H. Podoler and J. Henen (1983) Phytoparasitica 11(3-4): 167-176

A COMPARATIVE STUDY OF THE EFFECTS OF CONSTANT TEMPERATURES ON DEVELOPMENT TIME AND SURVIVAL OF TWO COCCINELLID BEETLES OF THE GENUS *CHILOCORUS*

H. PODOLER and J. HENEN*

The effect of constant temperatures on duration and rate of development and on survival of two species of predatory beetles of the genus *Chilocorus* (Coleoptera: Coccinellidae) (one endemic and one imported) was studied. The observed data were analyzed and compared applying three different methods. The methods based on the logistic curve provided a better fit to the observed data as compared with the widely used Blünck-Bodenheimer equation.

The imported species *C. kuwanae* had a faster rate of development than the endemic species *C. bipustulatus* at the lower temperatures tested (18°, 22°C), but it could not complete its development at 32°C. Survival of *C. kuwanae* was considerably lower than that of the endemic species. As both species are active during the summer, it was concluded that the sensitivity of *C. kuwanae* to high temperatures provides at least a partial explanation to the fact that this species has not become established yet in Israel.

KEY WORDS: Chilocorus bipustulatus; Chilocorus kuwanae; Coleoptera; Coccinellidae; temperature effects; development, duration and rate of; survival.

INTRODUCTION

The coccinellid beetle *Chilocorus bipustulatus* L. is the most important predator of diaspidid scale insects in citrus groves in Israel (*e.g.* 1, 5) and is also known to affect the populations of important pests in the Coccidae (*e.g.* 7, 8). In 1976 the Israel Cohen Institute for Biological Control of the Citrus Marketing Board of Israel, imported from Japan another predator of the same genus, *C. kuwanae* Silvestri, with the aim of strengthening the predatory complex and thus improving biological control of citrus pests. Several thousand individuals of this predator were released at various locations, but *C. kuwanae* has not yet been reported to be established in Israel. A study was therefore initiated to compare the two species and to determine the reasons for this failure.

Received March 20, 1983; received in final form July 31, 1983.

* Dept. of Entomology, The Hebrew University of Jerusalem, Faculty of Agriculture, Rehovot.

The part of this study which summarizes the effect of constant temperatures on the rate of development and survival is reported here; another part, which deals with the searching behavior of these species, is in preparation.

MATERIALS AND METHODS

Cultures

The stock culture of *C. bipustulatus* was started from field-collected adults. Special care was taken to ensure that only beetles free of the parasitic fungus *Hesperomyces virescens* Thaxter (3) were used. The stock culture of *C. kuwanae* was started from beetles received from the Israel Cohen Institute for Biological Control of the Citrus Marketing Board of Israel. The original culture in Israel was started from beetles sent by Dr. Nohara from Hagi (Japan) in 1976.

The cultures were maintained in wooden cages (30 x 40 x 30 cm) which had a glass roof, a side opening covered with cloth for ventilation and another opening with a cloth sleeve for access. The cages were held at 27°±1°C, 65% RH and 16:8 LD, a photophase regime which kept the adults from entering imaginal diapause.

Flannel strips were placed in the cages for oviposition by *C. bipustulatus* (6); strips of sponge, which had been found in the present study to meet the ovipositional requirements of *C. kuwanae*, were supplied for this species.

The Diaspidid scale insects *Aonidiella aurantii* Mask., *Chrysomphalus aonidum* L. and *Aspidiotus nerii* Bouché served as food for the predatory beetles.

Effect of constant temperatures

This effect was studied in plastic containers (13 x 30 x 20 cm) closed with a glass plate, and with ventilation apertures covered with copper net. Strips of sponge were glued to the edges of the cover plate to prevent the beetles from escaping the containers. Infested whole butternut squashes were placed on wooden frames at the bottom of these containers. A known number of eggs, up to 24 h of age for temperatures lower than 27°C and up to 48 h of age for the higher temperatures (on flannel strips for *C. bipustulatus* and on sponge strips for *C. kuwanae*), was placed on each squash. The containers were then transferred to incubators with the following constant temperatures: 18°, 22°, 24°, 26°, 28°, 30° and 32°C for *C. bipustulatus*, and all these except 24°C for *C. kuwanae*. The numbers of larvae, pupae and adults, as well as the moults, were recorded daily. The duration of each developmental stage was determined by employing the equation:

$$T = \frac{\Sigma(N_X \cdot t)}{\Sigma N_X}$$

where

T = mean development time (in days) from oviposition

x = developmental stage
N_x = number of insects entering stage x on day t
t = total time from oviposition;

and the equation:

$$T_x = T - T_y$$

where

T_x = mean development time of stage x
T_y = total development time of all stages preceding stage x.

