Reproductive biology of *Sclerodermus brevicornis*, a European parasitoid developing on three species of invasive longhorn beetles

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A R T I C L E   I N F O

A B S T R A C T

The reproductive performance of *Sclerodermus brevicornis* (Kieffer), a bethylid wasp native to Europe, was evaluated on three species of factitious hosts. These are longhorn beetles which have recently invaded Europe from Asia: *Anoplophora glabripennis* (Motschulsky), *Anoplophora chinensis* (Forster) and *Psacothea hilaris hilaris* (Pascoe) (Coleoptera: Cerambycidae). *Sclerodermus brevicornis* attacked all three species, but offspring only developed to maturity on medium and large sized host larvae. Host species influenced the duration of parasitoid development and the number of offspring maturing, both were greatest on *A. glabripennis*, with up to 373 adult parasitoids emerging from a single host. The sex ratios of *S. brevicornis* broods were strongly female biased (*ca.* 9% males). We conclude that *S. brevicornis* has the potential to be efficiently mass-reared and actively deployed in the biological control of invasive longhorn beetles. Further progress should be encouraged by the successful use of other species of *Sclerodermus* against beetle pests in China.

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1. Introduction

Many insect species have spread from their geographical origins to become invasive pests in new habitats (Pimentel et al., 2005; Pellizzari et al., 2005; Roques et al., 2009; Jucker and Lupi, 2011). Wood-boring beetles provide good examples of anthropogenic spread as their immature stages are often inside wood imported for building houses or furniture, or in wood packaging materials and timber imported for pulp (Haack, 2006; Liebhold et al., 2006; Cocquempot, 2007; Liebhold and Tobin, 2008; Gandhi and Herms, 2010; Marini et al., 2011; Lupi et al., 2013; Rassati et al., 2014, 2015). However, they can also arrive in living plants brought in from overseas (Roques, 2010; EPPO, 2012; Liebhold et al., 2012).

Many invasive wood-boring beetle species belong to the family Cerambycidae (Cocquempot and Lindelöw, 2010; Jucker and Lupi, 2011) with species in the genus *Anoplophora* considered some of the most dangerous invasive pests of woody plants worldwide (Haack et al., 2010). For instance, *Anoplophora chinensis* (Forster), the Citrus Longhorn Beetle (CLB), and *Anoplophora glabripennis* (Motschulsky), the Asian Longhorn Beetle (ALB), both native to the far east of Asia and considered quarantine pests, were detected in Italy in 2000 and in 2007, respectively (Colombo and Limonta, 2001; Maspero et al., 2007; Favaro et al., 2015). Specific eradication pro-

grams were subsequently implemented, at great social, environmental and economic cost (Faccoli and Gatto, 2016). CLB is currently restricted to several provinces in Lombardy (northern Italy) and some areas in central Italy, where active measures are being taken to eradicate it (EPPO, 2015a). The ALB is considered transient, targeted by current eradication actions, but with small isolated occurrences in several localities in the north and the center of the Italian peninsula (Hérard et al., 2009; EPPO, 2015b; Faccoli et al., 2015). Not included among quarantine pests (being officially controlled) or notifiable pests (a species that should be reported to plant health authorities if observed) but considered as a potential threat, is the Yellow Longhorn Beetle (YLB), *Psacothea hilaris hilaris* (Pascoe) (Coleoptera: Cerambycidae), a pest of Fig. and mulberry trees. The Asian YLB was first detected in southern Europe (Italy) in 2005, where it can kill infested plants. It is considered a potential threat for all Mediterranean countries where Figs. and mulberries are common trees (Jucker et al., 2006; Lupi et al., 2013, 2015a).

The containment of longhorn beetle populations is challenging both because these species are highly polyphagous on broad-leaf plants and because their larvae develop within the protection of woody trunks, protecting them from insecticidal spraying. While chemical control is an unrealistic and ineffective solution, biological control, via natural enemies, offers an environmentally sustainable approach to combating these species (Brabbs et al., 2015; Duan et al., 2016) and it can also be successfully combined with other tools, such as the use of lures and light-traps, in integrated pest management programs (Yang et al., 2014). There are a number of parasitoids that are

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natural enemies of cerambycids and the majority attack the larval and pupal stages (Hanks et al., 1995; Delvare et al., 2004; Zhang et al., 2005; Azevedo and Waichert, 2006; Loni et al., 2015).

