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Comparing longevity of *Pseudacteon* species of different sizes: effect of sugar feeding

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Abstract. Sugar feeding is known to enhance lifespan in many parasitoid species. Several species of phorid flies in the genus *Pseudacteon* (Diptera: Phoridae) have been introduced in the Southern U.S.A. for the biological control of imported fire ants of *Solenopsis* species (Hymenoptera: Formicidae). *Pseudacteon* species are short-lived flies and little is known about their nutritional ecology. Results from previous studies in our laboratory show that one of the introduced species, *Pseudacteon tricuspis* Borgmeier, is capable of feeding on sugar sources with a significant increase in lifespan. However, in *Pseudacteon* phorid flies, the degree to which sugar feeding can enhance the lifespan of other species is not clear, nor is it known whether there is a relationship between body size and longevity. In the present study, the effect of sugar feeding on the survival of three phorid fly species of different body sizes, *Pseudacteon cultellatus* Borgmeier, *Pseudacteon curvatus* Borgmeier and *Pseudacteon obtusus* Borgmeier, is investigated. For all three species, flies continuously provided with 40% or 20% sucrose solution live longer than individuals provided water only or 40% sucrose solution only on the first day of adult life. However, the degree to which sugar feeding enhanced longevity varies by species and is highest for *P. obtusus*. The data also indicate that longevity in *Pseudacteon* phorid flies is related to body size: the largest species (*P. obtusus*) lives significantly longer than the smaller species (*P. cultellatus* and *P. curvatus*). These results suggest that adults of all three *Pseudacteon* species are capable of feeding on sucrose solution and that sugar feeding can enhance their longevity. The significance of these results is discussed in relation to the field performance of *Pseudacteon* phorid flies as biological control agents of imported fire ants.

Key words. Body size, fire ant, longevity, *Pseudacteon* species, sucrose, sugar feeding.

Introduction

Parasitic phorid flies in the genus *Pseudacteon* (Diptera: Phoridae) are natural enemies of ants, and many species are specific to fire ants of *Solenopsis* spp. (Disney, 1994; Morrison, 2000; Porter & Gilbert, 2004). Imported fire ants are invasive pests that pose significant ecological, economical and medical threats to invaded areas (Lofgren, 1986; Porter *et al.*, 1992). In the last two decades, six *Pseudacteon* species (*Pseudacteon tricuspis* Borgmeier, *Pseudacteon curvatus* Borgmeier, *Pseudacteon litoralis* Borgmeier, *Pseudacteon obtusus* Borgmeier, *Pseudacteon nocens* Borgmeier and *Pseudacteon cultellatus* Borgmeier) have been introduced into the Southern U.S.A. for classical biological control of imported fire ants (Henne *et al.*, 2007; Porter & Calcaterra, 2013). These flies vary in size and are categorized based on their relative sizes as large species (i.e. *P. litoralis*), medium-large species (i.e. *P. tricuspis*, *P. obtusus* and *P. nocens*) and small species (i.e. *P. curvatus* and *P. cultellatus*) (Porter & Calcaterra, 2013). Size plays a role in the relationship between phorid flies and their fire ant hosts. Large-sized species typically parasitize large fire ant workers up to 6 mm in length, whereas smaller-sized species parasitize smaller fire ant workers that are only 2–3 mm in length (Porter & Calcaterra, 2013).

Adults of many parasitoid species are known to feed on sugar-rich food sources, such as nectar and honeydew, for maximum survival and reproduction (Fadamiro *et al.*, 2005; Lee & Heimpel, 2008; Tena *et al.*, 2013; Jamont *et al.*, 2014). However,

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the extent to which parasitoids derive fitness benefits from sugar feeding depends on their egg maturation strategy; specifically, whether they are pro-ovigenic (all eggs are mature upon emergence) or synovigenic (some eggs are immature at emergence) (Ellers *et al.*, 2000; Bernstein & Jervis, 2008). *Pseudacteon* phorid flies are short-lived and are presumed to have similar feeding habits across the genus (Morrison, 2000), although little is known about their nutritional ecology as a group (Fadamiro & Chen, 2005). In the only *Pseudacteon* species studied so far in terms of nutritional ecology, sugar feeding, even for only the limited period of 1 day post-emergence, is found to significantly increase the longevity of *P. tricuspis* (Chen *et al.*, 2005; Fadamiro *et al.*, 2005; Chen & Fadamiro, 2006). Among the various sugar types tested, sucrose is very beneficial to *P. tricuspis* in terms of increased longevity and body nutrient levels (Chen & Fadamiro, 2006). However, it is not clear whether other *Pseudacteon* species are capable of sugar feeding with significant increase in longevity. Also, it is not known whether there is a relationship between body size and lifespan in *Pseudacteon* species.

