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Diachasmimorpha longicaudata and *D. kraussii* (Hymenoptera: Braconidae), potential parasitoids of the olive fruit fly

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Abstract
The olive fruit fly, *Bactrocera oleae* (Tephritidae), is a significant threat to California's olive industry. As part of a classical biological control program started in 2002, the parasitoids *Diachasmimorpha kraussii* and *D. longicaudata* (Hymenoptera: Braconidae) were imported to California from laboratory colonies in Hawaii. Studies on their biology and behavior as parasitoids of the olive fruit fly were conducted in quarantine. Both species tend to oviposit into 2nd and young 3rd instars, with the offspring completing development in the flies' puparia. Most eggs are deposited in the first two weeks of adult life. Observed lifetime fecundity was low, possibly as a consequence of the relatively poor quality of the harvested olives used as a host substrate. Both pre-imaginal development and adult longevity were limited at constant temperatures above 30°C, which may indicate that these species will have difficulty establishing in the warmest regions of California.

Keywords: *Tephritidae, Braconidae, biological control, parasitoid biology, olive*

Introduction

The olive fruit fly, *Bactrocera oleae* (Rossi) (Diptera: Tephritidae), has long been a major pest of olives in the Mediterranean basin (Clausen 1978; White & Elson-Harris 1992). First reported in southern California in 1998, it spread throughout the state within four years to pose a serious threat to the state's olive industry (Collier & Van Steenwyk 2003; Rice et al. 2003). The costs, effectiveness, and practicality of insecticide treatments, particularly when infested trees in suburban and rural landscaping serve as reservoirs for reinvasion, argue for the development of more

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sustainable means of control. Furthermore, the successful biological controls that have been established for scale pests in California olives (Daane et al. 2005) may be disrupted by insecticides applied for olive fly. Because no effective natural enemies of olive fly were present in California, a classical biological control program was initiated in 2002 (Hoelmer et al. 2004). Importation efforts have to date included searches for associated parasitoids in the pest's likely native range (Africa and Asia) as well as evaluation of parasitoids that have been used to control other tephritid pests.

Among the parasitoid species imported to California for evaluation under quarantine conditions were *Diachasmimorpha kraussii* Viereck and *D. longicaudata* (Ashmead) (Hymenoptera: Braconidae, Opiinae). *Diachasmimorpha* species, particularly those in the *D. longicaudata* group (Fullaway 1951), have proved useful in the biological control of fruit-infesting Tephritidae (Wharton 1989). *Diachasmimorpha longicaudata* is a native of southeast Asia and one of the most widely found fruit-fly parasitoids in the world (Greany et al. 1976; Wharton 1989; Wang & Messing 2004). It attacks a relatively wide range of tephritid hosts and has been used for biological control, with some success, against the Mediterranean fruit fly, *Ceratitis capitata* (Wiedemann), Caribbean fruit fly, *Anastrepha suspensa* (Loew), oriental fruit fly, *Dacus dorsalis* Hendel, and Mexican fruit fly, *Anastrepha ludens* (Loew) (Clausen 1978; Duan & Messing 1997; Montoya et al. 2003; Wang & Messing 2004). One attempt was made to rear and release it against the olive fly in Greece, but it did not establish (Clausen 1978). The second species, *D. kraussii,* is native to the coastal areas of eastern and northern Australia and attacks a range of *Bactrocera* species (Rungrojwanich & Walter 2000a). It has been released in Hawaii to control *C. capitata* and the solanaceous fruit fly, *B. latifrons* (Hendel) (Messing & Ramadan 2000). In this report, we describe some of the biological characteristics of these species when they use olive fly as a host, and their performance under a range of temperatures found in the olive growing regions of California. Neither has been released in California, pending the completion of studies evaluating their potential effects on non-target species and comparing their efficacy as olive fly parasitoids with the performance of other parasitoid species.

