

Changes in Searching Responses with Temperature of *Cyrtorhinus lividipennis* Reuter (Hemiptera: Miridae) on the Eggs of the Brown Planthopper, *Nilaparvata lugens* (Stål.) (Homoptera: Delphacidae)

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Abstract. The functional response of Cyrtorhinus lividipennis Reuter attacking the brown planthopper (Nilaparvata lugens (Stål.), BPH) eggs on rice was determined at six constant temperatures of 20°C , 23°C , 26°C , 29°C , 32°C and 35°C . Rogers' (1972) random predator equations were fitted to the data for each temperature separately. The equation model adequately described a Holling's Type II functional response for C. lividipennis and produced biologically realistic estimates of attack rates and handling times at five experimental temperatures between 20°C and 32°C . However, at 35°C , a negative handling time (Th = -0.0029) was produced. The effect of temperature was incorporated into Rogers' equation by making the attack rate (a) and handling time (Th) functions of temperature within the range 20°C to 32°C . The attack rate and handling time were fitted as hyperbola and reciprocal hyperbola functions of temperature respectively. The temperature incorporating four-parameter composite model fitted the combined data as well as did separate Rogers' equations based on the parameter estimates.

Key words: Cyrtorhinus lividipennis, functional response, Nilaparvata lugens, temperature.

Introduction

The threat and reality of global climate change has had a major impact on scientific research. This is evident from recent voluminous materials published on the subject (e.g. Solomon and Shugart 1993; Walker and Steffan 1996), and a global scientific initiative, the International Geosphere-Biosphere Program (IGBP), established in 1986 by the International Council of Scientific Unions (ICSU). An important focus of this program is to determine possible impact of global climate change on agriculture.

Rice is a staple food for about 50% of the world's population (IRRI 1995) and the impact of climate on world rice production is of concern. In September 1990, the United States Environmental Agency and the International Rice Research Institute began a cooperative program to examine two aspects: the effects of likely changes in global climate on the rice plant and its production, and the effects of flooded rice cropping on gases that may con-

tribute to global climate change (Peng et al. 1995). An important consideration to understand the effects of global climate change on production is to understand their effects on pest-natural enemy dynamics.

There is now consensus among scientists that the lower atmosphere and the earth's surface will warm with certainty. Near the earth's surface, the global average warming will be between +1.5°C and +4.5°C, with a best guess of +2.5°C (IPCC 1990). Pest and natural enemy species in rice ecosystems may respond to these changes in several ways. Since climate defines distribution boundaries of arthropods, there are likely to be changes in distribution and species composition (Heong and Domingo 1992). Climate can also affect predation rates which might reduce natural mortality of the pest species and increase its pest status.

In rice, the brown planthopper (BPH), *Nilaparvata lugens* (Stål.) is an important pest of rice in tropical (Dyck and Thomas 1979) as well as temperate countries (Cheng et al. 1994; Kiritani and Naba 1994; Song 1995). In tropical rice, it is now well established that BPH is a secondary pest problem caused by ecological disruptions, especially insec-

ticides, that reduce natural biological control (see Way and Heong 1994 for review).

Cyrtorhinus lividipennis Reuter is an important egg predator of plant and leaf hoppers in both tropical and temperate rice fields (see Dobel and Denno 1994 for review) and its populations are often directly related to BPH densities (Heong et al. 1992; Teramoto et al. 1996). Predation rates of C. lividipennis under normal laboratory conditions have been measured by Sivapragasam and Asma (1985) and Heong et al. (1990).

Temperature is an important factor influencing poikilothermal activities of arthropod predators (Cave and Gaylor 1989). A number of studies have examined variations in search and handling rates as a function of temperature for a wide variety of species (Everson 1980; Mack and Smilowitz 1982; McCaffrey and Horsburgh 1986). However, there have been limited studies on predators of rice leafhoppers and planthoppers. The purposes of this study were to determine the functional response of *C. lividipennis* attacking BPH eggs at six constant temperatures from 20°C to 35°C and to build a composite model describing changes in predatory response along a temperature gradient.

