

Effects of Temperature, Sugar Availability, Gender, Mating, and Size on the Longevity of Phorid Fly *Pseudacteon tricuspis* (Diptera: Phoridae)

LI CHEN, EBENEZER O. ONAGBOLA, AND HENRY Y. FADAMIRO¹

Department of Entomology and Plant Pathology Auburn University, Auburn, AL 36849

Environ. Entomol. 34(2): 246–255 (2005)

ABSTRACT The phorid fly, *Pseudacteon tricuspis* Borgmeier, has been released for biological control of red imported fire ant, *Solenopsis invicta* Buren, in many parts of the southern United States. However, little is known about the nutritional ecology and the effects of environmental and physiological factors on lifespan of adult phorid flies under laboratory or field conditions. Here we report the effects of sugar feeding, temperature, gender, mating, and body size on longevity of *P. tricuspis*. Sugar availability and temperature were the two major factors influencing longevity. In general, sugar feeding increased lifespan by a factor of 2–3. Longevity of *P. tricuspis* was inversely related to temperature, and the greatest longevity (≈ 15 d) was recorded for sugar-fed flies kept at 20°C. Longevity declined from ≈ 15 d at 20°C to 4 d at 33°C for sugar-fed females and from 7 d at 20°C to 2 d at 33°C for sugar-starved females. Similar results were obtained for male *P. tricuspis*, and gender or mating did not significantly influence longevity. There was no significant difference in longevity between mated and unmated female and male flies, irrespective of diet and temperature. Gender, however, had a significant effect on wing length with females being larger than males. A positive correlation between wing length and longevity was recorded for sugar-starved female and male phorid flies kept at 20°C and for sugar-starved males kept at 28°C, but not for sugar-fed flies or flies exposed to high temperatures. These results suggest that provision of supplemental sugar sources and suitable microclimate near its release sites may enhance the success of *P. tricuspis* as a biological control agent.

KEY WORDS *Solenopsis invicta*, imported fire ant, survivorship, microclimate, parasitoid

DECAPITATING PHORID FLIES in the genus *Pseudacteon* (Diptera: Phoridae) have received considerable attention in the last decade as possible classical biocontrol agents of imported fire ants, *Solenopsis* spp. (Hymenoptera: Formicidae) in the United States (Feener and Brown 1992, Orr et al. 1995, Gilbert 1996, Porter et al. 1995a, Porter and Alonso 1999). After successful development of rearing procedures, two species of phorid flies, *P. tricuspis* and *P. curvatus*, were selected for mass production and release in southern United States (Pesquero et al. 1995, Porter et al. 1997, Porter 2000, Graham et al. 2003, Vogt and Streett 2003). Since their first release in Texas in 1995 (Gilbert 1996), phorid flies have also been released in Florida, Alabama, and other parts of the southern United States (Porter 2000, Graham et al. 2003). Several aspects of the biology of phorid flies and their potential to control imported *Solenopsis* fire ants have been studied (reviewed by Porter 1998, Morrison 2000), and attempts are currently being made to monitor and evaluate the establishment and impact of phorid flies at

various release sites. However, several pertinent questions remain unanswered regarding the biology and ecology of phorid flies. For instance, little is known about adult activity and life span of *Pseudacteon* spp. under laboratory or field conditions, and the effects of environmental and physiological factors on lifespan and reproduction have not been examined.

One major factor that can impact the field efficacy of parasitoids released in biological control programs is the longevity of adult parasitoids. Increased longevity could potentially enhance biological control performance of parasitoids by increasing fecundity through an increase in searching time for suitable hosts and/or increase in egg maturation (Heimpel and Jervis 2005). Parasitoid species with a synovigenic life history strategy, in particular, could benefit from an increased lifespan commonly associated with provision of food resources because more time is available for egg maturation (Jervis et al. 2001, Heimpel and Jervis 2005).

Apart from genetics, several environmental and physiological factors are known to influence the lifespan of adult parasitoids, including availability of food, temperature, humidity, photoperiod, host availability, size, gender, and mating status (Ridgway and Mahr

¹ Corresponding author: Department of Entomology and Plant Pathology, 301 Funchess Hall, Auburn University, Auburn, AL 36849 (e-mail: fadamhy@acesag.auburn.edu).

1990, Corrigan and Liang 1994, McDougall and Mills 1997). Numerous laboratory and field studies have reported increased longevity and/or fecundity of parasitoids when provided sugar resources (e.g., Jervis et al. 1993, Heimpel et al. 1997, Olson and Andow 1998, Olson et al. 2000, Fadamiro and Heimpel 2001, Lee et al. 2004). The majority of studies on the effect of food availability and other factors on longevity of adult parasitoids have focused on hymenopteran parasitoids, whereas little information is available on dipteran parasitoids. In a recent report by our group, we demonstrated sugar feeding by adult *P. tricuspis* and showed that sucrose feeding could considerably enhance lifespan of adult phorid flies for >15 d in the laboratory (Fadamiro et al. 2005). This prompted us to conduct further studies on the influence of other environmental and physiological factors on longevity of phorid flies.

In addition to food availability, temperature (as a fundamental component of the microclimate) is also likely to exert a major effect on the lifespan of phorid flies, especially in the hot and humid summer conditions in southern United States. In general, longevity of adult insects is inversely related to temperature (Hoffmann 1985, Lysyk 1991, Rahim et al. 1991). However, the degree to which temperature affects longevity varies with species and gender, and some species are more tolerant of temperature extremities than others (Hawkins and Smith 1986, McDougall and Mills 1997). The degree of sensitivity of *P. tricuspis* to high temperatures may significantly affect its impact as a biological control agent for *S. invicta* in Alabama. In addition, mating could potentially have a negative effect on longevity, in particular when energy is limited, if energy resources are allocated to reproduction (Reznick 1985, Ellers 1996). Courtship and mating are energy- and time-consuming activities that could result in a significant reduction in adult lifespan (Li et al. 1993). In this study, we investigated the effects of sugar feeding, temperature, gender, mating status, and possible interactions among these factors on the longevity of *P. tricuspis*. We also checked the potential effect of fly size on longevity at different diet and temperature regimens. Evaluating the effects of these factors on adult lifespan should improve our understanding of the biology of *P. tricuspis* and provide insights into its potential biological control impact in Alabama and other parts of the United States.

