Thermal regimes, age and sex modulate feeding attributes of *Zygogramma bicolorata* Pallister (Coleoptera: Chrysomelidae)

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Feeding attributes of phytophagous insects are greatly influenced by abiotic and biotic factors. Therefore, we assessed the combined effect of temperature, age and sex on food consumption and utilization efficiencies of *Zygogramma bicolorata* Pallister. This Mexican beetle is known as one of the most promising candidates for the biocontrol of *Parthenium hysterophorus* Linnaeus, a noxious weed of barren, grazing and farming lands. Temperature, age and sex influenced food consumption, its utilization and ecological efficiencies of the beetle. Temperature between 27°C and 30°C was found optimal for 20-day-old adults of *Z. bicolorata* to convert and utilize the food biomass to body mass. Above and below the optimal temperature and age, the feeding attributes declined. Young females kept at 27°C consumed more food and laid more number of eggs compared to other females at different temperatures. This study reveals that females are more voracious feeders than the males regardless of temperature regimes. The present findings can be helpful to mass-multiply *Z. bicolorata* in the laboratory for the biocontrol of *Parthenium* weed in fields and agricultural farms. The results also suggest that global climate change may affect the biocontrol potential of the insect, but field investigations are needed to support the present findings.

Keywords: Age, biocontrol, food, sex, temperature, *Zygogramma bicolorata.*

ALL insects require a certain amount of energy for their development, reproduction and survival. Favourable conditions with ample food and energy resources combined with an innocuous environment enhance the survival rate of insects. Both quantity[1–3] and quality[4–7] of food consumed by the insects are known to influence the survival and growth of immature stages as well as reproduction in adults. Studies were done to answer the questions of how and to what extent an organism can alter its physiological and behavioural processes like consumption rate and metabolism to achieve and maintain its optimal state. The result of study[8] reveals that the physiological afflictions linked with egg production in mated females were indicated by their higher relative consumption rate, prior and higher rate of egg laying, better lifetime relative metabolic rate and more net and gross production efficiencies than unmated adults. Previous studies reported that optimal temperature can promote accumulation of energy reserves in *Drosophila*[9] and fluctuation in temperature can modulate physiological development like metabolic rate in insects[10,11]. It has been observed that climate change has resulted in range shifts[12,13] and changes in the periodic biological phenomena in various insects[14].

Phytophagous insects act as a link in the matter and energy transmission in terrestrial ecosystems. Consequently, information about food consumption, its utilization along with ecological efficiencies of phytophagous insects is essential. Food consumption by phytophagous insects in relation to various parameters, viz. food quality[15–17], chemicals, like fertilizers[18,19], larval stages[20–23], sex[24,25], previous experience of food consumption[26] and age[22,27–31] have been frequently studied by various workers. These studies are not only helpful in understanding the quantitative utilization of food, but also bestow knowledge on important biological processes and the behaviour of insects.

Understanding the relationship between biotic and abiotic factors on different biological characteristics is necessary for the development of a good pest population calculation system and management programme. However, this combined study is lacking in *Zygogramma bicolorata* Pallister, which was imported from Mexico to India in 1983 by the Indian Institute of Horticultural Research, Bengaluru for the biocontrol of *Parthenium hysterophorus* Linnaeus[31]. The present study was done to quantify the combined effects of temperature, age and sex on food consumption, its utilization and ecological efficiency in *Z. bicolorata*, since for ecologically relevant problems it is necessary to have information about the optimal requirements of food, temperature and age of an organism. Another important verity is that food and temperature should not be considered separately because of their natural independence[32].

