

# Functional and numerical responses of *Propylea dissecta* (Col., Coccinellidae)

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**Abstract:** The functional response of a ladybeetle, *Propylea dissecta*, to increasing density of aphid, *Aphis gossypii*, was of the curvilinear shape depicting Holling's type II response with fourth instar larva being the most voracious stage when compared with adult male and female. Prey handling time by different predatory stages decreased from 65.45 to 8.72 min with increase in prey density from 25 to 800. The predator aggregation and high prey density reduces the searching efficiency of the predator. Area of discovery was highest (1.4437) when a single predator was searching at minimum aphid density (25) and lowest (0.0366) when eight predators were searching at a constant aphid density (200). Mutual interference and quest constants were 0.75 and 0.40, respectively. The reproductive numerical response, in terms of eggs laid, increased curvilinearly with prey density and female laid  $70.5 \pm 5.55$  eggs when exposed to highest prey density (400) and  $12.3 \pm 0.79$  eggs at lowest prey density (10). The similar shapes of both functional and reproductive responses indicate that both responses are interlinked and function simultaneously.

**Key words:** *Aphis gossypii*, *Propylea dissecta*, Coccinellidae, functional response, numerical response, prey density

## 1 Introduction

The traditional analytical assessment of the impact of insect predators on varying prey density referred to as functional and numerical responses (SOLOMON, 1949; HOLLING, 1959) can be used to predict the predators' efficacy in biocontrol of overgrowing pest populations (LAWTON et al., 1975; BEDDINGTON et al., 1978; O'NEIL and STIMAC, 1988; O'NEIL, 1990). The functional response of predators, i.e. attacking and killing more number of prey, with prey density was earlier promulgated in the form of three disc equations (HOLLING, 1959, 1965). Of these, type II response is curvilinear in shape and common in most ladybeetles (HASSELL, 1978; HODEK et al., 1984; OMKAR and JAMES, 2001; OMKAR and SRIVASTAVA, 2001; XIA et al., 2003); however, a few also exhibit type III response which is sigmoidal (HAJIZADEH et al., 1994). Functional response curves can be used to infer basic mechanisms underlying the predator–prey interactions, to clarify coevolutionary relationships and to enhance practical predictive powers for biocontrol.

Various models have been proposed in the past to explain predator–prey interactions. The pioneer and simplest of those was the Lotka–Volterra model (LOTKA, 1925; VOLTERRA, 1926) in the form of differential equations, explaining the dynamics of a pure resource–consumer system. Thereafter, the discrete time Nicholson–Bailey Model (NICHOLSON, 1933; NICHOLSON and BAILEY, 1935) was formulated to explicate the interactions in a host–parasitoid system, which can

also be applicable to prey–predator systems. According to the model, 'area of discovery', a measure for searching efficiency of predator, is constant and independent of prey and predator densities. It was refuted by an inductive population model (HASSELL and VARLEY, 1969), which suggested that searching efficiency of predators declines exponentially with increase in their density and incorporated a mutual interference constant ( $m$ ). Although the new population model was criticized (HASSELL, 1971; ROYAMA, 1971; STINNER and LUCAS, 1976), it is still widely accepted because of its simplicity (VEERAVEL and BASKARAN, 1997). Hence it is used in the present study to calculate mutual interference.

Numerical response of predator can be expressed in terms of progressive change in the number of its progeny in relation to increasing prey density (SOLOMON, 1949). It may be considered as a strategy of female ladybeetles to augment their progeny in prey abundance and in an aphidophagous ladybeetle, *Cheilomenes sexmaculata* (Fabricius), this response was found synchronous to the density of aphid, *Aphis craccivora* Koch (AGARWALA and BARDHANROY, 1999). Previous studies modelled on predaceous ladybeetles have dealt with the questions on functional (HODEK et al., 1984; HAJIZADEH et al., 1994; XIA et al., 1999; WANG and TSAI, 2001; WELLS and McPHERSON, 1999; OMKAR and JAMES, 2001; OMKAR and SRIVASTAVA, 2001; XIA et al., 2003) and numerical (PANDEY et al., 1984; AGARWALA and BARDHANROY, 1999) responses separately, with a few

