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The Relationship Between Temperature and the Functional Response of *Coccinella septempunctata* (L.) (Coleoptera:Coccinellidae)

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Abstract.- The foraging activities of the predators depend on environmental variables, including air temperature. In the present study, the searching behavior and maximum consumption of prey of all developmental stages of *Coccinella septempunctata* was carried out with respect to the changing values of the air temperature. A strong relationship between two important factors of functional response "instantaneous attack rate" (a´) and "prey handling time" (T_h) was found with respect to temperature changes. The prey intake ratio per unit time was increased with increasing temperature up to a certain level beyond which it levels off and goes down to the extent of '0'predation. The temperature range for the foraging activities falls between 10ºC-40ºC. However, maximum predation rates were observed between 20-23ºC and 23ºC-25ºC. The lower temperature where the foraging activities were completely ceased was between 10-12ºC irrespective of prey densities available. A parabolic (curvilinear) relationship with high scale of co-relation ($r^{2 =}$ 0.86 – 0.99 α = 0.01) (T_h) was found.

Key Words: Behavioural response, *Coccinella septempunctata***,** functional response, foraging activity, incremental temperature**,** maximum and minimum temperature threshold.

INTRODUCTION

The predation rate is described as the ratio of prey killed per unit time by an individual predator from available prey numbers. The findings of previous studies determined the ratios of positively dependent biological factors including prey density, prey size, and the predator's hunger level (Frazer and McGregor, 1982)**.** Some abiotic factors, for example environmental temperature, have important roles in the rate of prey encountered and consumption. Many researchers carried forward the idea of the effect of increasing temperature typically accelerate the biological activity of the insects in general **(**Butler, 1982, Michaels and Flanders, 1992) and thus the rate of food ingestion increased with the increasing demand of its consumption. However, little work has been done on the role of temperature in predators foraging rate and the functional responses.

In previous studies of functional responses the attack rate (a′) and the handling time (T_h) were considered simply to be the components of the predation mechanism (Frazer and Gilbert, 1976)) but in later studies Longstaff (1980) and Pastorok (1981) analyzed their experimental results of the effect of temperature as components of the high rate of food consumption, based on the idea that increasing temperature could extend the satiation level of insects and the length of digestion pause could be reduced. The present experiment was designed to determine the effect of temperature on foraging behaviour of *Coccinella septempunctata* along with other parameters of the functional response. The specific objective of the experiment is to acquire the basic information regarding the behavioral responses of *Coccinella septempunctata* to several prey densities of *Myzus persicae* at a range of temperatures to provide a broader prospective of foraging pattern and its functional response.

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MATERIALS AND METHODS

The predator (C*occinella septempunctata*) and its prey (*Myzus persicae*) were reared in the laboratory. Adults and 4th instars were used in this study because of their efficient prey searching ability. Disposable Petri dishes of 9 cm x 1.5 cm diameter were used for the experimental unit. Both larvae and adults males and females used in the experiment were taken from the same cohort to minimize the chances of variation. The feeding regimes consisted of a mixture of developmental stages of *Myzus persicae.* Individual larvae and adults were exposed to the experimental arena with seven feeding regimes of 15, 30, 45, 60, 75, 90 and 105 aphids/experimental unit arena for 12 hours. The experiment was repeated five times at seven temperature *i.e.* 12, 15, 20, 25, 30 and 35ºC. The experiment was carried out at the entomological laboratories of National Agriculture Research Centre, Islamabad.

The number of prey eaten by the predator was recorded hourly. An individual predator was introduced into the arena containing the counted number of prey M*yzus persicae* and was considered as one replicate. Each unit was replicated five times. Before placing in the experimental arena the predator larvae and adults were starved for two hours to maintain a uniform level of hunger for each individual. Molting and mortality in the pre-adult stage of *Coccinella septempunctata* was monitored at each temperature level. The number of aphid prey eaten per individual predator (larvae and adults) was recorded after every twelve hours at all the temperature levels.