The main parasitoids of ALB and CLB in Asia are the beetle *Dastarcus helophoroides* (Fairmaire) (Coleoptera: Bothrideridae) (Li et al., 2009; Wei and Niu, 2011) and wasp species in the genus *Sclerodermus* (Hymenoptera: Bethylidae) (Yao and Yang, 2008). In Europe, *Dastarcus* is represented by just one species, *D. cyprianus* Dajoz, which appears to occur only in Cyprus (Dajoz, 1989), while 17 species of *Sclerodermus* are recorded from Mediterranean areas (Andrè et al., 1904; Kieffer, 1914) some of which are associated with invasive exotic longhorn beetles (Hérard et al., 2007; Lupi et al., 2014). Members of the genus *Sclerodermus* (comprising at least 81 described species worldwide, Gordh and Móczár, 1990; Lanes and Azevedo, 2008), are idiobiont ectoparasitoids (Li and Sun, 2011; Hu et al., 2012) that mainly attack the larvae of wood-boring beetles. The wasps find hosts by entering preexisting galleries bored in the wood, aided by their morphological adaptations (e.g. small size, flattened body, prognathous head) are specifically selected for seeking hosts in enclosed spaces (Kühne and Becker, 1974; Evans, 1978; Yang et al., 2012; Baena and Zuzarte, 2013; Jiang et al., 2015).

The hosts of *Sclerodermus* range from small to large species (Mendel, 1986; Hsu and Wu, 1989; Yang et al., 2014). Within a *Sclerodermus* species, females may be most effective attacking younger (relatively small) hosts (Yang et al., 2014) but multiple females can cooperate in host attack, allowing them to suppress host defense and to lay eggs on larger hosts (Tang et al., 2014). After laying eggs, mothers remain at the host, tending the offspring until pupation into cocoons and emergence of adults (Hu et al., 2012; Yang et al., 2012; Tang et al., 2014). Multiple-female reproduction on a single host appears to be cooperative, without division of labor, and as such may be termed quasi-social (Li and Sun, 2011; Liu et al., 2011; Wang et al., 2016), an unusual life-history character among parasitoid hymenopterans.

Here we report empirical studies on the reproductive biology of *Sclerodermus brevicornis* (Kieffer) a native European species. *Sclerodermus brevicornis* was reported to be associated with the longhorn beetle *Oxypleurus nodieri* Mulsant in Europe approximately a century ago (Kieffer, 1914) and in 2011 it was recorded in association with YLB in northern Italy (Lupi et al., 2014). Subsequently, in 2013 more than 1,000 adult *S. brevicornis* emerged from a Fig. branch (100 cm long, 32 cm diameter) heavily infested by YLB in the same locality (D. Lupi, pers. obs.) confirming the new host-parasitoid association. We discuss the potential of *S. brevicornis* for the suppression of exotic and invasive longhorn beetle populations. In China, mass rearing and release of Asian species of *Sclerodermus* has formed an integral part of successful forest pest management programs (Chen and Cheng, 2000; Du et al., 2006; Tang et al., 2012; Yang et al., 2014; Jiang et al., 2015), suggesting the possible employment of similar measures within Europe.

2. Materials and methods

2.1. Host rearing

ALB: In the spring of 2013, logs infested with ALB larvae were collected from Cornuda in North East Italy (45°49′ N, 12°00′ E) and stored under ambient conditions outdoors in metallic mesh cages (2 × 1 × 1 m) until adult ALB emergence (Faccoli et al., 2016; Faccoli and Favaro, 2016). Newly emerged adults were then moved into maturation metallic mesh cages (2 × 1.5 × 1.5 m) and fed for around two weeks with fresh maple twigs (*Acer campestre* L.) to

allow adult sexual maturation and mating. Fresh willow logs (*Salix alba* L.) (10 cm diameter × 30 cm long) were also placed in the cages for egg laying.

CLB: Several adults of CLB were collected in an urban park of Milan (North Italy, 45°29′ N, 9°05′ E) in July 2013 placed in plastic cages (30 × 20 × 18 cm) under outdoor conditions and fed with fresh maple twigs. After a few days, maple branches (2–3 cm diameter × 10–15 cm long) were added to the cages for egg laying.

YLB: A laboratory rearing system for YLB was set up in summer 2013 with adult beetles emerged from infested fig logs collected in the infestation area of the Como province, near to Lake Como in northern Italy (45°49′ N, 9°13′ E) (Lupi et al., 2013, 2015a). Four-to-ten pairs of newly emerged YLB adults were placed in plastic cages (30 × 20 × 18 cm) and kept in a climate room (temperature 25 ± 1 °C, photoperiod L16/D8, relative humidity 60 ± 5%). Three times each week the adult beetles were provided with fresh fig twigs (10–15 cm length × 1.5–2.5 cm diameter) for feeding and laying eggs on.

Infested material was debarked once a week by a cutter, and freshly laid eggs were moved individually onto an artificial diet known to be suitable for longhorn beetles (Lupi et al., 2015b). Eggs were randomly collected from at least ten different logs/twigs infested by different females. Newly hatched larvae were reared singly in 10 cm-diameter petri dishes in a climate chamber (25 ± 1 °C, 16L:8D, RH 60 ± 5%). Every week each larva was moved into a new petri dish with fresh diet (Lupi et al., 2015b), until they reached a suitable size for presentation to parasitoids.

