Plasticity in predation behaviour of carabid beetles in agro-ecosystems

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ABSTRACT: A study on the feeding behaviour of three species of Chlaenius and two species of Calosoma (Coleoptera: Carabidae), the caterpillar and semi-looper hunting predatory ground beetles in agro-ecosystems, was carried out under laboratory conditions in the Department of Entomology, Rajasthan College of Agriculture, MPUAT, Udaipur, during September to November, 2016. The carabid predator species and the second/ third instar tobacco caterpillar prey relationship followed the typical Holling’s Type II functional response. Of the three species of Chlaenius evaluated, Chlaenius udaipurensis Chanu and Swaminathan consumed the maximum prey with a preference for the second instar tobacco caterpillar. Increase in second instar caterpillar prey density from 1 to 5 resulted in an increase in mean prey consumption up to 4.4 in 24 hours. Under enhanced prey provision from 5 to 25 to Ch. udaipurensis the maximum mean consumption was 9.0; whereas, the maximum third instar caterpillar consumption was only 2.0 in 24 hours. Both species of Calosoma could kill 11 to 13 third instar tobacco caterpillars per day. Increased prey density evinced a gradual decreasing trend in the per cent feeding propensity with little variation among the species for both the genera of carabids. The relationship between prey consumption and the body mass increase for the species of Chlaenius showed significant positive correlation (r = 0.902 for II instar prey and r = 0.711 for III instar prey); similarly, the relationship for Calosoma species had significant positive correlation (r = 0.795).

KEY WORDS: Calosoma, Chlaenius, Feeding Behaviour, Functional Response

INTRODUCTION

Insect predators are frequently reckoned as effective regulators of insect pest populations (DeBach and Rosen, 1991; Price, 1997; Obrycki, 1998; Cardoso and Lazzari, 2003; Padmalatha et al., 2003), which has led their increasing use in insect pest management programs (Wiedenmann and Smith, 1997; Riudavets and Castane, 1998). Functional response of a predator is one of the important factors regulating population dynamics of predator–prey systems, and functional response curves can be used to infer basic mechanisms underlying predator–prey interactions, clarify co-evolutionary relationships, and enhance biological control (Houck and Strauss, 1985).

The members of the family Carabidae (Coleoptera) are mostly carnivorous, larvae and adults are nocturnal and hence, less known. These beetles exhibit polyphagy of diverse order (Davies, 1953; 1959 and Thiele, 1977), Scher-
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between prey consumption and increase in body mass of *Calosoma imbricatum* Klug, *Calosoma orientale* Hope, *Chlaenius nitidicollis* Dejean, *Chlaenius distigma* Chaudoir and *Chlaenius udaipurensis* Chanu and Swaminathan, thus, the objective of this study was undertaken under laboratory conditions.

**MATERIALS AND METHODS**

The experiment was conducted in the Department of Entomology, Rajasthan College of Agriculture, MPUAT, Udaipur, during September to November, 2016. The adults of three species of *Chlaenius*, viz., *Chlaenius nitidicollis* Dejean, *Chlaenius distigma* Chaudoir, *Chlaenius udaipurensis* Chanu and Swaminathan, and two species of *Calosoma*, viz., *Calosoma imbricatum* Klug, *Calosoma orientale* Hope were collected from Ajmer, Bhilwara and Udaipur using light traps. The prey, i.e., *Spodoptera litura* (Fabricius) eggs as well as first instar larvae were collected from field and reared in the laboratory on the soybean leaves. The adult carabid beetles were kept individually in a desiccator (15cm mouth diameter), filled with moist sand at the base and grass above it to maintain humidity, covered with a muslin cloth and fastened with rubber band. All the three species of *Chlaenius* were provided second as well as third instar larvae at different prey densities, i.e., 1, 2, 3, 4 and 5 larvae per day. For the indigenous species, *Chlaenius udaipurensis* Chanu and Swaminathan, enhanced prey densities of second instar *S. litura* were provided, i.e., 5, 10, 15, 20 and 25 larvae per day because they were available in sufficient numbers for the study being locally abundant. For both the species of *Calosoma*, third instar *S. litura* was provided at prey densities 5, 10, 15, 20 and 25 larvae per day. The experiment on each species was replicated five times.