Statistical models

The estimated results were graphically shown using Excel 5.0. The number of aphids eaten (N_e) within twelve hours was plotted against the incremental temperature for different feeding regimes (prey densities) provided /predator (both larvae and adults) per experimental (unit) arena (N_t). Regression equation (curvilinear) $Y = a - N_t - N_t^2$ analysis was performed to fit the data. The ratios of prey (aphid) eaten to prey given (N_e / N_t) were also plotted against the incremental temperature again for both predator larvae and the adults exposed to various food regimes (N_t) to identify the functional response as effected by temperature. The regression analysis was again performed for each food regime. The instantaneous search rate (a´) was estimated (a´ / T_t) whereby the handling time $[(T_h) = a'/(T_t)]$ using Holling's typical disc equation $Ne = a'\ T_t\ N_t / (1+ a'\ T_h\ N_t)$.

RESULTS

The predation rate of C*occinella septempunctata* (4th instars and adults) is not only related to the prey density but also dependent on temperature (Table I). Initially with the increase in temperature the predation level increased up to a certain level beyond which the rate of predation goes decline of café predation. Within the range of 1ºC – 35ºC the maximum rate of predation predicted to be at 20 and 23ºC. This is valid for fourth instars including adults irrespective of the density of prey population (Fig. 1).

Table I.- The search rate (a´) Handling time (Th) and (R^2) of *C. septempunctata* 4th instar calculated for different temperatures under which they were fed on seven different food regimes (prey density).

Temperature (°C)	Instantaneous search rate (´a)	Prey handling time (T_h)	R^2	Max. no attacked
Larvae				
12	0.414	0.228	0.94	11c
15	0.540	0.197	0.97	19.0c
20	0.780	0.155	0.98	24b
25	0.975	0.105	0.98	45a
30	0.303	0.209	0.98	23b
35	0.489	0.536	0.94	13c
Adults				
12	0.508	0.242	0.90	9.0
15	0.653	0.185	0.96	19
20	0.766	0.177	0.94	22.5
25	0.816	0.124	0.96	33.5
30	0.600	0.202	0.98	13.7
35	0.359	0.216	90.0	6.1

The data on the rate of population when plotted against the increasing temperature fit very well into curvilinear parabolic model. With this parabolic curvilinear relationship the correlation co-efficient (ranging from 0.85–0.97) is significant at 0.01 levels. Beyond the optimal temperature for predation (*i.e.* 23–25ºC) the rate of predation quickly fell down and at around 38ºC the predator seemed to stop feeding totally. It can also be mentioned here that the predicted lower threshold of temperature where feeding activity started between around 10-12ºC. So there is a very wide spectrum of temperature (10-35ºC) in which feeding activity occurs. This is again true for both 4th instars and adults at all the prey levels of given 15 –105 aphids/ experimental arena. To understand the changing functional response of the predator *Coccinella septempunctata* in a more explicitly manner, the ratio of prey consumed (N_e) against prey offered ($N_{t)}$ *i.e*. (N_e / $N_{t)}$ is plotted against the increasing temperature for seven feeding regimes (15, 30, 45, 60, 75, 90, 105 / experimental arena). The relationship was found again parabolic (curvilinear) with high scale of co-relation ($r^2 = 0.86 - 0.99$ $\alpha = 0.01$). The changing of functional response in both adults and 4th instar larvae was in a same pattern.

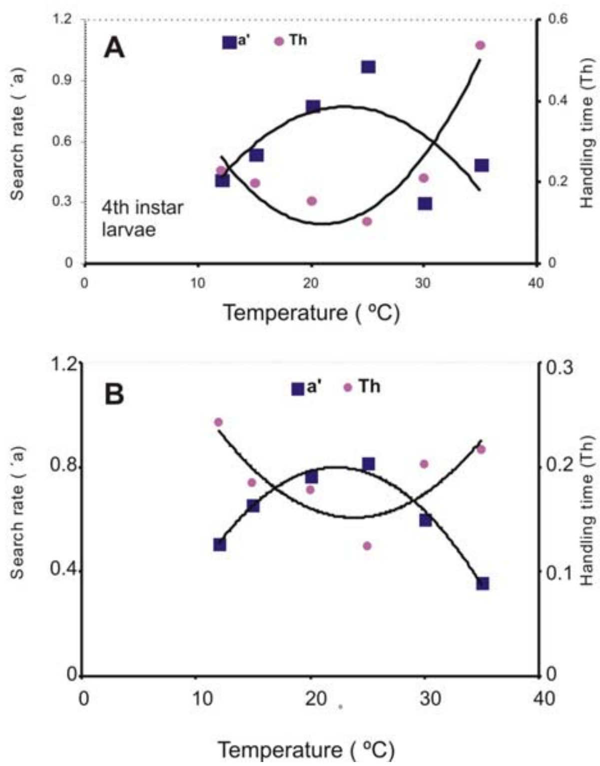

Fig. 1. Instantaneous search rate (a') and handling time (Th) plotted against different temperature regimes and the curve draw for the fourth instar larvae (A) and adult (B) of C. *septempunctata* fed on six different prey densities of *M. persicae.*

