Reproductive Biology and Search Behavior of *Amitus bennetti* (Hymenoptera: Platygasteridae), a Parasitoid of *Bemisia argentifolii* (Homoptera: Aleyrodidae)

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ABSTRACT   *Amitus bennetti* Viggiani & Evans is a recently discovered parasitoid of whiteflies in the genus *Bemisia*, including the serious pests *Bemisa tabaci* (Gennadius) and *Bemisia argentifolii* Bellows & Perring. The reproductive biology and the host searching behavior of *A. bennetti* was studied in the laboratory, using *B. argentifolii* as a host. The developmental time for *A. bennetti* from egg to adult at 27°C was 21.4 ± 0.2 d (range, 18–31 d). The primary behavioral pathway when searching for hosts was searching, grooming, host encounter, host antennation, followed by probing a host. Searching occupied 44.9% of the adults' time budget, whereas grooming represented 27.1%. There was a significantly greater preference to antennate and probe 1st and 2nd instars than older instars. Average longevity of *A. bennetti* adults exposed to hosts was 6.3 ± 0.9 d (range, 3–11 d). Oviposition occurred on days 0–6 of adult life, but was concentrated in days 0–3. The average number of progeny produced in the daily fertility study was 78.8 ± 8.1 (range, 47–122) female offspring per female; no males were produced in any experiment or colony. Life tables were constructed assuming a preimaginal survival of 100%, and yielded a net reproductive rate (R_o) of 73.1, a cohort generation time (T_c) of 21.7 d, and an intrinsic rate of increase (r_m) of 0.199, the highest ever recorded for a parasitoid of *Bemisia* spp. This parasitoid may be a suitable candidate for use in inundative release programs targeting *Bemisia* spp. whiteflies.

KEY WORDS   *Amitus bennetti*, *Bemisia argentifolii*, search behavior, biology, fertility

THE GENUS *Amitus* is primarily known from 2 species that have been used widely in biological control programs against 3 pest whiteflies. *Amitus hesperidum* Silvestri was used in conjunction with *Encarsia* spp. for biological control of the citrus blackfly, *Aleurocanthus woglumi* Ashby, in Mexico and the United States (Smith et al. 1964, Flanders 1969, Cherry et al. 1978, Cherry 1979, Dowell 1979, Dowell et al. 1981, Summy et al. 1983, Thompson 1985, Thompson et al. 1987, Debach and Rosen 1991). This parasitoid was credited as the most important natural enemy in the control of citrus blackfly in humid regions of Mexico (Smith et al. 1964, Thompson 1985). The whitefly *Aleurocanthus spiniferus* Quaintance & Baker, a pest in China and Guam, was reduced by 80–95% using *A. hesperidum* and *Encarsia smithi* (Silvestri) (Peterson 1955, Lin et al. 1975). *Amitus spiniferus* (Brèthes) was used together with *Cales noaki* Howard in California coastal areas to reduce populations of woolly whitefly, *Aleurothrixus floccosus* (Maskell), by up to 95% in citrus (Debach and Rose 1976, Miklasiewicz and Walker 1990, Debach and Rosen 1991). These 2 parasitoids are also credited with control of woolly whitefly in Italy (Longo et al. 1985), France, Spain, and North Africa (Debach and Rosen 1991).

Relatively few biological studies of *Amitus* speci have been conducted. The genus has 10 species d scribed from the Western Hemisphere (MacGo\ and Nebeker 1978, Viggiani and Evans 1992). *Amit* species are typically solitary endoparasitoids of whi fly nymphs (Gauld and Bolton 1988, Masner 199: *Amitus hesperidum* is presumed proovigenic and \ recorded to hold 200–300 ova before adult emergen (Flanders 1969). Preimaginal survival of immature *hesperidum* was estimated at 80%, and the sex ratio adults was 1:1 (Smith et al. 1964). This species pr erentially oviposited in 1st-instar *A. woglumi* (Do\ et al. 1981). Reproduction of *Amitus* spp. may be eitl thelytokous or arrhenotokous (Viggiani and Batta\ 1983, Gauld and Bolton 1988, Viggiani and Evans 19 Masner 1993). Searching and oviposition behavi lethal temperatures for pupae and adults, and long ity have been investigated for *A. hesperidum* (Che 1979, Dowell 1979, Dowell et al. 1981).

