



Comparison of life table parameters for *Maconellicoccus hirsutus*, *Anagyrus kamali*, *Cryptolaemus montrouzieri* and *Scymnus coccivora*

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Abstract. The pink mealybug *Maconellicoccus hirsutus* Green (Homoptera: Pseudococcidae) was recently introduced to Trinidad. *M. hirsutus* almost immediately attained pest status and despite the implementation of cultural and chemical control measures, the population increased above the economic injury level. Three natural enemies, *Anagyrus kamali* Moursi (Hymenoptera: Encyrtidae), *Cryptolaemus montrouzieri* Mulsant (Coleoptera: Coccinellidae) and *Scymnus coccivora* Ayyar (Coleoptera: Coccinellidae) were introduced. Life fecundity tables were constructed for the pest-natural enemies complex in the hope of understanding the interaction of each natural enemy with its host, and, in so doing, form a comparative approach to assessing the effectiveness of each natural enemy. The studies were carried out in the laboratory at 27.0 ± 3.0 °C and $58.0 \pm 3.0\%$ RH, which is within the average field conditions in Trinidad. The net reproductive rates (R_0), the innate capacity for increase (r_m) and the finite rate of increase (λ) were found to be higher for the natural enemies compared to the pest. The doubling time for *M. hirsutus* was 8.83 days, while *A. kamali*, *C. montrouzieri* and *S. coccivora* populations doubled in 2.09, 5.13 and 4.45 days respectively. The significantly higher population parameters of the natural enemies, coupled with their shorter doubling times, mean that their populations can grow faster and thus exert a controlling effect on pest numbers.

Key words: Coccinellidae, Coleoptera, Encyrtidae, Homoptera, Hymenoptera, life fecundity tables, *Maconellicoccus hirsutus*, Pseudococcidae

Introduction

Maconellicoccus hirsutus Green (Homoptera: Pseudococcidae), a pest of food plants, ornamentals, weeds, and fruit and forest trees in Grenada, was recorded for the first time in Trinidad in 1994. It quickly became a pest of major importance and by December, 1995 was designated a notifiable pest. After cultural methods and chemical control failed to effect control of an expanding pest population, natural enemies were introduced. The

parasitoid, *Anagyrus kamali* Moursi (Hymenoptera: Encyrtidae) along with two predatory coccinellids, *Cryptolaemus montrouzieri* Mulsant (Coleoptera: Coccinellidae) and *Scymnus coccivora* Ayyar (Coleoptera: Coccinellidae) were released at several sites on the island.

Mani (1989), Ranga Reddy and Lakshmi Narayan (1986) and Ghose (1972) provide accounts of various aspects of the biology of *M. hirsutus*. Developmental studies for various *Anagyrus* spp. include research by Nechols and Kikuchi (1985), Tingle and Copland (1989) and Cross and Moore (1992). Substantial research has been conducted on the biology of *C. montrouzieri* by Mineo (1967), Charansri and Nishida (1975), Chako et al. (1978), Murthy (1982) and Babu and Azam (1987). Various authors have presented data on reproduction in Scymni, (e.g., Davidson, 1923; Naranjo et al., 1990; Padamaja et al., 1995). Life fecundity tables of both pest and natural enemies generate data necessary for a biological control program. No such comparative studies exist for the *M. hirsutus*, *A. kamali*, *C. montrouzieri* and *S. coccivora* complex.

The population growth of the pest and the biological control agents were assessed by computation of the net reproductive rate (R_0), the intrinsic rate of natural increase (r_m), the mean generation time (T) and the finite rate of increase (λ). The stable age distribution was also obtained in each case using the methods of Birch (1948), Laughlin (1965) and Southwood (1991). The r_m value obtained was used to calculate the percentage distribution of each developmental stage for each species (Percentage distribution = $100L_x e^{-r_m(x+1)}$ where x = age in days and L_x = age specific survivorship). The sum of the percentages for each developmental stage reflects the percent stable age distribution for that particular stage in the life cycle.

