

ORIGINAL ARTICLE

Comparative life table statistics for the ladybeetle *Scymnus syriacus* reared on the green citrus aphid, *Aphis spiraecola*, fed on two host plants

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Abstract

Demographic statistics for the ladybeetle *Scymnus syriacus* Marseul (Coleoptera: Coccinellidae) were investigated when reared on the green citrus aphid, *Aphis spiraecola* Patch (Homoptera: Aphididae), fed on two host plants: spirea (*Spirea* sp.) and Thompson orange (*Citrus sinensis* cv. Thompson) under laboratory conditions ($25 \pm 1^\circ\text{C}$, $65 \pm 5\%$ relative humidity and 16 h light : 8 h dark). Mean developmental times from egg to adult were 20.32 ± 0.18 and 22.07 ± 0.15 days for spirea and Thompson orange, respectively. The survival rate from egg to adult was higher for spirea (85%) than for Thompson orange (72.5%). The oviposition periods were 41.8 ± 2.47 and 39.71 ± 2.6 days and the total number of eggs per female were 657.6 ± 29.5 and 587.9 ± 32.6 on spirea and Thompson orange, respectively. Fertility life tables were also constructed to compare the effects of host plants. The intrinsic rate of increase (r_m) on spirea was higher than that on Thompson orange. Jackknife estimates of r_m varied from 0.149 on spirea to 0.133 on Thompson orange. The mean population generation times on these host plants were 38.16 and 40.65 days, respectively. These results indicate that spirea-fed *A. spiraecola* is more suitable for *S. syriacus*, producing a higher survival rate and shorter developmental time.

Key words: demographic statistics, generation time, intrinsic rate of increase, ladybeetle, survival rate.

INTRODUCTION

The spirea (green citrus) aphid, *Aphis spiraecola* Patch, is a polyphagous species with a worldwide distribution. It is a pest of citrus (Cole 1925; Miller 1929; Yokomi & Tang 1995) and ornamentals (Blackman & Eastop 2000), and is a vector of the citrus tristeza virus (Yokomi & Garnsey 1987; Tsai & Wang 2001). When young shoots are fed upon by this aphid, foliage distortion often results, and the honeydew secreted by aphids not only promotes growth of sooty mold (Cole 1925; Miller 1929), but also attracts ants, which deter the natural enemies of aphids, resulting in additional pest damage (Yokomi & Tang 1995).

Plant species differ greatly with respect to their suitability as host plants; a plant's nutritional value, secondary metabolites, and architectural characteristics can all influence the fecundity, population growth and survival of herbivorous insects (Slansky & Feeny 1977; Norris & Kogan 1980; Montllor 1991; Rutledge & O'Neil 2005). Some plant species protect themselves from herbivorous insects by producing a variety of secondary metabolites (Nielsen 1978; Isman & Duffey 1982). Having a low nutritional value can also act as a defense against herbivory and decrease the herbivore's fecundity or increase its developmental time (Michaud 1999). The natures of both the host plant and prey species influence how natural enemies search, thus the quality of their dietary resources influences their biology (Dixon & Russell 1972; Price *et al.* 1980; Carter *et al.* 1984; Coll & Ridgeway 1995).

The ladybeetle *Scymnus syriacus* Marseul is a successful predator, with a proven ability to dramatically

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reduce the size of green citrus aphid populations. This predator has been reported from various parts of Iran, where it is important in green citrus aphid control (Rezvani *et al.* 1994; Emami 1996). Natural enemies of phytophagous insects function and develop in multitrophic systems (Price *et al.* 1980). Thus, their behavior and physiology, which determine their fitness, are influenced by both the plant (first trophic level) and the phytophagous host (second trophic level) (Vinson 1976; Takabayashi *et al.* 1991). Some herbivorous insects protect themselves against general predators by accumulating toxic substances in their bodies (Evans & Schmidt 1990; Fukunaga & Akimoto 2007); aphids have also been shown to assimilate secondary compounds from their host plants to produce substances which are toxic to predators. For example, larvae of the ladybeetle *Harmonia axyridis* Pallas suffer high mortality and lower growth rate when fed with the aphid *Aulacorthum magnoliae* Essig et Kuwana associated with elder, *Sambucus sieboldiana* Schwer (Fukunaga & Akimoto 2007). Okamoto (1978) found that *H. axyridis* larvae completely failed to develop when they were fed with *Aphis craccivora* Koch. The extent to which aphids are toxic to predators will change depending on seasonal factors and which part of the host plant the aphid colonizes (Takeda *et al.* 1964; Bristow 1991; Francis *et al.* 2000, 2001).