Observations were recorded on the number of *S. litura* larvae-prey consumed by the adult beetles in each replication after 24h of exposure. The beetles were pre-starved for 24h and weight for each adult beetle was taken before and after provision of prey. The functional response to the prey

### Table 1. Functional response parameters for *Chlaenius* species fed on 2nd and 3rd instar *Spodoptera litura* (Fabricius) larvae

| Prey per dessicator (Nos.) (H) | Total prey provided | 2nd instar larvae as prey | 3rd instar larvae as prey |
|-------------------------------|---------------------|---------------------------|--------------------------|
|                               | Total prey killed   | Average prey killed * (H)_i | 1/(HT) | 1/H_a | Total prey killed   | Average prey killed * (H)_i | Feeding propensity (%) | 1/(HT) | 1/H_a |
| Ch. nitidicollis              | Linear regression: Y = 0.167 + 0.813x (R²=0.958) | Linear regression: Y = 0.329 + 0.617x (R²=0.84) |
| 1                             | 5                   | 5                          | 1     | 1     | 5                   | 1                          | 100.00 | 0.5 | 1     | 5                   | 1     | 100.00 | 0.5 | 1     |
| 2                             | 10                  | 10                         | 2     | 0.5   | 4                   | 0.8                        | 26.67 | 0.33 | 1.25 |
| 3                             | 15                  | 15                         | 3     | 0.33  | 4                   | 0.8                        | 25.00 | 0.25 | 0.556 |
| 4                             | 20                  | 15                         | 3     | 56.00 | 0.2               | 0.357                     | 1       | 20.00 | 0.2 | 1     |
| 5                             | 25                  | 20                         | 2.8   | 56.00 | 0.2               | 0.357                     | 5       | 1     | 20.00 | 0.2 | 1     |
| Ch. distigma                  | Linear regression: Y = 0.099 + 0.877x (R²=0.973) | Linear regression: Y = 0.329 + 0.617x (R²=0.84) |
| 1                             | 5                   | 5                          | 1     | 1     | 5                   | 1                          | 100.00 | 0.5 | 0.5   | 5                   | 1     | 100.00 | 0.5 | 0.5   |
| 2                             | 10                  | 10                         | 2     | 0.5   | 10                  | 2                           | 100.00 | 0.33 | 0.5   | 4                   | 0.8   | 26.67 | 0.33 | 0.5   |
| 3                             | 15                  | 15                         | 3     | 75.00 | 0.25              | 0.333                      | 9       | 1.8   | 45.00 | 0.25 | 0.556 |
| 4                             | 20                  | 15                         | 3     | 60.00 | 0.2               | 0.333                      | 10      | 2     | 40.00 | 0.2  | 0.5   |
| 5                             | 25                  | 15                         | 3     | 60.00 | 0.2               | 0.333                      | 10      | 2     | 40.00 | 0.2  | 0.5   |
| Ch. udaipurensis (1)          | Linear regression: Y = 0.013 + 0.982x (R²=0.998) | Linear regression: Y = 0.305 + 0.645x (R²=0.877) |
| 1                             | 5                   | 5                          | 1     | 1     | 5                   | 1                          | 100.00 | 0.5 | 0.5   | 5                   | 1     | 100.00 | 0.5 | 0.5   |
| 2                             | 10                  | 10                         | 2     | 0.5   | 10                  | 2                           | 100.00 | 0.33 | 0.5   | 4                   | 0.8   | 26.67 | 0.33 | 0.5   |
| 3                             | 15                  | 15                         | 3     | 75.00 | 0.25              | 0.333                      | 9       | 1.8   | 45.00 | 0.25 | 0.556 |
| 4                             | 20                  | 15                         | 3     | 60.00 | 0.2               | 0.333                      | 10      | 2     | 40.00 | 0.2  | 0.5   |
| 5                             | 25                  | 20                         | 4     | 88.00 | 0.2               | 0.227                      | 10      | 2     | 40.00 | 0.2  | 0.5   |
| Ch. udaipurensis (2)          | Linear regression: Y = 0.084 + 0.602x (R²=0.95) | Not applicable |
| 5                             | 25                  | 36                         | 7.2   | 72.00 | 0.1               | 0.139                      | 10      | 50    | 36.00 | 0.04 | 0.111 |
| 10                            | 50                  | 40                         | 8     | 40.00 | 0.05              | 0.125                      | 20      | 100   | 40.00 | 0.05 | 0.125 |
| 15                            | 75                  | 45                         | 9     | 36.00 | 0.04              | 0.111                      |