Materials and methods

Fecundity life table for M. hirsutus

Five one-day-old *M. hirsutus* ovisacs were randomly collected from each of five *Hibiscus rosa-sinensis* L. plants kept in the laboratory under a 12L: 12D regime. From each ovisac, four eggs were randomly removed with a piece of ovisac intact; these eggs were not handled directly. One hundred eggs were thus obtained. Each was placed on an individually caged *H. rosa-sinensis* plant enclosed in a 6 cm × 12 cm ventilated chamber.

The experiment was set up in the laboratory at mean ± S.E. values of 27.0 ± 3.0 °C and 58.0 ± 3.0% RH. These conditions were used throughout the study, are in the range of field conditions, and, also allowed for the optimum growth of both pest and natural enemy cultures.

On hatching, the cages were covered with black cotton cloth for 24 hours to encourage the crawlers to settle and start feeding. Light was supplied directly above the plants in a 12L: 12D regime. This encouraged the crawlers to remain on the uppermost leaves. Observations were made with the aid of a stereomicroscope. Data on moulting, sex ratio and fecundity were collected daily. Plants were watered on alternate days and Blaukorn[®] 2g/l (12N: 12P₂O₃: 17K₂O₄: 2MgO) fertilizer was applied at weekly intervals. Adult female *M. hirsutus* were allowed to mate by introducing recently emerged males from culture cages into their chamber. The experiment continued until the death of the last adult female. *M. hirsutus* ovisacs were collected from each cage and the number of eggs in each ovisac was counted using the stereomicroscope.

Fecundity life table for A. kamali

Five potted *H. rosa-sinensis* plants which were infested for six weeks with *M. hirsutus* were individually placed in organza (40 mesh/cm²) cages in the laboratory at 27.0 ± 3.0 °C and $58.0 \pm 3.0\%$ RH. Each plant was then exposed to 10 pairs of *A. kamali* for 24 hours under a 12L: 12D regime. After 8 days, 20 parasitized mealybugs were randomly collected from each plant. One hundred mummies of varying sizes were thus collected and individually placed in 4 cm diameter petri dishes to await emergence of the adults.

On emergence, *A. kamali* adults were visually sexed. Males are smaller (about 1.8 mm in body length) and black, while females are orange-brown (about 2.8 mm in body length). In this study more females than males were obtained; hence males of comparable age from a culture maintained on *H. rosa-sinensis* were introduced to some females. Pairs of adult *A. kamali* were introduced into a 10 cm diameter organza (40 mesh/cm²) cage containing one *H. rosa-sinensis* plantlet infested with thirty, 3rd instar *M. hirsutus*. Fine streaks of honey on the cage sides and top were offered as a food source for *A. kamali*. Care was taken to ensure that the plantlets were all of the same size and had approximately the same population of *M. hirsutus*. Similarly infested plantlets were used to replace these at daily intervals.

Plantlets were removed and placed in separate ventilated cages under light. After 8 days mummies were brushed onto paper, counted and stored in the laboratory at 27.0 ± 3.0 °C and $58.0 \pm 3.0\%$ RH and 12L: 12D until emergence of *A. kamali* adults. Records were made on the longevity of both sexes as well as the fecundity of the emerging female. Males dying before females in any caged pair were replaced with another of same age from a separate culture cage. The experiment was terminated when all females died.

Fecundity life table for C. montrouzieri and S. coccivora

To construct the life fecundity table, 100 eggs of *C. montrouzieri* or *S. coccivora* were obtained by placing 50 *M. hirsutus* ovisacs into several cages containing *C. montrouzieri* or *S. coccivora* adults overnight. Five eggs were removed from each of twenty randomly chosen ovisacs. With the aid of a camel hair brush and fine probe the portions of waxy ovisacs containing the coccinellids' eggs were carefully placed in 4 cm Petri dishes. Surplus eggs were removed leaving only one egg per Petri dish. The chosen egg was not handled directly. One hundred labeled Petri dishes were thus arranged in the laboratory at 27.0 ± 3.0 °C and $58.0 \pm 3.0\%$ RH under a light: dark schedule of 12L:12D. Each egg was examined daily.

