

Food sources for adult *Diachasmimorpha longicaudata*, a parasitoid of tephritid fruit flies: effects on longevity and fecundity

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Abstract

We report the results of a study on potential food sources of the widely distributed Indo-Australian braconid fruit fly parasitoid *Diachasmimorpha longicaudata* (Ashmead) (Hymenoptera: Braconidae). Adults sustained life on diets of fruit juice or fruit pulp, a homopterian and its associated honeydew, or extrafloral nectary secretions. Longevities on all these foods and fecundity on fruit juice were comparable to those achieved on the honey that is typically provided in mass-rearing programs. Certain of the flower species *Bidens alba* (L.), *Spermacoce verticillata* L., *Lobularia maritima* (L.) Desv., *Brassica nigra* (L.), *Lantana camara* L., their nectar or pollen, provided a diet that resulted in longer maximum life spans than water alone. Unlike some tephritid flies, the braconid did not feed on fresh bird feces or leaf-surface exudates. Feeding by *D. longicaudata* on wounded host fruits of tephritid flies suggests that adult parasitoids would not need separate forays for adult food and oviposition sites, as these occur in the same locations. We conclude that an inventory of adult foods may help target inundative releases of *D. longicaudata* and lead to improvements in diets used for mass rearing.

Introduction

There is abundant evidence that adult feeding by many hymenopteran parasitoids has a substantial effect on their longevity, fecundity, and movement (Leius, 1961; Wäckers & Swaans, 1993; Morales-Ramos et al., 1996; Jervis & Kidd, 1999). However, much of this evidence has been gathered in the laboratory on unlikely to be encountered food sources, honey and sucrose blocks (Eijs et al., 1998), and largely stems from parasitoid species that attack herbivorous insects. What sorts of foods are consumed by parasitoids that attack fruit-infesting insects, such as fruit flies (Diptera: Tephritidae), has been a neglected field of study.

Although several species of opiine braconid parasitoids of pest tephritids are mass reared for augmentative or inundative release and are typically fed with honey or honey solutions (e.g., Wong & Ramadan, 1993; Sivinski et al., 1996),

little is known about their dietary requirements. Even less is known about potential food sources in the field. Because the sustained efficacy of a release may be impacted by the availability of adult food, it is important to determine the sorts of nutritional resources parasitoids may exploit in nature.

One such opiine is *Diachasmimorpha longicaudata* (Ashmead) (Hymenoptera, Braconidae), an endoparasitic koinobiont of several tephritid genera originally collected in the Indo-Philippine region attacking *Bactrocera* spp. (White & Elson-Harris, 1992). However, it has been introduced throughout much of the tropical and subtropical New World over the last half century (Ovruski et al., 2000) and is widely mass reared for use in inundative releases against both *Anastrepha* spp. and *Ceratitidis capitata* (Wiedemann) (e.g., Sivinski et al., 1996; Montoya et al., 2000). Unlike some other tephritid-attacking opiines, *D. longicaudata* forages extensively for larval hosts in fallen fruit (Purcell et al., 1994).

A survey of the hymenopteran parasitoid literature suggests a number of potential adult foods. These include flower nectar (Jervis et al., 1993), extrafloral nectaries (Koptur,

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1989), host fluids (Jervis & Kidd, 1986), homopteran honeydew (Wäckers, 1999, 2001), and fruit or fruit juices (Eijs et al., 1998). The last of these, although an obvious possible food source for a fruit fly parasitoid, has rarely been reported as a feeding substrate. The only example is the somewhat similar case of the *Asobara* spp. (Braconidae) parasitoids of drosophilids that feed on fermenting fruit (Eijs et al., 1998). Our aim was to first provide *D. longicaudata* with examples of the types of nutritional resources commonly exploited by the adults of parasitoid species that do not attack frugivorous Tephritidae (e.g., flowers, extrafloral nectaries, and homopteran honeydew), and determine whether or not they are consumed through their effects on longevity. Because adult fruit fly parasitoids often occur in the same habitats as adult flies and exhibit similar diet patterns of activity [e.g., *Doryctobracon areolatus* (Szepilgeti)] and its host *Anastrepha obliqua* (Macquart) (Aluja & Birke, 1993); we then ascertained if *D. longicaudata* exploits the types of nutritional resources available to flies, particularly fruit juices oozing from wounded or infested fruit (see Eijs et al., 1998), bird feces that are plentiful during the fruiting season (Hendrichs et al., 1993; Jácome et al., 1999; Aluja et al., 2000), and exudates (leachates) from leaf surfaces (Hendrichs et al., 1992). There are no known observations of host feeding in *D. longicaudata* in spite of an extensive history of oviposition behavior studies (Greany et al., 1976; Lawrence et al., 1976, 1978), and this was not considered in our experiments.