Materials and methods

Experiments

Greenhouse cultures of BPH were reared on rice (variety: Taichung Native 1, TN(1)) using a standard method described by Heinrichs et al. (1985). Cultures of C. lividipennis were initiated from adults caught in the Laguna rice area (Philippines) during April-May in 1993 and maintained on BPH eggs.

The searching responses of *C. lividipennis* on the BPH eggs were determined at six temperature conditions; 20°C, 23°C, 26°C, 29°C, 32°C and 35°C. Freshly emerged *C. lividipennis* female adults were preconditioned to the six different temperature regimes for one day and caged with seedlings of TN(1) rice plants for 14 h prior to release into the experimental arenas.

To prepare the experimental arenas, the seedlings of TN(1) rice were transplanted to clay pots (size 4, 15 cm diameter, 16 cm height) at five seedlings per pot. At thirty days after transplanting, the rice plants were trimmed to five tillers per pot. These plants were then enclosed in a cylindrical mylar cage (13 cm diameter, 50 cm height) with its top and a 15×15 cm² cut-out window covered by muslin cloth. Gravid BPH females (3-day-old adults) were introduced into the caged plants at densities of 1, 2, 4, 8 and 12 per pot for 24 h to obtain variation in BPH egg densities.

A total of 50 egg-laden arenas caged with one precon-

ditioned C. lividipennis female were placed in each temperature-controlled walk-in growth chamber with 12:12 h illumination and 70% relative humidity. After 24 h, the predators were taken out of the arenas. The number of BPH eggs consumed were counted and recorded. Consumed eggs were distinguished based on the remaining egg shell which was completely shrunken with no contents visible.

The whole set-up was replicated two times and the data were pooled together. Data from arenas in which the predators were missing or dead were excluded from the analysis.

Data analysis

The egg consumption data for each temperature were fitted to the Rogers' (1972) random predator equation:

$$Na = Nt(1 - \exp(-a Pt(Td - Th Na/Pt)))$$
 (1)

where, Na is the number of hosts attacked, Nt is the number of hosts available, a is the attack rate, Pt is the number of female predators, Td is the duration of the experiment, and Th is the handling time. Values for Pt and Td were pre-defined by the experimental design as Pt=1 female and Td=1 day, thus the equation (1) was simplified as:

$$Na = Nt(1 - \exp(-a(1 - Th Na)))$$
 (2)

The non-linear least-squares procedure was used to calculate the estimates of a and Th (PROC NLIN METHOD=DUD; SAS institute 1988).

The best fit two-parameter equations relating a and Th to temperature were selected based on r values and visual fit (CurveExpert 1.2: A comprehensive curve fitting software for Windows^{TR}, Copyright (c) 1995-1996 Daniel Hyams). The equation parameters were then estimated by using the SAS non-linear least-square procedure (PROC NLIN). Residuals of the regression models were plotted against the temperature variables and were examined for zero mean, uniform variance, and normality (PROC UNIVARIATE, SAS Institute 1988).

Results

The functional responses at different temperature regimes of C. lividipennis attacking BPH eggs were typically of Holling's Type II (Fig. 1), except for that at 35° C. Estimates of attack rates (a) and handling times (Th) are shown in Table 1. The data fitted the given random predator equation satisfactorily in all cases. However, at 35° C, a negative Th was obtained, implying that the Type II response did not adequately fit the data.

The attack rate increased with increase in temperature

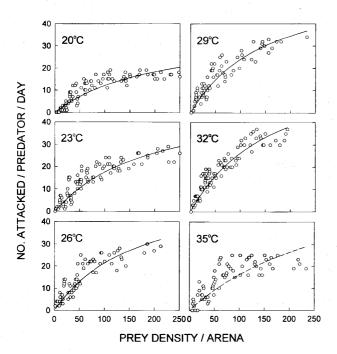


Fig. 1. Fit of Rogers' random predator functional response model for females of *Cyrtorhinus lividipennis* feeding on *Nilaparvata lugens* eggs at six constant temperatures.

up to 32°C, while at 35°C, a was lower than that at 20°C. Handling times Th correspondingly decreased with increase in temperature, up to 32°C.

