



## Performance of adult psyllids in no-choice experiments on juvenile and adult leaves of *Eucalyptus globulus*

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### Abstract

The presence of glaucous juvenile leaves and glossy adult leaves in the canopy of the heteroblastic plant *Eucalyptus globulus* Labill., is a source of within-tree variation that affects herbivory by three psyllid species (*Ctenarytaina eucalypti* Maskell, *C. spatulata* Taylor and *Glycaspis brimblecombei* Moore) (Homoptera, Psyllidae). In no-choice field experiments with adult female psyllids in clip-on cages, we compared (1) leaf-settling, honeydew production, and survival of the *Ctenarytaina* species on juvenile and adult leaves of *E. globulus*, (2) leaf-settling and survival of *G. brimblecombei* on juvenile and adult leaves, (3) leaf-settling and survival of the three species on waxy (untreated) juvenile leaves and de-waxed (rubbed) juvenile leaves, and (4) leaf-settling and survival of *C. spatulata* on juvenile leaves from which wax was repeatedly removed. Leaf-settling by *C. eucalypti* was significantly greater on juvenile than adult leaves, however, honeydew production and survival were equal on both leaf types. In contrast, leaf-settling, honeydew production, and survival by *C. spatulata* were significantly greater on adult than juvenile leaves. Similarly, leaf-settling and survival by *G. brimblecombei* were significantly greater on adult than juvenile leaves. Wax removal from juvenile leaves significantly increased leaf-settling and survival of *C. spatulata* and *G. brimblecombei*. Although wax removal decreased leaf-settling by *C. eucalypti*, it did not affect survival. Repeated removal of regenerating wax from juvenile leaves did not affect leaf-settling or survival of *C. spatulata*. These results suggest that the epicuticular wax of juvenile leaves plays a role in resistance to *C. spatulata* and *G. brimblecombei*, however other unknown factors are probably also involved.

### Introduction

*Eucalyptus globulus* is a heteroblastic plant with morphologically and anatomically distinct juvenile and adult leaves (Johnson, 1926; Reeve, 1949; Brennan, 2000). The glaucous, simple-shaped juvenile leaves contrast sharply with the glossy, sickle-shaped adult leaves. Although heteroblasty is a common source of within-tree variation in *Eucalyptus* and other large genera (e.g., *Acacia*), its effects on herbivores has received little attention. Brennan (2000) found ovipositional antixenosis of juvenile and adult shoots of *E. globulus* to three psyllid species. Two species (*Ctenarytaina spatulata* Taylor and *Glycaspis brimblecombei* Moore) preferred adult shoots, and *C. eu-*

*calypti* Maskell preferred juvenile shoots. These plant-insect interactions are some of the first examples of developmental resistance (Kearsley & Whitham, 1989) due to heteroblasty. In this paper, we test for antibiosis in the juvenile and adult leaves of *E. globulus* and study the role of epicuticular wax on psyllid resistance.

The juvenile leaves of *E. globulus* are glaucous due to light-scattering, tubular epicuticular waxes that are generally absent from the glossy adult leaves (Hallam & Chambers, 1970; Baker, 1982; Wirthensohn & Sedgley, 1996). Epicuticular waxes can affect plant resistance to insects by deterring or stimulating feeding and oviposition, and by reducing insect adhesion to plant surfaces (Eigenbrode & Espelie, 1995). Juvenile leaf waxes of *E. globulus* can be removed by gently

rubbing leaf surfaces with cotton swabs. Following its removal, wax regeneration has been detected on leaves within hours (Hallam, 1970; Wirthensohn & Sedgley, 1996). We hypothesize that the glaucous wax on juvenile leaves of *E. globulus* is involved in resistance to *C. spatulata* and *G. brimblecombei* because these psyllids only colonize glossy adult leaves of *E. globulus* and other nonglaucous species (i.e., *E. camaldulensis* Dehnh). In contrast, we hypothesize that the wax is a phagostimulant for *C. eucalypti* because this psyllid only colonizes glaucous juvenile leaves of *E. globulus* and other species with glaucous leaves (e.g., *E. pulverulenta* Sims., *E. cinerea* F. Muell. ex Benth.).

