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Reproductive biology of *Fopius arisanus* (Hymenoptera: Braconidae) on *Ceratitis capitata* and *Anastrepha* spp. (Diptera: Tephritidae)

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Abstract

The reproduction of the solitary endoparasitoid *Fopius arisanus* (Sonan) (Hymenoptera: Braconidae) in *Anastrepha ludens* (Loew), *Anastrepha obliqua* (Macquart), and *Anastrepha serpentina* (Wiedemann) was compared with that using *Ceratitis capitata* (Wiedemann), being the host in which it had been reared previously. Eggs of different ages (<4 h old, 1, 2, and 3 days old for *Anastrepha* spp., and ⩽4 h, 1 and 2 days old for *C. capitata*) of each host species were placed in pieces of papaya, exposed to parasitism for 24 h and then reared through to the adult stage. Host species had a marked effect on parasitoid reproduction with consistently higher parasitoid emergence from *C. capitata*, whereas emergence from *A. obliqua* was negligible and this host was not studied further. Host age did not significantly affect parasitoid emergence from *C. capitata* whereas parasitism of *A. ludens* and *A. serpentina* was significantly greater in eggs exposed at 3 days old than those exposed at younger ages. Adult parasitoid sex ratio was male biased in all cases. Despite significant differences in host developmental time, host species did not affect parasitoid developmental time. Parasitoid life expectancy at emergence was reduced by >60% for parasitoids that emerged from *A. ludens* compared to those that emerged from *A. serpentina* or *C. capitata*. The reproduction of parasitoid progeny was highest in parasitoids that emerged from and reproduced on *C. capitata* and lowest for parasitoids reproducing on *A. ludens*. Parasitoids that emerged from *A. ludens* were often deformed, but were larger than those that emerged from *A. serpentina*. Parasitoids that emerged from *C. capitata* were smaller than those from *Anastrepha* spp. We conclude that *F. arisanus* is capable of sustained reproduction in *C. capitata* and *A. serpentina* and merits further study as an agent for the control of these fruit flies.

Keywords: Fruit fly; *Anastrepha* spp.; *Ceratitis capitata*; *Fopius arisanus*; Endoparasitoid; Reproduction; Sex ratio; Longevity; Body size

1. Introduction

Tephritid fruit flies (Diptera: Tephritidae) attack a wide range of fruits and vegetables in most parts of the world (Aluja and Norrbom, 2000; Bateman, 1972). The genus *Anastrepha* represents the most important group of fruit flies in tropical and subtropical zones of the Americas (Hernández-Ortíz, 1996; Norrbom and Kim, 1988). In Mexico, extensive areas of citrus, mango, sapodilla, and plum are cultivated, all of which are subject to attack by *Anastrepha* spp. such as *A. ludens* (Loew), *A. obliqua* (Maquart), and *A. serpentina* (Wiedemann) (Aluja, 1993, 1994; Norrbom and Foote, 1989). The economic losses arising from fruit fly infestations have stimulated the Mexican government's Secretariat of Agriculture and Rural Development (SAGARPA) to implement extensive control programs, based to a large degree on integrated pest management strategies, in which biological control plays an important role in the reduction of pest *Anastrepha* populations (Montoya et al., 2000; Reyes et al., 2000).

As part of the National Fruit Fly Control Campaign, a facility for mass-rearing of the braconid parasitoid

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Diachasmimorpha longicaudata (Ashmead) has been established to permit inundative parasitoid release programs for *Anastrepha* control over wide areas of Mexico (Cancino, 2000). Nevertheless, the evaluation of new parasitoid species is considered to be an important aspect of the campaign in an effort to identify natural enemies that may compliment existing control measures, or contribute to the control of additional pest species of *Anastrepha* fruit flies.

Fopius (previously Biosteres) *arisanus* (Sonan) is a solitary braconid endoparasitoid originating from the Indoaustralasian region, where it is found parasitizing eggs of *Bactrocera* spp. (= *Dacus* spp.) (Clausen et al., 1965; Harris and Bautista, 1996; Nishida and Haramoto, 1953). This parasitoid develops in the egg and larval stages, and emerges from the pupa 18–20 days post-oviposition, some 2 days after the emergence of non-parasitized adult flies (Bess et al., 1961; Haramoto, 1957).

The dominance of this parasitoid observed in natural fruit fly parasitoid species complexes may be due to its ability to attack eggs and, therefore, competitively displace parasitoids that exploit later larval or pupal host stages (Bess et al., 1961; van den Bosch and Haramoto, 1953). In their revision of opiine parasitoids of *Ceratitis* and *Dacus* s.l., Wharton and Gilstrap (1983) suggested that *F. arisanus* has considerable potential as an agent for biological control of these pests, specifically because it attacks the egg stage of the host. For example, following its introduction to Hawaii, *F. arisanus* became the dominant parasitoid in coffee and guava plantations infested by the Mediterranean fruit fly, *Ceratitis capitata* (Wiedemann), and oriental fruit fly, *Bactrocera dorsalis* (Hendel), respectively (Vargas et al., 1993; Wong and Ramadan, 1987). Moreover, recent studies in Hawaii indicate that areawide integrated control of *C. capitata* may be feasible by the action of this parasitoid combined with the use of selective insecticides (e.g., spinosad or phloxine B) applied in bait formulations (Vargas et al., 2001).