* Data indicating average prey killed is a mean of 5 replications; R² indicates coefficient of determination value
Table 2. Functional response parameters for *Calosoma* species fed on 3rd instar *Spodoptera litura* (Fabricius) larvae

| Prey per dessicator (Nos.) (H) | Total prey provided | C. imbricatum |  | C. orientale | Feeding propensity (%) | 1/(HT) | 1/Hₐ | Total prey killed | Average prey killed * (Hₐ) | Feeding propensity (%) | 1/(HT) |
|-------------------------------|---------------------|---------------|---|--------------|------------------------|-------|-------|-----------------|------------------------|------------------------|-------|
| 5                             | 25                  | 25            | 5 | 100.00       | 0.2                    | 0.200 | 25    | 5               | 100.00                 | 0.2                    | 0.200 |
| 10                            | 50                  | 46            | 9.2 | 92.00       | 0.1                    | 0.109 | 50    | 10              | 100.00                 | 0.1                    | 0.100 |
| 15                            | 75                  | 54            | 10.8 | 72.00       | 0.07                   | 0.093 | 65    | 13              | 86.67                  | 0.07                   | 0.077 |
| 20                            | 100                 | 55            | 11  | 55.00       | 0.05                   | 0.091 | 64    | 12.8            | 64.00                  | 0.05                   | 0.078 |
| 25                            | 125                 | 55            | 11  | 44.00       | 0.04                   | 0.091 | 61    | 12.2            | 48.80                  | 0.04                   | 0.082 |

Linear regression: $Y = 0.051 + 0.711 x$ (R²=0.951)  
$Y = 0.034 + 0.789 x$ (R²=0.939)

* Data indicating average prey killed is a mean of 5 replications; R² indicates coefficient of determination value

Table 3. Effect of prey consumption on body mass increase in species of *Chlaenius*

| Carabid species | Prey provided (I) | Mean prey consumed in 24 h | Mean body mass increase (mg) after feeding on |
|-----------------|-------------------|---------------------------|---------------------------------------------|
|                 | Prey (II instar)  | Prey (III instar)        | Prey (II instar)                           | Prey (III instar)                       |
| *Ch. nitidicollis* | 1                 | 1.0                       | 1.0                              | 2.0                                    | 3.0                                 |
|                 | 2                 | 2.0                       | 1.0                              | 6.0                                    | 2.0                                 |
|                 | 3                 | 2.0                       | 0.8                              | 5.0                                    | 3.0                                 |
|                 | 4                 | 3.0                       | 1.0                              | 9.0                                    | 2.0                                 |
|                 | 5                 | 2.8                       | 1.0                              | 7.0                                    | 3.0                                 |
| *Ch. distigma*   | 1                 | 1.0                       | 1.0                              | 1.0                                    | 3.0                                 |
|                 | 2                 | 2.0                       | 2.0                              | 4.0                                    | 6.0                                 |
|                 | 3                 | 3.0                       | 2.0                              | 6.0                                    | 5.0                                 |
|                 | 4                 | 3.0                       | 1.8                              | 6.0                                    | 6.0                                 |
|                 | 5                 | 3.0                       | 2.0                              | 5.0                                    | 5.0                                 |
| *Ch. udaipurensis* | 1                | 1.0                       | 1.0                              | 1.8                                    | 7.0                                 |
|                  | 2                 | 2.0                       | 2.0                              | 4.8                                    | 14.0                                |
|                  | 3                 | 3.0                       | 2.0                              | 6.6                                    | 15.0                                |
|                  | 4                 | 4.0                       | 2.0                              | 8.0                                    | 15.0                                |
|                  | 5                 | 4.4                       | 2.0                              | 9.0                                    | 14.0                                |
| S. Em. ±         |                   |                           | 0.31                             | 0.51                                  |
| C. D.            |                   |                           | 1.17                             | 1.91                                  |

Correlation between prey consumption and body mass increase: 0.902** 0.711*

Calculated t-value: 7.55 3.64

*Ch. udaipurensis* (enhanced prey provision)

|                  | 5                 | 4.8                       | -                               | 11.0                                   | -                                    |
|                  | 10                | 7.2                       | -                               | 15.0                                   | -                                    |
|                  | 15                | 8.8                       | -                               | 19.0                                   | -                                    |
|                  | 20                | 8.0                       | -                               | 17.0                                   | -                                    |
|                  | 25                | 9.0                       | -                               | 17.0                                   | -                                    |
| S. Em. ±         |                   |                           | 0.49                            | -                                     |
| C. D.            |                   |                           | 1.83                            | -                                     |