In this study we report on the biology of *Am bennetti* Viggiani & Evans, a species first collected Fred Bennett in 1990 from *Bemisia tabaci* (Gen dius) infesting *Euphorbia heterophylla* L. in Pue Rico. Initial collections included both males and males (Viggiani and Evans 1992), but the species produced by thelytoky when maintained in colon quarantine at the University of California, Rivers The current study examined search behavior, de

opmental time, daily and lifetime fertility, and longevity of A. *bennetti* when attacking *Bemisia argentifolii* Bellows & Perring.

Materials and Methods

Insect Colonies. The colony of A. *bennetti* at the University of California, Riverside was started from adults obtained from Ru Nguyen at the Division of Plant Industry in Gainesville, FL. R. Nguyen's colony was started from the initial collections in Puerto Rico in 1990. *Amitus bennetti* was reared on colonies of *B. argentifolii* maintained on cotton (*Gossypium hirsutum* L.) at 27 ± 1°C in the Insectary Facility at the University of California, Riverside. Clean cotton plants were infested with adult *B. argentifolii* by shaking whiteflies off infested cotton plants taken from a *B. argentifolii* colony at University of California, Riverside. Leaves on the cotton plants were examined to ensure that whitefly oviposition had occurred. The adult whiteflies were removed from the experimental cotton plants after 24 h to develop a narrowly aged cohort of nymphal instars for subsequent oviposition by the parasitoid.

Amitus bennetti adults were allowed to oviposit on nymphal instars of *B. argentifolii* in the Insectary Facility at 27 ± 1°C. The colony reproduced by thelytoky, and no males were observed. Newly emerged A. *bennetti* adults were obtained by removing A. *bennetti* pupae from cotton leaves with a fine camel's-hair brush. Individual pupae were placed separately in 1-ml glass vials and a minute portion of honey was streaked on the inside wall of the glass vial. The vial was closed with a small piece of nonabsorbent cotton lint and placed in a humidity chamber at 24°C and 75% RH. The vials were checked daily for newly emerged females of A. *bennetti*. Newly emerged females were occasionally dissected and the ovaries examined to determine the shape and developmental stage of parasitoid ova.

Search Behavior. Cotton leaves with approximately equal proportions of 1st, 2nd, 3rd, and 4th nymphal instars of *B. argentifolii* were created by infesting cotton plants in the manner described above for colony maintenance. Cotton plants were reinfested in this manner every 4 d for a total of 5 infestations over a 16-d period. Both 1st- and 2nd-instar nymphs of *B. argentifolii* develop in ≈4 d at 27°C on a variety of host plants, including cotton (Yee and Toscano 1996).

A cotton leaf thus infested with nymphal instars of *B. argentifolii* was placed abaxial side up in the bottom half of a glass petri dish. A strip of cotton lint 1 cm in diameter moistened with water was stretched around the edge of the cotton leaf. The open petri dish was placed under a Zeiss dissecting microscope. One ocular was removed from the microscope and replaced with a video camera (Javelin JE33620). A newly emerged (0–24 h), adult female A. *bennetti* was placed into the petri dish arena for observation. Six females were filmed separately for a minimum of 30 min each. Behaviors were recorded on a video recorder and were visible during recording on a video monitor.

Time was recorded directly onto the video tape. Each tape was reviewed and sequential behaviors exhibited by each female were noted and their individual durations were recorded.

Data on the durations of behaviors and behavioral sequences were combined from all females, and the frequency and the proportion of the total number of events was calculated for each behavior. Mean durations for each behavior and the frequencies of behavioral sequences were also calculated. Tests for significant differences among the mean durations of behaviors were conducted by analysis of variance (ANOVA) using SAS (SAS Institute 1988), and tests for significant differences among frequencies of behaviors were conducted using chi-squared tests.

Developmental Time. Experiments were conducted in the Insectary Facility at the University of California, Riverside, Department of Entomology at 27 ± 1°C and 50% RH, with a photoperiod of 14:10 (L:D) h. Temperature and humidity were recorded hourly with an Omnidata Digital Recorder (model DP214).

Eleven newly emerged female A. *bennetti* were placed onto the leaves of 2 caged cotton plants with abundant 1st and 2nd nymphal instars. The adult parasitoids were removed after 24 h. Whitefly nymphs were then monitored daily for darkening, which indicated parasitoid pupation. Parasitoid adults that emerged were counted daily and the number of days for development from egg to adult was recorded. These data were used to calculate mean, standard error, and range of developmental time.

