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Life table of the parthenium beetle, *Zygogramma bicolorata* (Coleoptera: Chrysomelidae), under different environmental variables

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Abstract: The present study was aimed to understand the patterns in the development, survival and mortality of the immature stages of parthenium beetle, *Zygogramma bicolorata* Pallister along with the behavioural patterns associated with them under different environmental variables. This may aid in the improved mass multiplication of this weed biocontrol agent. For the purpose, life table of *Z. bicolorata*, a defoliator and biocontrol agent of a parthenium weed, *Parthenium hysterophorus* L., was studied in the laboratory under environmental variables, like food, temperature, photoperiod and different wavelengths of light. Kappa value, as mortality indicator, was lowest when beetles at various life stages were fed on inflorescence of weed, followed by leaves and stem, while the generation survival was highest on inflorescence. Temperature significantly affected the mortality and survival rate of key life stages of the beetle. Kappa value was lowest when beetles at immature stages were reared at 27℃, followed by 30, 25, 20 and 35℃. The generation survival and survival rate followed the same pattern. Mortality was significantly influenced by different photoperiods and it was least with best generation survival at 14L:10D (long day) followed by 12L:12D (equinox), 10L:14D (short day), 24L:0D (continuous light) and 0L:24D (continuous dark). In response to different wavelengths of light, Kappa value was lowest with highest generation survival under white light (broad spectrum), followed by yellow ($\lambda = ca.$ 570 nm), blue ($\lambda = ca.$ 475 nm) and red ($\lambda = ca.$ 650 nm). Egg experienced highest mortality. The life stages of the beetle can be best reared under long day white light at 27℃ feeding on inflorescence of parthenium. Mortality trend was rigidly and significantly stage-specific, showing an innate survival effect which was independent from the factors studied.

Key words: *Zygogramma bicolorata*; *Parthenium hysterophorus*; host plant; survival; mortality; life table

1 INTRODUCTION

Life tables are essential statistics and could be used as bioclimatic indices of population growth rates responding to selected conditions (Southwood and Henderson, 2000), and are helpful in understanding the effects of bioclimatic factors on growth and survival of an insect population (Hansen *et al.*, 1999; Wittmeyer and Coudron, 2001). Temperature is amongst the key abiotic factors that regulate insect population dynamics, developmental rates, phenology, physiology and seasonal occurrence (Logan *et al.*, 1976, Klok and Chown, 1997, 1998; Schowalter, 2000; Kingsolver *et al.*, 2001). Exposure to lights of different durations (McPherson, 1974; Saunders *et al.*, 2002; Mishra and Omkar, 2004; Omkar *et al.*, 2009a, 2009b) and wavelengths (White and Shardlow, 2011) largely affects the various physiological and behavioural processes of beneficial insects. Plant structures differing in morphological and/or biochemical features also have a great impact on development, survival (Norris and Kogan, 1980) and the demography of the attacking insects.

Parthenium weed, *Parthenium hysterophorus* Linnaeus, is an annual herb, native to the Gulf of Mexico and central South America and is widespread globally (Navie *et al.*, 1996). It is one of the worst weeds because of its invasiveness, potential for spread, along with economic, health and environmental impacts (Evans, 1997). It is spreading rapidly in Indian subcontinent (Javaid and Anjum, 2006) and could be managed to some extent using the parthenium beetle, *Zygogramma bicolorata* Pallister (Coleoptera: Chrysomelidae). This beetle became abundant in India within three years of its introduction, resulting in a significant reduction in

