

Biology and life history of *Hyperaspis trifurcata* feeding on *Dactylopius opuntiae*

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Abstract *Hyperaspis trifurcata* (Coleoptera: Coccinellidae) is a native predator of the wild cochineal scale, *Dactylopius opuntiae* (Hemiptera: Dactylopiidae) in North America. Here we have determined its life cycle and voracity when reared on first instar nymphs of *D. opuntiae* and estimated its population parameters using five diets based on different developmental stages of its prey: (a) first instar nymphs, (b) second instar nymphs, (c) young adults, (d) gravid adult females, and (e) a mixed diet which included all the developmental stages. The tests were conducted under laboratory conditions: 25 ± 2 °C, 60 ± 10 % RH and 12:12 (L:D) h. *H. trifurcata* developmental times were 5.9, 3.1, 3.6, 3.1, 8.9 and 11.4 days for the eggs, first, second, third and fourth instar larvae, and pupae, respectively. Overall there were 36.6 days from egg to adult emergence. Females consumed a mean of 5293 ± 361 first instar *D. opuntiae* nymphs during their lifetime, and there was no significant difference in developmental time between males and females. *H. trifurcata* could complete its life cycle

when reared on any developmental stage of *D. opuntiae*. Nevertheless, the highest fecundity (237.4 ± 25.8 eggs) was obtained when they were fed the mixed diet, and the lowest fecundity and fertility were obtained when they were fed first or second instar nymphs, with a fecundity of 57.8 ± 10 and 140.5 ± 13 eggs and a fertility of 72 and 80 %, respectively. Moreover, the mixed diet increased the net reproduction rate ($R_0 = 112$) and prolonged the generation time ($T = 68.4$ days) compared with females reared on first or second instar nymphs where $R_0 = 27.3$ and 66.3 and $T = 56.2$ and 62.4 days, respectively. These parameters indicate that *H. trifurcata* has potential as a biological control agent of *D. opuntiae*.

Keywords *Opuntia ficus-indica* · Cochineal scale · Native natural enemies · Biological control

Introduction

Dactylopius opuntiae (Cockerell) (Hemiptera: Dactylopiidae), or wild cochineal scale, is a primary pest of *Opuntia ficus-indica* (L.) Miller (Caryophyllales: Cactaceae) and other cultivated and wild *Opuntia* species throughout Mexico (Portillo and Viguera 2006; Vanegas-Rico et al. 2010), Brazil (Oliveira et al. 2013), Spain, Ethiopia, Italy, Turkey, Lebanon and Israel (Portillo 2009; García Morales et al. 2016;

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Spodek et al. 2014). Although *O. ficus-indica* is native to Mexico (Griffith 2004), it is the cactus that is most widely cultivated worldwide (Nobel 2002) and it is used in the food industry, as a forage plant for livestock and to prevent erosion in desert regions (Le Houérou 1996; Flores-Valdéz 1995; Stintzing and Carle 2005; Sáenz et al. 2006; Corrales-García 2009).

Dactylopius opuntiae feeds directly on the plant causing chlorosis and premature dropping of cladodes and fruits. Severe infestations (>75 % of the cladode surface) can result in death of the plant (Mann 1969; Vanegas-Rico et al. 2010, 2015). In Brazil, the damage caused by *D. opuntiae* on *O. ficus indica* used as forage resulted in the loss of 100,000 ha, valued at 25 million dollars (Lopes et al. 2009). In Mexico, damage to fruit and nopalitos (edible young *Opuntia* cladodes) resulted in lower yields and higher production costs (Badii and Flores 2001; Portillo and Viguera 2006).

Dactylopius opuntiae is controlled mainly by organophosphate insecticides (Badii and Flores 2001), which can have deleterious effects on human health (Galloway and Handy 2003) and the environment (Arias-Estévez et al. 2008). Residues of these insecticides on the crop also limit international trade. To reduce insecticide use, alternative management strategies have been explored, such as the use of mineral oils, resistant genotypes, detergents, plant extracts and mycoinsecticides (Palacios-Mendoza et al. 2004; de Brito et al. 2008; Viguera et al. 2009; de Santos et al. 2011; Borges et al. 2013a, b). However, the results have been unsatisfactory and new strategies, such as the use of natural enemies, require exploration.