The cohort life table gives the most comprehensive description of the survivorship, development and reproduction of a population and, as such, is fundamental to both theoretical and applied population ecology. Collection of life table data for relevant species of different trophic levels in a food chain is a basic and important task for conservation (Bevill & Louda 1999; Gabre *et al.* 2005) and pest management (Naranjo 2001). Estimating the growth parameters and reproduction potential of an insect population are essential requirements in their study. A fertility life table describes the potential reproduction capacities of females at different times and is created by following the survival of a cohort born at the same time and recording survival and death until all members of the cohort have died. Such life tables can be used to describe the developmental times and survival rates of each growth stage and to predict the size of a population (Carey 1993; Medeiros *et al.* 2000; Southwood & Henderson 2000).

The intrinsic rate of increase (r_m) summarizes the physiological qualities of an animal relative to its capacity to increase (Andrewartha & Birch 1954). The intrinsic rate of increase is also useful to estimate the population growth potential of insects and mites, which may help predict the outcomes of pest–natural enemy

interactions (Roy *et al.* 2003). Comparisons of intrinsic rates of increase often provide considerable insight beyond what is available from independent analysis of several life history parameters (Petitt *et al.* 1994). Although the components of r_m are affected by a large number of factors, there is a close and positive association between the mean relative growth rate and r_m (Guldmond *et al.* 1998). The mean relative growth rate is mainly determined by food quality; if r_m values are to be used effectively, levels of confidence must be assigned to the observed differences. However, without variance information, it is difficult to interpret estimates (Petitt *et al.* 1994). The use of jackknife techniques to estimate the variance of r_m enables us to test the statistical significance of r_m values.

The purpose of this study was to examine the effect of two host plants on the biology and life table parameters of *S. syriacus* under laboratory conditions.

MATERIALS AND METHODS

Plants and insects

Two host plants commonly found in the north of Iran (Guilan province) were used in this study. These were: *Spirea* sp. and Thompson orange. Plants were maintained in a greenhouse in pots (220 mm × 230 mm). Fertilizers (12:8:6 N : P : K) were added to the pots, which were watered as required.

A stock culture of spirea aphids originating from citrus trees in the greenhouse of Ramsar Citrus Research Center was used. The aphids were maintained on two potted Thompson oranges (Rutaceae) in an insect-rearing room at $25 \pm 1^\circ\text{C}$, $65 \pm 5\%$ relative humidity and a photoperiod of 16 h light : 8 h dark. After a month of rearing, the resulting colonies were transferred to potted spirea (Rosaceae) and Thompson orange and reared for 2 months. The ladybeetle predators used in this study were collected from spirea shrubs and cultured for a generation on aphids fed on potted spirea and Thompson orange host plants (as described above).

Development time and survival rate of immature stages

The biology of *S. syriacus* was studied using eggs produced by the first generation adults of a stock culture on each host plant. Spirea and Thompson orange leaves bearing *Aphis spiraeicola* were inserted in a cotton wool ball for moisture and placed in Petri dishes. Petri dishes were 80 mm in diameter and had a hole (15 mm in diameter) in the center of the lid, which was covered

with muslin for aeration. This experiment was performed on each host plant using 40 eggs (0–24 h old). These eggs were placed separately on each host plant leaf. After the eggs hatched, the larvae were fed on aphids and were observed daily to record different larval instars (i.e. through exuviae), mortality and the survival of immature stages. The leaves bearing aphids were replaced daily, except for during the pupal stage of the ladybeetle. Fine brushes were used to move insects onto fresh leaves.

Longevity and fecundity

To study the preoviposition, oviposition and postoviposition periods, and the longevity and fecundity of *S. syriacus*, ten pairs of 24-h-old adults were reared on each host plant separately. Then each pair was placed in a Petri dish containing host plant leaves (as described above) and was provided with 40–50 aphids every day. Petri dishes were observed daily to record longevity, fecundity and other events in the lives of the adult beetles.

Statistical analysis

Data analysis with respect to development, longevity and fecundity was performed using the *t*-test with SAS software.

Ratio of females

Sex ratios were calculated using the method of Maia *et al.* (2000).

Immature stages survivorship

The percentage of offspring that survived until adulthood (SURV), also known as pre-imaginal survivorship, was calculated by dividing the number of insects alive until adulthood (NA) by the number of eggs taken from each group (Ng):

$$\text{SURV} = \text{NA}/\text{Ng}$$

Calculation of parameters

Population growth parameters were calculated using the method of Carey (1993). The jackknife method proposed by Meyer *et al.* (1986) was used to estimate the variance for r_m . Population growth rates were calculated using the methods of Andrewartha and Birch (1954) and Southwood (1976):

$$1 = \sum e^{-rx} l_x m_x$$

where x is age in days, r is the intrinsic rate of increase, l_x is age-specific survival, and m_x is age-specific number of female offspring.