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parthenium density (Jayanth and Bali, 1994a; Jayanth and Visalakshy, 1996). Its importance in biocontrol of this weed has led to various studies on its occurrence, dispersal, thermal effects, diapause, feeding and reproductive behaviour (Jayanth and Bali, 1992, 1993a, 1993b, 1993c, 1994b; Jayanth and Visalakshy, 1994; Bhoopathi and Gautam, 2006; Omkar *et al*., 2008, 2009b, 2010; Omkar and Pandey, 2010; Sushilkumar and Ray, 2010; Omkar and Afaq, 2011) and biocontrol efficacy (Dhileepan *et al*., 2000; Dhileepan, 2001). However, little is known about its life table (Jayanth and Bali, 1994b; Bhumannavar *et al*., 1998; Bhoopathi *et al*., 2011) with almost no information on abiotic and biotic factors affecting the mortality of its population. Hence, the present study has been designed to investigate mortality based life table of *Z. bicolorata* under the influence of food, temperature, photoperiod and wavelength of light. The present investigation especially focuses on the mortality of the immature stages of *Z. bicolorata* and not on adult reproduction, as we aimed to understand the pattern of mortality in this beetle. Hence, the fertility based demographic attributes, such as intrinsic rate of increase is not included in this study. This study may increase the understanding of the patterns in the development and survival of the immature stages of *Z. bicolorata* along with the behavioural patterns associated with them when exposed to different environmental factors. Additionally, it will help improve the mass multiplication of this biocontrol agent by providing the information on mortality and survival, and thereby its use in *Parthenium* biocontrol programmes.

2 MATERIALS AND METHODS

2.1 Stock maintenance

Z. bicolorata adults were collected from *P. hysterophorus* plants available in the university campus and brought to the laboratory. They were paired in plastic Petri dishes (9.0 cm × 2.0 cm) and fed on leaves of *P. hysterophorus* kept in Environmental Test Chamber (ETC) (CH-6S, Remi Instruments, India) maintained at 27 ± 1℃, 65% ± 5% RH and 14L∶10D. Leaves were replenished daily. The eggs obtained after mating were reared separately till adult eclosion in plastic beakers (1 L) (diet as above). For pupation, mature larvae are kept in containers having sand because they pupate inside soil. The newly eclosed adults were reared (same diet) in isolation in Petri dishes. Sexually mature adults were paired and eggs obtained after mating were used in experiments.

2.2 Life table on different foods

Life table was evaluated after providing leaves, stem and inflorescence of *Parthenium* plants as food under controlled conditions (27 ± 1℃, 65% ± 5% RH and 14L∶10D). For this, one thousand eggs were taken from the F_2 stock and reared till adult eclosion on the above three foods (100 eggs per replicate, 10 replicates). The larvae were reared separately to avoid over-crowding in plastic Petri dishes (9.0 cm × 2.0 cm) under above-mentioned conditions in the ETC. Observations were taken on the developmental period and survival of every life stage (x). The newly eclosed beetles were sexed. Data on number of immature stages dying at each stage were subjected to analysis following Morris and Miller (1954):

Stage mortality $(dx) = d_n / x_0$;

Real mortality $(100rx) = d_n \times 100 / x_0$;

k-value (kx) or mortality within life stage $x = \log x_{n-1} - \log x_n$;

K (Kappa) $= \sum kx =$ Sum of k- values.

where $x =$ life stage (*i. e.*, eggs, all four instar larvae, and pupae), x_n = number of x stage survived, x_{n-1} = number of x stage survived in previous stage, x_0 = initial number of eggs taken, d_n = number of x stage died. Generation survival (number of daughters/number of initial eggs) was calculated following Harcourt (1969).

2.3 Life table at different temperatures

One thousand eggs (100 eggs per replicate, n = 10) of F_2 generation were kept in plastic Petri dishes (as above) at each of five constant temperatures, *viz.* 20, 25, 27, 30 and 35℃ at 65% ± 5% RH and 14L∶10D in ETC. The neonates hatching from eggs were recorded and reared till adult emergence on *P. hysterophorus* leaves (space as above). Life table calculations were done as given in section 2.2.

