



Figure 1. Panoramic view of a mature cork oak dehesa in the summer season. Dehesa La Vieja, Cornalvo Natural Park, Extremadura, Spain, July 2008. (Photo: Luis M. Torres-Vila / SSV.)

Billaea adelpha (Loew) (Diptera: Tachinidae) as a larval parasitoid of large oak-living cerambycids in Southwestern Spain

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Introduction

Oak forests are widespread in the Mediterranean Basin, occupying more than two million hectares in Southwestern Iberia alone. Most lowland oak forests in this area have experienced a huge man-made transformation during past centuries, so their primeval climax stage has almost completely disappeared. At present, oak forests occur as a savannah-like open woodland (the so-called *dehesa* in Spain and *montado* in Portugal) which sustain a well-defined traditional agro-silvo-pastoral use shaping landscape multiplicity. Lowland dehesas are typically populated by sclerophyllous and evergreen oak (*Quercus*) species, mostly holm oak (*Q. ilex* L.) and cork oak (*Q. suber* L.), over an often limited or absent woody understory and a grassland formed by annual and perennial species for pasture (Fig. 1). In higher or cooler areas, open woodlands may also be populated by marcescent/deciduous oaks, mainly pyrenean oak (*Q. pyrenaica* Willd.) but also gall oak (*Q. faginea* Lam.), though these species occur more typically in denser upland and hillside forests. Dehesa woodlands constitute the most important forest ecosystem in SW Iberia with outstanding socio-economic, ecological and biodiversity values (Montero *et al.* 1998, Moreno & Pulido 2009, Bugalho *et al.* 2011, Torres-Vila *et al.* 2017a), which hosts the highest levels of biological diversity in Europe (Cowling *et al.* 1996, Ramírez-Hernández *et al.* 2014, Vodka *et al.* 2009), so the dehesa ecosystem is considered a biodiversity hotspot (Medail & Quezel 1999, Myers *et al.* 2000) protected under the EU Habitats Directive (CEC 1992).

Three large xylophagous cerambycids are usually associated with these oak species, two Cerambycinae, namely *Cerambyx welensii* (Küster) (*Cw*) and *Cerambyx cerdo* L. (*Cc*), and one Prioninae, *Prinobius myardi* Mulsant (*Pm*) (López-Pantoja *et al.* 2008, 2011, Torres-Vila *et al.* 2017a,b). The life cycles of *Cw*, *Cc* and *Pm* typically occur in old, decayed and/or diseased oak trees, so that these longhorn beetles are included among the highly diverse assemblage of saproxylic (wood dwelling) insects. This functional group is important in wood degradation and