Two basic components of the functional response *i.e*., instantaneous search rate (a′) and prey handling time (T_h) of the predator were plotted against the temperature regimes. The instantaneous search rate (a′) initially increased with increasing temperature (10-25ºC) after which it quickly decreased, on the other hand, the handling time initially decreased but at 23±1ºC it began to increase. The relationship between both (a′) and the handling time ($T_{h)}$ were curvilinear with respect to temperature changes. Thus the relationship between search rates against temperature is 'concave' whereas that of between handling time and temperature is convex. The impact of the temperature on search rate (a′) and handling time (T_h) are more or less reciprocal with respect to changing temperature regimes.

This is true for both 4th instars and adults of *C. septempunctata*. These changes were reciprocal but the relationships of the basic parameters (*i.e*. a′ and T_h) determined the pattern of changes in the functional response in changing temperature.

DISCUSSION

The effect of temperature on the bionomics of various Coccinellids has been studied with their several aphid prey species as food (Frazer and McGregor, 1982; Evans and Dixon, 1986; Rhamhalinghan, 1987; Michaels and Flanders, 1992). Xia *et al.* (1999) determined the effect of temperature and various prey densities on life history parameters of various Coccinellids feeding on *Aphis gossypii,* on cotton. However, during the present study it was found that the activities especially the feeding and foraging of 4th instars larvae and adults are highly dependent on temperature.

This phenomenon was not unique to any particular predator species but is found in other predators including some of the Coccinellids (Honek, 1985; Spitze, 1985; Nakamuta, 1987; New, 1991; Elliott *et al*., 1989). During the present study, it was found that predation of both 4th instar larvae and adults were sensitive to temperature variation. Predation was observed between 12 and 35ºC, the maximum being 24±1ºC. The lower threshold of 10ºC for predation conforms to the biological threshold of C. *septempunctata* determined by Xia *et al*. (1999) *i.e*. 12.9–13.9ºC for the larval instars and pupae and 10.9–11.5ºC for eggs and adults. It shows the relationship between predation and other biological activity *i.e.* growth starting at 10ºC the rate of predation of *C. septempunctata* goes up with increasing temperatures up to certain level

(24±1ºC) beyond which the rate of predation decreased rapidly, predicted to reach zero at 40ºC. This pattern was not affected by the density of prey. Earlier, New (1991) expressed the view that temperature, a very common environmental variable markedly affected the functional response of *Ischnura elegens* larvae.

Elliott and Kieckher (1989) found that there is no searching by any coccinellids (adults and larvae) in cereals below 10 and 15ºC. They also estimated that the temperature at which walking speed is zero at 7°C, calculated from regression of walking speed verses temperature to be 7.3ºC. The maximum predation during this study occurred at 24 ± 2ºC, thus it could be expected that the maximum development of the beetles would occur at the temperature little above it but Kawcshi (1982) found that coccinellids attain this most rapid development at 35ºC. The phenomenon of maximum food consumption verses maximum development rate has to be well understood.

Elliott *et al*. (2000) while studying the activity and predation on adult coccinellids on aphids in spring cereal, constructed linear regression models to relate behavioural variables to abiotic and biotic factors. They did not incorporate non-linear terms in regression models. It has been stated that they did not have evidence of marked non- linearity in relationship among variables. In our current study the relationship between the predation and the temperature was found non-linear and parabolic. Furthermore, the predation at different prey density regimes of prey (functional response) and different temperature was also found to be non-linear and parabolic (12-35ºC) used during the experiment. Thus the predation rate and moreover the functional response was observed to be quadratic function of temperature for 4th instar larvae and adults the food regimes (prey densities) used in the experiment. Elliott *et al*. (2000) however, stated that the relationship existed among variables, than their exact parametric representation**.**