Arthropod natural enemies associated with *D. opuntiae* and other Dactylopiidae include only predators (Mann, 1969; Zimmermann et al. 1979; Vanegas-Rico et al. 2010) of which the Coccinellidae *Chilocorus cacti* L. and *Hyperaspis trifurcata* Schaeffer are the most abundant in Mexico and USA (Mann 1969; Gilreath and Smith 1988; Badii and Flores 2001; Rodríguez-Leyva et al. 2010; Vanegas-Rico et al. 2010, 2015). *Chilocorus cacti* preys on a variety of insects and insect scales such as *Diaphorina citri* Kuwayama (Hemiptera: Psyllidae), *Aulacaspis tubercularis* Newstead and *Aspidiotus destructor* Signoret (Hemiptera: Diaspididae) (Pluke et al. 2005; Vanegas-Rico et al. 2010; Hernández-Fuentes et al. 2012). On the contrary, *H. trifurcata* is a highly specific predator on the *Dactylopius* genus (Gilreath and Smith 1988;

Rodríguez-Leyva et al. 2010; Vanegas-Rico et al. 2010; 2015). *Hyperaspis trifurcata* preys on all developmental stages of Dactylopiidae (Vanegas-Rico et al. 2010). However, there are no formal studies on the basic biology of this predator, which could contribute to determining its regulatory capacity. The objective of this study was to determine the biological cycle, voracity and life history of *H. trifurcata* reared on *D. opuntiae*.

Materials and methods

Insect rearing

Opuntia ficus-indica cladodes were used for rearing *D. opuntiae*. The cladodes were one-year old, 2 to 4 cm thick and were grown in pots ($\varnothing = 20 \text{ cm} \times 20 \text{ cm}$ high) in a substrate of tezontle (porous volcanic gravel) and compost (30:70). The *D. opuntiae* colony was established from individuals collected from two regions of Mexico in May 2012: Milpa Alta, Mexico City (19°10'49"N, 98°59'24.7" W, 2554 masl) and Tlalnepantla, Morelos (19°00'22"N, 98°58'10"W, 2105 masl). A modified version of the 'cut cladode technique' of Aldama-Aguilera and Llanderal-Cázares (2003) was used to increase numbers. Briefly, this technique involved perforating the basal end of each cladode with a wooden stake, leaving them to scar for 24 h, and then hanging them vertically from metal grids. An open waxed paper bag (4 cm²) containing gravid *D. opuntiae* females was attached to the apex of each cladode with a wooden toothpick and other cladodes placed horizontally beneath to capture any nymphs that did not initially fasten on to the vertical cladodes. The infested cladodes were maintained under controlled conditions of $26 \pm 2 \text{ }^\circ\text{C}$, $60 \pm 10 \text{ \% RH}$ and 12:12 h L:D regime and the colony was allowed to grow for use in experiments.

The *H. trifurcata* colony was established from adults that were collected in June 2012 from the same regions as the *D. opuntiae*. Adults were placed in entomological cages (70 × 55 × 40 cm) comprised of a wooden frame covered by a mesh fabric to allow ventilation. Access to water was provided via a cotton wick inserted into a 25 ml glass vial of water. Cladodes infested with *D. opuntiae* were introduced into the cages to provide food and substrates for *H. trifurcata* oviposition. Infested cladodes were withdrawn weekly

and *H. trifurcata* larvae transferred to another cage with the same characteristics to complete their development. All of the assays with *H. trifurcata* were conducted at 25 ± 2 °C, 60 ± 10 % RH and 12:12 (L:D) h. In addition, all the ladybird adults, both during rearing and experimentation, were offered a complementary diet (mixture of water, honey and brewer's yeast in a 20:40:40 proportion), which was replaced daily. We offered this diet because in previous observations in the laboratory some adults of *H. trifurcata*, which had access only to fresh water, lived just six to eight weeks. In addition, Dreyer et al. (1997) indicated that honey was useful to increase longevity in the rearing of *Hyperaspis notata* Mulsant.

Determining the developmental time and longevity of *H. trifurcata*

We used a cohort of 100 *H. trifurcata* eggs that were 0–6 h old. Each egg was placed in a hard gelatin capsule No 2 (2 ml) and observed twice daily (at 10:00 and 18:00 h), and the times of hatching or ecdysis of each individual were recorded. The chorion or exuviae were removed as they were formed. Adults that emerged were placed individually into Petri dishes ($\varnothing = 3.0$ cm). Both larvae and adults of *H. trifurcata* were provided with an excess of first instar *D. opuntiae* nymphs as prey and the duration of each development stage and the longevity of the adults was recorded. When the *H. trifurcata* larvae became adults they were sexed using the methods of Gordon (1985).

