ENTOMOPHAGA 40 (2), 1995, 183-192

ASSESSMENT OF TEMPERATURE-DEPENDENT DEVELOPMENT IN THE GENERAL POPULATION AND AMONG ISOFEMALE LINES OF *COCCINELLA TRIFASCIATA (COL.: COCCINELLIDAE)*

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Temperature-dependent development of *Coccinella trifasciata* LeConte from Corvallis, Oregon, was assessed for the general population and compared among a subset of isofemale lines. All eggs died at 10 and 34°C. Survival ranged between 63.3-96.7% from 18-34°C. Development from oviposition to adult ranged from 44.2 days at 18°C to 11.1 days at 34°C. Mean adult weight did not differ among temperatures, and was 15.2 mg overall. For the species, heat-unit requirements for development from egg to adult were 227 degree-days above a developmental threshold of 12.7°C. Values for the developmental threshold differed among isofemale lines, and ranged from 11.4-14.5°C with heat-unit requirements ranging from 186-260 degree-days above their respective threshold. The isofemale line producing the fastest rate of immature development at 18°C was characterized by a heat-unit requirement of 260 degree-days above a developmental threshold of 11.4°C. The isofemale line producing the slowest rate of immature development at 18°C was characterized by a heat-unit requirement of 186 degree-days above a developmental threshold of 14.5°C. Implications of using isofemale lines in culturing biological control agents are discussed.

KEY-WORDS: *Coccinella trifasciata*, Coccinellidae, developmental threshold, degree-days, isofemale lines

Variation in life history traits within a population of natural enemies in classical biological control programs may be influenced by numerous factors. In particular, the source of the colony and the maintenance of the colony will affect genetic variation (Mackauer, 1972, 1976, 1980; Roush, 1990; Hopper *et al.*, 1993). The desire for a high or low degree of variation in a population of natural enemies being cultured for release may depend on the use of the biological control agent. Mackauer (1972) lists two purposes for release of natural enemies: 1) permanent establishment of the biological control agent, or 2) inundative release conducted to acquire seasonal pest suppression. We would propose that for some life history traits, such as development rate, a low degree of variation may be well suited to certain biological control programs, such as those requiring repeated inundative releases of natural enemies into annual crops or glasshouse environments.

Studies of insect developmental biology indicate that variation may exist among geographic locations and hosts (Haardt & Holler, 1992; Honek & Kocourek, 1988; Ruberson *et al.*, 1987, 1989) as well as among females and clones within local populations (Lamb *et al.*, 1987; Rodriguez-Saona, 1994). One life history trait that is pertinent to maximizing mass production of natural enemies is the temperature-dependent development rate of the immature stage. Models using age-specific life-table dynamics to predict population growth-potential demonstrate that increased rates of development result in shorter generation time and faster population growth (Gutierrez *et al.*, 1981; Taylor, 1981). Since variation in development rates exists among isofemale lines, individuals chosen as the source of a culture may determine the success of the mass production phase of a biological control project, especially if the objective is to rear millions of individuals for an inundative release (Rodriguez-Saona & Miller, 1995).

An investigation of the temperature-dependent development of *Coccinella trifasciata* LeConte, an early season lady beetle in various agroecosystems in the Pacific Northwest of North America, was conducted for a comparison among temperate zone aphidophagous coccinellid species and to address the issue of within-population variation of development rates. This study focused on two primary questions: 1) What are the values for the lower developmental threshold and degree-day requirements to complete immature development for the population of *C. trifasciata* from Corvallis, Oregon, and how do these compare to other temperate zone aphidophagous coccinellids?; 2)What values for development threshold and heat-unit requirements may be attributed to individual females based on the developmental rates of her progeny? The results of this study have implications for the (un)intentional selection of biological control agents during foreign exploration and conduct of laboratory mass culture programs.

MATERIALS AND METHODS

The study was conducted during the spring and summer of 1994. Adult beetles were collected from alfalfa fields in Corvallis, Oregon, during April and May. The field-collected adult beetles were kept individually at 22°C and fed pea aphid, *Acyrthosiphon pisum* (Harris) to obtain egg clusters. Only F_1 progeny from the field-collected adults were used in the study.