2.2. Parasitoid rearing

A laboratory stock culture of *Sclerodermus brevicornis* was founded by rearing individuals collected in September 2011 from fig trees infested by YLB in Ponte Lambro (Como province), northern Italy (45°49′40″ N; 9°13′07″ E). In 2013, the stock culture was enriched with specimens coming from a new finding in field. The parasitoid was reared for more than 30 generations on YLB infested branches kept inside ventilated containers in a climate chamber (25 ± 1 °C, 16L:8D RH, 60 ± 5%). Every 15 days new YLB-infested branches were added to the rearing containers, thus providing new hosts to the newly emerged parasitoids. Some of the newly emerged female *S. brevicornis* were collected from the rearing stock and used in the experiments.

2.3. Parasitoid reproduction

In order to evaluate the susceptibility hosts to attack by *S. brevicornis* and the effect of host characteristics on subsequent parasitoid performance, we presented hosts of different species and sizes to groups of adult female wasps. Host size was classified according to head capsule width: small, medium and large (Table 1). In most cases 20 replicates of each host species and host size combination were used. However, as the laboratory culture of CLB collapsed during the experiment, trials on this species were restricted to 16 replicates of medium sized larvae and no large larvae.

Host larvae were placed individually into plastic containers (5 cm diameter and 4 cm depth) in which there was a thin layer (ca. 1.5 mm) of cork oak granules to maintain the relative humidity and to allow the parasitoids to access the part of the host which otherwise would be in contact with the container. In another species of *Sclerodermus*, the exploitation of larger hosts usually requires larger numbers of foundresses (Tang et al., 2014). As we were primarily concerned with identifying conditions that might be productive for para-

Table 1
Classification larval size on the basis of head capsule width.

Species	Size class (mm)									Across size class differences[2]
	Small			Medium			Large			
	Range	Mean	S.E.	Range	Mean	S.E.	Range	Mean	S.E.	
ALB	1.6–2.1	1.674	±0.026	2.4–3.4	2.906	±0.091	3.6–3.8	3.709	±0.022	H = 52.99, d.f. = 2, P<0.001
CLB[1]	1.6–2.1	1.680	±0.036	2.2–3.3	2.623	±0.101	-			H = 23.20, d.f. = 1, P<0.001
YLB	1.1–1.6	1.593	±0.027	2.0–3.4	2.816	±0.109	3.5–4.1	3.748	±0.027	H = 51.94, d.f. = 2, P<0.001
Across species differences[2]	H = 0.847, d.f. = 2, P = 0.654			H = 3.471, d.f. = 2, P = 0.176			H = 2.904, d.f. = 1, P = 0.084			

[1] The laboratory culture of CLB collapsed during the experiment: we were able to carry out trials on 20 small and 16 medium larvae. There were 20 replicates of all other size class and species combinations.

[2] The size distributions of presented hosts were homogeneous across species within each size class, while distinct across size classes within each species (Kruskal-Wallis tests).

sitoid mass-rearing, small host larvae were exposed to two *S. brevicornis* 'foundress' females, medium sized host larvae to four, and large host larvae to eight. We note, however, that conclusions we draw concerning effects of host size can equally be interpreted in terms of effects of foundress number.

Rearing containers were checked daily, recording host paralysis, oviposition and hatching of eggs, removal of mature wasp larvae from the host by the adult females tending the brood (larval transfer) (ShaoLong et al., 2013), the spinning of cocoons following detachment from the host, the completion of pupal development, adult emergence and the sexes and polymorphic forms (winged or wingless) of adult offspring produced. The experiment was carried out at 25 ± 1 °C, 16L:8D and RH $60 \pm 5\%$.

2.4. Statistical analyses

Binary data on host acceptance and offspring production were analysed using logistic analyses assuming binomially distributed errors and the reported test statistic is change in deviance, G, which is approximately χ^2 distributed (Crawley, 1993). Other logistic analyses of proportional data, with denominators larger than unity, assumed quasi-binomial error distributions and the reported test statistic is the F-ratio (Crawley, 1993; Wilson and Hardy, 2002). All logistic analyses adopted a logit-link function. Integer data were explored using log-linear analyses assuming quasi-Poisson error distributions and a log-link function (Crawley, 1993). Data on host size and on developmental times were not normally distributed (assessed using normal probability pots) and were thus analysed using non-parametric ANOVAs, *i.e.* Kruskal-Wallis tests (Siegel and Castellan, 1988). Where we applied multiple hypothesis tests, each assuming a Type I error rate of 0.05, we used adjusted significance levels according the Bonferroni procedure (Quinn and Keough, 2002). All analyses were carried out using the statistical software package *GenStat* (version 17, VSN international, Hemel Hempstead, UK).

3. Results

3.1. Probability of offspring production on presented hosts

The overall probability of producing offspring was influenced significantly both by host species ($G_2 = 3.35$, $P = 0.035$) and host size ($G_2 = 29.09$, $P < 0.001$) but not by an interaction between these main effects ($G_3 = 0.02$, $P = 0.997$). No offspring were produced from small hosts of any host species and offspring were most likely to be produced when medium sized CLB hosts were presented (Fig. 1). Statistical model simplification by aggregation of factor levels within logistic analysis showed that production on medium and large hosts of either ALB or YLB did not differ significantly ($G_3 = 0.05$, $P = 0.984$) and that the probability of production on medium sized CLB was significantly greater than on medium or large ALB and YLB hosts ($G_1 = 7.23$, $P = 0.007$) (Fig. 1).