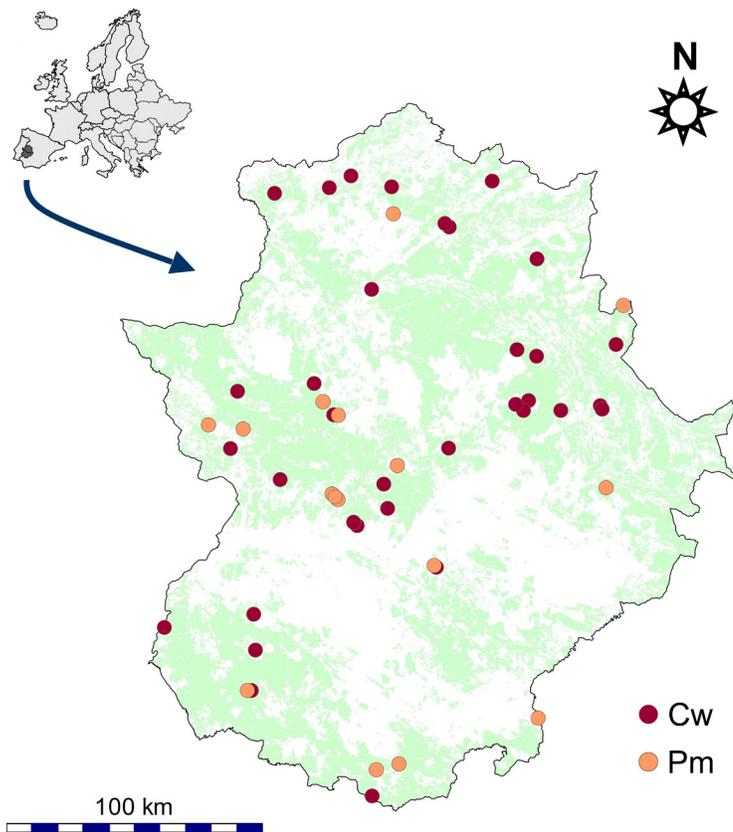


Figure 2. Records of *Billaea adelpha* parasitizing cerambycid larvae of either *Cerambyx welensii* (*Cw*) or *Prinobius myardi* (*Pm*) compiled during our 6-year study (2011–2016) in Extremadura (SW Spain). The forest cover layer (holm oak, cork oak, pyrenean oak and gall oak species pooled) is superimposed in green color. (Artwork: F. Javier Mendiola / Luis M. Torres-Vila.)

hollow formation in old trees, which will be later used as shelters by a large array of species, greatly contributing to the biodiversity in oak forests (Speight 1989, Grove 2002, Buse *et al.* 2008). However, as *Cw* and *Cc* are primary saproxylic beetles that need living wood for larval development, they also colonize young/healthy trees and can become harmful or pest species. The pest and legal status of the target cerambycids differs markedly depending on the geographical and forest context. *Cw* is an emerging pest involved in oak decline in Iberia (López-Pantoja *et al.* 2008, Torres-Vila *et al.* 2012, 2016); *Cc* is a protected species in Europe (CEC 1992, IUCN 2010) although also reported as a harmful or pest species in several circum-Mediterranean and Black Sea countries (Torres-Vila 2017); and *Pm* is a secondary/minor pest (López-Pantoja *et al.* 2011). The three longhorn species exhibit a typical western Palaearctic distribution with respective ranges widely overlapping in southern Europe. In SW Iberia, they are widespread, share a similar ecological niche, and often coexist in sympatry. Wood quality and host tree species are major factors shaping larval resource partitioning (Torres-Vila *et al.* 2017a).

In the described scenario, and despite its potential importance, very few data are reported in the literature about the natural enemies (particularly larval parasitoids) of these large cerambycids. In the last years our research group has studied the distribution, ecology and behavior of *Cw*, *Cc* and *Pm* in the region of Extremadura (SW Spain) in order to set up an integrated management strategy in dehesa woodlands. From a recent study on the larval ecology of these cerambycids (Torres-Vila *et al.* 2017a) we had the opportunity to collect and rear a large number of larvae and to obtain their parasitoids. Here we report on the field and laboratory results obtained, from which it is deduced that the tachinid *Billaea adelpha* (Loew) is by far the main larval parasitoid in the study area. We also provide some interesting data about the ecology and behavior of this fly species.

Study area

Our study area was the whole region of Extremadura (SW Spain), which extends over 41,634 km² (Fig. 2). The climate is typically Mediterranean with dry and hot summers (up to 40°C). Samples of cerambycid larvae were taken during six consecutive years (2011–2016) in the above mentioned oak species. Geographical coordinates were taken for each sampled tree. Sampling effort was standardized as far as possible to adequately cover geographical, altitudinal and host oak ranges.

Cerambycid species

Cw, *Cc* and *Pm* adults are large (about 25–60 mm), blackish-brown in color and show sexual dimorphism, with antennae longer in males (Fig. 3). The three species are univoltine, flying from late May to late August, with flight peaks occurring from late June to early July (*Cw* and *Cc*) or a little later (*Pm*). Adult daily activity occurs typically at dusk and early evening. *Cw* and *Cc* adults feed mainly on tree sap and exudates while *Pm* adults do not feed at all. Mated females lay eggs into bark crevices, pruning cuts and cork stripping wounds. Larvae are xylophagous mainly on oak species (see above). After hatching, neonate larvae bore subcortically and then tunnel increasingly wider and longer galleries into sapwood and heartwood (Figs. 5, 7). Larval development usually lasts 2–4 years and pupation occurs in early (*Pm*) or late summer (*Cw* and *Cc*) within a pupal cell constructed ad hoc by the larvae inside the sapwood. The pupal stage lasts about one month, but while *Pm* adults leave the tree to reproduce in the same summer, emerged *Cw* and *Cc* adults overwinter in a pre-reproductive stage until late spring in the following year. Colonized trees can be easily identified by the presence of adult exit holes and larval frass (Fig. 4). Larval galleries may cause huge physiological, mechanical and structural damage to oaks, and even tree death in the worst instances (Duffy 1953, Bense 1995, Vives 2000, López-Pantoja *et al.* 2011, Torres-Vila *et al.* 2016, 2017a,b).