The parameters a and Th were plotted as dependent variables against temperature by using the estimates from temperatures between 20°C and 32°C (Fig. 2). A hyperbola and a reciprocal hyperbola model were selected as the best two-parameter functions for a and Th, respectively, based on the r value and visual judgments using CurveExpert 1.2 (Hyams 1996). The best fit equation for attack rates, a', and temperature was:

$$a' = A0 + A1/T \tag{3}$$

where, T is temperature (°C), and A0 and A1 are constants

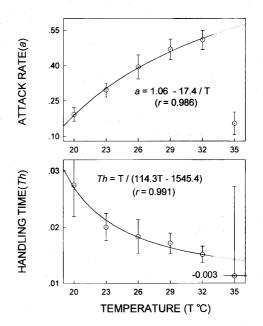


Fig. 2. Two parameters, attack rates (a) and handling times (Th), estimated from Rogers' equations at each temperature regressed against temperature (\pm asymptotic SE).

estimated by PROC NLIN; as $A0=1.0582\pm0.0232$, $AI=-17.365\pm0.578$; F=5114; df=2, 3; P<0.01; r=0.986. The equation fitted for handling time was:

$$Th' = T/(B0 T + B1) \tag{4}$$

where, B0 and B1 are constants (PROC NLIN; $B0=114.335\pm6.656$, $B1=-1545\pm146$; F=1303; df=2, 3; P<0.01; r=0.991). Because high-temperature inhibition appears to occur at 35°C, data from this temperature were not incorporated in the model, and this model thus must not be used for temperatures above 32°C.

The effect of temperature was incorporated into a Rogers' predator model by substituting equations (3) and (4) for both a' and Th' respectively, and establishing a composite model, as shown in equation (5), by using the combined data from the 20°C to 32°C range (PROC

Table 1. Attack rate (a) and handling time (Th) for Cyrtorhinus lividipennis female adults feeding on brown planthopper eggs estimated from fitting the random predator model (Rogers 1972) at different temperature regimes.

Temperature		Parameter	estimates	Asymptotic S.E.				
(°C)	а	Th	a	Th	\boldsymbol{F}	· . r	
2	20	0.1923	0.0274	0.0296	0.0056	321.7ª	0.88	
2	23	0.2950	0.0200	0.0292	0.0024	477.4a	0.92	
: 2	26	0.3938	0.0183	0.0516	0.0030	285.0a	0.90	
2	29	0.4687	0.0172	0.0437	0.0018	477.9a	0.94	
. 3	32	0.5085	0.0151	0.0412	0.0015	780.6a	0.95	
3	35	0.1550	-0.0029	0.0475	0.0159	196.4a	0.75	

^a Significant at 1% level (P<0.01)

NLIN; $A0=1.0844\pm0.0827$, $A1=-18.0976\pm1.8723$, $B0=103.9256\pm15.7668$, $B1=-1265.4122\pm401.513$, F=1201, df=4, 405, P<0.001; r=0.870).

$$Na = Nt(1 - \exp(-(A0 + A0/T)) + (1 - Na T/(B0 T + BI))$$
 (5)

The distribution of residuals for the composite model at each temperature was comparable to that of the separate Rogers' equations (Table 2). The composite model also provided estimates for the attack rate (a) and handling time (Th) close to those of separate Rogers' equations.

Discussion

Searching efficiencies of C. lividipennis attacking BPH eggs approximated that of Holling's (1959) Type-II functional responses as shown by others (e.g. Heong et al. 1990; Laba and Heong 1996; Sivapragasam and Asma 1985). The parameter estimates of a and Th obtained by Heong et al. (1990) (0.247 and 0.017) were more than twice that obtained by Laba and Heong (1996) (0.102 and 0.044). The latter attributed this difference to differences in the median temperatures under which the experiments were conducted. As the temperatures in the two studies were not kept constant and varied from 24°C to 32°C, it was difficult to directly implicate the difference as due to temperature. In this study, the same arena sizes were used and a and Th values varied from 0.192 to 0.509 and 0.0151 to 0.0274, respectively, between constant temperatures of 20°C and 32°C. It seems likely that the temperatures and periods of time the predators were exposed have extreme The estimates of effects on these parameters.