We further explored the probabilities of hosts being successfully utilized by *Sclerodermus* at the successive stages of offspring production, from presentation of hosts to foundresses to the eclosion of adult offspring. Offspring production never advanced as far as cocoon formation by hatched larvae on small hosts, while it yielded adult parasitoids on most medium and large hosts (Fig. 2). Significant influences of size and/or species were typically found during the earlier stages of offspring production, although note that the power to detect influential effects declines as the number of replicates for analysis decreases (Table 2).

3.2. Timing of offspring production on presented hosts

Host species and host size both influenced the time taken for parasitoid development, although effects of host size were found at only one developmental stage (smaller hosts were oviposited on earlier than larger hosts, following paralysis) and effects of host species were found at most stages (Table 3). Typically broods on YLB hosts developed the fastest and broods on ALB hosts the slowest (Table 4). Overall, eggs laid on ALB hosts took approximately one week longer (21.23 ± 0.70 days) to develop to adulthood than those laid on YLB hosts (28.50 ± 0.60 days), with intermediate developmental time on CLB hosts (24.00 ± 1.09 days).

3.3. Numbers of offspring produced on presented hosts

The number of offspring produced was influenced significantly both by host species ($F_{2,152} = 10.40$, $P < 0.001$) and host size ($F_{2,152} = 34.87$, $P < 0.001$) but not by an interaction between these main effects ($F_{3,148} = 0.06$, $P = 0.981$). Large ALB hosts yielded the largest total numbers of *S. brevicornis* adults (Table 5). Medium sized CLB hosts did not yield large numbers of parasitoids, despite being the most colonized host larvae (Fig. 1, Table 5). Model simplification within log-linear analysis showed that offspring production did not differ significantly between medium sized CLB and YLB hosts ($F_{1,151} = 0.01$, $P = 0.999$) or between medium ALB and large
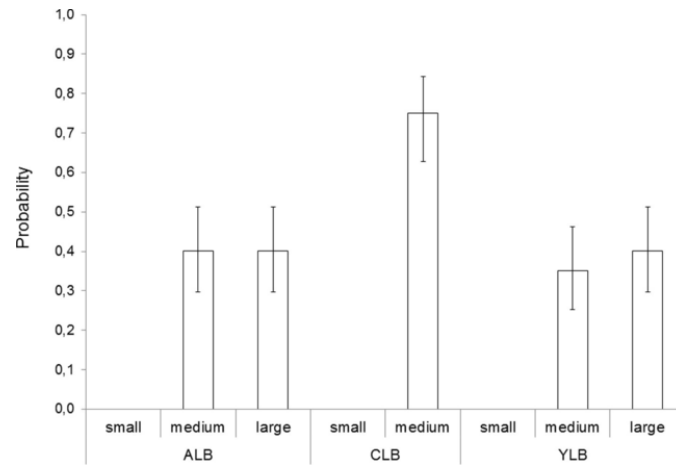
Fig. 1. Probability of *S. brevicornis* offspring production from hosts of different species and sizes. Bars show means ± S.E., back-transformed from the logit scale. Absence of bars denotes that no offspring were produced from the hosts provided.
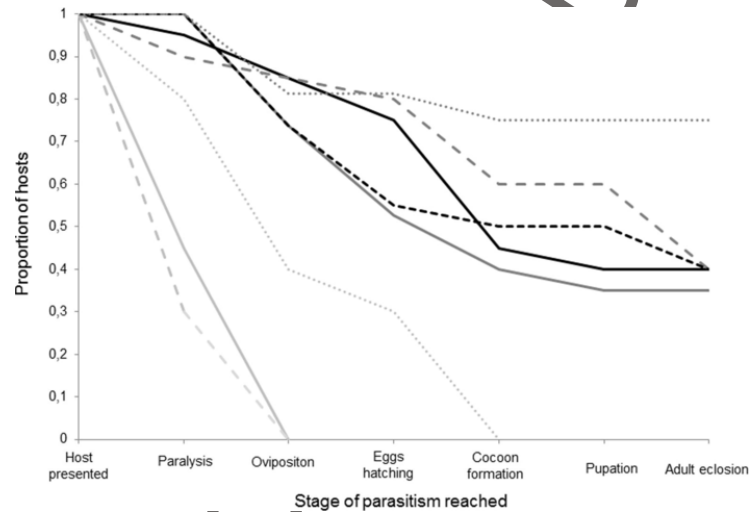

Fig. 2. The proportion of hosts that were successfully utilized by *S. brevicornis* at the successive stages of offspring production. Lines show how means for each host species and host size combination decline as parasitoid production progresses (YLB: solid lines; ALB: broken lines; CLB: pointed lines; Large larvae: black lines; Medium larvae: dark-grey lines; Small larvae: light-grey lines).