Daily and Lifetime Fertility and Longevity. Cotton plants were infested with 1st- and 2nd-instar whitefly nymphs in the manner previously described. Newly emerged female A. *bennetti* were caged individually on cotton leaves for both daily and lifetime fertility studies. Leaf cages were constructed from self-sealing plastic bags (17.5 by 20 cm). A square (10 by 10 cm) was cut from one side of the bag and this opening was covered with Tekron polyester material (105-μ mesh) attached to the bag with 2-sided tape to prevent parasitoid escape. This material also allowed for leaf transpiration without water condensation inside the plastic cage. A circle constructed from a 1-mm thick strip of mylar (2 cm wide by 36 cm long) was taped inside the center of the plastic bag cage to prevent the bag from collapsing and contacting the leaf. The cage was placed around the leaf with the ventilated side over the top surface of the leaf. A piece of cotton lint (1 by 1 cm) was wrapped around the leaf petiole where the cage closed around the leaf to prevent the parasitoid from escaping. Paper clips were used to secure the plastic bag tightly around the leaf petiole. Plastic bag cages were heated at 80°C for 8 h before use to remove any vapors associated with the plastic materials.

Parasitoids in the daily fertility and longevity experiments were moved to a new host-infested leaf every 24 h. Each leaf contained at least 200 1st and 2nd instars. Cages were moved to new leaves on the same plant until 1st and 2nd instars were no longer available on that plant. The parasitoid and cage were then
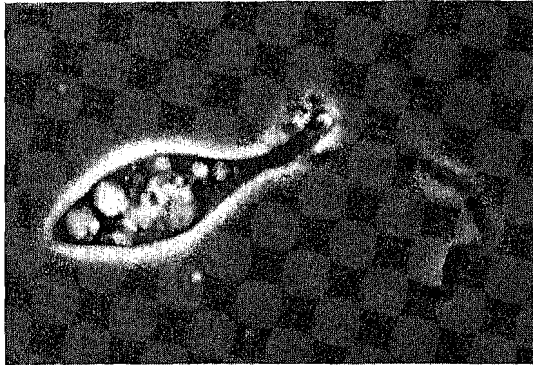
Fig. 1. Ovum of A. bennetti dissected from the parasitoid.

Fig. 2. The frequency of behavioral sequences of A. bennetti (n = 6 adults). S, searching; E, host encounter; A, antennation; P, probing; G, grooming. The number above each arrow indicates the frequency of the event after the prior behavior. Thickness of the arrows indicate relative frequency of behavioral pathways.

moved to a leaf on a new plant. This process was repeated daily until the parasitoid died, at which time the cage was removed from the leaf. This procedure was repeated for 9 female parasitoids.

The lifetime fertility and longevity experiment was performed in a similar manner; however, the plastic bag cage with the parasitoid remained on 1 leaf that initially had 1st and 2nd instars for the entire life of the parasitoid. Nine females were also used for the lifetime fertility and longevity experiment.

Leaves from both the daily and lifetime experiments were monitored daily for the presence of parasitoid pupae. At the 1st sign of A. bennetti pupae, the leaves were recaged with plastic bag cages. The leaf remained caged until the adult parasitoids had completed emerging. The numbers of emerged adults were counted, and the mean, standard error, and range of daily and lifetime fertility and longevity were calculated. Daily fertility data were used to construct life tables for A. bennetti and to calculate (Southwood 1978) net reproductive rate (R_o), intrinsic rate of increase (r_m), and cohort generation time (T_c).

Results

Parasitoid Ova. The eggs were observed and photographed after dissection of newly emerged females (Fig. 1). The eggs were narrowly ovoid in shape, with an elongate pedicel. The majority of the eggs in newly emerged females were in a similar stage of development and appeared mature.