Materials and Methods

Adult *Pseudacteon tricuspis* used in this study were reared on workers of red imported fire ants, *Solenopsis invicta*, at the fire ant rearing facility of the USDA-ARS, Center for Medical, Agricultural and Veterinary Entomology, Gainesville, FL, using methods described by Porter et al. (1995b, 1997). Parasitized fire ant worker heads were received in batches and kept in a plastic jar (25 by 13 cm) with a lid until emergence. Most adults seemed to emerge in the morning as has been reported (Porter et al. 1997). However, the jar was checked at least five times a day for fly emer-

gence. Emerging flies did not have access to food or water in the jar. Newly emerged flies were removed promptly with an aspirator and sexed immediately under a dissecting microscope.

This experiment simultaneously tested the effects and interactions of diet (sugar-fed versus sugar-starved), temperature (20, 25, 28, and 33°C), and mating status (mated versus unmated) on longevity of female and male *P. tricuspis*. The various combination of these factors resulted in a total of 16 treatment combinations for each gender. Newly emerged flies were placed in groups of two individuals either of the same gender (unmated treatments) or of opposite gender (mated treatments) in a 6-cm-diameter plastic petri dish. Water was provided in all treatments by filling a 0.5-ml microcentrifuge tube with distilled water and threading a cotton string through a hole in the cap of the tube. Water tubes were refilled as needed. For the treatments involving sugar feeding, 25% sucrose solution was smeared on the inside of the petri dish cover with a cotton-tipped applicator. Fresh sugar solution was smeared on the dish cover as needed (every 3–5 d depending on temperature). Petri dishes were kept in separate growth chambers at 20, 25, 28, or 33°C with a 14:10 (L:D) photoperiod and $75 \pm 5\%$ RH. Saturated brine was used to maintain constant relative humidity in the chambers. Female and male *P. tricuspis* emerging on the same day were distributed evenly across the treatment combinations. At least 16 flies of each gender were tested for each treatment combination. Petri dishes were checked once daily for dead flies, which were promptly removed from the dishes. We also evaluated the effect of fly size on longevity of female and male *P. tricuspis* exposed to the different treatment combinations. For this, one forewing was pulled from each dead fly, slide mounted, and measured to the nearest 0.05 mm. Measurements were taken from the outer edge of the anal cell to the outer edge of the tip of the wing using an ocular micrometer calibrated in 0.05-mm increments on a dissecting microscope.

We tested the effects of diet (sugar availability), temperature, gender, mating status, and wing length (as a measure of size) on survivorship using proportional hazard modeling, a nonparametric analysis designed to evaluate for effects of multiple factors on survivorship (SAS Institute 1998). This model also allowed testing for effects of two-way, three-way, four-way, and five-way interactions (a total of 26 possible interactions) among the five variables. Longevity data for each gender was analyzed separately using analysis of variance (ANOVA) followed by the Tukey-Kramer honestly significant difference (HSD) test for multiple comparisons of means at $P < 0.05$ (SAS Institute 1998).

Results

Proportional hazard analysis revealed significant effects of diet, temperature, and wing length on longevity of *P. tricuspis* (Table 1). Diet significantly in-

Table 1. Proportional hazard model testing for effects of diet, temperature, gender, mating, wing length, and interactions of these variables on longevity of *P. tricuspsis*

Source of variation	df	χ^2	<i>P</i>
Diet	1	159.51	<0.0001 ^a
Temperature	3	188.96	<0.0001 ^a
Gender	1	3.28	0.07
Mating	1	0.44	0.51
Wing length	1	4.78	0.03 ^a
Diet × temperature	3	5.81	0.12
Diet × gender	1	0.12	0.73
Diet × mating	1	0.94	0.33
Diet × Wing length	1	3.33	0.07
Temperature × gender	3	1.06	0.79
Temperature × mating	3	0.44	0.93
Temperature × wing length	3	2.25	0.52
Gender × mating	1	0.39	0.53
Gender × wing length	1	0.05	0.82
Mating × wing length	1	0.07	0.79
Diet × temperature × gender	3	1.72	0.63
Diet × temperature × mating	3	0.61	0.89
Diet × temperature × wing length	3	1.60	0.66
Diet × gender × mating	1	0.82	0.37
Diet × gender × wing length	1	0.0001	0.99
Diet × mating × wing length	1	0.05	0.83
Temperature × gender × mating	3	0.22	0.98
Temperature × gender × wing length	3	0.05	0.99
Temperature × mating × wing length	3	0.73	0.87
Gender × mating × wing length	1	0.90	0.34
Diet × temperature × gender × mating	3	1.04	0.79
Diet × temperature × gender × wing length	3	0.48	0.92
Diet × gender × mating × wing length	1	0.40	0.53
Diet × temperature × mating × wing length	3	0.35	0.95
Temperature × gender × mating × wing length	3	2.29	0.51
Diet × temperature × gender × mating × wing length	3	2.65	0.45

^a Significant variables.

fluenced longevity, with sugar-fed flies living significantly longer than sugar-starved flies ($\chi^2 = 159.51$, *df* = 1, *P* < 0.00001). Similarly, temperature had a significant effect on survivorship ($\chi^2 = 188.96$, *df* = 3, *P* < 0.00001): longevity was greater at lower temperatures than at higher temperatures. Longevity was also significantly influenced by wing length ($\chi^2 = 4.78$, *df* = 1, *P* = 0.03). The effects of gender ($\chi^2 = 3.28$, *df* = 1, *P* = 0.07) and mating ($\chi^2 = 0.44$, *df* = 1, *P* = 0.51) were not significant, suggesting that adult longevity did not vary as a result of gender or mating status

(Table 1). Mean (days ± SE) longevity of mated females fed sucrose at 20°C (14.75 ± 1.69) was similar to that of unmated sucrose fed females (14.81 ± 1.48) at the same conditions. Similar results were also obtained for female and male flies at the different diet-temperature treatment combinations, confirming that longevity was not affected by mating. There were no significant two-way, three-way, four-way, or five-way interactions among any of the five variables. Because the effect of mating on longevity of female and male flies was not significant, longevity data from unmated and mated flies were pooled and reanalyzed using ANOVA to test for the effect of temperature on lifespan of female and male flies fed sugar or water only (sugar-starved).

Phorid fly lifespan was influenced significantly by diet and temperature (Table 2). Survivorship curves depicting longevity of flies fed or starved sugar and kept at different temperatures are shown in Figs. 1 (female) and 2 (male). Longevity of sugar-fed flies was greatest at 20°C and lowest at 33°C. However, longevity at 28°C was not significantly different from longevity at 33°C, irrespective of diet and gender (Table 2). Similar results were recorded for sugar-starved flies, except that longevity of this group of flies was generally reduced by a factor of 2–3 in comparison with sugar-fed flies.