Correlation between prey consumption and body mass increase: 0.958*

Calculated t-value: 5.81

* indicates coefficient of correlation values significant at p = 0.05; ** indicates significance at p = 0.001
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The relationship between prey consumption with a prey density ranging from 1 to 5 caterpillars per day and the body mass increase for the species of Chlaenius and Calosoma indicated significant positive correlations. For Chlaenius, the correlation coefficient (r) was 0.902 (second instar prey) and 0.711 (third instar prey). Under enhanced prey density ranging from 5 to 25 caterpillars per day for Chlaenius, a significant positive correlation (r = 0.958) was recorded between mean prey-consumption and subsequent increase in body mass (Table 3). In the case of third instar tobacco caterpillar as prey, an increase in prey numbers from 1 to 5 resulted in a decrease in feeding propensity from 100 to 20 per cent for Ch. distigma, 100 to 40 per cent for both Ch. distigma and Ch. udaipurensis (Table 1). This shows that the carabid predator (Chlaenius) and the prey (second/ third instar tobacco caterpillar) relationship followed the typical Holling’s Type II functional response. Holling’s functional response when transformed into a linear regression showed an increasing trend in feeding. The linear regression equations species-wise have been presented in the Table (1). Likewise, the predator-prey relationship for the two species of Calosoma exhibited a typical Holling’s Type II response. The response transformed into a linear regression showed an increasing trend as depicted by the equations (Table 2). An increase in third instar tobacco caterpillar as prey from 5 to 25 depicted a decreasing feeding tendency from 100 to 44 per cent for C. imbricatum and 100 to 48.8 per cent for C. orientale.

The three species of Chlaenius when provided with different densities of second instar tobacco caterpillar as prey (1, 2, 3, 4 and 5) and enhanced prey provided for Ch. udaipurensis (5, 10, 15, 20 and 25) the maximum average prey consumed per day by Ch. nitidicollis and Ch. distigma were 3.0 each, 4.4 by Ch. udaipurensis and 9.0 by Ch. udaipurensis under enhanced prey provision. For the same three species of Chlaenius provided with third instar tobacco caterpillar as prey at prey densities 1, 2, 3, 4 and 5, the maximum average prey consumed per day were 1.0 for Ch. nitidicollis and 2.0 each for Ch. distigma and Ch. udaipurensis (Table 1). For the two species of Calosoma when third instar tobacco caterpillar was provided as prey in different densities (5, 10, 15, 20 and 25), the maximum average consumption per day was 11.0 for C. imbricatum and 13.0 for C. orientale (Table 2).

The carabid predator species of Chlaenius and the second/third instar tobacco caterpillar prey relationship followed the typical Holling’s Type II functional response. For all the three species of Chlaenius, an increase in caterpillar prey density for both the prey, i.e., second and third instar tobacco caterpillar, resulted in an increase in mean prey consumption initially, but later, leveled off after satiation with little variation among the species (Table 1). All the same, an increase in prey density evinced a gradual decreasing trend in the percent feeding propensity with little variation for Ch. nitidicollis fed on second instar S. litura. An increase in second instar prey numbers from 1 to 5 resulted in a decrease in feeding propensity from 100 to 56 per cent, then a slight increase to 75 per cent and decrease to 56 per cent for Ch. nitidicollis; the remaining species showed a regular decreasing trend and the corresponding values for Ch. distigma were 100 to 60 per cent; while for Ch. udaipurensis it was 100 to 88 per cent. When the prey density was enhanced ranging from 5 to 25 second instar caterpillars per day for Ch. udaipurensis, the feeding response showed a gradual decrease from 96 to 36 per cent (Table 1). In case of third instar tobacco caterpillar as prey, an increase in prey numbers from 1 to 5 resulted in a decrease in feeding propensity from 100 to 20 per cent for Ch. nitidicollis, 100 to 40 per cent for both Ch. distigma and Ch. udaipurensis (Table 1). This shows that the carabid predator (Chlaenius) and the prey (second/third instar tobacco caterpillar) relationship followed the typical Holling’s Type II functional response. Holling’s functional response when transformed into a linear regression showed an increasing trend in feeding. The linear regression equations species-wise have been presented in the Table (1). Likewise, the predator-prey relationship for the two species of Calosoma exhibited a typical Holling’s Type II response. The response transformed into a linear regression showed an increasing trend as depicted by the equations (Table 2). An increase in third instar tobacco caterpillar as prey from 5 to 25 depicted a decreasing feeding tendency from 100 to 44 per cent for C. imbricatum and 100 to 48.8 per cent for C. orientale.

The experiment was carried out following CRD and the data for increase in body mass after prey consumption for different species of Chlaenius and Calosoma were analyzed. The correlation between mean prey-consumption and subsequent increase in body mass was also calculated and the test of significance was worked out.

