

COMPARATIVE DEMOGRAPHICS OF A GENERALIST PREDATORY LADYBIRD ON FIVE APHID PREY: A LABORATORY STUDY

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Abstract Prey driven demographic parameters of an aphidophagous ladybird, *Propylea dissecta* (Mulsant) were studied in attempt to answer how ladybird overcomes the problem of seasonally fluctuating food base. The ladybird reared for five generations in laboratory derived differential nutrition from five food sources (*i.e.* aphid species, *Rhopalosiphum maidis* (Fitch), *Aphis craccivora* Koch, *Aphis gossypii* Glover, *Uroleucon compositae* (Theobald) and *Lipaphis erysimi* (Kalt.)). The order of relative prey suitability was *A. gossypii*, *A. craccivora*, *R. maidis*, *U. compositae* and *L. erysimi*. Neonates suffered maximum mortality followed by eggs. Estimates of net reproductive rate, intrinsic rate of increase and finite rate of increase were highest (407.18 , 0.2274 day^{-1} , 1.2553 day^{-1}) on *A. gossypii* and lowest (176.02 , 0.1533 day^{-1} , 1.1657 day^{-1}) on *L. erysimi*. Generation time was shortest (26.43 days) on *A. gossypii* and longest (33.73 days) on *L. erysimi*. The present study thus, provides an explanation to the high incidence of *P. dissecta* on *A. gossypii*, as it experienced high intrinsic rate of increase and optimal values for related demographic parameters.

Key words *Propylea dissecta*, *Aphis gossypii*, life table, intrinsic rate of increase

1 INTRODUCTION

Generalist aphidophagous ladybirds (Coleoptera: Coccinellidae) normally switch from one prey species to another during scarcity or availability of more suitable prey to improve their fitness (Hemptinne *et al.* 1996, Hattingh and Samways 1991). In fields, owing to the ephemeral nature of aphids, the ladybirds are not exposed to the same aphid species for many generations and move to other prey types. Thus, the ladybird has to derive its nutrition from different aphid resources, which are patchy and

less suitable. In addition, generalist ladybirds have wide range of accepted prey which differ in nutritive contents, energetic values and costs associated with their capture and ingestions (Soares *et al.* 2004). This causes difficulty in predicting its fitness in the fields where the ladybird is largely dependent on different food sources.

It is largely held that food quality has a major influence on the intrinsic growth and reproductive rates of ladybirds (Hodek and Honek 1996). Its encounter with suitable prey appears to enhance its intrinsic rate of increase, which is key

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demographic parameter useful for predicting its population growth potential (Roy *et al.* 2003). Life table studies give the most comprehensive description of survivorship, development and reproduction of a population, as such, are fundamental to both theoretical and applied population ecology.

The intrinsic rate of increase and related demographic parameters in predaceous ladybirds have been studied by many workers (Kawauchi 1985, Singh and Singh 1994, Kairo and Murphy 1995, Canhilal *et al.* 2001, Chi and Yang 2003, Roy *et al.* 2003). Most of them reported the influence of heterospecific predators (Obrycki *et al.* 1997), populations (Phoofolo and Obrycki 1995), seasons (Singh and Singh 1994), sexes (Chi and Yang 2003) and temperatures (Canhilal *et al.* 2001, Roy *et al.* 2003, Pervez and Omkar 2004a) on demographic parameters. However, the studies pertaining to the impact of seasonal prey are lacking. Thus, we attempted to question how an aphidophagous ladybird overcomes the problem of seasonally fluctuating food sources (different species of aphids). We tried to simulate the field conditions in the laboratory providing food in terms of seasonally available aphid species from local ladybird habitats.