Wing length of *P. tricuspsis* flies used in this study ranged between 0.8 and 1.4 mm, in agreement with previous reports (Borgmeier and Prado 1975, Fad-amiro et al. 2005). Wing length data obtained from individual flies were analyzed by using proportional hazard analysis to test for effects of diet, temperature, gender, and mating, and any interactions (a total of 11 possible interactions) among the four variables. Wing length did not vary with diet ($\chi^2 = 2.90$, *df* = 1, *P* = 0.09), temperature ($\chi^2 = 5.40$, *df* = 3, *P* = 0.15), or mating status ($\chi^2 = 0.04$, *df* = 1, *P* = 0.85), suggesting that flies were uniformly distributed in size across the different treatments (Table 3). However, wing length was significantly affected by gender ($\chi^2 = 126.62$, *df* = 1, *P* < 0.0001). The only significant interaction was recorded between temperature and gender (Table 3). Because no significant effects of diet, temperature, and mating were recorded on wing length, wing length data obtained from the different treatments were pooled and analyzed by gender. The results showed that male (mean ± SD = 1.04 ± 0.09 mm; *N* = 256) had a significantly shorter wing length than female (mean ± SD = 1.14 ± 0.08 mm; *N* = 256) *P. tricuspsis*

Table 2. Temperature-dependent longevity (days ± SE) of female and male *P. tricuspsis* fed or starved sugar

Temperature (°C)	Female		Male	
	Sugar starved	Sugar fed	Sugar starved	Sugar fed
20	7.3 ± 0.42a (b)	14.8 ± 1.11a (a)	6.1 ± 0.44a (b)	14.5 ± 1.48a (a)
25	3.3 ± 0.19b (b)	10.0 ± 0.75b (a)	2.8 ± 0.19b (b)	9.9 ± 1.12b (a)
28	2.3 ± 0.14c (b)	5.3 ± 0.61c (a)	2.3 ± 0.16b (b)	5.7 ± 0.70c (a)
33	2.1 ± 0.13c (b)	4.1 ± 0.30c (a)	2.0 ± 0.08b (b)	4.5 ± 0.41c (a)

Means within the same column having different letters are significant (*P* < 0.05, Tukey HSD test). Similarly, means across the same row having different letters indicated in parentheses are significant (*P* < 0.05, Tukey HSD test).

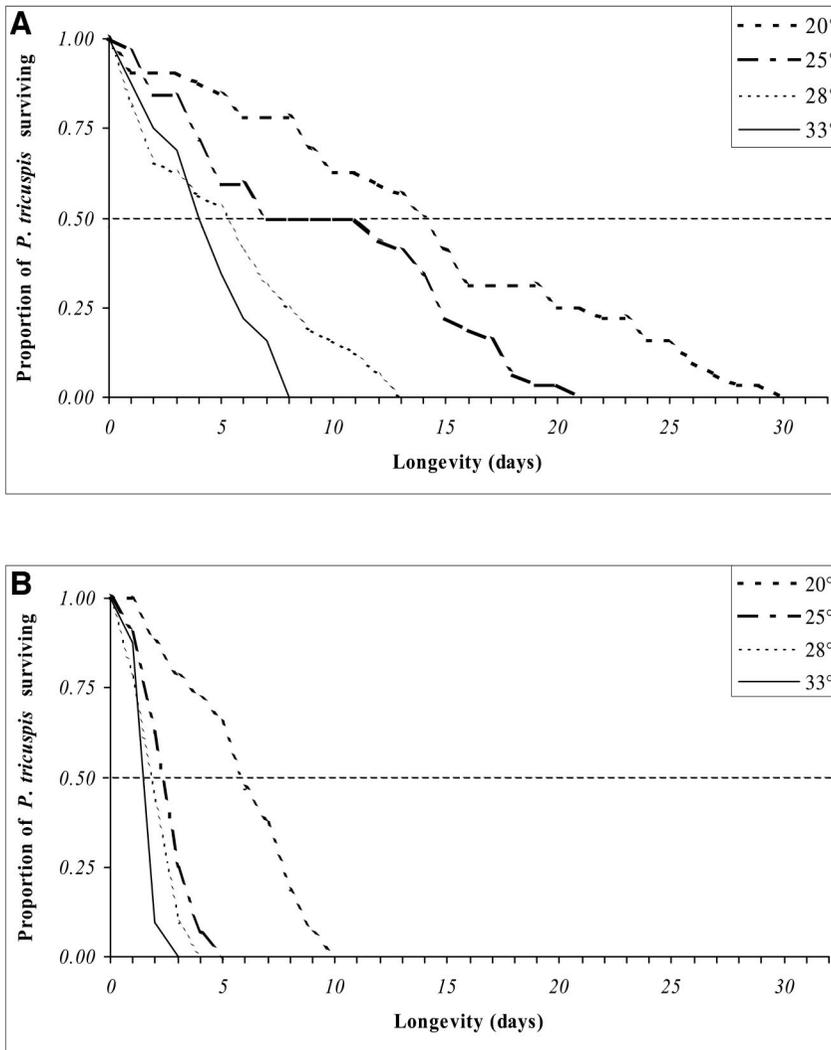


Fig. 1. Survivorship curves for sugar-fed (A) or sugar-starved (B) female *P. tricuspis* at different temperatures. Dashed line at 0.5 survivorship indicates median longevity for each treatment.

($t_{510} = 12.90$; $P < 0.001$). Wing length data from mated and unmated flies were again pooled and further analyzed by gender to test for any correlations between wing length and longevity in each of the diet-temperature treatment combinations. Longevity was correlated with wing length only in sugar-starved female and male flies kept at 20°C and in sugar-starved males kept at 28°C (Table 4; Fig. 3), suggesting that flies that emerged with relatively larger size have a lifespan advantage over smaller flies only when adult food is limited and when exposed to low-moderate temperature conditions.