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Materials and methods

Maintenance of stock culture

Adults of *Z. bicolorata* were collected from the campus of the University of Lucknow, Uttar Pradesh, India (26°50′N, 80°54′E) and brought to the laboratory to establish a stock culture. The stock culture was maintained in plastic petri dishes (9.0 cm × 2.0 cm) under controlled abiotic conditions (27° ± 1°C; 65% ± 5% relative humidity; 14 h light : 10 h dark) in environmental test chambers (CH-6S, Remi Instruments, Mumbai). The excised leaves of *P. hysterophorus* were used as a food; leftover leaves were replaced after every 24 h with fresh ones. Adults from stock culture were paired in plastic petri dishes and allowed to mate. The eggs were collected daily and hatched first instars were reared in plastic petri dishes of the same area on the same food source as above. The development of second, third and fourth instars were completed in petri dishes. The fully grown grubs were transferred to plastic beakers (9.0 cm × 6.5 cm) half filled with moist sand for pupation. Newly emerged adults were placed singly in petri dishes for further use in experiments.

Experimental protocol

Adults of different ages, viz. newly enclosed (<12-h-old), 5-days-old, 10-days-old, 15-days-old, 20-days-old, 25-days-old, 30-days-old, 35-days-old and 40-days-old, were weighed using an electronic balance (Sartorius CP225-D, Germany) with 0.1 mg precision. They were maintained at five constant temperatures, viz. 20°C, 25°C, 27°C, 30°C and 35°C, in plastic Petri dishes (size as above) and provided with preweighed amount of fresh *Parthenium* leaves (150 mg). The unconsumed leaves were weighed after 24 h. Adults were also weighed after 24 h. However, on the tenth day, males and females were paired for mating and after completion of mating each partner was provided with preweighed fresh *Parthenium* leaves (150 mg). Leftover leaves by the beetle and weights of the beetle were weighed after food consumption (every 24 h). Eggs laid by females at each age were also recorded. The experiment was repeated at each of the five constant temperatures mentioned above. All weights were taken at the time of food change. There were ten replicates per group.

Dry biomass was calculated by converting fresh weight into the dry weight. For the purpose, fresh weight were recorded then they were air-dried at 80°C for 24 h and again after drying their weight were recorded. For dry biomass of adults, fresh weight of adults (male and female) was recorded following which they were killed, air-dried at 80°C for 24 h and weighed. There were 15 replicates per group. The weights obtained were used for the calculation of dry biomass per milligram of fresh leaf, adults and eggs. The dry weight of the food consumed, efficiency of conversion of ingested food (ECI) and growth rate were calculated using the formulae given by Waldbauer[27].

Statistical analysis

All data were tested for normality using Kolmogorov–Smirnov test and Bartlett's test for homogeneity of variance prior to further analysis. Three-way ANOVA was conducted with all feeding attributes as dependent variables, and temperature, age and sex and their interactions as independent variables followed by Tukey's post-hoc comparison of means. Oviposition by females of *Z. bicolorata* was statistically analysed for the combined and individual effect of temperature and age using two-way ANOVA taking temperature as the row factor and age as the column factor. Dry food consumption of females was regressed against eggs laid by them. All statistical analyses were performed using MINITAB 16 on a portable personal computer.

Results

The three-way ANOVA reveals a significant influence of temperature, age, sex and their interactions on dry food consumption of the beetles (Table 1). Age-specific regression graphs show that dry food consumption increases with increase in age up to a certain duration, thereafter it decreases further increase in age. However, 20-day-old females at 27°C had the highest food consumption (Figure 1).

Temperature, age and their interactions had a significant effect on ECI; however, the effect of sex and its interactions was statistically not significant (Table 1). However, 20-day-old males at 27°C had the highest conversion efficiency (Figure 2). Further, growth rate and dry biomass gain of adult beetles were significantly influenced by the three independent factors (Table 1). Although males had a higher growth rate than the females (Figure 3), the latter exhibited higher dry biomass gain (Figure 4).

There was a significant effect of temperature and age of the beetles ($F = 470.40$; $P < 0.001$; $df = 6315$) on fecundity. It was maximum for 20-days-old females at 27°C and minimum for newly emerged beetles at 35°C (Figure 5). The interaction between temperature and age significantly influenced fecundity. Eggs laid by the female *Z. bicolorata* were strongly regulated by dry food consumption and the trend can be best depicted by a linear regression equation: $Y = 0.518X - 24.9$ ($R^2 = 0.275$; $P < 0.001$) with significant regression coefficient.