Materials and methods

Sources of insects and plants and colony maintenance

Laboratory cultures of olive fly were derived from infested olives collected near Davis, California (Yolo County). The flies were reared on olive fruit following guidelines set forth by Tzanakakis (1989). We found that flies could not develop in small, immature fruit (less than two months old), and that olives picked when ripe were likely to rot before the fly larvae (or their parasitoids) completed development. We therefore used a variety of olive cultivars (mostly Manzanillo, Sevillano, and Mission) that have different periods of ripening and that could be collected at different times across a wide area of the state (from south to north: Riverside, Kern, Tulare, Fresno, and Yolo Counties), providing fresh fruit acceptable to the flies for 9–10 months out of the year. Olives held in cold storage were used for the remaining period.

The olives were exposed to adult flies in an oviposition chamber consisting of a $45 \times 45 \times 45$ cm wooden cage with organdy sides and a glass top, which was kept in a temperature-controlled insectary room ($25 \pm 1^{\circ}$C, 16:8 L:D) at the U.C. Berkeley Insectary and Quarantine Facility. The adult flies had access *ad libitum* to water and

a mixture (approx. 2:1 by volume) of honey and a dry yeast extract (FisherBiotech, Fairlawn, New Jersey). Olives were left in the cage for 1–2 d or until 5–10 oviposition marks were seen on each one. The infested olives were then transferred to plastic boxes with mesh tops. To reduce mold growth, the olives were placed in the box no more than 2–3 layers deep and were raised about 2 cm off the bottom by a metal grid. After about 12 d under these conditions, the mature larvae typically exited the fruit and fly pupae began to accumulate on the bottom of the boxes. They were collected and transferred to the oviposition chamber to emerge as adults.

The *D. longicaudata* colony used in the following experiments was started with individuals from the USDA-ARS Pacific Basin Agricultural Research Center in Honolulu, Hawaii, that had been reared on *C. capitata*. The *D. kraussii* colony, originally from a population in Brisbane, Australia, was imported to California by way of cultures maintained for approximately four years on *B. latifrons* at the Kauai Agricultural Research Center, Hawaii. Shipments of both species were imported directly to the Berkeley quarantine facility in July and September 2003.

The adult parasitoids were kept in cages (as described for the olive fly) that were freely provisioned with water and a honey-water solution (50% by volume) and kept in a temperature-controlled room (22 ± 2 °C, partial natural light augmented by 16:8 L:D). Both *D. longicaudata* and *D. kraussii* prefer medium to large larvae of other tephritid species for oviposition (Messing & Jang 1992; Messing & Ramadan 2000; Eitam et al. 2004). For this reason, we presented them with infested olives from the insectary colony that contained 2nd to 3rd (last) instar fly larvae (this required a development period of 8–10 d, under the described conditions). The olive fly larvae were exposed to parasitoids for 1–3 d, with the exposure period varying depending on parasitoid densities in the oviposition chamber. The inoculated material was then transferred to plastic boxes of the type used for rearing olive fly. Olive fly larvae dropped to the bottom of these containers to pupate, at which time the puparia were collected and transferred to transparent plastic Petri dishes (9-cm diam) that were monitored daily for the emergence of adult flies and parasitoids.

Host stages used for oviposition

Host-stage preference and reproductive success on different olive fly developmental stages were examined in choice tests. To produce olive fly larvae of varying ages, fresh olives were exposed to adult flies for 8 h every 2 d and then held at 25 ± 1°C. The immature stages inside the olives were presented to the parasitoids at 2, 4, 6, 8, 10, and 12 d of age. A subsample of olives from each set was dissected immediately before each test to determine the olive fly stages present. Under these conditions, 2-d old olives contained eggs and, rarely, 1st instars; 4-d old olives contained 1st instars; 6-d old olives contained 2nd instars; 8-d old olives contained 2nd and young 3rd instars; 10-d old olives contained 3rd instars; and 12-d old olives contained mature 3rd instars, prepupal (emerging) larvae, and occasional pupae.