Our study addressed 4 main questions: (1) Are there differences in leaf-settling, honeydew production and survival of the two Ctenarytaina species on juvenile versus adult leaves? (2) Are there differences in leaf-settling and survival of *G. brimblecombei* on juvenile versus adult leaves? (3) Does juvenile epicuticular leaf wax affect leaf-settling and survival of the three psyllid species? (4) Are leaf-settling and survival of *C. spatulata* on juvenile leaves affected by repeated removal of regenerating wax?

## Materials and methods

The experiments were conducted in El Cerrito, California between June and September, 1999 on *E. globulus* trees containing both juvenile and adult shoots. Adult female psyllids from wild populations of the three species were used. In each experiment, sexually mature psyllids were confined in clip-on cages that each covered approximately 113 mm<sup>2</sup> of leaf area. In all of the experiments there was one psyllid per cage.

*Experiment 1a: Effect of leaf type on leaf-settling, honeydew production, and survival by C. eucalypti and C. spatulata.* Our objective was to compare leaf-settling, honeydew production, and survival of *C. eucalypti* and *C. spatulata* on the adaxial and abaxial surfaces of expanding juvenile and adult leaves of *E. globulus*. Leaf-settling refers to whether a psyllid was settled (i.e., not moving) on the leaf surface under a cage during the approximately 20-s observation period. Each replicate included four cages on a juvenile leaf and four cages on a nearby adult leaf in a similar region of the tree canopy. Within each leaf type, two cages were attached on the adaxial surface and two were attached on the abaxial surface, and the

two psyllid species were randomly distributed to either cage on each leaf surface. The experiment was replicated ten times among three trees and lasted for ten days from from 7 June to 17 June; although some of the psyllids were still alive at the end of this period, Brennan (2000) found that psyllid survival on the juvenile and adult leaves after ten days was consistent with the long-term survival (i.e., until death). To assess honeydew production and survival on a nearby non-host plant, ten psyllids of each species were caged on the adaxial and abaxial surfaces of adult *Hedera helix* L. (ivy) leaves. Survival was also assessed on a non-plant medium, by caging ten psyllids of each species on a plastic transparency sheet hanging within the canopy of an *E. globulus* tree. We recorded leaf-settling and survival three times daily (approximately 6 AM, 12 PM, 6 PM) during the first five days of the experiment and once daily thereafter. To quantify feeding we recorded the number of honeydew droplets present in each cage on day six. The honeydew droplets of both species were approximately equal in size. Droplets remained separate from each other and could be counted readily. Preliminary analyses showed that psyllid performance was the same on the adaxial and abaxial surfaces within each leaf type, so the data from both surfaces were combined. Paired *t*-tests (two-sided) were used to compare honeydew production and the cumulative number of leaf-settling observations on juvenile and adult leaves of *E. globulus* within each species. Due to the paired design of the experiment, leaf-settling and honeydew production were only compared for the time period that both individuals in each pair were alive. Sign tests (two-sided) were used to compare survival on the juvenile and adult leaves within each species. Statistical comparisons were not made between psyllid performance on *E. globulus* leaves and performance on the nonhost plant (ivy) or plastic sheets due to the design of the experiment.

*Experiment 1b: Effect of leaf type on leaf-settling and survival by G. brimblecombei.* This experiment was similar to experiment 1a, but focused on *G. brimblecombei* and was conducted from 13 June to 20 June. Honeydew production was not quantified because *G. brimblecombei* adults did not excrete honeydew as discrete droplets that were apparent in the cages. The experiment was replicated ten times and paired *t*-tests were used to compare psyllid performance on juvenile and adult leaves.