Seven constant temperatures were used: 10, 14, 18, 22, 26, 30, and 34°C. Eggs were placed among the seven temperatures within eight hours of oviposition and monitored every 12 hours to observe survival and time to larval eclosion. Larvae were reared individually in 1-oz plastic creamers with a cardboard lid. First instars were systematically placed into each temperature according to female source so that all females were represented by offspring in each temperature treatment. A total of 14 females provided a sufficient number of eggs to be reared at each temperature. Because no eggs hatched at 10 and 34°C we transferred first instars to these temperatures from eggs that had hatched at 18 and 30°C, respectively. Observations of survival and time to each molt, and provision of fresh food, were conducted every 12 hours. Larvae were fed the same aphid species, cultured on fava bean (*Vicia faba* L.), as given to the adults. The observations were terminated upon adult eclosion.

Only certain isofemale lines were assessed for female-progeny differences in development-rate. Female lines were excluded from the isofemale analysis if fewer than three progeny were represented in each temperature treatment. Statistical analyses of survival of larvae and pupae among temperatures were via G-test for independence (Sokal & Rohlf 1981). The developmental threshold and degree-day requirements were calculated using linear regression comparing temperature (independent variable) to the inverse of number of days for development (dependent variable). The linear portions of the growth curves for larvae and pupae, and for overall development, were determined by the greatest correlation coefficients from these regressions. Differences in developmental time among the progeny of isofemale lines were assessed by an analysis of variance (ANOVA) within a given temperature, and developmental rate parameters among isofemale lines were differentiated using linear regression. All ANOVA and regression analyses were performed using Statgraphics version 7 (Manugistics Inc., Rockville, MD). Statistical significance was accepted at the $P<0.05$ level of probability.

RESULTS AND DISCUSSION

MORTALITY

Egg, larval, and pupal mortality differed by temperature ($G = 164.4$, $df = 1$, $P < 0.001$, table 1). No larvae eclosed from eggs held at 10 or 34°C. Also, no larvae survived beyond the third instar at 10 and 14°C. Thus, the lowest temperature from which larvae completed development was 18°C where larval-pupal mortality averaged 13.3%. Larval-pupal mortality at the two highest temperatures, 30 and 34°C, was 23.3 and 36.7, respectively. Survival of larvae in the 18-34°C treatments averaged 84% but ranged from 71-100% depending on the isofemale line (see table 5).

Previous studies on larval-pupal survival in temperate zone aphidophagous coccinellids have reported a relatively high death rate in larvae at temperatures below 18°C. Miller (1992) observed 83% mortality at 17°C for *Hippodamia convergens* Guerin-Meneville. Orr and Obrycki (1990) noted that *Hippodamia parenthesis* (Say) exhibited 67% mortality at 14°C. Similarly, *Scymnus frontalis* (F.) experienced 74% mortality at 15°C (Naranjo *et al.*, 1990). The aforementioned studies typically documented mortality ranging between 85 and 100% at temperatures below 13°C. However, an exceptional species, *Eriopis connexa* Mulsant exhibited 33 and 4.8% mortality at 14 and 18°C, respectively (Miller and Paustian, 1992).

GROWTH AND DEVELOPMENT

Development from oviposition to adult ranged from 44.2 days at 18°C to 11.1 days at 34°C. Egg, larval, and pupal development ranged between 14-21%, 55-59%, and 24-27% of

TABLE 1

Age-class specific percent mortality among larvae and pupae of first generation Coccinella trifasciata *from field-collected adults. Corvallis, Oregon, 1994.*

Stage[a]	Temperature, °C						
	10	14	18	22	26	30	34
Instar I	0	0	0	0	0	0	0
Instar II	96	6	3	0	3	0	0
Instar III	4	21	0	3	0	3	10
Instar IV	x	23	3	0	0	10	13
Pupa	x	50	7	3	0	10	13
Cumulative mortality	100	100	13	6	3	23	36

[a]n = 30 first instars.

TABLE 2

Average (±S.D., n) time for development (days) and adult weight (mg) of first generation Coccinella trifasciata *from field-collected adults. Corvallis, Oregon, 1994.*