Larval sampling

Candidate oaks were selected based on the presence of adult exit holes in the bark and larval galleries in pruning cuts or debarked wounds, very often with larval frass (Fig. 4). Some samples were also taken from firewood piles/woodsheds when the log source was known (about 15% of samples). Selected trees/branches were cut with a chainsaw (Fig. 6) and the resulting bolts carefully dissected looking for cerambycid larvae, using metal wedges



Figure 3. Adults of the three species of large oak-living cerambycids: *Cerambyx welensii* (top), *Cerambyx cerdo* (middle) and *Prinobius myardi* (bottom), (males of each species on the left). (Photos: Emilio Echevarría. Plate: Luis M. Torres-Vila.)



Figures 4–9. Cerambycid host larvae, damage and field sampling. **4.** Abundant larval frass in an old cork oak. **5.** Large *Prinobius myardi* larvae surprised inside their galleries. **6.** Newly fallen branch with cerambycid galleries cut into bolts with a chainsaw. **7.** Cut section of a holm oak bolt showing larval damage in the inner heartwood. **8.** *Prinobius myardi* larvae in a newly-opened holm oak bolt. **9.** Laboratory rearing of field-collected cerambycid larvae. (Photos: Luis M. Torres-Vila / SSV.)

and a sledgehammer (Figs. 5–8). All larvae in each sampled bolt were collected, individually arranged in aerated plastic containers, referenced and taken to the laboratory in portable coolers. Larvae were scored according to their body length as small (<20 mm), medium (20–40 mm) or large (>40 mm). Larvae of *Cerambyx* and *Prinobius* were easily differentiated as the first possess a ferruginous-pigmented band on the pronotum frontal margin and rounded mandible tips while in the second the frontal band is missing and mandibles are pointed. Field-collected larvae were individually reared at room temperature (22–28°C and 50–70% relative humidity) in aerated 140 ml plastic containers on an agar-based artificial diet (Fig. 9) (Morales-Rodríguez *et al.* 2015). Rearing containers were regularly inspected and emergence of parasitoids noted. Tachinid larvae were maintained in the laboratory until adulthood (Fig. 13) and then identified to species (by the second author).