*Experiment 2a: Effect of juvenile epicuticular leaf wax on leaf-settling and survival of C. eucalypti and C. spatulata.* Our objective was to compare leaf-settling and survival of *C. eucalypti* and *C. spatulata* on regions of the adaxial surface of juvenile leaves with glaucous wax present (waxy) versus regions where the wax had been removed by gently rubbing with cotton swabs (de-waxed). Our use of the terms 'waxy' and 'de-waxed' refer only to epicuticular wax. Within each replicate (leaf) both psyllid species were evaluated for both the waxy and de-waxed treatments. Each replicate contained four cages at the middle of the leaf, with two on either side of the mid rib at a distal position, and the other two at a proximal position. Within each species, the waxy and de-waxed regions were the same distance from the petiole, but on opposite sides of the mid rib. We randomly assigned the two species to either the distal or proximal pair of cages. The experiment was conducted from 28 June to 8 July. We recorded leaf-settling and survival three times daily (approximately 6 AM, 12 PM, 6 PM) for the first three days, twice daily (6 AM and 6 PM) for days four to six, and once daily (6 AM) from day seven onwards. The experiment was replicated ten times, and paired *t*-tests were used to compare leaf-settling and survival on waxy and de-waxed regions, within each species.

*Experiment 2b: Effect of juvenile epicuticular leaf wax on leaf-settling and survival of G. brimblecombei.* This experiment was similar to experiment 2a, but focused on *G. brimblecombei* and was conducted from 10 to 14 June. The experiment was replicated ten times, and paired *t*-tests were used to compare performance on de-waxed and waxy regions.

*Experiment 3: Effect of repeated leaf wax removal on survival of C. spatulata on the adaxial surface of juvenile leaves.* Our objective was to determine whether repeated wax removal increased leaf-settling and prolonged the survival of *C. spatulata* on the adaxial surface of juvenile leaves. Each replicate included two cages on either side of the mid rib at the middle of a leaf. On day one, the wax was rubbed off of the leaf surface under each cage, and one psyllid was placed in each cage. At approximately 8 AM daily, we recorded leaf-settling and survival, and the cage that was randomly selected for repeated rubbing was removed (with the psyllid inside), the leaf surface was gently rubbed to remove regenerated wax, and the cage and psyllid were placed back on the leaf. At rerubbing, psyllids in both treatments were gently prodded

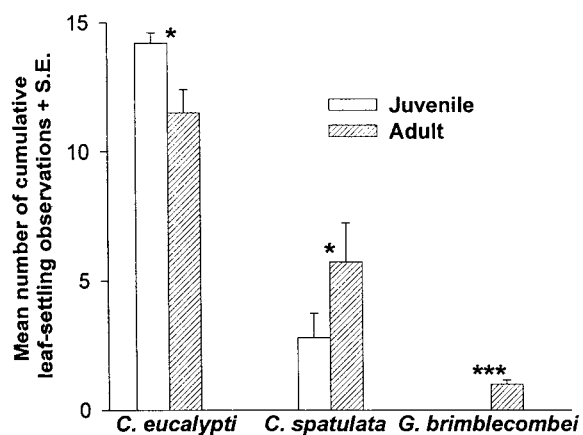


Figure 1. Leaf-settling of pairs of psyllids in experiments 1a (*C. eucalypti* and *C. spatulata*) and 1b (*G. brimblecombei*) on juvenile and adult leaves of *E. globulus*. In each experiment, leaf-settling was recorded until one psyllid in each replicate pair died. Within each species, \* and \*\*\* indicate significant differences between the mean number of cumulative leaf-settling observations on the juvenile versus adult leaves at the  $P < 0.05$  and  $P < 0.001$  levels, respectively.

with a thin wire to force them to move. This experiment was replicated ten times and was conducted from 1 September to 11 September until all psyllids had died. Paired *t*-tests were used to compare leaf-settling and survival on once-rubbed and repeatedly rubbed regions.