Discussion

The main purpose of this study was to evaluate the effects of environmental and physiological factors on the lifespan of *P. tricuspis*. Our results clearly showed

that sugar availability and temperature were the two main factors determining adult longevity. Sugar-fed female and male *P. tricuspis* had significantly greater longevity than their sugar-starved counterparts. This significant positive effect of sugar on lifespan was recorded at all temperatures. In general, sugar feeding increased phorid fly lifespan by a factor of 2–3 relative to sugar-starved flies, irrespective of the temperature. These results are in agreement with previous reports of the positive effect of sugar feeding on longevity of several hymenopteran parasitoids (Hagley and Barber 1992, Fletcher et al. 1994, Heimpel et al. 1997, Thompson 1999, Olson et al. 2000, Fadamiro and Heimpel 2001, Wäckers 2001). In one of the very few systematic studies on the effect of sugar availability on lifespan of dipteran parasitoids, Fadamiro et al. (2005) recently demonstrated sugar feeding by adult *P. tricuspis* and recorded a similar increase in longevity of sugar-fed

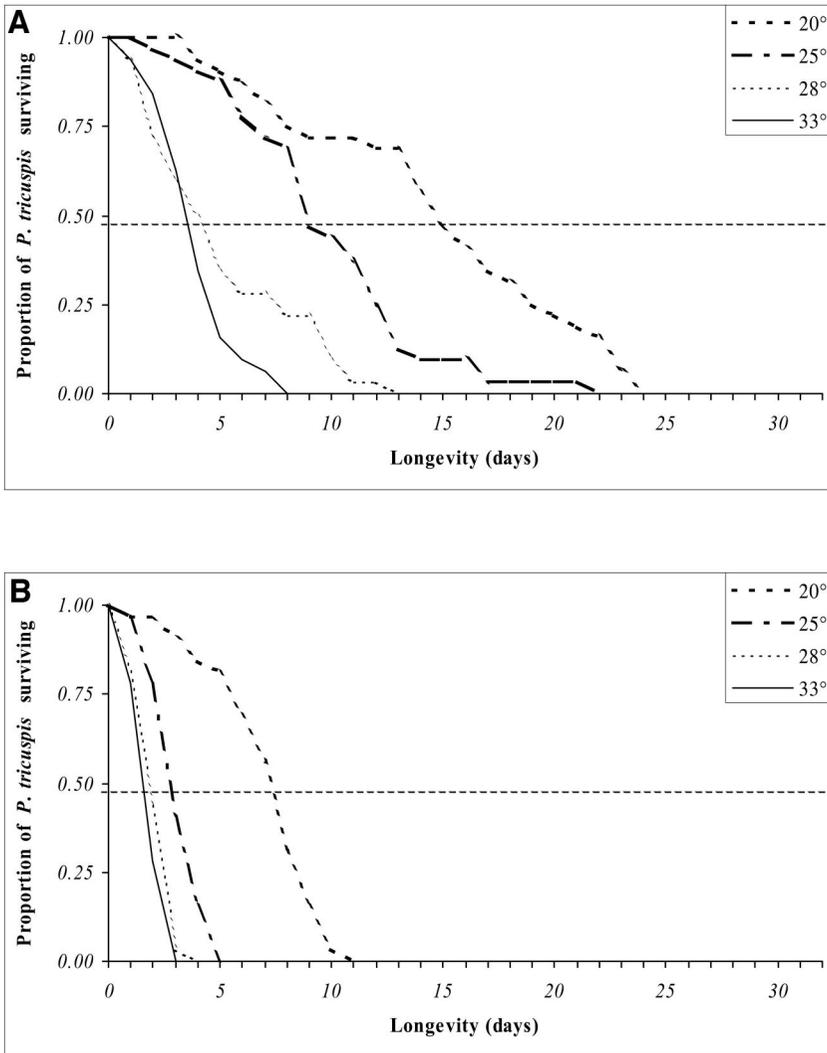


Fig. 2. Survivorship curves for sugar-fed (A) or sugar-starved (B) male *P. tricuspid* at different temperatures. Dashed line at 0.5 survivorship indicates median longevity for each treatment.

flies by a factor of two in comparison to sugar-starved flies. In this study, sugar feeding dramatically enhanced the longevity of both male and female phorid flies. Adult flies benefited proportionately more from sugar feeding at moderate temperatures, as reported for the parasitic wasp, *Eriborus terebrans* (Gravenhorst) (Dyer and Landis 1996). For instance, an approximately three-fold increase in the relative longevity of sugar-fed flies was recorded at 25°C compared with the two-fold increase recorded at 33°C. It is important to note that provision of water is crucial for the maintenance of adult lifespan beyond the first day of emergence. Fadamiro et al. (2005) reported that completely starved adults (flies provided no water and no sugar) rarely lived beyond 1 d at 28°C and that provision of water increased longevity by ≈2 d.

The significant effect of sugar feeding on lifespan suggests that *P. tricuspid* may benefit from sugar avail-

Table 3. Proportional hazard model testing for effects of diet, temperature, gender, mating, and interactions of these variables on wing length of *P. tricuspid*

Source of variation	df	χ^2	P
Diet	1	2.90	0.09
Temperature	3	5.40	0.15
Gender	1	126.62	<0.0001 ^a
Mating	1	0.04	0.85
Diet × temperature	3	1.80	0.61
Diet × gender	1	1.83	0.18
Diet × mating	1	0.41	0.52
Temperature × gender	3	10.73	0.01 ^a
Temperature × mating	3	3.25	0.36
Gender × mating	1	0.05	0.82
Diet × temperature × gender	3	0.73	0.87
Diet × temperature × mating	3	1.32	0.73
Diet × gender × mating	1	0.24	0.62
Temperature × gender × mating	3	4.41	0.22
Diet × temperature × gender × mating	3	0.16	0.98

^a Significant variables.

Table 4. Linear regression analyses testing for correlation between wing length and longevity of female and male *P. tricuspsis* at different diet-temperature treatment combinations

Diet-temperature treatment combination	df	Females			Males		
		MS	F	P	MS	F	P
Sugar starved, 20°C	1	43.47	10.14	0.003 ^a	27.01	4.81	0.04 ^a
Sugar starved, 25°C	1	1.57	1.42	0.24	0.13	0.12	0.73
Sugar starved, 28°C	1	2.33	3.85	0.06	6.05	8.72	0.006 ^a
Sugar starved, 33°C	1	1.39	2.89	0.10	0.31	1.40	0.25
Sugar fed, 20°C	1	77.41	2.05	0.16	94.00	1.35	0.25
Sugar fed, 25°C	1	14.83	0.81	0.37	12.09	0.30	0.59
Sugar fed, 28°C	1	0.26	0.02	0.88	0.06	0.004	0.95
Sugar fed, 33°C	1	9.51	3.46	0.07	2.95	0.55	0.46

^a Significant correlation between wing length and longevity.

ability in the field. In the field, parasitoids can potentially obtain sugar from different sources, including floral or extra-floral nectar and homopteran honeydew (Rogers 1985, Idoine and Ferro 1988, Jervis et al. 1996, Stapel et al. 1997, Heimpel and Jervis 2005). Future field studies on the nutritional ecology and foraging behavior of *P. tricuspsis* will address its possible use of sugar sources in the field and provide insights into the effects of sugar availability on the fecundity and performance of phorid flies as a biological control agent of imported fire ants in the southern United States.