RESULTS AND DISCUSSION

Where ‘H’ is the number of attacked prey, ‘H’ is the prey density per unit area, ‘a’ is the predator’s search rate, ‘T’ is the handling time per prey and ‘T’ is the total time that is equal to the sum of time spent on searching and time spent on handling.

Holling’s equation was transformed to a linear form (Livdahl and Stiven, 1983) as:

\[
H_a = \frac{aHT}{1 + aHT}
\]

The correlation between mean prey-consumption and subsequent increase in body mass was also calculated and the test of significance was worked out.

\[
H_a = \frac{\alpha H T}{1 + \alpha H T}
\]

\[
1 = \frac{1}{H_a} = \frac{1}{H} + \frac{1}{T}
\]

\[
y = \alpha H + \beta
\]
Chlaenius panagaeoides (Laferte) consumed 1.4 to 6.9 cow pea aphids per day (Rajagopal and Kumar, 1988). Chlaenius micans (Fabricius) and Chlaenius posticalis Motschulsky, particularly the larvae of these species were reported to have high consumption rates of diamondback moths per individual (91 and 92 early fourth instars) through the entire larval period (Suenaga and Hamamura, 1998). Under laboratory conditions, a single adult of Chlaenius viridis Chaudoir could consume 9-tobacco caterpillar [Spodoptera litura (F.)] larvae per day. An equal liking for the larvae of cotton leaf roller (Sylepta derogata) as prey was also observed; however the larvae of Chlaenius viridis Chaudoir were observed to prey upon the soybean leaf webber, Lamprosema sp. in the field (Swaminathan et al., 2001). Kanat and Mol (2008) studied the feeding capacity of Calosoma sycophanta L., which is one of the most important predators of Pine Processionary Moth (PPM) larvae and pupae. The adult beetles consumed as many as 7-8 times their body weight per day; one adult beetle consumed 210-280 PPM larvae per year and 840-1120 PPM larvae during its lifetime. A detailed study on the feeding behaviour of Calosomasa yi DeJean by Young (2008) evinced that there was a trend observed wherein initial offerings of prepupae and pupae of fall armyworm were eagerly consumed, but later offerings were less consumed but no such trend occurred with offerings of larvae and adult fall armyworm.

Earlier studies on the functional response of carabid beetles are very scanty and none for the species of Chlaenius and Calosoma. The present study on functional response of the above mentioned two genera is supported by the studies of Dinis et al. (2016), though in an indirect way, as the predator-prey relationship for both the predators Calathus granatensis (Vuillefroy) and Pterostichus globosus (Fabricius) with the prey Bactrocera oleae (Rossi) pupae exhibited a type II functional response.

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### Table 4. Effect of prey consumption on body mass increase in species of Calosoma

| Carabid species | Prey provided (№) | Mean prey (№) consumed in 24 h | Mean body mass increase (mg) after feeding |
|-----------------|-------------------|-------------------------------|-----------------------------------------|
| C. imbricatum   | 5                 | 5                             | 58                                      |
|                 | 10                | 9.2                           | 88                                      |
|                 | 15                | 10.8                          | 105                                     |
|                 | 20                | 11                            | 98                                      |
|                 | 25                | 11                            | 103                                     |
| C. orientale    | 5                 | 5                             | 85                                      |
|                 | 10                | 10                            | 146                                     |
|                 | 15                | 13                            | 178                                     |
|                 | 20                | 12.8                          | 180                                     |
|                 | 25                | 12.2                          | 184                                     |

S. Em. ± C. D. Correlation between prey consumption and body mass increase: Calculated t-value: * indicates coefficient of correlation values significant at p = 0.05

| Carabid species | Prey provided (№) | Mean prey (№) consumed in 24 h | Mean body mass increase (mg) after feeding |
|-----------------|-------------------|-------------------------------|-----------------------------------------|
| C. imbricatum   | 5                 | 5                             | 58                                      |
|                 | 10                | 9.2                           | 88                                      |
|                 | 15                | 10.8                          | 105                                     |
|                 | 20                | 11                            | 98                                      |
|                 | 25                | 11                            | 103                                     |
| C. orientale    | 5                 | 5                             | 85                                      |
|                 | 10                | 10                            | 146                                     |
|                 | 15                | 13                            | 178                                     |
|                 | 20                | 12.8                          | 180                                     |
|                 | 25                | 12.2                          | 184                                     |

S. Em. ± C. D. Correlation between prey consumption and body mass increase: Calculated t-value: * indicates coefficient of correlation values significant at p = 0.05

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