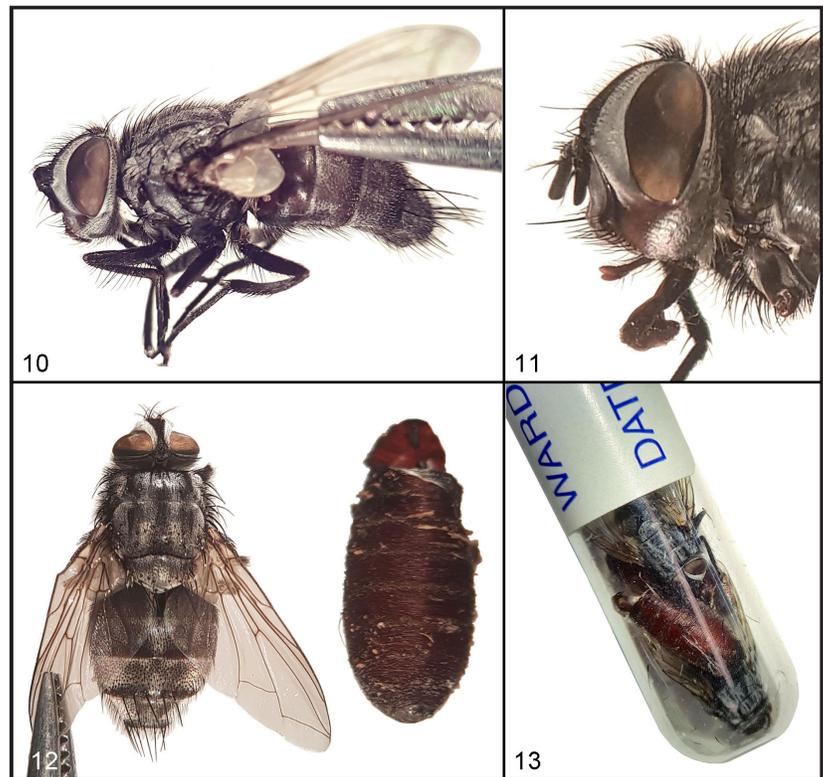
Data analysis

Mean parasitism rate (i.e., mean of parasitism percentages in larval samples, including 0% values) was used to assess the effects of host species (*Cw* vs. *Pm*), larval size (small, medium or large) and oak species (holm, cork or pyrenean oak) on parasitism pressure. The number of *Cc* larvae collected was very low (see Torres-Vila *et al.* 2017a about this fact), so this species was not considered in this study. The effect of host size on the number of parasitoids emerged per parasitized larva was also examined. Data were analyzed through Kruskal-Wallis tests (Mann-Whitney U test for two-sample contrasts) using SYSTAT software.

Vouchers and DNA barcoding

Voucher specimens of the reared tachinids (all *Billaea adelpha*) were deposited in the entomological collection of the senior author's institution. The specimens are preserved dry in 35 labeled vials (references 01T to 35T), each vial containing all individuals (adults and puparia) obtained from a single parasitized beetle larva.

Five *Billaea adelpha* adults among those obtained in this study were DNA barcoded (COI gene fragment) and sequences will be publicly available online through GenBank database.



Figures 10–13. *Billaea adelpha* individuals (all males) obtained in the laboratory from field-collected cerambycid larvae. **10.** Adult lateral view. **11.** Adult head lateral view. **12.** Newly-emerged fly and puparium remains. **13.** Tube with the set of parasitoids emerged from a single host larva. (Photos: Rafael López / Luis M. Torres-Vila / SSV.)

Results

More than 400 oak trees were inspected and 500 bolts from 348 trees (181 holm oaks, 113 cork oaks and 54 pyrenean oaks) were finally dissected. A summary of the number of larval samples recovered and larvae number (collected and parasitized) arranged by host cerambycid and oak species is shown in Table 1. The tachinid fly *Billaea adelpha* (Loew) (Figs. 10–12) was the only larval parasitoid detected in both *Cw* and *Pm*, being widespread throughout the entire region (Fig. 2) and over a broad altitudinal range (162–1315 m). However, parasitism rates by *B. adelpha* were rather low in both *Cw* and *Pm* (Table 1). Parasitism pressure was almost twice in *Cw* than in *Pm* (Table 1) although such difference was not significant (Mann-Whitney test, $U_1 = 24782.5$, $P = 0.95$).

Oak species in which host larvae lived did not affect parasitism rate in both *Cw* (Kruskal-Wallis test, $U_2 = 2.92$, $P = 0.23$) and *Pm* ($U_1 = 2079.0$, $P = 0.30$). Hence, oak species were pooled in subsequent analyses. Note that degrees of freedom in these tests differ between cerambycid species as *Pm* larvae were never found in pyrenean oak (Table 1).

Table 1. Mean parasitism rates by *Billaea adelpha* on *Cerambyx welensii* (*Cw*) and *Prinobius myardi* (*Pm*) larvae recorded in Extremadura (SW Spain) during our 6-year study (2011–2016).

Host cerambycid	Oak species	Larval samples ¹	Larve number		Parasitism rate (%)	
			Collected	Parasitized	mean ± SE	range
<i>Cw</i>	holm oak	105	417	17	5.03 ± 1.78	0-100
<i>Cw</i>	cork oak	138	747	12	2.44 ± 1.09	0-100
<i>Cw</i>	pyrenean oak ²	89	273	17	4.33 ± 1.48	0-100
Total <i>Cw</i>		332	1437	46	3.77 ± 0.82	0-100
<i>Pm</i>	holm oak	115	969	21	2.23 ± 0.71	0-50
<i>Pm</i>	cork oak	34	174	3	0.90 ± 0.75	0-25
<i>Pm</i>	pyrenean oak	0	0	–	–	–
Total <i>Pm</i>		149	1143	24	1.93 ± 0.57	0-50
Total <i>Cw</i> + <i>Pm</i>		481	2580	70	–	–

¹ number of dissected bolts with at least one cerambycid larva for each host species / oak species combination.