Temperature exerted a significant and major effect on longevity of *P. tricuspsis* in this study, with longevity being inversely related to temperature. The greatest mean longevity (≈ 15 d) was recorded for sugar-fed flies kept at 20°C. Longevity was consistently greater at the lower temperatures (20 and 25°C) than that at the higher temperatures (28 and 33°C), irrespective of the diet. Increasing the temperature from 20 to 33°C resulted in approximately three- to four-fold reduction in longevity. For instance, longevity of sugar-fed flies at 20°C was ≈ 15 d compared with ≈ 4.5 d at 33°C. Similar results have been reported for other insects, including several parasitoids (Lysyk 1991, Dyer and Landis 1996, McDougall and Mills 1997, Uckan and Ergin 2003).

The longevity of adult insects is generally lower at higher temperatures (Hoffmann 1985), and extreme temperatures have been shown to negatively impact insect lifespan (Tracy and Nechols 1987, Pullin 1994). The degree of tolerance to temperature extremes varies with species and may be influenced by the availability of food (Hawkins and Smith 1986, Dyer and Landis 1996, McDougall and Mills 1997, Uckan and Ergin 2003). The reduced lifespan of adult parasitoids at high temperatures may be the result of increased metabolism and possible destruction or denaturing of enzymes at high temperatures (Mendel et al. 1987, Mohan et al. 1992). In Alabama and other parts of the southern United States where *P. tricuspsis* has been released for biological control of imported fire ant, *S. invicta*, average daily temperatures in the summer are usually high and sometimes in excess of 30°C, and relative humidity is frequently >75% (the relative humidity condition at which this study was conducted). Our results showing that adult *P. tricuspsis* is

sensitive to high temperatures, coupled with the fact the parasitoid may likely experience more severe heat in the field from direct solar radiation, suggest that hot summer temperatures may potentially impact its establishment and performance in the southern United States. However, several habitats such as woodlots and other noncrop habitats near the release sites of *P. tricuspsis* could potentially provide cool or moderate microclimates for the parasitoid, thereby limiting its exposure to severe temperatures. For instance, *E. terebrans* was more abundant near wooded edges of cornfields and fencerows in Michigan because of availability of sugar source and cool microclimates at these habitats (Dyer and Landis 1996). Little is known about what phorid flies do or where they spend their time when they are not attacking fire ants or if they are more abundant in certain habitats. There are anecdotal reports that phorid adults would stop and drink water or lap up sugary substances if they contact them (Porter 1998). The presence of adult food resources, such as flowers and homopteran honeydew, may provide suitable microclimate, increase the attacking capability of phorid flies, and ultimately enhance the success of biological control efforts on fire ants. Field studies on the behavioral ecology, dispersal ability, and habitat use by *P. tricuspsis* will provide insights into how the parasitoid avoids stressful environmental conditions.

Fly gender did not have any significant effect on longevity, although a few sugar-fed males kept at 20°C lived beyond 25 d, whereas no sugar-fed females lived up to this age. In general, studies on several parasitoid species have recorded greater longevity for females than males (Mendel et al. 1987, Ueno and Tanaka 1994). In contrast, Uckan and Ergin (2003) reported a slight but not significant increase in longevity for sugar-fed male *Apanteles galleriae* Wilkinson (Hymenoptera: Braconidae) compared with female wasps at low to moderate temperatures, whereas females lived longer than males at extreme temperatures. Our data analysis did not detect any significant temperature-dependent effect of gender on survivorship of *P. tricuspsis*.

The mating status of *P. tricuspsis* had little influence on its longevity in this study. There was no significant difference in longevity between mated and unmated female and male flies, irrespective of diet and tem-