Materials and methods

Source of parasitoids

Diachasmimorpha longicaudata adults were obtained from colonies kept at the Florida Department of Agriculture and Consumer Services, Division of Plant Industry, and the USDA-ARS, Center for Medical, Agricultural, and Veterinary Entomology, both in Gainesville, Florida, USA. The colonies had been maintained for approximately 10 years and were only recently derived from a common cohort. All parasitoids were reared on larvae of the Caribbean fruit fly, *Anastrepha suspensa* (Loew), and the insects used in experiments were from a number of consecutive generations.

Exposure to food source

Adults were provided with water at the time of emergence and introduced to potential food sources within 24 h. The container and manner of presentation varied with the type of food offered. Screens used in cage construction were 13 × 13 lines per square centimeter. Unless otherwise stated, water was provided in 5-ml glass vials topped with a cotton wick.

Potential food sources were of two kinds: floral and non-floral. Flowers were selected because *D. longicaudata* was

observed flying to and apparently feeding upon them under seminatural conditions in a greenhouse or on the basis of literature reports indicating that they were fed upon by non-fruit fly natural enemies (references and description of each flower species used follows). All bore relatively small flowers in multiple-bloom inflorescences and initially appeared accessible to a relatively small insect. However, we were particularly interested in determining if there was an effect of the differences in the flowers' morphologies on parasitoid survival. Non-floral sources consisted of peeled, sectioned oranges and peaches, orange juice, a homopteran and its honeydew, cotton plant extrafloral nectaries, leaf surfaces, and bird feces. They were selected either because they, too, had been reported in the literature as food sources for parasitoids (e.g., homopteran honeydew, extrafloral nectaries; e.g., Bugg et al., 1989; Wäckers, 2001), because apparent feeding had been previously observed (i.e., leaf surfaces; J. Sivinski, pers. obs.), or because they are widely used by fruit flies in nature (fruit juices, bird feces, leaf surfaces; e.g., Aluja & Birke, 1993; Hendrichs et al., 1993). As noted in the introduction, we were interested in ascertaining if fruit fly parasitoids shared nutritional resources with the adult form of their hosts.

Survival on food sources other than flowers was compared to controls in the following manner. The mean proportions of parasitoid cohorts surviving on a particular day (= lx) were calculated. These means were obtained from both parasitoids provided with a candidate food source and water and those provided with water alone. In many instances, separate cohorts were also provided with an alternative food in the form of honey and water (for details see individual descriptions in succeeding discussions). The relative performance of the insects on the candidate food source compared to water (or honey) was then obtained by dividing the candidate food lx value by a control lx value (either water or honey and water). The slope of this relative performance over time was then compared to the slope of the performance on the control substrate [e.g., lx (water on day 1)/lx (water on day 1)]. Because all the control/control values equaled 1, control values over time generated straight and horizontal lines. Regressions of the treatments, lx (candidate food/control) and the lx (control/control) over time, were performed (PROC GLM; SAS Institute, 1989). The P value of the type III interaction between day and treatment revealed any significant differences between the slopes of the controls (either water or honey and water) and the candidate food source relative to the control. Fecundities of females maintained on honey and orange juice were compared through regression (PROC GLM; SAS Institute, 1989). Because of the non-linear nature of the relationships, significance was determined through the type I interaction factor 'treatment*day*day'.

Floral food sources

Flower morphology and parasitoid survival. Flower morphology is known to influence insect parasitoid access to nectar and pollen (Patt et al., 1997; Wäckers, 2004). Five species of flowers from four families (descriptions of each and experimental procedure follow) were dissected and measured with a micrometer under a binocular microscope. The characters considered to be most likely to effect access to nectar were corolla width at the bottom of the flower where nectar was present and corolla depth. The first because a relatively narrow corollar diameter might block the entrance of an insect's head and the latter because the typically short tongues of Braconidae might be better suited to feeding on shallow flowers (see Jervis, 1998). Means were obtained from measuring five flowers on each of five plants of each species. Following these measurements, relationships between flower morphology and parasitoid longevity when maintained with the various flowers were made. First, the mean days of parasitoid survival when maintained with a particular flower (or honey) was divided by the mean survival of insects maintained on water alone (see details in the following discussions). Flower height and width were correlated to the ratios of treatment survival to water-control survival (Zar, 1974). Feeding trials were carried out from September 2003 through May 2004. In all cases, particular pairs of parasitoids were held with flowers from individual plants.

