The biology of *Psyllaephagus bliteus* Riek (Hymenoptera: Encyrtidae), a parasitoid of the red gum lerp psyllid (Hemiptera: Psylloidea)

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**Abstract**

The red gum lerp psyllid, *Glycaspis brimblecombei* Moore (Hemiptera: Psylloidea), is native to Australia, where it feeds upon *Eucalyptus* species. It first appeared near Los Angeles, California, in 1998, and soon spread throughout the state. A biological control program directed against the psyllid was initiated and *Psyllaephagus bliteus* Riek (Hymenoptera: Encyrtidae) was imported from Australia and released in California. During quarantine screening, the taxonomic status of *Psyllaephagus quadricyclus* Riek was assessed by one of us (RLZ) and is proposed here as a new junior synonym for *P. bliteus*. The experiments discussed herein provide basic biological information on *P. bliteus* to supplement and improve the control program. We found that *P. bliteus* can oviposit into psyllid nymphs of any age but prefers third and fourth instars. Observations of host-handling behavior suggest that the large lerps of fifth instar psyllids increase host-handling time, thereby impeding oviposition and providing some protection from parasitism. Female *P. bliteus* were observed host-feeding on all psyllid nymphal development stages. Adults are relatively long-lived and, at constant temperatures of 17, 21, 23, 26, and 32 °C, longevity is a negative linear function of temperature. Females lived significantly longer than males. Adult females can live for several months, provided with hosts and held under glasshouse conditions (22 ± 3 °C), however, maximum egg deposition occurred within 22 days after adult emergence. Studies of larval development show that *P. bliteus* is a koinobiont and larval development is not initiated until the host reaches the late fourth or early fifth instar.

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1. Introduction

*Psyllaephagus* Ashmead (Hymenoptera: Encyrtidae) is a cosmopolitan genus containing over 200 described species with perhaps as many as 1000 in all (Noyes and Hanson, 1996). Their greatest taxonomic diversification occurs in Australia, where the endemic *Psyllaephagus* species, like almost all others in the genus, attack nymphs of Psylloidea, and a few are reported as hyper-parasitoids attacking other *Psyllaephagus* species (Noyes and Hanson, 1996; Riek, 1962). Their psyllid hosts, in turn, are often specialist on Myrtaceae, mainly species groups and subgenera of *Eucalyptus* (Moore, 1988; Yen, 2002). The effectiveness and specificity of the Australian
Psyllaephagus has made them especially attractive candidates for use in classical biological control programs that target psyllid pests of Eucalyptus, and they have been used for programs in California, Mexico, and the British Isles (Chauzat et al., 2002; Dahlsten et al., 1998a; Paine et al., 2000).

Psyllaephagus bliteus Riek was widely released in California from 2000 through 2002 to control the Australian red gum lerp psyllid, Glycaspis brimblecombei Moore (Hemiptera: Psylloidea) (Paine and Millar, 2002; Paine et al., 2000), after quarantine studies indicated that it would specifically attack this host (Dahlsten et al., unpublished data). This psyllid was first discovered in Los Angeles County in 1998 (Brennan et al., 1999) and had spread throughout California by 2000 (Paine and Millar, 2002) and Mexico by 2002 (J. Guerra, pers. comm.). Like other Glycaspis spp. and some related psyllids, the nymphs of G. brimblecombei are characterized by the shelters (lerps) they construct from excreted carbohydrates and proteins (Ernst and Sekhwela, 1987; Gilby et al., 1976; Moore, 1961). The accumulation of the sticky lerps on leaves and underneath infested trees creates a nuisance, while heavy infestations lead to defoliation, branch dieback, and occasionally tree death (Paine et al., 2000). The main host of G. brimblecombei in California, the river red gum (Eucalyptus camaldulensis Dehn.) (Brennan et al., 2001), is one of the most commonly planted shade and windbreak trees in both urban and rural environments and is also grown commercially for fuel wood (Cockerham, 2004; Helms, 1988). The biological control program with P. bliteus against the red gum psyllid has been largely successful in California’s coastal regions, but has provided, to date, only sporadic control in some of the warmer interior regions (Dahlsten et al., unpublished data). We report herein on basic biological information on P. bliteus that was collected to supplement and improve the control program, especially insectary operations and release strategies.