Quantifying the voracity of *H. trifurcata*

First instar larvae of *H. trifurcata* ($n = 30$) were maintained individually in gelatin capsules and provided daily with known densities of first instar *D. opuntiae* nymphs. As the larvae grew the number of first instar *D. opuntiae* nymphs provided was increased so that there were always more available than they required (i.e. 20, 40, 80, 160, 180 for first, second, third and fourth instar larvae, and adults, respectively). The number of *D. opuntiae* nymphs consumed daily by each life stage was recorded until the adults died and the mean daily consumption rate and total consumption rate for each life stage was calculated. A control group was established for each density of *D. opuntiae* nymphs provided (20, 40, 80, 160 and 180 nymphs, respectively) in gelatin

capsules to determine the mean number of nymphs that died from causes other than predation.

Quantifying the reproductive success of *H. trifurcata*

To quantify fecundity, 11 groups of ten adult male and ten adult female *H. trifurcata* (less than 8 h old) were placed into each of 11 Petri dishes ($\varnothing = 8$ cm) with an excess of first instar *D. opuntiae* for 48 h to allow copulation (Omkar and Srivastava 2002; Félix et al. 2004). Then each pair was placed in an individual Petri dish ($\varnothing = 8$ cm) and randomly assigned to one of five treatments, defined by the age of the prey they would subsequently be offered. These treatments were (a) first instar *D. opuntiae* nymphs (2–4 days old), (b) second instar *D. opuntiae* nymphs (8–10 days old), (c) young adult *D. opuntiae* females (20–25 days old), (d) gravid *D. opuntiae* females (26–33 days old), and (e) a mixed diet that included all development stages of *D. opuntiae*. All diets were offered *ad libitum*. Twenty-two replicate pairs of *H. trifurcata* were established per treatment, but those that did not oviposit within the first 14 days were excluded from subsequent analysis. Ultimately each treatment had at least 17 replicates. In all treatments the prey items were introduced into each dish on a labeled Petri dish lid ($\varnothing = 3.0$ cm), which was replaced daily. An artificial substrate for oviposition was also placed into each dish. This substrate consisted of thick black paper (4 cm^2) to which wax from adult *D. opuntiae* (dried at 50 °C for three days) was attached, making it attractive for oviposition. The inert substrate was replaced daily and the number of eggs quantified. The fertility was obtained by sampling eggs of six random females per day in each treatment. We maintained the daily group of eggs per female in a labeled Petri dish lid and checked emergence every six to seven days. All dishes were placed randomly in trays.

Data analysis

Longevity of females and males was compared using a t test ($p \leq 0.05$) with the software package SPSS ver. 21.0 (SPSS 2012). Daily voracity (V_0) during each development stage was estimated using the equation of Soares et al. (2003):

$$V_0 = (A - a_{24}) \text{ra}_{24}$$

where V_0 is the number of prey consumed, A is the number of prey offered, a_{24} is the number of prey alive after 24 h, and ra_{24} is the proportion of prey alive in the absence of a predator after 24 h. Daily and total voracity were compared between development stages and between sexes with ANOVA or a t test, respectively ($p \leq 0.05$) with SPSS (SPSS 2012).

Fecundity and fertility were recorded daily during the entire life of the females, but the data were grouped by week for the analysis and were limited to the first eight weeks of life to avoid bias in the last weeks when there were fewer surviving females. The pre-oviposition time, fecundity and fertility data were normalized (\log_{10}) prior to analysis using ANOVA and means comparisons (Tukey, $p \leq 0.05$) (Atlihan and Özögkçe 2002). The life table was constructed from the pivoting age (x), the specific survival age (lx) and the specific fecundity age (mx) using the Birch (1948) method. These values were obtained from the experiments on life cycle and fecundity and were used to estimate the population parameters using the computer programme of Maia et al. (2000) in the software package Lifetable SAS (SAS Institute 2000). The programme included a Jackknife method to estimate confidence levels for all parameters (Maia et al. 2000).