² one parasitized *Cw* larva from gall oak. Note that *Pm* larvae were never found in pyrenean oak.

SE: standard error of the mean.

Host larval size and the origin of the wood (trees vs. firewood) in which cerambycid larvae were collected had a noticeable effect on the parasitism exerted by *B. adelpha* (Fig. 14). Parasitism rate depended on larval size at collection time, with overall higher values in large than in small larvae and intermediate values in medium-sized larvae (see total panel in Fig. 14), both in *Cw* ($U_2 = 5.84$, $P = 0.05$) and in *Pm* ($U_2 = 5.26$, $P = 0.07$) although in the last species significance was close to the limit. Host larval size did not affect the number of flies that emerged from a single parasitized larva (large vs. medium plus small larvae pooled), in both *Cw* ($U_1 = 118.0$, $P = 0.55$) and *Pm* ($U_1 = 21.0$, $P = 0.70$). The number of parasitoids per larva did not differ either between cerambycid species ($U_1 = 311.5$, $P = 0.99$) with values of 3.08 ± 0.51 , 1–13 (mean ± SE, range) in *Cw*, and 2.94 ± 0.84 , 1–14 in *Pm*.

Regarding the effect of wood origin, the most striking outcome was observed in large larvae (Fig. 14). Thus, parasitism rate in large *Pm* larvae was significantly higher in firewood than in trees ($U_1 = 1096.0, P < 0.05$), the trend in large *Cw* larvae being similar although not significant ($U_1 = 3198.0, P = 0.12$).

