Parasitoid and ant interactions of some Iberian butterflies (Insecta: Lepidoptera)

R. Obregón, M. R. Shaw, J. Fernández-Haeger & D. Jordano

Abstract

As a result of recent field studies in the Iberian Peninsula, interactions between 17 parasitoid taxa and 17 butterfly species, and 9 species of Lycaenidae and 15 species of Formicidae are detailed and discussed. Several of these, which are presented quantitatively, are otherwise unrecorded in the literature, while others confirm previous records. Attention is drawn to the need for the deposition of voucher material and both careful and prolonged quantitative recording in order to understand and conserve these vulnerable aspects of biodiversity.

KEY WORDS: Insecta, Lepidoptera, parasitism, Hymenoptera, Diptera, myrmecophily, Formicidae, Spain.

Interacciones de parasitoides y hormigas con mariposas ibéricas (Insecta: Lepidoptera)

Resumen

Se aportan 17 especies de parasitoides para 17 especies de mariposas y 15 nuevas interacciones de hormigas con 9 especies de licénidos (Lycaenidae) como resultado del trabajo de campo en la península ibérica y la cría en cautividad de estadios preimaginales en el laboratorio. Muchas de estas interacciones no han sido nunca registradas, mientras que otras confirman citas previas. Cabe señalar la necesidad de conservar material tipo y guardar estos registros cuantitativos para comprender mejor y conservar estos aspectos vulnerables y poco conocidos de la biodiversidad.

PALABRAS CLAVE: Insecta, Lepidoptera, parasitismo, Hymenoptera, Diptera, mirmecofilia, Formicidae, España.

Introduction

Interactions between insect parasitoids and their arthropod hosts are important features of most terrestrial ecosystems. Insect parasitoids mostly belong to the orders Hymenoptera and Diptera, and have free-living adults. Their larvae, however, feed to their full development on the body of a single host individual, which is killed by the interaction. Because of this, parasitoids are important factors in limiting the populations of the host species they attack.

SHAW *et al.* (2009) outline the general biology of parasitoids of European butterflies. Some tiny Hymenoptera (Scelonidae (now often included within Platygastridae) and a few groups of Chalcidoidea) attack and develop completely inside the host egg, but parasitism of later (but always pre-adult) stages by other groups is often more noticeable. As far as European butterflies are concerned the most important groups of such parasitoids are in the Hymenoptera, families Braconidae, Ichneumonidae and to a lesser extent Pteromalidae and Eulophidae, and the Diptera, families Tachinidae and much more rarely Bombyliidae. Hymenoptera have a piercing tubular ovipositior with which to inject eggs into the host's body or to reach a concealed host, and/or to sting the host with

venom. Diptera lack these abilities and instead different groups of Tachinidae adopt different strategies. Some scrape a wound through the host's skin into which they can oviposit, while others stick the egg externally to the host's skin and leave the first instar larva to enter the host (sometimes incubated eggs or even first instar tachinid larvae are placed near the host rather than on it). In another group, minute eggs are laid on plants to be ingested by caterpillars and hatch in their gut.

Parasitoids may develop internally within the host's body (endoparasitism) or externally (ectoparasitism, but this is not seen in Diptera parasitizing butterflies in Europe, and most ectoparasitoid Hymenoptera parasitize only concealed hosts). Many parasitoids, including all Tachinidae, allow the host to continue its development for a time after being parasitized (koinobionts) while others permanently paralyse or kill the host at the time of attack (idiobionts). Many idiobionts are ectoparasitoids of concealed hosts, but parasitism of butterfly pupae by idiobiont endoparasitoids is common. Most koinobionts inject the egg (or eggs, as some are gregarious) into the young caterpillar and the fully fed parasitoid larvae later erupt from the host after it has continued to grow, but others oviposit into caterpillars (in this case usually well-grown ones) and delay killing the host until after it has pupated. Tachinidae pupate inside their own larval skins to form a puparium, but most Ichneumonidae and Braconidae construct tough cocoons in which to pupate, although the Ichneumonidae that pupate inside host pupae manage without making a discrete cocoon.

While some parasitoid species in most groups tend to have quite wide host ranges (especially seen in idiobionts and in some tachinids), it is more usual for parasitoids (especially braconid and ichneumonid koinobiont endoparasitoids) to be specialized to a narrow range of hosts, often congeners, or even to be absolutely specialized to just one species of host. However, even for well-studied host groups such as European butterflies, there have been very few detailed studies of parasitoid complexes (summarized in SHAW *et al*., 2009; also STEFANESCU *et al*., 2009, 2012), and reliable data on regular host-parasitoid relationships is also surprisingly meagre (SHAW *et al*., 2009). This is partly because the literature is cluttered with a plethora of misinformation, resulting largely from misidentification of parasitoids (sometime because taxonomic understanding has subsequently advanced), incorrect assumptions of the true host, and the unreferenced reiteration of supposed associations without new substantiation (SHAW, 1994). There is thus much value in gathering and presenting quantitative rearing records made under carefully controlled conditions. In this paper we present records of parasitism of butterfly species, with some emphasis on Lycaenidae, collected in the field in several provinces in Spain.

Caterpillars of butterflies have evolved defensive adaptations to limit attack from natural enemies, including parasitoids. The caterpillars of some species of Lycaenidae such as *Iolana debilitata* (Schultz, 1905), *Lampides boeticus* (Linnaeus, 1767)*, Leptotes pirithous* (Linnaeus, 1767) and *Tomares ballus* (Fabricius, 1787) can at least partly protect themselves from parasitoid attack by feeding endophytically, in the fruit pod of legumes (JORDANO *et al*., 1990; GIL-T., 2004) or within leaf or stem tissue, as in *Cacyreus marshalli* Butler, 1898. In addition, the caterpillars of some species such as *T. ballus* use silk to seal their entrance hole into the pod. They feed inside the pod on the seeds, protected from parasitoid attack (JORDANO *et al*., 1990; OBREGÓN *et al*., 2012). Larvae are believed to be exposed to parasitoid attack only when they have consumed all the seeds in a pod and have to search for a new one (JORDANO *et al*., 1990), although the *Cotesia* species reported in the present work almost certainly attack the young host before it has a chance to enter and seal itself into the pod.

But the most striking mechanism for avoiding attack from parasitoids is probably the mutualistic relationship that lycaenid larvae have developed with ants (PIERCE *et al*., 2002; SEYMOUR *et al*., 2003). Various scenarios have been proposed to explain this complex behavior. THOMANN (1901) first suggested that the ants keep parasitoids away, thereby benefiting the larval instars (see also PIERCE & EASTAL 1986; PIERCE *et al.,* 1987). Larvae seek to attract ants by secreting sugary and nutritious exudates highly appreciated by ants, through exocrine glands - myrmecophilous organs - first described by NEWCOMER (1912). LENZ (1917) proposed another interpretation of the origin of these exudates, as adaptation of Lepidoptera larvae to produce a sugary liquid to prevent aggression by ants. In this case, any effect those ants have in protecting the caterpillars would be a secondary consequence,

but equally effective. In addition, caterpillars and pupae of myrmecophilous Lycaenidae can use acoustic signals (stridulatory organs) to attract the ants (PIERCE, 1995; PIRCE *et al*., 2002). Recently, in ÁLVAREZ *et al*. (2012, 2014) the stridulatory organs are found in myrmecophilous and nonmyrmecophilous lycaenids that supported the idea that sound production is not necessarily related with myrmecophily within the Lycaenidae. Commensalism that becomes a mutualistic relationship is a common process in the evolution of many interactions (MARGALEF, 1974). But in some cases the larvae of certain butterfly species exploit ant nests as food resource and shelter, and behave as specialized social parasites (WITEK *et al*., 2008). In the genus *Phengaris* Doherty, 1891 some species prey on ant brood and are called predatory species, while others, termed "cuckoo" species, mimic ant larvae and are fed directly by workers (WITEK *et al*., 2008). Whatever the origin may be, the caterpillars are at least to some extent protected through the presence of ants from predators and parasitoids (FIEDLER *et al*., 1993; JORDANO *et al*., 1992.), although some parasitoids have successfully specialized on Lycaenidae and may inflict heavy mortality (BINK, 1970, SHAW, 1996, SHAW *et al.,* 2009), and some extraordinary associations and behaviors have resulted (THOMAS & ELMES, 1993; THOMAS *et al.*, 2002). Thus many Lycaenidae have associations with ants, which can be both facultative and obligatory, ranging from mutualism to parasitism (Pierce *et al*., 2002). As a result, more than half the species of the family Lycaenidae may have an association with ants at some stage of their development (PIERCE, 1987; FIEDLER, 1996, 2006).