combined studies on the two responses ignoring the impact of searching efficiency (OFUYA and AKINGBOHUNGBE, 1988; VEERAVEL and BASKARAN, 1997). For pragmatic utilization of ladybeetles, it is necessary to address both the questions simultaneously. We started with the hypothesis that the functional response of the predator in terms of number of prey consumed may have certain relationship with numerical response in terms of number of eggs laid and possibly work simultaneously. The hypothesis further suggests the success of a ladybeetle in biocontrol will be dependent on its efficiency of conversion of prey biomass into progeny. With an expectation of similar shapes of both the responses, experiments were designed on a ladybeetle, *Propylea dissecta* (Mulsant) as an experimental model. It is native to India with prominent sexual dimorphism (OMKAR and PERVEZ, 2000) and high specificity for aphid, *Aphis gossypii* Glover (PERVEZ, 2002; PERVEZ and OMKAR, 2003). It is a polymorphic species, exhibiting typical, intermediate and pale morphs (R.G. Booth, personal communication) with pale morph being largely abundant in local agro-ecosystems (approximately 60%) and thus selected.

## 2 Materials and Methods

### 2.1 Functional response

Individual fourth instar, adult male and female of pale morph of *P. dissecta* were kept separately without food for 12 h in a glass beaker (11.0 cm height  $\times$  8.5 cm diameter) in order to standardize their hunger. Thereafter, different densities, viz. 25, 50, 100, 200, 400 and 800 of *Aphis gossypii* infested on pieces of leaves of *Lagenaria vulgaris* Linnaeus were provided per predator to the predatory stages. The beakers were covered with muslin and kept in an environmental test chamber (ETC) maintained at 27°C and 65  $\pm$  5% RH. After 24 h, the beakers were taken from the ETC and the predators removed. The live aphids left in the beakers were counted to determine the number of aphids consumed. Ten replicates of the experiment were performed ( $n = 10$ ). The percentage prey consumed and handling time of prey (i.e. time taken by the predator for pursuing, subduing, consuming and digesting the prey, calculated as the ratio of exposure time to the number of prey consumed) were calculated and regressed with prey density using a statistical software MINITAB on personal computer.

Based on the assumptions that the coefficients of the 'disc equations' (HOLLING, 1959) are constant and independent of prey density, the disc equation was transformed according to the method suggested by LIVDAHL and STIVEN (1983) and thereafter followed by VEERAVEL and BASKARAN (1997). This transformation removes the statistical limitations associated with the ROYAMA (1971) and ROGERS (1972) transformations and permits a high degree of explanation of variants in the independent variable by regression.

### 2.2 Interference

The experiment on interference used only fourth instar predators and the data were used to estimate searching efficiency (area of discovery). Fifteen fourth instars of *P. dissecta* were kept separately without food in the glass beakers (11.0 cm height  $\times$  8.5 cm diameter) for 12 h to standardize their hunger. The predators were grouped: one,

two, four and eight individuals in four beakers (11.0 cm height  $\times$  8.5 cm diameter) containing 200 individuals of *A. gossypii* on pieces of host plant leaves. The open ends of the beakers were covered with muslin and kept in the ETC for 3 h. Thereafter, the beakers were taken out from the ETC and the predators were removed. The unconsumed aphids were counted to determine the number of prey consumed. The experiment was carried out 10 times ( $n = 10$ ). Number of prey consumed and prey consumed per predator in relation to predator density were subjected to regression analysis using statistical software MINITAB.

According to the Nicholson–Bailey model:

$$N(t+1) = \lambda N(t) \exp[-aP(t)] \quad (1)$$

$$P(t+1) = cN(t)[1 - \exp(-aP(t))] \quad (2)$$

where  $N(t)$  is the number of hosts (prey) at time  $t$ ,  $P(t)$ , the number of parasitoids (predators) at time  $t$ ,  $\lambda$ , the host reproductive rate, and  $a$ , the area of discovery. In order to estimate area of discovery, the above model (2) can be rearranged (HASSELL, 1978) after assuming that  $c = 1$

$$a = \frac{1}{P} \log_e \frac{N}{(N - N_a)} \quad (3)$$

where  $a$  is the area of discovery,  $N$ , the prey density exposed for predation,  $N_a$ , the number of prey consumed, and  $P$ , the predator density released for predation.

