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Construction of a Temperature-dependent Simulation Model to Predict Population Growth of the German Cockroach, *Blattella germanica*

Chon, Tae Soo and Tae Sung Kwon
(Department of Biology, Pusan National University)

바퀴, *Blattella germanica* 개체군 증가의 예측을 위한 溫度依存 Simulation Model의 구성

全 胎 秀·權 太 晟
(釜山大學校 生物學科)

ABSTRACT

By using temperatures as a key variable, a simulation model was constructed to predict the size and developmental speed of the German cockroach population. The following three research steps were conducted to implement the individual simulation technique to represent the basic life system of the cockroach.

First, informations on developmental periods and survival rates in each life stage were obtained through rearing experiments at five different temperatures. Secondly, biological parameters needed for modeling were obtained based on these rearing results. The logistic equation was applied to calculating the developmental speed, while the averages of survival rates were utilized as parameters determining population size.

And thirdly, a basic life model was constructed in a simulative framework in FORTRAN for predicting the population development on the individual basis. For this purpose the biological characteristics, such as life stage, age in days, developmental speed, fecundity, etc., were assigned as an inherent attribute of the transaction so that they could accompany each individual automatically all through the simulation. This gave the model flexibility and applicability in representing the insect life system. To save memory space in computer programing, two files were utilized in translocating the individual informations each other as time proceeded.

The developed model could be effectively used as a strategic tool in interpreting and managing the cockroach population. It was also suggested in this study that the individual simu-

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lation could efficiently serve as a basis to formulate a fundamental framework on which the advanced and complex life process could be built.

INTRODUCTION

As an inital step to produce a simulation system which can appropriately predict the temporal and spatial change in the cockroach population, it was tried to construct a model to represent a simple life system of the insect in this study. Since there are unlimited number of environmental factors relating to the complex of the cockroach life system, it is impossible to consider all the factors at the same time. As a first step, temperature, the foremost environmental factor for determining the development of the poikilothermic animals, was chosen, and a simulation model that can calculate the size and developmental speed of the cockroach population was constructed in this study.

Since the 19th century there have been many researches on calculating the relationship between temperature and insect development. Among numerous models the widely applicable logistic equation (Davidson, 1942, 1944) was utilized in this study as an algorithm to calculate the developmental speed of the insect. Because it has been recognized that the logistic model can be practically applicable to field situations where temperature varies in a wide range(Andrewartha and Birch, 1967, 1973).

Due to its economic and medical importance, measurement of the German cockroach, *Blattella germanica*, has been conducted by many researchers. Under the temperature of 30°C, Willis *et al.* (1958) observed that the cockroach required 41.0 ±0.5 days for females and 40.1±0.6 days for males. Izutzu *et al.* (1970) reported that the German cockroach developed faster when they were reared collectively than when reared alone. He said that if the insects were reared in the number of more than 2 in a container, it would require about 1 week faster to become adult under 25°C than the individual rearing.

Shin *et al.* (1973) reported that the total period required for the nymphal development was about 55 days at 25°C. This was similar to the results from Izutzu *et al.* (1970). The female produced 3 ~7 oothecae in its whole life span and carried the ootheca for 20 days. They also observed that the longevity of female adults was 176 days and that of male adults was 171 days. In 1975 Ree *et al.* also investigated life cycle of the German cockroach. At 25°C it took about 7~8 days for the stadium between the first and fourth instar. It required 10 days for the fifth instar nymphs and 13 days for the sixth instar nymphs. The whole period of the nymphal stage was 53.4 days (female; 54.7, male; 52.1). The observed mortality during this period was 11.6%, and more than half of the mortality occured during the first instar stage. They reported that the hatching period required 36.8 days, while the hatching rate was 76.1%.

However, these observations were conducted at one level of temperature mainly for the descriptive purpose of the development, and they do not include the processes to utilize these rearing results in quantifying the relationship between the developmental speed and the change in temperatures. For the purpose of formulating this temperature-development relationship mathematically, the development of the German cockroach was observed on the individual basis at different levels of temperature in this study. Based on the observed results it was further attempted to calculate parameters in determining developmental units, then a simulation model was constructed by using these parameters as inputs.