During quarantine screening, one of us (RLZ) also reviewed the taxonomic status of P. bliteus. Amongst the specimens that emerged in quarantine from material collected in Australia were male and female Psyllaephagus specimens: the females matched Riek’s (1962) description of P. bliteus and the males that of Psyllaephagus quadricyclus Riek. These males and females were observed to mate and reproduce, indicating that the species descriptions required review. Riek (1962) described P. bliteus from a series of females from Canberra (Australian Capital Territory), noting that it also occurred in South Australia, New South Wales and Queensland. Psyllaephagus bliteus had been reared from undetermined Glycaspis (= Spondyliaspis) species on Eucalyptus rossii, E. blakelyi, E. leucoxylon and E. camaldulensis, as well as from Creiis costatus (Froggatt) on E. blakelyi. In the same paper, he described P. quadricyclus from a series of males from Canberra, also recording it from South Australia and New South Wales. These had been bred from undetermined Glycaspis species on Eucalyptus melliodora, E. rossii, E. blakelyi, E. viminalis, and an undetermined Eucalyptus species. Thus, these species were essentially sympatric (one paralectotype of P. bliteus and both paratypes of P. quadricyclus were collected from the same site, “Black Mountain,” within a few days of each other) and probably share the same hosts. We examined the lectotype (assigned by John Noyes) and three paralectotypes of P. bliteus, and the holotype (male, not female as reported in Riek, 1962) and two paratypes of P. quadricyclus. These specimens were conspecific with the females and males, respectively, imported to California—including F1 and F2 specimens from the importation cultures, as well as field-collected specimens. Additional verified P. bliteus specimens have been reared from G. brimblecombei on a Eucalyptus sp. from Sao Paulo, Brazil, in 2003, and from Ulupalakua, Maui, Hawaii, in 2004. The junior author (RLZ) herein proposes the synonymization of P. quadricyclus Riek under P. bliteus Riek as follows:

Psyllaephagus bliteus Riek
Psyllaephagus bliteus Riek, 1962: 722–723 (Holotype female, Australia, ANIC)
Psyllaephagus quadricyclus Riek, 1962: 751–752 (Holotype male, Australia, ANIC) syn. nov.

2. Materials and methods

2.1. Insect and plant materials

Laboratory cultures of red gum lerp psyllids were derived from field-collected material on infested red gum eucalyptus in Alameda and Sacramento Counties, California. The psyllids were reared on potted (2.2 L) red gums that were either grown from seed (about 80% of the plants) or purchased from commercial nurseries. Red gums were maintained in a glasshouse at the University of California, Berkeley, Insectary and Quarantine Facility, at 22±3°C and with natural lighting. Small red gums (0.5–1 m) were inoculated with adult psyllids and, by manipulating the numbers and periods of ovipositing females, we were able to produce trees infested with 200–800 psyllids of the desired developmental stages. We periodically reintroduced field-collected psyllids to reduce inbreeding. These infested trees were used in all described experiments.

The P. bliteus used in experiments were reared from psyllids that were field-collected on red gum foliage in the Ardenwood Regional Preserve (Alameda County, California). This parasitoid population had originated from P. bliteus imported from southern Australia in 1999, reared in quarantine and released throughout California in 2000 and 2001 (Paine et al., 2000). Each
week, infested red gum foliage was collected and placed inside wood-sided sleeve cages (45 × 45 × 45 cm) that were provisioned with dilute honey (1:1 honey and water by volume). Unless noted otherwise, adult *P. bliteus* were collected daily as they emerged, placed in glass vials that were provisioned with dilute honey, and held in an incubator at 12 ± 2 °C for 1–10 days until used. On each day we collected all parasitoids found; therefore, we assume the collected parasitoids were less than one day old. Voucher specimens of red gum lerp psyllids and *P. bliteus* have been deposited in the Essig Museum, University of California, Berkeley.