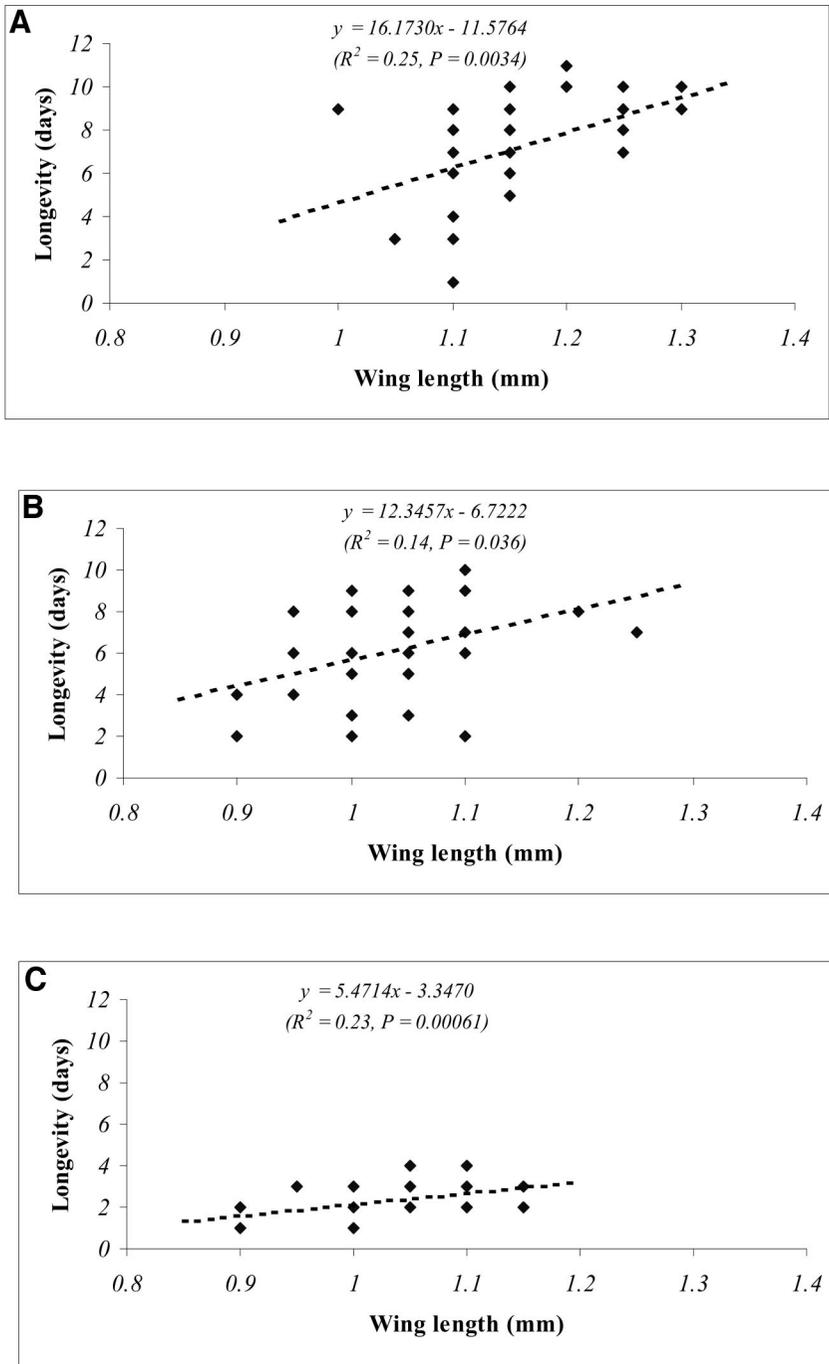


Fig. 3. Regression of significant linear relationship between wing length and longevity of *P. tricuspis* provided water only at different temperatures: females kept at 20°C (A), males kept at 20°C (B), and males kept at 28°C (C).

perature. Several studies have documented a trade-off between mating and longevity in insects, including parasitoids (Fowler and Partridge 1989, Li et al. 1993, Carpenter 1995, Jacob and Evans 2000, Sagarra et al. 2002). Mating is widely presumed to impact insect longevity, in particular when energy resources are limited, by allocating resources to reproductive activ-

ities (Partridge and Farquhar 1981, Reznick 1985, Ellers 1996), and by stimulating oogenesis and egg maturation in female insects (Wheeler 1996). Jacob and Evans (2000) tested the effect of mating on longevity of the parasitoid wasp *Bathyplectes curculionis* (Thomson) provided different diets. The authors did not allow female wasps to oviposit and found that

mating reduced longevity of females provided water only or inferior food plants but not when a superior food such as honey-water was provided. Partridge and Farquhar (1981) reported that the negative effect of mating on longevity was more pronounced for male fruitflies than females, possibly because of the higher intense courtship and mating behavior of the males. In this study, we did not detect any effect of mating on longevity of female and male *P. tricuspsis* or any interaction between gender and mating effects on longevity. The lack of effect of mating on longevity of female and male phorid fly is interesting and may suggest reduced allocation of resources to reproduction or reduced mating related activities such as courtship. It should be noted that we did not morphologically confirm mating in this study, although adult pairs in the mating treatment were frequently observed in courtship. It is not clear whether or not *P. tricuspsis* mates multiply. However, if single mating (first mating) does not require a lot of energy resources and flies are not stimulated to mate again (multiple mating) in the absence of hosts to oviposit on, it is conceivable that mating will not likely affect longevity. However, it is unlikely that flies will mate only when provided hosts, because imported fire ant worker hosts spend most of their time in ground tunnels.

Our data showed a positive correlation between wing length and longevity of *P. tricuspsis*. Wing length is commonly used as a measure of parasitoid body size, and body size is usually considered as a measure of parasitoid quality and fitness (Jervis and Copland 1996, Olson et al. 2000, Fadamiro and Heimpel 2001, Roitberg et al. 2001, Sagarra et al. 2001). Further analyses of our data showed that wing length had a positive effect on longevity only for sugar-starved female and male phorid flies kept at 20°C and for sugar-starved males kept at 28°C, indicating that larger flies only had an advantage over smaller flies when the food resource was limited and at low temperatures. When food was available or when flies were placed at high temperatures, smaller flies had similar longevity as larger flies. Of all the factors tested, only gender had a significant effect on wing length with phorid fly females being larger than males. Correlation between body size and parasitoid longevity has been reported for several species; larger individuals tended to live longer and have a higher fecundity than smaller individuals (Jervis and Copland 1996, Sagarra et al. 2001). The effect of body size on phorid fly fecundity remains to be examined.

In summary, our data showed significant effects of sugar availability and temperature on lifespan of *P. tricuspsis*. We also recorded a positive correlation between wing length and lifespan, but gender and mating did not significantly influence lifespan. These results suggest that availability of adult food sources and suitable microclimate are important factors that could potentially influence the survival, establishment, distribution, and overall impact of *P. tricuspsis* released in different parts of the southern United States for biological control of imported fire ants. Provision of supplemental sugar sources and suitable microclimate

near release sites may likely enhance the success of phorid flies as a biological control agent.

Acknowledgments

We thank D. Roberts (USDA APHIS PPQ CPHST Laboratory, Gainesville, FL) for the supply of adult *P. tricuspsis* for this study. This research was funded partly by a Alabama Fire Ant Management Program grant to HYF and the Alabama Agricultural Experiment Station.