On hatching, *M. hirsutus* eggs and nymphs of varying stages were provided to each coccinellid larva *ad lib*. Records of larval growth and moults were made on a daily basis. Exuviae and fecal matter was promptly removed. For fecundity and age specific mortality investigations, adults were paired within 24 hours of emergence and introduced into a 6 cm × 5 cm plastic container. The container was fitted with a mesh lid (40 mesh/cm²) and food comprising of *M. hirsutus* eggs, nymphs and adults was replenished at daily intervals.

C. montrouzieri adults were visually sexed by examination of the first pairs of legs; in males they are reddish brown to yellow while in females they may range from grey to black (Pang and Gordon, 1986). In the case of *S. coccivora*, females have a tip on the last abdominal segment, while in males it is rounded. Occasionally a fine mist of water was sprayed over the insects. This enhanced mating among most of the pairs, especially when misting was done during the first week after eclosion. *C. montrouzieri* or *S. coccivora* eggs were laid within the *M. hirsutus* ovisacs which were checked and restocked on a daily basis. The amber colour and larger size of the coccinellids' eggs can easily be differentiated from the pink/orange eggs of *M. hirsutus*. Any dead *C. montrouzieri* or *S. coccivora* male was replaced with another of comparable age from a culture cage. The experiment was terminated when all test coccinellid females died.

Results

Fecundity life table for M. hirsutus

Figure 1 shows the relationship between the age specific survival (l_x) and the various stages of development of *M. hirsutus*. The developmental success from egg to adult was 19%, and an adult sex ratio of 1.4♂: 1♀ was obtained.

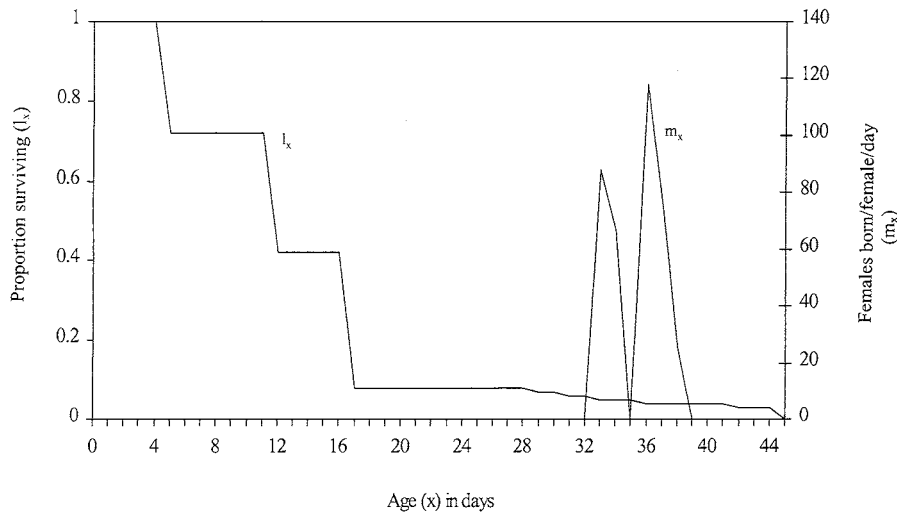


Figure 1. Survivorship and age-specific fecundity curves for *Maconellicoccus hirsutus* at 27.0 ± 3.0 °C and $58.0 \pm 3.0\%$ R.H. (12L: 12D).