Reproduction of *F. arisanus* in members of the genus *Anastrepha* has only been reported for *A. suspensa*, which is apparently a suitable host for *F. arisanus* (Lawrence et al., 2000). Given the paucity of information on *F. arisanus* reproduction in *Anastrepha* spp., and the excellent results of previous programs involving the release of this parasitoid for control of other tephritid flies, the objectives of the present study were threefold. First, we wished to compare the effect of host age on parasitism and emergence of *F. arisanus* from three economically important *Anastrepha* species and from *C. capitata*, the host used to culture the parasitoid. Second, we determined the development time and pattern of adult emergence on each host. Third, we evaluated the effect of the developmental host on the body size, longevity, and reproductive capacity of *F. arisanus* progeny; parameters of direct relevance to the performance of this parasitoid as a natural enemy of *Anastrepha* fruit fly pests.

2. Materials and methods

This study was performed in the biological control laboratory of the National Fruit Fly Control Campaign, located in Metapa de Domínguez, Chiapas, Mexico. The colony of *F. arisanus* used for experiments originated from a strain already adapted to laboratory conditions using *B. dorsalis* as a host and was obtained from the ARS-USDA laboratory in Honolulu, Hawaii (Bautista et al., 1998, 1999; Harris et al., 1991). Prior to our experiments, this strain was reared for at least 28 generations using *C. capitata* eggs placed in pieces of papaya, *Carica papaya* L., at 24 ± 2 °C, 60–80% RH, and 12:12 (L:D) h photoperiod as described previously (Bautista and Harris, 1996; Harris and Bautista, 1996). Eggs of *A. ludens*, *A. obliqua*, and *A. serpentina* were obtained from insect colonies maintained in the neighboring Moscamed and Moscafrut mass-rearing facilities (SAGARPA-IICA), following culture methods described elsewhere (Domínguez et al., 2000; Schwarz et al., 1985).

2.1. Experimental parasitism units

Fruit fly eggs were placed in pieces of ripe papaya var. maradol (3 cm long × 4 cm wide × 2 cm thick). Nine holes were made to a depth of 3–5 mm in the surface of each piece of fruit. Groups of approximately 450 *Anastrepha* spp. eggs or 600 *C. capitata* eggs were placed in each hole using a fine paintbrush, giving a total of approximately 4050 and 5400 eggs in each papaya piece for *Anastrepha* spp. and *C. capitata*, respectively. Artificially infested papaya pieces were placed in Hawaii-type cages ($30 \times 30 \times 30$ cm) (Wong and Ramadan, 1992) containing 30 pairs of 16-day-old parasitoids for a period of 24 h as described by Bautista et al. (1998).

Male *F. arisanus* reach sexual maturity 5–6 days post-emergence and require bright light to initiate mating (Hagen, 1953; Ramadan et al., 1992). Consequently, to facilitate mating, cages containing parasitoids were placed outside the laboratory for 4 h periods each morning during 5–9 days post-emergence. The temperature during this period was typically 26.8 ± 0.4 °C and 60–70% RH.

2.2. Effect of host species and age on parasitoid reproduction

For tests involving *Anastrepha* spp., four papaya pieces containing eggs that were either recently laid ($\leqslant$4 h old) or 1, 2, or 3 days of age, were placed in Hawaii cages and exposed to parasitization as described

above. For tests involving *C. capitata*, three artificially infested papaya pieces containing eggs that were newly laid ($\leqslant$4 h old) or 1 or 2 days old were placed in the cages. In this way, each cage contained 30 male and 30 female parasitoids exposed to three or four pieces of fruit infested with eggs of different ages, but of only one host species. At the end of each hour during the first 9 h of exposure, we recorded the number of parasitoids that showed apparent ovipositional behavior, defined as insertion of the ovipositor in a hole containing eggs followed by a motionless stance during >30 s. After 24 h exposure, all the eggs of each age class were gently extracted from the fruit, using a hand-held water sprayer, and placed on a cotton cloth separated by perforated plastic strips 28 × 17 cm. Eggs were moistened with a fusellerone solution (3.3 g/l fusellerone + 0.3 g/l sodium benzoate) and placed in humid containers, kept damp by wet cotton wool until ready for hatching. Eggs were then transferred to plastic trays (20 cm long × 15 cm wide × 4 cm deep) containing 300 g artificial diet (Domínguez et al., 2000). Following a larval developmental period of 7–9 days, *C. capitata* larvae were placed in wheat bran for 9 days, whereas *Anastrepha* spp. larvae were placed in vermiculite for 12 days for pupation. Pupae were then separated from the substrate and placed in ventilated plastic containers. The number of flies and parasitoids that emerged was noted. In the case of parasitoids exposed to 3-day-old *A. ludens* and *A. serpentina* eggs, and newly laid ($\leqslant$4 h old) *C. capitata* eggs, the emergence and sex of parasitoids was recorded on a daily basis. The experiment was performed seven times.