References Cited

- Borgmeier, T., and A. P. Prado. 1975. New or little known Neotropical phorid flies, with description of eight new genera (Diptera: Phoridae). *Stud. Entomol.* 18: 3–90.
- Carpenter, J. E. 1995. *Ichneumon promissorius* (Erichson) (Hymenoptera: Ichneumonidae): factors affecting fecundity, oviposition, and longevity. *J. Entomol. Sci.* 30: 279–286.
- Corrigan, J. E., and J. E. Liang. 1994. Effects of the rearing host species and the host species attacked on performance by *Trichogramma minutum* Riley (Hymenoptera: Trichogrammatidae). *Environ. Entomol.* 23: 755–760.
- Dyer, L., and D. A. Landis. 1996. Effects of habitat, temperature, and sugar availability on longevity of *Eriborus terebrans* (Hymenoptera: Ichneumonidae). *Environ. Entomol.* 25: 1192–1201.
- Ellers, J. 1996. Fat and eggs: an alternative method to measure the trade-off between survival and reproduction in insect parasitoids. *Neth. J. Zool.* 46: 227–235.
- Fadamiro, H. Y., and G. E. Heimpel. 2001. Effects of partial sugar deprivation on lifespan and carbohydrate mobilization in the parasitoid *Macrocentrus grandii* (Hymenoptera: Braconidae). *Ann. Entomol. Soc. Am.* 94: 909–916.
- Fadamiro, H. Y., L. Chen, E. O. Onagbola, and L. 'Fudd' Graham. 2005. Lifespan and patterns of accumulation and mobilization of nutrients in sugar fed phorid fly *Pseudacteon tricuspsis*. *Physiol. Entomol.* (in press).
- Feener, D. H., Jr., and B. V. Brown. 1992. Reduced foraging of *Solenopsis geminata* (Hymenoptera: Formicidae) in the presence of parasitic *Pseudacteon* spp. (Diptera: Phoridae). *Ann. Entomol. Soc. Am.* 85: 80–84.
- Fletcher, J. P., J. P. Hughes, and I. F. Harvey. 1994. Life expectancy and egg load affect oviposition decisions of a solitary parasitoid. *Proc. R. Soc. Lond.* 258(B): 163–167.
- Fowler, K., and L. Partridge. 1989. A cost of mating in female fruitflies. *Nature (Lond.)* 338: 760–761.
- Gilbert, L. E. 1996. Prospects of controlling fire ants with parasitoid flies: the perspective from research based at Brackenridge field laboratory, pp. 77–92. *In* W. E. Cohen (ed.), *Texas Quail Short Course II*. Texas Agricultural Extension Service, Texas A & M University, Kingsville.
- Graham, L.C.F., S. D. Porter, R. M. Pereira, H. D. Dorough, and A. T. Kelley. 2003. Field releases of the decapitating fly *Pseudacteon curvatus* (Diptera: Phoridae) for control of imported fire ants (Hymenoptera: Formicidae) in Alabama, Florida, and Tennessee. *Florida Entomol.* 86: 334–339.
- Hagley, E.A.C., and D. R. Barber. 1992. Effect of food sources on the longevity and fecundity of *Pholetesor ornigis* (Weed) (Hymenoptera: Braconidae). *Can. Entomol.* 124: 341–346.
- Hawkins, B. A., and J. W. Smith. 1986. *Rhaconotus roslinensis* (Hymenoptera: Braconidae), a candidate for biological control of stalkboring sugarcane pests (Lepidoptera: Pyralidae)