Spermacoce verticillata L. (Rubiaceae; shrubby false button-weed). *Spermacoce verticillata* is a perennial whose small flowers (1.5 mm corolla depth, 1.0 mm corolla width at the juncture of the calyx) occur in dense ball-shaped inflorescences. There is a distinct 'honey guard' above the interior base of the corolla. The flowers are known to be attractive to a number of Hymenoptera, and stands have been planted to support and monitor populations of *Larra* spp., sphecid ectoparasitoids introduced to control *Scapteriscus* spp. mole crickets (Sailer, 1985; Frank, 1990). In this and in all following cases, flowers were left intact and attached to living plants in order to preserve a natural production of nectar and any other floral products. Flowers were presented to *D. longicaudata* in 2.5×11 cm plastic cylinders fitted at the end with a moistened cotton wick contained in a small plastic water-filled vial. The cylinders were placed over blooming inflorescences, then held in place by a cotton ball, and arranged so that none of the stem or leaves could be contacted. Controls consisted of identical cylinders, without flowers but containing either water alone or water and a small drop of honey at the mouth of the cylinder. The honey was replenished every other day and inflorescences on the plant were switched daily. A single male and female were placed in each cylinder and their condition monitored

daily. All cylinders were held in a greenhouse under natural photoperiods, ambient humidity, and temperatures typically ranging daily from 24 to 36 °C. Eleven replicates of each treatment were observed until all insects died. In this and in all subsequent floral cases, data were analyzed by multivariate regression (PROC GLM; SAS Institute, 1989), in which the variables were parasitoid sex, flower species, and treatment (i.e., candidate flower + water, water, or honey + water). Additional paired comparisons were made between the maximum longevities of male and female parasitoids in water-only and flower-containing cages by Wilcoxon paired-sample test (Zar, 1974).

Bidens alba (L.) (Asteraceae; Spanish needle, common beggar's tick). The daisy-like inflorescence contains numerous small flowers whose individual corollas are 0.13 mm wide at the junction with calyx and 0.5 mm deep. It is attractive to a range of Hymenoptera (e.g., Grombone-Guaratini et al., 2004). Flowers were presented in the same manner as those of *S. verticillata* and with the same controls. There were 10 replicates of each treatment.

Brassica nigra (L.) (Brassicaceae; mustard). Mustard plants have flat, open flowers 1.4 mm in width above the petiole and with essentially no corollar depth. There have been frequent reports of *Brassica* spp. used as a food plants by ichneumonid parasitoids (e.g., Idris & Grafius, 1995). Presentation and controls were as described for *S. verticillata*. There were 10 replicates of each treatment.

Lantana camara L. (Verbenaceae; lantana). Lantana is frequented by a number of nectar-feeding insects (e.g., Habeck, 1985) and has flowers 1.0 mm wide at the junction with the calyx and is 11 mm deep. Presentation and controls were as described for *S. verticillata*. There were 10 replicates of each treatment.

Lobularia maritima (L.) Desv. (Brassicaceae; sweet alyssum). Sweet alyssum is a hardy, non-weedy annual herb that produces small, cruciform-stalked flowers (0.67 mm wide corolla at the junction with the calyx with a 1.4 mm deep corolla) that occur in indeterminate clusters. *Diachasmimorpha longicaudata* was observed flying to and apparently feeding upon the flowers of sweet alyssum under seminatural conditions in a greenhouse, and the flowers are demonstrated food sources of braconid [*Cotesia marginiventris* (Cresson)] and ichneumonid (*Diadegma insulare* (Cresson)) parasitoids (Johanowicz & Mitchell, 2000). Again, inflorescences alone were presented to single male and female *D. longicaudata*, but this time in 100-ml clear plastic cups whose lids had been cut to their center. Stems were placed in the incision, which was then sealed with tape. Controls

again consisted of either water alone or water and a drop of honey that was replenished every day. Inflorescences were switched daily as well, and the condition of the insects was monitored at the same time. There were 10 replicates of each treatment.

Non-floral food sources

Oranges (*Citrus sinensis* Osbeck; *Rutaceae*): Oranges were peeled, and their sections were presented to 25 male and 25 female parasitoids in 20 × 20-cm screen cages. The surface of the fruit section was repeatedly pricked with a pin to expose pulp. Controls consisted of cages containing only water or cages with water and several small drops of honey that were replenished every other day. There were five replicates of each treatment. This and other non-floral feeding trials were performed in the laboratory where mean temperature was 25 °C, 60% r.h., and L12:D12. The extrafloral nectaries were examined in a greenhouse and under the same conditions as the floral resources described previously. Feeding trials for non-floral food sources were performed from May 2003 through March 2004.

Orange juice. Cotton balls were saturated with commercially available unsweetened orange juice ('organically grown') and placed in a 20 × 20-cm screen cage. Juice was replaced every other day. Controls consisted of water alone or water and drops of honey that were replenished every other day. Twenty-five males and 25 females were held in the cages and their condition monitored daily. There were five replicates of each treatment.

Orange juice and fecundity. Ten females from separate cohorts of 25 male and 25 female parasitoids maintained on orange juice and water and honey and water (see previous discussions) were dissected every 5 days with the first dissections occurring at <24 h after emergence and the last dissections on day 30. Mature oocytes (i.e., large, homogeneously sized eggs in the vicinity of the ovarian calyx) were counted under a binocular microscope (see Sivinski et al., 2001). Because of early mortality, females maintained on water alone were dissected only on day 5. Differences in mean fecundity were examined by t-test comparisons of the different age classes, with the exception of age day 5 where the three means were compared through ANOVA followed by Waller's test to discriminate among the means (SAS Institute, 1989).