## Results

*Experiments 1a and 1b: Effect of leaf type on leaf-settling, honeydew production, and survival by the 3 psyllid species.* There were significant differences in leaf-settling by the psyllids on juvenile and adult leaves (Figure 1). *Ctenarytaina eucalypti* settled more often on juvenile than adult leaves ( $t = 2.8$ ;  $df = 9$ ;  $P < 0.05$ ), while *C. spatulata* settled more on adult than juvenile leaves ( $t = 2.7$ ;  $df = 7$ ;  $P < 0.05$ ). Leaf-settling by *G. brimblecombei* was observed rarely, but occurred significantly more often on adult than juvenile leaves ( $t = 6.0$ ;  $df = 9$ ;  $P < 0.001$ ). There were several times more leaf-settling observations for *C. eucalypti* than *C. spatulata* and *G. brimblecombei* because replicate pairs of *C. eucalypti* survived longer on both leaf types.

Both *Ctenarytaina* species produced honeydew by day six (Figure 2). There was no significant difference in honeydew production by *C. eucalypti* on juvenile and adult leaves ( $t = 0.53$ ;  $df = 8$ ;  $P = 0.61$ ),

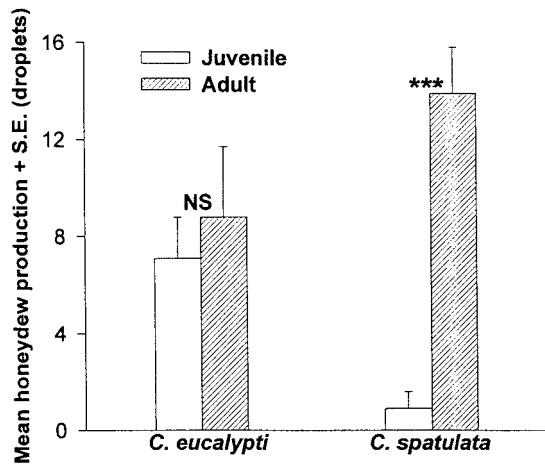


Figure 2. Honeydew production by *C. eucalypti* and *C. spatulata* in experiment 1a on juvenile and adult leaves of *E. globulus* by day six. Within each species, NS is not significant ( $P > 0.05$ ), and \*\*\* is significant at  $P < 0.001$ .

however, *C. spatulata* produced significantly more honeydew on adult than on juvenile leaves ( $t = 6.5$ ;  $df = 8$ ;  $P < 0.001$ ). *Ctenarytaina eucalypti* produced honeydew in all nine juvenile and adult leaf replicates, whereas *C. spatulata* produced honeydew in only two of nine juvenile leaf replicates, and on all nine adult leaf replicates. Neither *Ctenarytaina* species produced honeydew while caged on ivy leaves or plastic sheets.

There were differences in psyllid survival on juvenile and adult leaves of *E. globulus*, ivy leaves, and plastic sheets (Figure 3). Survival of all species was shortest on plastic sheets followed by ivy leaves. *Ctenarytaina spatulata* survived significantly longer ( $z = 3.16$ ;  $P < 0.01$ ) on adult (mean ten-day survival  $\pm$  s.e.;  $10.0 \pm 0$  days) than juvenile leaves ( $2.1 \pm 0.3$  days). Similarly, *G. brimblecombei* survived significantly longer ( $t = 3.9$ ;  $df = 9$ ;  $P < 0.01$ ) on adult ( $3.6 \pm 0.4$  days) than juvenile leaves ( $1.6 \pm 0.2$  days). In contrast, there was no significant difference ( $z = 1.0$ ;  $P = 0.3$ ) in mean ten-day survival of *C. eucalypti* on juvenile ( $9.9 \pm 0.2$  days) and adult leaves ( $10.0 \pm 0$  days).