In the present study, the effect of sucrose feeding on the longevity of three *Pseudacteon* species of varying sizes (*P. cultellatus*, *P. curvatus* and *P. obtusus*) is compared. The central hypothesis tested is that sucrose feeding will significantly increase lifespan of the three species, as reported for *P. tricuspis* (Chen *et al.*, 2005; Fadamiro *et al.*, 2005; Chen & Fadamiro, 2006). In addition, because bigger animal species tend to live longer than smaller ones (Speakman, 2005), it is expected that *P. obtusus* (larger-sized species) will live longer than the smaller-sized species (*P. cultellatus* and *P. curvatus)*, with and without sugar feeding.

Materials and methods

Parasitoids

The three phorid fly species tested (*P. cultellatus*, *P. curvatus* and *P. obtusus*) were reared on workers of red imported fire ants, *S. invicta*, at the fire ant rearing facility of the USDA-APHIS-PPQ-CPHST Laboratory/Florida DPI, Gainesville, Florida, U.S.A., as described by Porter *et al.* (1995). Because larvae of *Pseudacteon* spp. have the habit of decapitating fire ant workers and pupating inside the empty head capsule (Porter *et al.*, 1995), heads of parasitized fire ant workers were received in batches and maintained in a plastic jar with a lid (diameter 25 cm, height 13 cm) under a LD 14 : 10 h photocycle at 26 ± 1 °C and 65 ± 5% relative humidity until emergence. The jar was checked at least five times daily for fly emergence. Emerging flies were not given access to food or water in the jar and were removed with an aspirator five times daily. The sex was determined by the presence or absence, and shape of the distinct female ovipositor upon examination under a stereomicroscope.

Species categorization based on body size

Using the average thorax width of females as a measure of body size, Porter & Calcaterra (2013) categorized the three *Pseudacteon* species tested as medium-large species (i.e. *P. obtusus*, with an average female thorax width of 0.53 mm) and small species (i.e. *P. curvatus* and *P. cultellatus*, both with an average female thorax width of 0.33 mm). These measurements were confirmed, and the same categorization was used in the present study.

Effect of sugar feeding on parasitoid lifespan

The effect of sugar feeding on longevity of the three phorid fly species (both sexes) was determined as described by Chen *et al.* (2005). Based on previous studies showing sucrose to be very beneficial to *P. tricuspis* (Chen *et al.*, 2005; Fadamiro *et al.*, 2005; Chen & Fadamiro, 2006) and the reported variation in the ability of parasitoids to utilize different sugar concentrations (Wäckers, 1999, 2001; Beach *et al.*, 2003; Makatiani *et al.*, 2014), sucrose was tested at two concentrations: 40% and 20% (w/v) (i.e. 1.2 and 0.6 mol L^{-1}, respectively). Thus, the longevity of each of the three species was compared under four diet treatments: (i) water only (i.e. sugar-starved control); (ii) 20% (w/v) sucrose solution provided continuously from emergence throughout life (i.e. 20% sucrose); (iii) 40% (w/v) sucrose solution provided continuously from emergence throughout life (i.e. 40% sucrose); and (iv) 40% (w/v) sucrose solution provided only during the first day (24 h) of emergence and starved thereafter until death (i.e. 40% sucrose for 24 h).

Adult females and males of *P. cultellatus*, *P. curvatus* and *P. obtusus* emerging on the same day from the same batch of decapitated imported fire ant heads were distributed evenly across the four diet treatments. Flies were fed *ad libitum* for 24 h during the day of feeding. 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. Each fly was tested individually in a plastic Petri dish (diameter 6 cm). For the treatments involving sugar feeding, the sucrose solution was applied to the underside of each Petri dish cover with a cotton-tipped applicator. Flies that were fed only during the first day of emergence and then starved until death (i.e. 40% sucrose for 24 h) were transferred to new dishes without sucrose (but with water tubes) after exposure in sucrose-smeared dishes for 24 h. Petri dishes were checked once daily for dead flies.