2.4 Life table at different photoperiods

The mortality based life table was evaluated at five photoperiods. Wooden photoperiodic chambers of 40 cm × 40 cm × 40 cm dimensions were designed, each containing a 60 W white electric bulb (*Phillips* brand). The walls, ceiling and floor of each chamber were covered with white paper. Relative humidity (65% ± 5%) was maintained by keeping 1 N NaCl solution in a glass beaker in each of the chambers. One thousand F_2 eggs (100 eggs per replicate, n = 10) were kept in plastic Petri dishes (9.0 cm × 2.0 cm) at each of five photoperiods, 24L∶0D (continuous light), 14L∶

10D (long day), 12L: 12D (equinox), 10L: 14D (short day) and 0L: 24D (continuous dark) at 27℃. The neonates were recorded and reared till adult emergence (diet and the rest procedures were the same as in the experiment of section 2.3).

2.5 Life table at different wavelengths of light

Life table was evaluated at different wavelengths of light. Wooden light chambers of 40 cm × 40 cm × 40 cm dimensions were designed with constant and unfluctuating light source. White, yellow (λ = *ca.* 570 nm), blue (λ = *ca.* 475 nm) and red (λ = *ca.* 650 nm) lighted bulbs were used in different chambers to provide exposure to different wavelengths. Blue and red bulbs of 100 W, yellow bulb of 11 W and white (milky, broad spectrum) bulb of 60 W (brand Phillips) were used to ensure 190 – 200 lux light intensity (measured using Eurisem EP-628 Digital Luxmeter, Eurisem Technics Leicester Leicestershire, U. K.). Inner surface of chambers were covered with glossy paper of the colour as the light bulb, thus enhancing the effect and providing a completely coloured arena. The colours blue, yellow and red were selected because they make up a broad portion of the visible spectrum (VIBGYOR). 1 N NaCl solution in a glass beaker was kept in each chamber to maintain 65% ± 5% RH. One thousand F_2 eggs (100 eggs per replicate, n = 10) were kept in plastic Petri dishes (9.0 cm × 2.0 cm) in chamber illuminated with either blue (*ca.* 475 nm), yellow (*ca.* 570 nm), red (*ca.* 650 nm), or white light (broad spectrum, control). The neonates on hatching were reared till adult emergence (diet and the rest procedures were the same as in the experiment of section 2.3).

2.6 Data analysis

Data on real mortality (100*rx*) were pooled and subjected to one-way ANOVA to determine the stage specific mortality using statistical software SAS (2002). The comparison of means was done using Bonferroni's method. The pooled data of each treatment were then subjected to two-way ANOVA using 'factor' and 'life stage' as independent variables and 'real mortality' as dependent variable using SAS Institute (2002). Kappa value was correlated with the generation survival using Pearson correlation (SAS Institute, 2002).

3 RESULTS

3.1 Mortality of *Z. bicolorata* on different foods

The different life table attributes, *viz.* life stage (*x*), stage mortality (*dx*), *k*-value (*kx*) and Kappa value of *Z. bicolorata* on three foods are presented in Table 1. Mortality indicator Kappa value was lowest when beetles at various life stages were fed on inflorescence, followed by leaves and stem. However, there were no much difference in the mortality of beetles at various life stages between on inflorescence and leaves (Chi square test; $\chi^2 = 0.5$; $P > 0.1$). The generation survival was maximum on inflorescence. The stage specific real mortality was statistically significant ($F = 6.26$; $P < 0.01$; *d. f.* = 5, 12) (Fig. 1).

Table 1 Mortality based life table of *Zygogramma bicolorata*, when fed on different structures of *Parthenium hysterophorus*

Life stage (*x*)		Inflorescence		Leaves		Stem	
		dx	*k* value	*dx*	*k* value	*dx*	*k* value
Egg		0.18	0.09	0.29	0.15	0.51	0.31
Larva	1st instar	0.09	0.05	0.06	0.04	0.10	0.09
	2nd instar	0.05	0.03	0.03	0.02	0.09	0.12
	3rd instar	0.07	0.05	0.06	0.04	0.08	0.13
	4th instar	0.06	0.04	0.03	0.03	0.06	0.13
Pupa		0.07	0.06	0.11	0.10	0.09	0.36
Kappa		0.32		0.38		1.14	
Generation survival		0.26		0.29		0.05	

