechun, W. & Song, Q.M. (1988) Biological characters of ladybeetle, *Propylaea japonica* (Thunberg). *Natural Enemies of Insects* **10**, 22-33.

Soroushmehr, Z., Sahragard A. & Salehi L. (2008) Comparative life table statistics for the ladybeetle *Scymnus syriacus* reared on the green citrus aphid, *Aphis spiraecola*, fed on two host plants. *Entomological Science* **11**, 281-288.

Speight, M.C.D. (1990) *Hippodamia tredecimpunctata* (Coleoptera: Coccinellidae) and other insects from All Saints bog, Co. Offaly, Irish Republic. *Bulletin of the Irish Biogeographical Society* **13**, 200-212.

Spíndola, A.F., Silva-Torres, C.S.A., Rodrigues, A.R.S. & Torres, J.B. (2013) Survival and behavioural responses of the predatory ladybird beetle, *Eriopis connexa* populations susceptible and resistant to a pyrethroid insecticide. *Bulletin of Entomological Research* **103**, 485-494.

Srivastava, A.S., Katiyar, R.R., Upadhyay, K.D. & Singh, S.V. (1987) Studies on the food preference of *Coccinella repanda* Thunberg (Coleoptera-Coccinellidae). *Indian Journal of Entomology* **49**, 551-552.

Stathas, G. (2000) *Rhyzobius lophanthae* prey consumption and fecundity. *Phytoparasitica* **28**, 203-211.

Stathas, G. (2001) Studies on morphology and biology of immature stages of the predator *Rhyzobius lophanthae* Blaisdell (Col.: Coccinellidae). *Anzeiger für Schädlingskunde* **74**, 113-116.

Stathas, G.J., Eliopoulos, P.A., Japoshvili, G. & Kontodimas, D.C. (2009) Phenological and ecological aspects of *Protopulvinaria pyriformis* (Cockerell) (Hemiptera: Coccidae) in Greece. *Journal of Pest Science* **82**, 33-39.

Stenlokk, J. (2004) Mass outbreak of the heather leaf beetle (*Lochmaea suturalis*) in Vestlandet. *Insekt Nytt* **29**, 23-26.

Storch, R. & Vaundell, W. (1972) The effect of photoperiod on diapause induction and inhibition in *Hippodamia tredecimpunctata* (Coleoptera: Coccinellidae). *The Canadian Entomologist* **104**, 285-288.

Stork, N.E., Hammond, P.M., Russell, B.L. & Hadwen, W.L. (2001) The spatial distribution of beetles within the canopies of oak trees in Richmond Park, U.K. *Ecological Entomology* **26**, 302-311.

Stuart, R.J., Michaud, J.P., Olsen, L. & McCoy, C.W. (2002) Lady beetles as potential predators of the root weevil *Diaprepes abbreviatus* (Coleoptera: Curculionidae) in Florida citrus. *Florida Entomologist* **85**, 409-416.

Sugiura, K. & Takada, H. (1998) Suitability of seven aphid species as prey of *Cheilomenes sexmaculata* (Fabricius)(Coleoptera: Coccinellidae). *Japanese Journal of Applied Entomology and Zoology* **42**, 7-14.

Suja, G. & Beevi, S.N. (2007) Biology and efficiency of the potential coccinellid predators of cowpea aphid, *Aphis craccivora* Koch. in cowpea. *Entomon* **32**, 97-102.

Sullivan, D.J., Castillo, J.A. & Bellotti, A.C. (1991) Comparative biology of six species of coccinellid beetles (Coleoptera: Coccinellidae) predaceous on the mealybug, *Phenacoccus herreni* (Homoptera: Pseudococcidae), a pest of cassava in Colombia, South America. *Environmental Entomology* **20**, 685-689.

Suzuki, N., Osawa, N. & Nishida, T. (2013) Larval performances for prey capture in hatchlings of two sibling ladybird beetles *Harmonia yedoensis* and *H. axyridis*. *IOBC/WPRS Bulletin* **94**, 65.

Taghizadeh, R.,Fathipour, Y. & Kamali, K. (2008) Influence of temperature on life-table parameters of *Stethorus gilvifrons* (Mulsant) (Coleoptera: Coccinellidae) fed on *Tetranychus urticae* Koch. *Journal of Applied Entomology* **132**, 638-645.

Tang, L., Wu, J., Ali, A. & Ren, S. (2013) The influence of different aphid prey species on the biology and life table parameters of *Propylaea japonica*. *Biocontrol Science and Technology* **23**, 624-636.

Tank, B.D., Korat, D.M. & Borad, P.K. (2007) Determination of dominant species of predatory coccinellid in Anand region of Gujarat. *Karnataka Journal of Agricultural Sciences* **20**, 637-638.

Tavadjoh, Z., Hamzehzarghani, H., Alemansoor, H., Khalghani, J. & Vikram, A. (2010) Biology and feeding behaviour of ladybird, *Clitostethus arcuatus*, the predator of the ash whitefly, *Siphoninus phillyreae*, in Fars province, Iran. *Journal of Insect Science* **10**, 1-12.

Tavares, C., Jactel, H., van Halder, I., Mendel, Z. & Branco, M. (2014) A case of ecological specialization in ladybirds: *Iberorhyzobius rondensis* (Coleoptera: Coccinellidae), potential biocontrol agent of *Matsucoccus feytaudi* (Hemiptera: Matsucoccidae). *Bulletin of Entomological Research* **104**, 367-375.

Tezcan, S. & Uygun, N. (2003) Evaluation of the Coccinellidae (Coleoptera) fauna of ecologically managed cherry orchards in Izmir and Manisa provinces of Turkey. *Turkiye Entomoloji Dergisi* **27**, 73-79.