The results were summarized and analyzed applying the following methods: (i) the law of heat summation according to the Blünck-Bodenheimer equation; (ii) the logistic curve as suggested by Davidson (2); and (iii) the modified logistic curve as suggested by Pradhan (9). The first equation (i):

$$t(T-c) = C(\text{onstant})$$

where

t = development time at temperature T
c = lower temperature threshold
C(onstant) = thermal constant

This equation can be rearranged to represent a rectilinear curve:

$$\frac{1}{t} = V = -\frac{c}{C} + \frac{1}{C}T$$

where V = rate of development. This equation provides the values of lower threshold temperature (c) and of the total heat required for the development of the insect (C).

The logistic equation (ii):

$$\frac{1}{t} = V = \frac{K}{1+e^{a-bT}}$$

where
V = the rate of development at temperature T
K = the upper asymptote

a and b define the location of the curve on the axes and the rate of change of the curve, respectively.

This equation can be rearranged to represent a rectilinear curve:

$$\ln\frac{K - V}{V} = a - b\,T$$

This equation takes into account the upper asymptote, which represents the maximal rate of development that the insect can attain.

The last equation (iii):

$$V = Y_0 e^{-\frac{1}{2}a\,(T_0 - T)}$$

where

Y_0 = highest value of developmental index

T_0 = the temperature at which Y_0 is attained

a = constant which represents the inhibiting effect of the temperature on the rate of the process.

This equation takes into account not only the maximal rate of development but also the decrease in this rate as the temperature exceeds a certain value. The parameters of this equation were calculated using the program for non-linear regression of BMDP on the CDC Cyber 74 computer of The Hebrew University of Jerusalem.

The calculated values were compared with the observed data employing the chi-square test.

RESULTS AND DISCUSSION

The effects of constant temperatures on the duration and rate of development of the two species of *Chilocorus* are presented in Table 1. The three methods employed to analyze the data provided satisfactory results for both species, with very low, nonsignificant values of χ^2. Among these methods, the one suggested by Pradhan (9) had the best fit to the observed data (smallest value of χ^2). Similar results were obtained recently by Kay (4), who compared these methods for analyzing the effect of temperature on the duration of development of eggs of the pest *Heliothis armiger* (Hbn.) (Noctuidae: Lepidoptera). The main advantages of the widely used equation of Blünck-Bodenheimer over the other methods are its simplicity in application and that it provides the parameters of lower temperature threshold (c) and total heat requirements of the insect for development (presented as days x degrees). On the other hand, the availability of computers in recent years, and especially of microcomputers, does not justify any but the most suitable method in all future analyses of such data. Moreover, as Pradhan's equation provided the best fit to the observed data, the biological validity of c and C when calculated by linear extrapolation of the Blünck-Bodenheimer equation should be tested biologically whenever other methods provide a better fit. This is important because the discrepancy between the line predicted by the Blünck-Bodenheimer equation and those based on the logistic curve is

TABLE 1

DURATION AND RATE OF DEVELOPMENT (EGG TO ADULT) OF TWO SPECIES OF *CHILOCORUS* AT CONSTANT TEMPERATURES

(Data analyzed by three different methods; see text for details)