Discussion

Abiotic and biotic factors are known to influence the growth, consumption and food utilization efficiencies of phytophagous insects[33]. Among the biotic factors, diet plays a key role in survival, behaviour, development, metamorphosis,

Table 1. Effect of temperature, age, sex and their interactions on feeding attributes of *Zygogramma bicolorata*

Independent variables	Dependent variables			
	Dry food consumption	ECI	Growth rate	Dry biomass
Temperature	$F = 722.53$; $P < 0.001$; d$f = 4392$	$F = 44.96$; $P < 0.001$; d$f = 4392$	$F = 159.67$; $P < 0.001$; d$f = 4392$	$F = 193.30$; $P < 0.001$; d$f = 4392$
Age	$F = 91.70$; $P < 0.001$; d$f = 8392$	$F = 87.45$; $P < 0.001$; d$f = 8392$	$F = 156.10$; $P < 0.001$; d$f = 8392$	$F = 175.13$; $P < 0.001$; d$f = 8392$
Sex	$F = 537.53$; $P < 0.001$; d$f = 1392$	$F = 0.28$; $P > 0.05$; d$f = 1392$	$F = 12.68$; $P < 0.001$; d$f = 1392$	$F = 20.29$; $P < 0.001$; d$f = 1392$
Temperature * age	$F = 3.12$; $P < 0.001$; d$f = 32,392$	$F = 11.94$; $P < 0.001$; d$f = 32,392$	$F = 24.26$; $P < 0.001$; d$f = 32,392$	$F = 27.03$; $P < 0.001$; d$f = 32,392$
Age * sex	$F = 3.11$; $P < 0.01$; d$f = 8392$	$F = 0.96$; $P > 0.05$; d$f = 8392$	$F = 0.51$; $P > 0.05$; d$f = 8392$	$F = 0.81$; $P > 0.05$; d$f = 8392$
Temperature * sex	$F = 16.98$; $P < 0.001$; d$f = 4392$	$F = 1.05$; $P > 0.05$; d$f = 4392$	$F = 1.50$; $P > 0.05$; d$f = 4392$	$F = 0.67$; $P > 0.05$; d$f = 4392$

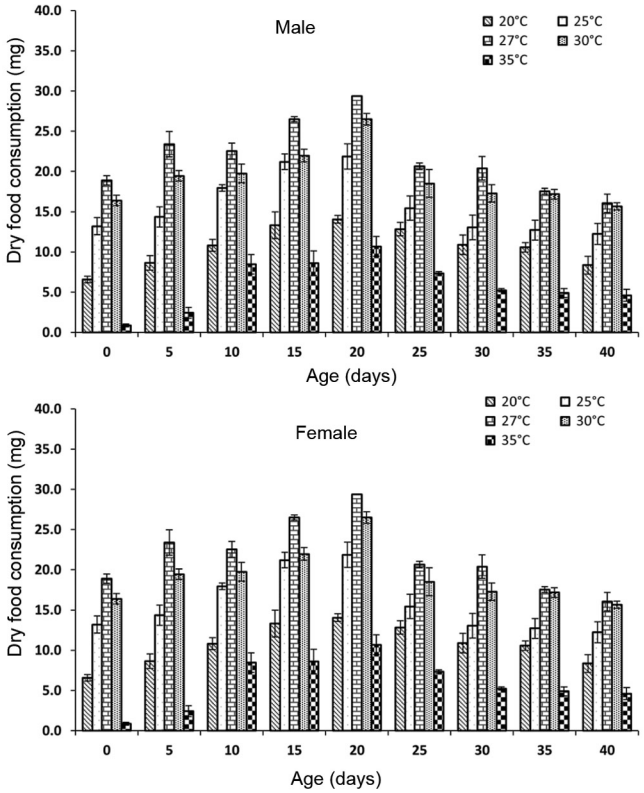

Figure 1. Temperature and age-specific dry food consumption (mg) in *Zygogramma bicolorata*.