MATERIALS AND METHODS

Rearing To measure developmental periods of the cockroach nymphs, individuals were reared at the temperatures of 19.6±1.9, 25.6±2.4, 29.0±3.5, 34.6±1.2 and 37.5±1.1°C in the laboratory (light conditions; 12~14hrs. light (100~200 lux) and 10~12 hrs. dark). The first instar nymphs reared in each temperature were collected from 2~5 oothecae. A transparent plastic container (diameter; 4.5cm, height; 7cm) was used as the rearing cage. For each container 3 nymphs were reared, and daily observations were made on the development of each individual. Food for the cockroaches was provided according to Cornwell (1976). That was the 9 : 9 : 1 : 1 mixture of rolled oats, wheat feed, fish meal and dried yeast powder (Bicellase®; Korea Bayer) respectively. The prepared food was provided into the cage in a sphere form (diameter; 0.7~1.0cm).

For the supply of water, a 4cm plastic hose(diameter; 1cm) was inserted through the top of the container with the tissue paper stuffed at its end. Then the tissue paper was wrapped with an aluminium foil so that the supplied water could not drip onto the floor of the cage. Through this method it was possible to supply fresh water daily. For ventialation the top of the container was cut out about 20cm², and saran cloth (0.05cm mesh) was covered. To provide a shaded shelter, a 0.5mm thick paper plate (3.5×4.5cm²) was vertically set along the wall of the cage, then the same portion of the outside of the cage was covered with another sheet of the paper. By providing the food, water and shaded shelter in this way, the cage was efficiently managed for rearing the German cockroach in the laboratory.

Relative humidities (R.H.) during the experiment was 70±15% for 25.6, 29.0 and 34.6°C, 55±12% for 19.6°C, and 75±5% for 37.5°C. Adults were reared under the same rearing conditions for nymphs except that a larger container (diameter; 8cm, height; 12cm) was used. 1~4 couples of the 1~3 days old adults were observed on their oviposition in one container daily. For tracing each individual the coloured maniqure was marked on the pronotum of the cockroach.

To compare the results of the model with the actual rearing data, mass rearing tests were conducted under variable temperature conditions in the laboratory on April 26, May 2 and May 4 in 1984, and on March 8, May 12 and July 18 in 1985. For each rearing test 10, 19, 22, 30, 24 and 34 individuals of the first instar nymph hatched newly were used respectively. The nymphs for each test were collected from the same ootheca. The rearing conditions were same as those for the tests on the inidvidual basis except for the container (diameter; 8cm, height; 10cm).

Modeling The results of the rearing experiments were analyzed and used for obtaining parameters in the logistic equation to calculate daily developmental units in the model. The term, developmental units, was used in this study to mean the proportional development of the cockroach occured in each stage in one day under given temperature conditions. If the cumulative developmental unit reaches 1, it represents that the cockroach changes its life stage, i.e., molting. The logistic equation suggested by Davidson, (1942, 1944) is:

$$y=\frac{K}{1+e^{a-bx}} \qquad (1)$$

where y is the developmental units (or reciprocal of the developmental period in each life stage). K is the asymptote of the developmental units y, e is the natual logarithm, x is temperature, and a and b are constants.

K was obtained by the graphic method based on the rearing results at various temperatures. The constants a and b are calculated through the least square method after transforming the logistic equation to the linear regression form. Namely the equation, (1), can be rewritten as: $\log_e(K/y-1)=a-bx$. This is a form of the linear regression of x on $\log_e(K/y-1)$.

The obtained logistic equation for each life stage was integrated into a simulative framework written in FORTRAN to calculate developmental units for the generated individual on the daily basis. To provide variations in the calculated data for each individual, they were generated in the manner of the normal distribution pattern by using the means and standard deviations of the developmental units. To estimate the variance of y, $V(y)$, Taylor's theorem was applied (Snedecor and Cochran, 1967).

If we let $z(y) = \log(K/y-1)$, then

$$V(z) \doteq \left(\frac{dz}{dy}\right)^2 V(y),$$

where $V(z)$ is the variance of z. After calculating the derivative of z on y, and rearranging the equation on $V(y)$, it becomes: $V(y) = V(z)\{y(y/K-1)\}^2$.