Stage		Temperature (°C)						
		10	14	18	22	26	30	34
Egg	ave.	28.0	15.6	6.1	4.5	3.2	2.4	2.3
	s.d.	0	1.1	0.7	0.3	0.3	0.5	0.6
	n	1	37	58	61	73	31	9
Instar	ave.	x	12.6	6.4	3.3	2.3	1.8	1.6
I	s.d.	x	2.2	0.9	0.4	0.2	0.2	0.2
	n	0	27	29	30	29	30	29
Instar	ave.	x	10.8	4.5	2.6	1.5	1.1	0.9
II	s.d.	x	2.9	1.8	0.3	0.3	0.3	0.2
	n	0	21	29	29	29	29	26
Instar	ave.	x	13.5	4.6	2.7	1.8	1.3	1.1
III	s.d.	x	1.6	0.4	0.3	0.3	0.3	0.2
	n	0	17	28	29	29	24	22
Instar	ave.	x	x	10.6	5.7	3.9	2.8	2.5
IV	s.d.	x	x	1.4	0.3	1.2	0.6	0.2
	n	0	0	27	28	29	23	18
Instar	ave.	x	x	26.1	14.3	9.5	7.0	6.1
I-IV	s.d.	x	x	2.4	0.8	1.2	0.8	0.4
	n	0	0	27	28	29	23	18
Pupa	ave.	x	x	12.0	6.4	4.3	3.0	2.7
	s.d.	x	x	1.3	0.6	0.2	0.5	0.4
	n	0	0	26	28	29	23	18
Egg to	ave.	x	x	44.2	25.2	17.0	12.4	11.1
Adult	s.d.	x	x	4.3	1.5	1.9	1.4	1.9
	n	0	0	26	28	29	23	18
Adult	ave.	x	x	15.3	15.6	15.1	15.0	14.6
weight	s.d.	x	x	2.0	1.3	2.4	2.2	2.2

the total developmental period, respectively. These data suggest that the pattern of development for each life stage of *C. trifasciata* is similar to that of other aphidophagous coccinellids (Obrycki & Tauber, 1981; Naranjo *et al.*, 1990; Miller, 1992; Miller & Paustian, 1992).

Live adult weight did not differ among the temperature treatments (one-way ANOVA, F = 0.65, df = 4,119, P = 0.63), and averaged between 14.7 mg at 34°C to 15.6 mg at 28 °C (table 2). Data for other aphidophagous coccinellids suggest that *C. trifasciata* is similar to the cold-adapted species, *Calvia quatuordecimguttata* L., in attaining equivalent mass at different temperatures (LaMana & Miller, 1995). However, Schanderl *et al.* (1985) showed that *Harmonia axyridis* Pallas were significantly lighter when reared at temperatures close to their developmental-threshold.

The lower temperature-threshold for development was determined from data on growth rates between 18 and 34°C (fig. 1, table 3). The lower developmental thresholds differed according to life stage. The developmental threshold for eggs was the lowest of the values at 10.9°C. The developmental threshold for the second instar was the highest of the values at 14.6°C. Analysis of the development of all four instars resulted in an estimated threshold