YLB hosts ($F_{1,152} = 0.52$, $P = 0.47$). Other host categories differed significantly in terms of offspring production (Table 5).

Similar results were found when analyzing production in terms of the number of offspring produced per foundress (Table 5): production was greater on larger hosts ($F_{2,155} = 29.47$, $P < 0.001$) and differed according to host species ($F_{2,155} = 9.72$, $P < 0.001$). Production was greatest on ALB and there was no significant difference in production between CLB and YLB hosts ($F_{1,154} = 0.55$, $P = 0.458$). There was also no significant interaction effect between host size and host species ($F_{3,152} = 0.07$, $P = 0.976$).

3.4. Characteristics of produced offspring groups

Offspring were produced from 43 of the 156 replicates in which a host was presented to foundress females. The number of adults in these offspring groups ranged widely, from 2 to 373, with a mean of 85.80 (+S.E = 15.70, −S.E. = 13.27, Table 5). As with analysis across all replicates, above, offspring group size was influenced by host species ($F_{2,43} = 16.83$, $P < 0.001$) and host size ($F_{1,43} = 15.83$, $P < 0.001$) but not by their interaction ($F_{1,42} = 0.52$, $P = 0.473$). Model simplification showed that the number of adults produced did not differ significantly between medium sized CLB and YLB hosts

Table 2
Influences on the probability of transition between stages of offspring production. Results are from 2-way logistic ANOVAs of host species and hosts size and their interaction. The number of replicates, N, from which data are analysed declines due to failures on some hosts as the stage of production progressed (Fig. 2). Similarly, $d.f.$ become smaller as the number of species and size classes decline due to reproductive failures. Note that statistical power also declines with decreasing N. Asterisks indicate those hypothesis tests that remain significant after Bonferroni adjustment due to multiple-testing (as a family of 18 hypothesis tests were carried out each assuming a Type I error rate of 0.05, the adjusted significance level is $0.05/18 \approx 0.003$, Quinn and Keough, 2002).

Stage of offspring production	N	Host	G	$d.f.$	P
Paralysis of presented host	156	Species	6.32	2	0.002
		Size	28.84	2	<0.001
		Species × Size	1.39	3	0.245
Oviposition on paralysed host	124	Species	2.48	2	0.084
		Size	15.78	3	<0.001
		Species × Size	4.04	3	0.007
Hatching of eggs	83	Species	2.12	1	0.120
		Size	0.52	2	0.593
		Species × Size	3.08	2	0.079
Cocoon formation by larvae	71	Species	1.37	2	0.254
		Size	8.71	2	<0.001
		Species × Size	2.31	1	0.128
Pupation of larvae in cocoons	51	Species	2.21	2	0.109
		Size	0.14	1	0.708
		Species × Size	0.00	1	1.000
Eclosion of adults from pupae	49	Species	5.56	2	0.004
		Size	0.03	1	0.481
		Species × Size	0.10	1	0.998

Table 3
Influences on the duration of stages of offspring production. Results are from separate Kruskal-Wallis tests of host species and hosts size. H values are adjusted for ties. As in Table 2, the number of replicates, N, and $d.f.$ decline due to failures on some hosts as the stage of production progressed. Asterisks indicate those hypothesis tests that remain significant after Bonferroni adjustment due to multiple-testing (as 12 hypothesis tests were carried the adjusted significance level is $0.05/12 = 0.004$, Quinn and Keough, 2002).

Temporal variable	N	Host	H	$d.f.$	P
Host presentation-to-paralysis	116	Species	28.99	2	<0.001
		Size	0.95	2	0.622
Paralysis-to-oviposition	77	Species	38.13	2	<0.001
		Size	15.92	2	<0.001
Oviposition-to-hatching	63	Species	0.05	2	0.974
		Size	0.36	1	0.057
Hatching-to-pupation	49	Species	10.31	2	0.005
		Size	3.54	2	0.060
Pupation-to-eclosion	41	Species	22.91	2	<0.001
		Size	2.16	1	0.138
Total egg-to-adult development	39	Species	21.84	2	<0.001
		Size	0.702	1	0.402

($F_{1,39} = 1.67$, $P = 0.204$) or between medium ALB and large YLB hosts ($F_{1,40} = 0.66$, $P = 0.42$) but other differences in offspring production were significant.

Offspring sex ratios were strongly female biased: the mean proportion of offspring that were male was 0.0899 (+S.E. = 0.006, −S.E. = 0.005). Sex ratios were affected by the species of host offered ($F_{2,39} = 17.51$, $P = 0.001$): they were less female biased on ALB hosts but did not differ significantly between CLB and YLB hosts ($F_{1,41} = 2.20$, $P = 0.146$). Sex ratios were not significantly affected by host size ($F_{1,40} = 0.01$, $P = 0.925$) or by an interaction between host species and size ($F_{1,39} = 0.29$, $P = 0.596$). Sex ratios were less female biased in larger offspring groups ($F_{1,41} = 11.51$, $P = 0.002$), with largest groups being produced on ALB hosts.