RESULTS AND DISCUSSION

Rearing Table 1 shows the observed developmental period in each instar at different temperatures. Except for 37.5°C the development required a longer period as temperature decreased. The development of the cockroach was delayed at 37.5 and 19.6°C. As shown in the table, the sum of the periods of the nymphal stages were 291.9, 66.9, 57.1, 36.1 and 78.6 days respectively at temperatures from 19.6°C to 37.5°C. When the whole nymphal period was calculated on the individual basis from hatching to emergence, the averages were 271.0, 64.5, 57.3, 36.6 and 73.0 days respectively from 19.6°C to 37.5°C.

One problem in measuring the developmental speed of the insect is the physiological stress produced by extremely low or high temperatures in the previous stages. If this is to be considered in modeling, it causes complicated situations. To predict the developmental speed of the fourth instar nymph, for example, three combinations of the lowest, highest and optimal temperatures are required in each previous instar (3^3 experiments). In order to cover all the instars of the German cockroach, $\sum_{n=2}^{6} 3^{(n-1)}$ treatments (n; instar) are needed unless an assumption is made on simplifying the effect of the physiological stress. As an initial step in constructing the basic life model, it was assumed for simplicity of modeling that the model was generally run under favorable tempeature conditions and that the physiological stress was not produced.

To eliminate the physiological stress in previous stages other series of experiments were conducted at 19.6°C and 37.5°C. In these tests the individuals had been reared at optimal temperatures (25∼28°C) in previous stages before their development was observed at the specific instar. The results were 35.4, 27.6, 34.5, 34.2 and 39.1 days at 19.6°C respectively at the stages from the second to sixth instar when 42, 42, 51, 71 and 45 ndividuals were observed. The developmental periods at 37.5°C were 5.6, 11.0, 11.0, 17.4 and 10.0 days respectively from the second to the sixth instar when 5, 2, 4, 5 and 1 individuals were observed.

In this study the development took a relatively longer period than that observed by other researchers. Ree *et al.* (1975) reported that it required 53.4 days for the nymphs to emerge at 25°C and 60% R.H.. According to Shin *et al.* (1973) it was 55.1 days at 25.2°C and 75% R.H.. Considering that the humidity conditions were the similar range among these rearing tests, this delayment may be due to other rearing environments including diet conditions or due to physiological variability in growth of the German cockroach. But it needs further study. Shin *et al.* (1973) reported that the development was delayed (69.7 days) when the rearing periods of the dead ones during the experiment were included, and that the total period for the nymphal stage was in a wide range of 34∼101 days. Ree *et al.* (1975) also observed the variability in growth of the cockroach. They said that the developmental period for the fastest growing nymph until emergence was equal to the period from the first to fourth molting of the slowest growing individual. Considering that urban environments where the German cockroach inhabits are very complex, the development of the insect on the populational basis would quite vary in field situations. This leads to a necessity of studying the relationship between the development and environmental impacts in more complex conditions. This basic life study would provide a basis to this advanced approach.

As previously mentioned, the logistic equation, (1), was applied to these rearing results to be able to calculate the daily developmental units for each individual in the model. Table 2 lists the obtained parameters in the logistic equation for each instar. There have been reports that it requires

Table 1. Developmental periods in days in nymphal stages of the German cockroach at different temperatures