Thakur, J.N., Rawat, U.S. & Pawar, A.D. (1989) Investigations on the occurrence of natural enemies of San Jose scale, *Quadraspidiotus perniciosus* Comstock (Hemiptera: Coccidae) in Jammu & Kashmir and Himachal Pradesh. *Entomon* **14**, 143-146.

Thakur, J.N., Rawat, U.S. & Pawar, A.D. (1989) Investigations on the occurrence of natural enemies of San Jose scale, *Quadraspidiotus perniciosus* Comstock (Hemiptera: Coccidae) in Jammu & Kashmir and Himachal Pradesh. *Entomon* **14**, 143-146.

Tifft, K.H., Leppla, N.C., Osborne, L.S. & Cuda, J.P. (2006) Rearing *Diomus terminatus* (Coleoptera: Coccinellidae) on the corn leaf aphid, *Rhopalosiphum maidis* (Homoptera: Aphididae). *Florida Entomologist* **89**, 263-265.

Timms, J.E., Oliver, T.H., Straw, N.A. & Leather, S.R. (2008) The effects of host plant on the coccinellid functional response: Is the conifer specialist *Aphidecta obliterata* (L.) (Coleoptera: Coccinellidae) better adapted to spruce than the generalist *Adalia bipunctata* (L.) (Coleoptera: Coccinellidae)? *Biological Control* **47**, 273-281.

Toccafondi, P., Covassi, M. & Pennacchio, F. (1991) Studies on the predator complex of *Matsucoccus* Cock. occurring in Italy. II. Bio-ethological notes on *Rhyzobius chrysomeloides* (Herbst) in the pine woods of Liguria (Coleoptera: Coccinellidae). *Redia* **74,** 599–620**.**

Ulgenturk, S. & Toros, S. (1999) Natural enemies of the oak scale insect, *Eulecanium ciliatum* (Douglas) (Hemiptera: Coccidae) in Turkey. *Entomologica* **33**, 219-224.

Ulgenturk, S., Szentkiralyi, F., Uygun, N., Fent, M., Gaimari, S.D., Civelek, H. & Ayhan, B. (2013) Predators of *Marchalina hellenica* (Hemiptera: Marchalinidae) on pine forests in Turkey. *Phytoparasitica* **41**, 529-537.

Uygun, N. & Elekcioglu, N.Z. (1998) Effect of three diaspididae prey species on development and fecundity of the ladybeetle *Chilocorus bipustulatus* in the laboratory. *Biocontrol* **43**, 153-162.

Valenciaga, N., Barrientos, A. & Mora, C. (1999) Performance of the beneficial entomofauna in *Leucaena leucocephala* Lam de Wit areas. *Cuban Journal of Agricultural Science* **33**, 319-324.

Van Driesche, R.G, Idoine, K., Rose, M. & Bryan, M. (1998a) Evaluation of the Effectiveness of *Chilocorus kuwanae* (Coleoptera: Coccinellidae) in Suppressing Euonymus Scale (Homoptera: Diaspididae). *Biological Control* **12**, 56-65.

Van Driesche, R.G., Idoine, K., Rose, M. & Bryan, M. (1998b) Release, establishment and spread of Asian natural enemies of Euonymus scale (Homoptera: Diaspididae) in New England. *Florida Entomologist* **81**, 1-9.

Vandenberg, N. (1990) First North American records for *Harmonia quadripunctata* (Pontopiddian) (Coleoptera: Coccinellidae); a lady beetle native to the Palaearctic. *Proceedings of the Entomological Society of Washington* **92**, 407-410.

Vandenberg, N. (2004a) Contributions to the knowledge of *Olla casey* (Coleoptera: Coccinellidae: Coccinellini): New species from the Galapagos Islands, updates on the distribution of *O. v-nigrum* (Mulsant). *Proceedings of the Entomological Society of Washington* **106**, 619-626.

Vandenberg, N. (2004b) Homonymy in the Coccinellidae (Coleoptera), or something fishy about *Pseudoscymnus Chapin*. *Proceedings of the Entomological Society of Washington* **106**, 483-484.

VanDyk, J. (2014) BugGuide. Available online at BugGuide.net.

Vanegas-Rico, J.M., Lomeli-Flores, J.R., Rodriguez-Leyva, E., Mora-Aguilera, G. & Valdez, J.M. (2010) Enemigos naturales de *Dactylopius opuntiae* (Cockerell) en *Opuntia ficus-indica* (L.) Miller en el centro de México. *Acta zoológica mexicana* **26**, 415-433.

Vanhaelen, N., Gaspar, C. & Francis, F. (2002) Aphid prey suitability as environmental effect on *Adalia bipunctata* reproduction. Mededelingen (Rijksuniversiteit te Gent. Fakulteit van de Landbouwkundige en Toegepaste Biologische Wetenschappen) **67**, 563-568.

Vantaux, A., Roux, O., Magro, A., Ghomsi, N.T., Gordon, R.D., Dejean, A. & Orivel, J. (2010) Host-specific myrmecophily and myrmecophagy in the tropical coccinellid *Diomus thoracicus* in French Guiana. *Biotropica* **42**, 622-629.

Varma, G., Vyas, R. & Brar, K. (1993) Biology of *Menochilus sexmaculatus* (Fabricius) Coccinellidae: Coleoptera. *Journal of Research Punjab Agricultural University* **30**, 27-31.

Varty, I. (1969) Ecology of *Mulsantina hudsonica* Casey, a ladybeetle in fir-spruce forest. *Internal report M-42*, Department of Fisheries and Forestry Canada, Forest Research Laboratory, Fredericton, New Brunswick, Canada, January 1969.