Uncertainty associated with parameter estimates

After r_m was computed for the original data (r_{all}), the differences in r_m values were tested for significance by estimating the variance using the jackknife method to facilitate calculation of the standard errors of r_m estimates (Sokal & Rohlf 1995; Meyer *et al.* 1986). The jackknife pseudo-value r_j is calculated by omitting data for the j th individual of the cohort using the following equation:

$$r_j = n \times r_{all} - (n - 1) \times r_i$$

where n is the total number of female individuals used in the life table analysis, and r_j is the intrinsic rate estimated using data from the remaining $n - 1$ individuals. The mean values of n jackknife pseudo-values and their standard error were then computed.

Comparisons of parameters between groups

To perform pairwise comparisons between groups, Student's *t*-test for independent samples with different variances was used.

RESULTS

Development and survivorship of immature stages

The embryonic developmental time for *S. syriacus* was significantly longer on aphids fed on Thompson orange than on those fed spirea (Table 1). In all immature stages except for the first larval stage, there were no differences in the development period on the two host plants, but the total post-embryonic developmental time (four larval stages) on Thompson orange was longer than on spirea, and there were statistical differences between the two host plants. The fourth larval and pupal periods were longer than the other stages on both host plants. The total developmental time (egg to adult) on Thompson orange was significantly longer than on spirea.

The survival rate of eggs was higher on spirea. In the immature stages, mortality occurred in the first and fourth larval stages on spirea and in the first larval and pre-pupal stages on Thompson orange. The total survival rate of the immature stages on spirea (85%) was higher than on Thompson orange (72.5%; Table 2).

The mean durations of the pre-oviposition, oviposition and post-oviposition periods, and longevity data for females are given in Table 3. Only the pre-ovipositional period differed significantly for the two host plants (it was longer on Thompson orange). The ovipositional

Table 1 Mean developmental times (days; mean \pm SE) of *Scymnus syriacus* on spirea and Thompson orange

Plant	Egg stage	First larval instar	Second larval instar	Third larval instar	Fourth larval instar	Total larval instar	Pupa	Larva + Pupa	Egg to adult
Spirea	4.64 \pm 0 ^a	2.31 \pm 0.08 ^a	1.83 \pm 0.06 ^a	1.57 \pm 0.1 ^a	3.15 \pm 0.0 ^a	8.82 \pm 0.1 ^a	5.41 ^a	15.7 \pm 0.14 ^a	20.32 \pm 0.18 ^a
Thompson orange	4.97 \pm 0 ^b	2.62 \pm 0.08 ^b	1.97 \pm 0.07 ^a	1.62 \pm 0.0 ^a	3.31 \pm 0.0 ^a	9.51 \pm 0.1 ^b	5.89 ^b	17.03 \pm 0.15 ^b	22.07 \pm 0.15 ^b

Means within columns followed by the same letter are not statistically significantly different according to the *t*-test ($P = 0.05$).

Table 2 Survival rates (%) of eggs and immature stages of *Scymnus syriacus* on spirea and Thompson orange

Host plant	Egg	First larval instar	Second larval instar	Third larval instar	Fourth larval instar	Prepupa	Pupa	Egg to adult
Spirea	90	97.2	100	100	97.1	100	100	85
Thompson orange	85	94.1	100	100	100	100	90.6	72.5

Table 3 Biological parameters, longevity (days) and fecundity of *Scymnus syriacus* on spirea and Thompson orange (mean \pm SE)

Plant	Premating	Mating to oviposition	Preoviposition	Oviposition	Postoviposition	Longevity	No. eggs per female
Spirea	2.7 \pm 0.15 ^a	3.4 \pm 0.22 ^a	5.51 \pm 0.17 ^a	41.8 \pm 2.47 ^a	3.43 \pm 0.6 ^a	50.3 \pm 2.9 ^a	657.6 \pm 2 ^a
Thompson orange	2.9 \pm 0.18 ^a	3.5 \pm 0.16 ^a	6.1 \pm 0.018 ^b	39.71 \pm 2.6 ^a	3.6 \pm 0.4 ^a	47.9 \pm 3.1 ^a	587.9 \pm 3 ^a

Means within a column followed by the same letter are not statistically significantly different according to the *t*-test ($P = 0.05$).

and post-ovipositional periods were longer on spirea, but the difference was not significant.