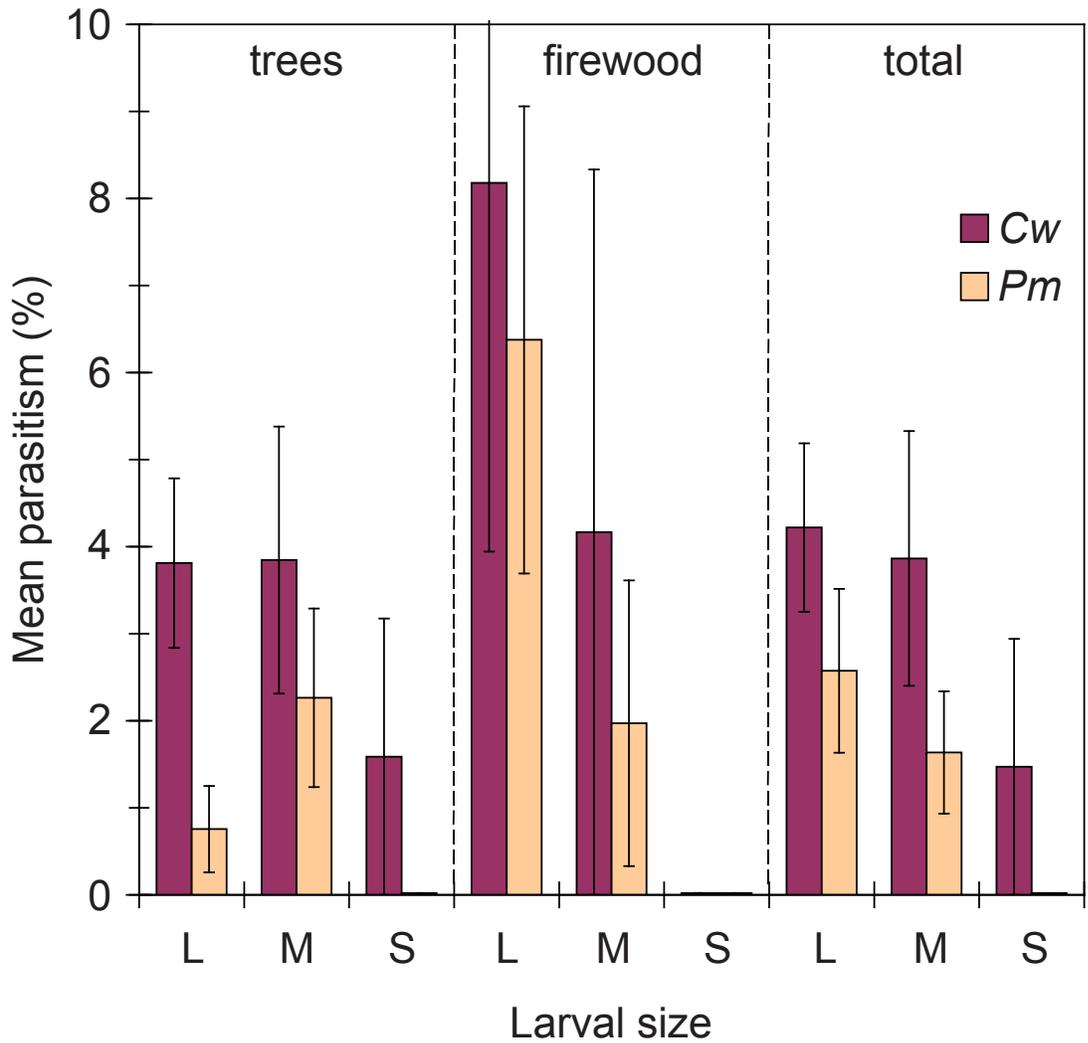


Figure 14. Effects of wood origin (trees vs. firewood) and larval size of *Cerambyx welensii* (*Cw*) and *Prinobius myardi* (*Pm*) on mean parasitism rate by *Billaea adelpha*. Data recorded in Extremadura (SW Spain) during our 6-year study (2011–2016). Host larvae were scored according to their body length at collection time as small (S: <20 mm), medium (M: 20–40 mm) or large (L: >40 mm). Vertical lines are the standard error of the mean. See text for a detailed statistical analysis.

The dextine *Billaea* Robineau-Desvoidy is a large genus of worldwide distribution (O'Hara 2013) that includes seven known species in the Iberian Peninsula (Tschorsnig & Báez 2002). Our target species, *B. adelpha*, has a mainly western Palaearctic distribution and towards the east it reaches Azerbaijan (Herting 1984). *Billaea adelpha* occurs in practically all of Europe (Tschorsnig *et al.* 2004) including Iberia (Tschorsnig 1992, Almeida *et al.* 2017). However, this tachinid fly prefers dry and warm areas so it is rare in North and Central Europe and more common in Southern Europe (Tschorsnig & Herting 1994). Its occurrence in Extremadura (both in Cáceres and Badajoz provinces) had already been previously reported from field-captured adults on umbels of Apiaceae plants and in the shade of large stones (Tschorsnig 1992), as well as from laboratory-obtained adults emerged from field-collected parasitized larvae (Tschorsnig 2017). Like other *Billaea* species (Allison *et al.* 2000, Tschorsnig 2017), *B. adelpha* exhibits a clear parasitic specialization on coleopteran larvae, mainly cerambycids (including several subfamilies such as Cerambycinae, Lamiinae and Prioninae), having been also cited from a buprestid and a scarabaeid (Tschorsnig 2017). Although the distribution of *B. adelpha* is relatively well known, information on its biology, ecology and especially host range remains scarce and fragmentary (as in most tachinids) (Cerretti & Tschorsnig 2010, Dindo 2011); this despite the fact that tachinid flies are a main group of parasitoids of insect pests in agriculture and forestry. The data provided in this paper attempt to reverse a little this undesirable situation.

Our results show that *B. adelpha* is widespread in SW Spain across a broad spatial and altitudinal range. Hence, *B. adelpha* is able to complete its life cycle in an ample array of habitats, from the warmer and drier lowland woodlands inhabited by evergreen sclerophyllous oaks to the wetter and colder mountains populated by deciduous oaks where it usually snows in winter. This fly species was the only larval parasitoid detected on *Cw* and *Pm* larvae despite intense field sampling, which suggests that the pressure exerted by this group of natural enemies on large oak-living cerambycids is rather low. Kenis & Hilszczanski (2007) already noted in their review the lack of published information on the natural enemies of *Cw* (as *C. velutinus* Brullé) and they compiled the few available data about *Cc*. In fact, the present study constitutes the second record (*Cw*) and the first formal report (*Pm*) about the parasitism of *B. adelpha* on large oak-living cerambycid species, two host-parasitoid associations recently compiled by Tschorsnig (2017).