For each replicate, four female parasitoids were held for 24 h in an oviposition chamber (a round plastic container 13-cm deep $\times$ 20-cm diam, with a fine mesh top) with four olives of each of the six age classes. The olives were placed in the bottom of the container in open plastic Petri dishes (5-cm diam) marked with the days elapsed since the olives had been infested. There were 11 replicates for each parasitoid species. During the first 7–8 h of the exposure period, ten 30-s observations were made, at

approximately 40-min intervals, of activity inside the containers. The age of the larval host in olives contacted by parasitoids was recorded. Also noted was whether the parasitoids probed the olives with their ovipositors or simply stood on or off the olives, but in the Petri dish. After the parasitoids were removed from the oviposition chamber, the olives were held at $25 \pm 1^{\circ}$C to rear either adult parasitoids or olive flies.

Adult longevity at different temperatures

Adult male and female longevity was measured at six temperatures (15.2 ± 0.3, 21.9 ± 0.2, 24.8 ± 0.4, 27.8 ± 0.2, 30.1 ± 0.2, and $32.0 \pm 0.5^{\circ}$C). Newly emerged parasitoids were placed singly in glass vials (5-cm long $\times$ 1-cm diam, with a mesh lid), provisioned with a streak of honey-water (50% solution by volume), and randomly assigned to a temperature cabinet. The vials were kept in sealed plastic containers to prevent desiccation. The parasitoids were checked daily for mortality. The honey-water was replenished every 2–3 d or as needed. For both *D. longicaudata* and *D. kraussii*, 10 male and 10 female parasitoids were tested at each temperature.

Adult longevity with various provisions

Female longevity was compared in five treatments with access to: 1) olives containing hosts, plus honey-water (50% by volume) and water; 2) olives without hosts, plus honey-water and water; 3) honey-water and water only; 4) water only; and 5) no provisions. To begin, newly emerged females were collected daily, transferred to a small container with males, supplied with water and honey-water, and held for 2 d to mate, a period thought to be more than adequate for successful mating (Greany et al. 1976; Rungrojwanich & Walter 2000b). Females were then randomly assigned to one of the five treatments, with each parasitoid isolated in a small plastic container (15-cm diam $\times$ 6-cm deep) with a hole ($\approx$7-cm diam) cut in the lid and covered with nylon mesh for ventilation. The olives (four per container) were replaced every other day. Where olives with hosts were offered, the fly larvae were at a suitable stage for parasitoid oviposition (mostly 3rd instars). Honey-water, streaked along the sides of the container, and distilled water, in a soaked cotton wick, were freely available. The parasitoids were checked daily for mortality. All treatments were kept in a temperature-controlled room ($22 \pm 2^{\circ}$C). Each treatment was replicated 10 times for each species.

Lifetime fecundity

The infested olives provided in the longevity study described above were collected every other day and held in plastic cups for the emergence of adult flies or parasitoids. The number and sex of the emerging offspring were recorded.

Pre-imaginal development at different temperatures

Development rate (egg to adult) of each parasitoid species was assessed at moderate to high constant temperatures (21.9, 24.8, 27.8, 30.1°C, all $T \pm 0.2^{\circ}$C). Olives infested with 2nd and 3rd instar flies were exposed to the parasitoid colonies for 20–24 h. Each replicate consisted of six infested olives in a paper cup (9-cm diam $\times$ 4.5-cm deep), which after exposure to the parasitoids was covered with a clear, ventilated plastic lid

and randomly assigned to a temperature cabinet. The cups were then checked daily for fly or parasitoid emergence. There were 10 replicates for each species and temperature.

Statistics

Results are presented herein as means per treatment (± standard error). Treatment effects were analyzed using analysis of variance (ANOVA), with treatment means separated using Tukey's HSD test (three or more treatments) or *t* tests (two-way comparisons).

Results and discussion

Host stages used for oviposition

The parasitoids (both species) were most often observed searching on and probing into olives that had been infested 6 to 10 days earlier (i.e., olives containing 2nd and young 3rd instar flies) (Figure 1). The results from rearing the parasitoid offspring corroborate these observations, with most parasitoids reared from olive flies that were 6 to 12 d old at exposure (Figure 2).