The longevity of females was also shorter on spirea than on Thompson orange, but the difference was not statistically significant. Fecundity on spirea was higher, with a peak observed on the 31st day from the onset of the egg-laying period. On Thompson orange, the highest fecundity was observed on the 32nd day.

The sex ratio of the ladybeetles' offspring was close to 1:1 (51:49, $\chi^2 = 0.841$; 47.5:52.5, $\chi^2 = 0.812$ on spirea and Thompson orange, respectively). The survival rates of adults on both plants decreased gradually after a peak in egg production (Fig. 1).

Population growth parameters

The demographic parameters calculated using approximate and iterative methods revealed no differences, thus the jackknife method was deemed to be most appropriate for analysis of the data (Meyer *et al.* 1986). Net reproductive rate (R_0), intrinsic rate of increase (r_m) and finite rate of increase (λ) were significantly higher on spirea, and generation time (T) and doubling time (DT) were significantly higher on Thompson orange. Jackknife estimates, respective standard errors and *P*-values

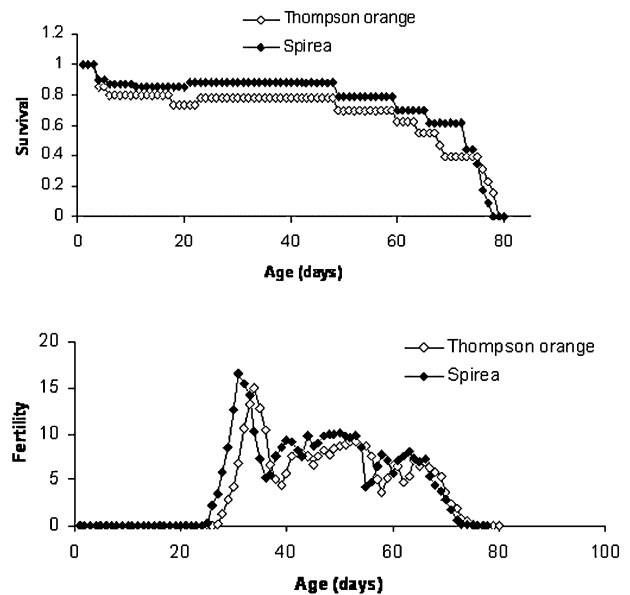


Figure 1 Age-specific survival rate (l_x) for pre-adult and adult stages, and age-specific fertility (m_x) of *Scymnus syriacus* on Thompson orange and spirea.

Table 4 Associated life table estimates for *Scymnus syriacus* on spirea and Thompson orange

Parameters	Spirea			Thompson orange		
	True calculation \pm SEM	Jackknife estimate	95% CI	True calculation \pm SEM	Jackknife estimate	(95% CI) <i>P</i>
Net reproductive rate (R_0) (female/female)	292.24 \pm 13.61	292.19	(261.39–322.99)	219.006 \pm 12.43	218.98	(190.85–247.11) 0.003255
Intrinsic rate of increase (rm) (female/female/day)	0.149 \pm 0.0007	0.149	(0.147–0.150)	0.133 \pm 0.001	0.133	(0.130–0.135) 0.0000001
Finite rate of increase (λ)(female/female/day)	1.16 \pm 0.0008	1.16	(1.158–1.162)	1.14 \pm 0.0012	1.14	(1.139–1.145) 0.0000001
Mean generation time (T) (days)	38.16 \pm 0.39	38.16	(37.28–39.04)	40.65 \pm 0.45	40.65	(39.63–41.67) 0.002484
Doubling time (Dt) (days)	4.66 \pm 0.023	4.66	(4.61–4.71)	5.23 \pm 0.41	5.23	(5.1–5.3) 0.0000012

CI, confidence interval.

are shown in Table 4. The values of parameter $b + d$ as an index of vital occurrences per capita population were 13.96 and 7.04 on spirea and Thompson orange, respectively.

DISCUSSION

Plant species differ greatly in terms of their suitability as hosts for specific insects when assessed in terms of insect mortality and reproductive rate. Shorter development times and greater total reproduction indicate that a plant is a suitable host. Although developmental rates and reproduction provide important clues concerning the ability of the host to support a complete insect life cycle, these data should be linked to other parameters (e.g. mortality) before definite conclusions can be drawn concerning host suitability for reproductive purposes (Van Lenteren & Noldus 1990). Host plants sometimes indirectly influence the performances of predators and parasitoids of phytophagous insects (Price *et al.* 1980; Ohgushi 2005). For example, there is variation in the fatty acid content of the aphid *Acyrtosiphon pisum* depending on its host plant, and this in turn affects the performance of its insect natural enemies (Giles *et al.* 2000, 2002). Fukunaga and Akimoto (2007) found that the aphid *A. magnoliae* has the potential to assimilate toxic substances from its host plants: larvae of the ladybeetle *H. axyridis* fed with aphids reared on elder (*S. sieboldiana*) suffered significantly higher mortality and grew more slowly. In the present study, although developmental times in some preadult stages were similar, significant