2.2. Host-stage preference for oviposition

Infested trees were selected that had 300–500 psyllid nymphs, with the population comprised of all five development stages in similar proportions, as estimated by lerp size. For each replicate, 3–4 infested red gums were placed in cloth-sided tree cages (32 × 45 × 96 cm) and held at 25 ± 2 °C under fluorescent lighting with a 16:8 (L:D) photoperiod. At the start of each trial, 15–20 female and 4–5 male *P. bliteus* were released into the cage. After 24 h, the parasitoids were removed and all psyllids found were transferred to 70% ethanol. To determine whether or not the exposed psyllids were parasitized and their development stage, the psyllids were transferred to a clearing solution of chloralphenol (10 g phenol, 10 g chloral hydrate, and 3–5 ml distilled water). After 24 h in chloralphenol, the psyllid’s body becomes transparent and *P. bliteus* eggs are visible under a dissecting microscope. At the same time, we determine the psyllid development stage by counting the number of antennal segments, as described by Moore (1961). The parasitism rates for psyllids in each of the five nymphal stages were compared. There were five replicates, with new parasitoids used for each replicate.

2.3. Host-handling behavior

We used direct observations of the host-handling behavior of experienced *P. bliteus* to further assess host-stage preference and oviposition success. An individual female was provided with a single red-gum leaf infested with 70–100 lerps, which were estimated (by size) to house psyllids in all five developmental stages and in similar proportions. The leaf was placed in a transparent plastic cylinder (21 cm long × 7 cm diameter), which was ventilated by a cloth mesh covering one end and a 4 cm diameter hole in the side. The *P. bliteus* was added and her host-handling behavior was observed under a dissecting microscope for 1 h, beginning when the parasitoid first touched a psyllid. The tested *P. bliteus* were discarded if they showed no interest in the psyllids during the initial 10 min of observation. Oviposition and host-feeding events and duration were recorded. During each trial, the psyllid’s developmental stage was estimated by the lerp size. At the end of each trial, the lerps were removed and presence or absence of psyllids was noted, as red gum psyllid nymphs often move from their lerps (Moore, 1961). The psyllids were then transferred into 70% ethanol, cleared in chloralphenol, and the presence of *P. bliteus* eggs and the development stages of parasitized nymphs were recorded, as described previously. We completed 18, 1-h trials.

2.4. Adult longevity and fecundity

Adult longevity was determined at five temperatures (17, 21, 23, 26, and 32 °C). Males and females were tested separately. Newly emerged (12–16 h) *P. bliteus* were collected, placed in 35 ml glass vials that were provisioned with dilute honey–water, and randomly assigned to a temperature treatment. Thereafter, the vials were checked every 24 h and the *P. bliteus* condition (live or dead) was recorded. The honey–water was refreshed daily and the vials were changed weekly. Temperature cabinets maintained temperatures (*T*) at *T* ± 1 °C, with a 16:8 (L:D) photoperiod. We tested 20 females and 7–10 males at each temperature.

Adult fecundity, as estimated by life-time egg deposition, was also determined. Newly emerged (12–16 h) female and male *P. bliteus* were collected and held together for 24 h. The mated females were individually isolated in clear plastic tubes (4 × 8 cm) that each enclosed a single infested leaf on a potted red gum tree in the glasshouse (22 ± 3 °C). Each leaf was infested with 10–30 psyllids, primarily in the third instar development stage. The plastic tubes were covered with a nylon mesh on the open end, to provide ventilation, and plastic foam on the other end, to wrap around the leaf petiole and enclose the leaf. The parasitoid was transferred to a new leaf every 2 days throughout her lifetime. After each transfer, the exposed psyllids were placed into 70% ethanol, cleared in chloralphenol, and the presence of *P. bliteus* eggs and the development stages of parasitized psyllids were recorded, as described previously.