Temp. (°C)	Instar	I	II	III	IV	V	VI	Sum
19.6	N*	46	42	39	38	32	26	291.9
	Range	15.0～26.0	15.0～49.0	19.0～55.0	29.0～127.0	26.0～186.0	45.0～243.0	
	Mean	18.1±13.6	35.4±13.3	33.3±14.7	44.8± 22.9	64.3± 46.0	96.0± 56.9	
25.6	N	46	46	46	46	45	28	66.9
	Range	6.0～ 9.0	6.0～14.0	6.0～16.0	6.0～ 25.0	7.0～ 36.0	10.0～ 32.0	
	Mean	7.3± 0.9	8.4± 2.2	9.5± 1.9	11.9± 6.2	13.4± 4.0	16.4± 6.2	
29.0	N	40	39	39	38	36	24	57.1
	Range	4.0～ 9.0	5.0～16.0	5.0～34.0	5.0～ 22.0	6.0～ 26.0	9.0～ 21.0	
	Mean	6.3± 0.8	7.8± 6.8	8.6± 5.9	10.1± 6.3	10.6± 5.4	13.7± 4.5	
34.6	N	54	53	53	53	53	42	36.1
	Range	4.0～ 7.0	4.0～ 6.0	4.0～ 7.0	4.0～ 7.0	5.0～ 23.0	7.0～ 17.0	
	Mean	5.4± 0.8	4.2± 0.7	4.9± 0.7	5.3± 0.7	6.6± 0.9	10.0± 1.8	
37.5	N	63	50	5	4	4	2	78.6
	Range	5.0～ 8.0	4.0～13.0	6.0～19.0	5.0～ 21.0	6.0～ 35.0	6.0～ 21.0	
	Mean	5.9± 0.8	6.8± 2.5	13.8± 6.3	8.8± 1.3	25.3± 14.1	18.0	

*N is the number of the observed individuals.

Table 2. Parameters in the logistic equation* for determining developmental units in nymphal stages of the German cockroach

Instar	K	a	b
I	0.190	7.0954	0.3125
II	0.240	10.0887	0.3922
III	0.205	11.7585	0.4767
IV	0.188	11.5358	0.4586
V	0.114	9.2844	0.3896
VI	0.110	5.7498	0.2314
V′**	0.065	5.1056	0.2272

* $y=\frac{K}{1+e^{a-bx}}$, where y is developmental units and x is temperature.

** V′ represents the last nymphal stage of the male German cockroach.

different number of moltings for the German cockroach to reach adult (Wills *et al.* 1958, Tanaka and Hasegawa 1979). In this study males emerged from the fifth or the sixth instar, and the parameters were separately obtained (V and V′). When they emerged directly from the fifth instar, it required relatively longer periods, showing 23.4±8.1, 18.6±4.9 and 16.4±6.3 days respectively at 25.6, 29.0 and 34.6°C.

Table 3 shows the survival rates in nymphal stages at different temperatures. The survival rates at 37.5°C were lowest and most unstable between instars, ranging from 0.119 in the third instar to 0.937 in the first instar. The high survival rate in the first instar at this temperature needs further study since the highest mortality is usually shown in the youngest instar of insects in adverse environmental conditions. For the purpose of measuring survival rates of the cockroach nymph in optimal conditions, the means at temperatures between 25.6 and 34.6°C were obtained in Table 3. It was lowest in the first instar with 0.938, followed by 0.973 in the second instar. When the survival rates were calculated cumulatively from the first to the last instar, the probability of the survival of a first instar nymph until emergence

Table 3. Survival rates in nymphal stages of the German cockroach at different temperatures

Temp. (°C)	N*	I	II	III	IV	V	VI
19.6	50	0.880	0.750	0.970	0.938	0.999	0.999
25.6	46	0.999	0.999	0.999	0.999	0.999	0.999
29.0	39	0.951	0.999	0.999	0.999	0.999	0.923
34.6	53	0.964	0.931	0.999	0.999	0.999	0.974
37.5	159	0.937	0.450	0.119	0.875	0.714	0.600
Mean (25.6∼34.6°C)		0.938	0.973	0.999	0.999	0.999	0.994
Shin *et al.* (1973)		0.966	0.965	0.928	0.956	0.949	0.957
Average		0.952	0.969	0.964	0.978	0.974	0.976

*The size of the initial population.

was 0.904. Shin *et al.* (1973) observed that the overall mortality rate during the nymphal period was 23.8%, while Ree *et al.* (1975) reported that it was 11.6%. The results in this study was similar to those observed by Ree *et al.* (1975). As parameters determining the population size in the model, the averages of the results from Shin *et al.* (1973) and those from this study were utilized as inputs. In simulation the survival of each individual was determined randomly by using random numbers generated within the system.