These results are similar to published descriptions of *D. kraussii* and *D. longicaudata* attacking other tephritid hosts. Messing and Ramadan (2000) reported that *D. kraussii* can reproduce successfully on all three instars of *C. capitata* and *B. latifrons*. When *C. capitata* was used the most progeny were obtained from flies attacked as young 3rd instars, and on *B. latifrons* from flies attacked as middle 3rd instars. Similarly, *D. longicaudata* oviposits mainly into 2nd and 3rd instar oriental fruit flies (Purcell et al. 1998) and Caribbean fruit flies (Ashley & Chambers 1979; Eitam et al. 2004). Lawrence et al. (1976) and Messing and Ramadan (2000) obtained relatively few offspring when oviposition was into mature 3rd instars, and assumed that the

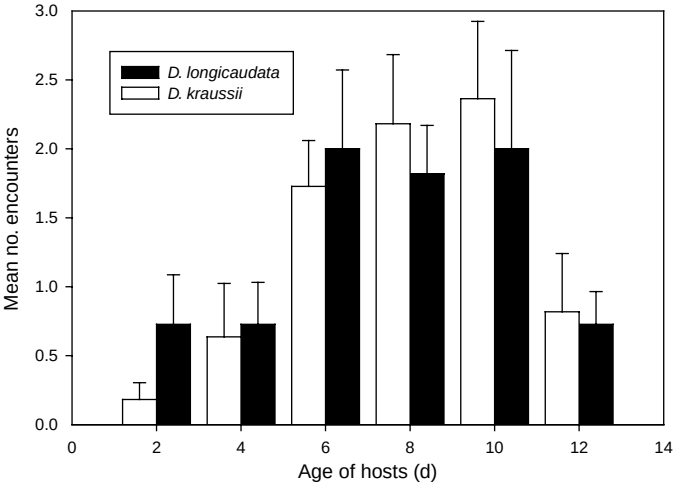

Figure 1. Host-stage preference of *D. kraussii* and *D. longicaudata*, measured as the sum of contact and probing encounters with olives infested by olive fly 2–12 days earlier. Both species favored 6–10 d old hosts (i.e., 2nd to medium 3rd instar larvae) (*D. kraussii*, $F = 4.7212$, df = 5, 60, $p = 0.0011$; *D. longicaudata*, $F = 2.1575$, df = 5, 60, $p = 0.071$; pairwise comparisons, $0.05 < p < 0.10$).

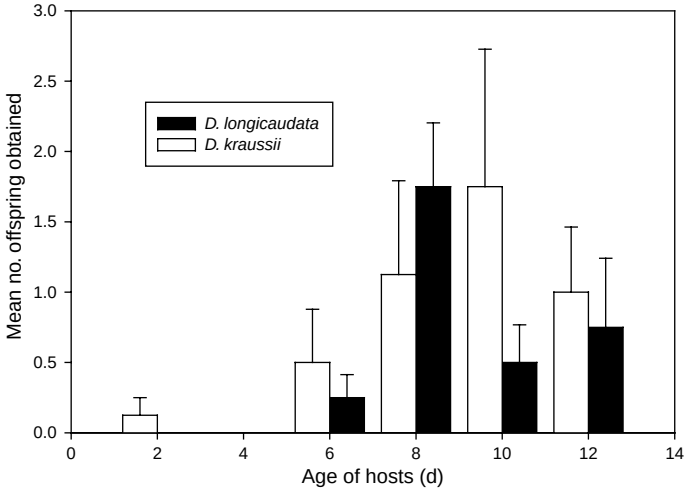

Figure 2. Parasitoid offspring obtained from six age classes of fly larvae. For *D. longicaudata*, most offspring were obtained from hosts exposed at 8 d (2nd and young 3rd instars) ($F = 4.797$, df = 5, 42, $p = 0.0015$, Tukey's HSD, $p < 0.05$). For *D. kraussii*, most offspring were obtained from hosts exposed at 6–12 d ($F = 1.50$, df = 5, 42, $p = 0.21$, Tukey's HSD, $p < 0.05$).

parasitoid's survival was adversely affected when host pupation occurred too soon after parasitoid oviposition, perhaps because the parasitoid did not have enough time to complete its development.