Mean parasitism rates by *B. adelpha* were rather modest in both *Cw* and *Pm* irrespective of oak species, but values ranged widely from one stand to another reaching levels of even 100% in *Cw* (Table 1). Such a parasitism pressure is similar to that displayed by *B. monohammi* (Townsend) on either *Monochamus scutellatus* (Say) (0.6–7.5%) (Soper & Olson 1963) or *Monochamus carolinensis* (Olivier) (<5%) (Reagel *et al.* 2012), but appreciably lower than the 9.3–18.9% of *B. irrorata* (Meigen) on *Saperda populnea* (L.) (Tsankov & Georgiev 1991), the 27.9% of *B. triangulifera* (Zetterstedt) on *Saperda scalaris* (L.) (Campadelli & Gardenghi 1991), or the >28% of an undescribed *Billaea* species on *Acanthocinus princeps* (Walker in Lord) (Allison *et al.* 2000). The higher parasitism detected in large rather than in small larvae suggests that parasitization by *B. adelpha* in early host stages should be rare. A similar fact occurs in the congeneric species *B. irrorata*, which usually emerges from full-grown host larvae (Smith *et al.* 2004).

Neither cerambycid species or host size had a significant effect on the number of parasitoids that emerged from a single host larva, which averaged about 3 flies per larva, even if in large larvae it was not infrequent to obtain more than 10 parasitoids. In our case, the number of parasitoids per larva was similar to that reported in *B. triangulifera* parasitizing *S. scalaris* (Campadelli & Gardenghi 1991), but quite a bit lower than in *Rasiliverpa agrianomei* (Mesnil) parasitizing *Agrianome fairmairei* (Montrouzier) (whose large larvae are the so-called

“ver de bancoule”), as in this parasitoid-host association an average of 15 parasitoids per host larva occurs in a range of 2–59 (Cochereau 1970). It is interesting to note here that in our study, parasitoids often emerged from their host some days after the field collection date, which suggests that the high stress suffered by host larvae when extracted from the wood could somehow accelerate the emergence pattern of *B. adelpha*. Such a temporal asynchrony is not trivial since, if parasitoids in the wild emerge from a host larva before it has completed their future exit gallery, then the adult flies will inevitably die cloistered inside the tree.

The effect of wood origin on *B. adelpha* parasitism rate (especially on large *Cw* larvae) was an unexpected finding. The three cerambycid species studied require living trees and do not oviposit in firewood under natural conditions. However, larvae already present in the wood before being cut can continue their development and successfully complete their life cycle, sometimes at the cost of a reduced final adult size (Torres-Vila *et al.* 2018). Higher *B. adelpha* parasitism rates in firewood than in trees could occur if cerambycid larvae are less protected in the firewood. The oviposition strategy of *B. adelpha* females has not been observed or described but is very likely practically the same as it is for the closely related species *Billaea pectinata* (Meigen), as studied by Tölg (1910) and summarized by Herting (1960). *Billaea pectinata* lays thin membranous eggs from which neonate larvae immediately hatch and begin actively searching for host beetle larvae in their immediate surroundings (decayed wood). Tölg (1910) found that the tachinid larvae must find a host in one day, otherwise it will die. Experimental survival was nevertheless observed up to four days after ovi(larvi)position, but parasitization of host larvae was no longer possible. Indirect ovi(larvi)position has also been reported in the congeneric species *B. triangulifera* (Campadelli & Gardenghi 1991).

Indirect oviposition requires that newly-hatched tachinid larvae (planidia) must locate suitable host larvae on their own, either by waiting for them to pass by or by actively searching for them. This behavioral process is mediated by semiochemical compounds (Dindo & Nakamura 2018). Indirect oviposition likely evolved as an adaptive response whereby tachinid females may reach (otherwise inaccessible) endophytic host larvae living concealed within their host plants in galleries often protected by frass plugs – a case well exemplified by our wood-boring cerambycid species. In this so cryptic scenario, our results suggest that parasitization success by *B. adelpha* is substantially improved in firewood piles, possibly because female flies can penetrate through the large holes in the cut sections of the logs, accessing more easily the host galleries and laying their eggs (larvae) closer to host larvae.

We have found that *B. adelpha* is widespread in SW Spain, and conclude that despite rather low parasitism rates in oak-living cerambycids, the large variability among larval samples suggests that this tachinid could exert a significant parasitic pressure in some instances.

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