More than a quarter of the offspring groups produced contained no adult males (mean proportion of all-female broods = 0.279 (+S.E. = 0.073, −S.E. = 0.063). The probability that an offspring group was all-female declined significantly with increase in brood size ($G_1 = 5.86$, $P = 0.015$) and was influenced by host species ($G_2 = 3.66$, $P = 0.026$) but not by host size ($G_1 = 0.02$, $P = 0.896$) (Fig. 3).

Most *S. brevicornis* females were apterous (wingless) but a minority were alate (winged) (Table 5). The mean proportion of females that were alate was 0.0985 (+S.E. = 0.016, −S.E. = 0.014). Logistic analyses indicated that there were no significant relationships between the proportion of females that were alate and any of the variables we measured or controlled experimentally. As expected, given the constant proportion of alate females within broods, the number of females that were alate increased significantly with overall brood size (log-linear analysis: $F_{1,41} = 27.82$, $P < 0.001$) and with the number of apterous females ($F_{1,41} = 19.10$, $P < 0.001$) and the number of males ($F_{1,41} = 20.50$, $P < 0.001$).

4. Discussion

We have shown that it is possible to rear *Sclerodermus brevicornis* on all three species of exotic longhorn beetles presented. This implies that *S. brevicornis*, which is native to Europe, has potential in conservation biological control approaches to the management of invasive longhorn pests and that it would be feasible to use these host species to mass-produce it for inundative field release.

While at least some hosts of all three species and sizes were attacked and paralysed, paralysis of small ALB and YLB hosts was not frequent. Paralysis of small CLB was, however, common. One possibility is that two foundresses are in principle sufficient to successfully attack a host but that ALB and YLB hosts may be better able to defend themselves than are CLB hosts. It may, alternatively, be that small hosts constitute insufficient or unsuitable resources for parasitoid development and, in the case of ALB and YLB, were typically assessed as such by the *S. brevicornis* females either before or after attack. Further work in which host size and foundress number are varied independently (e.g. Tang et al., 2014) will be required to evaluate these possibilities. Only around half of the CLB hosts that were paralysed were subsequently oviposited on and all eggs that were laid failed to complete larval development: these results are suggestive of low host quality. Small hosts do however, have some value to the parasitoids, as we observed that they were fed upon by the adult wasps. Females were seen biting the host's epidermis near the tracheal spiracles and also the intersegmental membranes. This resulted in browning of the epidermis and sometimes in visible lacunae. Host feeding appeared to promote the longevity of the adult parasitoids and is likely to enhance future fecundity as *Sclerodermus* are synovigenic anautogenous species (oogenesis takes place after foundress feed on a suitable host) (Liu et al., 2011). In conclusion, this behavior may have some pest control value as *S. brevicornis* attacks and kills small hosts, even if it does not generate recruits into the next generation of parasitoids.

S. brevicornis offspring production increased with host size in all three species studied. We observed that foundresses continued to oviposit on the host larva until the surface was completely covered by eggs; hence, more parasitoid offspring were allocated to larger hosts. This is a commonly observed result across many host-parasitoid associations (e.g. Godfray, 1994; Mousseau and Fox, 1998; Jervis et al., 2008; Lupi et al., 2015a) and the most effective long-term suppression of pest populations is most likely to be achieved when large numbers of (female) parasitoids are produced from each host parasitized (Hassell, 2000). Differences in offspring production obtained from hosts of similar size, but belonging to different species, further

Table 4
Number of days (mean±SEM) *S. brevicornis* offspring took to reach each development stage on the different host species and sizes.

Host species	Host size	Host presentation-to-paralysis	Paralysis-to-oviposition	Oviposition-to-hatching	Time to larval transfer (a)	Transfer spinning cocoon (b)	Hatching-to-pupation (a + b)	Pupation-to-eclosion	Total egg-to-adult development
YLB	Small	2.86 ± 0.80	–	–	–	–	–	–	–
	Medium	2.60 ± 0.29	4.20 ± 0.89	5.10 ± 0.59	5.50 ± 1.28	0.71 ± 0.18	5.57 ± 1.26	11.14 ± 1.16	21.71 ± 1.21
	Large	2.84 ± 0.32	5.59 ± 0.56	4.20 ± 0.45	6.56±0.88	1.00 ± 0.00	7.13 ± 0.88	9.75 ± 0.96	20.67 ± 0.96
ALB	Small	3.25 ± 0.25	–	–	–	–	–	–	–
	Medium	4.72 ± 0.45	8.24 ± 0.45	4.63 ± 0.29	6.08 ± 0.48	1.00 ± 0.00	7.08 ± 0.48	18.88 ± 0.30	30.25 ± 0.56
	Large	4.95 ± 0.59	7.71 ± 0.50	3.55 ± 0.34	5.40 ± 0.31	1.00 ± 0.00	6.40 ± 0.31	17.38 ± 0.38	26.75 ± 0.62
CLB	Small	4.50 ± 0.51	2.33 ± 0.49	4.75 ± 0.75	–	–	–	–	–
	Medium	4.25 ± 0.43	4.15 ± 0.42	4.23 ± 0.36	3.50 ± 0.34	1.33 ± 0.40	3.82 ± 0.58	16.25 ± 1.09	24.00 ± 1.09
Grouped by host size									
	Small	3.78 ± 0.39	2.33 ± 0.49	4.75 ± 0.75	–	–	–	–	–
	Medium	3.80 ± 0.26	5.90 ± 0.45	4.62 ± 0.23	4.97 ± 0.43	1.07 ± 0.16	5.53 ± 0.48	15.70 ± 0.80	25.26 ± 0.88
	Large	3.92 ± 0.38	6.55 ± 0.42	3.92 ± 0.30	5.95 ± 0.46	1.00 ± 0.00	6.72 ± 0.42	13.56 ± 1.10	24.14 ± 0.98