Results

Life cycle

The incubation period of eggs lasted a mean of 5.9 days, and there was no significant difference between the sexes ($t = -0.374$, $df = 81$, $p = 0.709$). *H. trifurcata* has four larval instars. The duration of the third and fourth instars was significantly longer in females than males (third instar $t = 2.3$, $df = 81$, $p = 0.03$; fourth instar $t = 2.3$, $df = 81$, $p = 0.02$). The overall larval developmental time of females (36.6 days) was, therefore, longer than that of males (35.1 days) ($t = 2.8$, $df = 81$, $p = 0.006$). Eighty-three percent of *H. trifurcata* survived to adulthood and emerged at a 1:1 sex ratio. Adult female *H. trifurcata* lived significantly longer (48.0 ± 1.8 days) than males (40.6 ± 1.9 days) ($t = 2.76$, $df = 81$, $p = 0.007$). Mortality of eggs (6 %), first instar larvae

(5.3 %) and the remaining larval instars (4.6 %) was higher than pupal mortality (2.3 %) (Table 1).

Voracity of *H. trifurcata*

Voracity of *H. trifurcata* against first instar nymphs of *D. opuntiae* varied significantly between developmental stages ($F_{4,10} = 1100.721$, $p < 0.001$) (Table 2). Individual females and males consumed around 5293 ± 361 and 4932 ± 436 nymphs each in total throughout their lives, and there was no significant difference between the sexes ($t = 0.64$, $df = 22$, $p = 0.526$). Total prey intake during the larval stage (over all instars) was only 9 % of the total number of prey consumed throughout the entire life cycle (Table 2). Of the larval instars, fourth instars were the most voracious. Maximum consumption was recorded on day 21 (69.4 ± 0.3 nymphs). Recently emerged adults killed 89.0 ± 0.24 nymphs and their voracity increased gradually up to a maximum of 152.3 ± 0.45 nymphs at 32 days of age.

Reproductive success of *H. trifurcata*

Females of *H. trifurcata* laid their eggs individually, and in 99 % of cases they were located amongst the wax fibres of their prey, particularly gravid female prey. The period of pre-oviposition was between five and six days, and there were significant differences among treatments ($F_{4,92} = 2.934$, $p = 0.025$). Females reared on first instar nymphs had a longer pre-oviposition time than those feeding on a mixed

Table 1 Development time and adult longevity (days; mean \pm SE) of *Hyperaspis trifurcata* ($n = 100$) reared on first instar nymphs of *Dactylopius opuntiae* under laboratory conditions (25 ± 2 °C, 60 ± 10 % RH, 12:12 [L:D] h)

| Developmental stage | Females | Males |
|---------------------|----------------|------------------|
| Egg | 5.9 ± 0.0 | 5.9 ± 0.1 |
| First instar | 3.1 ± 0.1 | 3.0 ± 0.1 |
| Second instar | 3.6 ± 0.1 | 3.7 ± 0.1 |
| Third instar | 3.1 ± 0.5 | 3.0 ± 0.0 * |
| Fourth instar | 8.9 ± 0.1 | 8.4 ± 0.2 * |
| Pupa | 11.4 ± 0.1 | 10.9 ± 0.2 |
| Egg to adult | 36.0 ± 0.1 | 35.1 ± 0.4 * |
| Longevity of adult | 48.0 ± 1.8 | 40.6 ± 1.9 * |

Asterisks indicate significant differences between the sexes (Student's t test, $p \leq 0.05$)

Table 2 Voracity (mean numbers of prey eaten \pm SE) of *Hyperaspis trifurcata* ($n = 30$) reared on first instar *Dactylopius opuntiae* nymphs

| Developmental stage | Voracity | |
|------------------------|------------------|--------------------|
| | daily | total |
| First instar | 8.2 \pm 1.5a | 25.4 \pm 0.8a |
| Second instar | 13.4 \pm 4.8a | 39.9 \pm 0.8b |
| Third instar | 30.4 \pm 1.8b | 119 \pm 2.3c |
| Fourth instar | 50.1 \pm 3.9c | 399 \pm 4.1d |
| First to fourth instar | – | 560.5 \pm 5.6 |
| Adult | 117.2 \pm 2.9d | 4860.6 \pm 482.2 |

Means within a column followed by the same letter are not significantly different (Tukey's test, $p > 0.05$)

diet, although the difference was only one day (Table 3).

There were significant differences amongst treatments in longevity ($F_{4,92} = 6.525$, $p \leq 0.001$), fecundity ($F_{4,92} = 26.2$, $p \leq 0.001$) and fertility ($F_{4,92} = 21.2$, $p \leq 0.001$). Overall the three parameters were similar when adult females of *D. opuntiae* were included in the diet, and superior to treatments fed only first or second instar nymphs (Table 3). The females fed with young adults or the mixed diet lived 25 and 14 days longer, respectively, than those reared on first or second instar nymphs (Table 3). *H. trifurcata* reared on adult females produced 35–170 % more eggs than those reared on first or second instar nymphs, while those fed on the mixed diet had higher fecundity. The lowest fecundity was seen in treatments with first and second instar nymphs, which was significantly different from the treatments with adult prey (Table 3).