2.3. Effect of host species on parasitoid progeny

To determine the effect of host species on parasitoid body size, fecundity and longevity, groups of parasitoids (10♀♀ + 10♂♂) that emerged from the previous experiment were placed in Hawaii cages with 10% honey solution. Only those parasitoids that emerged from *Anastrepha* spp. eggs exposed at 3 days old or *C. capitata* eggs exposed when newly laid ($\leqslant$4 h old) were used. It was not possible to perform this study with parasitoids from *A. obliqua* due to a lack of material. Adult mortality was recorded daily. Each cohort was exposed to natural light to facilitate mating as described above. At 10 days post-emergence, these parasitoids were exposed to pieces of papaya containing 2000 eggs of the species from which they emerged (i.e., parasitoids that emerged from *A. ludens* were offered *A. ludens* eggs for oviposition, whereas parasitoids from *C. capitata* were offered *C. capitata* eggs, etc.). Eggs were $\leqslant$4 h or 3 days old in the case of *C. capitata* and *Anastrepha* spp., respectively. Eggs were replaced at 24 h intervals until the last female of the cohort died. Eggs that had been exposed to parasitism were removed, incubated, and reared to determine the prevalence of parasitoid emergence as described above. The progeny production per female parasitoid was thereby estimated in terms of gross fecundity ($\sum m_x$) and net fecundity ($\sum l_x m_x$) following the procedures described by Carey (1993). The experiment was performed six times. Following death, parasitoid body length from the tip of the head to the tip of the abdomen, ovipositor length, right anterior wing length and hind tibia length were measured for 30 randomly selected male–female pairs using a dissecting microscope fitted with an eyepiece graticule.

2.4. Statistical analysis

Due to marked differences in the host biology and host suitability for *F. arisanus* development, in most cases the results from *C. capitata* were analyzed separately from those from *Anastrepha* spp. For parasitoids reared on *C. capitata*, a one-way ANOVA was employed followed by Tukey test for means separation (Statistica, 1999). The number of ovipositions observed in each 9 h period and fruit fly emergence for *Anastrepha* spp. were subjected to two-way ANOVA with species and age as factors. For the other parameters, only the results from *A. ludens* and *A. serpentina* were analyzed because reproduction in *A. obliqua* was negligible. Emergence of *Anastrepha* flies was subjected to $\log_e(1+x)$ transformation prior to analysis by two-way ANCOVA with the number of emerged parasitoids as a covariable. Percentage parasitism data were subjected to range transformation (Potvin and Roff, 1993) prior to analysis whereas parasitoid and host developmental time were $\log_e(x)$ transformed prior to ANOVA. Survival and fecundity curves were elaborated following the procedures described by Carey (1993). Parasitoid body size measurements were subjected to multivariate discriminate analysis as a set of dependent variables (Everitt and Dunn, 1991).

3. Results

3.1. Effect of host species and age

Parasitoid reproduction in *C. capitata* and *Anastrepha* spp. were analyzed separately (Table 1). In *C. capitata*, host age did not significantly affect the number of apparently ovipositing parasitoids observed at hourly intervals during a 9 h period ($F_{2,18} = 1.74,\ P = 0.20$). However, host age did affect *C. capitata* adult emergence with significantly fewer flies emerging from eggs that had been exposed to parasitism at 2 days old ($F_{2,18} = 7.25,\ P = 0.004$). In contrast, parasitoid emergence from *C. capitata* eggs did not differ significantly according to host age ($F_{2,18} = 1.04,\ P = 0.38$). Percentage parasitoid emergence from *C. capitata* ranged from

Table 1
Parasitoid behavior, host emergence, and reproduction of *Fopius arisanus* in four species of fruit flies exposed as eggs of different ages

Host species	Age of eggs	Number parasitoids observed apparently ovipositing	Number of adult flies emerging	Number of parasitoids emerging			Parasitoid emergence (%)	Adult parasitoid sex ratio (propn. ♂)
				♂♂	♀♀	Total		
C. capitata	<4 h	201 a	28,998 a	294 a	229 a	523 a	4.5 a	0.56
	1 day	235 a	30,230 a	421 a	193 a	614 a	4.9 a	0.69
	2 days	147 a	16,868 b	660 a	113 a	773 a	9.0 a	0.85
A. ludens	<4 h	141 Aa	10,180 Aa	—	—	—	—	—
	1 day	129 Aa	11,150 Aa	11 Aa	4 Aa	15 Ab	0.1 Ac	0.73
	2 days	140 Aa	11,838 Aa	96 Aa	56 Aa	152 Aab	1.3 Ab	0.63
	3 days	144 Aa	7823 Aab	320 Aa	70 Aa	390 Aa	4.7 Aa	0.82
A. serpentina	<4 h	120 Aa	2819 Bb	–	–	–	–	–
	1 day	105 Aa	7722 Bab	49 Ba	21 Aa	70 Ab	0.9 Bc	0.70
	2 days	146 Aa	4089 Bb	40 Ba	33 Aa	73 Aab	1.7 Bb	0.55
	3 days	141 Aa	3050 Bb	126 Ba	93 Aa	219 Aa	6.7 Ba	0.58
A. obliqua	<4 h	144 Aa	3824 Bb	—	—	—	—	—
	1 day	179 Aa	7884 Bab	—	—	—	—	—
	2 days	198 Aa	4670 Bb	—	—	—	—	—
	3 days	100 Aa	3118 Bb	—	—	—	—	—

Results of reproduction in *Ceratitis capitata* were analyzed separately from results of reproduction in *Anastrepha* spp.