The sex ratio is shown in Table 4 with the average of 0.58 when the cockroaches were reared at 23∼28°C. Also the number of males that emerged directly from the fifth instar is listed in Table 4. Thirtyfive individuals out of eightyfive male nymphs had the fifth instar as their last nymphal stage. This was about 41.1% of the total nymphs. Some variations exist in the last instar of male nymphs. Tanaka and Hasegawa (1979) observed that males usually emerged from the fifth instar while females emerged from the fifth or the sixth instar. Willis *et al.* (1958) reported that it required 5, 6 or 7 molts in males of the German cockroach and 6 or 7 molts in females when they were reared alone at 30°C. These observations suggest that there exists variability in the number of molting in cockroach development. For the simplicity of modeling in this study, the observed result, 41%, was used as the input determining the number of moltings in male nymphs. Although the result was 0.58 in this study, the sex ratio was assumed 0.5 in the basic life system. Because it has been generally recognized by many researchers.

Table 4. Emergence and the sex ratio (S.R.) of the German cockroach

Trial	No. of females	No. of Males		Total	S.R.
		Last instar (V)	Last instar (VI)		
1	21	3	10	34	0.62
2	24	16	4	44	0.55
3	15	7	9	31	0.48
4	26	7	16	49	0.53
5	31	2	11	44	0.70
Total	117	35	50	202	0.58

As shown in Table 5, the preovipositional periods from emergence to the formation of the first ootheca were 19, 11 and 7 days respectively at 25.6, 29.0 and 34.6°C. Table 6 shows the periods between ootheca formations at different temperatures. For simplicity of modeling the periods for ootheca formations and those for hatching were pooled after the production of the initial ootheca. As shown in the table, the periods for the initial (the period between the first and the second ootheca formation) and subsequent ootheca formations were similar in the range of 39∼41, 25∼26 and 22∼25 days at the temperatures of 25.6, 29.0 and 34.6°C respectively.

The incubation periods from ootheca formation

Table 5. The periods in days from the emergence to the formation of the first ootheca produced by female German cockroachhes at different temperatures

Temp. (°C)	N*	Days
25.6	15	19.2±12.0
29.0	30	10.5± 7.5
34.6	22	7.3± 4.7

*No. of tested oothecae

Table 6. The periods in days between ootheca formations by the female German cockroach at different temperatures

Temp. (°C)	N*	1st Ootheca-2nd Ootheca	Subsequent Oothecae	Mean
25.6	23	39.14±11.08	40.82±11.05	39.57± 9.74
29.0	65	25.04± 4.32	26.25± 3.85	25.74± 5.25
34.6	23	24.69±12.48	22.32± 8.11	23.35±10.99

*The initial number of tested oothecae at each temperature.

to hatching are shown in Table 7. The hatching periods for the first ootheca were 25.8, 16.0 and 13.7 days at the temperatures from 25.6 to 34.6°C respectively. These periods appeared to be relatively longer than those observed by other researchers. Similar to the case of the nymphal development this may be related to physiological variability or to difference in rearing environments. But this needs further study.

By utilizing the periods for the preoviposition, ootheca formation and hatching, it was possible to calculate the oviposition and hatching time in the model. Similar to the determination of the nymphal development, the logistic equation, (1), was applied to the oviposition results. Table 8 lists the obtained parameters, *K*, *a* and *b* to calculate the developmental units needed for oviposition and hatching. In the oviposition test, however, observations were made at 3 levels of temperature due to difficulties in rearing at the highest and lowest temperatures. Hence it was assumed that oviposition and hatching were practically inhibited at the temperatures below 18°C and above 38°C. In fact it was shown in the previous test that almost all the cockroaches were dead in the nymphal stage when reared at 37.5°C. Only 4 adults emerged out of 159 first instar nymphs of the initial population. Also 42 couples of the adult cockroaches have been reared at 19.6°C since April 21, 1984 until present time (October 2, 1985) and 4 females still survive. Among these only 3 females were able to produce the first ootheca from which alive nymphs hatched. The other eighteen females were successful to produce the first ootheca, but all the eggs did not hatch. A few females were able to produce more than two oothecae but they could not hatch.

Table 7. The incubation periods in days for the first and subsequent oothecae produced by the female German cockroach at different temperatures

Temp. (°C)	First		Subsequent		Mean	
	N*	Day	N*	Day	N*	Day
25.6	6	25.83±7.31	19	23.2±7.07	25	23.8±7.18
29.0	27	16.0 ±2.65	45	16.9±4.06	72	16.8±3.78
34.6	6	13.7 ±0.82	—	—	6	13.7±0.82

*Number of the tested oothecae.