Adult males lived an average of 2.73 ± 0.14 days ($n = 13$) while adult females lived an average of 13.87 ± 2.25 days ($n = 5$). In females, mating occurred from the first day of adult life and eggs were produced on the 9th day. A pre-oviposition period of 8 days was observed. Females produced an overall average of 178.00 ± 32.92 eggs per female during their adult reproductive lifetime. Maximum oviposition of 280 eggs/day (i.e. $m_x = 117$) occurred on the 4th day after the start of oviposition. Most eggs were laid in the first 5 days after oviposition began and then oviposition rate declined rapidly. The net reproductive rate (R_o), representing the total female births, was 15.51 (Table 1). This meant that the population of *M. hirsutus* would be able to multiply 15.51 times on *H. rosa-sinensis* at the end of each generation ($T = 34.23$ days). The finite rate of increase (λ) was 1.08 indicating that the population had the capacity to multiply 1.08 times per female per day. The percentage contribution of the egg stage to the value of the intrinsic rate of natural increase was 57.23% (when $r_m = 0.0801$), while the combined nymphal stages and adult stages contributed 41.04% and 1.73% respectively to the stable age distribution.

Fecundity life table for A. kamali

The developmental success of *A. kamali* from egg to adult was 96%, and an adult sex ratio of $1\sigma^7: 2\varphi$ was obtained. Mating occurred on the day of eclosion and eggs were produced one day later. A preoviposition period of

Table 1. Life table parameters for *M. hirsutus* and its exotic natural enemies under laboratory conditions of $27.0 \pm 3.0^\circ\text{C}$ and $58.0 \pm 3.0\%$ RH and 12L: 12D

Parameter	<i>M. hirsutus</i>	<i>A. kamali</i>	<i>C. montrouzieri</i>	<i>S. coccivora</i>
Net reproductive rate R_0	15.51	994.00	227.18	220.02
Innate capacity for increase r_m	0.0801	0.3301	0.1352	0.1559
Finite rate of increase $\lambda = e^{r_m}$	1.08	1.39	1.14	1.17
Generation time $T = \log_e R_0 / r_m$	34.23	20.05	40.13	35.60
Doubling time $\ln 2 / r_m$	8.83	2.09	5.13	4.45
Preoviposition period (days)	8.00	1.00	7.00	5.00
Longevity (days)	$\sigma^{\circ} = 2.73 \pm 0.14$	$\sigma^{\circ} = 5.94 \pm 0.33$	$\sigma^{\circ} = 94.18 \pm 4.01$	$\sigma^{\circ} = 32.74 \pm 2.06$
(Mean \pm S.E.)	$\varphi = 13.87 \pm 2.25$	$\varphi = 7.23 \pm 0.44$	$\varphi = 98.08 \pm 1.60$	$\varphi = 39.21 \pm 1.67$

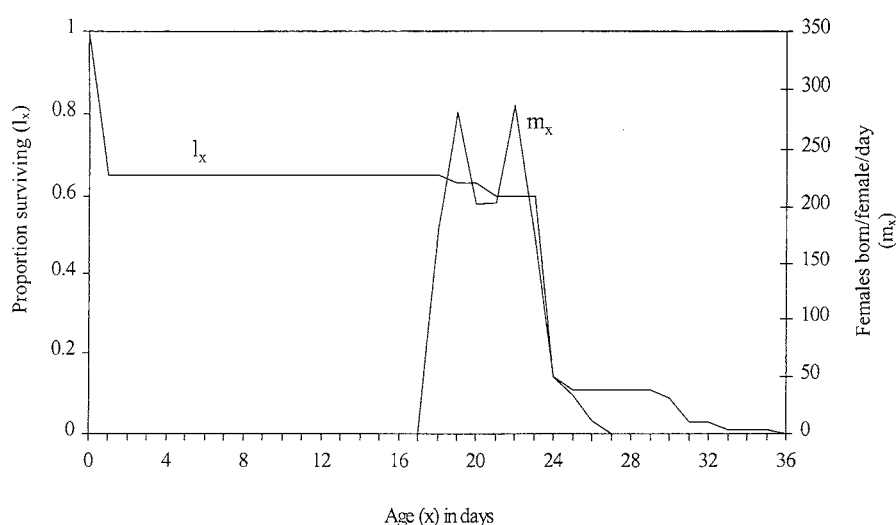


Figure 2. Survivorship and age-specific fecundity curves for *Anagyrus kamali* at 27.0 ± 3.0 °C and $58.0 \pm 3.0\%$ R.H. (12L: 12D).