For many of the Iberian Lycaenidae, interactions with ants constitute a facultative and slack mutualism and, therefore, this association is not strictly necessary for the full development of the larva. Just in a few species, such as *Plebejus argus* (Linnaeus, 1758) (THOMAS, 1985; SEYMOUR *et al.*, 2003), an obligate myrmecophily occurs and, in the most extreme case, mutualism becomes obligate parasitism, as in genus *Phengaris*, regarded as social parasitism (THOMAS *et al.*, 1991; MUNGUIRA & MARTÍN, 1997; ALS *et al.*, 2001; WITEK *et al.*, 2008.).

Although some recent papers describe associations between ants and certain Iberian lycaenids (MUÑOZ-SARIOT, 2011; OBREGÓN & GIL-T., 2011; ÁLVAREZ *et al.*, 2012; GARCÍA-BARROS *et al*., 2013), there is still much to learn about myrmecophily and other aspects of the ecology and biology of many lycaenid and other Iberian butterflies. In this paper we provide new information on these interactions observed during our several years of study of Iberian butterflies, and summarize the observations already recorded by other authors in the literature.

Materials and methods

Our data are the results of field observation and rearing larvae in a range of instars of various species of butterflies, particularly Lycaenidae, found and collected while feeding on their host plants.

Parasitoids (Hymenoptera and Diptera) were obtained from laboratory rearing of wild-collected larvae and pupae, preserved in alcohol and subsequently identified by the second author (except as indicated in Acknowledgements). The adults are deposited in the National Museums of Scotland. We give the rearing data quantitatively as an indication of the level at which a particular parasitoid interaction was occurring. However, it is important to recognize that it is not possible to use these data to suggest an overall percentage parasitism for the host population for three main reasons (SHAW *et al*., 2009): (a) At the time of host collection, some parasitoids may have already killed their hosts and would then be unaccounted for, and some parasitoid attack may not occur until after the sampling date, whether at the same or a subsequent host stage; (b) healthy and parasitized mobile hosts are neither ecologically nor behaviorally equivalent, and may not be equally amenable to sampling; and (c) parasitism by koinobionts often alters the growth rate of the host, usually by retarding it so parasitism can appear to be much higher than it really is if sampling is done after a proportion of healthy hosts have left the arena (for example to pupate elsewhere).

Ants with which lycaenid larvae were interacting directly were captured and preserved in alcohol (90%) and identified in the laboratory, avoiding possible errors from "in situ" identification or through

photographs. The ant samples are deposited in the collection of the Department of Botany, Ecology and Plant Physiology, in the University of Córdoba. Nomenclature is that of Fauna Europaea.

Results

Parasitoid interactions

Table I summarizes the parasitoids identified obtained from the Lepidoptera species collected in the field (butterfly families: Lycaenidae, Pieridae, Hesperiidae and Nymphalidae) and the stage of the life history of the butterfly that is finally killed. It also includes the locality, province, 10 km UTM grid and altitude where the observations were made.

Table I.– Ecological and distribution data of the parasitoids reared during this study.

Parasitoid species	Butterfly species	Parasitoid family	Host stage killed	Butterfly foodplants	Locality	Province	10 Km UTM square	Altitude (m)
Cotesia astrarches (Marshall)	*Tomares ballus*	Braconidae	Larva	*Erophaca baetica* (Linnaeus)	Los Villares	Córdoba	30SUH40	530
Cotesia astrarches	*Tomares ballus*	Braconidae	Larva	*Erophaca baetica*	Cabeza Aguda, Parrillas	Córdoba	30SUH12	610
Cotesia astrarches	*Tomares ballus*	Braconidae	Larva	*Erophaca baetica*	Erillas	Córdoba	30SUH02	724
Cotesia glabrata (Telenga)	*Carcharodus alceae*	Braconidae	Larva	*Lavatera cretica* Linnaeus	Huerta El Caño	Córdoba	30SUG49	120
Cotesia glabrata	*Carcharodus tripolinus*	Braconidae	Larva	*Malva sylvestris* Linnaeus	Barragem do Arade	Silves, Portugal	29SNB51	25
Cotesia inducta (Papp)	*Leptotes pirithous*	Braconidae	Larva	*Medicago sativa* Linnaeus	Huerta El Caño	Córdoba	30SUG49	120
Cotesia inducta	*Leptotes pirithous*	Braconidae	Larva	*Rosmarinus officinalis* Linnaeus	Los Idolos	Córdoba	30SUG29	325
Cotesia inducta	*Zizeeria knysna*	Braconidae	Larva	*Tribulus terrestris* Linnaeus	Córdoba	Córdoba	30SUG49	120
Cotesia saltatoria (Balevski)	*Callophrys rubi*	Braconidae	Larva	*Cistus monspeliensis* Linnaeus	Erillas	Córdoba	30SUH02	724
Cotesia saltatoria	*Zizeeria knysna*	Braconidae	Larva	*Tribulus terrestris*	Huerta El Caño	Córdoba	30SUG49	120
Cotesia specularis (Szépligeti)	*Lampides boeticus*	Braconidae	Larva	*Erophaca baetica*	Los Villares	Córdoba	30SUH40	530
Cotesia specularis	*Lampides boeticus*	Braconidae	Larva	*Erophaca baetica*	Guadiatillo	Córdoba	30SUH20	350
Cotesia tenebrosa- agg. (Wesmael)	*Polyommatus icarus*	Braconidae	Larva	*Medicago* spp.	Pandiello	Asturias	30TUN49	390

Cotesia vanessae (Reinhard)	*Vanessa cardui*	Braconidae	Larva	*Malva sylvestris*	Huerta El Caño	Córdoba	30SUG49	120
Cotesia vanessae	*Vanessa atalanta*	Braconidae	Larva	*Urtica urens* Linnaeus	Huerta El Caño	Córdoba	30SUG49	120
Cotesia vestalis (Haliday)	*Vanessa*	Braconidae *cardui*	Larva	*Malva sylvestris*	Huerta El Caño	Córdoba	30SUG49	120
Cotesia vestalis	*Vanessa cardui*	Braconidae	Larva	*Malva sylvestris*	Barragem do Arade	Silves, Portugal	29SNB51	25
Meteorus pulchricornis (Wesmael)	*Charaxes jasius*	Braconidae	Larva	*Arbutus unedo* Linnaeus	Las Tonadas	Córdoba	30SUH21	500
Anisobas seyrigi- agg. Heinrich	*Lampides boeticus*	Ichneumonidae	Pupa	*Erophaca baetica*	Los Villares	Córdoba	30SUH40	530
Anisobas seyrigi- agg.	*Glaucopsyche melanops*	Ichneumonidae	Pupa	*Erophaca baetica*	Cuesta Traición	Córdoba	30SUG49	120
Anisobas seyrigi- agg.	*Leptotes pirithous*	Ichneumonidae	Pupa	*Erophaca baetica*	Guadiatillo	Córdoba	30SUH20	350
Anisobas rebellis Wesmael	*Lycaena phlaeas*	Ichneumonidae	Pupa	*Erophaca baetica*	Tonadas	Córdoba	30SUH21	500
Anisobas rebellis	*Lycaena phlaeas*	Ichneumonidae	Pupa	*Rumex pulcher* Linnaeus	Idolos	Córdoba	30SUG29	325
Hyposoter ebeninus (Gravenhorst)	*Pieris brassicae*	Ichneumonidae	Larva	*Capparis spinosa* Linnaeus	Niebla	Huelva	29SQB03	39
Neotypus intermedius Mocsary	*Lampides boeticus*	Ichneumonidae	Pupa	*Erophaca baetica*	Guadiatillo	Córdoba	30SUH20	350
Brachymeria tibialis (Walker)	*Aporia crataegi*	Chalcididae	Pupa	*Crataegus monogyna* Jacq.	Campos H. Perea	Jaén	30SWH20	1700
Catolaccus crassiceps (Massi)	*Sloperia proto*, via Cotesia	Pteromalidae	Cocoon, secondary parasitoid	*Phlomis purpurea* Linnaeus	Sierra Gallinera	Córdoba	3SUG84	800
Pteromalus puparum (Linnaeus)	*Aglais io*	Pteromalidae	Pupa	*Urtica dioica* Linnaeus	Puerto Panderrueda	León	30TUN37	1470
Pteromalus puparum	*Pieris brassicae*	Pteromalidae	Pupa	*Brassica sp.*	Río Bailón	Córdoba	30SUG85	650
Aplomya confinis (Fallén)	*Tomares ballus*	Diptera	Larva	*Erophaca baetica*	Guadiatillo	Córdoba	30SUH20	350
Aplomya confinis	*Lycaena phlaeas*	Diptera	Larva	*Rumex pulcher*	Tonadas	Córdoba	30SUH21	500

This table clearly shows that the large koinobiont endoparasitoid braconid genus *Cotesia*, which contains many species (both solitary and gregarious) associated with butterflies in Europe, includes several parasitoids of Lycaenidae (see also SHAW, 2007; SHAW *et al*., 2009). Unfortunately this

includes some poorly characterized species in aggregates that are difficult to resolve morphologically (SHAW, 2007), and their taxonomy remains to some extent in a state of flux (SHAW, unpublished data). Recently, a substantial number of reared samples have been barcoded, and this CO1 sequence data has informed some of the determinations given in this paper.