2.5. Immature development time

The development time of *P. bliteus* immature stages was assessed at three constant temperatures: 22, 26, and 30 °C. For each trial, infested red gums were selected that had 100–300 psyllids; all stages of psyllids were present on each tree, but the populations were dominated by third and fourth instars, which were identified by the host-stage preference study as the preferred stages for oviposition. The trees were placed individually in the cloth-sided tree cages and 25–30 female *P. bliteus* were placed in each cage for a 48 h period (and then removed). This oviposition period occurred at 25 ± 2 °C. The trees were then randomly assigned to different temperature
cabinets (treatment). The temperature cabinets used maintained temperatures at $T \pm 1\, ^\circ C$, with a 16:8 (L:D) photoperiod. Thereafter, 20 psyllids were collected every 3–4 days, placed into 70% ethanol and later cleared in chloralphenol, as described previously. The presence of \textit{P. bliteus} eggs or larvae and the development stages of parasitized psyllids were recorded. We completed four trials at each temperature.

2.6. Statistics

Results are presented herein as means per treatment ($\pm$ SEM). Treatment effects were analyzed using analysis of variance (ANOVA), with treatment means separated using Tukey’s HSD test (three or more treatments) or a $t$ test (two-way comparisons) at $P < 0.05$. We used regression analysis to describe the relationship between \textit{P. bliteus} host-handling duration and psyllid development stage, and adult \textit{P. bliteus} longevity and temperature.

3. Results and discussion

3.1. Host-stage preference for oviposition

From 2279 exposed and examined psyllids, we found 164 \textit{P. bliteus} eggs in 155 hosts, with an average 7.9 $\pm$ 2.7% parasitism across all trials. Percentage parasitism was determined by the mean of means for each replicate, which ranged from 1.3 to 31.7%. We believe the wide range in percentage parasitism was an artifact of the variation in number of psyllids provided in each replicate, while the number of parasitoids remained the same. Because the psyllids are covered by lerps, before the trial started we could only estimate the actual number of live psyllids under the lerps; in some trials there proved to be more empty lerps. Of the parasitized psyllids, significantly more of the \textit{P. bliteus} eggs were recovered from third (49.6 $\pm$ 10.5%) and fourth (35.5 $\pm$ 7.3%) instar psyllids than from the first (0.23 $\pm$ 0.23%), second (8.12 $\pm$ 3.15%), and fifth (6.60 $\pm$ 2.93%) instars (Fig. 1). There was no significant difference in the number of parasitized first, second or fifth instar psyllids (Fig. 1); however, only a single first instar was parasitized. There was no significant difference in the numbers of each psyllid developmental stage provided ($df = 4.30$, $F = 1.789$, $P = 0.156$) and there was an overabundance of psyllids in each development stage, with the exception of one trial where no first instars were found. Therefore, the encounter frequency of the different psyllid development stages did not impact oviposition decisions and we conclude that \textit{P. bliteus} preferentially deposits eggs in third and fourth instar psyllids, although it will attack all nymphal stages in a host-choice test arena. A similar finding has been reported for \textit{Psyllaephagus pulvinatus} (Waterston) on the citrus psylla, \textit{Trioza erytreae} (Del Guercio), which strongly prefers to attack third instars (while the offspring feed on and emerge from fifth) (McDaniel and Moran, 1972), and for \textit{P. pilosus} Noyes on the on blue gum psyllid, \textit{Ctenarytaina eucalypti} Maskell (Dahlsen et al., 1998b) and \textit{P. euphyllurae} (Masi) on \textit{Euphyllura olivina} (Chermiti et al., 1986), though the latter two appear to prefer older (fourth and fifth instar) psyllids. In contrast, \textit{P. yaseeni} Noyes typically attacks smaller (first and second instar) psyllids (Patil et al., 1993).