Vidya, M., Patil, R.K. & Lingappa, S. (2004) Coccinellid predators of sugarcane woolly aphid, *Ceratovacuna lanigera* Zehntner. *Insect Environment* **10**, 38-39.

Vieira, M.R. & Correa, L.S. (2001) Whiteflies (Hemiptera: Aleyrodidae) and the predator *Delphastus pusillus* (Le Conte) (Coleoptera: Coccinellidae) on papaya tree (*Carica papaya* L.) grown under screened conditions. *Neotropical Entomology* **30**, 171-173.

Villacarlos, L.T. & Robin, N.M. (1992) Biology and potential of *Curinus coeruleus* Mulsant, an introduced predator of *Heteropsylla cubana* Crawford. *Philippine Entomologist* **8**, 1247-1258.

Villanueva, R.T., Michaud, J.P. & Childers, C.C. (2004) Ladybeetles as predators of pest and predacious mites in citrus. *Journal of Entomological Science* **39**, 23-29.

Vohland, K. (1996) The influence of plant structure on searching behaviour in the ladybird, *Scymnus nigrinus* (Coleoptera: Coccinellidae). *European Journal of Entomology* **93**, 151-160.

Wang, J.-J. & Tsai, J.H. (2001) Development and functional response of *Coelophora inaequalis* (Coleoptera: Coccinellidae) feeding on brown citrus aphid, *Toxoptera citricida* (Homoptera: Aphididae). *Agricultural and Forest Entomology* **3**, 65-69.

Wang, S., Chen, C., Zou, D. & Chen, H. (2010) Preliminary study on biological characteristics of *Scymnus frontalis* Fabricius. *Chinese Journal of Biological Control* **26**, 397-403.

Watson, W.Y. (1976) A review of the genus *Anatis* Mulsant (Coleoptera: Coccinellidae). *The Canadian Entomologist* **108**, 935-944.

Weng, W. & Huang, Y. (1988) A preliminary study on a predacious insect, *Brumoides lineatus* (Weise). *Insect Knowledge* **25**, 105-108.

Wenlong, C. & Longshu, L. (1993) Preference of *Stethorus chengi* Sasaji to its preys. *Journal of Southwest Agricultural University* **2**, 014.

Wheeler Jr., A.G. (2003) *Brumoides septentrionis* Davisi (Leng) (Coleoptera: Coccinellidae): distribution, host-plant associations, and habitats of a seldom-collected lady beetle. *Proceedings of the Entomological Society of Washington* **105**, 50–58.

Wheeler Jr., A.G. (2010) *Hyperaspidius venustulus* (Mulsant) (Coleoptera: Coccinellidae): A rarely collected lady beetle associated with the mealybug *Dysmicoccus dennoi* Kosztarab on big cordgrass, *Spartina cynosuroides* (Poaceae). *Proceedings of the Entomological Society of Washington* **112**, 149-154.

Wheeler Jr., A.G. (2013) *Hyperaspis paludicola* Schwarz (Coleoptera: Coccinellidae): association with *Miscanthus* mealybug, *Miscanthicoccus miscanthi* (Takahashi) (Hemiptera: Pseudococcidae), with a review of its distribution. *Entomological News* **123**, 220-224.

Wiggins, G., Hakeem, A., Follum, R., Rhea, R., Lambdin, P.L. & Grant, J.F. (2010) Seasonality of established populations of *Sasajiscymnus tsugae* on Eastern Hemlock in the Southern Appalachians. pp. 203–205 in Onken, B. & Reardon, R. (Eds.) *Fifth Symposium on Hemlock Woolly Adelgid in the Eastern United States* organized by the *U.S. Department of Agriculture, Forest Service*, Asheville, NC, U.S.A., 17–19 August 2010.

Winiarska, W. (1996) Natural enemies of the fir bark aphid, *Dreyfusia piceae* (Ratz.) (Homoptera, Adelgidae). *Sylwan* **140**, 43-47.

Wiryadiputra, S., Priatno, N., Junianto, Y.D. & Sulistyowati, E. (1987) *Harmonia octomaculata* (F.) as a predator of the Leucaena psyllid [Indonesian]. *Pelita Perkebunan* **3**, 73-77.

Witter, J.A. (1969) Laboratory Studies on the Developmental Period and Feeding Behavior of *Aphidecta obliterata* (L.) (Coleoptera: Coccinellidae), an introduced predator of the Balsam Woolly Aphid. *Annals of the Entomological Society of America* **62**, 1004-1008.

Woin, N., Volkmar, C. & Wetzel, T. (2000) Seasonal activity and diversity of ladybirds (Coleoptera: Coccinellidae) as ecological bioindicators in paddy fields. *Mitteilungen der Deutschen Gesellschaft für allgemeine und angewandte Entomologie* **12**, 203-206.

Wright, R.J. & Vries, T.A.D. (2000) Species composition and relative abundance of Coccinellidae (Coleoptera) in South Central Nebraska field crops. *Journal of the Kansas Entomological Society* **73**, 103-111.

Wu, J., Yang, J. & Ren, S. (2010) Influence of *Bemisia tabaci* (Gennadius) and *Myzus persicae* (Sulzer) as preys on biological characteristics of *Phrynocaria congener* (Billberg). *Chinese Journal of Biological Control* **26**, 260-266.

Wylie, H.G. (1958) Observations on *Aphidecta obliterata* (L.) (Coleoptera: Coccinellidae), a predator of conifer-infesting Aphidoidea. *The Canadian Entomologist* **90**, 518-522.