differences were found in total preadult development time between *S. syriacus* reared on *A. spiraecola* fed on the two host plants. The net reproductive rate and mean generation time of *S. syriacus* were found to be significantly higher for spirea than for Thompson orange. However, the fecundity curves and survival rates of *S. syriacus* on the two host plants were similar.

Survival rate data provides detailed information on not only survival but also stage transitions. Since it takes into account variation in developmental rates among individuals, it is possible to demonstrate stage overlap during the development of a cohort (Amir-Maafi & Chi 2006). The generation time for *S. syriacus* on spirea was similar to that for *S. apetzi* (~40.7 days) and that on Thompson orange was similar to that for *S. subvillosus* (~38.3 days) (Atlihan & Kaydan 2002), and these values were higher than those reported for *S. buffmanni* (~20.5 days) (Kawauchi 1985) and *S. marginicollis* Mannh (~22 days) (Buntin & Tamaki 1980). The doubling time for *S. syriacus* on spirea was less than that on Thompson orange, suggesting that spirea is more suitable for an increase in the predator's population. However, the doubling time was the same as has been reported for *S. coccivora* (Persad & Khan 2002). Recent studies on other ladybeetles have also demonstrated that development, survivorship and reproduction vary significantly with the host plant (LeRu & Mitsipa 2002; Vatansever *et al.* 2003; Du *et al.* 2004; Fukunaga & Akimoto 2007). The results of this study indicate that spirea-fed *A. spiraecola* are more suitable for *S. syriacus* than those fed on Thompson orange, leading to a higher survival rate and shorter developmental time.

The intrinsic rate of increase (r_m) is a more useful statistic for comparing the population growth potential of different species than is R_0 (Price 1997). According to Southwood (1981) and Huffaker *et al.* (1984), r -strategists are characterized by a high r , a large fecundity (large R_0) and short generation time (T). In *S. syriacus*, the finite rate of increase (λ) is greater than 1, suggesting that it is an r -strategist. The value of r_m obtained here for *S. syriacus* on spirea was greater than that for Thompson orange. However, it was similar to the r_m value calculated for *S. levaillanti* (0.151) (Uygan & Atlihan 2000). The r_m values for *S. frontalis* feeding on *Duraphis noxia* (Mordvilko), *A. pisum* (Harris), and *A. graminum* were 0.73, 0.65 and 0.63, respectively (Gibson *et al.* 1992) and 0.236 for *S. huffmanni* (Kawauchi 1985), which are all higher than the r_m calculated for *S. syriacus*. The values of r_m for *S. apetzii* and *S. subvillosus* have been reported to be 0.121 and 0.11 when fed on *Hyalopterus pruni* (Atlihan & Kaydan 2002), which are lower than the corresponding value obtained in the present study. The life table parameters obtained in this study for *S. syriacus* can be used to estimate the rate of increase of a natural or released population (El Hag & Zaitoon 1996) and to determine when to release laboratory-reared coccinellids. The parameter r_m is of especial interest because it integrates the effects of mortality and fertility in a single value (Kontodimas *et al.* 2007).

Chi (1990) used life table data to simulate timing of pest control based on the change of age stage structure during the growth of a population. The inclusion of predator and prey age structure is important in understanding the predator-prey relationship in biological control (e.g. Hassell 1978). Chi and Yang (2003) studied the predation rate of *Propylaea japonica* based on an age-stage life table and showed how changes in predation rate with age and stage could be incorporated into a life table study. Life table data obtained under laboratory conditions can be used as a basis for simulation models for field use that include other factors (Gutierrez 1996). Life history parameters need to be determined in the laboratory, which usually involves rearing insects under controlled conditions, despite the fact that they are subjected to more complex and fluctuating conditions in their natural environment. Nevertheless, life tables remain a very useful tool for evaluating the effectiveness of natural enemies for controlling pests under various climatic conditions and in different habitats (Birch 1948; Jervis & Copland 1996). The results of the current study, in which the life table parameters of *S. syriacus* on two different host plants were compared,

provide useful information that will facilitate more effective control of *A. spiraeicola* by this ladybeetle.