We observed \textit{P. bliteus} eggs deposited in the psyllid thorax and abdomen, without any apparent preference for either region. Most of the parasitized psyllids (94.5%) in this trial had a single egg deposited, while eight third instars and a single fifth instar had two eggs; however, in this trial there was an overabundance of host-material provided. From field-collected material we commonly found two eggs per host and in a laboratory study with restricted host-material provided we found up to 26 eggs per host. In both of these situations, the number of available hosts was restricted and adult \textit{P. bliteus} may have competed for host-material. Moreover, in all laboratory trials and field collections, we have never reared more than one \textit{P. bliteus} adult per host nor found more than one large \textit{P. bliteus} larva per host. Therefore, we believe that hosts with more than one egg are superparasitized and, although some solitary parasitoids lay multiple egg clutches (Rosenheim and Hongkham, 1996), we prefer the simpler explanation that competition for a limited resource resulted in more than one egg per host. Regardless, our experimental designs do not allow us to determine whether psyllids containing more than one egg
were attacked by one, or more than one, parasitoid. This observation implies that, during host-handling, *P. bliteus* has either little or no ability to discriminate previously parasitized hosts. Several wasps probed empty lerps, which suggests that there is little recognition of host-condition under the lerp and that chemical cues on the lerp itself may initiate oviposition. We do not know, in cases of superparasitism, if the numbers of parasitoid larvae are reduced through resource or direct competition.

3.2. Host-handling behavior

Direct observations of host-handling revealed a different pattern of host-stage preference as compared with that revealed by dissecting individuals for deposited eggs (Fig. 1). Here, we estimated the lerp size (and stage of the psyllid underneath) during the oviposition attempt, and after clearing and examining the psyllid we later determined the nymphal stage and whether the oviposition attempt resulted in successful egg deposition. This study showed that the *P. bliteus* made significantly more oviposition attempts in the larger psyllids (third to fifth instars) (Fig. 2), and that host-handling time (as measured by oviposition attempts either for host-feeding or oviposition) was a positive linear function of psyllid developmental stage (*y* = −1.37 + 1.29*x*, *r*² = 0.96, *df* = 1.4, *F* = 82.92, *P* < 0.003). The pattern is essentially the same as that found in the host-preference study with one exception—the largest lerps (fifth instar nymphs) were the most commonly attacked. However, when the exposed psyllids were cleared and examined, we found *P. bliteus* eggs in third and fourth instar psyllids, but not fifth instars.

In the comparison of oviposition duration, we used measurements from only those *P. bliteus* that oviposited in both small and large lerps during the same 1 h period, to conduct a paired *t* test. Handling times for oviposition were significantly shorter on the smaller (first, second, third instar) than larger (fourth and fifth instar) lerps, measuring 69.0 ± 3.3 and 232.3 ± 47.1 s, respectively (*t* = −3.801, *P* = 0.003). We believe the difference is explained by the lerp structure. The psyllids have some free space within the lerp, and the large lerps have both a greater external diameter and internal free space, relative to the nymph size. During our observations, the psyllids could be seen through the more translucent lerps, moving within the lerp to avoid the parasitoid’s probing ovipositor; the parasitoid, in turn, would move from side to side on top of the lerp and repeat its drilling attempts in different locations. The greater internal free space therefore allows the psyllid to move to avoid oviposition attempts. For these larger lerps, successful oviposition typically occurred when the ovipositor was quickly slipped under the edge of the lerp, which is loosely fixed to the leaf surface and provides small gaps, rather than through the lerp (as was reported by Moore, 1961). This same oviposition location was reported for *Metaphycus annekei* Guerrieri and Noyes to oviposit in black scale, *Saisssetia oleae* (Olivier), and was suggested as a method to reduce oviposition time (Barzman and Daane, 2001).

We found that *P. bliteus* had significantly greater oviposition success in second and third instar psyllids (Fig. 1), while there was a clear preference in oviposition attempts for larger lerps (Fig. 2). We suggest this discrepancy is explained by the increased handling times and lower oviposition success in these larger nymphs. Therefore, one function or realized benefit of the large lerps is protection from *P. bliteus*. Moore (1961), citing the occasionally high rates of parasitism of *Glycaspis* species in Australia, argued that the main function of the lerp was not to protect the nymphs from natural enemies but to either reduce desiccation or provide a fortuitous method of disposing of waste. Ours is the first indication that the lerps can also play a role in deterring at least one natural enemy.