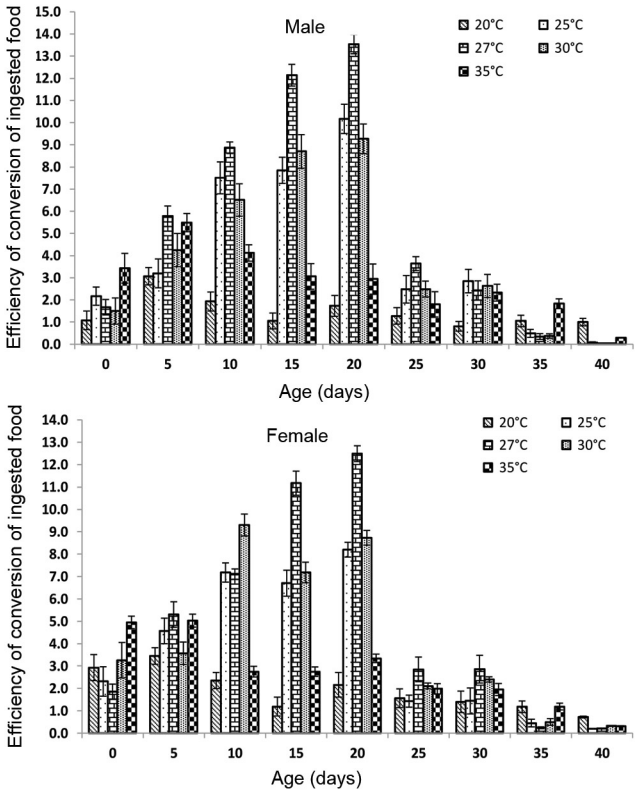

Figure 2. Temperature and age-specific efficiency of conversion of ingested food in *Z. bicolorata*.

reproduction, life-table parameters and population dynamics of phytophagous insects[34]. The present study reveals that temperature, age and sex of this insect play a key role in food consumption, its utilization and ecological efficiencies. Several growth parameters like dry food consumption and growth rate were significantly influenced by temperature as well as age of the beetles. However, ECI was significantly affected by temperature and age, but not by sex of the beetles. The efficiency of conversion of ingested food, also known as 'growth efficiency index', is a reliable indicator for examining the overall ability of the insect to use its food to produce biomass.

The dry food consumption, ECI and growth rate of *Z. bicolorata* were found to increase up to 20 days from their emergence. This enhanced consumption of food by the adult beetles at an young age can be attributed to: (a) their elevated demand of energy for development of gonads and to attain sexual maturity and (b) senescence. Several studies reported that food consumption modulates reproduction as well as fitness of an individual[23,35,36]. Senescence can facilitate

decrease in consumption of food by adult beetles, characterized by decrease in oviposition, assimilation and pace of locomotion with age. The enhanced voracity by female beetles can be ascribed to their bigger size[37], as large size has more food nutrients requirement due to high-energy expenditure for sustenance and reproduction[23].

The decreased growth rate in adult beetles with ageing can be ascribed as a physiological consequence of senescence which results in decreased consumption rates. On the other hand, the resultant higher growth rates of females can be ascribed to their larger size and high consumption rates, as the females require more energy for reproduction and egg production[23,36].

The increased conversion efficiency of young adults might be a physiological effect of their age. However, higher conversion efficiency of males than females can be ascribed to their smaller size. The present findings are in agreement with those reported earlier[23]. Further, increased mean body biomass of adults with ageing propounds that their digestive capabilities improve with age to compensate for their increasing nutritional requirements.