Adult longevity at different temperatures

For both parasitoid species, adult longevity declined with increasing temperature (Figure 3). Males and females of both species tended to have similar life spans. Exceptions are at 30°C: *D. longicaudata* females lived longer than males at this temperature (2.8 ± 0.2 d vs. 5.7 ± 1.1 d, $t = 2.58$, $p = 0.02$, df = 18), but *D. kraussii*

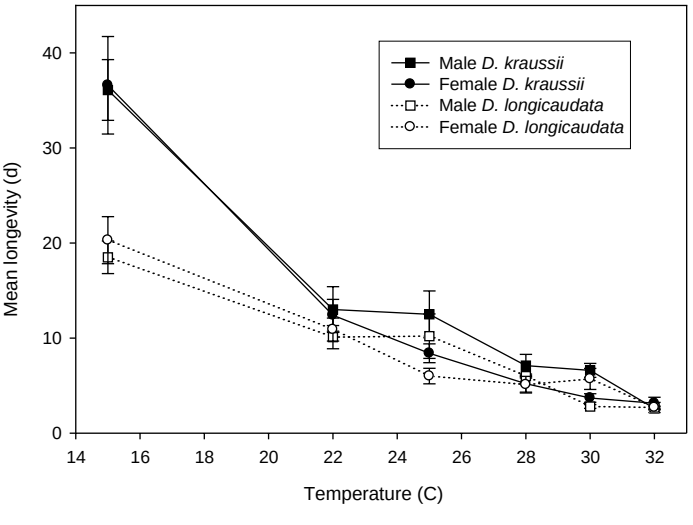

Figure 3. Adult longevity under various constant temperatures.

males lived longer than females (6.6 ± 0.73 d vs. 3.7 ± 0.45 d, $t = 3.37$, $p = 0.0034$, $df = 18$).

There were no significant differences between *D. longicaudata* and *D. kraussii* overall except at 15°C, the lowest temperature tested, where both male and female *D. longicaudata* had significantly shorter life spans than those of *D. kraussii* ($t = 5.15$, $p < 0.0001$, $df = 38$). The relatively poor performance of *D. longicaudata* at this lower temperature appears to support the hypothesis of Eitam et al. (2004) that the distribution of *D. longicaudata* in Florida (there as a parasitoid of *A. suspensa*) is delimited in part by temperature minima, because it is absent from areas with low winter temperatures (mean lows below 10.5°C) and appears to be less tolerant of cool weather than this host. An inability to survive cool winter weather might also curb the effectiveness of this species in the Central Valley of California, where winter temperatures often drop below 10°C. The longevity of adults of both species drops below three days at constant temperatures above 30°C. Because summer temperatures are usually over 30°C and often reach 40°C in the Central Valley, neither species may perform well during the summer months in that region. Because these experiments were conducted at constant temperatures, however, it is also possible that the parasitoids may live long enough under natural conditions, with temperatures above 30°C for only part of the day, to prove effective. Temperatures along the California coast are rarely below freezing or much above 30°C, which improves the potential for establishment there.

Adult longevity with various provisions

Both species lived longest when provisioned with uninfested olives, honey, and water, or just honey and water (Figure 4). Provision with water alone, or with nothing, significantly decreased longevity. Life span also declined when hosts were available,