We selected a generalist aphidophagous ladybird, *Propylea dissecta* (Mulsant) for the present study as it has a wide aphid prey range (Omkar and Pervez 2000, 2004a) and occurs seasonally throughout the year on different aphid food bases. Laboratory experiments revealed seven aphid species as its essential food, *i.e.* the food which can support both pre-imaginal development and adult reproduction (Pervez and Omkar 2004b). It is a eurytopic species, *i.e.* it exists in different types of zoo-geographical habitats and

can survive in prey scarcity by switching over to non-insect diets to overcome stress of prey deprivation (Omkar and Pervez 2003). *Propylea dissecta* is polymorphous with co-occurrence of three forms, *viz.* pale, intermediate and typical (R.G. Booth personal communication). Predominance of pale morph (>60% in a population) in the field was a criterion for its selection as an experimental model. High incidence of *P. dissecta* on colonies of aphids, *Rhopalosiphum maidis* (Fitch), *Aphis craccivora* Koch, *Aphis gossypii* Glover, *Uroleucon compositae* (Theobald) and *Lipaphis erysimi* (Kalt.) in different seasons was a reason to use them as prey resources in different laboratory reared generations in the present study.

2 MATERIALS AND METHODS

2.1 Stock maintenance

Adults of pale morph of *P. dissecta* were collected from agricultural fields of Lucknow, India and brought to the laboratory during August 2000. For the stock, groups of 20 adult beetles (sex-ratio 1:1) were kept in glass jars (15.0 × 10.0 cm) containing moist filter papers for adults to oviposit at 27 ± 1°C, 65% ± 5% R.H. and LD 14: 10 h photoperiod. These jars were covered with fine muslin. Adults were fed daily an *ad libitum* supply of specific prey.

2.2 Experimental design

Life tables of *P. dissecta* for five generations under laboratory conditions during August 2000 to March 2001 were constructed. Life stages of *P. dissecta* were constantly reared for five generations using different prey species, which were seasonally available, *i.e.* F₁ (*R. maidis* infesting *Zea mays*), F₂ (*A. craccivora* infesting *Dolichos*

lablab), F₃ (*A. gossypii* infesting *Lagenaria vulgaris*), F₄ (*U. compositae* infesting *Carthamus tinctorius*) and F₅ (*L. erysimi* infesting *Raphanus sativus*). Five hundred eggs of *P. dissecta* were obtained from the adults reared on *R. maidis*. These were placed in Petri dishes (100 eggs per Petri dish of size 16.0 × 2.6 cm) and incubated in an Environmental Test Chamber (ETC) maintained at 27 ± 1 °C and (65 ± 5)% R.H. Three observations per day were made to record egg hatching and number of hatched first instars recorded. Neonates were reared individually in isolation in glass beakers on *ad libitum* supply of *R. maidis* till adult emergence (F₁ generation). Mortality of different life stages were recorded. After emergence, the adults were sexed (Omkar and Pervez 2000), paired and reared on *R. maidis*. Females mated and laid eggs, which were recorded daily. Both adult male and female ladybirds were kept together throughout the oviposition period. No incidence of egg cannibalism was observed possibly due to *ad libitum* prey supply. The eggs obtained were reared simultaneously as next generation eggs (*i.e.* F₂) on the available aphid for next filial generation. The experiment was continued for five generations, using 500 eggs reared on different aphid species.

Mortality of different life stages, *viz.* eggs, larval instars, pre-pupae and pupae were recorded and *k*-value (or *k*_{*x*} = mortality within life stages) calculated following formula proposed by Morris and Miller (1954).

$$k\text{-value} = \log_{10} a_x - \log_{10} a_{x+1},$$

where *a*_{*x*} = initial number of individuals and *a*_{*x*+1} = number of individuals surviving to the next developing stage. The *K* (Kappa) = Total of *k*-values. Generation survival (number of female emergence/ number of eggs) was calculated fol-

lowing Harcourt (1969).