Yang, P. (2006) Laboratory study of predation by *Curinus coeruleus* (Coleoptera: Coccinellidae) on eggs of *Aedes albopictus* (Diptera: Culicidae). *Procedings of the Hawaiian Entomological Society* **38**,127–129.

Yang, X., Shen, M., Guo, Z. & Xiong, J. (1997) Predation of the ladybeetle *Chilocorus kuwanae* on the scale *Unaspis yanonensis*. *Insect Science* **4**, 249-258.

Yang, X., Shen, M., Xiong, J. & Guo, Z. (1996) Approaches to enhance the effectiveness of biocontrol of *Panonychus citri* (Acari: Tetranychidae) with *Stethorus punctillum* (Coleoptera: Coccinellidae) in citrus orchards in Guizhou. *Systematic and Applied Acarology* **1**, 21-27.

Yanik, E., Unlu, L. & Yucel, A. (2011) Determination of insect predator species found on almond and wild almond trees adjacent to pistachio orchards. *Acta Horticulturae* **912**, 743-749.

Yaşar, B. & Özger, Ş. (2005a) Development, feeding and reproduction responses of *Adalia fasciatopunctata revelierei*(Mulsant) (Coleoptera : Coccinellidae) to *Hyalopterus pruni*(Geoffroy) (Homoptera : Aphididae). *Journal of Pest Science* **78**, 199-203.

Yaşar, B. & Özger, Ş. (2005b) Functional response of *Oenopia conglobata* (L.)(Coleoptera: Coccinellidae) on *Hyalopterus pruni* (Geoffroy) (Homoptera: Aphididae) in three different size arenas. *Türkish Entomology Dergisi* **29**, 91-99.

Yazdani, M. & Zarabi, M. (2010) Predation of *Clitostethus arcuatus* (Col.: Coccinellidae) on *Trialeurodes vaporariorum* (Hem.: Aleyrodidae). *Biocontrol Science and Technology* **20**, 353-358.

Yigit, A. & Canhilal, R. (2005) Establishment and dispersal of *Serangium parcesetosum* Sicard (Coleoptera, Coccinellidae), a predatory beetle of citrus whitefly, *Dialeurodes citri* Ashm. (Homoptera, Aleyrodidae) in the East Mediterranean region of Turkey. *Zeitschrift Fur Pflanzenkrankheiten Und Pflanzenschutz-Journal of Plant Diseases and Protection* **112**, 268-275.

Young, G.R. (2003) Life history, biology, host plants and natural enemies of the lilly pilly psyllid, *Trioza eugeniae* Froggatt (Hemiptera: Triozidae). *Australian Entomologist* **30**, 31-38.

Yu, J.-Z., Chi, H. & Chen, B.-H. (2013) Comparison of the life tables and predation rates of *Harmonia dimidiata* (F.) (Coleoptera: Coccinellidae) fed on *Aphis gossypii* Glover (Hemiptera: Aphididae) at different temperatures. *Biological Control* **64**, 1-9.

Zarpas, K.D., Margaritopoulos, J.T. & Tsitsipis, J.A. (2007) Life histories of generalist predatory species, control agents of the cotton aphid Aphis gossypii (Hemiptera: Aphididae). *Entomologia Generalis* **30**, 85-102.

Zhang, F. (1997) Functional response of *Coccinella transversoguttata* on the prey *Macrosiphum avenae*. *Natural Enemies of Insects* **19**, 156-160.

Zhang, F., Han, D., Zhang, J. & Fu, Y. (2010) Predation of *Stethorus parapauperculus* on *Eotetranychus sexmaculatus*. *Chinese Bulletin of Entomology* **47**, 1236-1239.

Zhang, S., Zhang, F. & Hua, B. (2007) Suitability of various prey types for the development of *Propylea japonica* (Coleoptera: Coccinellidae). *European Journal of Entomology* **104**, 149-152.

Zhang, S.-Z., Li, J.-J., Shan, H.-W., Zhang, F. & Liu, T.-X. (2012) Influence of five aphid species on development and reproduction of *Propylaea japonica* (Coleoptera: Coccinellidae). *Biological Control* **62**, 135-139.

Zilahi-Balogh, G.M., Kok, L.T., Salom, S. M. (2002) A review of world-wide biological control efforts for the Family Adelgidae. pp. 129-140 in Onken, B., Reardon, R. & Lashomb, J. (Eds) *Proceedings of the Symposium on Hemlock Woolly Adelgid in the Eastern United States*, East Brunswick, NJ, U.S.A, 5-7 February 2002.

Zulfiqar, A., Shah, H.A. & Yousuf, M. (1999) Studies on the biology of *Brumoides suturalis* (F.) (Coccinellidae: Coleoptera). *Pakistan Entomologist* **21**, 57-59.

VII. Conclusions

This work can be divided into two parts:

First, we addressed in detail the biology and ecology of the poorly known coccinellid, *Iberorhyzobius rondensis* (Eizaguirre), in view of using it in a program of classical biological control of the maritime pine bast scale, *Matsucocccus feytaudi* Ducasse. We studied *I. rondensis*'s life traits, phenology, phylogeny, phylogeography, prey and habitat specialization, and life cycle synchronization with its prey. Our results contribute to the risk assessment of *I. rondensis* as a biological control agent of *M. feytaudi*, and so far support the idea of this ladybird's effectiveness as such an agent.

Second, considering the importance of prey specificity in predators used as biological control agents, we performed a review concerning several aspects of prey specialization in ladybirds. We studied the association between prey specialization, several life traits, taxonomy, habitat specialization and habitat specialization of the prey. We further analyzed the relationship between biological control success and the predator's degree of prey specialization.