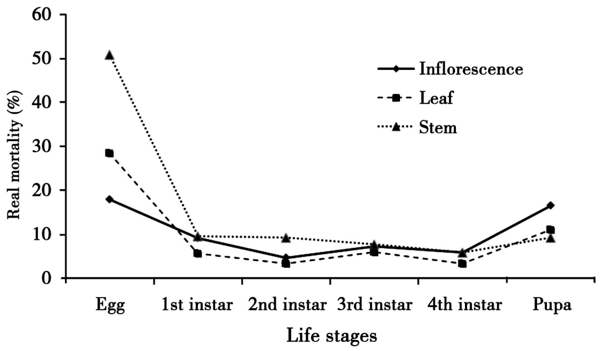

Fig. 1 Stage specific real mortality of *Zygogramma bicolorata* on different foods

3.2 Mortality of *Z. bicolorata* at different temperatures

Temperature affected the Kappa value, which was lowest when beetles at immature stages were reared at 27℃, followed by 30, 25, 20 and 35℃ (Table 2). The generation survival followed the same pattern except the survival rate of the 4th instar larvae, which survived maximum at 27℃, followed by 25, 30, 20 and 35℃. Temperature dependent stage specific real mortality was statistically significant ($F = 12.12$; $P < 0.0001$; *d. f.* = 5, 24) (Fig. 2).

Table 2 Mortality based life table of *Zygogramma bicolorata* at different temperatures

Life stage (x)		20℃		25℃		27℃		30℃		35℃	
		dx	*k* value	*dx*	*k* value	*dx*	*k* value	*dx*	*k* value	*dx*	*k* value
Egg		0.44	0.22	0.25	0.12	0.12	0.06	0.18	0.09	0.44	0.22
Larva	1st instar	0.05	0.04	0.01	0.01	0.01	0.01	0.02	0.01	0.05	0.04
	2nd instar	0.06	0.07	0.04	0.03	0.03	0.02	0.03	0.02	0.08	0.08
	3rd instar	0.06	0.07	0.03	0.03	0.03	0.02	0.04	0.02	0.08	0.10
	4th instar	0.05	0.07	0.05	0.03	0.03	0.02	0.07	0.04	0.07	0.11
Pupa		0.07	0.10	0.06	0.05	0.06	0.04	0.08	0.05	0.08	0.18
Kappa		0.57		0.27		0.17		0.23		0.73	
Generation survival		0.15		0.28		0.38		0.31		0.09	

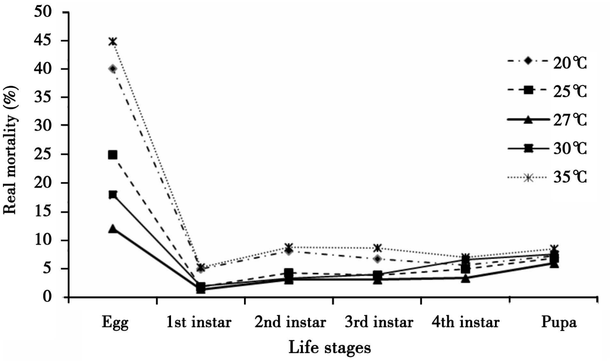

Fig. 2 Stage specific real mortality of *Zygogramma bicolorata* at different temperatures

3.3 Mortality of *Z. bicolorata* at different photoperiods

Kappa value was minimum at 14L∶10D, followed by 12L∶12D, 10L∶14D, 24L∶0D and 0L∶24D (Table 3). The generation survival was maximum after exposing life stages of *Z. bicolorata* to 14L∶10D (long day), followed by 12L∶12D (equinox), 10L∶14D (short day), 24L∶0D (continuous light) and 0L∶24D (continuous dark). The photoperiod dependent stage specific real mortality was statistically significant ($F = 10.53$; $P < 0.0001$; *d. f.* = 5, 24) (Fig. 3).