Demographic natality parameters, *viz.* net reproductive rate ($R_0 = (\sum l_x m_x)$), mean generation time ($T_0 = \sum x l_x m_x / R_0$), intrinsic rate of increase ($r_m = \log_e R_0 / T_0$), finite rate of increase ($\lambda = \text{antilog}_e r_m$), and doubling time (D.T. = $\log_e 2 / r_m$), were calculated following Birch (1948). Where, *x* = pivotal age, *l*_{*x*} = number of females surviving and *m*_{*x*} = net fecundity of an emerging female in each generation. The sex-ratios were compared using Chi-square Goodness-of-fit test using a statistical software MINITAB. The five generations were reared in the laboratory within a short phase of time due to their overlapping nature. For instance, while rearing F₁ generation to study the intrinsic rate of increase of *P. dissecta* on *R. maidis*, we simultaneously reared F₂ generation to determine mortality life table of immature stages of *P. dissecta* on *A. craccivora*.

3 RESULTS

The demographic parameters were differentially affected by the quality of food base provided to the immature stages of *P. dissecta* during different generations. The immature stages of *P. dissecta* suffered minimum mortality when fed on *A. gossypii* in F₃ generation, while maximum on *L. erysimi* in F₅ (Fig. 1). The first instars suffered maximum mortality as evident from their *k*-values followed by eggs, second instars, thirds instars, fourth instars, pupae and pre-pupae (Fig. 2). This prey quality dependent life table revealed that, though predatory stages developed completely on the five prey species provided, their fitness components in terms of survival and fecundity were higher using *A. gossypii* as prey. Fitness trend supports best F₃ followed by F₂, F₁,

Table 1 Demographic attributes based on mortality and natality of *Propylea dissecta* on five prey species (*Rm*= *Rhopalosiphum maidis*, *Ac*=*Aphis craccivora*, *Ag*=*Aphis gossypii*, *Uc*=*Uroleucon compositae*, and *Le*=*Lipaphis erysimi*).

Demographic Parameters	Aphid species				
	<i>Rm</i>	<i>AC</i>	<i>Ag</i>	<i>Uc</i>	<i>Le</i>
Female proportion in adult emergence	0.58	0.60	0.62	0.56	0.54
Generation survival	0.32	0.36	0.42	0.29	0.24
Kappa (<i>K</i>)	0.26	0.22	0.17	0.29	0.36
Net Reproductive rate (R_0)	244.21	365.76	407.18	231.32	176.02
Generation Time (T_c) (in days)	27.67	27.23	26.43	30.89	33.73
Intrinsic rate of Increase (r_m) (in day $^{-1}$)	0.20	0.22	0.23	0.18	0.15
Finite rate of Increase (λ) (in day $^{-1}$)	1.22	1.24	1.26	1.19	1.17
Doubling Time (D.T.) (in days)	3.49	3.20	3.05	3.93	4.52

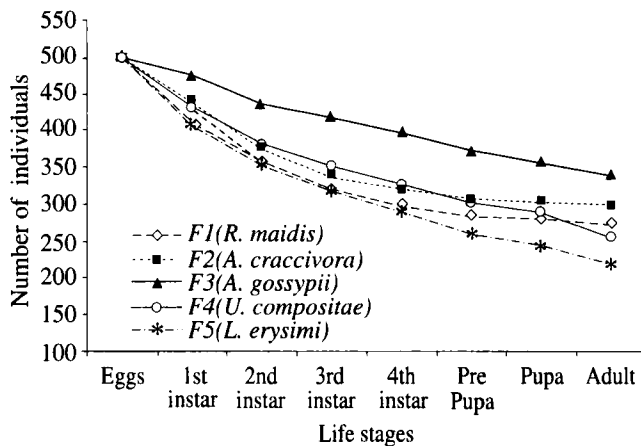


Fig. 1 Number of individuals of different life stages of *P. dissecta* survived starting from original cohort size of 500 eggs during five generations.

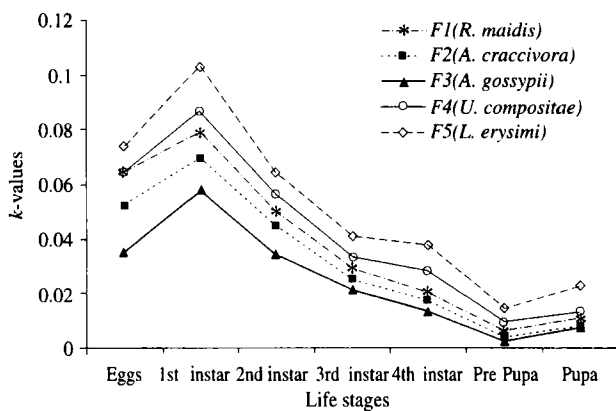


Fig. 2 k -values for different life stages of *P. dissecta* in different generations.