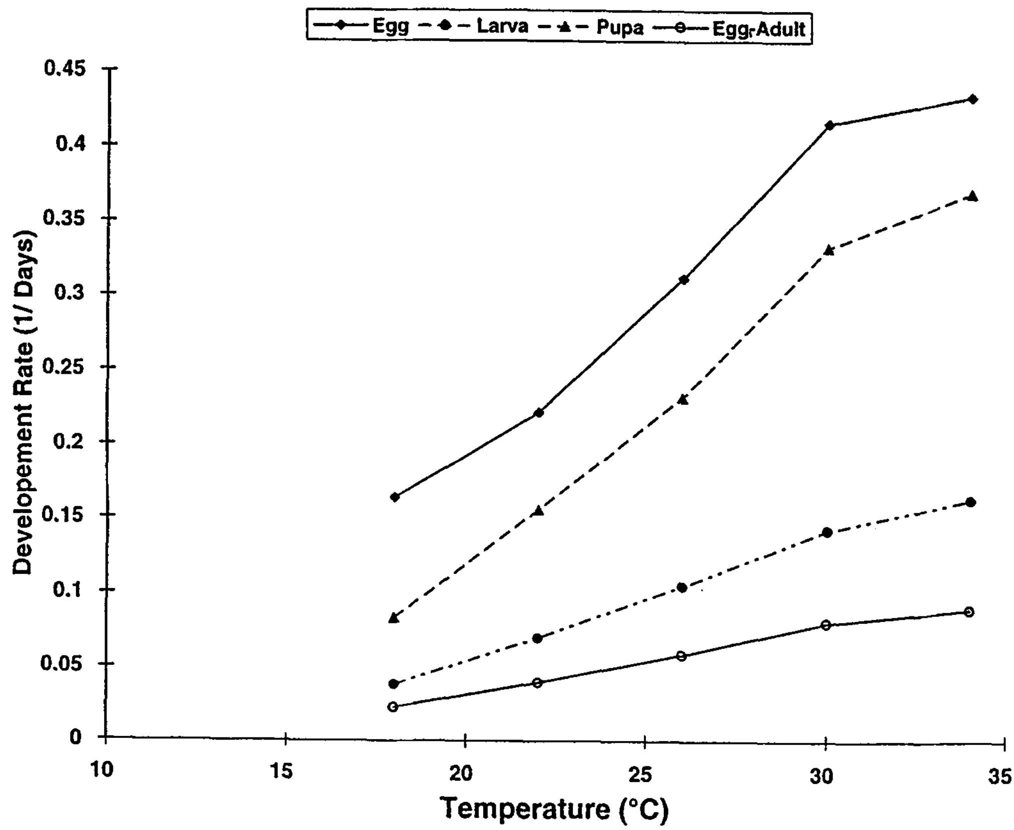

Fig. 1. Developmental rate (1/days) for eggs, larvae, pupae, and egg to adult for *Coccinella trifasciata* at various constant temperatures.

of 13.2°C, which did not differ from the pupal threshold of 15.5°C. As with *C. trifasciata*, threshold of coccinellid eggs are often lower than those of larvae and pupae (e.g LaMana & Miller, 1995 ; however see Honek & Kocourek, 1988). Calculation of the developmental threshold and heat-unit requirements for development from oviposition to adult eclosion for *C. trifasciata* resulted in an estimated heat-unit requirement of 227 degree-days above a threshold of 12.7°C.

A comparison a heat-unit requirements and threshold values for temperate zone aphidophagous coccinellids shows that *C. trifasciata* possesses the highest developmental threshold reported to date (table 4). Only *H. convergens* has exhibited a similarly high value at 12.5°C (Miller 1992). Since the accumulation of heat-units is dependent upon the estimated developmental threshold, comparison of degree-day requirements are best conducted by assessing predicted days for development at various temperatures. The time required for complete development by *C. trifasciata* at 20 and 30°C is approximately midway in the range of the other species that have been studied (table 4). However, at cooler temperatures the rate of development in *C. trifasciata* decelerates sharply because of

TABLE 3

Developmental threshold [D_{th}] and degree-day [DD°] requirements (± SE) for first generation Coccinella trifasciata *from field-collected adults. Corvallis, Oregon, 1994.*

Life stage	Developmental parameter (± S.E.)[a]		
	D_{th}	DD°	R^2
Egg	10.9 ± 1.0	47.1 ± 2.1	0.985
Instar I	12.1 ± 0.9	33.6 ± 1.2	0.985
Instar II	14.6 ± 0.3	17.4 ± 0.4	0.994
Instar III	13.3 ± 0.3	22.4 ± 0.4	0.996
Instar IV	13.1 ± 0.8	50.4 ± 1.5	0.989
Instar I-IV	13.2 ± 0.4	123.4 ± 2.9	0.993
Pupa	13.5 ± 0.8	53.3 ± 1.8	0.986
Egg - Adult	12.7 ± 0.8	227.4 ± 7.1	0.989

[a] Data on development rates between 18 - 34°C were used in the linear regression analyses.

TABLE 4

Summary of developmental threshold [D_{th}], degree-day [DD°] requirements and predicted duration of development from oviposition to adult eclosion at 20 and 30°C for temperate zone aphidophagous coccinellids.

Genus Species	D_{th}	DD°	Reference	Development[a]		
				15°C	20°C	30°C
Calvia quatuordecimguttata	8.2	274	LaMana & Miller, 1995	47	23	13
Adalia bipunctata	9.0	263	Obrycki & Tauber, 1981	44	24	13
Eriopis connexa	9.2	259	Miller & Paustian, 1992	45	24	13
Harmonia axyridis	10.5	231	Schanderl *et al.* 1985	50	24	12
Hippodamia parenthesis	10.8	235	Orr & Obrycki, 1990	56	26	12
Coleomegilla maculata	11.3	236	Obrycki & Tauber, 1978	64	27	13
Propylaea quatuordecimpunctata	11.7	195	Baumgartner *et al.*, 1987	59	25	11
Scymnus frontalis	11.7	312	Naranjo *et al.* 1990	95	38	17
Coccinella septempunctata	12.1	197	Obrycki & Tauber, 1981	68	25	11
Coccinella transversoguttata	12.2	218	Obrycki & Tauber, 1981	78	28	12
Hippodamia convergens	12.5	228	Miller, 1992	95	30	13
Coccinella trifasciata	12.7	227	This study	99	31	13

[a] Predicted number of days for development calculated from respective lower developmental thresholds and heat-unit requirements.

the sensitivity conferred by its high D_{th} value. Time for completion of development at 15°C is the longest of the species studied (99 d), and is similar to such warm-adapted species as *H. convergens* and *S. frontalis*.