Peaches [*Prunus persica* Batsch. (*Rosaceae*)]. To determine if *D. longicaudata* fed upon fruits other than oranges, peaches were sliced into approximately six sections and presented in the same manner as orange slices. Longevity was compared to water alone. There were four replicates of each treatment.

Homopteran honeydew. Honeydew, the waste product of certain plant-feeding Homoptera, is a major source of carbohydrates for a number of parasitoids (e.g., Wäckers, 2001). Citrus mealybug, *Planococcus citri* (Risso) (Pseudococcidae), produces a copious honeydew that serves as a substrate for the growth of sooty molds (Quayle, 1941). Insects were originally obtained from the Florida Division of Plant Industry culture and reared on acorn squash [*Cucurbita moschata* (Duchesne ex. Lam.) (Cucurbitaceae)]. After mealybug populations were established across more than half the dorsal surfaces of the squash, mealybugs and honeydew were presented to 20 male and 20 female *D. longicaudata* in 30 × 30 × 45 cm screen cages. Controls consisted of water alone and water with uninfested squash of the same age as the infested squash. Insects appeared to feed on honeydew, but it is possible that other insect products or the mealybugs themselves were consumed. There were eight replicates of each treatment.

Cotton extrafloral nectaries. Cotton [*Gossypium hirsutum* L. (Malvaceae)] bolls have four prominent subbracteal extrafloral nectaries that were observed to be highly attractive to ants (*Camponotus* spec.) in our greenhouse. Extrafloral nectaries are visited by a broad range of insect natural enemies (Koptur, 1989), and the presence of cotton nectaries increases parasitism of noctuid eggs by the *Trichogramma* spp. that feed upon them (Treacy et al., 1987). The nectaries on a single boll were exposed in split cups as previously described for *L. maritima*, with a short portion of the stem and base of the boll alone available to insects. Controls consisted of cups containing only water or water and a drop of honey that was replenished every other day. There were 10 replicates of each treatment, and experiments were performed in a greenhouse.

Leaf surface. Certain tephritid fruit flies, including the pest species *Rhagoletis pomonella* (Walsh) feed upon the minerals and carbohydrates that leach from the surfaces of leaves (Hendrichs et al., 1993). 'Food hairs' on the foliage of lesser burdock, *Arctium minus* (Hill) Bernh., are consumed by the ichneumonid *Giraudia plana* Prov., which can live up to 1 month on no other diet (Leius, 1960). On several occasions, *D. longicaudata* were seen to apply their faces to leaf surfaces of a *Brassica* species, suggesting that they, too, may gain nutrients in a similar manner. Leaves of kale, *Brassica oleracea* L. var. *acephala*, purchased from an organic grocery were individually placed in a vial of water and presented to single female *D. longicaudata* in 400-ml clear plastic cups along with a supply of water in a wicked vial. The control consisted of water alone. Leaves were changed daily and there were 10 replicates of each treatment. Kumquat, *Fortunella margarita* Swing., a host of *Anastrepha suspensa*

(Loew) a pest fruit fly attacked by *D. longicaudata* (Norrbon & Kim, 1988), was used to present parasitoids with intact leaves attached to the plant. Individual leaves on the tree were placed in 100-ml clear plastic cups in the manner described for presentation of *L. maritima*. Single male and female parasitoids were held in the containers and their condition monitored daily. Controls consisted of identical cups containing only water. There were 10 replicates of each treatment.

Bird (parrot) feces. Bird feces occur on fruit tree foliage and are commonly exploited by tephritid fruit fly hosts of *D. longicaudata* (Aluja & Birke, 1993; Prokopy & Vargas, 1993; Jácome et al., 1999). Less than 1-day-old parrot feces (various species of Psittacidae) were obtained from a local pet store and presented in boluses of >5 g to 15 male and 15 female *D. longicaudata* held in 20 × 20 cm screen cages. Feces were replaced every day. The control consisted of water only and there were three cages of each treatment.

Results

Floral food sources

In no instance, in either sex, did the ratio of longevity of parasitoids maintained on a flower species equal that of parasitoids simultaneously maintained on honey. Parasitoids exposed to certain flowers had a somewhat longer mean life span than those exposed to water alone, but none were individually significant and there was no statistical difference overall ($F = 3.41$, d.f. = 201, $P = 0.07$). However, the maximum longevity of males and females in flower-containing cages were significantly greater than in water-only cages ($n = 8$; $T = 3$, $P = 0.025$). There were no significant correlations between either corolla width or depth and the ratios of longevity of flower- and water-maintained parasitoids (Figure 1).

Non-floral food sources

Orange pulp. Females lived as long as 71 days in the presence of orange slices and water and up to 84 days on honey and water (Figure 2). Maximum male longevity was 61 days on orange slices and 69 days on honey. Neither females nor males survived longer than 6 days on water alone.