Table 3 Mortality based life table of *Zygogramma bicolorata* at five photoperiods

Life stage (x)		14L:10D		12L:12D		10L:14D		24L:0D		0L:24D	
		dx	*k* value	*dx*	*k* value	*dx*	*k* value	*dx*	*k* value	*dx*	*k* value
Egg		0.10	0.05	0.16	0.07	0.16	0.08	0.19	0.09	0.28	0.14
Larva	1st instar	0.05	0.02	0.05	0.03	0.08	0.04	0.09	0.05	0.15	0.10
	2nd instar	0.02	0.01	0.03	0.02	0.03	0.02	0.08	0.05	0.09	0.07
	3rd instar	0.03	0.02	0.03	0.02	0.04	0.02	0.04	0.03	0.04	0.04
	4th instar	0.08	0.05	0.10	0.07	0.13	0.09	0.13	0.11	0.14	0.16
Pupa		0.10	0.06	0.12	0.09	0.14	0.12	0.14	0.31	0.15	0.28
Kappa		0.21		0.30		0.37		0.64		0.79	
Generation survival		0.41		0.33		0.28		0.20		0.11	

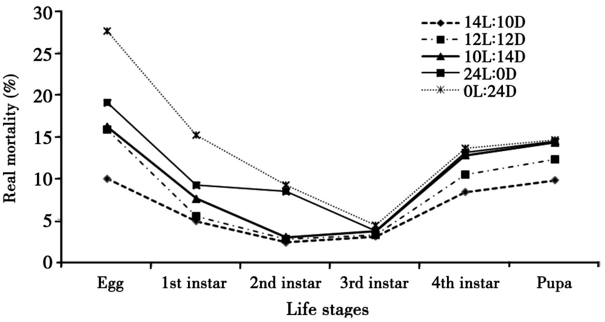

Fig. 3 Stage specific real mortality of *Zygogramma bicolorata* at different photoperiods

3.4 Mortality of *Z. bicolorata* at different wavelengths of light

The key life stages also responded to the lights of various wavelengths (Table 4), and Kappa value was lowest when beetles at immature stages were reared under white light (broad spectrum), followed by yellow, blue and red light. The generation survival also followed the same trend. The stage specific real mortality was statistically significant ($F = 9.28$; $P < 0.001$; *d. f.* = 5, 13) (Fig. 4).

Table 4 Mortality based life table of *Zygogramma bicolorata* under lights of different wavelengths

Life stage (x)		White		Yellow		Blue		Red	
		dx	*k* value	*dx*	*k* value	*dx*	*k* value	*dx*	*k* value
Egg		0.14	0.07	0.25	0.12	0.39	0.22	0.51	0.31
Larva	1st instar	0.06	0.03	0.07	0.04	0.14	0.06	0.09	0.08
	2nd instar	0.07	0.04	0.08	0.05	0.17	0.08	0.09	0.11
	3rd instar	0.04	0.02	0.07	0.05	0.15	0.07	0.07	0.11
	4th instar	0.04	0.03	0.06	0.05	0.21	0.10	0.08	0.20
Pupa		0.06	0.04	0.07	0.07	0.32	0.17	0.08	0.30
Kappa		0.23		0.38		0.70		1.11	
Generation survival		0.30		0.19		0.11		0.04	

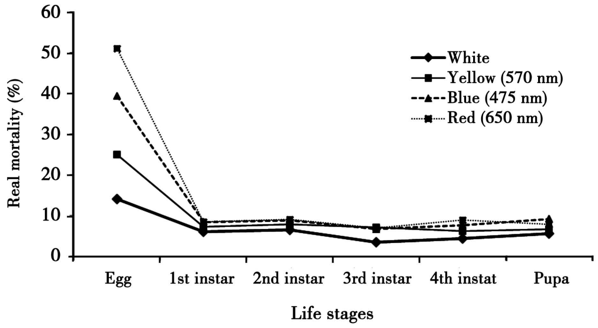

Fig. 4 Stage specific real mortality of *Zygogramma bicolorata* under lights of different wavelengths