Numbers followed by the same letter are not significantly different for comparisons within columns. Capital letters refer to comparisons between *Anastrepha* species. Lower case letters refer to comparisons between host ages of the same species (ANOVA, Tukey; $P < 0.05$).

4.5% in eggs exposed at $\leqslant$4 h old to 9.0% in eggs exposed at 2 days old, but this difference was not significant ($F_{2,18} = 1.13,\ P = 0.34$). However, secondary sex ratio changed from 56% male in parasitoids that emerged from eggs exposed when $\leqslant$4 h old to 85% male in parasitoids that emerged from hosts exposed as 3-day-old eggs ($\chi^2 = 136.8,\ \mathrm{df} = 2,\ P < 0.001$).

For *Anastrepha* spp., no significant differences were detected in the number of parasitoids that were observed apparently ovipositing, according to host age ($F_{3,72} = 0.84,\ P = 0.48$), or host species ($F_{2,72} = 1.02,\ P = 0.37$). However, emergence of adult flies was affected by host species ($F_{2,72} = 42.8,\ P < 0.001$) and host age ($F_{3,72} = 13.3,\ P < 0.001$) with *A. ludens* generally showing higher prevalence of adult fly emergence than *A. obliqua* or *A. serpentina* (Table 1). Host age at exposure to parasitization did not significantly affect the number of male ($F_{2,35} = 1.82,\ P = 0.18$) or female parasitoids ($F_{2,35} = 0.007,\ P = 0.99$), but the total number of emerging parasitoids was significantly greater in eggs exposed at 3 days old than those exposed at younger ages ($F_{2,36} = 8.44$, $P < 0.001$).

The number of male parasitoids that emerged from *A. ludens* was significantly greater than those from *A. serpentina* ($F_{1,35} = 5.44,\ P < 0.03$), whereas the number of female parasitoids ($F_{1,35} = 0.03,\ P = 0.86$) or the total number of emerged parasitoids ($F_{1,36} = 0.33,\ P = 0.57$) were not significantly affected by host species (Table 1).

Percentage emergence of parasitoids was significantly higher in *A. serpentina* than in *A. ludens* ($F_{1,36} = 5.56$, $P = 0.02$) and increased significantly with host age at the moment of exposure to parasitization for both *Anastrepha* species ($F_{2,36} = 16.6,\ P < 0.001$). Parasitoid sex ratio at emergence was generally male biased in all egg age classes and for both host species, but no clear patterns were apparent (Table 1).

3.2. Developmental time and patterns of adult emergence

Emergence of adult *C. capitata* ($n = 28{,}998$) occurred between 19 and 24 days post-oviposition with a peak emergence at 21 days (Fig. 1A). *Anastrepha* spp. developed significantly more slowly than *C. capitata* with a mean ($\pm$SE) overall developmental time of 27.4 ± 0.5 days for *A. ludens* ($n = 7823$, range: 25–32 days) and 27.5 ± 0.4 days for *A. serpentina* ($n = 3050$, range 26–31 days) ($F_{2,18} = 215.5,\ P < 0.001$) (Fig. 1B and C).

Host species did not significantly affect the developmental time of male ($F_{2,18} = 3.35,\ P = 0.06$) or female parasitoids ($F_{2,18} = 2.06,\ P = 0.16$). Emergence of male and female *F. arisanus* from *C. capitata* that had been exposed as $\leqslant$4-h-old eggs occurred at 23.0 ± 0.7 days (range 21–25 days) and 24.0 ± 0.7 days (range 22–26 days) post-parasitism, respectively (Fig. 1A). Emergence of *F. arisanus* from *A. ludens* that had been exposed as 3-day-old eggs occurred at 24.5 ± 0.8 days (range 22–27 days) for males and 26.0 ± 0.6 days (range 24–28 days) post-parasitism for females ($n = 390$ total) (Fig. 1B). Emergence of *F. arisanus* from *A. serpentina* exposed as 3-day-old eggs occurred at 25.0 ± 0.6 days (range 24–26 days) for males and 26.0 ± 0.6 days (range 25–27 days) post-parasitism for females ($n = 219$ total) (Fig. 1C).