In the present study the ratio of the prey consumed (N_e) to the number of prey offered (N_t) when plotted against changing temperature for different Prey densities was again found to be curvilinear (parabolic) implying that the functional response of *C. septempunctat*a increased with increasing temperature to the certain level from where it sharply declined. The functional response in turn basically depended on two behavioural components of predator *i.e*. instantaneous search rate (a′) and prey handling time (T_h)

During a field study Elliott *et al*. (2000) found that the frequency of encounter with aphids was correlated with aphid density for two coccinellid species *Hippodemia deceimpunctata* and *H. convergens.* The frequency with which aphids were eaten was correlated with temperature for both the species and was positively correlated with aphid density. Some Coccinellids displayed the effect of ambient temperature on searching due to thermoregulatory basking and circadian rhythm (Frazer and Gill, 1981; Honek, 1985; Nakamuta, 1987).

According to Thompson (1975) the attack co-efficient increased with temperature (almost a five fold increase between 5ºC and 27.5 ºC) while the handling time decreased logarithmically from 5ºC to 16ºC and remained constant at higher temperatures. The part of the reason for increasing attack rate in this case was found to be less activity of prey (*Daphnia*) at lower temperature. The authors also concluded that other sub-components influencing the attack might also be influenced. This variation indicates the need for detailed investigation of the biology of the predator and prey as a basis for any reliable predictive modeling. If capture efficiency remains fairly constant or increases, the attack rate (a′) should also increase with temperature (Spitze, 1985). The rate of digestion should also increase with temperature. Handling time, with digestion as its major component, should then decrease as temperature increases (Spitze, 1985). During the present study (a′) increased initially with increasing temperature (10ºC-25ºC) after which it quickly ceases downward. On the other hand (T_h) declined with the temperature up to 23±1ºC and started increasing.

Although Zhang *et al*. (1996) while working with *Cardiochiles phlipinensis,* a brachonid larval parasitoid of a lepidopterous rice insect pest *Craphalocroin medinalis*, found that the instantaneous search rate (a′) was a linear function of temperature and handling time (T_h) was a quadratic function. In the present study both of these components were found to have quadratic (parabolic) relationship with temperature (T_t) except the fact that the curve whereas, the one between T_h and TºC is a down up (concave) curve when both were seen from the top.

According to New (1991) the increasing digestion rate could decrease the prey handling time and thus the rate of prey encounter increased. Increasing temperature might have accelerated the metabolic rate of the predator which results in the more demand of prey.

Longstaff (1980) analyzed the components of functional response of a predatory mite in relation to the temperature and argued that increasing temperature could extend the satiation level of the predator and the length of digestion pause could be reduced due to the (i) greatest distance from which the predator reacts to a prey by attacking it (ii) speed of the movement of both predator and prey, and (iii) proportion of attacks started which are successful.

Handling time also depends on the (i) time spent on persuing subduing a prey item, (ii) time spent eating it, and (iii) the time spent cleaning and /or resting after feeding during which the predator is not actively searching for more food.

It seems that all these aspects of both the components are affected either positively or negatively by temperature fluctuations. The resultant effect on the search rate (a´) and handling time (T_h) however, determine the change in functional response.

Despite the numerous variable factors (T_h) and (a´) have commonly been assumed to be constant for a given predator species and because of this assumption, quantitative data on predation can be described simply, indeed, perhaps in many cases too simply. The various cases are discussed in several recent accounts and the factors causing variation were reviewed by Hassell *et al*. (1977).

It can be inferred from the present study that a´ and T_h may be constant at certain temperature in the laboratory but as the temperature is a continuously changing biotic factor of environment and has a tremendous influence, both positively and negatively, depending on the level of regimes of temperature. It is rightly said that foraging studies on insect predators, in laboratory arenas may highlight important factors involved in the predator prey interaction (Haugh *et al*., 1984) but can not be expected to provide an advocate towards understanding of field interactions (O'Neil, 1989; Hodek (1973) and Honek **(**1985) cited by Elliot *et al.* (2000). The temperature and aphid density are important factors to regulate the coccinellids foraging activity and predation in field (Frazer and Gilbert, 1976; Honek, 1985; Takahashi, 1993).

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