The above rearranged model (3) was used to relate area of discovery to prey density. However, it has a weakness when correlated with predator density, for it was proposed for host–parasitoid systems, where one parasitized host gives rise to one new parasitoid. This is not true in predator–prey systems, as single prey does not lead to the emergence of new predator. Moreover, with a realization that area of discovery is not constant and there is mutual interference amongst predators, we used HASSELL and VARLEY (1969) model instead of Nicholson–Bailey's model.

HASSELL and VARLEY (1969) model is as follows,

$$a = QP^{-m} \quad (4)$$

where  $a$  is the area of discovery,  $Q$ , the quest constant (area of discovery when only one predator was searching),  $m$ , the mutual interference constant (slope of regression of  $\log a$  on  $\log P$ ), and  $P$ , the predator density. The data obtained from the experiment on 'Functional response' concerning fourth instar larva were used to estimate  $a$  for  $P = 1$  at prey densities.

### 2.3 Numerical response

Eight (15-day old) sexually mature adult female ladybeetles of *P. dissecta* were starved for 12 h to standardize their hunger. Thereafter, they were exposed to different densities, viz. 10, 25, 50, 75, 100, 200, 300 and 400 of *A. gossypii* infested on pieces of *L. vulgaris* leaves kept in glass beakers for 24 h. The glass beakers were kept in the ETC. After 24 h, the females were removed from the beakers and the number of prey consumed recorded. Thereafter, the females were paired individually with sexually mature (15-day old) male ladybeetles in Petri dishes (diameter 9 cm  $\times$  height 2 cm) and allowed to mate. After mating, the females were isolated in Petri dishes and the oviposition recorded after 24 h. Egg cannibalism by females fed at low prey densities was observed and remnants of the eggs on the surface of Petri dishes minimized the sampling error. The experiment was performed 10 times ( $n = 10$ ). The efficiency of conversion of ingested food (ECI) (in number) into egg biomass (in

number) was calculated (number of eggs laid × 100/number of prey consumed) at different prey densities. The data on oviposition and ECI at different prey densities were fitted using regression analysis to determine the relationship between (i) oviposition and prey density, and (ii) ECI of female beetle and prey density.

### 3 Results

#### 3.1 Functional response

Prey consumption by fourth instar, adult male and female *P. dissecta* increased from 24.10 ± 0.35 to 165.10 ± 3.63, 22.00 ± 0.63 to 136.80 ± 2.98 and 23.00 ± 0.58 to 142.50 ± 2.97 with increase in density of *A. gossypii* from 25 to 800, respectively. The increase in prey consumption by above predatory stages with increased prey density was curvilinear in shape (figs 1–3). The handling time per prey (*b*) and attack rate (*a*) (obtained from transformation followed by least square estimates) of fourth instar were 6.51 min and 1.06 ( $r^2 = 0.99$ ;  $P < 0.001$ ), adult male were 9.26 min and 0.97 ( $r^2 = 0.96$ ;  $P < 0.001$ ), and adult

female were 8.96 min and 1.01 ( $r^2 = 0.96$ ;  $P < 0.001$ ), respectively.

Percentage prey consumption by fourth instar, adult male and female ladybeetles decreased significantly ( $P < 0.001$ ) with increase in prey density (table 1). Similarly, the handling time by fourth instar, adult male and female ladybeetles decreased significantly with prey density ( $P < 0.001$ ; table 2).

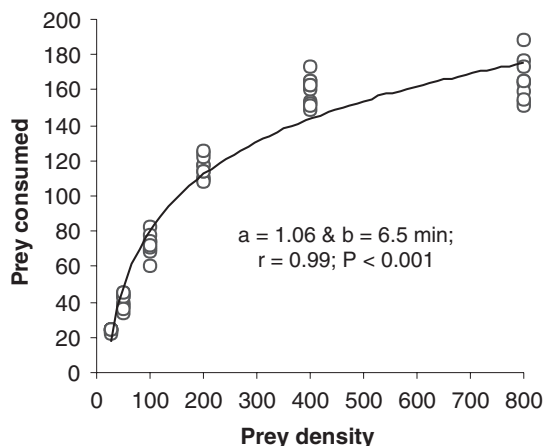


Fig. 1. Prey consumed by fourth instar of *Propylea dissecta* at different densities of *Aphis gossypii*