Table 8. Parameters in the logistic equation for determining the developmental units in oviposition and hatching of the German cockroach

	K	*a*	*b*
Preoviposition*	0.150	9.1984	0.3349
Ootheca Formation**	0.044	8.6946	0.3588
Incubation***	0.079	6.6278	0.2653

*The periods from emergence to the formation of the first ootheca.

**The periods of ootheca formations in female adults.

***The periods from ootheca formation to hatching.

As shown in Table 9, the hatching rate of the ootheca was highest at 29.0°C. It was 0.967 and 0.804 respectively for the initial and subsequent oothecae. At 19.6 and 34.6°C, it appeared to be very low. For the initial ootheca the hatching rates were 0.250 and 0.318 respectively. Hatching was not successful for the subsequent oothecae. In simulation the means of hatching rates at 25.6 and 29.0°C were used as parameters for determining hatching.

Table 9. Hatching rates in the first and subsequent oothecae produced by the female German cockroach at different temperatures

Temp. (°C)	N*	First	Subsequent	Mean
19.6	8	0.250	0.000	0.250
25.6	15	0.667	0.792	0.730
29.0	30	0.967	0.804	0.886
34.6	22	0.318	0.000	0.270

*Number of the tested oothecae.

The average number of nymphs hatched from the first ootheca was 31.6±8.3 and that from the subsequent oothecae was 26.1±8.9. These numbers were used as parameters for generating the number of produced nymphs by adults in the model. In order to give variation in the number they were generated in the normal distribution pattern by using the means and standard deviations.

Simulation Individual uniqueness is one of the principle characteristics observed in the biological phenomena. Although it is unique, it causes a difficulty when mathematical or mechanical modeling techniques are applied to this complex biological system. Because the techniques deal with the biological population collectively, not individually. As a way of coping with this problem it was tried in this study to construct a simulation model that conducts calculation on the individual basis. By simulating individually it gives more flexibility in representing biological characteristics and leads us to a better position to analyze the complex of a life system.

For inidvidual simulation, a simulation language, GPSS (General Purpose Simulation System) can be utilized, and it has an example of application to an insect life system (Chon 1982). But the GPSS is originally designed to represent engineering or business management systems where the individuals (transactions) require frequent waiting (qued) times. In this study the qued situation did not appear. The other disadvantage is that it requires a relatively longer computer time in representing the life process of each individual. Especially this problem appears in the situations where many individuals have to be generated. Because of the high biotic potential, individuals increase geometrically in the insect life system. Hence memory space and calculation speed become very important in simulating individuals of insects. Due to this reasoning a compile language, FORTRAN, was utilized in the manner that it could properly calculte data of each individual in a relatively less computer time.

Figure 1 shows the overall process of the individual calculation. Instead of providing the total population size and other collective data as inputs, each individual was generated as a transaction in the similar manner to GPSS, and a set of individual information was given to the created insect. The set of data for each individual included: 1) the sequential number of the individual which is unique in the simulation system, i.e., the name of an individual (INUM), 2) the number representing the life stage of the individual, egg, from the first to sixth instar nymph and adult (female and male) (ISTA), 3) age in days of the individual in each life stage (IDAY), 4) daily calculated developmental units for nymphs (or for ovipostion of females) (IDEV), 5) cumulative developmental units from the first day in each life stage (ICUDEV), 6) the calculated number of the oothecae that a female will produce in its life span (ICALO), 7) the number of oothecae already produced by a female (IACTO), 8) the number of eggs produced from an ootheca (IEGG), and 9) survival rate in each life stage (or life span of adults) (ISURV).

The informations on each individual were read from the file A at the beginning of each day, *t*.