Orange juice (longevity and fecundity). Females lived as long as 95 days on a diet of orange juice and water and up to 99 days on honey and water (Figure 2). Males lived as long as 45 days on both orange juice and honey. Neither females nor males survived longer than 6 days on water alone. Female fecundity (number of mature eggs per ovary) was similar in insects fed on orange juice and honey (Figure 3). Comparisons with females maintained on water alone were possible only on day 5 due to relatively

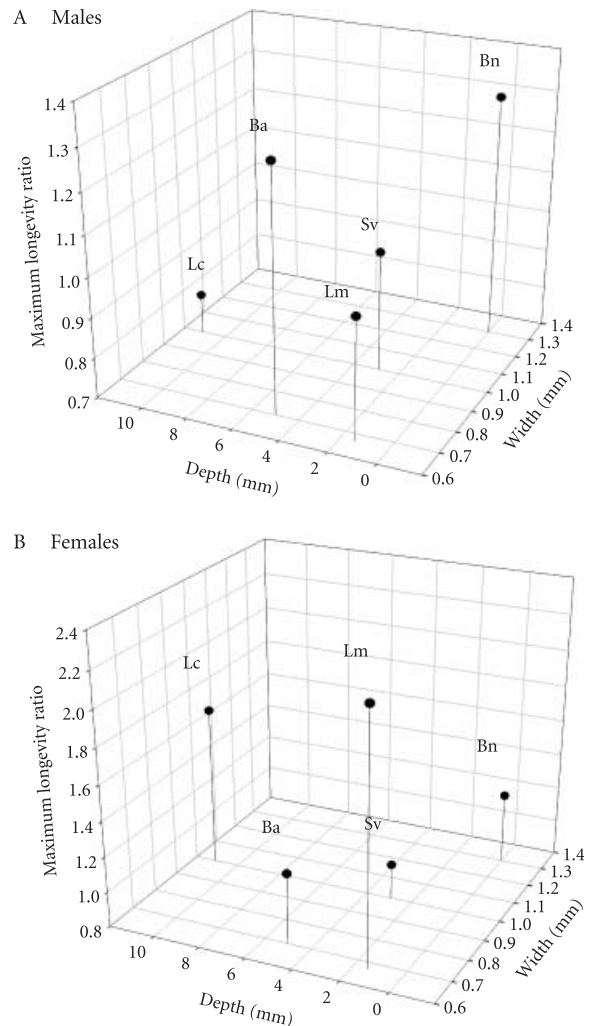


Figure 1 The relationships between the corolla widths and depths of various flowers and the ratio of maximum life span in (A) male and (B) female *Diachasmimorpha longicaudata* fed on these flowers relative to a water-only control (i.e., longest lifespan on a particular flower/longest lifespan on a water-only control). The letters within the graphs refer to various flower species: Ba (*Bidens alba*), Bn (*Brassica nigra*), Lc (*Lantana camara*), Lm (*Lobularia maritima*), and Sv (*Spermacoce verticillata*).

early mortality. The water-alone females had significantly fewer eggs than either the orange juice-fed or honey-fed females (Figure 4).

Peach pulp. Females fed peach pulp lived up to 50 days on peaches and males 34 days. Males and females on water alone lived no longer than 2 days (Figure 2).

Homoptera and their honeydew. Female parasitoids lived as long as 31 days in the presence of citrus mealybugs,