Temperature, T (°C)	*Development*							
	Observed		*As predicted by the equations of:* Blünck-Bodenheimer		Davidson		Pradhan	
	t (days, mean±SE)	V (100/day)	t (days)	V (100/day)	t (days)	V (100/day)	t (days)	V (100/day)
				CHILOCORUS BIPUSTULATUS				
18	80.50±3.53	1.24	76.15	1.31	90.26	1.11	82.01	1.22
22	53.92±4.45	1.85	49.28	2.03	49.14	2.03	49.99	2.00
24	38.17±1.94	2.62	41.89	2.38	39.83	2.51	41.23	2.42
26	27.78±3.06	2.65	36.43	2.74	34.22	2.92	35.28	2.83
28	27.80±1.89	3.60	32.23	3.09	30.83	3.24	31.31	3.19
30	31.15±2.67	3.21	28.90	3.46	28.79	3.47	28.83	3.47
32	27.14±0.90	3.68	26.19	3.82	25.57	3.13	27.53	3.63
Development Equations:			$t(T-10.66) = 558.92$		$V = \frac{3.89}{1+e^{5.480-0.253T}}$		$V=3.671e^{-0.0046(33.51-T)^2}$	
			$\Sigma\chi^2 = 1.88$		$\Sigma\chi^2 = 2.46$		$\Sigma\chi^2 = 0.11$	
				CHILOCORUS KUWANAE				
18	66.23±2.78	1.51	67.30	1.48	84.03	1.19	68.10	1.40
22	49.75±4.35	2.01	45.66	2.19	41.17	2.43	45.87	2.21
26	31.93±1.54	3.13	34.55	2.89	31.50	3.17	34.17	3.00
28	30.00±1.31	3.33	30.80	3.24	30.03	3.33	30.64	3.29
30	29.20±0.84	3.42	27.79	3.60	29.33	3.41	28.17	3.50
32*	–	–	–	–	29.00	3.45	28.32	3.53
Development Equations:			$t(T-9.56) = 568$		$V = \frac{3.48}{1+e^{7.372-0.373T}}$		$V=3.53e^{-0.0049(31.75-T)^2}$	
			$\Sigma\chi^2 = 0.67$		$\Sigma\chi^2 = 5.56$		$\Sigma\chi^2 = 0.034$	

*Complete egg mortality.

least at the middle of the temperature range, and increases toward the lower or upper ranges of the temperature scale.

The development time of *C. kuwanae* was considerably shorter than that of *C. bipustulatus* at the lower range of temperatures tested (Table 1). However, this advantage disappeared as the temperature exceeded 28°C. Moreover, while *C. bipustulatus* completed its development normally even at 32°C, eggs of *C. kuwanae* did not hatch, and died when exposed to this temperature.

The duration of each developmental stage was calculated for both species (Table 2) and the data were analyzed employing the three above mentioned methods (Table 3). Again, Pradhan's method provided a better fit to the observed data, as is shown by the lower values of χ^2. The faster rate of development of *C. kuwanae* is obvious at the lower range of temperatures. The main difference between these species is in the rate of development of the eggs and L I stage. For example, at 18°C, the developmental time of eggs plus L I of *C. bipustulatus* was 34.5 days as compared with 19 days for *C. kuwanae.* Another interesting conclusion which was drawn from the data in Table 2 is that in most cases *C. bipustulatus* stays at the egg stage longer than at any other developmental stage. In *C. kuwanae* the duration of L IV and the pupal stage usually equals, or is sometimes even longer than, that of the egg stage.

The effect of the temperature on survival (1x) of the developmental stages of both species is summarized in Fig. 1 and in Table 4. In both species the highest mortality occurred usually during the egg stage. This phenomenon was more apparent in *C. kuwanae* but occurred also in *C. bipustulatus,* other than at 28°C. *C. kuwanae* suffered a much higher mortality than *C. bipustulatus* throughout the range of temperatures studied. Survival of *C. kuwanae* reached its highest value, ∿20%, at 18°C, while at all other temperatures it oscillated around 10%. In *C. bipustulatus* the highest rate of survival, 52%, was achieved at 28°C, while at the other temperatures it varied from 47% (at 26°C) to 10% (at 32°C).