F_4 and F_5 generations, revealing the prey quality in decreasing order to be *A. gossypii*, *A. craccivora*, *R. maidis*, *U. compositae* and *L. erysimi*.

The sex-ratio of emerging adults was not significantly ($\chi^2 = 4.663$; $P=0.324$; d.f.=4) affected by prey type. Natality table based on survival (l_x) and age-specific fecundity (m_x) also supported *A. gossypii* to be the best food which resulted in the optimal demographic values. That is, R_0 , r_m and λ -values were maximum when *A. gossypii* was provided as food. This also resulted in shortest generation and doubling times (Table 1). Reverse was the case when *L. erysimi* was used as prey. High generation survival of F_3 might suggest *A. gossypii* to be the best food base amongst the five aphid foods.

4 DISCUSSION

Demographic analysis based on the empirical data revealed prey quality as a crucial factor affecting survival and intrinsic rate of increase of different generations of *P. dissecta*. Consistency in the ranking of prey was evident in the mortality of immature stages and natality based demo-

graphic parameters. The prey suitability was in the order *A. gossypii*, *A. craccivora*, *R. maidis*, *U. compositae* and *L. erysimi*. The results also support the previous studies on differential effects of prey types on the life attributes of generalist ladybirds (Sugiura and Takada 1998, Omkar and James 2003, Omkar and Bind 2004). The striking differences in the values of demographic parameters in the present study might be due to difference in prey suitability, which largely depends on the physiological status of its host plant and aphid performance, their nutritional requirements, enzyme equipments and nutritional budgets (Soares *et al.* 2004). It also depends on the nutritive requirement of predator, its prey capture efficiency, number of prey eaten and amount of biomass ingested.

Being a generalist, *P. dissecta* effectively utilized all five prey species to increase its fitness and number and the generation supplied with *A. gossypii* gave best results. This may be attributed to the better nutritive quality of prey infested on *L. vulgaris*. This also explains the abundance of *P. dissecta* in the fields of *L. vulgaris* infested with *A. gossypii* (Pervez 2002). The generation survival increased with increase in generations from F_1 to F_3 and thereafter decreased. *Rhopalosiphum maidis* used in F_1 appears to be inferior in terms of nutritive contents as compared to *A. gossypii* and *A. craccivora*, as also supported by a recent study on its prey suitability (Pervez and Omkar 2004b). *Lipaphis erysimi* was the least suitable prey as compared to the other four aphid species.

Amongst immature stages, neonates were most sensitive to food quality. Food quality affected the generation survival, which increased progressively from F_1 to F_3 and thereafter decreased. Female biased sex-ratio was highest

when *A. gossypii* was used as prey, which also resulted in maximum R_o -value. The differences in the sex-ratio, however, did not vary significantly. Maximum R_o -value in F_3 revealed that females of this generation produced maximum daughters per female, while reverse was the case in F_5 . R_o -value of *P. dissecta* (407.18) in F_3 was found larger than those recorded in other ladybirds, *Harmonia axyridis* (Pallas) (289.11 by Abdel-Salam and Abdel-Baky 2001), *Propylea japonica* (Thunberg) (179.8 by Kawauchi 1985), *Adalia bipunctata* (Linn.) (18.49 by Lanzoni *et al.* 2004), *Rodolia iceryae* Janson (50.11 by Kairo and Murphy 1995), *Hippodamia variegata* (Linn.) (52.75 by Lanzoni *et al.* 2004), however lesser than that recorded in *Coccinella septempunctata brucki* Mulsant (575.4 by Kawauchi 1985).