HYMENOPTERA
BRACONIDAE

Cotesia astrarches (Marshall, 1889), a gregarious species with usually rather small broods (typically from two or three up to about ten) and pale yellow cocoons, was previously recorded from *Cupido minimus* (Fuessly, 1775) (but doubtfully, as only from males (SHAW, 2007)), *Aricia agestis* ([Denis & Schiffermüller], 1775), *A. artaxerxes* (Fabricius, 1793) and *Polyommatus thersites* (Cantener, [1835]) (SHAW, 2007; SHAW *et al*., 2009). In this paper it is recorded from *T. ballus* (Fig. 1) (previously recorded in MUÑOZ-SARIOT, 2011) as well as from *P. abencerragus* (Pierret, 1837) (OBREGÓN *et al*., 2014). The braconid was identified from a sample of 78 adult wasps (41 females and 37 males) reared from 11 *P. abencerragus* larvae (out of 28 captured as 4th instar larvae) and another 82 adult wasps (48 females and 34 males) reared from 21 *T. ballus* larvae (96 parasitized from a total of 326 larvae in 2009 and 56 parasitized larvae from 304 captured in 2012). The parasitoid was present at all sites sampled.

Cotesia glabrata (Telenga, 1955), is a gregarious parasitoid, recorded from certain *Carcharodus* spp. and *Pyrgus* spp. (SHAW *et al.*, 2009), although recent CO1 sequence data suggest that specimens reared from *Pyrgus* may belong to a different (cryptic) species (M. R. Shaw, unpublished). We have reared this parasitoid from both of the two *Carcharodus* species that are consistently parasitised by it: *C. alceae* (6 broods from 18 larvae collected in the 3rd instar) and *C. tripolinus* (Verity, 1925) (the latter in southern Portugal, 1 parasitized out of 4 larvae collected in the 3th instar).

Cotesia inducta (Papp, 1973), a solitary parasitoid, is known from *Tomares ballus, Callophrys avis* Chapman, 1909, *Satyrium w-album* (Knoch, 1782)*, Celastrina argiolus* (Linnaeus, 1758) and *Glaucopsyche melanops* (Boidsduval, [1828]) (SHAW, 2007; SHAW *et al.*, 2009). In this study we have found this species parasitizing larvae of *Leptotes pirithous* (7 parasitized from 38 larvae reared) and *Zizeeria knysna* (Trimen, 1862) (1 from 6). It is a highly distinctive species that was described only in 1973, since when it appears to have spread widely in Europe and become a rather common parasitoid of a range of Lycaenidae.

Cotesia saltatoria (Balevski, 1980) is a solitary parasitoid that has previously been recorded from *Aricia agestis, A. artaxerxes, Polyommatus amandus* (Schneider, 1792)*, P. icarus* (Rottemburg, 1775) and *P. coridon* (Poda, 1761) (SHAW, 2007; SHAW *et al.*, 2009). In this study it is tentatively recorded for the first time parasitizing *Callophrys rubi* (Linnaeus, 1758), from a single female that emerged from its very pale yellow cocoon (out of 15 collected as 2nd instar larvae). However, this is rather a poorly characterized species and definitive identification is awaiting molecular studies. The identity of a series of both sexes from *Zizeeria knysna* has been confirmed from CO1 sequences (unpublished).

Cotesia specularis (Szepligeti, 1896), is previously known as a gregarious parasitoid of endophytic lycaenids feeding in fruit pods of legumes: *Lampides boeticus, Iolana debilitata* (Schultz, 1905) and *Glaucopsyche alexis* (Poda, 1761) (SHAW *et al*., 2009). This study confirms parasitism of *L. boeticus*. The parasitoid is morphologically very difficult to separate from *C. astrarches*, but tends to be smaller with much larger brood sizes, and to have pure white cocoons. Unfortunately the CO1 barcodes of the two species overlap, but despite these difficulties we are confident that the species are distinct. We reared 59 broods from a batch of 211 larvae in 2009, and 15 from 77 larvae in 2012, but unfortunately losses from disease were high in both years.

Cotesia tenebrosa (Wesmael, 1837), has been described as parasitizing the following lycaenids: *Cupido alcetas* (Hoffmansegg, 1804), *Plebejus argus, Aricia morronensis* (Ribbe, 1910)*, Polyommatus icarus*, *P. daphnis* ([Denis & Schiffermüller], 1775), *P. bellargus* (Rottemburg, 1775), *P. coridon, P. albicans* Gerhard and *P. admetus* (Esper, 1785) (SHAW, 2007; SHAW & GIL-T., 2008; SHAW *et al*., 2009, MUÑOZ-SARIOT, 2011). In this paper it is recorded from *P. icarus*, as a single brood of 4 females

and 1 male from the only larva collected. The host is presumably *P. icarus*, because of the northern locality of this record (Cantabrian mountains) in the Iberian Peninsula, where its cryptic sister-species *P. celina* (Astaut, 1879) seems not to fly (DINCA *et al.*, 2011). However, recent molecular genetic results (M.R. SHAW, unpublished) suggest that *C. tenebrosa* auctt. is an aggregate of at least three species, and it is not clear to which the name *C. tenebrosa* should be applied. This uncertainty also affects the published records outlined above. The CO1 sequence from the series found in this study clusters with sequences from *Cotesia* ex *P. icarus* (Scotland), *P. admetus* (Greece) and *Plebejus* sp. (France).

Cotesia vanessae (Reinhard, 1880), is a common and widespread gregarious species recorded parasitizing the nymphalidae hosts *Vanessa atalanta* (Linnaeus, 1758)*, Vanessa cardui* (Linnaeus, 1758) and *Aglais urticae* (Linnaeus, 1758) (SHAW *et al.*, 2009; STEFANESCU *et al.*, 2012.). Its presence was confirmed in wintering populations of *V. cardui* and *V. atalanta* in the province of Cordoba (Spain). In more northern areas of Europe, where vanessine larvae are not available in the winter months, the overwintering generation parasitizes certain noctuid larvae (NIXON, 1974), and this is also the case in Canada (HERVET *et al.*, in press).

Cotesia vestalis (Haliday, 1834), is a solitary parasitoid that has been recorded from early instar larvae of *Vanessa cardui, Aglais urticae, Nymphalis polychloros* (Linnaeus, 1758)*, Maniola jurtina* (Linnaeus, 1758) and *Hipparchia semele* (Linnaeus, 1758) larvae (SHAW *et al.*, 2009; STEFANESCU *et al.*, 2012) as well as several other Lepidoptera, the best known of which is the pest plutellid *Plutella xylostella* (Linnaeus, 1758). Its winter nymphalid host *V. cardui* is confirmed in this study in southern Spain and Portugal.

Meteorus pulchricornis (Wesmael, 1835), is a solitary koinobiont endoparasitoid parasitizing an extremely wide range of Lepidoptera larvae (STIGENBERG & SHAW, 2013). Among butterfly hosts it was previously known from *Iphiclides podalirius* (Linnaeus, 1758), *Thecla betulae* (Linnaeus, 1758) and *Charaxes jasius* (Linnaeus, 1767) (SHAW *et al.*, 2009). Our specimen was from the last of these. Only one of the 22 larvae reared in captivity was parasitized, but the parasitoid killed the host in its 3rd instar while some of the collected hosts were more advanced than that.