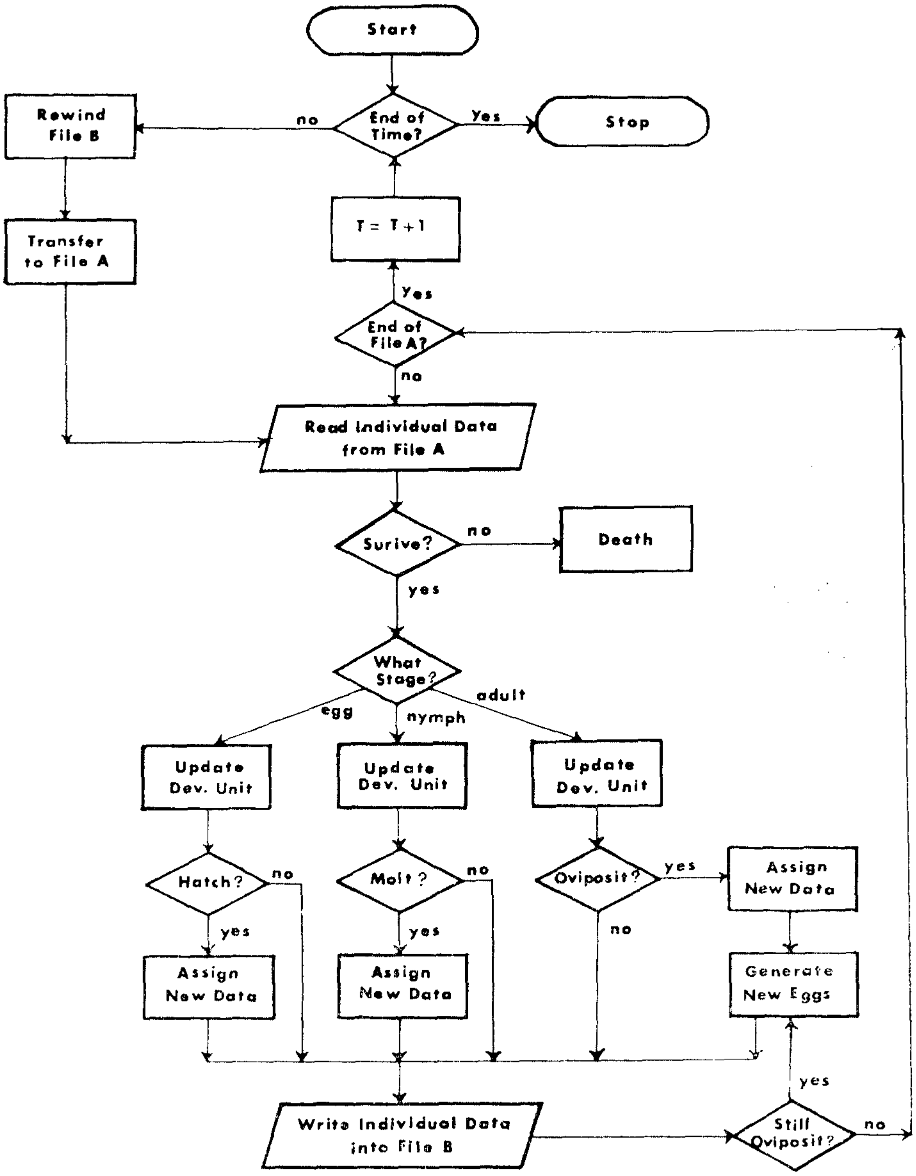

Fig. 1. A modified flowchart for representing individual simulation in the basic life system of the German cockroach.

Then these informations were updated in the aspects of survival, daily development and life stage advancement. After being updated, or being given new data for a new life stage, the data were written on the file B, which was read again as inputs for the next day, $t+1$.

As previously mentioned, a problem in constructing the individual simulation model is that it requires a large memory space since the insect population increases rapidly due to its high biotic potential. If the informations for all the individuals are kept in all days as time proceeds, this could require a great amount of memory space. Then the computer memory capacity would become a limiting factor in simulation. As one way of solving this problem, the memory space for the previ-