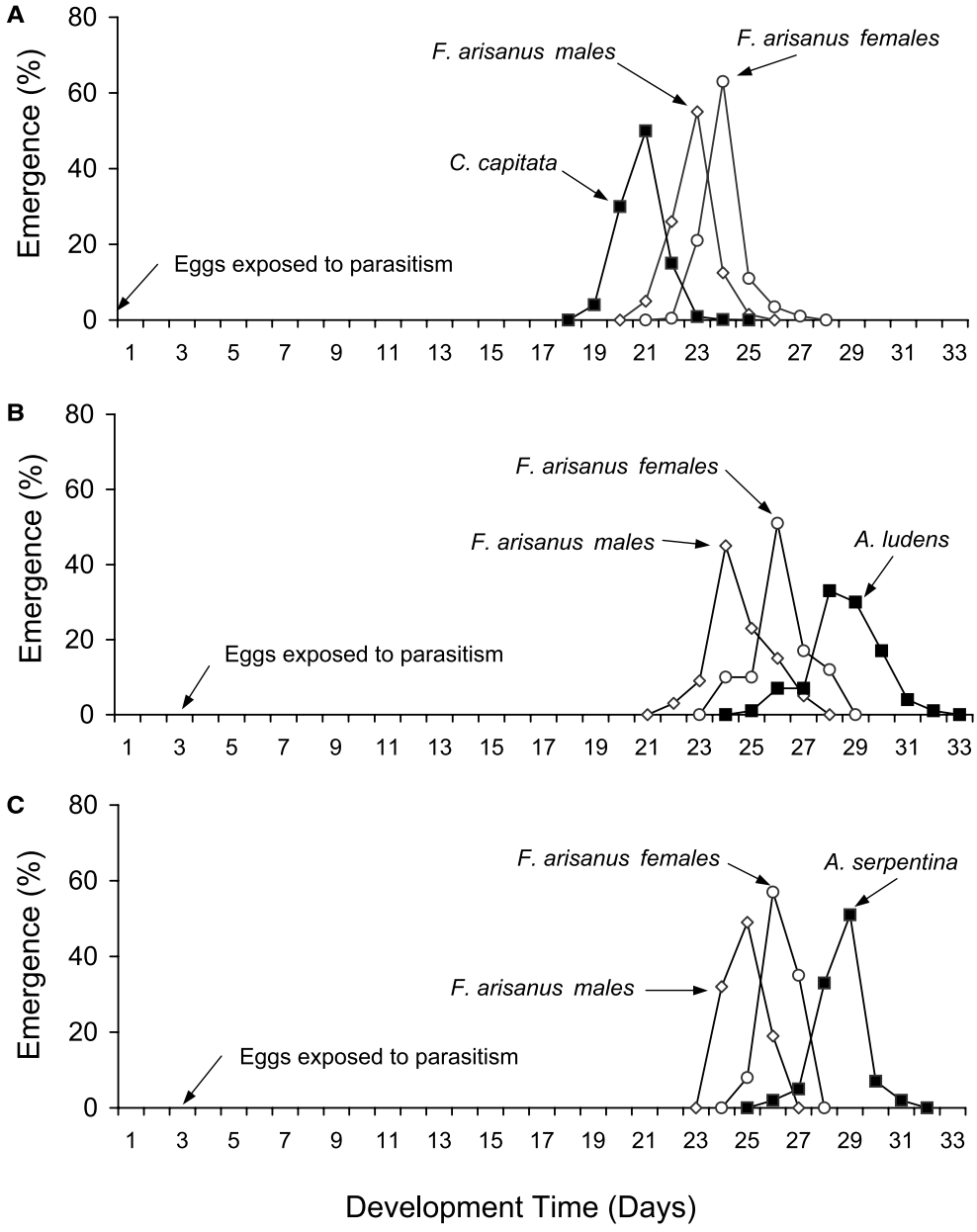

Fig. 1. Pattern of emergence of adult hosts and male and female *Fopius arisanus* from (A) *Ceratitis capitata* exposed as newly laid eggs, (B) *Anastrepha ludens* exposed as 3-day-old eggs and (C) *Anastrepha serpentina* exposed as 3-day-old eggs.

3.3. Longevity, body size, and reproduction of progeny

Life expectancy was reduced by more than 60% for parasitoids that emerged from *A. ludens* compared to those that emerged from *A. serpentina* or *C. capitata* ($F_{2,15} = 29.4$, $P < 0.001$) (Table 2, Fig. 2). This difference was reflected in the observation that mortality of parasitoids originating from different host species reached 50% at 5, 30, and 33 days post-emergence from *A. ludens*, *C. capitata*, and *A. serpentina*, respectively. A few individuals that emerged from *A. serpentina* lived up to 70 days post-emergence.

When offered eggs of the species from which they emerged, total egg production (gross fecundity, $\sum m_x$) was greater in parasitoids that emerged from *C. capitata* compared to parasitoids that had developed in *Anastrepha* spp. ($F_{2,14} = 10.6$, $P = 0.001$). Net fecundity ($\sum l_x m_x$) was also markedly affected by host species being highest in parasitoids that emerged from and reproduced on *C. capitata* and lowest in parasitoids that emerged from and reproduced on *A. ludens* ($F_{2,14} = 25.9$, $P < 0.001$), reflecting the short lifespan of parasitoids reproducing in *A. ludens* (Table 2, Fig. 3).

Table 2
Mean life expectancy at emergence, gross and net fecundity of *Fopius arisanus* that reproduced in different hosts (mean ± SE)

Host species	Life expectancy	Gross fecundity	Net fecundity
C. capitata	29.6 ± 0.1 a	157.8 ± 0.8 a	117.4 ± 0.8 a
A. ludens	9.1 ± 0.1 b	70.7 ± 1.7 b	14.5 ± 0.4 c
A. serpentina	31.0 ± 0.1 a	91.9 ± 0.6 b	58.0 ± 0.7 b

Numbers followed by the same letter are not significantly different for comparisons within columns (ANOVA, Tukey; $P < 0.05$).