The second objective of this study was to address the possibility that isofemale lines would exhibit different developmental rates that may be assessed in terms of heat-unit requirements. Among isofemale lines the time required for development at 18°C differed by 21% (table 5). Values for the developmental thresholds ranged from 11.4-14.5°C with heat-unit requirements ranging from 186-260 degree-days above respective thresholds. The isofemale line 'A' produced the fastest immature development characterized by a heat-unit requirement of 260 degree-days above a developmental threshold of 11.4°C. The isofemale line 'H' produced the slowest rate of immature development and was characterized by a heat-unit requirement of 186 degree-days above a developmental threshold of 14.5°C. Using linear regression, the heat-unit requirements of female-lines were demonstrated to be strongly correlated to lower threshold ($F = 20.8$, $df = 1,6$, $P = 0.004$, $r^2 = 0.78$) (fig. 2). In other words, maternal progeny-lines that showed increased heat-unit requirements partly compensated for this by having reduced temperature-threshold for the onset of development. However, as Honek & Kocourek (1988) point out, and is corroborated in our study, this compensation is not perfect. Thus, those beetles with reduced thresholds but higher heat-unit requirements are predicted to complete development more quickly.

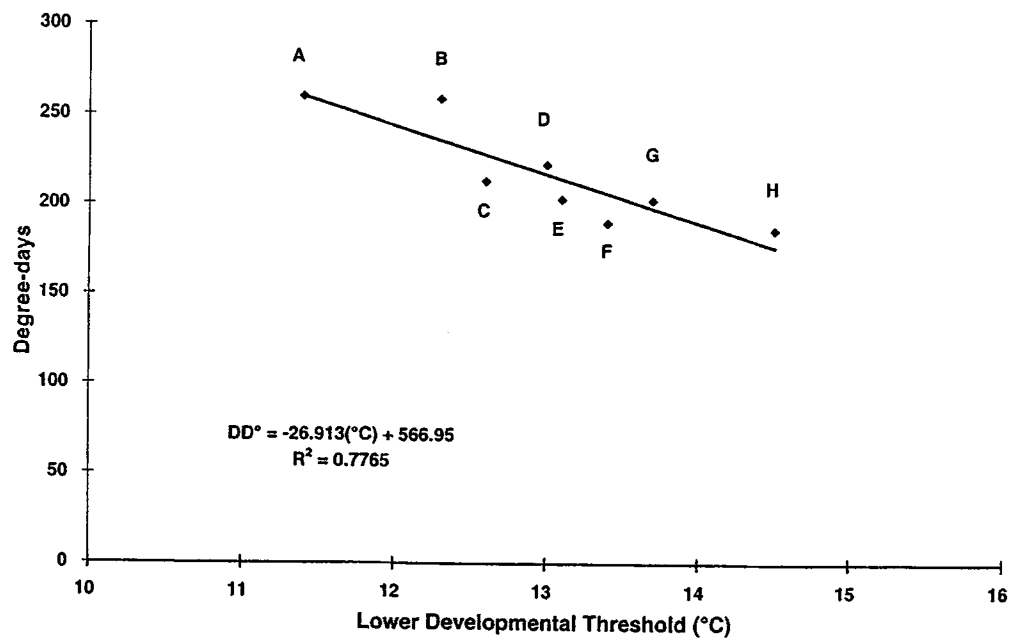

Fig. 2. Relationship between the lower developmental threshold temperature (D_{th}) and degree-days (DD°) among 8 isofemale lines of *Coccinella trifasciata*.