*Experiments 2a and 2b: Effect of juvenile epicuticular leaf wax on survival and leaf-settling of the three psyllid species.* There were significant differences in leaf-settling of the three psyllid species on waxy versus de-waxed regions of juvenile leaves (Figure 4). *Ctenarytaina eucalypti* settled more often on waxy than on de-waxed regions ( $t = 5$ ;  $df = 9$ ;  $P < 0.001$ ), but *C. spatulata* ( $t = 4$ ;  $df = 2$ ;  $P < 0.05$ ) and *G. brim-*

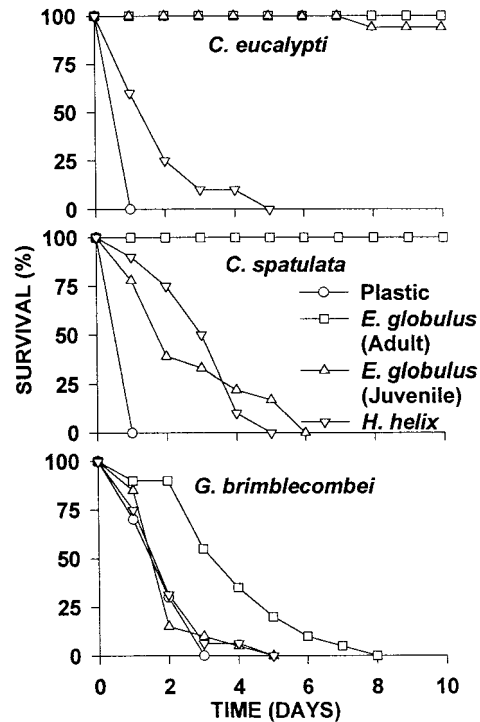


Figure 3. Survival of the *Ctenarytaina* spp. (experiment 1a) and *G. brimblecombei* (experiment 1b) in clip-on cages on plastic transparency sheets, *H. helix* leaves, and juvenile and adult leaves of *E. globulus*.

*blecombei* ( $t = 1.8$ ;  $df = 9$ ;  $P < 0.05$ ) settled more often on de-waxed regions.

Removing the wax from juvenile leaves of *E. globulus* affected survival of the three psyllid species differently (Figure 5). *Ctenarytaina spatulata* ( $t = 7.5$ ;  $df = 8$ ;  $P < 0.001$ ) and *G. brimblecombei* ( $t = 3.4$ ;  $df = 9$ ;  $P < 0.001$ ) survived significantly longer on de-waxed than on waxy regions, however, *C. eucalypti* survived equally well on both regions ( $t = 1.0$ ;  $df = 6$ ;  $P = 0.36$ ). Mean ten-day survival times ( $\pm$  s.e.) on waxy and de-waxed regions, respectively, were  $0.3 \pm 0.3$  and  $3.9 \pm 0.5$  days for *C. spatulata*, and  $1.0 \pm 0.1$  and  $2.0 \pm 0.3$  days, for *G. brimblecombei*. Most *C. eucalypti* were alive at the end of the experiment (day ten), however mean ten-day survival was  $9.2 \pm 0.5$  days on waxy regions and  $9.7 \pm 0.3$  days on de-waxed regions.

*Experiment 3: Effect of repeated leaf wax removal on leaf-settling and survival of C. spatulata on the adaxial surface of juvenile leaves.* There was no significant difference in leaf-settling on rerubbed versus once-rubbed surfaces of juvenile leaves ( $t = 1.9$ ;  $df = 9$ ;

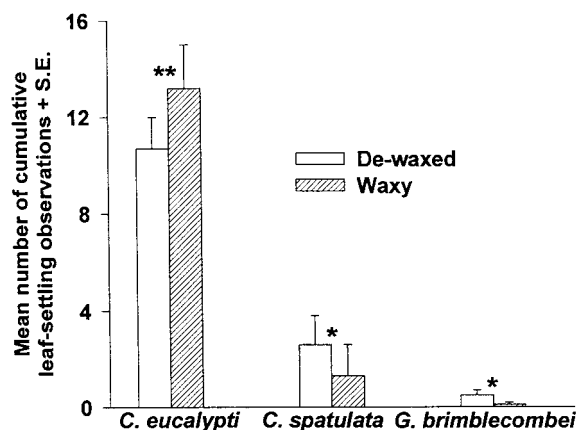


Figure 4. Leaf-settling of pairs of psyllids on de-waxed and waxy regions of the adaxial surface of juvenile leaves of *E. globulus* until one psyllid in each replicate pair died. Within each species, \* and \*\* indicate significant differences between the mean number of cumulative leaf-settling observations on the juvenile versus adult leaves at the  $P < 0.05$  and  $P < 0.01$  levels, respectively.