ICHNEUMONIDAE

Anisobas seyrigi Heinrich, 1934, is a solitary larva-pupal koinobiont parasitoid, that oviposits into the final instar host, either when it exposes itself after it has finished feeding or using its somewhat exserted ovipositor to inject its egg into the host through the membrane of the pod or through the silk-sealed entry hole made by the caterpillar. The parasitoid adults emerge from the lycaenid pupa. HORSTMANN (2007) records it from the univoltine lycaenid *Glaucopsyche melanops*, in the pupa of which the parasitoid remains dormant for many months and emerges the following spring so as to coincide with the next generation of the host. However, the distribution of the parasitoid extends well beyond that of the rather restricted *G. melanops*, and therefore HORSTMANN (2007) concluded that there must be other hosts. In this study we reared it from *G. melanops*, confirming its univoltinism in that host (with prolonged summer as well as winter diapause). We also reared a female and a male from *Lampides boeticus* (from 29 final instar larvae collected), and a series of three females and three males from *Leptotes pirithous* (from 33 collected in the final larval instar), with the adult parasitoid emerging from the host pupa just a week or two after the host had pupated in all of these cases (Fig. 2). Because the phenology was so different from the material known from *G. melanops*, all available material was submitted to Dr. Klaus Horstmann for his opinion. His view was that, morphologically, the material all belongs to one species, *A. seyrigi*. Our rearings thus explain the wider geographical distribution of this parasitoid in its broad sense, but it seems to us that the most parsimonious hypothesis is that in fact two cryptic species are involved, one a univoltine specialist of *G. melanops* and the other, apparently as yet undescribed, a plurivoltine species with a different distribution and host range. Experiments to further investigate this possibility are easy to envisage, but have not been attempted.

Anisobas rebellis Wesmael, 1845, is a solitary larva-pupal koinobiont parasitoid that oviposits into final instar larvae and emerges as an adult from its host's pupa. It is a specialist parasitoid of *Lycaena*

species, and has been previously recorded from *L. phlaeas* (Linnaeus, [1760]), *L. dispar* (Haworth, 1802) and *L. virgaureae* (Linnaeus, 1758) (SHAW *et al.,* 2009). We reared a female and a male from 36 *L. phlaeas* collected as final instar larvae: 1 at Tonadas (n=16) and 1 at Morilla (n=20). Under laboratory conditions, the adults emerged nine (female) and twelve (male) days after the host had pupated.

Hyposoter ebeninus (Gravenhorst, 1829), is a solitary koinobiont endoparasitoid of the larvae of various Pieridae in the genera *Pieris*, *Euchloe*, and less commonly *Pontia* and *Anthocharis*, with an unusual extension of host range to include the pyrgine hesperiid, *Carcharodus alceae* (SHAW *et al*., 2009). It is a common parasitoid of both host groups in southern Europe, and molecular studies have not revealed a corresponding difference in CO1 sequences (SHAW & QUICKE, unpublished data). However, successful cross-rearing experiments have not been undertaken. The parasitoid pupates in its cocoon spun within the larval skin of the host. We collected 42 *Pieris brassicae* (Linnaeus, 1758) larvae in their third instar, only 5 of them parasitized and in each case the host was killed in its fourth instar.

Neotypus intermedius Mocsary, 1883, a solitary koinobiont larva-pupal species that may attack the host at an earlier stage than in the case of *Anisobas* species, and may be a specialist parasitoid of *Lampides boeticus* (SHAW *et al*., 2009). As in *Anisobas*, the adults emerge from the pupa of the lycaenid. The host, from which we reared three females and three males, is confirmed in this paper. We obtained the 6 parasitized pupae from a batch of 211 larvae reared in 2009.

CHALCIDIDAE

Brachymeria tibialis (Walker, 1834), is a solitary idiobiont pupal parasitoid previously recorded from a wide range of Lepidoptera pupae, including various butterflies (NOYES, 2013). It is also capable of behaving as a pseudohyperparasitoid. Adults emerge directly from the pupae of their hosts. In this paper we have obtained a female specimen from 1 of 5 *Aporia crataegi* (Linnaeus, 1758) pupa collected.

PTEROMALIDAE

Catolaccus crassiceps (Masi, 1911), is an idiobiont ectoparasitoid that is frequently a solitary pseudohyperparasitoid in Braconidae: Microgastrinae cocoons, among a wide recorded host range (NOYES, 2013). In our observations the host was a *Cotesia* parasitoid (either *C. glabrata* or a species closely related to that) of *Sloperia proto* (Ochsenheimer, 1808).

Pteromalus puparum Linnaeus, 1758, is a common and widespread gregarious idiobiont endoparasitoid that specializes on butterfly pupae, though other hosts have been recorded (NOYES, 2013). It is particularly common on Pieridae, Papilionidae and Nymphalidae (especially Nymphalini). The adult female prefers to oviposit through fresh soft pupal cuticle, and often sits on the host prepupa waiting for the chance to do this. The resulting small adults emerge direct from the host pupa, often the whole brood through a single hole. Our brood, from the single pupa collected, was reared from *Aglais io* (Linnaeus, 1758), a known host (though not recorded at first hand by SHAW *et al*., 2009).

DIPTERA
TACHINIDAE

Aplomya confinis (Fallén, 1820) (Exoristinae), is a specialist parasitoid of many species of Lycaenidae (SHAW *et al*., 2009). We reared this species from *Tomares ballus* feeding on *Erophaca baetica* seeds inside the pods (only 1 parasitized from 304 larvae collected) and *Lycaena phlaeas* (1 from 47 larvae), the parasitoid larva erupting always from late instar hosts. The parasitoid puparia formed near the host remains, and adult flies emerged after twelve days under laboratory conditions.

Myrmecophilous interactions

In this study ant interactions have been seen in the following species of lycaenid: *Glaucopsyche*

alexis, Leptotes pirithous, Lampides boeticus, Laeosopis roboris (Esper, [1793])*, Polyommatus celina, Pseudophilotes abencerragus, Favonius quercus* (Linnaeus, 1758), *Tomares ballus* and *Zizeeria knysna*, as shown in Table II. Because these interactions are, in many cases, facultative and geographically variable, data characterizing the observation (date, locality, 10 km. UTM square and altitude) as well as the ant species are included.

Table II.– Interactions between ants and Lycaenidae observed in this study and data on the locations where the interactions were stated.

Lycaenid species	Ant species	Date	Locality	Province	UTM 10 Km. Grid square	Altitude
G. alexis	*Plagiolepis schmitzii* Forel	9-VI-2012	Sierra de La Sagra	Granada	30SWG49	1165 m
G. alexis	*Iberoformica subrufa* (Roger)	9-VI-2012	Sierra de La Sagra	Granada	30SWG49	1165 m
L. pirithous	*Tapinoma nigerrimun* (Nylander)	6-IV-2012	Pinares de Aznalcázar	Sevilla	29SQB42	30 m
L. pirithous	*Plagiolepys pygmaea* (Latreille)	7-XI-2013	Los Ídolos	Córdoba	30SUG29	325 m
L. pirithous	*Plagiolepis schmitzii*	6-IV-2012	Pinares de Aznalcázar	Sevilla	29SQB42	30 m
L. pirithous	*Iberoformica subrufa*	19-IV-2012	Río Guadiatillo	Córdoba	30SUH20	350 m
L. pirithous	*Tetramorium forte* Forel	19-IV-2012	Río Guadiatillo	Córdoba	30SUH20	350 m
L. pirithous	*Crematogaster sordidula* (Nylander)	12-XI-2013	Los Ídolos	Córdoba	30SUG29	325 m
L. boeticus	*Tapinoma nigerrimun*	6-IV-2012	Pinares de Aznalcázar	Sevilla	29SQB42	30 m
L. boeticus	*Crematogaster auberti* Emery	19-IV-2012	Río Guadiatillo	Córdoba	30SUH20	350 m
L. boeticus	*Tetramorium forte*	19-IV-2012	Río Guadiatillo	Córdoba	30SUH20	350 m
L. boeticus	*Aphaenogaster gibbosa* (Latreille)	19-IV-2012	Río Guadiatillo	Córdoba	30SUH20	350 m
L. boeticus	*Crematogaster sordidula*	24-IV-2012	Cabeza Aguda, Parrillas	Córdoba	30SUH12	610 m
L. roboris	*Formica gerardi* Bondroit	3-VI-2012	Sierra Madrona	Ciudad Real	30SUH86	740 m
P. ¿ celina	*Camponotus fallax* (Nylander)	19-VII-2012	Sierra Mágina, Camino del Aguadero	Jaén	30SVG67	1120 m
P. abencerragus	*Plagiolepis schmitzii*	30-V-2012	Canteras de Asland	Córdoba	30SUG49	160 m
F. quercus	*Formica gerardi*	7-VI-2012	Sierra Madrona	Ciudad Real	30SUH86	750 m
F. quercus	*Pheidole pallidula* (Nylander)	3-VI-2012	Sierra Madrona	Ciudad Real	30SUH85	720 m
T. ballus	*Tetramorium forte*	19-IV-2012	Río Guadiatillo	Córdoba	30SUH20	350 m
T. ballus	*Plagiolepys pygmaea*	7-V-2012	Las Erillas	Córdoba	30SUH02	724 m
T. ballus	*Aphaenogaster gibbosa*	19-IV-2012	Río Guadiatillo	Córdoba	30SUH20	350 m
T. ballus	*Crematogaster auberti*	19-IV-2012	Río Guadiatillo	Córdoba	30SUH20	350 m
T. ballus	*Camponotus pilicornis* (Roger)	24/IV/2012	Cabeza Aguda, Parrillas	Córdoba	30SUH11	610 m
Z. knysna	*Formica cunicularia* Latreille	3-XI-2013	Parque urbano	Córdoba	30SUG49	150 m
Z. kysna	*Lasius niger* (Linnaeus)	5-XI-2013	Parque urbano	Córdoba	30SUG49	150 m