Aphis gossypii contributes to shorter generation time in *P. dissecta* with high r_m and λ -values in F_3 , which reveals that the predator needs minimum time to complete a generation in presence of suitable prey. The significantly high r_m -value when the ladybird was fed on *A. gossypii* also indicates its high numerical response. Recently, it has been found that *P. dissecta* can efficiently convert its prey biomass into progeny when fed on *A. gossypii* (Omkar and Pervez 2004b). The high numerical response and shorter generation time might encourage the field releases of *P. dissecta* for biocontrol of *A. gossypii*. However, comparative demographic studies of predator and prey along with field studies are needed prior to using the predator as a biocontrol tool. Short generation time results in high prey depletion, as the change in numbers of individuals tends to be large and adults multiply faster than those of long generation (Kindlmann and Dixon 1999). Generation time was lower than that recorded on *C.*

septempunctata brucki, *P. japonica* (Kawauchi 1985), *R. iceryae* (Kairo and Murphy 1995), *A. bipunctata* and *H. variegata* (Lanzoni *et al.* 2004).

High r_m - value of *P. dissecta* was obtained using *A. gossypii* as prey. Because r_m - value is a composite statistic, taking into account life history parameters, such as fecundity, survival and sex-ratio (Carey 1993), it can be used as an important criterion for evaluating potential of biocontrol agents. The r_m -value of *P. dissecta* in present study (0.23 day^{-1}) was higher than that obtained on *C. septempunctata brucki* (0.145 day^{-1} by Kawauchi 1985), *P. japonica* (0.187 day^{-1} by Kawauchi 1985 and 0.1133 day^{-1} by Chi and Yang 2003), *R. iceryae* (0.064 day^{-1}) (Kairo and Murphy 1995), *A. bipunctata* (0.081 day^{-1}) and *H. variegata* (0.114 day^{-1}) (Lanzoni *et al.* 2004). The r_m value of *P. dissecta* is comparable to those of specialist parasitoids, in which high r_m -values are considered a key factor for their success in biological control (DeBach 1964).

Thus, laboratory experiments revealed that *P. dissecta* can easily exploit all five food bases. The prey suitability, however, varies with different prey species. The order of prey suitability was *A. gossypii*, *A. craccivora*, *R. maidis*, *U. compositae* and *L. erysimi*. The high r_m and R_o -value in F_3 support *A. gossypii* as most suitable prey amongst the other seasonally available prey. The life stages were most sensitive to nutritional quality of the diet. First instars suffered maximum mortality. High r_m -value of *P. dissecta* reveals its immense biocontrol potential against the overgrowing population of *A. gossypii*.

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多食性瓢虫捕食 5 种蚜虫的统计学比较：实验室研究

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通过食蚜瓢虫 *Propylea dissecta* (Mulsant) 的捕食统计学参数的比较, 尝试回答瓢虫是如何克服食物基础季节性的变动问题。在实验室中饲养五世代的瓢虫从五种蚜虫 (*Rhopalosiphum maidis* (Fitch), *Aphis craccivora* Kock, *Aphis gossypii* Glover, *Uroleucon compositae* (Theobald) 和 *Lipaphis erysimi* (Kalt)) 为食物来源获得营养。相对适合的猎物次序是 *A.gossypii*, *A.craccivora*, *R. maidis*, *U.compositae* 和 *L.erysimi*。新生幼虫的死亡率最高, 其次是卵。统计表明, 净生殖率、内禀增长率和有限增长率为 (407.18, 0.2274 天⁻¹, 1.2553 天⁻¹) 最高的在 *A.gossypii* 和最低的 (176.02, 0.1533 天⁻¹, 1.1657 天⁻¹) 在 *L.erysimi*, 一个世代时间最短的 26.43 天是捕食 *A.gossypii*; 而最长的 33.73 天为捕食 *L.erysimi*。本研究为 *P.dissecta* 捕食 *A.gossypii* 高发生提供一种解释, 因为它经历了高内禀增长率和统计参数最佳值。

关键词: *Propylea dissecta*, 桃蚜, 生命表, 内禀增长率