Two modes of host-utilization for adult nutrients were observed. In the first, the wasps simply lapped at the surface of the lerp without disturbing the nymph underneath. Because the lerp is composed of excreted carbohydrates and proteins (Ernst and Sekhwela, 1987; Gilby et al., 1976) it may provide some of the nutritional requirements gained through host-feeding (Jervis and Kidd, 1986); however, as the lerp composition is primarily sugars, we suggest that lerp utilization is primarily for adult longevity rather than for increased egg load or...
development (Godfray, 1994). In the second mode, *P. bliteus* females host-fed on the psyllid after either sliding their ovipositors under or drilling through the lerps. Only 7 of 18 *P. bliteus* host fed during the total observation period (18 h). In these cases, the parasitoid probed briefly with her ovipositor, presumably piercing the nymphs, and then turned around and imbibed fluids that flowed out from under the edge of the lerp. With the exception of two, relatively short (8 and 13 s) events, host-feeding involved repeated bouts of drilling, probing and drinking over the course of several minutes (833.2 ± 224.3 s), which was significantly longer in duration than oviposition time on either small or large lerps (F = 11.245, df = 2, 28, P < 0.001). In each case, the *P. bliteus* host-fed only 1–2 times, with psyllid nymphs of all stages attacked in the following frequency: 1, 4, 3, 3, and 1 for first, second, third, fourth, and fifth instar psyllids, respectively. While there were more first and second instar psyllids used for host-feeding than expected based on egg deposition, observed host-feeding events were relatively rare and we could not clearly determine if *P. bliteus* has concurrent and/or nonconcurrent host-feeding mechanism(s) (Heimpel and Collier, 1996).

3.3. Adult longevity and fecundity

We tested adult longevity under a range of temperatures that could be used in insectary operations. From 17 to 32 °C, female and male *P. bliteus* longevity were negative linear functions of temperature (Fig. 3), ranging from 40.8 ± 3.3 days (at 17 °C) to 14.2 ± 0.9 days (at 32 °C). At each temperature, females lived significantly longer than males (Fig. 3). Excluding two individuals that were lost during the first week, lifetime egg deposition was 125.7 ± 24.6 eggs per female (range 34–302). Most eggs (88.1%) were deposited during the initial 22 days, although one parasitoid lived for 90 days and deposited eggs up to 70 days after emergence (Fig. 4). The average longevity of adult females, provided host material, was 60.4 ± 6.4 days (under described glasshouse conditions). During the initial 22 days, there were 7.0 ± 0.8 eggs per female per day deposited (range 0–39). The longevity and observed

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**Fig. 3.** *Psyllaephagus bliteus* adult female and male longevity was a negative linear function of five tested constant temperatures (17, 21, 23, 26, and 32 °C). Longevity was significantly different among tested temperatures for females (F = 41.52, df = 4, 89, P < 0.001) and males (F = 23.70, df = 4, 43, P < 0.001); within each gender, means followed by the same letter are not significantly different (Tukey’s HSD test, P < 0.05). Female longevity was significantly greater than male longevity at each tested temperature (17 °C, t test = 3.306; P = 0.003; 21 °C, t test = 5.106; P < 0.001; 23 °C, t test = 2.789; P = 0.009; 26 °C, t test = 5.307; P < 0.001; 32 °C, t test = 3.774, P = 0.001).

**Fig. 4.** *Psyllaephagus bliteus* lifetime fecundity, as estimated by egg deposition under glasshouse conditions with an overabundant host supply.
host-feeding behaviors of adult *P. bliteus* indicate synovigenic egg production; however, the fact that most eggs are deposited during the initial 22 days indicates that *P. bliteus* may have a significant proportion of its eggs available soon after emergence. Under the laboratory conditions imposed, parasitoid longevity may have been greatly overextended compared to longevity under field conditions. A truly synovigenic species would continue to develop and mature eggs during the entire lifetime, which rarely occurred in our experiment (Fig. 4). As differences between pro-ovigenic and synovigenic species often represent a continuum of life history strategies (Jervis et al., 2001), we suggest that while *P. bliteus* is synovigenic, it cannot produce and mature eggs throughout the long lifespan realized under laboratory conditions.