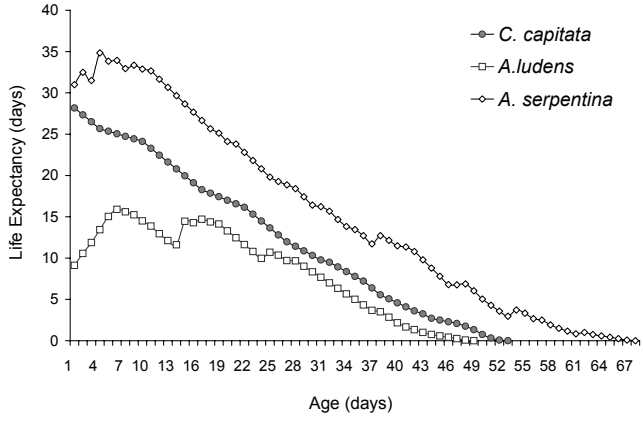

Fig. 2. Life expectancy of *Fopius arisanus* adults that emerged from *Ceratitis capitata*, *Anastrepha ludens*, or *A. serpentina*.

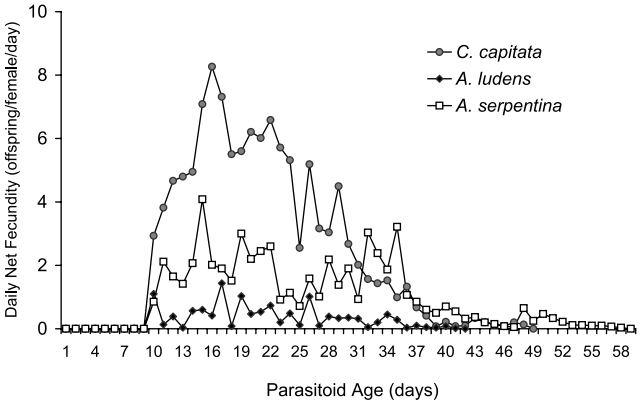

Fig. 3. Daily net fecundity ($l_x m_x$) of *Fopius arisanus* females that emerged from *Ceratitis capitata*, *Anastrepha ludens*, or *A. serpentina*. For oviposition, parasitoids were offered the same host species from which they had emerged.

Discriminate analysis applied to parasitoid body size measurements revealed significant differences among *F. arisanus* individuals that developed on different host species for both male (Wilks' $\lambda = 0.184$, $F_{6,170} = 37.6$, $P < 0.001$) and female (Wilks' $\lambda = 0.113$, $F_{8,168} = 41.3$, $P < 0.001$) parasitoids (Fig. 4A and B). For parasitoids that developed in *C. capitata* all individuals of both sexes were correctly assigned to the *C. capitata* group. There was a moderate degree of overlap in the classification of parasitoids that emerged from *Anastrepha* with 73% of females and 77% of male parasitoids correctly assigned to the *A. ludens* group compared to 87% of female and 67% of male parasitoids from *A. serpentina* correctly assigned. None of the parasitoids that emerged from *Anastrepha* were assigned to the *C. capitata* group based on body size characteristics, with the exception of one male individual that emerged from *A. serpentina*. *F* statistics calculated from the Mahalanobis squared distance generated by discriminant analysis confirmed the smaller body size of male and female parasitoids that emerged from *C. capitata* compared to those from *A. ludens* (♀♀$F_{4,84} = 71.3$, $P < 0.001$; ♂♂$F_{3,85} = 67.0$, $P < 0.001$). Similarly, parasitoids that emerged from *A. serpentina* were smaller than those that emerged from *A. ludens* (♀♀$F_{4,84} = 10.7$, $P < 0.001$; ♂♂$F_{3,85} = 6.0$, $P < 0.001$).

4. Discussion

The present study demonstrated the marked effects of host species on the development, reproduction and survival of *F. arisanus*. The number of parasitoids observed apparently ovipositing did not differ with host species or age of host, even though the size of the *Anastrepha* eggs (1.2–1.6 mm long) was considerably greater than *C. capitata* eggs of just under 1.0 mm length. Similarly, no ovipositional preferences were reported by Ramadan et al. (1992) when *F. arisanus* was offered *B. dorsalis* and *C. capitata* eggs in coffee berries.

Parasitism of newly laid *C. capitata* eggs resulted in the greatest production of female parasitoids, which is why eggs of this age and host species were routinely employed to maintain the *F. arisanus* colony. Insomuch as the number of ovipositions observed on 2-day-old *C. capitata* eggs was slightly lower than seen in younger eggs, the number of emerging parasitoids increased and became more male biased compared to parasitoids that emerged from eggs exposed at younger ages. This may be due to the quality of the older host being judged inferior by the ovipositing female parasitoid. The embrion of 2-day-old eggs was well developed and, in many cases, about to hatch. Selectively assigning male eggs to lower quality hosts and females eggs to high quality hosts may be selectively advantageous when fitness gains accrue through the production of high quality (large) female progeny to a greater degree than through the production of large male offspring (Godfray, 1994). Moreover, the puncture wound