The longevity (in days) of each fly was recorded. Thirty-five flies per sex per species were tested for each treatment. All experiments were conducted under a LD 14 : 10 h photocycle at 28 ± 1 °C and 65 ± 5% relative humidity. This temperature was selected because it is within the temperature range at which the flies are most active in the field (Graham *et al.*, 2003). For each sex and species, data were subjected to analysis of variance followed by a Tukey–Kramer honestly significant difference comparison test using SIGMAPLOT, version 13.0 (Systat Software Inc., Chicago, Illinois) to establish significant differences among the diet treatments. $P < 0.05$ was considered statistically significant.

Results

Pseudacteon cultellatus

Survivorship curves for both sexes of *P. cultellatus* are shown in Figs 1(A) and 2(A), whereas Tables 1 and 2 show the average longevity of females and males, respectively, under different diet treatments. Females with access to 40% sucrose continuously throughout their lifespan had significantly greater longevity than either females provided 20% sucrose continuously throughout their lifespan, females provided 40% sucrose for only 24 h or females provided with water only ($F_{3,136} = 12.1$; $P < 0.0001$) (Table 1). Similar results were obtained for male *P. cultellatus*. Males with access to 40% sucrose throughout their lifespan lived significantly longer than males in the other three treatments ($F_{3,136} = 25.71$; $P < 0.0001$) (Table 2). Feeding on 40% sucrose increased average longevity by 1 day for females and by approximately 2 days for males compared with individuals provided with only water. The effect of sex was not significant: males and females under each diet treatment had similar lifespans.

Pseudacteon curvatus

Survivorship curves for both sexes of *P. curvatus* are shown in Figs 1(B) and 2(B). Females provided 40% sucrose continuously throughout their lifespan, 20% sucrose continuously throughout their lifespan and 40% sucrose for 24 h all had significantly greater longevity than females provided water only ($F_{3,136} = 7.9$; $P < 0.0001$) (Table 1). Males that had access to 20% sucrose continuously during their lifespan had significantly