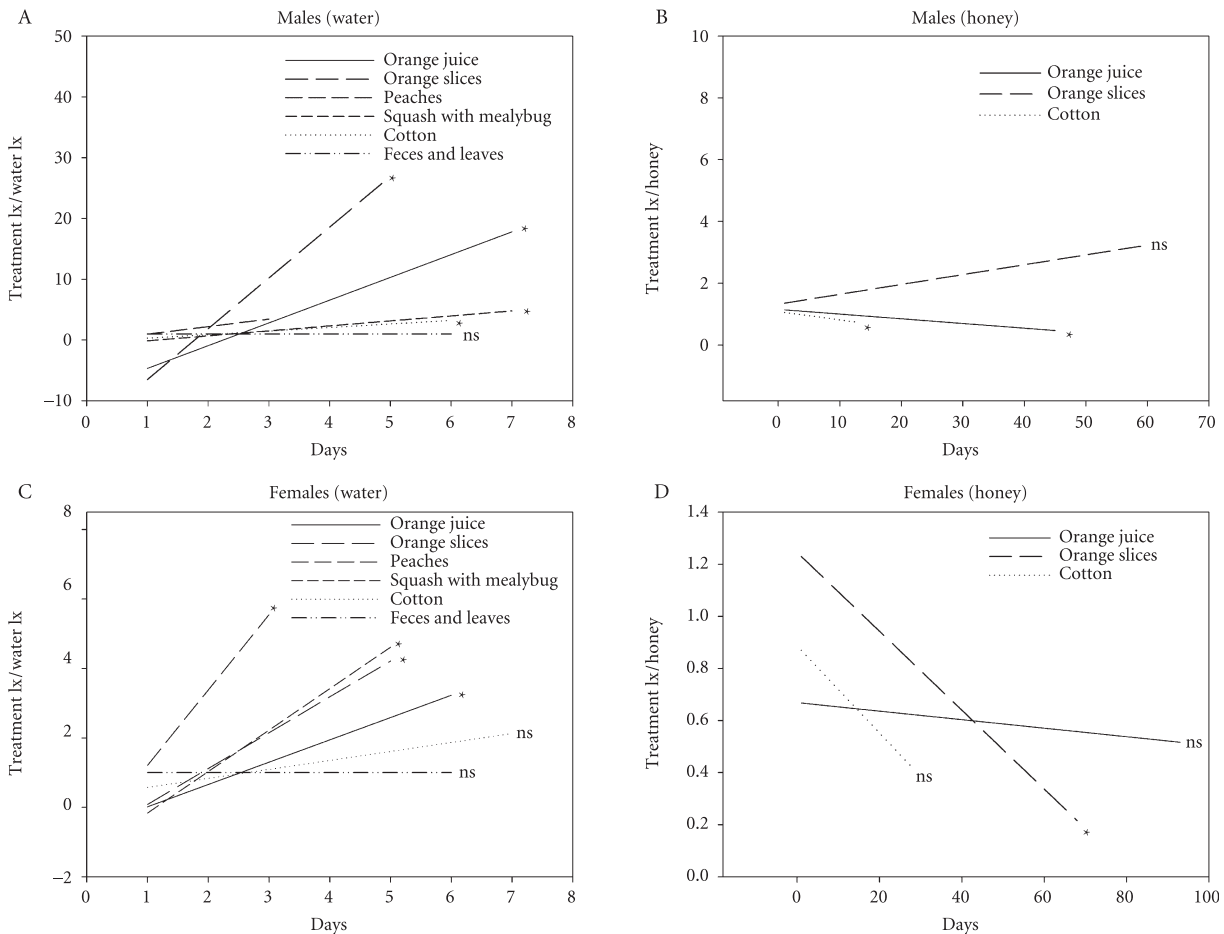


Figure 2 The relationships of male and female *Diachasmimorpha longicaudata* provided with food sources and their individual controls. The mean proportions of parasitoid cohorts surviving on a particular day (= lx) on a candidate food source was divided by a control lx value (either water or honey and water) for the same day. The slope of these relative performances over time was then compared to the slope of the performance on the control substrate [e.g., lx (water on day i)/lx(water on day i)]. Because all the control/control values equaled 1, these values over time generated straight and horizontal lines. Positive lines in the graph indicate increasingly greater lx values relative to a particular control, and negative lines indicate that the lx values in candidate food cohorts declined relative to the control. Those lines marked by an '*' have slopes significantly different from the control/control line, and those marked by 'ns' are not significantly different. The length of the line reflects the longevity of the shortest lived treatment used to calculate the candidate food/control ratio. These are typically the water control in A and C and the candidate food in B and D.

whereas the longest lived females on uninfested squash or with water alone lived 5 days (Figure 5). Males lived as long as 10 days in the presence of mealybugs and in their absence 5 days.

Extrafloral nectaries. Females lived as long as 28 days in the presence of cotton extrafloral nectaries and males 15 days. On water alone, males and females lived as long as 7 days. When fed honey and water, the longest-lived female was 34 days and the longest-lived male 13 days (Figure 2).

Leaf surfaces. Neither sex when provided with intact leaves survived longer than those provided with water only. All

individuals kept with *B. oleracea* and *F. margarita* leaves and water were dead after 5 days, as were all individuals kept with water alone.

Bird feces. Neither sex when provided with fresh bird feces survived longer than those provided with water only. All individuals in both treatments were dead after day 6.

Discussion

Diachasmimorpha longicaudata sustained life on diets of fruit juice or juicy fruit pulp, homopteran honeydew (or associated products), or extrafloral nectary secretions.

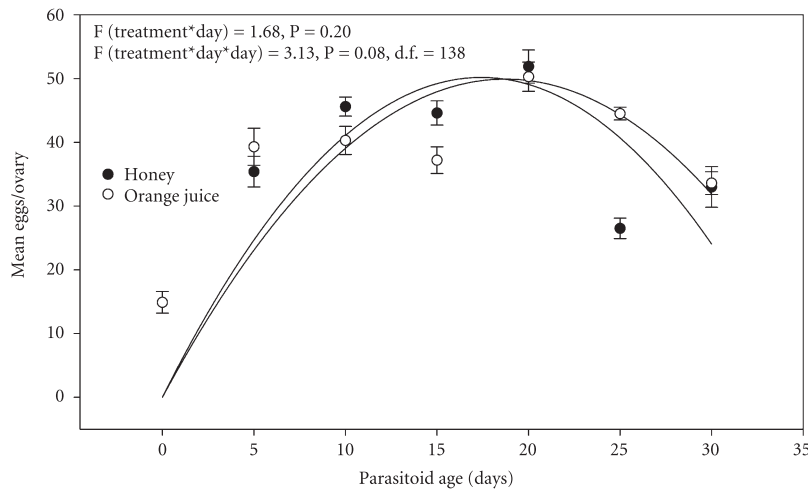


Figure 3 Mean ($\pm$ SE) numbers of mature eggs/ovary over time in *Diachasmimorpha longicaudata* females fed either orange (*Citrus sinensis*) juice and water or honey and water.