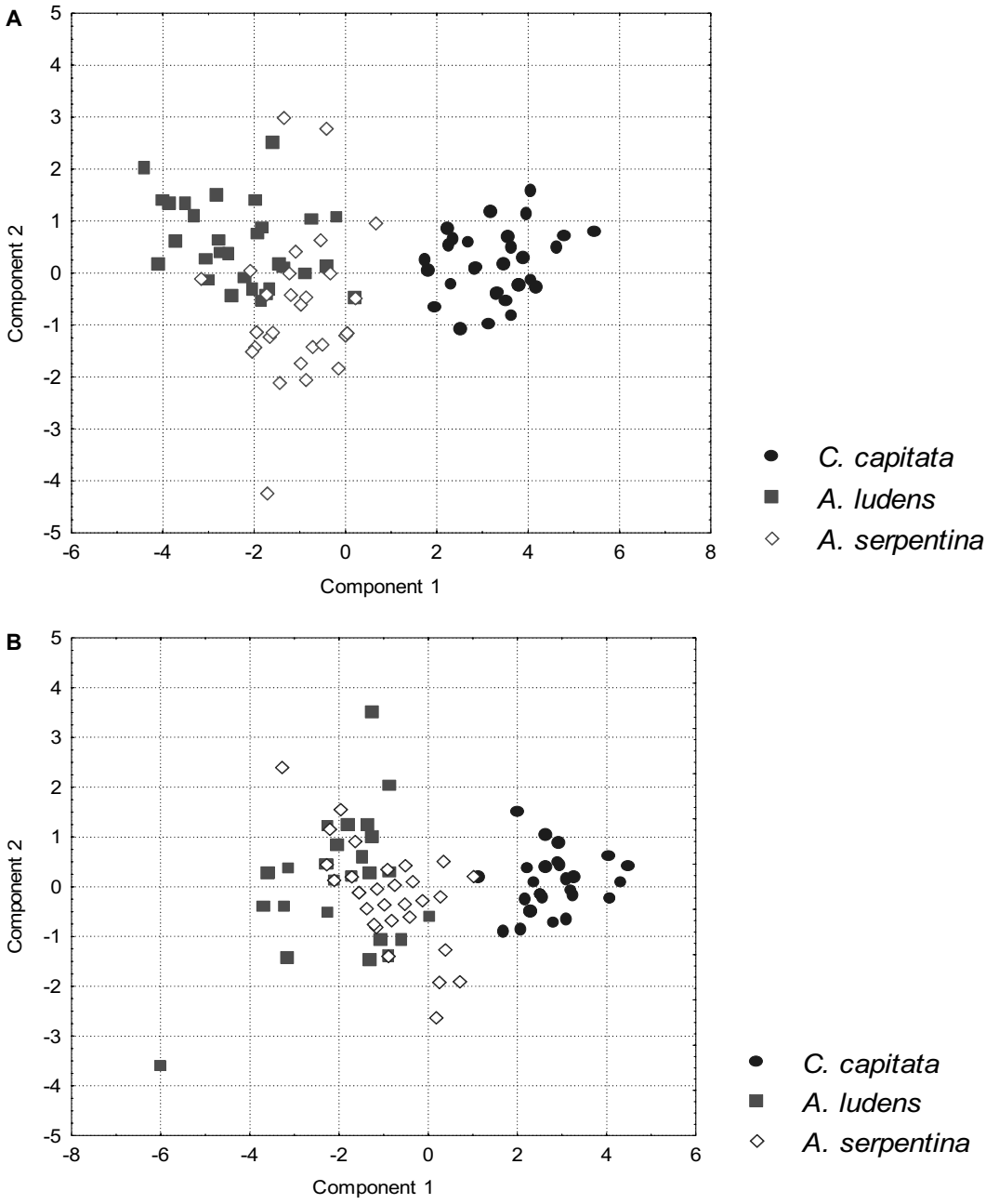

Fig. 4. Scatter plot generated by discriminant analysis of body size characteristics of *Fopius arisanus* (A) females and (B) males that emerged from *Ceratitis capitata*, *Anastrepha ludens*, and *A. serpentina* indicating the separation of the parasitoids that emerged from different host species into distinct groups based on the length of the wing, hind tibia, ovipositor, and overall body length.

inflicted by the parasitoid ovipositor may cause direct mortality of host eggs, although the relationship between egg age and its ability to survive such wounds has not, to our knowledge, been investigated in detail (Nishida and Haramoto, 1953).

Preliminary observations with *C. capitata* confirmed that *F. arisanus* spent more time ovipositing in sites containing eggs rather than first-instar larvae, although parasitoid reproduction was confirmed as possible in first-instar hosts as previously reported (Bess et al., 1961; Haramoto, 1957). Egg age had a marked effect of on the suitability of *A. ludens* and *A. serpentina* as hosts for *F. arisanus*. The greatest number of parasitoids emerged from hosts that were exposed as 3-day-old eggs whereas no parasitoids emerged from hosts exposed as eggs of <4 h old, despite the frequent observations of ovipositional behavior recorded during the exposure period. This may be related to the biology of *Anastrepha* spp. that require 3–4 days of incubation at 26–28 °C for embrion development (Domínguez et al., 2000), such

that newly laid eggs were not at a suitable stage for parasitoid development.