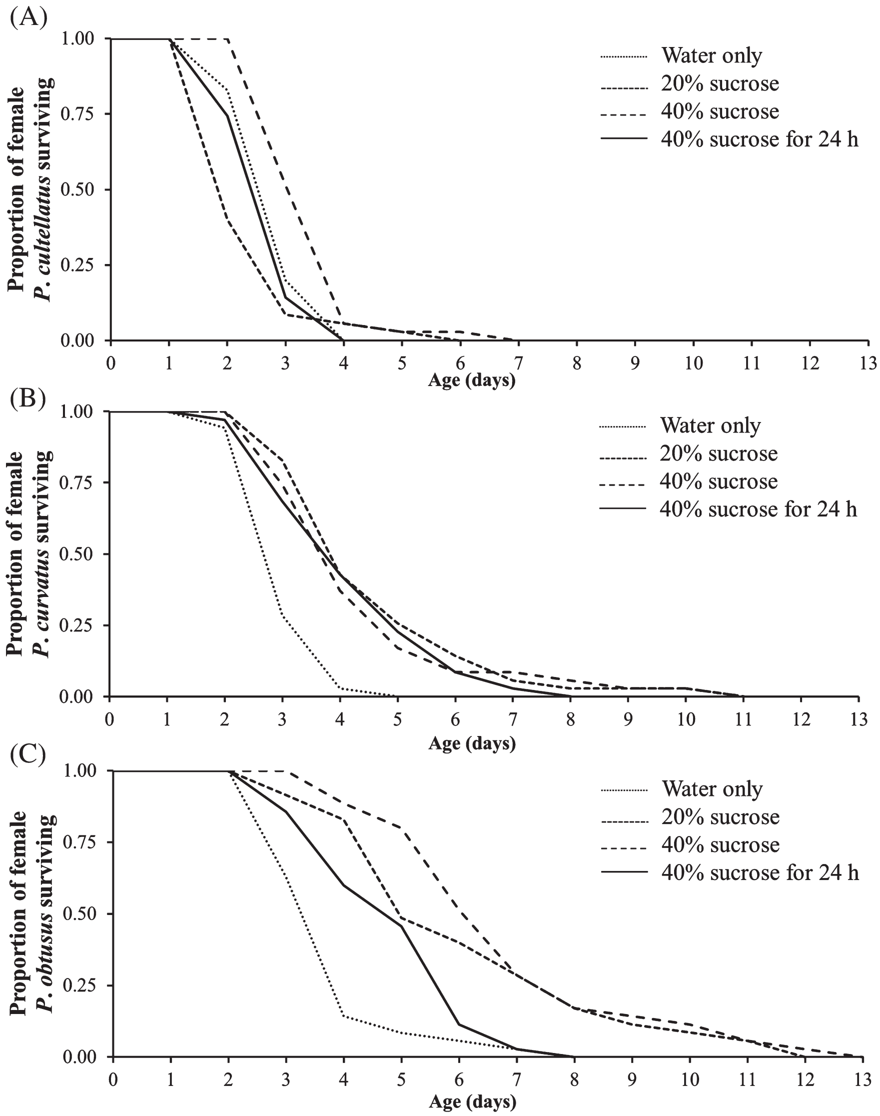

Fig. 1. Survivorship curves for females of (A) *Pseudacteon cultellatus*, (B) *Pseudacteon curvatus* and (C) *Pseudacteon obtusus* provided different diet treatments.

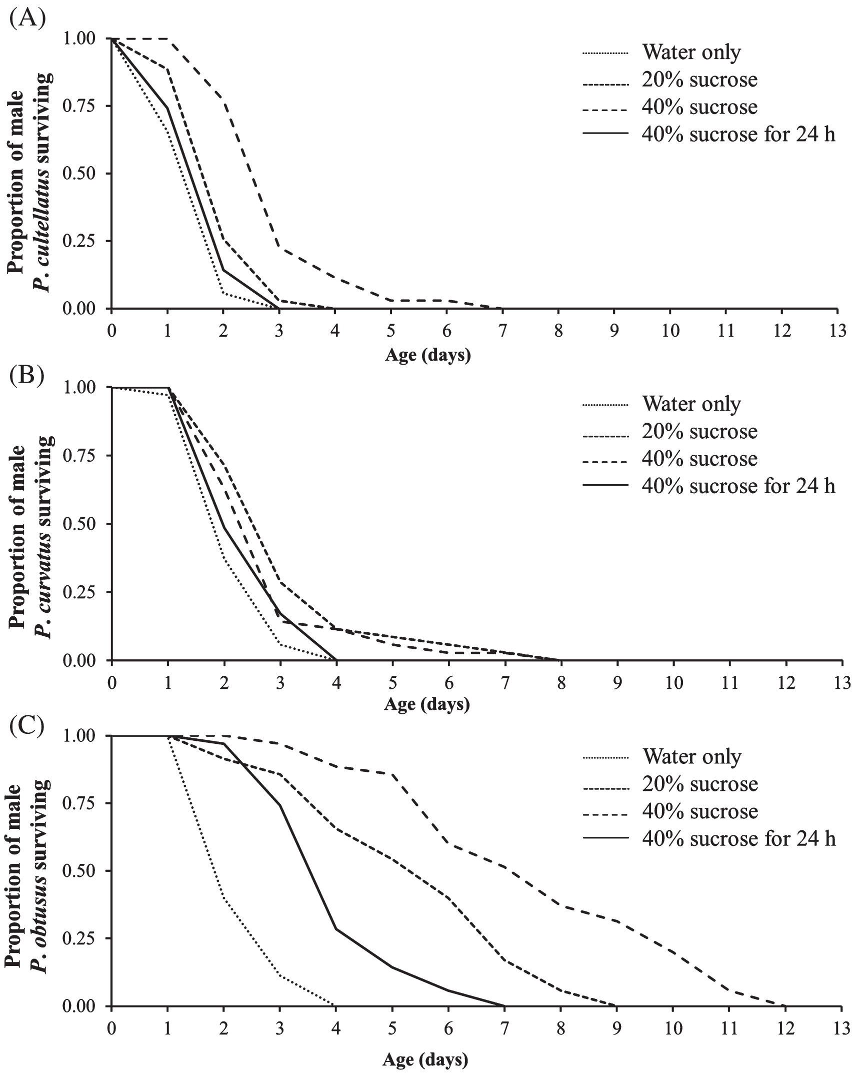

Fig. 2. Survivorship curves for males of (A) *Pseudacteon cultellatus*, (B) *Pseudacteon curvatus* and (C) *Pseudacteon obtusus* provided different diet treatments.