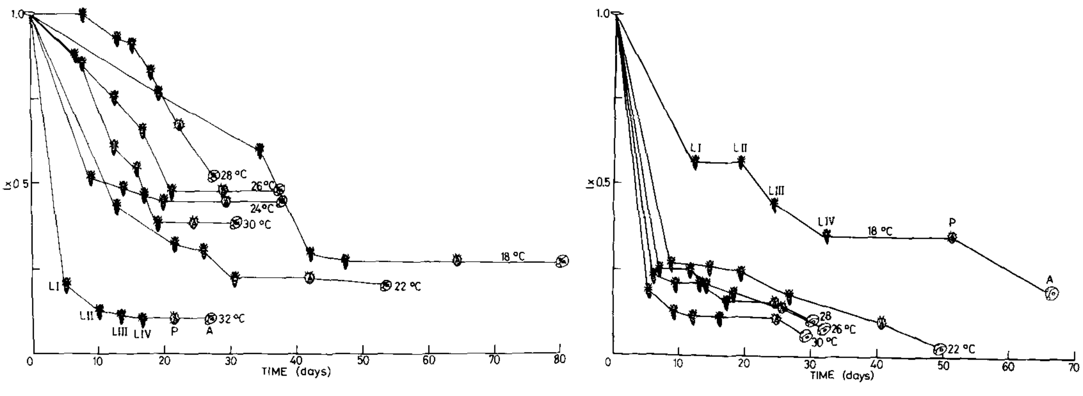

Fig. 1. **Survival curves of developmental stages of the predatory bettles *Chilocorus bipustalatus* (left) and *C. kuwanae* (right) at constant temperatures.**
L I – L IV, larval stages; P, pupal stage; A, adult stage; lx, proportion of survivors at start of age interval.

TABLE 2

MEAN DURATION OF DEVELOPMENTAL STAGES (EGG TO ADULT) OF TWO SPECIES OF *CHILOCORUS* AT CONSTANT TEMPERATURES

Temperature, T (°C)	*Number of eggs*	*Duration (days, mean ± SD)* *Developmental stage* Egg	L I	L II	L III	L IV	P
		CHILOCORUS BIPUSTULATUS					
18	57	19.03±0.96	15.51±3.36	7.64±3.18	5.32±1.58	16.90±4.93	16.10±3.58
22	184	12.95±1.93	8.57±3.59	4.50±2.96	4.64±3.30	11.22±4.09	12.04±4.45
24	95	9.10±0.68	4.68±0.73	3.08±1.82	3.16±1.28	9.45±1.40	8.69±1.94
26	120	6.54±1.33	6.19±1.56	4.29±3.08	4.30±3.17	7.68±1.44	8.78±3.06
28	120	8.03±0.89	5.09±0.73	2.08±1.01	2.93±1.48	4.34±0.98	5.34±1.84
30	150	7.52±0.92	5.06±1.55	3.40±1.99	3.04±1.88	5.70±1.70	6.48±2.67
32	95	5.13±0.74	4.87±1.22	3.00±1.41	3.42±0.69	5.44±0.38	5.28±0.90
		CHILOCORUS KUWANAE					
18	83	12.22±1.51	6.97±1.54	5.24±2.58	8.14±2.61	18.58±4.17	15.07±2.79
22	146	8.74±1.75	5.58±2.17	4.59±1.57	4.68±1.32	17.13±4.25	9.02±4.35
26	178	11.46±1.38	4.39±1.38	2.74±1.07	3.66±1.31	7.83±1.87	6.24±1.54
28	96	6.00±0.48	3.38±0.81	3.88±1.50	3.88±1.04	7.25±1.36	5.75±1.31
30	80	5.13±0.74	4.05±1.17	2.93±0.93	4.11±1.09	8.56±0.98	4.44±0.84

TABLE 3

COMPARISON OF DIFFERENT METHODS OF DESCRIBING THE EFFECT OF TEMPERATURE ON RATE OF DEVELOPMENT OF VARIOUS STAGES OF TWO SPECIES OF *CHILOCORUS*

(The parameters are of the equations listed at the end of the table; see text for explanations)

Stage	Method of: Blünck-Bodenheimer			Davidson				Pradhan			
	c	C	$\Sigma\chi^2$ *	K	a	b	$\Sigma\chi^2$	Y_0	$\frac{1}{2}a$	T_0	$\Sigma\chi^2$
					CHILOCORUS BIPUSTULATUS						
E	12.18	112.14	1.663	17.4	3.78	.165	4.066	19.598	.0033	38.04	1.747
L I	8.47	104.44	4.023	20.0	8.70	.424	2.343	20.720	.0090	29.30	2.337
L II	6.81	65.55	12.947	37.0	3.14	.162	14.970	34.650	.0078	29.20	9.457
L III	2.96	107.20	3.777	32.0	3.53	.155	3.510	27.030	.0021	44.86	1.379
L IV	12.80	92.79	3.450	19.33	4.24	.188	6.014	21.082	.0043	35.59	3.114
P	12.17	104.58	1.447	19.00	3.53	.155	3.510	27.030	.0021	44.86	1.379
					CHILOCORUS KUWANAE						
E	9.35	110.50	0.110	19.5	3.94	.197	0.406	4339.000	.0002	190.1	0.036
L I	6.18	90.33	1.930	27.0	3.44	.194	2.142	34.126	.0027	28.1	0.926
L II	2.28	82.03	3.110	35.3	1.36	.084	5.440	33.583	.0248	33.5	3.050
L III	8.88	77.82	2.317	25.8	5.03	.255	2.940	28.093	.0036	33.9	2.030
L IV	10.15	144.00	0.963	12.7	3.40	.202	1.810	13.250	.0052	31.6	0.728
P	12.98	80.47	0.191	22.5	4.72	.215	0.588	46.3	.0022	38.6	0.132