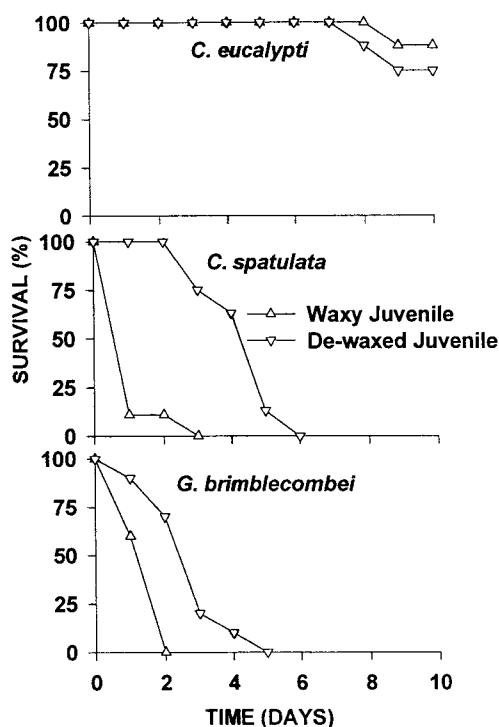


Figure 5. Survival of the *Ctenarytaina* spp. (experiment 2a) and *G. brimblecombei* (experiment 2b) on de-waxed and waxy regions of the adaxial surface of juvenile leaves of *E. globulus*.

$P = 0.09$ ). *Ctenarytaina spatulata* settled  $2.5 \pm 0.5$  times on the once-rubbed region and  $3.4 \pm 0.8$  times on the rerubbed region. The survival of *C. spatulata* was  $3.4 \pm 0.5$  days (mean  $\pm$  s.e.) in the rerubbed region and  $2.5 \pm 0.9$  days on the once-rubbed region, but these were not significantly different ( $t = 1.0$ ;  $df = 9$ ;  $P = 0.16$ ).

## Discussion

Our study demonstrates that heteroblasty in *E. globulus* significantly affects leaf-settling, honeydew production, and survival of adult female psyllids. These results are consistent with those of choice experiments that found ovipositional preferences of *C. spatulata* and *G. brimblecombei* for adult shoots, and ovipositional preferences of *C. eucalypti* for juvenile shoots (Brennan, 2000). Interestingly, both *C. spatulata* and *G. brimblecombei* survived as poorly on juvenile leaves of their host plant as on leaves of a non host-plant (ivy). In contrast, although *C. eucalypti* settled more often on juvenile than adult leaves, it survived equally well on both types of leaves. The ten-day survival of *C. eucalypti* on juvenile and adult leaves reported here is consistent with the long-term survival (i.e., until death) of adults of this species caged on both leaf types in field experiments (Brennan, 2000). Preliminary results suggested that nymphs of *C. eucalypti* cannot survive on adult leaves (Brennan, 2000) which may explain the ovipositional preference of this psyllid for juvenile shoots.

Honeydew production and longevity are indirect measures of feeding and host plant resistance to homopteran insects (Paguia et al., 1980; Eenink et al., 1984; Lewis, 1986; Shanks & Garth, 1992; Kaloshian et al., 1997). Our data suggest that the differential survival of *C. eucalypti* and *C. spatulata* on juvenile and adult leaves were due to differences in feeding behavior. Based on honeydew production, *C. eucalypti* fed equally on the adult and juvenile leaves, whereas *C. spatulata* fed mainly on adult leaves. The lack of honeydew production by *C. spatulata* on the juvenile leaves suggests that this species died sooner on the juvenile leaves than on the adult leaves due to starvation. If *C. spatulata* died sooner on the juvenile than adult leaves due to starvation, we would conclude that the juvenile leaves are antixenotic to this species. Although we were unable to quantify honeydew production by *G. brimblecombei*, the significantly longer

survival on adult leaves suggests that more feeding occurred there than on juvenile leaves.