Table 1. Mean ± SE longevity (days) of females of three *Pseudacteon* spp. provided different diet treatments.

	Females			
Species	Water only	20% sucrose	40% sucrose	40% sucrose for 24 h
Pseudacteon cultellatus	2.6 ± 0.15 c(c)	3.0 ± 0.10 c(b)	3.6 ± 0.14 b(a)	2.8 ± 0.11 b(bc)
Pseudacteon curvatus	3.3 ± 0.10 b(b)	4.8 ± 0.28 b(a)	4.6 ± 0.29 b(a)	4.4 ± 0.24 a(a)
Pseudacteon obtusus	3.9 ± 0.19 a(d)	6.3 ± 0.41 a(b)	7.3 ± 0.40 a(a)	5.1 ± 0.23 a(c)

Means within the same column with different lowercase letters are significantly different [$P < 0.05$, Tukey–Kramer honestly significant difference (HSD) test]. Similarly, means across the same row with different lowercase letters indicated in parentheses are significantly different ($P < 0.05$, Tukey–Kramer HSD test). $n = 35$ per species per treatment.

greater longevity than males provided water only ($F_{3,136} = 4.5$; $P = 0.0045$) (Table 2). Access to 20% sucrose increased average longevity by approximately 2 days for both females and males compared with individuals provided water only. The effect of sex was not significant because males and females under each diet treatment had similar longevity.

Pseudacteon obtusus

Survivorship curves for both sexes of *P. obtusus* are shown in Figs 1(C) and 2(C). Females provided 40% sucrose continuously throughout their lifespan had significantly greater longevity than either females provided 20% sucrose continuously throughout

Table 2. Mean ± SE longevity (days) of males of three *Pseudacteon* spp. provided different diet treatments.

	Males			
Species	Water only	20% sucrose	40% sucrose	40% sucrose for 24 h
Pseudacteon cultellatus	2.7 ± 0.09 b(b)	3.2 ± 0.11 c(b)	4.2 ± 0.18 b(a)	2.8 ± 0.11 c(b)
Pseudacteon curvatus	3.4 ± 0.11 a(b)	4.3 ± 0.24 b(a)	4.0 ± 0.22 b(ab)	3.6 ± 0.13 b(ab)
Pseudacteon obtusus	3.5 ± 0.12 a(c)	6.6 ± 0.34 a(ab)	8.7 ± 0.42 a(a)	5.2 ± 0.19 a(b)

Means within the same column with different letters are significantly different [$P < 0.05$, Tukey–Kramer honestly significant difference (HSD) test]. Similarly, means across the same row with different lowercase letters indicated in parentheses are significantly different ($P < 0.05$, Tukey–Kramer HSD test). $n = 35$ per species per treatment.

their lifespan, females provided 40% sucrose for 24 h or females provided water only ($F_{3,136} = 20.5$; $P < 0.0001$) (Table 1). The mean longevity of females provided with 40% sucrose continuously was 61% higher than that of females provided water only (Table 1). Males that had access to 40% sucrose continuously throughout their lifespan had significantly greater longevity than males provided 40% sucrose for 24 h or males provided water only ($F_{3,136} = 57.4$; $P < 0.0001$) (Table 2). The mean longevity of males provided 40% sucrose continuously was 85% higher than that of males provided water only (Table 2). There was no difference between males fed 40% and 20% sucrose continuously. Also, there was no difference between males fed 20% sucrose continuously and 40% sucrose for 24 h. Compared with females provided water only, continuous provisioning of 40% sucrose increased longevity by 3 days for females and 5 days for males. The effect of sex was not significant because males and females under each diet treatment had similar longevity.

Species comparison and effect of body size

Water only. Female *P. obtusus* had significantly greater longevity than female *P. curvatus* and female *P. cultellatus* ($F_{2,102} = 19.7$; $P < 0.0001$) (Table 1). Male *P. obtusus* and male *P. curvatus* both had significantly greater longevity than male *P. cultellatus* ($F_{2,102} = 15.8$; $P < 0.0001$) (Table 2).