3.5 Correlation of generation survival with the Kappa value

Generation survival had a strong negative correlation with the Kappa value in all experimental treatments ($r_{\text{food}} = -0.99$; $P < 0.0001$; $r_{\text{temperature}} = -0.99$; $P < 0.0001$; $r_{\text{photoperiod}} = -0.97$; $P < 0.001$; $r_{\text{wavelength}} = -0.97$; $P < 0.001$). The pooled data subjected to two-way ANOVA revealed a significant main effect of 'life stage' ($F = 34.9$; $P < 0.0001$; *d. f.* $= 5$) and significant effect of interaction between 'life stage' and 'factor' ($F = 1.81$; $P < 0.05$; *d. f.* $= 15$). However, the main effect of 'factor' was not statistically significant ($F = 1.14$; $P = 0.3385$; *d. f.* $= 3$). The comparison of means revealed a strong significant difference between 'egg' as key life stage and the other life stages of *Z. bicolorata* under all experimental conditions.

4 DISCUSSION

The results reveal that immature stages of *Z. bicolorata* thrived best on inflorescence with least mortality values. Reproductive parts of plants, especially inflorescence, contain essential nutrients needed for the growth of insects and are usually more attacked by them (Kelly and Dyer, 2002). Excess feeding on reproductive parts of plants by the life stages of beetle potentially limits plant fitness and population growth directly through consumption of gametes (Cunningham, 1995; Krupnick and Weis, 1999) and/or developing seeds (Louda and Potvin, 1995). Additionally, the removal of inflorescence negatively influences pollinators' visit and subsequent seed production (Krupnick *et al.*, 1999; Mothershead and Marquis, 2000), thereby indirectly advantageous to weed biocontrol.

Survival of the 2nd instar larvae was highest on inflorescence, which may possibly be attributed to palatability and the softness of inflorescence that might have enabled ease in eating, as mouthparts of early instar larvae are less developed. Females fed on inflorescence laid more viable eggs than those females fed on stem, as more than half the cohort of eggs did not hatch in the latter case. It could be predicted that females would strategically lay more eggs on inflorescence as it is advantageous to the early instar larvae. Neonates are often less mobile and indirectly depend on mothers for their feeding preference (Omkar *et al.*, 2006). The ovipositing females who discriminate plant characteristics associated with survival usually have a selective advantage over females that do not discriminate. This discrimination is an adaptive feature of females to halt or reduce egg survival under poor food conditions. Thus females abstain from wasting their energy and reproductive efforts by producing offsprings with a low probability of survival (Slansky, 1982). Egg mortality was also highly dependent on the mother's age during mating as middle aged ones can lay more fertile eggs (Omkar *et al.*, 2010). Egg mortality may also be ascribed to infertility, as the mothers feeding of less nutritive diet lay some eggs which fail to hatch (Dixon, 2000). High mortality of all instar larvae of *Z.*

bicolorata on stem may possibly be due to the coarseness of stem texture, non-palatability, and poor nutritional quality. Lesser palatability of food decreases the food consumption. Moulting to next instar stage is highly dependent on the food consumption, especially in the later instars (Omkar and Afaq, 2011). Hence, inadequate food consumption at larval stage when stem was provided as food may be a reason for increased larval and pupal mortality.

Temperature significantly affected the mortality of life stages of *Z. bicolorata* and mortality was maximum at 35℃. Sushilkumar and Ray (2010) reported similar results of highest adult mortality (57.0%) at 35℃ indicating thermal intolerance of the species to the upper extreme of temperature. Both low and high temperature extremes may be unsuitable for the survival of immature key life stages of *Z. bicolorata* but could be advantageous in reducing the incidence of adult diapause (Sushilkumar and Ray, 2010). There was a high risk of adult diapause in the fields, especially in favourable conditions (Jayanth and Bali, 1993c; Gupta *et al.*, 2010). Egg was the susceptible key stage at high temperature and its mortality was probably a result of its dehydration at extremes of temperature (Piesik, 2006). The 1st instar larvae were vulnerable due to their small size and soft cuticle. This is in close agreement with findings on other coleopterans (Ponsonby and Copland, 1996; Srivastava and Omkar, 2004; Pervez and Omkar, 2004a) including chrysomelids (Jayanth and Bali, 1993a; Kumar, 2005). Low temperature also reduces the survival in key life stages probably due to immense slowing down of the metabolic rate affecting ecdysis in instars (Piesik, 2006; Zheng *et al.*, 2008).