Interestingly, *C. eucalypti* and *C. spatulata* died much sooner on the plastic sheets than on ivy leaves. The lack of honeydew production on ivy leaves suggests that differences in survival were not due to feeding. Rather, we speculate that the humidity was higher in cages on ivy leaves than in cages on plastic and that the higher humidity reduced psyllid desiccation and thus prolonged survival. This reasoning is consistent with aphid survival in cages on resistant plants and in cages without plant tissue (McMurtry & Stanford, 1960).

Epicuticular wax on juvenile leaves is clearly involved in resistance to *C. spatulata* and *G. brimblecombei* because wax removal increased leaf-settling (Figure 4) and nearly doubled psyllid survival (Figure 5). The ten-day survival of *C. eucalypti* reported here is consistent with its long-term survival (i.e., until death) (Brennan, 2000). We reject our initial hypothesis that wax is a phagostimulant for *C. eucalypti*, because this psyllid produced equal amounts of honeydew and survived equally on juvenile and adult leaves. Although wax did not affect survival of *C. eucalypti*, it did affect leaf-settling, suggesting that wax may affect acceptance of juvenile versus adult leaves. Epicuticular wax may affect insects by (1) altering their ability to adhere to plant surfaces (Stork, 1980; Edwards, 1982; Edwards & Wanjura, 1990; Eigenbrode et al., 1998, 1999), (2) changing their biting (Eigenbrode et al., 1991) and stylet probing behavior (Powell et al., 1999), (3) influencing oviposition (Städler, 1986; Blua et al., 1995; Udayagiri & Mason, 1997), and (4) changing host plant reflectance (Prokopy et al., 1983; Eigenbrode, 1996; Brennan, 2000). Because wax removal significantly increased leaf-settling of *C. spatulata* and *G. brimblecombei*, and these psyllids were rarely seen walking on waxy leaves, we hypothesize that wax reduces adhesion to the leaf surface which, in turn, prevents or hinders them from feeding.

Although wax removal increased survival of *C. spatulata* and *G. brimblecombei* by a few days, both species still died earlier than anticipated if the de-waxed juvenile leaves were as acceptable a food source as adult leaves. This trend was particularly clear for *C. spatulata* (Figure 5). However, because daily wax removal did not affect survival or leaf-settling of *C. spatulata* on juvenile leaves (experiment 3), it appears that factors other than wax regenera-

tion are involved in the relatively short-lived positive effects of wax removal on survival.

Leaf-settling of females of *C. eucalypti* and *C. spatulata* in these no-choice experiments was consistent with leaf-settling in choice experiments where the males and females were caged in bags on pairs of juvenile and adult shoots (Brennan, 2000). This consistency suggests that morphological differences (i.e., leaf size, leaf shape, stem and bud shape) between juvenile and adult shoots that were present in the choice experiments but absent in the no-choice experiments, do not mediate leaf-settling. Apparently *C. eucalypti* and *C. spatulata* can distinguish between juvenile and adult shoots and leaves based on cues on the surface or within the leaf because these were the only cues present in the clip-on cages.

In conclusion, this study showed that heteroblasty in *E. globulus* significantly affected the performance of adult female psyllids. *C. spatulata* and *G. brimblecombei* settled more and survived longer on adult than juvenile leaves. Epicuticular wax on juvenile leaves is involved in the resistance to these two species, however, other unknown factors are probably also involved. In contrast, although *C. eucalypti* preferred to settle on juvenile leaves, it survived equally well on both juvenile and adult leaves. In future studies it may be interesting to determine if feeding by *C. eucalypti* on adult leaves affects psyllid fecundity, and why adults of this species survive well on adult and juvenile leaves, but nymphs only survive on juvenile leaves.

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