Fecundity in the first eight weeks of life was significantly different amongst treatments ($F_{4,92} =$

12.7, $p < 0.001$). Overall the highest fecundity (eggs per female per day) was recorded during the third week for the following treatments: first instar nymphs (12.4 \pm 0.9), gravid females (22.5 \pm 1.3) and mixed diet (25.6 \pm 1.2). The average number of eggs produced in the mixed diet treatment was double that in the first instar nymph treatment (Fig. 1). Of the total number of eggs, 50 % were obtained on days 23, 34, 40, 37 and 41 in the first instar nymphs, second instar nymphs, young adults, gravid females and mixed diet treatments, respectively (Fig. 1).

During the first eight weeks of life, there were days when no oviposition occurred. These days were more frequent in the first instar nymph treatment (1.6 \pm 0.7 days), while there was on average <0.6 days without oviposition in the other treatments. After the ninth week, the number of days with no oviposition increased in all treatments: first instar nymphs, 2.2 \pm 0.3; second instar nymphs, 2.6 \pm 0.4; young adults, 2.2 \pm 0.5; gravid females, 0.6 \pm 0.2; and mixed diet, 1.9 \pm 0.6 days (Fig. 2). Fertility oscillated between 88 and 90 % in treatments that included adult female prey during the eight weeks of assessment, while it oscillated between 72 and 81 % in the first and second instar prey treatments.

Life tables

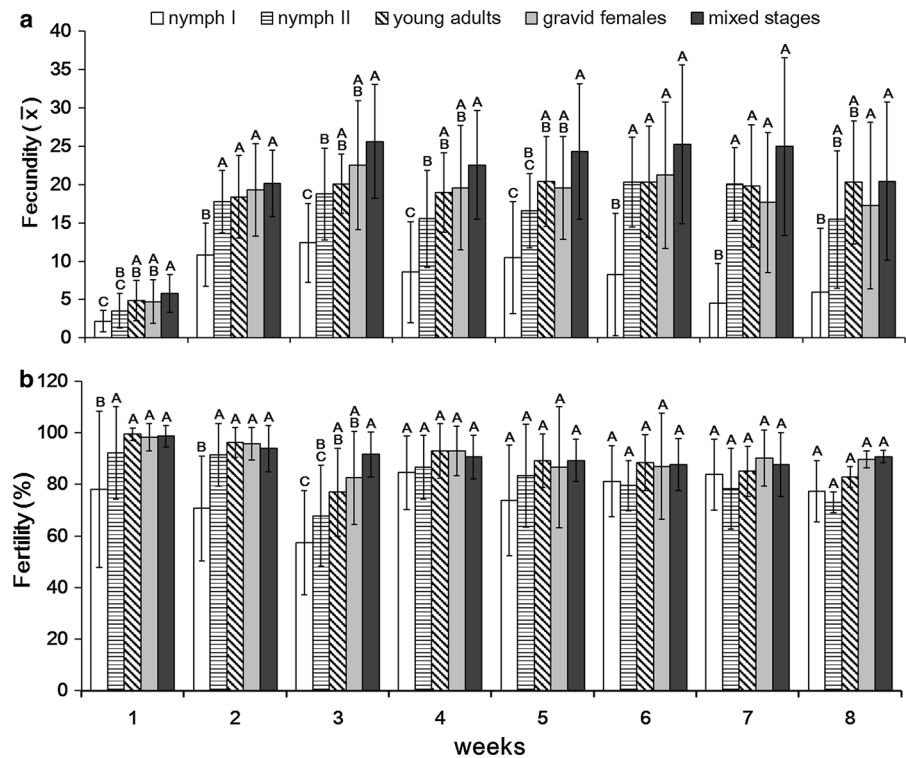
The treatments that included adult females in the diet had higher values for generation time and net reproduction rate than those fed with first instar nymphs, and resulted in an important difference in the intrinsic rate of increase (r_m) for the first instar nymph treatment relative to all the other treatments ($p < 0.05$) (Table 4). The intrinsic rate of increase (r_m), the finite rate of increase (λ) and the doubling