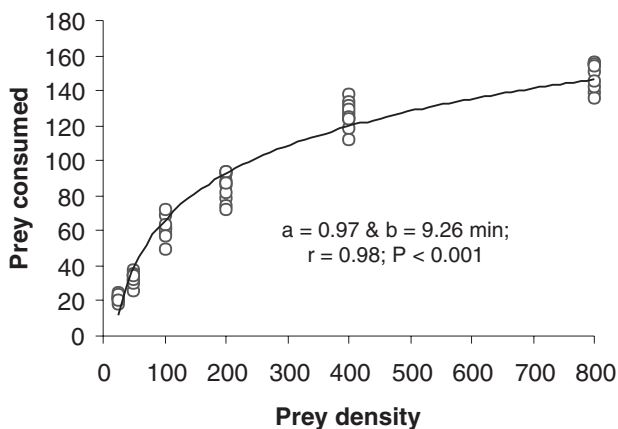


Fig. 2. Prey consumed by adult male of *Propylea dissecta* at different densities of *Aphis gossypii*

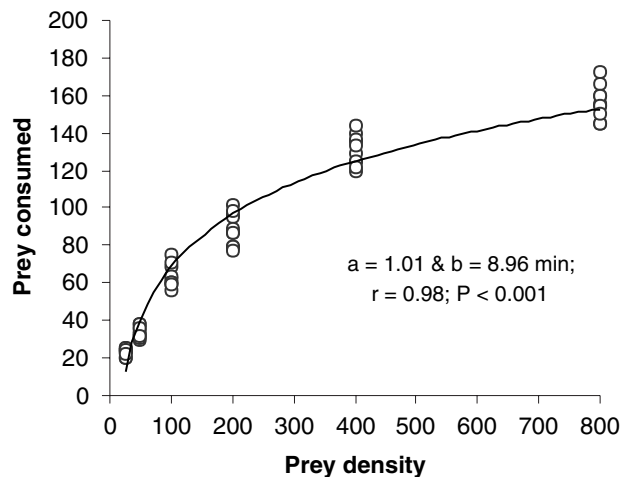


Fig. 3. Prey consumed by adult female of *Propylea dissecta* at different densities of *Aphis gossypii*

Table 1. Percent prey consumption by the predatory stages of *Propylea dissecta* at various densities of *Aphis gossypii*

Prey density	Fourth instar	Male ladybeetle	Female ladybeetle
25	96.40 ± 1.39	88.00 ± 2.53	92.00 ± 2.31
50	81.00 ± 2.55	65.60 ± 2.14	68.00 ± 1.82
100	72.50 ± 1.70	61.50 ± 1.95	63.40 ± 1.95
200	58.20 ± 1.03	42.45 ± 1.26	44.45 ± 1.38
400	39.88 ± 0.61	31.58 ± 0.59	32.73 ± 0.63
800	20.64 ± 0.46	17.00 ± 0.30	17.81 ± 0.34
$r^2$ value*	0.95	0.89	0.89

Values are mean ± SE.  
\* Significant at  $P < 0.001$ .

Table 2. Handling time of the prey by the predatory stages of *Propylea dissecta* at various densities of *Aphis gossypii*

Prey density	Handling time (in min)		
	Fourth instar	Male ladybeetle	Female ladybeetle
25	59.75 ± 0.89	65.45 ± 2.02	62.61 ± 1.68
50	35.56 ± 1.17	43.90 ± 1.56	42.35 ± 1.13
100	19.86 ± 0.55	23.41 ± 0.77	22.71 ± 0.66
200	12.37 ± 0.22	16.96 ± 0.53	16.20 ± 0.51
400	9.03 ± 0.14	11.40 ± 0.22	11.00 ± 0.53
800	8.72 ± 0.19	10.59 ± 0.16	10.11 ± 0.16
$r^2$ value*	0.75	0.77	0.78

Values are mean ± SE.  
\* Significant at  $P < 0.001$ .