Sivapragasam and Asma (1985) were very high (2.21 and 0.034), probably because of the smaller arena size used.

At the temperature extreme of 35°C, attack rate of C. lividipennis was inhibited. This might be due to destructive effects of high temperature on BPH eggs (Bae 1995). Reduction in searching ability may also be due to the extremely high temperature affecting biological functions and survival (Heong et al. 1995). Cave and Gaylor (1989) also found a significant decrease in attack rate at 35°C in Telenomus reynoldsi Gordh and Coker, an egg parasitoid of Geocoris spp.

The relationships between search parameters a and Th with temperature appear to be a hyperbola and a reciprocal hyperbola, respectively. These relationships may be best described in equation (3) and (4), respectively. Curvilinear responses have been obtained by Cave and Gaylor (1989) using T. reynoldsi, Mack and Smilowitz (1982) using Coleomegilla maculata (DeGeer), and Flinn (1991) using Cephalonomia waterstoni (Gahan). Linear responses have also been found in a damselfly, Ischnura elegans (Van der Linden) (Thompson 1978), Orius insidiosus (Say) (McCaffrey and Horsburgh 1986) and Phytoseiulus persimilis Athias-Henriot (Everson 1980). Zhang et al. (1996), however, found that the attack rates of the parasitoid, Cardiochiles philippinensis Ashmead attacking larvae of rice leaf folders declined with increase in temperature.

The model using separate estimates from Rogers' model would require parameter estimates from a series of experiments conducted at different temperatures. In the composite model, however, temperature is an independent variable and predator responses at various temperatures may be predicted. The outputs of these two models did

Table 2. Composition of residuals (observed-predicted) of independent Rogers' models and the composite functional response model by temperature.

 Temperatu (°C)	re	N		Mean	Variance	Skewness		Kurtosis	r	
Independer	nt Roge	rs' model	s							
20		88		1.092	16.146	-0.1035		-0.0283	0.7901	
23		92	<i>t</i> .	1.197	21.154	-0.4013	11.71	-1.1482	0.8426	
26		66	i 7	1.468	27.977	-0.1105		0.0921	0.8125	
29		72		1.224	22.412	0.0230		-0.3188	0.8791	
32		91		1.179	22,490	-0.3691		0.3502	0.8971	
Over all		409	, ,	1.219	21.493	-0.1951		0.3022	0.8698	
Composite	model									
20		88	:	1.120	16.137	-0.1784		0.0342	0.7966	
23		92		1.266	21.004	-0.3669		1.0389	0.8407	
26		66	,	1.545	27.749	-0.1042		0.0836	0.8136	
29		72	2	1.165	22.614	-0.0123		-0.2803	0.8819	
32		91		1.139	22.605	-0.3158		0.2833	0.8951	
Over all		409		1.234	21.490	-0.1898		0.2700	0.8703	

not differ significantly, implying that the composite model can adequately represent functional response-temperature relationships.

The models may provide convenient ways to predict the possible impact of global warming on searching behavior of C. lividipennis on eggs of BPH. They predicted increase in search with increase in temperatures between 20°C and 32°C. Thus, it might be reasonable to infer that in areas with such temperatures, there will likely be increase in predation. However, in areas where temperatures are likely to exceed 32°C, egg predation can be markedly reduced. Based on data collected in the Philippines, C. lividipennis also has more limited tolerance to high temperature extremes than BPH (Heong and Domingo 1992), suggesting that range dissociation between these two species can occur, that might result in reduced egg predation. In a similar study in Central Thailand, where peak temperatures can exceed 40°C in April, the C. lividipennis population was found to be 30 times more tolerant than that in the Philippines, suggesting that local populations are well adapted to such extremes and the possibility of global warming causing species range dissociation that will reduce predation is small (Heong et al. 1995). It will be interesting to estimate the functional responses of the central Thailand populations of C. lividipennis using the same methods.

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