one day was observed. Females had two peak egg laying periods, days 2 and 5 when they produced 422 and 430 eggs respectively (i.e. $m_x = 281$ and 287 respectively) (Figure 2). Most eggs were laid in the first 6 days after oviposition began (on Day 18) and then declined rapidly thereafter. Females produced an overall average of 39.09 ± 1.44 eggs per female throughout their adult reproductive lives. Egg production continued in some cases to within hours before dying. The net reproductive rate (R_0) and generation time (T) were 994 and 20.05 days respectively. The finite rate of increase (λ) was 1.39. The immature and adult stages contributed 95.09% and 4.91% respectively (when $r_m = 0.3301$) to the stable age distribution.

Fecundity life table for C. montrouzieri and S. coccivora

Fifty eight percent of *C. montrouzieri* eggs survived to adulthood while the adult sex ratio was $1.6\sigma^7: 1\text{f}$. In females, mating occurred 4 days after eclosion and eggs were produced 3 days later. A preoviposition period of 7 days was observed. Females produced an overall average of 118.68 ± 1.82 eggs per female throughout their lives. Most eggs were laid in the first 16 days after oviposition began (Figure 3). However, egg production, though significantly reduced, continued in some cases to within 1–2 days of death. The first female death occurred on day 77 and mortality increased afterward until the last death (Day 135).

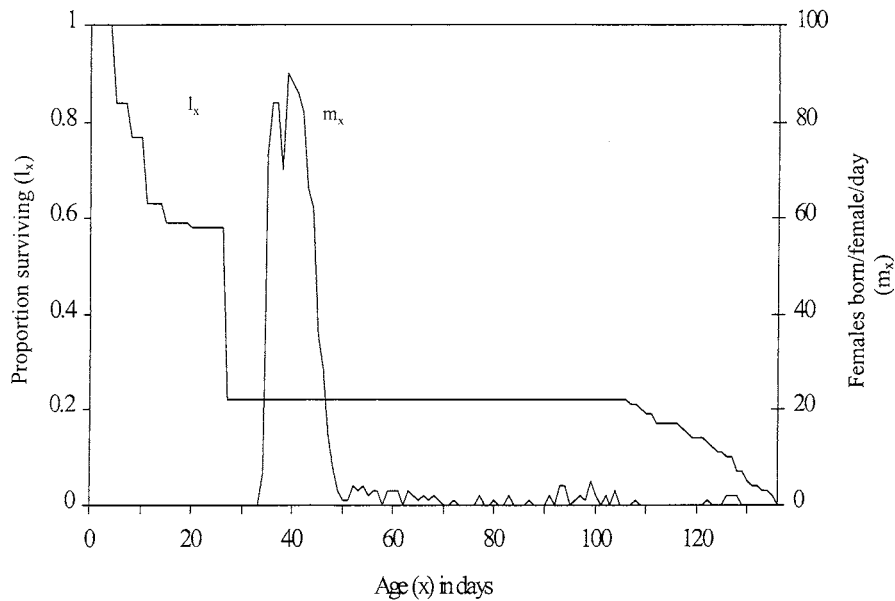


Figure 3. Survivorship and age-specific fecundity curves for *Cryptolaemus montrouzieri* at 27.0 ± 3.0 °C and $58.0 \pm 3.0\%$ R.H. (12L: 12D).

The net reproductive rate (R_0) was 227.18 while the generation time (T) was 40.13 days. The finite rate of increase (λ) was 1.14. The egg stage contributed 52.30% while the combined larval stages, the pupal stages and the adult stage contributed 45.91%, 1.44% and 0.35% to the stable age distribution respectively (when $r_m = 0.1352$).