Table 5
Characteristics of *S. brevicornis* offspring developing on the different host species and sizes. Data (number of wasps) are expressed as mean ± SEM of replicates that yielded some adults. No wasps reached maturity on small hosts.

Host species	Host size	Adult offspring	Apterous females	Alate females	Males	Offspring per foundress
YLB	Medium	37.71 ± 14.54	26.86 ± 11.40	9.00 ± 6.95	1.86 ± 1.16	9.43 ± 3.64
	Large	67.38 ± 14.66	58.38 ± 12.12	5.00 ± 3.75	3.88 ± 1.03	8.42 ± 1.83
ALB	Medium	90.75 ± 26.68	75.63 ± 23.27	5.50 ± 1.81	9.63 ± 2.64	22.70 ± 6.70
	Large	243.88 ± 43.14	196.38 ± 35.5	22.00 ± 4.98	25.50 ± 5.06	30.48 ± 5.40
CLB	Medium	17.58 ± 5.36	16.42 ± 5.01	0.58 ± 0.28	0.58 ± 0.35	4.40 ± 1.34
Grouped by host size						
	Medium	44.48 ± 10.61	36.67 ± 9.00	4.22 ± 1.91	3.59 ± 1.12	11.12 ± 2.65
	Large	155.62 ± 31.68	127.38 ± 25.42	13.56 ± 3.72	14.69 ± 3.75	19.45 ± 4.00
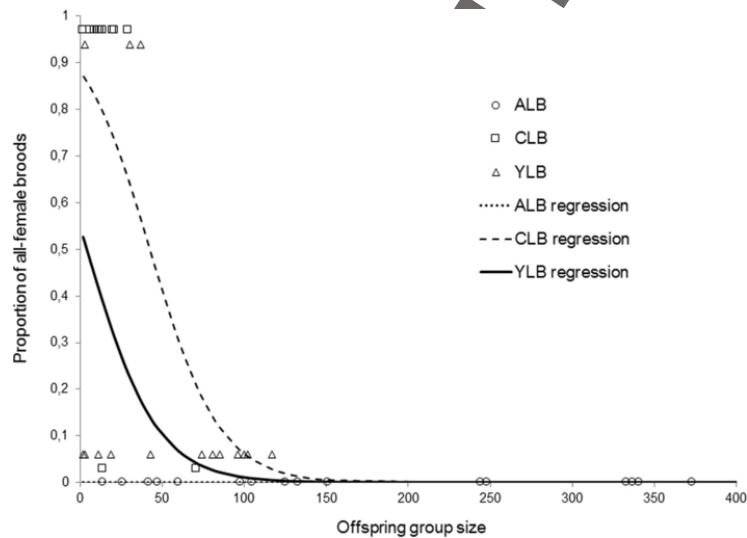
Fig. 3. The influences of offspring group size and host species on the proportion of broods that were all-female. The fitted regression lines are from logistic analyses. Some data points are displaced from their binary positions to reduce overlap.

imply that there are biochemical components to host quality (immunological differences are relatively unlikely to affect externally feeding larvae), even though the different host species were all reared on the same artificial diet. Juvenile nutrition has been shown to have important implications on adult phenotype, and therefore on fitness, in many species (Underwood and Rausher, 2000; Lupi et al., 2015b).

Nutritional quality can also directly affect trophic interactions by influencing the morphology, behavior, and life-histories of insects (Harvey et al., 2003; Bukovinszky et al., 2008). Future assessment of the key nutritional differences between ALB, CLB and YLB, and their effects on the biochemical profiles of *Sclerodermus* offspring

produced, could employ a metabolomics approach (Snart et al., 2015; Kapranas et al., 2016a).