**3.2 Interference**

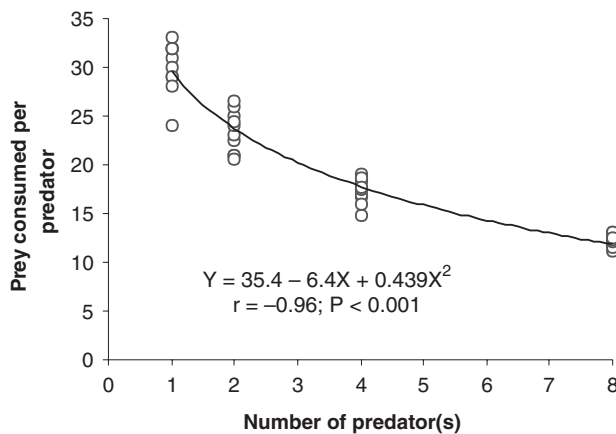
The prey consumption by fourth instar of *P. dissecta* increased, while prey consumption per predator decreased significantly ( $P < 0.001$ ; table 3) with increase in predator density at a constant prey density. The decrease in prey consumption per predator was curvilinear when fitted with predator density (fig. 4). The area of discovery decreased curvilinearly with

predator density (fig. 5). It was highest (0.0706) when one predator was searching and lowest (0.0366) when eight predators were searching at constant prey density. The mutual interference and quest constants were 0.75 and 0.40, respectively. There was also a curvilinear decrease in area of discovery at varying prey density (fig. 6) with highest value (1.4437) at the initial prey density and lowest (0.1132) at the highest prey density when a single predator searched.

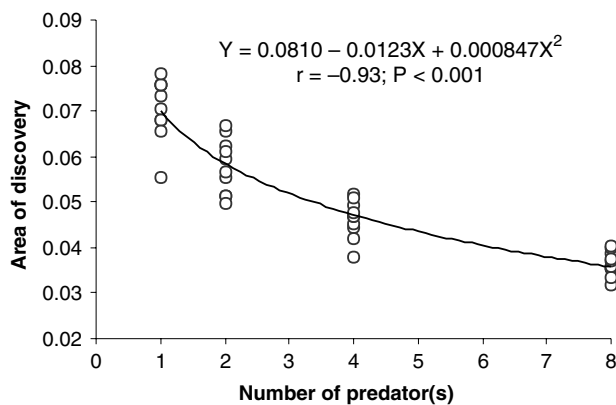
**Table 3.** Prey consumption by fourth instar of *Propylea dissecta* at various predator densities and constant density (200) of *Aphis gossypii*

Predator density	Total number of prey consumed*	Prey consumed per predator*
1	30.00 ± 0.84	30.00 ± 0.84
2	46.80 ± 1.36	23.40 ± 0.68
4	69.30 ± 1.62	17.36 ± 0.41
8	98.00 ± 1.61	12.25 ± 0.20
r <sup>2</sup> value*	0.97	0.92

Values are mean ± SE.  
\* Significant at  $P < 0.001$ .



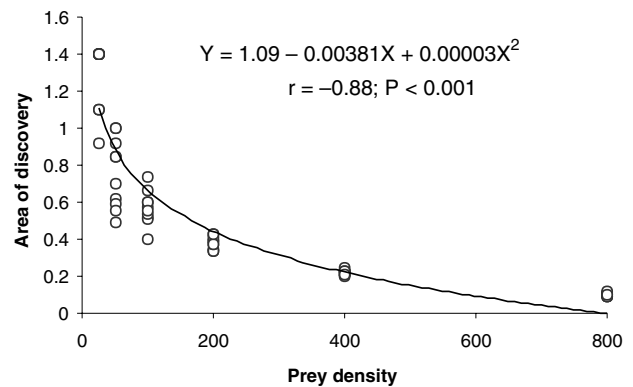
**Fig. 4.** Relationship between number of prey consumed per predator at different predator densities



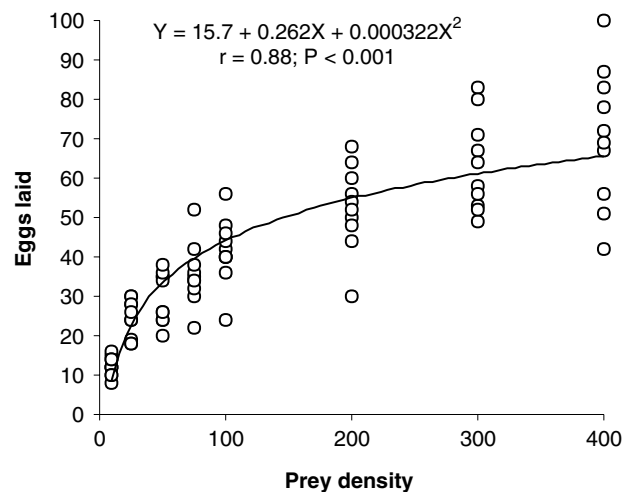
**Fig. 5.** Relationship between area of discovery and predator density of fourth instar *Propylea dissecta*