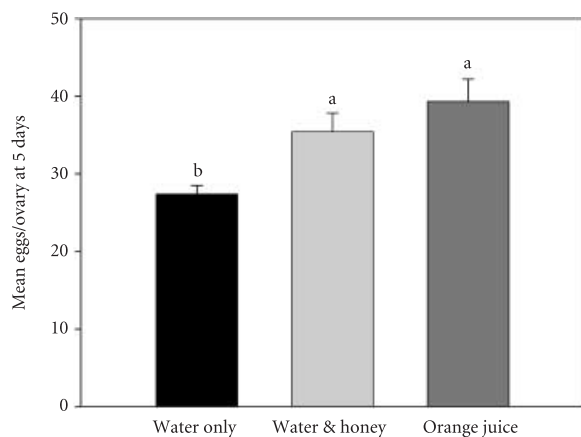


Figure 4 Mean ($\pm$ SE) daily proportional survival (lx) of (A) female and (B) male *Diachasmimorpha longicaudata* presented with either citrus mealy bugs (*Planococcus citri*) living on acorn squash (*Cucurbita moschata*), their honeydew and water, unfested squash and water, or water alone. Treatments sharing a letter are not significantly different.

Furthermore, egg production of females fed on orange juice was similar to those fed on honey. None of several species of flowers, their nectar, or pollen offered nutritional resources whose quality approached that of honey. The mean longevity of flower-provided parasitoids were no longer than those provided with water alone, although maximum life spans were significantly greater, suggesting that some individuals acquired sufficient floral resources. Perhaps the simplest explanation for the lack of difference in mean longevity, but a significant difference in maximum lifespan, is that the limited resources offered in the small container were marginal for survival and that they were only occasionally sufficient to maintain particularly fit

individuals. Flowers that sustained *D. longicaudata* for a longer period of time were not unusually accessible (i.e., they did not have unusually short or wide corollas). Unlike its tephritid fruit fly hosts, *D. longicaudata* did not acquire measurable nutrition from bird feces or leaf surfaces.

Of the potential food sources that unequivocally provided nutrients, the consumption of fruit or fruit juice in particular has implications for the time and energy allocations of adult parasitoids that must forage for both food and larval hosts. Because adult food in the form of wounded tephritid host fruit and parasitoid oviposition sites occur in the same locations, separate forays by *D. longicaudata* to acquire one or the other would be unnecessary. Such fruits would be particularly accessible to *D. longicaudata* because it forages extensively over fallen, likely to be injured, and oozing, fruits for larval hosts (Purcell et al., 1994). This is not the case in other sympatric fruit fly attacking New World opiines, such as *D. areolatus*, whose host searches are concentrated in fruit tree canopies where fruit is less likely to be damaged (Sivinski et al., 1997).

In parasitoids whose host substrates do not provide adult nutrition, travel between feeding and oviposition sites may be even longer than those of *D. areolatus* and more energetically expensive. For example, more flower-dependent parasitoids of herbivorous insects often feed in different habitats some distance from their oviposition sites (e.g., Powell, 1986). Feeding on the host's fruit substrate may save both time and energy that could be expended in performing searches for larval hosts (Eijs et al., 1998, see Van Emden, 1990; Kriven & Sirot, 1997). A competitive advantage may then accrue to efficient individuals that concentrate their feeding and breeding within the same resource patches. If this is the case, there may be little selection for exploitation of floral foods in *D. longicaudata*, which is consistent with the relatively limited life spans