REFERENCES

- Amir-Maafi M, Chi H (2006) Demography of *Habrobracon hebetor* (Hymenoptera: Braconidae) on two pyralid hosts (Lepidoptera: Pyralidae). *Annals of the Entomological Society of America* **99**, 84–90.
- Andrewartha HG, Birch LC (1954) *The Distribution and Abundance of Animals*. University of Chicago Press, Chicago.
- Atlihan R, Kaydan MB (2002) Development, survival and reproduction of three coccinellids feeding on *Hyalopterus pruni* Geoffr (Homoptera: Aphididae). *Turkish Journal of Agriculture and Forestry* **26**, 119–124.
- Bevill TS Jr, Louda SM (1999) Comparison of related rare and common species in the study of plant rarity. *Conservation Biology* **13**, 493–498.
- Birch LC (1948) The intrinsic rate of natural increase of an insect population. *Journal of Animal Ecology* **17**, 15–26.
- Blackman RL, Eastop VF (2000) *Aphids on the World's Crops. An Identification and Information Guide*. Wiley, New York.
- Bristow CM (1991) Are ant aphid associations a tritrophic interaction? Oleander aphids and Argentine ants. *Oecologia* **87**, 514–521.
- Buntin LA, Tamaki G (1980) Bionomic of *Scymnus marginicollis* (Coleoptera: Coccinellidae). *Canadian Entomologist* **112**, 675–680.
- Carey JR (1993) *Applied Demography for Biologists*. Oxford University Press, New York.
- Carter MC, Sutherland D, Dixon AFG (1984) Plant structure and searching efficiency of coccinellid larvae. *Oecologia (Berl.)* **63**, 394–397.
- Chi H (1990) Timing of control based on the stage structure of pest population: a simulation approach. *Journal of Economic Entomology* **83**, 1143–1150.
- Chi H, Yang TC (2003) Two sex life table and predation rate of *Propylaea japonica* Thunberg (Coleoptera: Coccinellidae) fed on *Myzus persicae* (Sulzer) (Homoptera: Aphididae). *Environmental Entomology* **32**, 327–333.
- Cole FR (1925) The natural enemies of the citrus aphid, *Aphis spiraeicola* Patch. *Journal of Economic Entomology* **18**, 219–316.
- Coll M, Ridgeway RL (1995) Functional and numerical responses of *Orius insidiosus* (Heteroptera: Anthicoridae) to its prey in different vegetable crops. *Ecology and Population Biology* **88**, 732–747.
- Dixon AFG, Russell RJ (1972) The effectiveness of *Anthocoris nemorum* and *A. confusus* (Hemiptera: Anthicoridae) as predators of the sycamora aphid, *Drepanosiphum platanoides*, 11. Searching behavior and the incidence of predation in the field. *Entomologia Experimentalis et Applicata* **15**, 35–50.