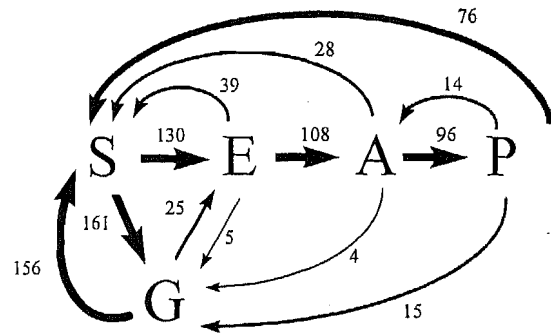Search Behavior. The behaviors exhibited by A. bennetti included searching, grooming, host encoun-

ter, host antennation, probing the host with the ovipositor, and feeding. A searching female walked rapidly while drumming her antennae against the leaf surface. Grooming females typically used their fore-tarsi to remove wax and honeydew from their bodies A host encounter was recorded when any portion o: a parasitoid's body contacted a whitefly nymphal in star. Females that spent >1 s evaluating a host b) tapping their antennae on or around the host wer< recorded as antennating the host. Probing was char acterized by a female positioning herself perpendic ular to the margin of the host and contacting the hos with the basal portion of her abdomen. The oviposito was occasionally observed on video recordings durin the act of probing. Feeding upon leaf nectaries an surface water also was observed occasionally, but nc analyzed as part of this study. On 1 occasion a par< sitoid appeared to be feeding upon the surface of nymphal whitefly. This host feeding was not precede by a probe of that nymph, and the adult may have bee feeding on water or honeydew on the nymph.

Behavioral Pathway. In total, 879 individual beha' ioral events were recorded from 6 females (Table 1 Behavioral frequencies were used to create an eth(gram showing the relationships among behaviors f< adult female A. bennetti (Fig. 2). Each behavior w: followed by one or more subsequent behaviors.

Female A. bennetti began searching when placed c a cotton leaf with hosts. Searching was the 1st step the behavioral pathway. Searching was the most fr

Table 1. Frequencies of behavioral events and duration of each behavior for data from all female A. bennetti (n = 6) and all inst of B. argentifolii combined

Behavior	Frequency	% of total	Duration, s mean ± SE	Total time spent in behavior, s	% of total ti
Search	300	34.1	18.3 ± 1.1	5,515	44.9
Groom	186	21.2	17.1 ± 2.0	3,328	27.1
Encounter	158	18.0	2.0 ± 0.4	310	2.5
Antennate	128	14.6	5.6 ± 0.5	710	5.8
Probe	107	12.2	22.6 ± 1.9	2,420	19.7
Total	879	100.0	—	12,283	—

Table 2. Total number of encounters, number of encounters that led to antennation, and antennations that led to probing for the parasitoid *A. bennetti* searching for instars of *B. argentifolii*

Instar	Total no. encounters	No. antennations preceded by encounters (%)	No. probes preceded by antennations (%)
First	96	75 (78.1)a	75 (100.0)a
Second	16	12 (75.0)a	11 (91.7)b
Third	19	4 (21.1)b	2 (50.0)c
Fourth	28	17 (60.7)a	8 (47.1)c

Numbers in columns followed by the same letter were not significantly different (chi-squared test, $P = 0.05$) (see text for details).
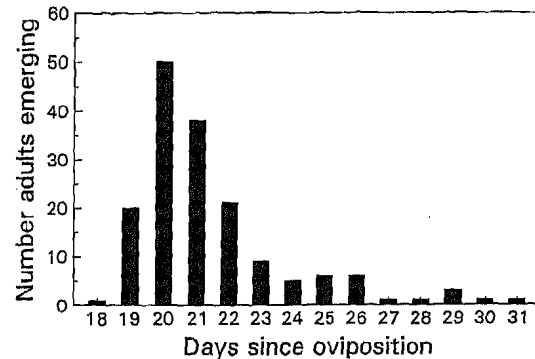

Fig. 3. Preimaginal developmental time for *A. bennetti* at 27°C. The number of adult *A. bennetti* that emerged on each day after oviposition is shown ($n = 163$, mean time from oviposition to adult emergence was 21.4 ± 0.2 d).

quent activity and occupied the largest portion of time (44.9%, Table 1). Searching was followed primarily by grooming (161 times, 55.3% of the time) or by host encounters (130 times, 44.7% of the time) (Fig. 2). Grooming was followed by 1 of 2 events, searching in 86.2% of cases and by a host encounter in 13.8% of cases. The most common behavioral pathway was searching followed by grooming, and then searching followed sequentially by encounters, antennations, and probes.