The numbers of females founding natural enemy cultures in classical biocontrol programs has often been quite low, and the expression of ecologically important traits in natural enemies may be further restricted during the ensuing mass-culturing. For instance, only five females provided the original stock population for *Tetrastichus incertus* (Ratzburg), a parasitoid released into North America for control of the alfalfa weevil, *Hypera postica*

TABLE 5

Survival, developmental thresholds, and degree-day requirements among isofemale lines of Coccinella trifasciata *ranked by actual and predicted number of days for development of instar I to adult at 18°C. Corvallis, Oregon, 1994.*

Female	Development (days) at 18 °C[a]		Survival (%)	D_{th}	DD°	R^2
	Actual	Predicted				
A	40.3 ± 0.6a	39.4	71	11.4	260.0	0.999
B	40.6 ± 0.7a	39.5	73	12.6	213.1	0.998
C	41.6 ± 0.7a	41.5	100	13.1	203.1	0.995
D	42.6 ± 1.0ab	41.3	80	13.4	190.1	0.988
E	45.6 ± 0.8bc	44.5	91	13.0	22.3	0.992
F	46.6 ± 0.7c	45.4	90	12.3	258.9	0.993
G	47.9 ± 1.1cd	47.2	100	13.7	202.8	0.999
H	51.1 ± 1.0d	53.2	86	14.5	186.3	0.993

[a] Different letters following values for actual development denote significant differences among isofemale lines. ANOVA, $P<0.05$.

(Gyllenhal) (Coles & Puttler, 1963). Also, only 17 females founded the initial culture of *Aphidius smithii* Sharma & Sabba Rao, a parasitoid released into North America for control of the pea aphid, *Acyrthosiphon pisum* (Harris) (Angelet & Coles, 1966). Although both of these projects were successful, the effects of a small founding gene pool are unknown.

Instead of haphazard selection of founding stock for mass culture, future biological control programs could manipulate the populations of natural enemies reared for release. Assume a classical biological control program involved an exploration trip to Oregon for the collection of *C. trifasciata*. A culture of fast developing larvae would result if isofemale lines such as 'A, B, or C' (see table 5) served as the founding source for mass culture. Similarly, a culture of slow developing larvae would result if isofemale lines such as 'H' served as the founding source for mass culture.

The following considerations emerge as a consequence of the results of this study: 1) degree-day assessments for insect pests and their natural enemies should be based on equal numbers of progeny from numerous females, otherwise certain isofemale lines will be under or over represented resulting in an inaccurate estimate of heat-unit requirements that characterize the overall population; 2) progeny from each female should be assessed as a family unit to analyze female source as a treatment effect; 3) a biological control program utilizing an innundative approach to natural enemy releases might be best served if individuals with genotypes expressing rapid development were screened and intentionally selected for propagation; 4) artificial selection for rapid development to improve natural enemies may lower the developmental threshold, which may increase survival at low temperatures (see Rodriquez-Saona & Miller, 1995). Artificial selection of natural enemies for faster development and enhanced survival at low temperatures may facilitate conservation and augmentation of these beneficial species/populations in temperate zone agroecosystems.

ACKNOWLEDGEMENT

Laboratory assistance was provided by J. W. Paustian and C. Rodriquez-Saona. The research was funded by USDA Special Grant Program 89-34205-4298. This is Oregon State University Experiment Station Technical Paper No. 10697.

RÉSUMÉ

Evaluation de l'effet de la température sur le développement de *Coccinella trifasciata* (Col. : Coccinellidae) et comparaison entre lignées isofemelles

L'effet de la température sur le développement de *Coccinella trifasciata* (provenant de Corvallis, Oregon) a été étudié pour la population générale et comparé entre lignées isofemelles. Aucun œuf ne survit à 10 et 34 °C. Le taux de survie est compris entre 63,3 % et 96,7 % pour des températures situées entre 18 et 34 °C. La durée du développement, de la ponte à l'état adulte, dure de 44,2 jours à 18 °C à 11,1 jours pour une température de 34 °C. Le poids moyen de l'adulte ne change pas en fonction de la température et il est de 15,2 mg. Pour l'espèce, les besoins pour le développement complet de l'œuf à l'adulte, sont de 227 degrés-jour au-dessus du seuil de développement de 12,7 °C. Les valeurs de ce seuil diffèrent entre les lignées isofemelles et sont comprises entre 11,4 et 14,5 °C pour des durées se situant entre 186 et 260 degrés-jour au-dessus des seuils respectifs. La lignée isofemelle ayant la vitesse de développement larvaire la plus rapide à 18 °C est caractérisée par un besoin de 260 degrés-jour au-dessus du seuil de 11,4 °C. Celle ayant la vitesse de développement la plus lente à 18 °C est caractérisée par un besoin de 186 degrés-jour au-dessus du seuil de 14,5 °C. L'intérêt de l'utilisation de lignées isofemelles dans l'élevage d'agents de lutte biologique est discuté.

Received : 19 December 1994 ; Accepted 22 January 1995

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