- Du L, Ge F, Zhu S, Parajulee MN (2004) Effect of cotton cultivar on development and reproduction of *Aphis gossypii* (Homoptera: Aphididae) and its predator, *Propylaea japonica* (Coleoptera: Coccinellidae). *Journal of Economic Entomology* **97**, 1278–1283.
- El Hag EA, Zaitoon AA (1996) Biological parameters for four coccinellid species in Central Saudi Arabia. *Biological Control* **7**, 316–319.
- Emami MS (1996) Biological studies and possibility of mass rearing of *Scymnus syriacus* Marseul (Coleoptera: Coccinellidae) (MSc Thesis). University of Tarbiat Modares, Tehran.
- Evans DL, Schmidt JO (1990) *Insect Defenses*. State University of New York Press, Albany.
- Francis F, Haubruge E, Gasper C (2000) Influence of host plant on specialist/generalist aphids and on the development of *Adalia bipunctata* (Coleoptera: Coccinellidae). *European Journal of Entomology* **97**, 481–486.
- Francis F, Lognag G, Wathelet J, Haubruge E (2001) Effects of allelochemicals from first (Brassicaceae) and second (*Myzus persicae* and *Brevicoryne brassicae*) trophic levels on *Adalia bipunctata*. *Journal of Chemical Ecology* **27**, 243–256.
- Fukunaga Y, Akimoto S (2007) Toxicity of the aphid *Aulacorthum magnoliae* to the predator *Harmonia axyridis* (Coleoptera: Coccinellidae) and genetic variance in the assimilation of the toxic aphids in *H. axyridis* larvae. *Entomological Science* **10**, 45–53.
- Gabre RM, Adham FK, Chi H (2005) Life table of *Chrysomya megacephala* (Fabricius) (Diptera: Calliphoridae). *Acta Oecologia* **27**, 179–183.
- Gibson RL, Elliott NC, Schaefer P (1992) Life history and development of *Scymnus frontalis* Fabricius (Coleoptera: Coccinellidae) on four species of aphids. *Journal of the Kansas Entomological Society* **65**, 410–415.
- Giles KL, Madden RD, Payton ME, Dilwith JW (2000) Survival and development of *Chrysoperia rufilabris* (Neuroptera: Chrysopidae) supplied with pea aphids (Homoptera: Aphididae) reared on alfalfa and faba bean. *Environmental Entomology* **29**, 304–311.
- Giles KL, Madden RD, Stockland R, Payton ME, Dillwith JW (2002) Host plants affect predator fitness via the nutritional value of herbivore prey: investigation of a plant-aphid-ladybeetle system. *Biocontrol* **47**, 1–21.
- Guldemond JA, van den Brink WJ, den Belder E (1998) Methods of assessing population increase in aphids and the effect of the growth stage of the host plant on population growth rates. *Entomologia Experimentalis et Applicata* **86**, 163–173.
- Gutierrez AP (1996) *Applied Population Ecology: A Supply-Demand Approach*. Wiley, New York.
- Hassell MP (1978) *The Dynamics of Arthropod Predator-Prey Systems*. Princeton University Press, New York.
- Huffaker CB, Beryman AA, Laing JE (1984) Natural control of insect populations. In: Huffaker CB, Rabb RL (eds) *Ecological Entomology*, pp 359–398. Wiley, New York.
- Isman MB, Duffey SS (1982) Toxicity of tomato phenolic compounds to the fruitworm, *Heliothis zea*. *Entomologia Experimentalis et Applicata* **31**, 370–376.
- Jervis MA, Copland MJW (1996) The life cycle. In: Jervis MA, Kidd NAC (eds) *Insect Natural Enemies. Practical Approaches to their Study and Evaluation*, pp 63–161. Chapman and Hall, London.
- Kawauchi SE (1985) Comparative studies on the fecundity of three aphidophagous coccinellids (Coleoptera: Coccinellidae). *Applied Entomology and Zoology* **29**, 203–209.
- Kontodimas DC, Milonas PG, Stathas GJ, Economou LP, Kavallieratos NG (2007) Life table parameters of the pseudococcid predators *Nephus includens* and *Nephus bisignatus* (Coleoptera: Coccinellidae). *European Journal of Entomology* **104**, 407–415.
- LeRu BP, Mitsipa A (2002) Comparative life table statistics of *Exochomus flaviventris* reared on the cassava mealybug, *Phenacoccus manihoti*, fed on four host plants. *Insect Science and its Application* **22**, 175–182.
- Maia AHN, Luiz AJB, Campanhola C (2000) Statistical inference on associated fertility life table parameters using the jackknife technique: computational aspects. *Journal of Economic Entomology* **93**, 511–518.
- Medeiros RS, Ramalho FS, Lemos WP, Zanuncio JC (2000) Age-dependent fecundity and fertility life tables for *Podisus nigrispinus* (Heteroptera: Pentatomidae). *Journal of Applied Entomology* **124**, 319–324.
- Meyer JS, Igersoll CG, McDonald LL, Boyce MS (1986) Estimating uncertainty in population growth rates: jackknife vs. bootstrap techniques. *Ecology* **67**, 1156–1166.
- Michaud JP (1999) Sources of mortality in colonies of the brown citrus aphid, *Toxoptera citricida* Kirkaldy. *Biocontrol* **44**, 347–367.
- Miller RL (1929) A contribution to the biology and control of the spirae aphid, *Aphis spiraecola* Patch. *Florida Agricultural Experimental Station Bulletin* **203**, 431–476.
- Montllor C (1991) The influence of plant chemistry on aphid feeding behavior. In: Bernays EA (ed.) *Insect-Plant Interactions*, Vol. 3, pp 125–173. CRC, Boca Raton, FL.
- Naranjo SE (2001) Conservation and evaluation of natural enemies in IPM systems for *Bemisia tabaci*. *Crop Protection* **20**, 835–852.
- Nielsen JK (1978) Host plant discrimination within Cruciferae: feeding responses of four leafbeetles (Coleoptera: Chrysomelidae) to glucosinolate, cucurbitactins and cardenolides. *Entomologia Experimentalis et Applicata* **24**, 41–54.
- Norris DM, Kogan M (1980) Biochemical and morphological bases of resistance. In: Maxwell FC, Jennings PR (eds) *Breeding Plants Resistant to Insects*, pp 23–61. Wiley, New York.