Once a female *A. bennetti* encountered a whitefly nymph, she exhibited 1 of 3 behaviors (Fig. 2). She antennated the nymph 70.6% of the time. Her 2nd most frequent behavior after an encounter was to search again away from the nymph (25.5%), which led back to the beginning of the behavioral pathway. Grooming followed 3.3% of encounters.

Antennations led to probing 75.0% of the time, a return to searching 21.9% of the time, and to grooming 3.1% of the time. The final step in the principal pathway was probing a nymphal instar. Searching, grooming, and antennations all followed probing, and represented 72.4, 14.3, and 13.3% of the subsequent behaviors, respectively (Fig. 2).

Frequency and Duration of Behaviors. Searching for hosts occupied nearly 1 half the total time observed (44.9%) (Table 1). Grooming accounted for 27.1% of the total time, and probing 19.7% of the time. Host antennations represented 5.8%, and encounters 2.5% of the total time.

The mean duration differed among behaviors (Table 1). An average of 18.3 s was spent in each search, and 17.1 s during each grooming behavior. Encounters lasted an average of 2.0 s. Antennations lasted an average of 5.6 s. There was no significant difference in duration of antennations which led to probing of a whitefly instar and antennations which led to other, nonprobing behaviors. Mean duration was longest for probing (22.6 s). The mean duration of probing before antennation of the same host again (11.4 s) was significantly shorter than the mean duration of probing followed immediately by further searching (25.6 s) ($F = 3.29$; df $= 1, 102$; $P = 0.041$).

Host Stage Preference. The frequency of host encounters that resulted in antennation and then probing was of particular interest to determine if there was a significant behavioral preference to probe a particular instar (Table 2). A chi-squared analysis of the

proportion of encounters leading to antennation showed the observed values to differ significantly from the expected values among the 4 nymphal stages ($\chi^2 = 24.78$, df $= 3$, $P < 0.05$). Third instars in particular were antennated much less frequently than expected. Analysis of the frequency of antennation of the 1st, 2nd and 4th instars indicated no difference among these stages ($\chi^2 = 3.44$, df $= 2$, $P > 0.05$). Thus, in the principal behavioral pathway, the parasitoids antennated 3rd instars less frequently per encounter than the other stages.

Analyses of frequencies of antennations that led to probing (Table 2) for all 4 instars found the observed values were significantly different from the expected values ($\chi^2 = 45.71$, df $= 3$, $P < 0.05$). Fourth instars were probed least often per nymph antennated. A comparison of the 1st, 2nd, and 3rd instars showed significant differences among these stages ($\chi^2 = 30.88$, df $= 2$, $P < 0.05$); 3rd instars were probed less frequently than expected. Similarly, a comparison between 1st and 2nd instars showed significant differences ($\chi^2 = 6.32$, df $= 1$, $P < 0.05$). Proportions of 3rd and 4th instars probed after antennation were not significantly different ($\chi^2 = 0.01$, df $= 1$, $P > 0.05$) (Table 2). Overall, the proportions of antennations that led to probing were significantly higher for 1st and 2nd instar nymphs that for 3rd and 4th instar nymphs (Table 2).

Developmental Time. The 1st adult *A. bennetti* emerged 18 d after oviposition, and parasitoids continued to emerge over a 2-wk period (Fig. 3). The mean developmental period from egg to adult was 21.4 ± 0.2 d. The range of developmental time was 18–31 d ($n = 163$); the median and modal times were 21 d and 20 d, respectively (Fig. 3).

Daily and Lifetime Fertility and Longevity. The average number of progeny for female *A. bennetti* in the daily fertility study was 78.8 (Table 3). Progeny emerged from hosts that females encountered on days 0–6 (Fig. 4). The average number of progeny was highest on the 1st d of adult parasitoid life (42.3), and declined as the adults aged (Fig. 4). Females in the

Table 3. Longevity and progeny production in both the daily fertility and lifetime fertility experiments for *A. bennetti*

Experiment	n	Adult longevity, d mean ± SE (range)	Total no. progeny mean ± SE (range)
Daily fertility	9	6.3 ± 0.9 (3–11)	78.8 ± 8.1 (47–122)
Lifetime fertility	9	6.3 ± 0.4 (4–8)	56.1 ± 8.8 (15–110)

daily fertility study lived an average of 6.3 d (Table 3; Fig. 5a). There was 100% survival of adults on the first 2 d. One adult died on day 3, 4 died on day 5, 2 died on day 6, and the final 2 died on the 11th d of adult life. There appeared to be an increase in overall fertility with an increase in longevity for *A. bennetti*. A regression of fertility on longevity was significant ($P = 0.032$, Fig. 5b).