Sushilkumar and Ray (2010) opined that photoperiod possibly may affect diapause initiation but perhaps be not important in the control of diapause development and termination, as diapausing beetles stay deep inside the soil where there is a condition of extreme darkness. Our result with continuous darkness reveals that light does significantly affect the mortality in key life stage with generation survival almost reduced to one fourth of that in favourable long day conditions. This indicates that absence of light possibly affects the diapause development and termination. In India, *Z. bicolorata* usually undergo diapause during winter and onset of summer, *i. e.*, a short day condition. Our result indicates that there is a high risk of mortality to the key life stages in the short day condition. This possibly could explain the onset of diapause of *Z. bicolorata* during short day. Long day (14L∶10D) favours the survival in various life stages possibly because of prevalence of long day condition in tropical and subtropical regions, where this beetle prevails. The daily light-dark cycle is known to be the major environmental synchronizer or photic-Zeitgeber affecting mortality and survival in different life stages (Filchak *et al.*, 2001).

The extreme wavelengths of visible spectrum were deleterious to the key life stages of *Z. biocolorata*. High egg mortality indicates that embryogenesis was affected when eggs were exposed to short and long wavelengths. Ultraviolet and short visible spectra had inhibitory effect on courtship and mating of other insects (Sakai *et al.*, 2002). Insects usually face difficulties in foraging and survival when exposed to broader wavelengths, *i. e.*, red, infrared and beyond (Arikawa *et al.*, 1987), as they negatively affect diel rhythms related to ecdysis, pupation and eclosion (White and Shardlow, 2011). There was a significant stage-specific effect on the real mortality, which was rigid and not affected by the external factors. This was largely due to heavy mortality of both immobile key stages, *i. e.*, egg and pupa, with the former leading in terms of real mortality. The optimal conditions reduce the mortality but there seems to be an innate stage specific mortality driven probably by the genetic factors. Optimal conditions improved the generation survival of *Z. bicolorata* which had a strong negative correlation with Kappa value, not affected by these factors.

Hence, it is concluded that these environmental variables largely affect the mortality and survival of *Z. bicolorata*. The survivor of immature stages of the beetle could be rearing them on inflorescence under long day white light at 27℃. Further detailed studies on demographic attributes under these variables are needed to conclusively explore the effects, especially on population trends.

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不同环境变量下银胶菊叶甲的生命表

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摘要：在室内研究了不同环境变量（如食物、温度、光周期和不同光波长）下银胶菊杂草 *Parthenium hysterophorus* L. 的食叶昆虫和生物防治因子银胶菊叶甲 *Zygogramma bicolorata* Pallister 的生命表。不同发育阶段的该种叶甲取食银胶菊不同部位时，取食花的甲虫死亡率指标 Kappa 值最低，其次是取食叶片和茎；而取食花时甲虫世代存活率最高。温度显著影响主要发育阶段该种叶甲的死亡率和存活率。27℃下饲养的未成熟期甲虫的 Kappa 值最低，其次是30，25，20 和35℃。世代存活和存活率表现相同的趋势。不同光周期显著影响死亡率，在14L:10D（长日照）下世代存活最好，其次是 12L:12D（昼夜相等），10L:14D（短日照），24L:0D（连续光照）和 0L:24D（连续黑暗）。甲虫对不同波长光的反应上，在白光（广谱）下 Kappa 值最低，世代存活率最高，其次是黄光（$\lambda \approx 570$ nm）、蓝光（$\lambda \approx 475$ nm）和红光（$\lambda \approx 650$ nm）。卵的死亡率最高。不同发育阶段的甲虫在27℃长日照白光下用银胶菊花饲养最佳。死亡率趋势具有严格和显著的阶段特异性，表现出内在的存活效应，与研究的因素无关。

关键词：银胶菊叶甲；银胶菊；寄主植物；存活；死亡率；生命表

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