Despite larger hosts being more suitable for parasitoid production than small hosts, failure to reproduce on medium and large hosts was common (as also observed in *S. harmandi*, Tang et al., 2014). In some instances, failure to reproduce on large and medium sized hosts was due to the death of the foundresses or to the host resources being exhausted by parasitoid larval feeding before larvae were large enough to pupate. Sometimes we observed *S. brevicornis* foundresses, which had earlier exhibited maternal care, switch to killing and eating all developing offspring when the host began to decay noticeably. Such infanticidal behavior has been reported to other insects and it generally occurs when a species kills the offspring of some other parents (Hager and Johnstone, 2004; Goubault et al., 2007; Tena et al., 2008), but self-infanticide is quite unusual in insects.

We found that the time taken for *S. brevicornis* to reproduce differed according to host species. Following host presentation, time to paralysis was lower on YLB than on ALB or CLB. All foundresses used in our experiments were themselves reared on YLB, hence they appear to need more time to recognize a different host species as suitable. In some other species of parasitoids, females prefer hosts belonging to the same species on which they developed (Schoonhoven et al., 1998; Wei et al., 2013) although such preferences may also be absent (Pérez-Lachaud and Hardy, 2001). All else being equal, mass rearing programs will be more efficient when parasitoids develop more rapidly. However, for *S. brevicornis* the host species which yielded the most offspring, ALB, was also the species on which parasitoid development took the most time.

The sex ratios of *S. brevicornis* broods were typically female biased: overall, 9% of offspring were males. Similar degrees of sex ratio bias have previously been reported in other species of *Sclerodermus* and it is thought that this is due to local resource enhancement (LRE) rather than local mate competition (LMC), the more commonly applied explanation of female bias among parasitoids (Li and Sun, 2011; Hu et al., 2012; Kapranas et al., 2016b; Wang et al., 2016). Whether *S. brevicornis* sex ratios are more strongly influenced by LMC or LRE, the female bias will be an asset for biocontrol programs employing mass-rearing and release because are females that attack pest larvae (Ode and Hardy, 2008). Moreover, under predominantly LRE, cooperation between foundress females is likely to enhance the range of host sizes that can be attacked successfully (Tang et al., 2014; Kapranas et al., 2016b) and thus also biocontrol potential of the parasitoid.

Despite the strong female bias overall, *S. brevicornis* broods, containing no male were most common when relatively few adults emerged. As a consequence of arrhenotoky the following generation would include male offspring only. In other species in the same genus it was further shown that the occurrence of all-male broods at emergence was related to high developmental mortality and to broods produced by few unmated foundresses (Kapranas et al., 2016b). On the basis of evidence from other *Sclerodermus* species (Mamaev, 1979; Liu et al., 2011; Tang et al., 2014; Kapranas et al., 2016b), it is likely that *S. brevicornis* foundresses each lay a small number of male eggs in every clutch and the proportion of all-female broods reflects the probability of those eggs failing to develop to adulthood. We noted that there were no all-female broods produced on ALB hosts and that this host species also yielded the largest *S. brevicornis* broods, suggesting a low preimaginal mortality. Conversely all-female broods were most common on CLB hosts, which yielded the smallest broods, suggestive of high-preimaginal mortality.

Many species of *Sclerodermus* are dimorphic in both sexes: in bethylid males dimorphism is normally associated with mating strategies while female wing dimorphism may be associated with different dispersal tactics (Bridwell, 1920; Evans, 1963; Godfray, 1994; Wang et al., 2016). Apterous specimens are often confined to a given tree, while winged forms can colonize hosts at greater distances, improving the parasitoid performance in host finding and colonization and influencing the efficacy of programs of mass rearing and release. Moreover, wing polymorphism in some bethylids has a genetic basis (Kearns, 1934; Godfray, 1994) and may also be influenced by environmental conditions (Wang et al., 2016). In the present research all the *S. brevicornis* male obtained were alate while around 10% of emergent females possessed wings, with this percentage unaffected by characteristics of the host presented or size of the offspring group produced. Further work will be required to assess environmental influences on the production of alate and apterous female of *S. brevicornis* and the consequences for subsequent reproductive performance.

5. Conclusions and prospects

Sclerodermus species appear to be among the most effective bethylids utilized as agents of biological pest control (Yang, 2004; Yang et al., 2014; Jiang et al., 2015). To date successes have been most notable in China, with native *Sclerodermus* species deployed against a range of wood boring beetles. Given that the morphologies and life-histories of *Sclerodermus* species are generally similar (Jiang et al., 2015), European species of *Sclerodermus* have promise for the biological control of invasive wood boring beetle within Europe. We have shown that *S. brevicornis* can attack and develop on three invasive longhorn beetle species becoming a strong candidate for biological control programs based on mass-rearing and release protocols. We, however, note that our study, like some studies on congenerics (Liu et al. 2011), has been restricted to evaluating parasitoid performance when hosts are exposed directly to foundresses. It would be informative to evaluate *S. brevicornis* performance under more natural conditions given that females must forage for hosts within wood and may encounter a variety of host species at different development stages, in competition with other foundresses.

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