In the lifetime fertility experiment where parasitoids were confined to a single leaf, females produced an average of 56.1 adult progeny (Table 3). The average longevity of the females in the lifetime fertility study was 6.3 d (Fig. 5c). One individual died on day 4. Mortality was highest on day 6 when 5 individuals died. One individual died on day 7, and the last adult died on day 8 (Fig. 5c). Fertility was positively correlated with longevity in this experiment as well (Fig. 5d); the relationship was marginally significant ($P = 0.09$).

Life tables using preimaginal survival rates of 60, 80, and 100% were constructed for *A. bennetti* with data from the daily fertility study. Generation time for each case was 21.7 d. Net reproductive rate varied with survival from 43.8 to 73.1 females per female, and intrinsic rate of increase varied from 0.175 to 0.199 (Table 4).

Discussion

Search Behavior. Searching (34.1%) and grooming (21.2%) were the most frequent behaviors observed for *A. bennetti* (Table 1). Parasitoids were observed to accumulate whitefly waxes and honeydew while
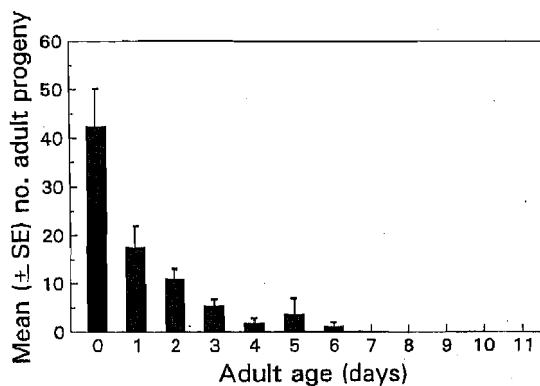

Fig. 4. Average number of adult progeny produced each day for *A. bennetti* ($n = 9$) in the daily fertility experiment. No adult progeny were reared from days 7–11 from the 2 females that lived 11 d.

searching. These accumulations may interfere with perception of olfactory cues or chemoreception involved in host location or evaluation (van Lenteren et al. 1980, Viggiani 1984, Sankaran 1992). Grooming removed these materials.

Feeding from substrates (water, honeydew, nectaries) was observed during this study. Feeding on these materials may be an important source of water or carbohydrates to the adult parasitoid. We did not observe probing of a host followed by feeding on the host hemolymph in this parasitoid. Host feeding has been suggested as necessary in synovigenic species to obtain nourishment for the development of ova (Flanders 1953). Adult female *A. bennetti* appear to be principally proovigenic and may not require host feeding to obtain nutrition for egg production (Flanders 1969).

Behavioral Pathway. The behavioral pathway in Fig 2 shows that *A. bennetti* had several interconnecting behavioral cycles. One such cycle consisted of searching, grooming, and searching again. Searching was followed by grooming 55.3% of the time, and grooming was followed by searching in 86.2% of cases (Fig. 2) This cycle is similar to that observed for the aphelinid parasitoid *Eretmocerus eremicus* Rose & Zolnerowic on *B. argentifolii* (Headrick et al. 1995). Grooming was the 2nd most frequent event for *E. eremicus* after searching (18.0%), after which the parasitoid returned to searching.

Searching by *A. bennetti* led to host encounters i 44.7% of cases (Fig. 2). Once a host was encountered it was antennated in 70.6% of cases. This contrasts with the behavior of *E. eremicus*, where only 34% of encounters led to antennation (Headrick et al. 1995 and for *Encarsia formosa* Gahan where 99% of encounters led to antennation (van Lenteren et al. 1980 The majority of nymphs encountered by *A. benne* appeared to be suitable to antennate to evaluate for oviposition. Host antennation by *A. bennetti* result in probing 75.0% of the time. This was much high than the 33% of antennations that led to probes for *eremicus* (Headrick et al. 1995). The higher frequen of encounters leading to antennations and antenn tions leading to probes for *A. bennetti* may be adaptation to the proovigenic nature of the parasite and its relatively short lifespan compared with up elinid parasitoids.