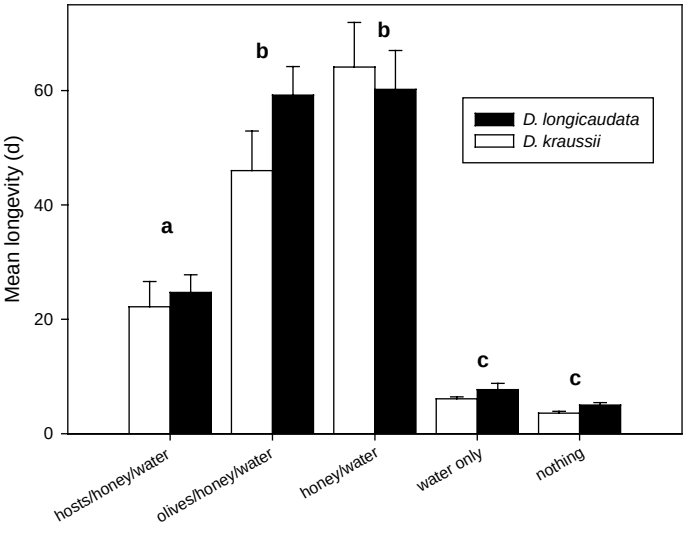

Figure 4. Adult female longevity was significantly affected by provision (*D. kraussii*, $F = 26.66$, $df = 4, 45$, $p < 0.0001$; *D. longicaudata*, $F = 44.25$, $df = 4, 45$, $p < 0.0001$). Treatments indicated by the same letter are not significantly different for either species (Tukey's HSD test, $p < 0.05$). There were no differences between the two species for any treatment except for "nothing", where *D. longicaudata* females lived significantly longer than *D. kraussii* ($t = 2.689$, $p = 0.015$, $df = 18$).

suggesting that energy was expended in searching and probing for hosts and producing eggs (Quicke 1997).

Lifetime fecundity

The mean lifetime fecundity was similar for both species: *D. longicaudata* produced 23.60 ± 5.29 offspring, and *D. kraussii* produced 22.70 ± 5.51 offspring (mean ± S.E.). They also had similar oviposition patterns (Figure 5). Oviposition rates peaked during the first 16 d and then dropped off, although the parasitoids continued to live to an average of 25.0 ± 3.0 d and 22.0 ± 4.0 d, respectively (Figure 4). The mean proportions (± S.E.) of female offspring obtained were 0.43 ± 0.08 (*D. longicaudata*) and 0.50 ± 0.11 (*D. kraussii*), which do not differ significantly from 1:1.

Reported fecundity varies for the two species on other hosts. Rungrojwanich and Walter (2000a) reported a much higher lifetime fecundity of 112 offspring for *D. kraussii* attacking *Bactrocera tryoni* (Froggatt) reared on artificial diet. For *D. longicaudata*, 18–20 progeny were obtained from *A. suspensa* reared on diet (Greany et al. 1976). The latter reported a significant discrepancy between egg production and lifetime fecundity. Comparable totals have been reported for both species when reared on the Mediterranean fruit fly on artificial diet (Larios et al. 2002). Our low result could indicate that olive fly is a poor host for these species. The native ranges of the two species—Australia for *D. kraussii* and the Indo-Philippine region for *D. longicaudata*—do not overlap with the native range of the olive fly (Africa and Central Asia), so they have no evolutionary history with this host species. Because both parasitoid species had similar low fecundities, it is also likely that the low numbers are at least in part a consequence of our rearing techniques. Fruit quality often suffered after picking due to dehydration or rot, and quality changed as the fruit ripened. The olive fly larvae may also have been overcrowded in some fruit, which could have increased mortality or lowered their quality as hosts. Testing the parasitoids on olive fly in artificial diets was not an objective of this study, however, and further investigation is clearly necessary to improve mass rearing techniques for the olive fly (Tzanakakis 1989).

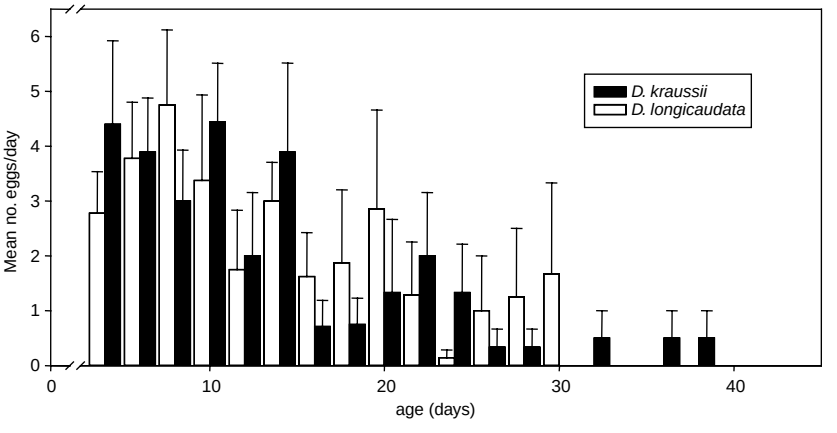

Figure 5. Lifetime offspring production, starting from age 2 days.