7.1. Biology, ecology and phylogeography of *Iberorhyzobius rondensis*

Iberorhyzobious rondensis is a ladybird species unique in its genus, belonging to the tribe Coccidulini, subfamily Coccidulinae. In this study we validated its unique genus status with molecular methods, but the taxonomic position of the beetle in the tribe Coccidulini is not yet established.

I. rondensis is a coccidophagous species, specialized on the maritime pine bast scale *M. feytaudi*, which uses the prey pheromone as a kairomone (Branco *et al.*, 2006). In this study we demonstrate that *M. feytaudi is I. rondensis*'s essential prey, and that in nature the latter cannot entirely complete its life cycle with other prey species. Further, the ladybird is only found on the prey's host, the maritime pine, *Pinus pinaster* Aiton, although *I. rondensis* if confined to the Iberian Peninsula.

The degree of adaptation of the ladybird to its prey was found to be extremely high, and it was measured in several ways:

Habitat restriction

Three species of pine trees (*P. pinaster*, *Pinus nigra* JF Arnold and *Pinus sylvestris* L.) known to harbor *Matsucoccus sp.* were surveyed in several regions of the Iberian Peninsula, for the presence of *I. rondensis*. The beetle was only present on *P. pinaster* trees, even when other pine species co-occurred. Only *M. feytaudi* is present on *P. pinaster,* whilst *M. pini* is found on *P. sylvestris* and *P. nigra* (Foldi, 2004). This demonstrates how unlikely it is for the beetle to prey on other species of *Matsucoccus*, besides *M. feytaudi*, in its natural habitat.

The ladybird is present in all the distribution area of *P. pinaster* in the Iberian Peninsula, except in the region of Catalonia. Densities of the beetle were found to be high in Central Portugal and South and Central Spain, and low in the region of Valencia. It is absent from the rest of the natural range of the prey in southern Europe (France) and in its area of expansion (Italy and Corsica). We lack information about its presence in North Africa, more specifically in the Atlas Mountains, where a population of *M. feytaudi* is known to exist (Burban *et al.*, 1999).

Prey Specialization

In this work we demonstrated that the unique natural prey of *I. rondensis* is *M. feytaudi*. Several diets (different Hemiptera prey and artificial *Ephestia kuehniella* Zeller eggs) were tested for their effect on the survival, development, RGR and prey preference (choice-tests) of the beetle.

The beetle could only complete its pre-imaginal development on eggs of *M. feytaudi,* with a high survival rate (98%). Complete development was also achieved when the larvae were fed with *E. kuehniella* eggs, but survival was extremely low (28%). Further, development took 10 days longer when larvae were fed with *E. kuehniella* eggs than with *M. feytaudi* eggs, which indicates its low suitability. Survival on *E. kuehniella* eggs increased from the 2nd instar onwards (80%).

Third and fourth instars larvae are able to complete their life cycle on other prey besides *M. feytaudi*, especially insects which are frequently present on *P. pinaster*, such as *Cinara maritimae* Dufour and *Pineus pini* Koch. Those prey species may serve as alternative food when *M. feytaudi* eggs are not immediately available. We believe that *I. rondensis* could prey on other species of the *Matsucoccus* genus (like *Matsucoccus* *josephi* Bodenheimer & Harpaz and *Matsucoccus. pini* (Green)), since the ladybird was able to develop from the 2nd instar onwards on *M. josephi* eggs in laboratory conditions.

RGR of *I. rondensis* larvae was highest when they were reared on *M. feytaudi* eggs, except for the 3rd instar larvae (for which RGR was almost the same as with eggs of *E. kuehniella).* When reared on other prey species, RGR was generally null or negative, and displayed high variability.

Third and fourth instar larvae showed a preference for *M. feytaudi* eggs over other prey, except for *P. pini* eggs, for which no preference was determined. In the field, preference for *M. feytaudi* is possible much stronger, because larvae are quickly attracted by the female sex pheromone which also impregnates the eggs (Branco *et al.*, 2006; Branco *et al.*, 2011).

We observed a density dependent relationship between *I. rondensis* and *M. feytaudi*, since there was a significant and positive correlation between the number of ladybird larvae and the number of *M. feytaudi* males caught per region in the Iberian Peninsula.

Foraging behavior

M. feytaudi females with eggs are generally hidden deep within the bark. Yet, *I. rondensis* can quickly find them out, since it searches for the prey using the sex pheromone as a kairomone, which greatly reduces prey searching time (Branco *et al.*, 2011). Our observations in the field confirmed this behavior for all the populations sampled in the Iberian Peninsula.

Reproduction

We found that *I. rondensis* presents an obligatory reproductive diapause of 5-6 months. Even when several different photoperiods, temperatures and/or regimes were tested, diapause was not broken. Mating was not observed during the diapause period. We conclude that reproductive diapause allows for reproduction of the ladybird to match with the period when *M. feytaudi* eggs are already available.

After the diapause, oviposition was only possible if beetles were fed with *M. feutaudi* or *E.kuehniella* eggs, which allowed the production of ovocytes. Oviposition never occurred with ladybirds fed with honey and pollen only. *I.rondensis* exhibits a low fecundity, around 73 eggs/ female which is typical of ladybird monovoltine species. Fecundity was found to be higher in beetles fed with *M. feytaudi* eggs.

Life cycle synchronization with Matsucoccus feytaudi

The ladybird completes its pre-imaginal development in 40 days at 22ºC. Optimal temperature for egg development ranges from 22ºC to 28ºC. Adults can live up to 2 years and reproduce during 8 months. During its pre-imaginal development a larvae can eat 4 to 7 egg masses of *M. feytaudi*.