Probing Preference. The analysis of the proportion encounters that led to antennation for *A. benne* found that 3rd instars were antennated significan less frequently than 1st, 2nd, and 4th instars (Table There is a clear behavioral avoidance of antennati of the 3rd instar. Large size is not likely to be t deterrent from antennating this instar, because instars did not have a significantly lower proportion encounters leading to antennations (Table 2). T analysis of the frequency of antennations that led probes showed there were significantly fewer 2 3rd, and 4th instars probed than 1st instars, and t 2nd instar nymphs were preferred significantly o 3rd- and 4th-instar nymphs. The combination of frequent antennation of 3rd-instar nymphs and sig
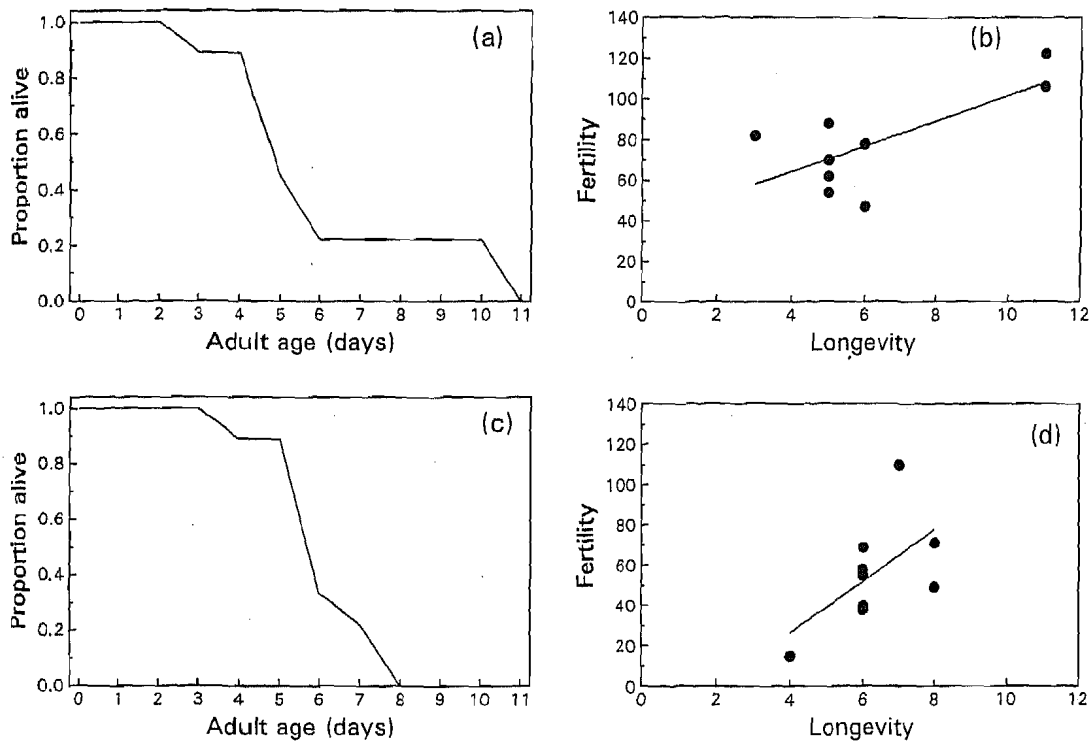
Fig. 5. (a) Proportion of *A. bennetti* adults alive during each day of the daily fertility study ($n = 9$). (b) Lifetime fertility was significantly related to longevity for *A. bennetti* ($n = 9$) in the daily fertility study ($r^2 = 0.501$; $F = 7.184$; $P = 0.03$; $y = 39.59 + 6.19x$ [SE $= 2.31$]). (c) Proportion of *A. bennetti* adults alive on each day the lifetime fertility study ($n = 9$). (d) Relationship between total adult progeny and longevity for each female *A. bennetti* ($n = 9$) in the lifetime fertility study ($r^2 = 0.341$; $F = 3.61$; $P = 0.09$; $y = -23.94 + 12.64x$ [SE $= 6.64$]).

icantly smaller proportion of probes in 2nd, 3rd, and 4th instars demonstrates there was a significant behavioral preference to probe 1st nymphal instars, and to a lesser degree 2nd instars, of *B. argentifolii* over 3rd and 4th instars. This result is similar to observations that *A. hesperidum* females prefer to oviposit in 1st instar nymphs (Dowell et al. 1981).