Pre-imaginal development at different temperatures

Development rates for both flies and parasitoids increased as a function of temperature from 22 to 28°C (Table I). Moderate temperatures (22–25°C) appear to be optimal for development under these conditions. At all temperatures, most of the flies emerged before the first parasitoids. Male parasitoids emerged before females at most temperatures. Male *D. longicaudata* emerged significantly earlier than females at 25°C (*t*-test, $t = 3.300$, $p = 0.0092$, $df = 9$). Male *D. kraussii* emerged earlier than females at the three temperatures that produced females: 22°C: $t = 5.589$, $p < 0.0001$, $df = 14$; 25°C: $t = 1.984$, $p = 0.0807$, $df = 13$; 28°C: $t = 4.439$, $p = 0.0003$, $df = 18$.

At 30°C, very few parasitoids emerged (no *D. longicaudata*, and only 5 male *D. kraussii*). There is some indication that *D. kraussii* performs better than *D. longicaudata* at higher temperatures, but this distinction, along with the apparent upper threshold for development between 28 and 30°C (suggested by these data), is probably artificial. The data on numbers of wasps completing development at the higher temperatures must be viewed with caution because the olives tended to dry out and shrivel within about a week, or even less at higher temperatures. Olives still on the tree will of course remain turgid at temperatures exceeding 40°C. At all temperatures we obtained many more dead puparia than adult flies or parasitoids, suggesting that rearing conditions were not optimal. Shriveling of the olives at higher temperatures may have killed some fly larvae and pupae inside. To obtain a more accurate estimate of the upper threshold for development, it would be instructive to repeat these experiments using artificial diet or fruit kept on branches in water rather than picked fruit.

Our studies provide some biological information on the development of *D. kraussii* and *D. longicaudata* on olive fly under laboratory conditions, and provide some predictions on their performance under various climatic conditions. Both parasitoid species readily attacked and developed on 2nd and 3rd instar olive fly larvae, and produced most offspring within the first two weeks of adult life. The parasitoids' adult longevity, and possibly pre-imaginal survival rates, decreased at higher temperatures, suggesting that they will be most effective in the coastal areas of California. This information will be useful in planned comparisons of *D. kraussii* and *D. longicaudata* with other imported parasitoid species as potential biological control agents for olive fly in California. While the ease of rearing these species on olive fly suggests that they will compare favorably to other parasitoids, this advantage may be negated by the

Table I. Development times (days) for parasitoids from oviposition to emergence of adults (mean ± S.E.) at various constant temperatures. The times shown for *B. oleae* are for individuals that escaped parasitism and represent the periods following exposure to parasitoids (i.e., duration of the pupal stage plus the latter portion of the 3rd instar). Under these conditions, *B. oleae* adults emerged earlier than parasitoids at all temperatures.

	Temperature (°C)			
Species	22	25	28	30
B. oleae	16.33 ± 0.18	13.19 ± 0.50	10.95 ± 0.21	11.00 ± 0.71
D. longicaudata ♂	22.75 ± 0.56	17.02 ± 0.69	17.50 ± 2.34	(none)
D. longicaudata ♀	23.25 ± 1.25	20.79 ± 0.92	(none)	(none)
D. kraussii ♂	23.30 ± 0.50	18.15 ± 0.82	14.95 ± 0.15	13.20 ± 0.58
D. kraussi ♀	28.78 ± 0.91	21.65 ± 1.74	16.62 ± 0.34	(none)

results of non-target host studies (which are currently underway). As neither species is a specialist on olive fly, it is necessary to determine the level of risk their release might pose to other tephritids present in California, which include a variety of native species and introduced beneficials (Duan et al. 1996; Hoddle 2004; Messing 2000).

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