Glaucopsyche alexis (Poda, 1761) is a univoltine, rare and local lycaenid species in the southern Iberian Peninsula, only present in habitats with limestone soils in the Betic mountains where its food plants of the genus *Onobrychis* Miller, 1754 grow. It has been recorded associated with many ants species: *Myrmica scabrinodis* Nylander, 1846, *Crematogaster auberti* Emery, 1869, *Tapinoma erraticum* (Latreille, 1798), *Formica cinerea* Mayr, 1853, *F. selysi* Bondroit, 1918, *F. fusca* Linnaeus, 1758 *F. pratensis* Retzius, 1783, *F. sanguinea* Latreille, 1798, *F. forsslundi* Lohmander,1949, *Iberoformica subrufa* (Roger, 1859), *Camponotus aethiops* (Latreille, 1798), *C. massiliensis* Schmitz, 1950, *C. cruentatus* (Latreille, 1802), *Lasius alienus* (Foerster, 1850) (FIEDLER, 2006) and *Camponotus piceus* (Leach, 1825), *Lasius niger* (Linnaeus, 1758) and *L. brunneus* (Latreille, 1798) (ÁLVAREZ *et al*., 2012). In the present study, caterpillars were attended by *Plagiolepis schmitzii* Forel, 1895 and we also confirmed its interaction with *Iberoformica subrufa*. Larvae were found feeding on *Onobrychis argentea* Boissier, 1840. It is clearly a lycaenid that can be attended by many different ant species, having therefore a strong and facultative interaction with all of them.

Leptotes pirithous (Linnaeus, 1767) is a multivoltine, polyphagous and migratory lycaenid (TOLMAN & LEWINGTON, 1997). For this reason, probably, its association with ants is considered to be loose and facultative (MARTÍN-CANO, 1984). In southern Spain the larvae are frequently found feeding on *Erophaca baetica* and other legumes during the winter and early spring, although host plants change throughout the year. In November 2013, several third instar larvae attended by *Plagiolepis pygmaea* (Latreille, 1798) and *Crematogaster sordidula* (Nylander, 1849), were observed on flowering buds of *Rosmarinus officinalis* Linnaeus, 1753 in Cordoba, on which they fully developed to the adult stage. Interactions with *Lasius* sp. has been recorded (MARAVALHAS, 2003), in addition to *Crematogaster auberti* Emery, 1869 and *Plagiolepis pygmaea* (OBREGÓN & GIL-T., 2011).

Lampides boeticus (Linnaeus, 1767) is also a multivoltine and migratory species, which feeds on many species of legumes. Its life cycle has been described by MARTÍN-CANO (1984) and OBREGÓN (2011). It is considered a facultative myrmecophilous lycaenid (MARTÍN-CANO, 1984) and has been observed attended by the ants *Camponotus compressus* (Fabricius, 1787), *C. cruentatus, C. sylvaticus* (Olivier, 1792), *C. foreli* Emery, 1881, *Paratrechina clandestine* (Mayr, 1870), *Lasius* sp., *Anoplolepis gracilipes* Smith, 1857, *Plagiolepis* sp., *Tapinoma melanocephalum* (Fabricius, 1793), *Linepithema humile* (Mayr, 1868), *Iberoformica subrufa* and *Crematogaster auberti* (FIEDLER, 2006; OBREGÓN & GIL-T., 2011; ÁLVAREZ *et al*., 2012). We provide new records of attending ants: *Tapinoma nigerrimum* (Nylander, 1856), *Crematogaster auberti* Emery, 1869, *Tetramorium forte* Forel, 1904, *Aphaenogaster gibbosa* (Latreille, 1798) and *Crematogaster sordidula* (Nylander, 1849), all of them observed on larvae feeding on *Erophaca baetica* in Sierra Morena (southern Spain).

Laeosopis roboris (Esper, [1793]) is a univoltine and monophagous species on different species of ash trees (*Fraxinus* spp.). Interaction of the pupal stage with the ant *Lasius grandis* Forel, 1909 has been recorded, through which the pupa is protected until adult emergence (OBREGÓN & GIL-T., 2012). MUÑOZ-SARIOT, 2011 records *Lasius niger* as pupa-attending ant. In this study, we found several (n=26) pupa inside *Formica gerardi* Bondroit, 1917 nests, located under large stones at the base of ash trees (*Fraxinus angustifolia* Vahl, 1804) in June, in Sierra Madrona, southern Ciudad Real province.

Polyommatus celina (Astaut, 1879) is a multivoltine lycaenid distributed through the centre and south of the Iberian Peninsula, Balearic Islands, Sicily, Sardinia and Northern Africa (including the Canary Islands). This species was recently separated from *P. icarus*, a species widely distributed in the Palearctic region (DINCA *et al*., 2011). Both are common species in Spain and their larvae feed on a wide range of legumes (Fabaceae). Because of its wide distribution, the unresolved aggregate taxon (*P. icarus* + *P. celina*) has been recorded (as *P. icarus*) attended by many species of ants: *Myrmica sabuleti* Meinert, 1861, *M. lobulicornis* Nylander, 1857, *M. tenuispina* Ruzsky, 1905, *Lasius alienus* (Foerster, 1850), *L. niger, Iberoformica subrufa, Formica subpilosa* Ruzsky, 1902, *F. rufibarbis* Fabricius, 1793 and *Plagiolepis pygmaea* (FIEDLER, 2006). In the present study the larvae of *P. ? celina* (tentatively determined as this species and not *P. icarus* on the basis of wing colour and genitalia of specimens, and also because *P. icarus* has not been found in the immediate area) were located feeding on *Medicago sativa* Linnaeus, 1753 and were attended by *Camponotus fallax* (Nylander, 1856).

Pseudophilotes abencerragus (Pierret, 1837) is a univoltine lycaenid with a fragmented distribution and very loose interactions with ants. It has been observed attended by *Plagiolepis pygmaea* (OBREGÓN & GIL-T., 2012; OBREGÓN *et al.*, 2013) and *Crematogaster auberti* (ÁLVAREZ *et al.*, 2012; GARCÍA-BARROS *et al.*, 2013). In this work we found *Plagiolepis schmitzii* attending larvae feeding on *Cleonia lusitanica* (L.).

Favonius quercus (Linnaeus, 1758) is a univoltine and monophagous butterfly feeding on various species in the genus *Quercus* (oak). It has been recorded to be attended by *Lasius* sp. (FIEDLER, 2006). In June 2012, several pupae were found sheltered under large stones in nests of *Formica gerardi* and *Pheidole pallidula* (Nylander, 1849). Fully grown caterpillars presumably drop from the branches of the oaks or go down the trunk before finding shelter in ant nests at the base of trees; however, it is unknown if the caterpillars are carried to the nest by ants or if the caterpillars can find the nest by themselves.