Duration of Behaviors. The mean duration of probing before antennation of the same host again (11.4 s) was significantly shorter than the mean duration of probing before leaving the host and searching for another host (25.6 s). The longer time spent probing by *A. bennetti* before searching suggests the female was ovipositing (van Lenteren et al. 1980). This suggests that the mean time for probes resulting in an egg being laid for *A. bennetti* was 25.6 s. The mean time of

Table 4. Life table values for *A. bennetti* ($n = 9$) parasitizing *B. argentifolii* assuming preimaginal survival of *A. bennetti* of 0.6, 0.8, and 1.0

Preimaginal survival	R_o	T_c	r_m
0.60	43.8	21.7	0.175
0.80	58.5	21.7	0.188
1.00	73.1	21.7	0.199

R_o, net reproductive rate; T_c, generation time; r_m, intrinsic rate of increase.

egg deposition for *Amitus hesperidum* in its whitefly host *A. woglumi* was recorded as 15 s by Flanders (1969) and 28 s by Dowell et al. (1981).

Developmental Time. *Amitis bennetti* took an average of 21.4 d to develop at 27°C and emergence occurred from 18 to 31 d after oviposition. Aphelinid whitefly parasitoids in the genera *Encarsia* and *Eretmocerus*, which generally oviposit in later nymphal instars than *A. bennetti*, require less time for development from egg to adult. *Encarsia luteola* Howard takes 11–14 d at 25°C for preimaginal development (Gerling et al. 1987). An *Eretmocerus* species took an average of 16.4, 16.8, and 17.6 d to develop at 26°C in 1st, 2nd, and 3rd instars, respectively, of *B. argentifolii* (McAuslane and Nguyen 1996).

Daily and Lifetime Fertility and Adult Longevity. In the daily fertility study, oviposition occurred on days 0–6; although some females lived 11 d with suitable hosts present throughout their lifespan. The abundance of hosts may have led to the entire egg complement being laid before females died. The majority of *A. bennetti* progeny emerged from days 0–3 of oviposition (Fig. 4). *Encarsia pergandiella* Howard, a synovigenic species, was found to oviposit all eggs in the first 70% of life, provided hosts were available (Gerling 1966).

The mean total progeny produced in the lifetime fertility study was 56.11, which was lower than the mean total progeny in the daily fertility study (78.8). Female *A. bennetti* were confined to 1 leaf that initially had 1st- and 2nd-instar nymphs. Lower fertility in the lifetime fertility study may have been caused by the loss of suitable (young) hosts as the hosts matured to older stages, and therefore females produced fewer progeny.

Longevity of *Amitus bennetti* averaged 6.3 d in both the daily and lifetime fertility studies (Table 3). This was close to the average longevity of 6 d for female *A. hesperidum* (Flanders 1969). Dowell (1979) reported that *A. hesperidum* without food or water lived an average of 2 d, with water an average of 2.3 d, and with a 1:1 mixture of honey:water an average of 4.1 d. There was a significant correlation between fertility and longevity for *A. bennetti*, with longer-lived females producing a larger number of progeny. Aphelinid whitefly parasitoid species generally live longer that *Amitus* species. Mated females of *E. luteola* at 25°C allowed to oviposit lived an average of 17 d (Gerling et al. 1987). An *Eretmocerus* species at 26°C lived an average of 12.5 d with honey, but with access to hosts lived an average of 8.4 d (McAuslane and Nguyen 1996).

The reproductive rates calculated for this species compare favorably with other whitefly parasitoids used for biological control of pest species. Powell and Bellows (1992) reported instantaneous growth rates for 2 *Eretmocerus* sp. populations attacking *B. tabaci* ranging from 0.06 to 0.21. Arakawa (1982) reported a value of r_m of 0.2 for *E. formosa* parasitizing *Trialeurodes vaporariorum* (Westwood). Vet and van Lenteren (1981) reported values of 0.137 and 0.124 for *E. formosa* and *E. pergandiella* parasitizing *T. vaporariorum*. The values estimated here for *A. bennetti* of 0.175–0.199 are thus among the higher values reported for whitefly parasitoids. Thus, this species' reproductive biology and search behaviors may make it a suitable candidate for evaluation as an agent in inundative release programs targeting *B. tabaci* and *B. argentifolii* in agronomic systems.

Acknowledgments

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