Fecundity was found to be influenced by the age of the female beetles. It was maximum for 20-day-old beetles. This increment in fecundity is the result of increased consumption of food to accomplish their high energy demands, as females require more nutrients and energy to increase their reproductive fitness. It has been reported earlier that depletion in the quality as well as quantity of food consumed results in delay in the onset and decline in the rate of egg production in females[38]. The quantity, quality and rate of food consumption by adults are known to have a significant influence on fecundity[39,40]. It has been previously reported by many workers that daily and lifetime fecundity are influenced differently by the food and nutrients ingested by the adults[41]. The better quality and quantity of food probably causes early ovariole ripening and leads to more efficient conversion of food into eggs[41,42]. Thus, it can be demonstrated that the feeding of adults affects the reproductive performance of *Z. bicolorata.*

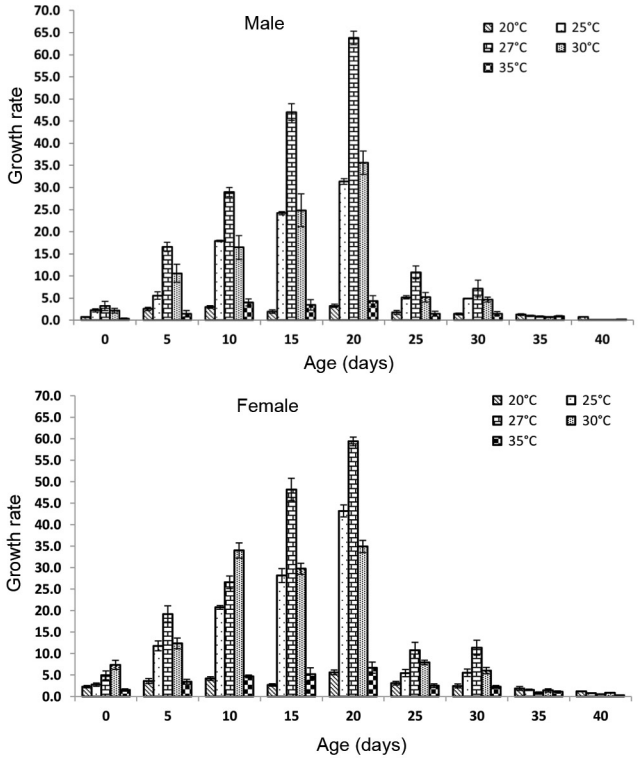

Figure 3. Temperature and age-specific growth rates of *Z. bicolorata*.

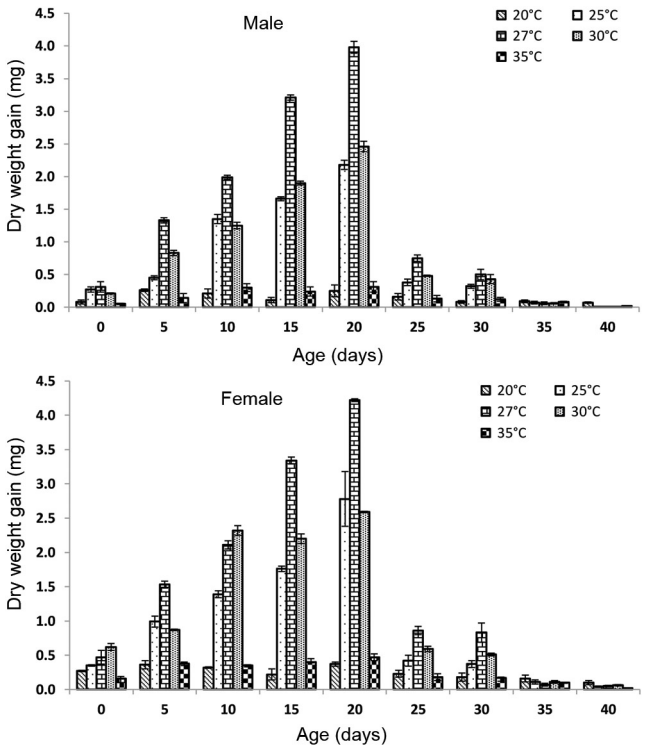

Figure 4. Temperature and age-specific dry weight gain in *Z. bicolorata*.