Tomares ballus (Fabricius, 1787) is a univoltine species, with an early flight period in the south of the Iberian Peninsula where the adults are on the wing in early February (or even in late January), and it is considered a facultatively myrmecophylous species (DOWNEY, 1987; TOLMAN & LEWINGTON, 1997). Its life cycle has been extensively studied by JORDANO *et al.* (1990) and OBREGÓN (2011). Its association with ants has been previously cited: *Plagiolepis pygmaea* (FIEDLER, 2006) and *Crematogaster auberti, C. sordidula* (Fig. 3), *Iberoformica subrufa, Lasius grandis* and *Tapinoma nigerrimum* (Nylander, 1856) (OBREGÓN & GIL-T., 2011). In this work, it was found in association with other ants: *Tetramorium forte* Forel, 1904*, Aphaenogaster gibbosa* (Latreille, 1798) and *Camponotus pilicornis* (Roger, 1859), and we can also confirm its association with *P. pygmaea* and *C. auberti*. Larvae and the attending ants were located inside the fruit pods of *Erophaca baetica*.

Zizeeria knysna (Trimen, 1862) is a bivoltine lycaenid. The flight period lasts from April to November in two generations, and it is most abundant in early autumn. It is a Mediterranean species, flying mostly in wetlands and grasslands near water-courses, reservoir edges and urban parks and gardens. We found several caterpillars at the base of a *Tribulus terrestris* Linnaeus, 1753 (Zygophyllacea) plant in an urban garden in Córdoba, attended by *Lasius niger* from a nearby nest. In addition, a final instar caterpillar attended by a major ant of *Formica cunicularia* was also observed. This lycaenid species was previously recorded attended by *Pheidole pallidula* (OBREGÓN & GIL-T., 2011), a eurytopic species, and one of the most frequent and abundant ants in the Iberian Peninsula. It seems to be associated with *Z. knysna* very often, probably influenced by similar habitat requirements. We observed females actively seeking Fabaceae plants (i.e. *Medicago sativa* or *Trifolium repens*) for oviposition near *P. pallidula* nests (Fig. 4), or with the nests at the base of the host plant in the case of *T. terrestris*.

Some general aspects of the ecology of the species of Formicidae included in this work are summarized in Table 3. The database of Iberian ants "hormigas.org" and SUAY-CANO *et al.* (2002) were used as references. Most of the ant species associated with lycaenid caterpillars included in this paper are polyphagous or nectarivorous, which probably facilitates this interaction. Other species of ants with granivorous feeding regimes or with a strictly carnivorous diet are less often found interacting with lycaenid larvae.

Table III.– Trophic preferences, abundance in study area and distribution of the ants considered in this study, attending Lycaenid larvae.

Ant species	Trofic preferences	Abundance	Distribution	Habitat
Aphaenogaster gibbosa	Polyphagous (not nectar)	Very common	Western Mediterranean	Preferably under stones
Camponotus fallax	Strictly nectarivorous	Very common	Europe	Trees, occasionally under stones
Camponotus pilicornis	Strictly nectarivorous	Very common	Iberian endemism	Under stones, dry and sunny soils
Crematogaster auberti	Polyphagous (including nectar)	Very common	Western Mediterranean	Under stones, wet soils
Crematogaster sordidula	Polyphagous (including nectar)	Very common	Mediterranean basin	Under stones, on siliceous or calcareous dry soils

Formica cunicularia	Polyphagous (including nectar)	Common	Europe	Preferably in forest soils, occasionally in mature urban green
Formica gerardi	Polyphagous (including nectar)	Infrequent	Paleartic region	Under stones
Iberoformica subrufa	Polyphagous (including nectar)	Very common	Iberian Peninsula, and Southern France	Under stones
Lasius niger	Polyphagous (including nectar)	Common	Europe	Variety of habitats
Pheidole pallidula	Polyphagous (including nectar)	Very common	Paleartic región and Northern Africa	Variety of habitats
Plagiolepis pygmaea	Polyphagous (including nectar)	Very common	Mediterranean basin	Under stones, dry soils
Plagiolepis schmitzii	Polyphagous (including nectar)	Common	Southern Europe and Northern Africa	Under stones, wet soils
Tapinoma nigerrimum	Polyphagous (including nectar)	Very common	Mediterranean basin	On soil and under stones
Tetramorium forte	Oportunistic seed feeder	Very common	Mediterranean basin	On soil and under stones

Discussion

The data provided in this paper are valuable for understanding the key ecological interactions of Lepidoptera preimaginal stages with parasitoids and ants, for which detailed and reliable overall information necessarily accrues from many studies such as the one presented here. Interactions between 17 parasitoid taxa with 17 species of Lepidoptera, and nine lycaenid species and 15 ant species are recorded here, for just one relatively small corner of Europe. While some of these biological observations for parasitoids and ants are apparently not previously recorded in the literature, the concept of "new records" is not of great value: what is far more important is that quantitative records are made, as here, with careful evaluation and, crucially, with the deposition of voucher specimens in named depositories that thus allows for the scrutiny of others in cases of doubt. Only through these means will the vast amount of incorrect and questionable data, often replicated by unreferenced transcription, that has accrued in the literature for example for the host ranges of parasitoids (see SHAW, 1993, 1994; NOYES, 1994; SHAW *et al.*, 2009) gradually become marginalized. There is still a long way to go before the strength and specialization, or otherwise, of interactions such as the ones recorded in this paper become as clearly known on as broad a front as - for example - the food plants of butterflies. Nevertheless, we regard that as a highly worthy aim, and progress towards it makes a real contribution to the knowledge necessary for the conservation of these most fragile and vulnerable aspects of biodiversity (SHAW & HOCHBERG, 2001).

It is very remarkable that in the guild *T. ballus - L. boeticus - L. pirithous*, which feed simultaneously in *Erophaca baetica* (Linnaeus) Boisser, 1840 in Sierra Morena (southern Spain), each species of butterfly larvae is parasitized by a different *Cotesia* species despite being frequently found within the same fruits competing for their seeds. This observation suggests that among these three species there is no apparent competition (HOLT, 1970; HOLT & LAWTON, 1993) mediated by the same parasitoid. Thus each lycaenid species has its specific parasitoid with the result that, when a high density of any one of the hosts occurs, stimulating a corresponding increase in the population of its parasitoid, it would not adversely affect the less abundant host(s) through increased parasitism.

In addition to new data recorded in the ant interactions, it is interesting to note that two of the species of ants, *Tetramorium forte* and *Aphaenogaster gibbosa*, had not previously been recorded attending lycaenid caterpillars. The association of the genus *Tetramorium* and Lycaenidae was previously cited by FIEDLER (2006) but he had not identified any *Tetramorium* species. Some authors

have reported that some species of the genus *Tetramorium* also interact with other insect groups that produce honeydew, such as aphids (KROMBEIN *et al.*, 1979). Regarding the genus *Aphaenogaster*, there are only two other records of attending caterpillars, *A. subterranea* (Latreille) and *A. smythiesii japonica* Forel (FIEDLER, 2006). Our observations of *A. gibbosa* represent the first records of this species attending lycaenid larvae.

Acknowledgements

BIBLIOGRAPHY

ALS, T. D., NASH, D. R. & BOOMSMA, J. J., 2001.– Adoption of parasitic *Maculinea alcon* caterpillars (Lepidoptera: Lycaenidae) by three *Myrmica* ant species.– *Animal Behaviour*, **62**: 99-106.

ÁLVAREZ, M., MUNGUIRA, M. L. & MARTÍNEZ-IBÁÑEZ, M. D., 2012.– Nuevos datos y recopilación de las relaciones entre Lycaenidae y Formicidae en la Península Ibérica (Lepidoptera: Lycaenidae; Hymenoptera: Formicidae).– *SHILAP Revista de lepidopterología*, **40**(157): 45-59.

BINK F. A., 1970.– Parasites of *Thersamonia dispar* Haw. and *Lycaena helle* Den. & Schiff. (Lep., Lycaenidae).– *Entomologische Berichten,* **30**: 30-34.

DINCA, V., DAPPORTO, L. & VILA, R., 2011.– A combined genetic-morphometric analysis unravels the complex biogeographical history of *Polyommatus icarus* and *Polyommatus celina* Common Blue butterflies.– *Molecular Ecology*, **20**: 3921-3935.

DOWNEY, J., 1987.– Lycaenidae (Papilionoidea), p. 443-445. *In* F. W. STERH. *Inmature Insects*: 650 pp. Kendall/Hunt, Dubuque, Iowa.