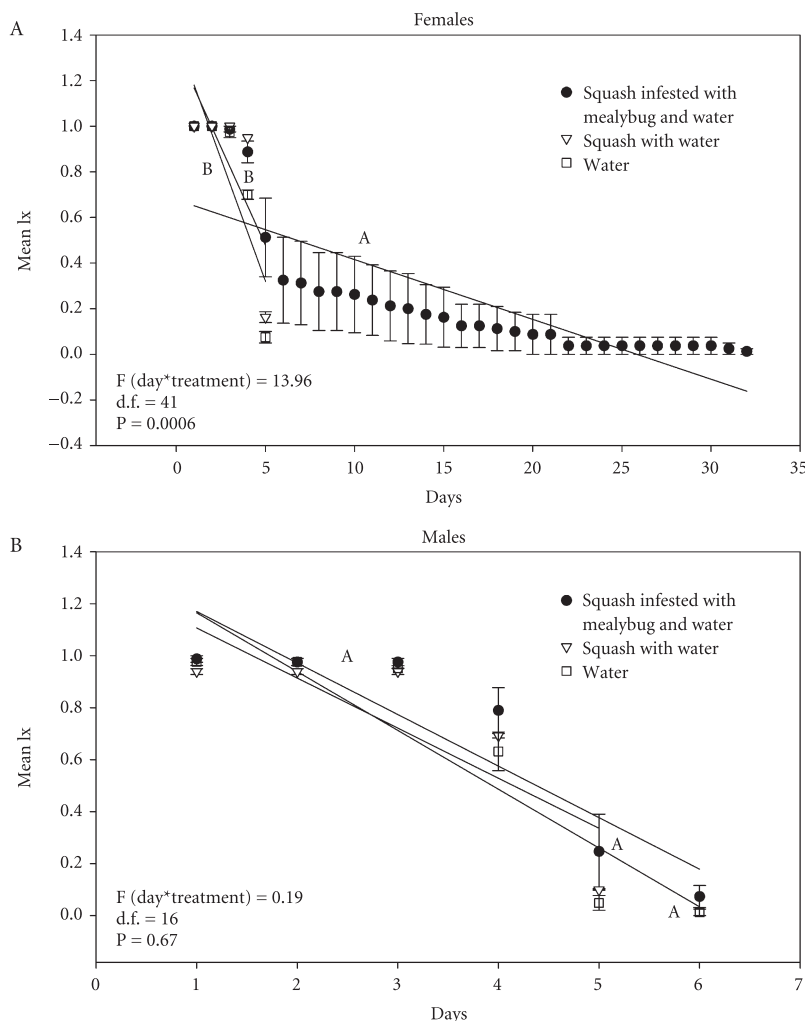


Figure 5 Mean (SE) numbers of eggs at 5 days of age in females fed either orange juice and water, honey and water, or water alone. Means sharing a letter are not significantly different.

they displayed when maintained in the presence of various flowers.

Another low travel-cost alternative to feeding on the host's substrate is to consume hosts themselves or fluids from wounded hosts. This is an important and widespread nutritional strategy in a phylogenetically broad range of hymenopteran parasitoids, including Braconidae (Jervis & Kidd, 1986), but has not been observed in *D. longicaudata* or, to our knowledge, in other tephritid-attacking opiines. However, beneficial for adults, host feeding may eliminate or lower the quality of potential larval hosts (Heimpel & Collier, 1996; Jervis et al., 1996). In situations where hosts are difficult to discover and subsequently attack, this cost to reproduction could be excessive. One correlate of host encounter rates, and by inferring the difficulty involved in their discovery, is the number of mature eggs held in the calyxes of ovarioles. This is low in tephritid-attacking opiines relative to some other ichneumonoid wasps

(compare Price, 1975 to Sivinski et al., 2001), and it may be that host feeding has not evolved because of an unfavorable trade-off between adult and offspring survival. In addition to the potential expense, host feeding may be difficult to accomplish for tephritid parasitoids given the depths at which larval hosts frequently feed within fruit tissues (see Sivinski et al., 1997, 2001).

Bird feces and leaf leachates were other potential food sources not exploited by *D. longicaudata*. Because these are important components of tephritid diets (Hendrichs et al., 1993) and abundant in their shared habitat (Jácome et al., 1999), it remains to be seen why they are not used by the parasitoid as well. Perhaps they are less accessible to the chewing mouthparts of Braconidae compared to the sponging mouthparts of fruit flies (see Downes & Dahlem, 1987). Alternatively, they may not provide required nutrients peculiar to the parasitoid.

Applied benefits may be derived from knowledge of tephritid parasitoid nutritional ecology. Given the co-

occurrence of food and oviposition sites, it appears that the sometimes elaborate schemes to concentrate parasitoid activities in agricultural environments by providing adult foods, such as spraying crops with sucrose solutions (e.g., Canas & O'Neil, 1998; Jacob & Evans, 1998), would not be necessary in the case of *D. longicaudata*. As previously noted, *D. longicaudata* has been mass reared for inundative releases (e.g., Sivinski et al., 1996; Montoya et al., 2000). An inventory of adult food sources could improve such biologic control programs by (1) targeting release points and times so that adults are best able to sustain themselves in the field and (2) suggesting improvements in the diets offered in rearing facilities and so optimizing adult performance immediately after release. The present experiments may also suggest improvements to be pursued in the mass-rearing technologies of cage design and climate control. Parasitoids provided with identical honey and water diets, obtained from the same colonies, and reared on the same hosts, but maintained in different containers, had life spans that differed by nearly an order of magnitude. The designs of those that resulted in greater longevity might be further investigated to determine what qualities they provided that others lacked.

In closing, we offer the following caveat: there are sometimes difficulties in the interpretation of negative results where preliminary behavioral observations suggested different results, particularly in regard to the lack of nutritional value of leaf surfaces. It may be that other leaves would have different effects on life span, or that products gleaned from these sources are used for purposes that do not necessarily translate into greater longevity in captivity (e.g., pheromones or defensive compound precursors).

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