In two years of field surveys in Portugal, larvae of *I. rondensis* were only observed between February and May, with a peak in April. A significant lag-correlation with an interval of 2 months was found between the number of *I. rondensis* larvae and the number of *M. feytaudi* males.

Based on this new information we predict the following life cycle for *I.rondensis* (Fig. 1):

Winter. In early December – January, *M. feytaudi* adults emerge and start reproducing, having their peak in February-March (Riom & Gerbinot, 1977; Branco *et al.*, 2001). *I. rondensis* starts its reproduction some weeks after *M. feytaudi* males start their flight, sometime between December and February, when its reproductive diapause ends and *M. feytaudi* egg masses are available. We showed that eggs of *I. rondensis* are adapted to survive at low temperatures and diapause for several months if temperatures are low (as low as 4ºC).

Spring. *M. feytaudi* oviposition is finished around late April - early May, so ladybirds are likely to lay eggs until late May. The majority of *I. rondensis* adults emerge in May - June. Emerged adults enter reproductive diapause.

Summer/Autumn**.** Reproductive diapause of *I. rondensis* lasts until late October - November. Adults may have a kind of aestivation period during summer which corresponds to the L2 phase of *M. feytaudi*, when the bast scale also aestivates (Foldi, 2004). During this period, it is also possible for *I.rondensis* to survive on other food resources such as pollen and honey.

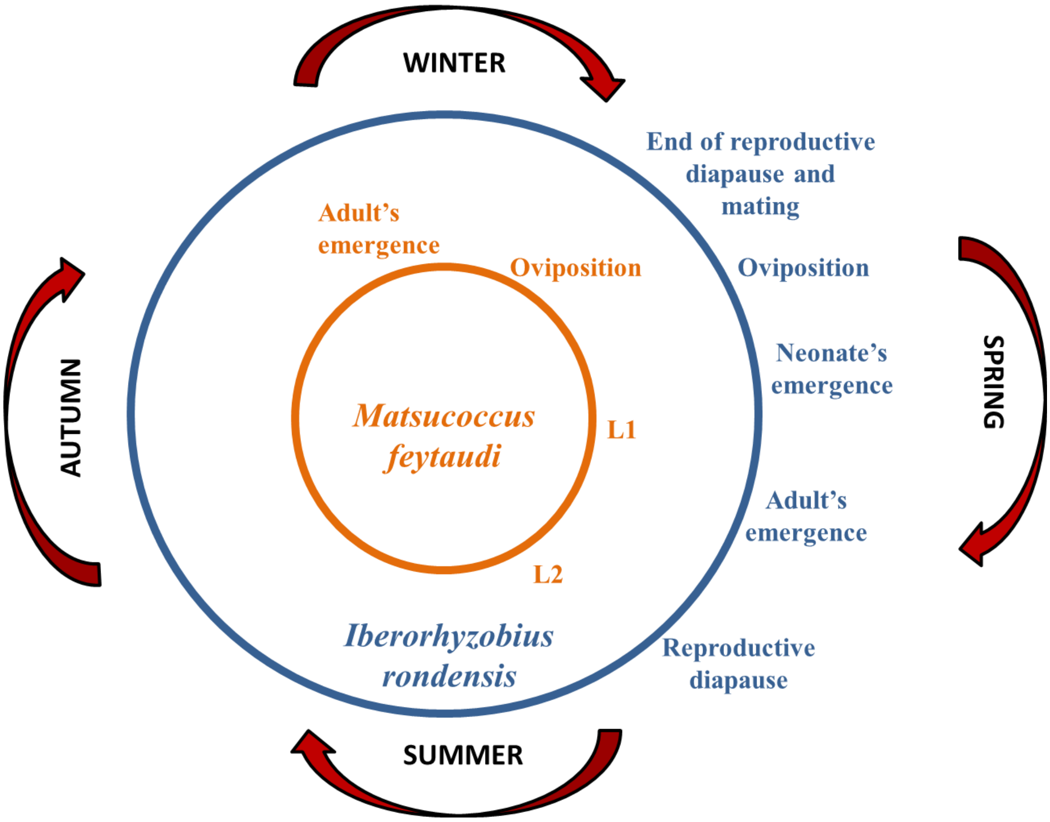

Fig. 1 Synchronization of the life cycles of *M. feytaudi* and *I.rondensis*.

Comparative Phylogeography of I.rondensis and M. feytaudi

Phylogeography of the ladybird using COI and 18S markers, revealed two main different genetic groups within the Iberian Peninsula: i) Western and Central Iberian Peninsula and ii) Eastern Iberian Peninsula. *M. feytaudi*, which is also native to the Iberian Peninsula and North Africa (Burban *et al*., 1999), has a similar phylogeographic pattern. To some extent, the same phylogeographic pattern was also found for the host tree, *P. pinaster*. This is evidence of a common biogeographic history, in which the three species are closely associated.

7.2. Review on prey specialization in coccinellids

Review on prey specialization of 186 species of coccinellids, revealed some interesting global patterns. The majority of ladybird species are oligophagous – feeding on prey species from a single family or superfamily, which supports the idea that ladybirds are a very specialized guild of predators (Hodek & Honěk, 1996). A strong association was also found between prey and habitat specialization.

Specialist predatory ladybeetles consume indifferently specialist or generalist prey species whereas generalist predators rather feed on generalist preys, or include generalist preys on their diet. The degree of prey specialization was related with feeding guilds, as with taxonomic groups.

Predators' traits such as fecundity, size and voltinism were found to be related to their degree of prey specialization. Specifically, polyphagous species are usually larger and more fecund than specialized species; and univoltinism is more frequent in specialized ladybeetles. By contrast, chemical cues are used by both generalist and specialist species and biological control success was not associated with high levels of prey specialization.