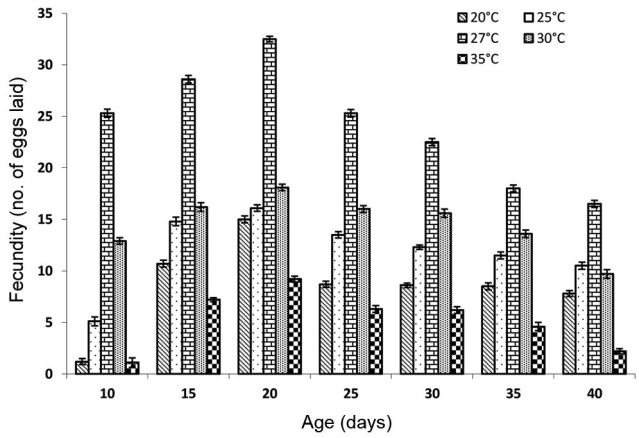

Figure 5. Temperature and age-specific oviposition by female *Z. bicolorata*.

The results of the present study demonstrate a direct action of temperature on dry food consumption, ECI and growth rate in adults of *Z. bicolorata*. These growth parameters were maximum at 27°C and minimum at 35°C. This may be ascribed to the fact that thermal regime modulates developmental time by controlling the processes underlying weight gain. The quantification of daily consumption of food by ectotherms has revealed that temperature has a linear relationship and a positive effect on the rate of food consumption[43,44]. However, studies have reported that food consumption in insects increases up to a certain age with increase in temperature, and subsequently it varies in different studies; either increase or decrease with further increase in temperature[44,45]. Decreased growth rate and food consumption at 20°C and 35°C may also be attributed to the deterioration in food quality at extreme high and low temperatures. Previous studies have confirmed that food quality is significantly altered by temperature[46,47]. Food exposed to low or high temperatures may undergo deterioration of varying degrees in its sensory characteristics and nutritional value, which results in decreased consumption and growth rate. An individual may show reduced growth rate due to food consumed that has deteriorated in nutritional quality[48]. The efficiency of food conversion and growth rate of adults primarily increased from 20°C to 27°C, and thereafter decreased with further increase in temperature. The temperature between 27°C and 30°C was optimal for *Z. bicolorata* adults to convert and utilize the food biomass to body mass. Above the optimal temperature, the feeding attributes decreased[49]. The results of the present study reveal the likelihood that along with the quality of food, temperature below the optimal level reduces the metabolic rate of *Z. bicolorata* adults, which in turn results in lower food utilization efficiencies of the adult beetles. On the other hand, temperature above the optimal level may induce thermal stress in adults that again reduces their conversion efficiency and growth rate.

Conclusion

In brief, the present study shows decreased consumption rate, conversion efficiency and growth rate of *Z. bicolorata* adults with increase in age up to 20 days and 27°C. Thereafter, there is a decrease with further increase in age and temperature. Adult females were more efficient consumers and converters of food than adult males. Temperature of 27°C and 30°C was found optimal for 20-day-old females of *Z. bicolorata* to convert and utilize food biomass to body mass above and below the optimal temperature and age, the feeding attributes showed a decline. Young females maintained at 27°C consumed more food and laid more eggs compared to other females at different temperatures. Thus, temperature between 27°C and 30°C, and age of 20 days can be considered optimal for converting and utilizing food biomass into body mass maximally by *Z. bicolorata* adults. The results of the present study can be helpful in developing strategies to control *Parthenium* weed in fields and agricultural farms by *Z. bicolorata*, viz. during which season should the beetles be released so that they can survive and build their population. Moreover, the above findings can be used for rapid mass-multiplication of this biocontrol agent in the laboratory for augmentative biocontrol of *P. hysterophorus*.

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