Equations: $V = -\frac{c}{C} + \frac{1}{C} T$ $\qquad V = \frac{K}{1+e^{a-bT}}$ $\qquad V = Y_0 e^{-\frac{1}{2}a(T_0-T)}$

* Calculated values were compared with the observed.

TABLE 4

SURVIVAL OF TWO SPECIES OF *CHILOCORUS* FROM EGG TO THE ADULT STAGE, AT DIFFERENT CONSTANT TEMPERATURES

Temperature, T (°C)	*% Survival*	
	C. bipustulatus	*C. kuwanae*
18	27	19
22	20	3
24	44	–*
26	47	9
28	52	11
30	29	6
32	10	0

* Not studied.

Summarizing these findings it can be concluded that while *C. kuwanae* had a faster rate of development at low temperatures, this advantage almost disappeared at the higher temperatures. This species suffered very high egg mortality throughout the whole range of temperatures studied, and particularly at or above 22°C. As both species are active during late spring and summer, *C. kuwanae* has a very poor chance to establish and maintain a population under the environmental conditions of Israel, where the temperature during this period usually exceeds 22°C. These results might explain in part the fact that there have been no indications that the mass releases of this species resulted in establishment of this predator in the citrus groves of Israel.

ACKNOWLEDGMENTS

This work was partially supported by grant No. I-138-79 from the United States – Israel Binational Agricultural Research and Development Fund (BARD). The authors wish to thank Dr. Y. Nitzan of the Israel Cohen Institute for Biological Control, in Rehovot, for providing the initial stocks of *Chilocorus kuwanae.*

REFERENCES

1. Bodenheimer F.S. (1951) Citrus Entomology in the Middle East. W. Junk, The Hague.
2. Davidson, J. (1944) On the relationship between temperature and rate of development of insects at constant temperatures. *J. Anim. Ecol.* **13:** 26-38.

ıburov, S.S., Nadel, D.J. and Kenneth, R. (1967) Observations on *Hesperomyces virescens* Thaxter, a fungus associated with premature mortality of *Chilocorus bipustulatus* L. *Israel J. agric. Res.* **17:** 131-136.

4. Kay, I.R. (1981) The effect of constant temperatures on the development time of eggs of *Heliothis armiger* (Hubner) (Lepidoptera: Noctuidae). *J. Aust. ent. Soc.* **20:** 155-156.

5. Kehat, M., Greenberg, S. and Gordon, D. (1970) Factors causing the seasonal decline of *Chilocorus bipustulatus* L. (Coccinellidae) in citrus groves in Israel. *Entomophaga* **15:** 337-345.
6. Nadel, D.J. and Biron, S. (1964) Laboratory studies and controlled mass rearing of *Chilocorus bipustulatus* L., a citrus scale predator in Israel. *Riv. Parassit.* **25:** 195-206.
7. Podoler, H., Bar-Zacay, I. and Rosen, D. (1979) Population dynamics of the Mediterranean black scale, *Saissetia oleae* (Olivier), on citrus in Israel. 1. A partial life table. *J. ent. Soc. sth. Afr.* **42:** 257-266.
8. Podoler, H., Dreishpoun, Y. and Rosen, D. (1981) Population dynamics of the Florida wax scale, *Ceroplastes floridensis* (Homoptera: Coccidae), on citrus in Israel. 1. A partial life-table. *Acta ecol. Oecol. appl.* **2:** 81-91.
9. Pradhan, S. (1946) Dynamics of temperature effect on insect development. *Proc. natn. Inst. Sci. India* **12:** 385-404.