20% sucrose. Female *P. obtusus* had significantly greater longevity than female *P. curvatus* and female *P. cultellatus* ($F_{2,102} = 31.8$; $P < 0.0001$) (Table 1). The mean longevity of female *P. obtusus* was more than double that of female *P. cultellatus*. Similar results were obtained for the males. Male *P. obtusus* had significantly greater longevity than male *P. curvatus* and male *P. cultellatus* ($F_{2,102} = 50.4$; $P < 0.0001$) (Table 2). The mean longevity of male *P. obtusus* was 69% higher than that of male *P. cultellatus* (Table 2).

40% sucrose. Female *P. obtusus* had significantly greater longevity than female *P. curvatus* and female *P. cultellatus* ($F_{2,102} = 39.9$; $P < 0.0001$) (Table 1). The longevity of female *P. obtusus* was two times that of female *P. cultellatus*. Similar results were obtained for the males. Male *P. obtusus* had significantly greater longevity (74% higher) than male *P. curvatus*, and 70% more than that of male *P. cultellatus* ($F_{2,102} = 103.69$; $P < 0.0001$) (Table 2).

40% sucrose for 24 h. Average longevities of female *P. obtusus* and female *P. curvatus* were significantly greater than that of female *P. cultellatus* ($F_{2,102} = 30.9$; $P < 0.0001$) (Table 1). Mean longevity of female *P. obtusus* was 58% higher than that of female *P. cultellatus*. Male *P. obtusus* had significantly greater longevity than male *P. curvatus* and *P. cultellatus* ($F_{2,102} = 41.5$; $P < 0.0001$) (Table 2). Mean longevity of male *P. obtusus* was 60% higher than that of male *P. cultellatus*.

In general, these results suggest a relationship between body size and lifespan in *Pseudacteon* phorid flies in which the larger *P. obtusus* (with an average female thorax width of 0.53 mm; Porter & Calcaterra, 2013) live significantly longer than the smaller *P. curvatus* and *P. cultellatus* (both with average female thorax width of 0.33 mm; Porter & Calcaterra, 2013).

Discussion

As predicted, the results of the present study show that continuous feeding on 20% or 40% sucrose solution significantly increases the longevity of males and females of all three species compared with individuals provided water only. Although not the primary focus of the present study, the data also suggest a relationship between body size and lifespan in *Pseudacteon* phorid flies, with the larger *P. obtusus* living significantly longer than the smaller species, *P. curvatus* and *P. cultellatus*.

A key trait shared among the three *Pseudacteon* species investigated in the present study, as well as *P. tricuspis* studied previously (Fadamiro *et al.*, 2005), is their apparent ability to utilize sucrose with a significant increase in their lifespan, as is reported for a number of other flies in the family Phoridae (Disney, 1994) and hymenopteran parasitoids (Olson *et al.*, 2000; Fadamiro & Heimpel, 2001; Lee & Heimpel, 2008; Jamont *et al.*, 2014). Under the conditions of the present study, continuous provisioning of 20% or 40% sucrose solution increases longevity in the three species. Interestingly, most plants that can serve as potential sugar sources for phorid flies in the field in Southern U.S.A. have sucrose concentrations in the range 20–50% (van Handel *et al.*, 1972). This suggests that sucrose concentrations in the nectars of several flowering plants in the areas where *Pseudacteon* phorid flies have been released are potentially suitable to these flies. However, the main challenge with nectar is its accessibility to parasitoid flies such as *Pseudacteon* spp. (Fadamiro & Chen, 2005). Other sugar sources in the field that may also provide suitable sucrose concentrations to the *Pseudacteon* spp. include honeydew, fruits and extrafloral nectar. However, the short mouthparts of *Pseudacteon* phorid flies is likely to restrict their utilization of sugar sources in the field to relatively accessible floral nectar and exposed sources such as honeydew and extrafloral nectar (Gilbert & Jervis, 1998; Jervis, 1998; Fadamiro & Chen, 2005). Continuous feeding on sucrose solution increases the lifespan of *P. obtusus* by two-fold, as also reported for *P. tricuspis* (Fadamiro *et al.*, 2005). By contrast, the effects of sucrose feeding on the longevity of the two other tested species (*P. curvatus* and *P. cultellatus*) are marginal, although significant. The extent to which parasitoid species can utilize sucrose varies, even within members of the same genus (Wäckers, 2001; Sigsgaard *et al.*, 2013). This aspect of the results in the present study implies that the preferred sucrose concentration for each species should be used for their mass-rearing. Variation in the response of parasitoids to sugar may be attributed to the presence or absence of saliva, which breaks down disaccharides such as sucrose (Wäckers, 2001; Wäckers *et al.*, 2006; Harvey *et al.*, 2012) in the gut lumen of koinobionts, and this may also be the case in *Pseudacteon* species.