**3.3 Numerical response**

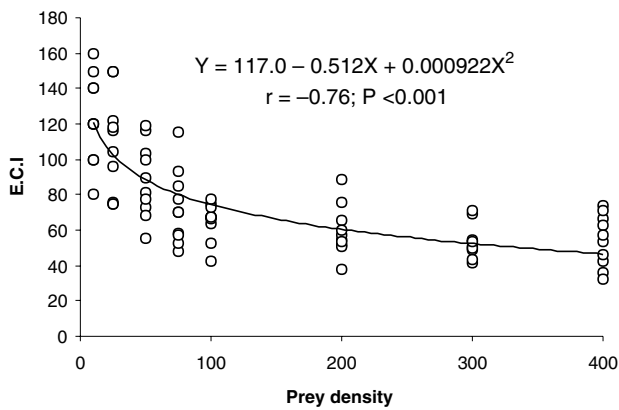
The oviposition by adult female *P. dissecta* increased, while the ECI decreased significantly ( $P < 0.001$ ; figs 7 and 8) with prey density. The female laid maximum (70.5 ± 5.55) eggs at highest prey density (400) and minimum (12.3 ± 0.79) at lowest prey density. The data on eggs laid per female ladybeetle at varying prey density and ECI at varying prey density when fitted exhibited curvilinear shapes but in reverse directions (figs 7 and 8).



**Fig. 6.** Relationship between area of discovery of fourth instar of *Propylea dissecta* and prey density



**Fig. 7.** Relationship between number of eggs laid by female *Propylea dissecta* at varying densities of *Aphis gossypii*



**Fig. 8.** Relationship between E.C.I. of *Propylea dissecta* at varying densities of *Aphis gossypii*

## 4 Discussion

### 4.1 Functional response

The functional response exhibited by the predatory stages of *P. dissecta* exemplified type II predatory response described by HOLLING (1959). The increased prey consumption with increase in prey density may be ascribed to the simultaneous action of various phenomena, such as handling time, level of hunger of the predator and the nature of the experimental arena (O'NEIL and STIMAC, 1985, 1988).

At low prey density, the aphids were sparsely distributed, which required the predator to spend more time and energy foraging. Prey handling time of the three predatory stages was relatively lesser and almost constant (ranging 11.40–8.72 min) at higher densities of *A. gossypii* (400 and 800 aphids). The empirical data on handling time at high aphid density may be comparable with field conditions where the prey density is high due to heavy aphid infestation. AKHTARUZZAMAN and AHMAD (1998) reported that handling time of predators was higher with low foraging rate at lower prey density. Recent reports documented higher handling time for the fourth instars than adults, owing to fewer aphids consumed at highest aphid density, as in *Hippodamia convergens* Guerin-Meneville (WELLS and MCPHERSON, 1999) and *Coelophora inaequalis* (Fabricius) (WANG and TSAI, 2001). The present finding disagrees with these reports, as fourth instars of *P. dissecta* processed the aphids at a faster rate than adults. WELLS and MCPHERSON (1999) remarked that although fourth instars of *H. convergens* took longer to process aphids, they were more efficient searchers than adults due to relatively high area of discovery (searching efficiency).

Satiation reduces the feeding performance of the predators, which was not achieved at low prey densities as exhibited by high percentage prey consumption. The predator's satiation level seems to be higher than the number of prey given. The mutilated remnants of the prey were scarce when predatory stages were exposed to prey at lower densities, suggesting that satiation was not achieved.

At high aphid densities, prey encounters were more and predators continued to feed till satiation. The mutilated remnants of prey increased with prey

density, as predators did not completely devour the prey, extracted progressively smaller proportions of the contents of each aphid killed. This aspect of predator–prey association encourages the pragmatic utilization of ladybeetles, as they tend to increase prey mortality. The predator's aggravation due to occasional disturbance by another prey during feeding possibly resulted in killing of more prey than normal, as also reported in *Cheilomenes lunata* (Fabricius) (OFUYA and AKINGBOHUNGBE, 1988). HODEK and HONEK (1996) opined that hungry ladybeetles completely devour the first few prey they encounter and utilize subsequent prey with gradually reduced voracity.