Table 3 Biological characteristics (mean \pm SE) of *Hyperaspis trifurcata* reared on different developmental stages of *Dactylopius opuntiae*

| Developmental stage | Pre-oviposition period (days) | Longevity (days) | Fecundity (eggs per female) | Fertility (%) |
|----------------------|-------------------------------|------------------|-----------------------------|-----------------|
| First instar nymphs | 6.4 \pm 0.3a | 49.6 \pm 5.4a | 57.8 \pm 10.1a | 71.9 \pm 2.7a |
| Second instar nymphs | 5.8 \pm 0.2ab | 61.1 \pm 4.5b | 140.5 \pm 13.2b | 80.3 \pm 2.7b |
| Young adults | 5.5 \pm 0.2ab | 75.7 \pm 6.0c | 193.4 \pm 16.3c | 88.5 \pm 2.5c |
| Gravid females | 5.6 \pm 0.2ab | 69.7 \pm 5.8bc | 183.9 \pm 21.0c | 90.1 \pm 1.6c |
| Mixed stages | 5.3 \pm 0.2b | 76.0 \pm 8.2c | 237.4 \pm 25.8d | 90.7 \pm 1.5c |

Means within a column followed by the same letter are not significantly different (Tukey's test, $p > 0.05$)

Fig. 1 Weekly records on the fecundity and fertility of *Hyperaspis trifurcata* (mean \pm SE) reared on different developmental stages of *D. opuntiae*. Only the first eight weeks of life are presented. **a** Average number of eggs laid per treatment; **b** Percentage of fertile eggs per treatment. Bars with the same letter are not significantly different in the same week (Tukey's test, $p > 0.05$)



time (DT) of the treatments with second instar nymphs were similar ($p > 0.05$) to those of the treatments that included adult female *D. opuntiae* as prey (Table 4).

Discussion

In Mexico and the USA there are at least 20 species of native predators that feed, at least occasionally, on *Dactylopius* species (Mann 1969; Gilreath and Smith 1988; Rodríguez-Leyva et al. 2010). However, the basic biology of most of these species is unknown. In this study, we determined that *H. trifurcata* could complete its life cycle when reared on first instar nymphs of *D. opuntiae*. The development time was 36.0 days for females, which is within the range found for other species in the genus, such as *Hyperaspis raynevali* Mulsant and *Hyperaspis pantherina* Fürsch reared on Pseudococcidae and Ortheziidae, respectively (Kanika-Kiamfu et al. 1992; Booth et al. 1995). It was also within the range of values reported for *Cryptolaemus montrouzieri* Mulsant (Coleoptera: Coccinellidae) reared on *Dactylopius tomentosus* Lamarck (Baskaran et al. 2002).

Hyperaspis trifurcata has a higher survival rate (83 %), compared with previous studies on *C. montrouzieri* (70.7 %) (Baskaran et al. 2002) and *Symphorobius barberi* (Banks) (16 %) (Neuroptera: Hemerobiidae) (Pacheco-Rueda et al. 2011) reared on *Dactylopius* species. That could suggest that *H. trifurcata* is better adapted to exploit this type of prey, which, among other distinguishing characteristics of the family, produces and accumulates carminic acid. This is thought to be a deterrent against predation (Eisner et al. 1994) and a component of the immune system (Hernández-Hernández et al. 2003) and could contribute to the prevention of parasitism (Stanley 2006). On the other hand, this adaptation of *H. trifurcata* to consume *Dactylopius* species does not avoid that *Homalotylus cockerelli* (Hymenoptera: Encyrtidae) reaches parasitism levels from 3 to 46 % on larvae and pupae of this coccinellid in some regions of Mexico and the USA (Gilreath and Smith 1988; Vanegas-Rico et al. 2015).

The voracity of *H. trifurcata* reared on first instar nymphs increased progressively with age. This is likely to be a function of the increase in size and nutritional requirements (Omkar and Bind 2004) and