FIEDLER, K., 1991.– Systematic, evolutionary and ecological implications of myrmecophily within the Lycaenidae (Insecta: Lepidoptera: Papilionoidea).– *Bonner Zoologische Monographien*, **31**: 1-210.

FIEDLER, K., 1996.– Host-plant relationships of lycaenid butterflies: Large-scale patterns, interactions with plant chemistry and mutualism with ants.– *Entomologia Experimentalis et Applicata*, **80**(1): 259-267.

FIEDLER, K., 2006.– Ant associates of Palaearctic lycaenid butterfly larvae (Hymenoptera: Formicidae; Lepidoptera: Lycaenidae) - a review.– *Myrmecologische Nachrichten*, **9**: 77-87.

FIEDLER, K., KRUG, E., & PROKSCH, P., 1993.– Complete elimination of hostplant quinolizidine alkaloids by larvae of a polyphagous lycaenid butterfly, *Callophrys rubi*.– *Oecologia*, **94**(3): 441-445.

GARCÍA-BARROS, E., MUNGUIRA, M. L., STEFANESCU, C. Y VIVES MORENO, A., 2013. *Lepidoptera Papilionoidea,* En: *Fauna Ibérica*, vol. 37, RAMOS, M.A. et al, (Eds.) Museo Nacional de Ciencias Naturales. CSIC. Madrid. 1213 pp.

HERVET, V. A., MURILLO, H., FERNÁNEZ-TRIANA, J. L., SHAW, M. R., LAIRD, R. A. & FLOATE, K. D., in press. First report of *Cotesia vanessae* (Hymenoptera: Braconidae) in North America.– *Canadian Entomologist*.

HOLT, R. D., 1970: Predation, apparent competition, and the structure of prey communities.– *Theoretical Population Biology*, **12**: 197-229.

HOLT, R. D. & LAWTON J. H., 1993: Apparent competition and enemy-free space in insect host-parasitoid communities.– *American Naturalist,* **142**: 623-645.

HORSTMANN, K., 2007.– Revision der Westpaläarktischen Arten von *Anisobas* Wesmael, 1985 (Hymenoptera, Ichneumonidae, Ichneumoninae).– *Entomofauna Zeitschrift für Entomologie*, **28**: 93-116.

JORDANO, D., FERNÁNDEZ-HAEGER, J. & RODRÍGUEZ J., 1990.– The life-history of *Tomares ballus* (Fabricius, 1787) (Lep: Lycaenidae): phenology and host plant use in southern Spain.– *Journal of Research on Lepidotera*, **28**: 112-122.

JORDANO, D., RODRÍGUEZ, J., THOMAS, C. D. & FERNÁNDEZ-HAEGER, J., 1992.– The distribution and density of a lycaenid butterfly in relation to *Lasius* ants.– *Oecologia*, **91**: 439-446.

KROMBEIN, K. V., HURD, JR., P. D., SMITH, D. R. y BURKS, B. D., 1979.– *Catalog of Hymenoptera in American North of Mexico*, **2**: 1011 pp. Smithsonian Institution Press. Washington, D. C.

MARAVALHAS, E., 2003.– *As Borboletas de Portugal*: 455 pp. Apollo Books, Stenstrup.

MARGALEF, R., 1974.– *Ecología*: 951 pp. Omega. Barcelona.

MARTÍN-CANO, J., 1984.– Biología comparada de *Lampides boeticus* (L.), *Syntarucus pirithous* (L.) y *Polyommatus icarus* (Rot.).– *Graellsia*, **40**: 163-193.

MUNGUIRA, M. L. & MARTÍN, J., 1997.– Action Plan for the *Maculinea* Butterflies in Europe.– *Nature and Environment*, **97**: 64 pp. Council of Europe Publishing, Strasbourg.

MUÑOZ-SARIOT, M. G., 2011.– *Biología y ecología de los Licénidos Españoles:* 383 pp. M. G. Muñoz Sariot, Granada

NEWCOMER, E. J., 1912.– Some observations on the relation of ants and lycaenid caterpillars, and a description of the relational organs of the latter.– *Journal of the New York Entomological Society*, **20**: 31-36.

NIXON G. E. J., 1974.– A revision of the north-western European species of the *glomeratus*-group of *Apanteles* Förster (Hymenoptera, Braconidae).– *Bulletin of Entomological Research,* **64**: 453-524.

NOYES, J. S., 1994.– The reliability of published host-parasitoid records: a taxonomist's view.– *Norwegian Journal of Agricultural Sciences,* **16**: 59-69.

NOYES, J. S., 2013.– Universal Chalcidoidea Database. Available from http:/www.nhm.ac.uk/chalcidoids (accessed 6th April 2014).

LENZ, F., 1917.– Der Erhaltungsgrund der Myrmekophilie.– *Zeitschrift für Induktive Abstammgs-und Vererbungslehre*, **18**: 44-48.

OBREGÓN, R., 2011.– El ciclo biológico de *Tomares ballus*.– *Danaus*, **3**: 7-10.

OBREGÓN, R. & GIL-T., F., 2011: Twenty-seven new records of associated ants with thirteen myrmecophilous lycaenid butterflies from Spain.– *Atalanta*, **42**: 139-143.

OBREGÓN, R., ARENAS-CASTRO, S., GIL-T., F., JORDANO, D. & FERNÁNDEZ-HAEGER, J., 2014.– Biología, ecología y modelo de distribución de las especies del género *Pseudophilotes* Beuret, 1958 en Andalucía (Sur de España) (Lepidoptera: Lycaenidae).– *SHILAP Revista de lepidopterología,* (in press).

OBREGÓN, R., DE HARO, S., JORDANO, D. & FERNÁNDEZ-HAEGER, J., 2012.– *Lampides boeticus* (Lepidoptera: Lycaenidae) preys on cocoons of its own specific parasitoid *Cotesia specularis* (Hymenoptera: Braconidae).– *Journal of Insect Behaviour,* **25**: 514-517.

PIERCE, N. E., 1987.– The evolution and biogeography of associations between lycaenid butterflies and ants.– *Oxford Surveys in Evolutionary Biology*, **4**: 89-116.

PIERCE, N. E., 1995.– Predatory and parasitic Lepidoptera: carnivores living on plants.– *Journal of the Lepidopterists' Society*, **49**: 412-453.

PIERCE, N. E., KITCHING, R. L., BUCKLEY, R. C., TAYLOR, M. F. J. & BENBOW, K. F., 1987.– The costs and benefits of cooperation between the Australian lycaenid butterfly, *Jalmenus evagoras*, and its attendant ants.– *Behaviour Ecology and Sociobiology,* **21**: 237-248.

PIERCE, N. E., BRABY, M. F., HEATH, A., LOHMAN, D. J., MATHEW, J., RAND, D. B. & TRAVASSOS, M. A., 2002.– The ecology and evolution of ant association in the Lycaenidae (Lepidoptera).– *Annual Review of Entomology*, **47**: 733-771.

PIERCE, N. E. & EASTEAL, S., 1986.– The selective advantage of attendant ants for the larvae of a lycaenid butterfly, *Glaucopsyche lygdamus*.– *Journal of Animal Ecology*, **55**: 451-462.

SEYMOUR, A. S., GUTIÉRREZ, D. & JORDANO, D., 2003.– Dispersal of the lycaenid Plebejus argus in response to patches of its mutualist ant *Lasius niger*.– *Oikos* **103**:162-174.

SHAW, M. R., 1993.– An enigmatic rearing of *Dolopsidea indagator* (Haliday) (Hymenoptera: Braconidae).– *The Entomologist's Record and Journal of Variation,* **105**: 31-36.

SHAW, M. R., 1994.– Parasitoid host ranges.– In B. A. HAWKINS & W. SHEEHAN (eds). *Parasitoid community ecology*: 111-144. Oxford University Press, Oxford.

SHAW, M. R., 1996.– Parasitism of *Aricia* species: preliminary results… and a call for help.– *Butterfly Conservation News,* **62**: 14-15.

SHAW, M. R., 2007.– The species of *Cotesia* (Cameron) (Hymenoptera: Braconidae: Microgastrinae) parasitising Lycaenidae (Lepidoptera) in Britain.– *British Journal Entomology Natural History*, **20**: 255-267.

SHAW, M. R. & HOCHBERG, M. E., 2001.– The neglect of parasitic Hymenoptera in insect conservation strategies: The British fauna as a prime example.– *Journal of Insect Conservation,* **5**: 253-263.