The results of the present study suggest a relationship between body size and lifespan in *Pseudacteon* species. The relatively larger *P. obtusus* live significantly longer than the two smaller species, *P. cultellatus* and *P. curvatus*, irrespective of the diet treatment. This relationship becomes even stronger when the results of the present study are combined with our previous data for *P. tricuspis* (Fadamiro *et al.*, 2005). Similar to *P. obtusus*, *P. tricuspis* is larger than both *P. curvatus* and *P. cultellatus*. Combining the data for females of these species when fed on 40% sucrose solution, *P. obtusus* (average female thorax width of 0.53 mm; female longevity = 7.3 ± 0.40 days) and *P. tricuspis* (average female thorax width of 0.51 mm; female longevity = 8.5 ± 1.3 days when fed 50% sucrose solution and 7.5 ± 1.2 days when fed 25% sucrose solution; data from Fadamiro *et al.*, 2005) have greater longevity than the two smaller species, *P. curvatus* (average female thorax width of 0.33 mm; female longevity = 4.6 ± 0.29 days) and *P. cultellatus* (average female thorax width of 0.33 mm; female longevity = 3.6 ± 0.14 days). It is known that bigger animals live longer than smaller ones (Speakman, 2005). Although studies on the rate of metabolism in *Pseudacteon* phorid flies are lacking, the results of the present study lend support to the rate of living theory, which is based on the observation that larger animals outlive smaller ones because larger animals have slower metabolic rates (Rubner, 1908). It is likely that the smaller species, *P. cultellatus* and *P. curvatus*, have higher metabolic rates than the larger species. To the best of our knowledge, this is the first report to suggest that longevity in *Pseudacteon* species may be a function of their body size, and this may have practical implications in the future selection of species as potential biocontrol agents. Further studies are needed to compare the metabolic rates of various *Pseudacteon* spp. and test whether the recorded differences in lifespan in this genus can be explained by the rate of living theory.

Egg maturation studies on *Pseudacteon formicarum* (Wasmann, 1918), *Pseudacteon wasmanni* (Zacaro & Porter, 2003) and *P. obtusus* (O. S. Ajayi & H. Y. Fadamiro, unpublished data) indicate that all three species are likely pro-ovigenic because only mature eggs are found in their ovaries at emergence. If truly pro-ovigenic, females of *Pseudacteon* spp. are unlikely to increase their fecundity through sugar feeding because they would not mature additional eggs during their lifetime. However, access to sucrose and other sugar sources could still provide some fitness benefits to the short-lived phorid flies in the form of increased longevity. This is particularly important when environmental conditions are not conducive for oviposition. For example, high wind speed and heavy rainfall could pose challenges for airborne insects foraging for hosts and oviposition sites. Thus, increased longevity as a result of sugar feeding can indirectly benefit parasitoids, even those with a pro-ovigenic life history strategy, because they can spend more time on resource foraging (Thompson & Hagen, 1999; Witting-Bissinger *et al.*, 2008). The utilization of sugars in the field might also increase the host searching intensity of parasitoids (Tena *et al.*, 2015). This highlights the importance of sugar feeding in these parasitoids which invest high amount of resources into egg-laying within a short lifespan.

The present study demonstrates that sugar feeding can increase the lifespan of the tested *Pseudacteon* species. It represents a first step in the identification of factors that can be manipulated in the field to enhance survival and performance of phorid flies as biological control agents. A previous study on the nutritional ecology of *P. tricuspis* shows that this species is able to successfully utilize aphid honeydew. It is also observed foraging on buckwheat flowers but with no confirmed increase in longevity (Fadamiro & Chen, 2005). Further studies are needed to identify the flowering plants that can serve as potential nectar sources for *Pseudacteon* species in the field because this information may be important for conservation biological control of *Solenopsis* fire ants.

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