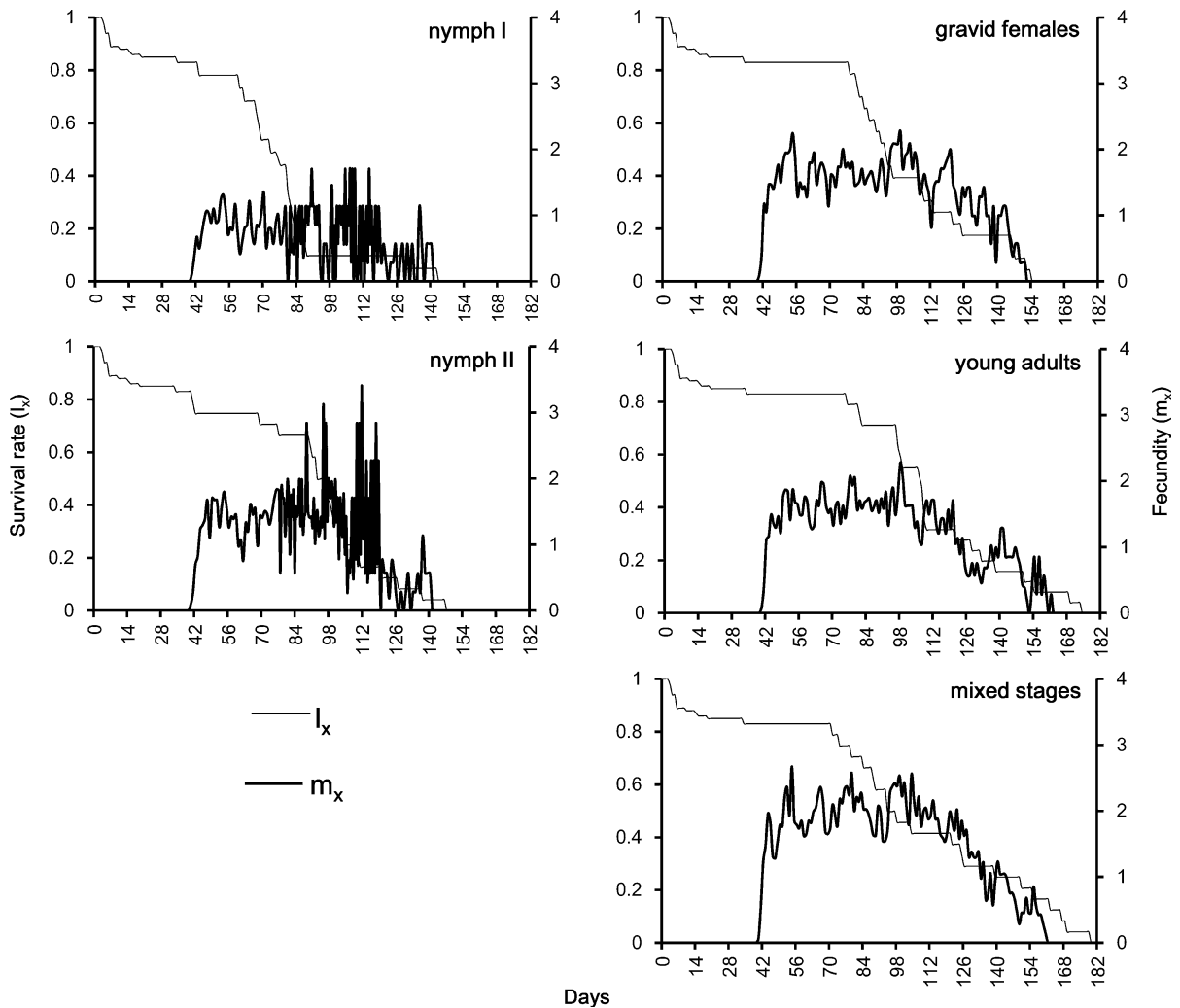


Fig. 2 Weekly records of age-specific fecundity (m_x) and age-specific survival (l_x) in relation to feed treatment

has also been observed in other *Hyperaspis* species (Reyd et al. 1991). Although the consumption of first instar nymphs was greater than that of other species (Santos et al. 2009), the proportion of prey consumed during the larval stages of *H. trifurcata* was only 9 % of the total amount consumed during the insect’s lifetime. This figure differs from that reported for *H. raynevali* (Reyd et al. 1991), *H. notata* (Dreyer et al. 1997) and *Hyperaspis marmottani* Fairm (Umeh 1982), which consumed around 50 % of their lifetime food requirements during the larval stages. *Hyperaspis trifurcata* adults consumed 91 % of their total prey requirement and thus have greater potential to exert a major effect on *D. opuntiae* populations.