Our review further reinforces the idea that *I. rondensis* represents a unique case of extreme specialization – it is a monophagous predator feeding on a monophagous species, restricted to the prey's habitat, univoltine, small, with a low fecundity and it uses the prey's sexual pheromone as a chemical cue. In this case we predict that prey characteristics may have driven such an ecological specialization of this specific predator.

7.3. *Iberorhyzobius rondensis* as a possible biological control agent of *Matsucoccus feytaudi*

When studying the biology of *I. rondensis*, we focused on several traits that are important in risk assessment of any potential biological control agent. We concluded that *I. rondensis* presents several traits common among successful biological control agents (Dixon, 2000; Van Lenteren *et al.*, 2006).

First, *I .rondensis* is a coccidophagous ladybird. This guild of ladybirds is known to be a better biological control agent than the aphidophagous species (Dixon, 2000). Further, *I. rondensis* is a monophagous species, highly specialized in the maritime pine bast scale *M. feytaudi*, and only present in the prey's habitat. These two components of specialization are probably the most important ones for any biological control agent (McEvoy, 1996; Van Lenteren *et al.*, 2006). They will insure effectiveness, since the ladybird will remain within the prey's habitat, and specificity, since they will not prey on non-target species.

I. rondensis is univoltine like its prey. This may be an advantage, since in the field, ladybirds are known to effectively control univoltine scales (Iperti, 1999; Dixon, 2000). The ladybird reproductive period occurs when the bast scale is also reproducing, so when the beetle larvae hatch, eggs masses of the prey are available for feeding. The fact that its life cycle is synchronized with that of the prey is another piece of evidence for its high degree of prey specialization. Further, the ladybirds present a density-prey response which suggests that they can follow the demography of prey populations.

Due to its foraging mode, the ladybird has a high searching capacity specifically adapted to *M. feytaudi*, which insures that it quickly finds its prey. During its lifetime, a larva eats around 2000 eggs of *M. feytau*di, but due to its feeding mode, possibly destroys several other egg masses.

The phylogeographic study suggests a co-evolutionary process in the predator-prey relationship, which further supports the beetle's specificity.

Recommendations for the use of Iberorhyzobius rondensis *as a biological control agent of* Matsucoccus feytaudi *in the area of invasion*

Iberorhyzobius rondensis specimens from the Central System and Western Iberian Peninsula should be collected for rearing and release since those are the areas of origin of the invasive populations of *M. feytaudi* introduced in Italy, France and Corsica (Kerdelhué *et al.*, 2014) and present a high degree of genetic variability.

We predict that the major constraint related with the use of the beetle as a classical biocontrol agent will be its mass rearing on the laboratory. First, larvae are only able to survive when fed with *M. feytaudi* eggs masses, which are hard to obtain in great quantities, and are only available once in a year. So, we suggest that the rearing of the beetle would have to take place in the invaded range, such as Corsica, where the prey, *M. feytaudi*, makes huge outbreaks and is quite abundant. Further, the beetle’s long reproductive diapause will not allow for its continuous reproduction. Advantageously adults can be reproduced with *E. kuehniella* eggs.

Alternatively we can consider the use of the beetles in an acclimation program, where only a few beetles are introduced in the invaded range. In this case, the rearing of a large quantity of beetles would not be necessary.

7.4. Future perspectives

Future studies in this line of research should first address the information which is lacking to complete the risk and feasibility assessment of using *I. rondensis* as a biocontrol agent for *M. feytaudi* in Corsica and Italy:

- *Dispersal capacity. I. rondensis* dispersal capacity should be tested since it would be advantageous on the acclimation approach, for the beetle to colonize the area of invasion by itself. This would not be so relevant in an innundative release approach. A certain degree of dispersal is required in any biological control agent, so the beetles are able to disperse to new affected areas. Yet a high flight capacity may result in migration to other habitats and effects on non-target prey (Van Lenteren *et al.*, 2006). For this purpose one could use flight-mills to estimate the maximum dispersal capacity of the insect under controlled conditions. We believe that *I. rondensis* has a low dispersal capacity, since the beetle has rarely been seen flying; when observed, though, that behavior was most common among recently emerged adults. When considering the best time for release of the beetle on areas affected by *M. feytaudi*, this behavior and flight dispersal should be taken into consideration. Wing-polymorphism is present in *Rhyzobius litura* (Fabricius*)* and *Rhyzobius chrysomeloides* (Herbst), which implies wing reduction in some individuals (Pope, 1977). This trait should also be verified with *I. rondensis,* since it would impede some individuals to fly.
- *Climate matching*. If the climate between the region of origin of *I.rondensis* and its region of release is similar, the probability of establishment and success of

the biocontrol agent is higher (Van Lenteren *et al.*, 2006). Climate matching could be predicted with some appropriate programs, such as Climex or Maxent, Further, some minimum threshold temperatures for larval development of *I. rondensis* should be estimated. These are important data when predicting thermal requirements of the beetle.