The developmental success from egg to adult for *S. coccivora* was 51%, and the emergent adult sex ratio was $1\sigma^a: 1.07\varphi$. The first female death occurred on the 13th day of adult life, mortality continued until the last death on the 60th day (Figure 4). In females, mating occurred 2 days after eclosion and eggs were produced 3 days later. Females started to lay eggs on the 6th day after eclosion and produced a maximum of 122 eggs (i.e. $m_x = 61$) on the 12th day after eclosion. Females produced an overall average of 57.29 ± 2.86 eggs per female throughout their adult reproductive lives. Oviposition was substantially reduced from the second week onwards.

The net reproductive rate (R_0) was 220.02 with a generation time of 35.60 days and finite rate of increase (λ) of 1.17. The egg stage, combined larval stages, prepupal and pupal and adult stages contributed 48.67%, 42.80%, 5.03% and 3.50% respectively to the stable age distribution ($r_m = 0.1559$).

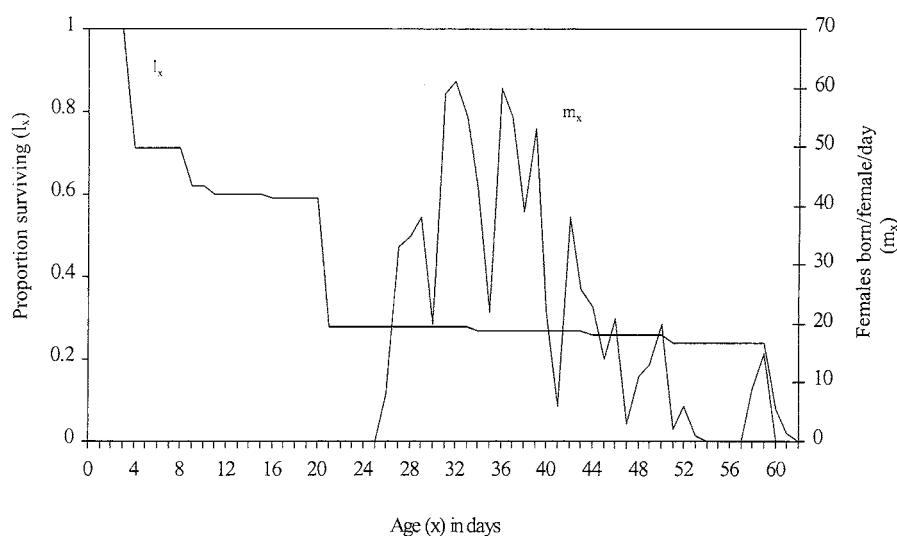


Figure 4. Survivorship and age-specific fecundity curves for *Scymnus coccivora* at 27.0 ± 3.0 °C and $58.0 \pm 3.0\%$ R.H. (12L: 12D).

Discussion

The combination of survivorship and fecundity curves (Figure 1) give an estimation of biological parameters that can be used in a biological control programme for *M. hirsutus*. Various authors have reported pre-oviposition periods for *M. hirsutus* ranging from 0.5 to 6 days (e.g. Singh and Ghosh, 1970; Ghose 1972; Mani, 1986). The slightly longer pre-oviposition period of 8–9 days obtained here may be due to the lower temperature under which this experiment was conducted.

Females produced an average of 178.00 ± 32.92 eggs per female throughout their reproductive lifetime. Dutt et al. (1951) reports an average number of 194 eggs while Ranga Reddy and Lakshmi Narayan (1986) report an average of 500 eggs. The age-specific fecundity (female progeny/female), m_x , curve of *M. hirsutus* is highly skewed to the right of the survivorship/fecundity complex (Figure 1). This indicates that females in the 33rd to 37th day of adult life contributed most to the female progeny of the cohort, two oviposition peaks three days apart were observed, this produced a phased effect on the production of crawlers.

The immature stages (egg and nymphal) contributed 99.65% to the intrinsic rate of natural increase. A preponderance of immatures is advantageous to the population of *M. hirsutus* since mortality is high in these stages and hence it is necessary to ensure that some offspring survive to adulthood.

This high mortality may be due to the fact that some of the younger stages are devoid of wax and consequently liable to desiccation.