The fourth instar was the most voracious stage followed by adult female and male. High levels of energy are required by fourth instar to complete development and attain a critical weight for pupation (FERRAN and LARROQUE, 1977). Adult female was more voracious than male, owing to her larger size and high nutrient requirements for egg production and oviposition (RHAMHALINGHAN, 1987; OMKAR and JAMES, 2001).

### 4.2 Interference

The increase in predator density resulted in increased prey consumption, which indicates that in order to kill more number of prey, more predators are required. However, doubling in the number of predators employed for predation did not result in doubling in the number of prey consumed, owing to mutual interference. The significantly decreased prey consumption per predator with increased predator density suggests that interferences amongst predators also increased at higher predator density. This was probably due to closed experimental arena with limited predation time and high probability of mutual interference. Although empirical data do not adequately explain these interactions in the spatial field conditions, the data possibly indicate that predator aggregation in the specific prey patch increases intraspecific interactions.

Estimates of area of discovery and mutual interference through new inductive population models (HASSELL and VARLEY, 1969) are useful to predict the efficacy of *P. dissecta* in field conditions. The high mutual interference constant (0.75) predicts the tendency of the predator to interact the prey and become more stable in the nature (HASSELL and VARLEY, 1969; HASSELL and MAY, 1973; ROGERS and HASSELL, 1974). The quest constant denotes the value of optimal searching efficiency of the predator, which is obvious when only one predator searches. High prey density reduces the searching efficiency of predators, as it is evident that predators search less on encountering prey clump at higher prey densities and continue feeding on them. The reduced searching at higher predator densities may be a consequence of greater mutual interferences.

### 4.3 Numerical response

Oviposition by female *P. dissecta* increased curvilinearly with prey density and reached a plateau at higher densities. There was a rapid and significant increase in

oviposition at lesser aphid densities but the rate gradually declined at high densities possibly because of satiation of the nutrient requirements for egg production. Other constraints such as limitation of females to lay not more than certain amount of eggs possibly explain the attainment of plateau at high prey densities. The prey density-dependent fecundity was sigmoidal in *C. lunata* (OFUYA and AKINGBOHUNGBE, 1988) and curvilinear in *C. sexmaculata* (AGARWALA and BARDHANROY, 1997).

It is evident from the metabolic pool model that only a part of the energy derived from the prey biomass is converted into egg production and the rest is lost as metabolic costs of food conversion and respiration to maintain life (BAUMGÄRTNER et al., 1987). The ECI in the present study reveals that this conversion of prey biomass was more at low prey density, which subsequently decreased at higher prey densities. This probably indicates that female ladybeetles at low prey density probably allocate most of their energy in egg production and in the process invest less in maintenance and metabolic activities. The decreased ECI at higher prey densities possibly suggests that well-fed females laid large number of eggs, besides investing much in maintenance and metabolic costs. This probably explains the better fitness of the females exposed to high prey densities in terms of growth in previous studies (BAUMGÄRTNER et al., 1987; HODEK and HONEK, 1996). Besides prey density, other factors such as temporary prey isolation (EVANS and DIXON, 1986) and body size (AGARWALA and BARDHANROY, 1999) also affect egg production.

The prey density-dependent oviposition in *P. dissecta* was curvilinear in function and can be compared with type II functional response of the predator. This comparison primarily reveals a prominent saturation level in prey consumption and egg production at optimal prey density, where the curve ends shaping a plateau. It also reveals that both functional and numerical responses are inter-linked, i.e. prey biomass consumed by the predator is directly proportional to egg production. The increased reproductive numerical response of *P. dissecta* in prey abundance may also be considered as its strong adaptive strategy to promote its progeny.

## 5 Conclusion

It may thus be inferred that predatory stages of *P. dissecta* exhibit Holling's type II functional response with fourth instar being most efficient in detecting and consuming prey. Its searching efficiency decreases with prey density and predator aggregation. Female response to increasing prey density in the form of oviposition was curvilinear. Similar shapes of functional and numerical responses to prey density lend support to the hypothesis that probably both are linked and function simultaneously. The increased aphid consumption tends to enhance numerical response of the predator: (i) by a direct and rapid improvement in its fitness, and (ii) by enhancement of its progeny. Thus present study provides a better

understanding of the predator-prey interactions, which may be helpful in efficient utilization of *P. dissecta* for the management of *A. gossypii* infestations.

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