- *Intraguild competition.* Other natural predators can prey upon *M. feytaudi*. In particular, in the Iberian Peninsula, *Elatophilus* sp. (Hemiptera, Anthocoridae) and *I. rondensis* co-occur in the natural habitat of the maritime pine bast scale and prey specifically on the bast scale. Based on our previous field and laboratory observations, it seems that there is no apparent competition. Thus, some niche partitioning might exist between these two species (Schoener, 1974). However, before releasing the beetle in a new range, it would be necessary to better evaluate the mechanisms regulating the coexistence of *I. rondensis* and other predators such as *Elatophilus nigricornis* Zetterstedt in Corsica. This would be of importance, since, in the areas invaded by *M. feytaudi*, *E. nigricornis* is present, and it is not desirable to decrease its populations.
- *Feeding preference of adults*. Although prey preference and consumption rate of *I. rondensis* instars have been determined, the same is not known for the adults. Previous observations leads us to believe that adults have a much lower efficacy of consumption than larvae, and that adults prefer *M. feytaudi* egg batches over other prey species. However, before their release, consistent information on this topic should be accumulated.

Further, information on the presence or absence of *I. rondensis* in North Africa, in particular in Morocco, where *M. feytaudi* is present, would help complement our knowledge on its life history. For instance, more phylogeographic studies could be made in order to improve our understanding of evolutionary patterns in the prey-predator relationship.

7.5. To conclude.

Iberorhyzobius rondensis is a unique species among ladybirds. Its traits reveal that it is a highly adapted species to its sole prey species, the maritime pine bast scale, *M. feytaudi.* Its study thus constitutes an important contribution to our knowledge on the ecology and biology of ladybirds in general, especially because inconspicuous and specialized species are often less studied (Sloggett, 2005). From an applied perspective *I. rondensis* has so far fulfilled the prerequisites which make it a promising biological control agent of *M. feytaudi* in its invaded range.

7.6. References

Branco, M., Brito, O., Jactel, H., Mendel, Z., Franco, J. & Pellizzari, G. (2001) Seasonal history of the Maritime Pine Bast Scale *Matsucoccus feytaudi* Ducasse (Hemiptera: Matsucoccidae) in Portugal. *Bollettino di Zoologia Agraria e di Bachicoltura* **33**, 319-329.

Branco, M.,van Halder, I.,Franco, J.C., Constantin, R. & Jactel, H. (2011) Prey sex pheromone as kairomone for a new group of predators (Coleoptera: Dasytidae, Aplocnemus spp.) of pine bast scales. *Bulletin of Entomological Research* **101**, 667-674.

Branco, M., Franco, J.C., Dunkelblum, E., Assael, F., Protasov, A., Ofer, D. & Mendel, Z. (2006) A common mode of attraction of larvae and adults of insect predators to the sex pheromone of their prey (Hemiptera: Matsucoccidae). *Bulletin of Entomological Research* **96**, 179-185.

Burban, C., Petit, R.J., Carcreff, E. & Jactel, H. (1999) Rangewide variation of the maritime pine bast scale *Matsucoccus feytaudi* Duc. (Homoptera: Matsucoccidae) in relation to the genetic structure of its host. *Molecular Ecology* **8**, 1593-1602.

Dixon, A.F.G. (2000) *Insect predator-prey dynamics: ladybird beetles and biological control*. 288 pp. New York, USA, Cambridge University Press.

Eizaguirre, S. (2004) Revisión de la tribu Coccidulini en la Península Ibérica (Coleoptera: Coccinellidae). *Estudios del Museo de Ciencias Naturales de Álava* **18-19**, 153-170.

Foldi, A.I. (2004) The Matsucoccidae in the Mediterranean basin with a world list of species (Hemiptera: Sternorrhyncha: Coccoidea). *Annales de la Société entomologique de France* **40**, 145-168.

Hodek, I. & Honěk, A. (1996) *Ecology of Coccinellidae*. p. 464. Dordrecht, The Netherlands, Kluwer Academic Publishers.

Iperti, G. (1999) Biodiversity of predaceous coccinellidae in relation to bioindication and economic importance. *Agriculture, Ecosystems & Environment* **74**, 323-342.

Kerdelhué, C., Boivin, T. & Burban, C. (2014) Contrasted invasion processes imprint the genetic structure of an invasive scale insect across southern Europe. *Heredity*, 1-11.

McEvoy, P.B. (1996) Host specificity and biological pest control. *BioScience* **46**, 401-405.

Pope, R.D. (1977) Brachyptery and wing-polymorphism among the Coccinellidae (Coleoptera). *Systematic Entomology* **2**, 59-66.

Raimundo, A., Canepari, C., Mendel, Z., Branco, M. & Franco, C. (2006) *Iberorhyzobius* Raimundo & Canepari gen. nov., for *Coccidula rondensis* Eizaguirre (Coleoptera: Coccinellidae). *Zootaxa* **1312**, 49-58.

Riom, J. & Gerbinot, B. (1977) Étude biologique et écologique de la cochenille du pin maritime *Matsucoccus feytaudi* Ducasse, 1942 (Coccoidea, Margarodidae, Xylococcinae) dans le Sud-Est de la France. I - Biologie générale et phénologie. *Annales de Zoologie et Écologie Animale* **9,** 11-50.

Schoener, T.W. (1974) Resource partitioning in ecological communities. *Science* **185**, 27-39.

Sloggett, J.J. (2005) Are we studying too few taxa? Insights from aphidophagous ladybird beetles (Coleoptera: Coccinellidae). *European Journal of Entomology* **102**, 391–398.

Tavares, C., Jactel, H., van Halder, I., Mendel, Z. & Branco, M. (2014) A case of ecological specialization in ladybirds: *Iberorhyzobius rondensis* (Coleoptera: Coccinellidae), potential biocontrol agent of *Matsucoccus feytaudi* (Hemiptera: Matsucoccidae). *Bulletin of Entomological Research* 104, 367-375.

Van Lenteren, J., Bale, J., Bigler, F., Hokkanen, H. & Loomans, A. (2006) Assessing risks of releasing exotic biological control agents of arthropod pests. *Annual Review of Entomology* **51**, 609-634.