Percentage parasitism in *C. capitata* and *Anastrepha* species was low (less than 10% in all cases). This was probably due to the high number of eggs (540 host eggs/parasitoid female) exposed to parasitism during each 24 h period. We selected this density of eggs to ensure abundant parasitoid reproduction and because host eggs were readily available from the mass-rearing facilities of Moscamed and Moscafrut. When presented with a density of 20 *B. dorsalis* eggs/female, Bautista et al. (1998) reported 52.3% parasitoid emergence, which in terms of numbers of developing parasitoids, is between half and one quarter of the *per capita* daily parasitoid production we observed using *C. capitata* as the host. Moreover, offering large numbers of host eggs is the preferred method for mass-rearing this parasitoid, even though the percentage parasitism is relatively modest (14–21%) at high host densities (Bautista et al., 1999).

Irrespective of host species or age at time of parasitization, males consistently outnumbered female parasitoids at emergence, which may indicate that parasitoids perceived the hosts as being of low quality, or may reflect differential survival of the sexes. Alternatively, the procedures used to induce parasitoid mating may not have functioned particularly well and the male bias may have arisen through the reproduction of virgin females that lay only haploid male eggs. Difficulties in successful mating in *F. arisanus* have previously been reported using other host species (Harris and Okamoto, 1983, 1991; Ramadan et al., 1992, 1994). Moreover, mass-rearing of *F. arisanus* in the oriental fruit fly *B. dorsalis* resulted in a consistently male-biased parasitoid population over a period of 13 months, and as such, sex ratio appears to be a major factor limiting the efficiency of mass-rearing of *F. arisanus* (Bautista et al., 1999).

Only two parasitoids emerged from the *A. obliqua* eggs exposed to parasitism. Marked differences in the ability of *F. arisanus* to reproduce in different hosts has been reported previously (Harris and Bautista, 1996; Ramadan et al., 1992). For example, Harris et al. (1991) observed that *C. capitata* eggs were less attractive and less suitable than *B. dorsalis* eggs for reproduction of *F. arisanus*. Moreover, in areas where *B. dorsalis* and *B. cucurbitae* are sympatric, *F. arisanus* caused considerable mortality of *B. cucurbitae* eggs despite being unable to develop in this host (Nishida and Haramoto, 1953).

Developmental times and the patterns of parasitoid emergence from *C. capitata* in this study were very similar to those reported previously using *B. dorsalis* as the host (Bautista et al., 1998) with parasitoid emergence occurring at 1–3 days after the peak emergence of adult flies. In contrast, parasitoids that developed in *Anastrepha* spp. emerged several days prior to the adult hosts. This was not due to a change in the developmental time of *F. arisanu* s in *Anastrepha* spp., which was almost identical to that seen in *C. capitata* hosts, but rather the longer developmental time required by *Anastrepha* spp. flies (Celedonio et al., 1988; Domínguez et al., 2000).

Host species also had marked effects on the size, longevity, and reproductive capacity of parasitoid progeny. Discriminant analysis applied to a set of parasitoid body characteristics was found to be particularly effective in detecting differences between the size of parasitoids emerging from different hosts. Pupae of *Anastrepha* spp. were larger than *C. capitata* pupae and most of the parasitoids that emerged from *A. ludens* had large bodies and approximately 20% had deformed wings. Half of the parasitoids that emerged from *A. ludens* were dead within 5 days post-emergence. In contrast, parasitoids that emerged from *C. capitata* and *A. serpentina* had similar life expectancies at emergence and deformities were not commonly observed in parasitoids from these hosts. The fecundity of parasitoids offered the host species from which they had emerged was, however, lower in parasitoids reproducing on *A. serpentina* than on *C. capitata*, possibly because this was the first generation of reproduction in this host.

Parasitoid longevity and reproductive success is usually positively correlated with body size which reflects the quantity and quality of host resources consumed in the parasitoid larval stage (Godfray, 1994). Clearly, this was not the case for parasitoids that developed in *A. ludens*. This host may represent too large a resource for development of *F. arisanus* resulting in the bodily deformations and reduced survival that we observed. Although the costs of ovipositing in hosts that are too small for progeny development are well recognized (Salt, 1941), some parasitoids may also suffer reduced survival or deformations when developing in host species that are too large (e.g., Flanders et al., 1961; Takagi, 1985).

In conclusion, *F. arisanus* was observed to oviposit in all of the species tested and reproduced in all species except *A. obliqua*. In general, *C. capitata* appeared to be a more suitable host than *A. serpentina*, which in turn was more suitable than *A. ludens*. This may be due to the fact that *F. arisanus* had been reared in *C. capitata* for at least 28 generations prior to the study. The high prevalence of inbreeding in continuously reared insect colonies tends to reduce the genetic heterogeneity of experimental insect populations (Bartlett, 1985). A parasitoid colony established using individuals collected from wild populations of *C. capitata* or *B. dorsalis* may have been better able to adapt to novel *Anastrepha* hosts.

Further studies are merited, particularly directed at the reproduction of this parasitoid in *A. serpentina*, for which we recommend exposure of eggs to parasitization at 3 days old. It is also desirable to investigate the

responses of *F. arisanus* to different fruits commonly infested by these fruit fly species to determine whether or not the parasitoid can find and successfully parasitize *Anastrepha* spp. eggs in such fruits. We conclude that *F. arisanus* has potential as a natural enemy of *C. capitata* and *A. serpentina* and that egg age at the moment of parasitization has a marked effect on the performance of the parasitoid.

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