SHAW, M. R.; STEFANESCU, C. & VAN-NOUHUYS, S., 2009.– Parasitoids of European Butterflies.– *In* J. SETTELE, T. G. SHREEVE, M. KONVICKA & H. VAN DYCK (Ed.). *Ecology of Butterflies of Europe*: 130-156. Cambridge University Press, Crambidge.

STEFANESCU, C., ASKEW, R. R., CORBERA, J. & SHAW, M. R., 2012.– Parasitism and migration in southern Palaearctic populations of the painted lady butterfly *Vanessa cardui* (Lepidoptera: Nymphalidae).– *European Journal of Entomology,* **109**: 85-94.

STEFANESCU, C., PLANAS, J. & SHAW, M. R., 2009.– The parasitoid complex attacking coexisting Spanish populations of *Euphydryas aurinia* and *Euphydryas desfontainii* (Lepidoptera: Nymphalidae, Melitaeini).– *Journal of Natural History*, **43**(9): 553-568.

STIGENBERG, J. & SHAW, M. R., 2013.– Western Palaearctic Meteorinae (Hymenoptera: Braconidae) in the National Museums of Scotland, with rearing, phenological and distribution data, including six species new to Britain, and a discussion of a potential route to speciation.– *Entomologist's Gazette*, **64**: 251-268.

SUAY-CANO, V. A., TINAUT, A. & SELFA, J., 2002.– Las hormigas (Hymenoptera, Formicidae) asociadas a pulgones (Hemiptera, Aphididae) en la provincia de Valencia.– *Graellsia*, **58** (1): 21-37.

THOMANN, H., 1901.– Schmetterlinge und Ameisen. Beobachtungen Über eine Symbiose zwischen *Lycaena argus* L. und *Formica cinerea* Mayr.– *Jahresbericht der Naturforschenden Gesellschaft Graubünden*, **44**: 1-40.

THOMAS, C.D., 1985.– Specializations and polyphagy of *Plebejus argus* (Lepidoptera: Lycaenidae) in North Wales.– *Ecological entomology*, **10**(3): 325-340.

THOMAS, J. A. & ELMES, G. W., 1993.– Specialized searching and the hostile use of allomones by a parasitoid whose host, the butterfly *Maculinea rebeli*, inhabits ant nests.– *Animal Behaviour*, **45**: 593-602.

THOMAS, J. A., MUNGUIRA, M. L., MARTÍN, J. & ELMES, G. W., 1991.– Basal hatching in *Maculinea* butterfly eggs: a consequence of advanced myrmecophily?.– *Biological Journal of the Linnean Society*, **4**: 175-184.

THOMAS, J. A., KNAPP, J. J., AKINO, T., GERTY, S., WAKAMURA, S., SIMCOX, D. J., WARDLAW, J. C. & ELMES, G. W., 2002.– Parasitoid secretions provoke ant warfare.– *Nature,* **417**: 505-506.

TOLMAN, T. & LEWINGTON, R., 1997.– *Butterflies of Britain and Europe*: 320 pp. Harper Collins, London – Glasgow – New York – Sydney – Auckland – Toronto - Johannesburg.

WITEK M., SLIWINSKA, E. B., SKÓRKA, P., NOWICKI P., WANTUCH M., VRABEC, V., SETTELE, J. & WOYCIECHOWSKI, M., 2008.– Host ant specificity of large blue butterflies *Phengaris* (*Maculinea*) (Lepidoptera: Lycaenidae) inhabiting humid grasslands in East-central Europe.– *European Journal of Entomology*, **105**: 871-877.

R. O.*, D. J., J. F.–H.
Dept. Botany, Ecology and Plant Physiology
University of Córdoba
Campus de Rabanales
E-14071 Córdoba
ESPAÑA / *SPAIN*
*E-mail: rafaobregonr@gmail.com
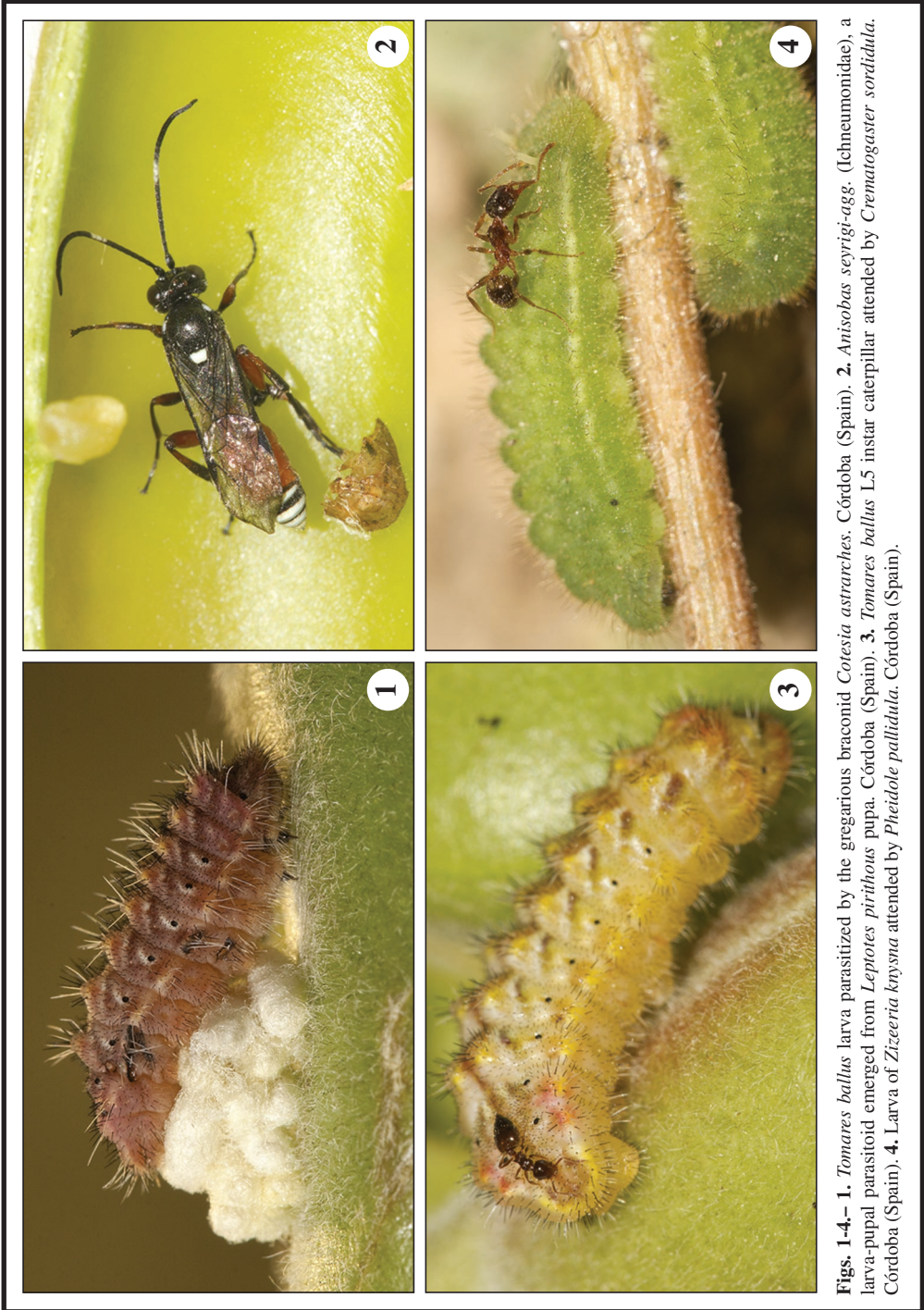E-mail: bvljobad@uco.es
E-mail: bv1fehaj@uco.es

M. R. S.
Honorary Research Fellow, National Museums of Scotland
Chambers Street
Edinburgh EH1 1JF,
REINO UNIDO / *UNITED KINGDON*
E-mail: markshaw@xenarcha.com

*Autor para la correspondencia / *Corresponding author*

Figs. 1-4.– 1. *Tomares ballus* larva parasitized by the gregarious braconid *Cotesia astrarches*. Córdoba (Spain). **2.** *Anisobas seyrigi-agg.* (Ichneumonidae), a larva-pupal parasitoid emerged from *Leptotes pirithous* pupa. Córdoba (Spain). **3.** *Tomares ballus* L5 instar caterpillar attended by *Crematogaster sordidula*. Córdoba (Spain). **4.** Larva of *Zizeeria knysna* attended by *Pheidole pallidula*. Córdoba (Spain).