These results have implications for insectary operations and release strategies in classical biological control programs. Although adults may survive for long periods, most egg deposition occurs early in the adult’s lifetime. Insectary colonies should therefore be supplied with the needed number of third or fourth instar psyllids for an oviposition period of 2–3 weeks. Because they are used for host-feeding, first or second instars should be provided as well. Rearing temperatures should range from 21 to 24°C. We suggest that for release programs, adults should be collected and released within 3–7 days after emergence in order to provide highly fecund individuals.

### 3.4. Immature development time

There was considerable variation in the immature development time, regardless of the temperature treatment. We found that *P. bliteus*, like other *Psyllaephagus* spp. studied in detail (McDaniel and Moran, 1972; Patil et al., 1993), is a koinobiont and the offspring will delay development until the psyllid reaches the proper stage or size (Godfray, 1994). In this trial, eggs were found in third, fourth, and young fifth instar psyllids (the relative age of fifth instars is indicated by the degree of sclerotization). Larvae and pupae were only found in fifth instar psyllids, however, and the psyllids appeared outwardly unaffected until the fifth instar, when the parasitoid larva presumably begins to develop and feed. Eggs deposited into younger nymphs that had still not reached the fifth instar were still eggs at the end of the trial, but larval development was rapid when eggs were deposited into fourth or fifth instars. These results indicate that *P. bliteus* is a koinobiont that delays larval development until the host reaches the late fourth or early fifth instar.

In our trial, while examining the cleared specimens, we identified newly parasitized psyllids by the presence of the encyrtiform egg, attached to the host-integument via an aeroscopic plate. We were able to clearly distinguish second and third instar *P. bliteus*, but we were unable to locate first instars and we suspect this development stage may have been destroyed during the clearing process with chloralphenol. Across all temperatures (22, 26, and 30°C) and psyllid development stages (second through fifth), average *P. bliteus* development time, from egg to pupa, was 18.3 ± 0.9 days. With no regard to the initial psyllid stage attacked, *P. bliteus* development was 22.6 ± 1.9, 18.0 ± 1.1, and 12.6 ± 1.2 days at 22, 26, and 30°C, respectively. When *P. bliteus* oviposited initially into fifth instar psyllids, development (egg to pupa) was only 7, 6, and 8 days at 22, 26, and 30°C, respectively (no variation).

In summary, this study has several implications for mass rearing and release of *P. bliteus*. Third-instar nymphs are the most suitable for oviposition and are suitable for host-feeding as well. The development time of offspring, however, depends on the psyllid stage attacked as well as on temperature, decreasing with increasing temperature. For the adults, high rates of oviposition can be sustained for up to about 22 days after emergence, at moderate temperatures, and because adult longevity decreases sharply with temperature, high temperatures may decrease lifetime fecundity. This last set of observations has important consequences for the evaluation of the biological control program in California. To date, about four years after the initial mass releases, *P. bliteus* remains less effective, with lower parasitism rates, in the interior of California compared to coastal regions, where it rapidly established and lowered psyllid populations (Dahlsten, unpublished data; Sime et al., 2004). While the coastal regions tend to be mild year-round, the inland Sacramento and San Joaquin valleys are characterized by hot summers, with temperatures commonly reaching 40°C. This study suggests that such temperatures would dramatically decrease adult longevity, to much less than the 22 days during which oviposition rates are high. Lowered lifetime fecundity, in turn, would be expected to slow and reduce the success of *P. bliteus* as a control agent. To test this hypothesis we are currently investigating the longevity and fecundity of *P. bliteus* in the field, comparing coastal and inland sites. It may prove necessary to import additional *Psyllaephagus* species, or different populations of *P. bliteus*, to improve effective biological control throughout California.

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