- development, life tables, and intraspecific competition. *Ann. Entomol. Soc. Am.* 79: 905-911.
- Heimpel, G. E., and M. A. Jervis. 2005. Does floral nectar improve biological control by parasitoids? *In* F. Wäckers, P. van Rijn, and J. Bruin (eds.), *Plant-Provided Food and Plant-Carnivore Mutualism*. Cambridge University Press, Cambridge, UK (in press).
- Heimpel, G. E., J. A. Rosenheim, and D. Kattari. 1997. Adult feeding and lifetime reproductive success in the parasitoid *Aphytis melinus*. *Entomol. Exp. Appl.* 83: 305-315.
- Hoffmann, K. H. 1985. *Environmental physiology and biochemistry of insects*. Springer, Berlin.
- Idoine, K., and D. N. Ferro. 1988. Aphid honeydew as a carbohydrate source for *Edovum putleri* (Hymenoptera: Eulophidae). *Environ. Entomol.* 17: 941-944.
- Jacob, H. S., and E. W. Evans. 2000. Influence of carbohydrate foods and lifetime longevity of the parasitoid *Bathyplectes curculionis* (Hymenoptera: Ichneumonidae). *Environ. Entomol.* 29: 1088-1095.
- Jervis, M. A., and M. J. W. Copland. 1996. The life cycle, pp. 63-160. *In* M. A. Jervis, and N. Kidd (eds.), *Insect natural enemies, practical approaches to their study and evaluation*. Chapman & Hall, London.
- Jervis, M. A., N. A. C. Kidd, G. E. Heimpel. 1996. Parasitoid adult feeding behaviour and biological control—a review. *Biocontrol News and Information* 17: 11N-26N.
- Jervis, M. A., N. A. C. Kidd, M. G. Fitton, T. Huddleston, and H. A. Dawah. 1993. Flower-visiting by Hymenopteran parasitoids. *J. Nat. History*. 27: 67-105.
- Jervis, M. A., G. E. Heimpel, P. N. Ferns, J. A. Harvey, and N. A. C. Kidd. 2001. Life-history strategies in parasitoid wasps: a comparative analysis of 'ovigeny'. *J. Anim. Ecol.* 70: 442-458.
- Lee, J. C., G. E. Heimpel, and G. L. Leibe. 2004. Comparing floral nectar and aphid honeydew diets on the longevity and nutrient levels of a parasitoid wasp. *Entomol. Exp. Appl.* 111: 189-199.
- Li, S. Y., G. Sirois, D. L. Lee, C. Maurice, and D. E. Henderson. 1993. Effects of female mating status and age on fecundity, longevity and sex ratio in *Trichogramma minutum* (Hymenoptera: Trichogrammatidae). *J. Entomol. Soc. B. C.* 90: 61-66.
- Lysyk, T. J. 1991. Effects of temperature, food, and sucrose feeding on longevity of the house fly (Diptera: Muscidae). *Environ. Entomol.* 20: 1176-1180.
- McDougall, S. J., and N. J. Mills. 1997. The influence of hosts, temperature and food sources on the longevity of *Trichogramma platneri*. *Entomol. Exp. Appl.* 83: 195-203.
- Mendel, M. J., P. B. Shaw, and J. C. Owens. 1987. Life history characteristics of *Anastatus semiflavus* (Hymenoptera: Eupelmidae), an egg parasitoid of the range caterpillar, *Hemileuca oliviae* (Lepidoptera: Saturniidae) over a range of temperatures. *Environ. Entomol.* 16: 1035-1041.
- Mohan, B. R., A. N. Verma, and S. P. Singh. 1992. Biology of *Apanteles flavipes* (Cameron) - a potential parasitoid of *Chilo partellus* (Swin.) infesting forage sorghum. *J. Insect Sci.* 5: 144-146.
- Morrison, L. W. 2000. Biology of *Pseudacteon* (Diptera: Phoridae) ant parasitoids and their potential to control imported *Solenopsis* fire ants (Hymenoptera: Formicidae). *Recent Res. Devel. Entomol.* 3: 1-13.
- Olson, D. M., and D. A. Andow. 1998. Larval crowding and adult nutrition effects on longevity and fecundity of female *Trichogramma nubilale* Ertle & Davis (Hymenoptera: Trichogrammatidae). *Environ. Entomol.* 27: 508-514.
- Olson, D. M., H. Y. Fadamiro, J. G. Lundgren, and G. E. Heimpel. 2000. Effects of sugar feeding on carbohydrate and lipid metabolism in a parasitoid wasp. *Physiol. Entomol.* 25: 17-26.
- Orr, M. R., S. H. Seike, W. W. Benson, and L. E. Gilbert. 1995. Flies suppress fire ants. *Nature (Lond.)* 373: 292-293.
- Partridge, L., and M. Farquhar. 1981. Sexual activity reduces lifespan of male fruitflies. *Nature (Lond.)* 294: 580-582.
- Pesquero, M. A., S. D. Porter, H. G. Fowler, and S. Campiolo. 1995. Rearing of *Pseudacteon* spp. (Dipt., Phoridae), parasitoids of fire ants (*Solenopsis* spp.) (Hym., Formicidae). *J. Appl. Entomol.* 119: 677-678.
- Porter, S. D. 1998. Biology and behavior of *Pseudacteon* decapitating flies (Diptera: Phoridae) that parasitize *Solenopsis* fire ants (Hymenoptera: Formicidae). *Florida Entomol.* 81: 292-309.
- Porter, S. D. 2000. Host specificity and risk assessment of releasing the decapitating fly *Pseudacteon curvatus* as a classical biocontrol agent for imported fire ants. *Biol. Control.* 19: 35-47.
- Porter, S. D., and L. E. Alonso. 1999. Host specificity of fire ant decapitating flies (Diptera: Phoridae) in laboratory oviposition tests. *J. Econ. Entomol.* 92: 110-114.
- Porter, S. D., D. F. Williams, and R. S. Patterson. 1997. Rearing the decapitating fly *Pseudacteon tricuspis* (Diptera: Phoridae) in imported fire ants (Hymenoptera: Formicidae) from the United States. *J. Econ. Entomol.* 90: 135-138.
- Porter, S. D., H. G. Fowler, S. Campiolo, and M. A. Pesquero. 1995a. Host specificity of several *Pseudacteon* (Diptera: Phoridae) parasitoids of fire ants (Hymenoptera: Formicidae) in South America. *Florida Entomol.* 78: 70-75.
- Porter, S. D., M. A. Pesquero, S. Campiolo, and H. G. Fowler. 1995b. Growth and development of *Pseudacteon* phorid fly maggots (Diptera: Phoridae) in the heads of *Solenopsis* fire ant workers (Hymenoptera: Formicidae). *Environ. Entomol.* 24: 475-479.
- Pullin, A. S. 1994. Cold tolerance of an insect parasitoid *Cotesia (Apanteles) glomeratus* and a comparison with that of its host *Pieris brassicae* and a hyperparasitoid *Tetrastichus galactopus*. *Cryo-Letters* 15: 67-74.
- Rahim, A., A. A. Hashmi, and N. A. Khan. 1991. Effects of temperature and relative humidity on longevity and development of *Ooencyrtus papilionis* Ashmead (Hymenoptera: Eulophidae), a parasite of the sugarcane pest, *Pyrilla perpusilla* Walker (Homoptera: Cicadellidae). *Environ. Entomol.* 20: 774-775.
- Reznick, D. 1985. Costs of reproduction: an evaluation of the empirical evidence. *Oikos* 44: 257-267.
- Ridgway, N. M., and D. L. Mahr. 1990. Reproduction, development, and longevity of *Pholetesor ornigis* (Hymenoptera: Braconidae), a parasitoid of spotted tentiform leafminer (Lepidoptera: Gracillariidae), in the laboratory. *Ann. Entomol. Soc. Am.* 83: 790-794.
- Rogers, C. A. 1985. Extrafloral nectar: entomological implications. *Bull. Entomol. Soc. Am.* Fall: 15-20.
- Roitberg, B. D., G. Boivin, and L. E. M. Vet. 2001. Fitness, parasitoids, and biological control: an opinion. *Can. Entomol.* 133: 429-438.
- Sagarra, L. A., C. Vincent, and R. K. Stewart. 2001. Body size as an indicator of parasitoid quality in male and female *Anagyrus kamali* (Hymenoptera: Encyrtidae). *Bull. Entomol. Res.* 91: 363-367.
- Sagarra, L. A., C. Vincent, and R. K. Stewart. 2002. Impact of mating on *Anagyrus kamali* Moursi (Hym., Encyrtidae) lifetime fecundity, reproductive longevity, progeny emergence and sex ratio. *J. Appl. Entomol.* 126: 400-404.

- SAS Institute. 1998. JMP Statistics and Graphics Guide, Version 5.1. SAS Institute, Cary, NC, USA.
- Stapel, J. O., A. M. Cortesero, C. M. de Moraes, J. H. Tumlinson, and W. J. Lewis. 1997. Extrafloral nectar, honeydew, and sucrose effects on searching behavior and efficiency of *Microplitis croceipes* (Hymenoptera: Braconidae) in cotton. *Environ. Entomol.* 26: 617–623.
- Thompson, S. N. 1999. Nutrition and culture of entomophagous insects. *Annu. Rev. Entomol.* 44: 561–592.
- Tracy, J. L., and J. R. Nechols. 1987. Comparisons between the squash bug egg parasitoids *Ooencyrtus anasae* and *O.* sp. (Hymenoptera: Encyrtidae): development, survival, and sex ratio in relation to temperature. *Environ. Entomol.* 16: 1324–1329.
- Uckan, F., and E. Ergin. 2003. Temperature and food source effects on adult longevity of *Apanteles galleriae* Wilkinson (Hymenoptera: Braconidae). *Environ. Entomol.* 32: 441–446.
- Ueno, T., and T. Tanaka. 1994. Comparative biology of six polyphagous solitary pupal endoparasitoids (Hymenoptera: Ichneumonidae): differential host suitability and sex allocation. *Ann. Entomol. Soc. Am.* 87: 592–598.
- Vogt, J. T., and D. A. Streett. 2003. *Pseudacteon curvatus* (Diptera: Phoridae) laboratory parasitism, release and establishment in Mississippi. *J. Entomol. Sci.* 38: 317–320.
- Wäckers, F. L. 2001. A comparison of nectar- and honeydew sugars with respect to their utilization by the hymenopteran parasitoid *Cotesia glomerata*. *J. Insect Physiol.* 47: 1077–1084.
- Wheeler, D. 1996. The role of nourishment in oogenesis. *Annu. Rev. Entomol.* 41: 407–431.

Received for publication 28 October 2004; accepted 30 December 2004.