The effect of prey age structure has implications for the biological control effectiveness of *H. trifurcata*. This result is similar to previous reports on *H. raynevali* (Reyd and Le Rü 1992) and *Hyperaspis senegalensis hottentotta* Mulsant (Kiyindou et al. 1990) consuming *Phenacoccus manihoti* Matilde-Ferrero (Homoptera: Pseudococcidae). The mixed diet, which included all of the developmental stages of *D. opuntiae*, was the treatment that resulted in the highest fecundity in *H. trifurcata*: 59, 81 and 408 % higher than when provided with young adults, second instar nymphs or first instar nymphs, respectively. There was also an increase in their longevity and fertility. This phenomenon has been observed in other

Table 4 Life table parameters (means and 95 % confidence levels) calculated for *Hyperaspis trifurcata* reared on different developmental stages of *Dactylopius opuntiae*

| Developmental stage | Generation time (T) (days) | Net reproductive rate (R ₀) | Intrinsic rate of increase (r _m) | Finite rate of increase (λ) | Doubling time (DT) (days) |
|----------------------|----------------------------|---|--|-----------------------------|---------------------------|
| First instar nymphs | 56.6a (49.1–64.1) | 27.3a (17.2–37.4) | 0.059a (0.053–0.064) | 1.060a (1.055–1.066) | 11.8a (10.8–12.8) |
| Second instar nymphs | 62.5ab (58.3–66.8) | 66.3b (53.3–79.3) | 0.067b (0.063–0.071) | 1.070b (1.065–1.073) | 10.3b (9.8–10.9) |
| Young adults | 66.4bc (62.0–70.7) | 91.5c (75.4–107.6) | 0.068b (0.065–0.071) | 1.070b (1.067–1.073) | 10.2b (9.8–10.6) |
| Gravid females | 64.9bc (59.5–70.4) | 86.8bc (65.9–197.7) | 0.069b (0.065–0.072) | 1.071b (1.067–1.075) | 10.1b (9.6–10.6) |
| Mixed stages | 68.6c (63.9–73.2) | 112.0c (86.5–137.6) | 0.069b (0.067–0.071) | 1.071b (1.069–1.072) | 10.1b (9.7–10.4) |

Life table parameters and confidence levels (95 %) were calculated using the SAS programme of Maia et al. (2000) with Jackknife estimations. Means within a column followed by the same letter are not significantly different by Student's t test for pairwise group comparison ($p > 0.05$). Non-independence of pairwise comparison were adjusted using Sidák's inequality test implemented in the programme (Maia et al. 2000)

species of Coccinellidae suggesting that their prey in certain development stages, or a combination of stages, may be important to maximizing egg production (Ponsonby and Copland 2007).

A diet based on first instar nymphs can be considered as standard for small coccinellid larvae (Ponsonby and Copland 2000), but they may be an insufficient source of nutrients for adult coccinellids. This nutrient deficit could lead to cannibalism (Hemptinne et al. 2000; Snyder et al. 2000; Cottrell 2005) or predation of other development stages of the prey (Ponsonby and Copland 2007). In our study, we observed that *H. trifurcata* first took immature prey from the mixed diet, probably because they were more vulnerable (Honda and Luck 1995; Ponsonby and Copland 2007) or because they contained less carminic acid than adults (Flores-Alatorre et al. 2014). Moreover, *H. trifurcata* consumed only a small portion of the biomass of the adult prey. Overall a daily maximum of five adult female *D. opuntiae* with feeding marks were recorded, but none were consumed entirely. Partial feeding on the adult prey may be due not only to nutritional requirements, but also to other factors such as a functional response (Vanegas-Rico et al. unpublished data) or greater gains may be achieved from consuming only a part of their prey (Cohen 1995). The mixed diet was probably the model most closely resembling field conditions where the pest populations overlap and each development stage is used according to the needs of the predator.

The mixed diet offered to *H. trifurcata* was assumed to be nutritionally different from the other development stages offered individually and, in general, increased longevity, fecundity and fertility. Nevertheless, with the mixed diet, generation time was longer than when first instar nymphs were provided (Table 4). In other words, the mixed diet improved the net reproduction rate but prolonged generation time. This phenomenon resulted in a difference in the intrinsic rate of increase (r_m) that was significant only for those provided with a diet of first instar nymphs (0.059), contrasting with the other diets that included second instar nymphs or adults (0.067, 0.068, 0.069, 0.069). The population parameters of *D. opuntiae* were not previously reported. However, each female is capable of laying up to 154 eggs in her lifetime in a 1:1 sex ratio (Flores-Hernández et al. 2006). This fecundity rate is lower than any fecundity rate of *H. trifurcata* reared in the present study on diets that contained *D. opuntiae* adults.

This paper reports aspects of the basic biology of *H. trifurcata* reared on *D. opuntiae*. Although its biological potential has not been completely assessed, the parameters measured for *H. trifurcata* indicate that it is a potential candidate for testing as a biological control agent of *D. opuntiae* in *Opuntia* ecosystems and agroecosystems.

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