- Ohgushi T (2005) Indirect interaction webs: herbivore-induced effects through trait change in plants. *Annual Review of Ecology and Systematics* **36**, 81–105.
- Okamoto H (1978) Laboratory studies on food ecology of aphidphagous lady beetles Coleoptera: Coccinellidae). *Memoirs of the Faculty of Agriculture, Kagawa University* **32**, 1–94. (In Japanese with English summary.)
- Persad A, Khan A (2002) Comparison of life table parameters for *Maconellicoccus hirsutus*, *Anagyrus kamali*, *Cryptolaemus montrouzieri* and *Scymnus coccivora*. *Biocontrol* **47**, 137–149.
- Pettitt FL, Loader CA, Schan MK (1994) Reduction of nitrogen concentration in the hydroponic solution on population growth rate of the aphids (Homoptera: Aphididae) *Aphis gossypii* on cucumber and *Myzus persicae* on pepper. *Environmental Entomology* **23**, 930–936.
- Price PW (1997) *Insect Ecology*, 3rd edn. Wiley, New York.
- Price PW, Bouton CE, Gross P, McPherson BA, Thompson JN, Weis AE (1980) Interaction among three trophic levels: influence of plants on interaction between insect herbivores and natural enemies. *Annual Review of Ecological Systems* **11**, 4–65.
- Rezvani A, Termeh F, Mosavi M (1994) *Aphids of Iran and their Host Plants*. Research Institute of Plant Pests and Diseases, Ministry of Agriculture, Tehran.
- Roy M, Brodeur J, Cloutier C (2003) Effect of temperature on intrinsic rates of natural increase (rm) of a coccinellid and its spider mite prey. *Biocontrol* **48**, 57–72.
- Rutledge CE, O'Neil RJ (2005) *Orius insidiosus* (Say) as a predator of the soybean aphid, *Aphis glycines* Matsumara. *Biological Control* **33**, 56–64.
- Slansky F, Feeny P (1977) Stabilization of the rate of nitrogen accumulation by larvae of the cabbage butterfly on wild and cultivated food plants. *Ecological Monographs* **47**, 209–228.
- Sokal RR, Rohlf FJ (1995) *Biometry*, 3rd edn. WH Freeman, San Francisco.
- Southwood TRE (1976) *Ecological Methods*. Chapman and Hall, London.
- Southwood TRE (1981) Bionomics strategies and population parameters. In: May RM (ed.) *Theoretical Ecology: Principles and Applications*, 2nd edn, pp 30–52. Blackwell, Oxford.
- Southwood TRE, Henderson PA (2000) *Ecological Methods*, 3rd edn. Blackwell, Oxford.
- Takabayashi J, Dicke M, Posthumus MA (1991) Variation in composition of predator-attracting allelochemicals emitted by herbivore-infested plants: relative influence of plant and herbivore. *Chemoecology* **2**, 1–6.
- Takeda S, Hukushima S, Yamada H (1964) Seasonal abundance in coccinellid beetles. *Research Bulletin of the Faculty of Agriculture, Gifu University* **19**, 55–63. (In Japanese with English summary.)
- Tsai JH, Wang JJ (2001) Effects of host plants on biology and life table parameters of *Aphis spiraeicola* (Homoptera: Aphididae). *Environmental Entomology* **30**, 44–50.
- Uygan N, Atlihan R (2000) The effect of temperature on development and fecundity of *Scymnus levaillanti*. *Biocontrol* **45**, 453–462.
- Van Lenteren JC, Noldus JJ (1990) Whitefly plant relationship: behavioral and ecological aspects. In: Gerling D (ed.) *Whiteflies: their Bionomics, Pest-Status and Management*, pp 47–89. Intercept, Andover, UK.
- Vatansever G, Ulusoy MR, Bakirciolu PL (2003) Improving the mass rearing possibilities of *Serangium montazerii* Fursch (Coleoptera: Coccinellidae) on different host plants of *Bemesia tabaci* Genn (Homoptera: Aleyrodidae). *Turkish Journal of Agriculture* **27**, 175–181.
- Vinson SB (1976) Host selection by insect parasitoids. *Annual Review of Entomology* **21**, 109–133.
- Yokomi RK, Garnsey SM (1987) Transmission of citrus tristeza virus *Aphis gossypii* and *Aphis citricola* in Florida. *Phytophylactia* **19**, 169–172.
- Yokomi RK, Tang YQ (1995) Host preference and suitability of two aphelinid parasitoid (Hymenoptera: Aphelinidae) for aphids (Homoptera: Aphididae) on citrus. *Journal of Economic Entomology* **88**, 840–845.