Three methods can be used to assess parasitoid fecundity; dissection of the ovaries, dissection of the parasitized hosts and the method employed in this study; post emergence host mummy counts (Iziquel and Le Ru, 1992). The emergent σ^7 : q sex ratio of 1: 1.7 and 1: 2 at 25 °C and 30 °C respectively was obtained for the related species, *Anagyrus dactylopii* Howard (Hymenoptera: Encyrtidae) by Mani and Krishnamoorthy (1992). This compares favourably with that obtained for *A. kamali* (1 σ^7 : 2 q).

The age specific fecundity (m_x), curve extended from the 18th to the 26th day when egg laying occurred. This period had two small oviposition peaks on the 19th and 22nd days (Figure 2). The life fecundity curve also indicates a pre-oviposition period of 1 day after which an average of 39.11 ± 1.02 eggs were produced per female of the group studied.

Generally females in the younger age classes (from the 2nd to the 10th day after adult emergence) contributed most to the female progeny of the cohort. Table 1 indicates $R_0 = 994$, $T = 20.05$ and $r_m = 0.3301$ for *A. kamali*. Iziquel and Le Ru (1992) provide values of $R_0 = 269.90$, $T = 33.90$ and $r_m = 0.2130$ for *Epidinocarsis lopezi* De Santis (Hymenoptera: Encyrtidae). The high R_0 obtained may be attributed to the fact that the *M. hirsutus* third instar nymphs are the preferred stages for oviposition (Sagarra and Vincent, 1999), hence the tested *A. kamali* females may have oviposited optimally.

The age-specific fecundity, (m_x) curve of *C. montrouzieri* is also highly skewed to the left. A pre-oviposition period of 7 days occurs before eggs can be produced from newly emerged females. An overall average of 118.68 ± 1.82 eggs per female was obtained over the reproductive lifetimes of the females in this study. This is in variance with the pattern noted by Tirumala and David (1956) who cited a pre-oviposition period of 9–13 days and an average egg production of 207 eggs per female. However the difference in egg quantity could be due to the higher temperature (30 °C) of their experiments. Babu and Azam (1987) have shown that egg production increases with temperature until 30 °C. Immature stages dominated the stable age distribution of the coccinellids, this is of importance in a biological control program as most prey is consumed by the larval stages of *C. montrouzieri*. Adults tend to prefer feeding on the eggs and crawlers of *M. hirsutus* (Babu and Azam, 1987).

The intrinsic rate of natural increase was higher for the natural enemies compared to the pest (Table 1). According to Huffaker et al. (1976), and Iziquel and Le Ru (1992) this means that these natural enemies can be effective against the pest. Theoretically the natural enemies all have the ability

to reproduce faster than the pest and in so doing are able to exert some measure of control.

The parasitoid, *A. kamali*, has the shortest pre-oviposition period and generation and doubling times compared to that of the predators. Its' net reproductive rate and its' finite rate of increase are also comparatively higher. This suggests that the parasitoid, given suitable conditions, may exert more sustained control on expanding *M. hirsutus* populations. The two predatory coccinellids, *S. coccivora* and *C. montrouzieri* had similar life table parameters on *M. hirsutus* suggesting that between them, they are almost equally competent at managing *M. hirsutus* populations.

In Trinidad, *M. hirsutus* populations have now been reduced below the economic injury level. Occurrence of *M. hirsutus* is incidental and often restricted to *Hibiscus* spp., and some ornamentals as well as legumes. The presence of one or more or a combination of all three exotic natural enemies at one infestation is not uncommon, and, after five years of initial releases, the existence of all three natural enemies in the field suggests that they may be established. However control by one natural enemy or a combination of parasitoid and predators remains uncertain and needs to be further evaluated.

The data generated in this paper provides critical information on biological parameters that is useful in field related studies on this new pest and is essential to formulating a biological control program for *M. hirsutus*. Control of *M. hirsutus* by introduced exotic natural enemies as described here, adds to the international list of successful programmes of biological control.

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