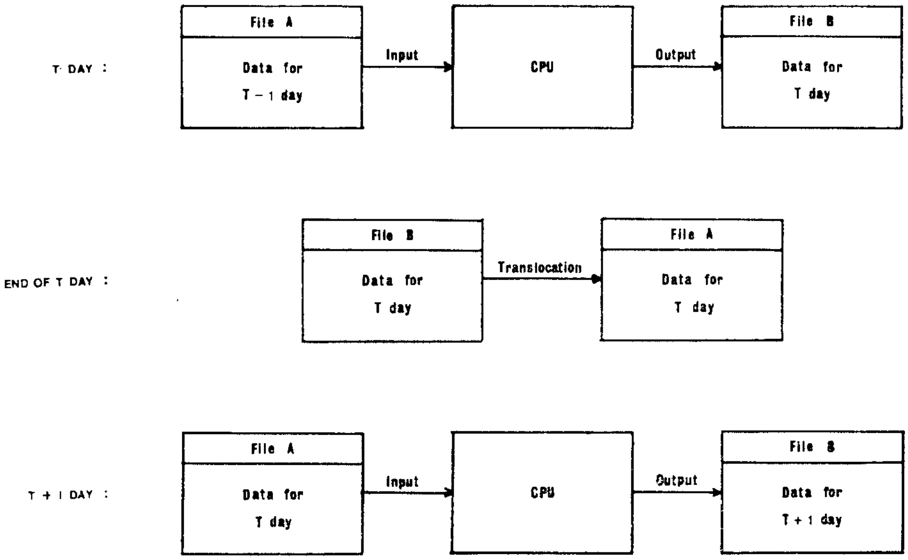

Fig. 2. Translocation of the individal informations between two files as time proceeds.

ous days were designed to be automatically eliminated. Before beginning of the next day the data file for the previous day was translocated to a new file, which was to be read for the simulation on the next day. Then the data in the former file was eliminated, and the file was used again to receive the updated results on the next day (Figure 2).

In each life stage the quantitative and temporal aspects of the population were considered. The survival rates for each stage were used as parameters to determine quantitative size of the population, while the developmental units calculated by the logistic equation were utilized to represent the temporal development of the population. For simplicity of modeling all the other environmental factors except for temperature are assumed to be in the favorable range (in the empirical sense) in the basic life system.

Figure 3 shows the flowchart for representing nymphal stages. In determining the advancement of life stage--hatching, molting or emerging--1000 was multiplied to the calculated developmental units for the convenience of calculation. At the time when the cumulative developmental units were over 1000 as time proceeded, the individual was de-

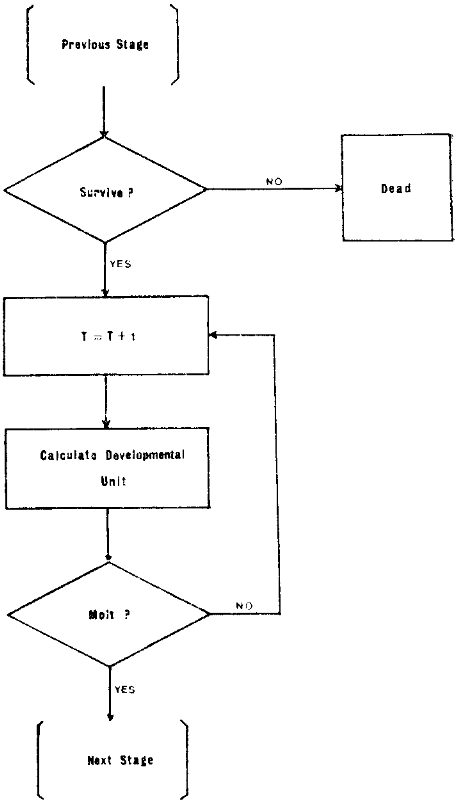

Fig. 3. A modified flowchart for representing nymphal stages of the German cockroach.

signed to experience molting, and became a new instar (or adult). As previously mentioned, variations were given to the calculated developmental units in the normal distribution pattern by using the means and standard deviations calculated from the regression equation.

The same process was conduced in the egg stage except that the eggs from one oothecae was designed to hatch at the same time. Since only the first instar nymphs hatched from an ootheca was recorded in the rearing test, the eggs that did not hatch from the same ootheca were not included in the model.

For the simulation of oviposition, the fecundity was considered as parameters determining the quantitative size of the population, while oviposition time--previposition period, duration of ootheca formation, etc.--was regarded to determine the temporal development. Figure 4 shows the flowchart representing simulation of the oviposition. By assuming the sex ratio as 1 : 1, the half of the generated adults were randomly chosen as females. As

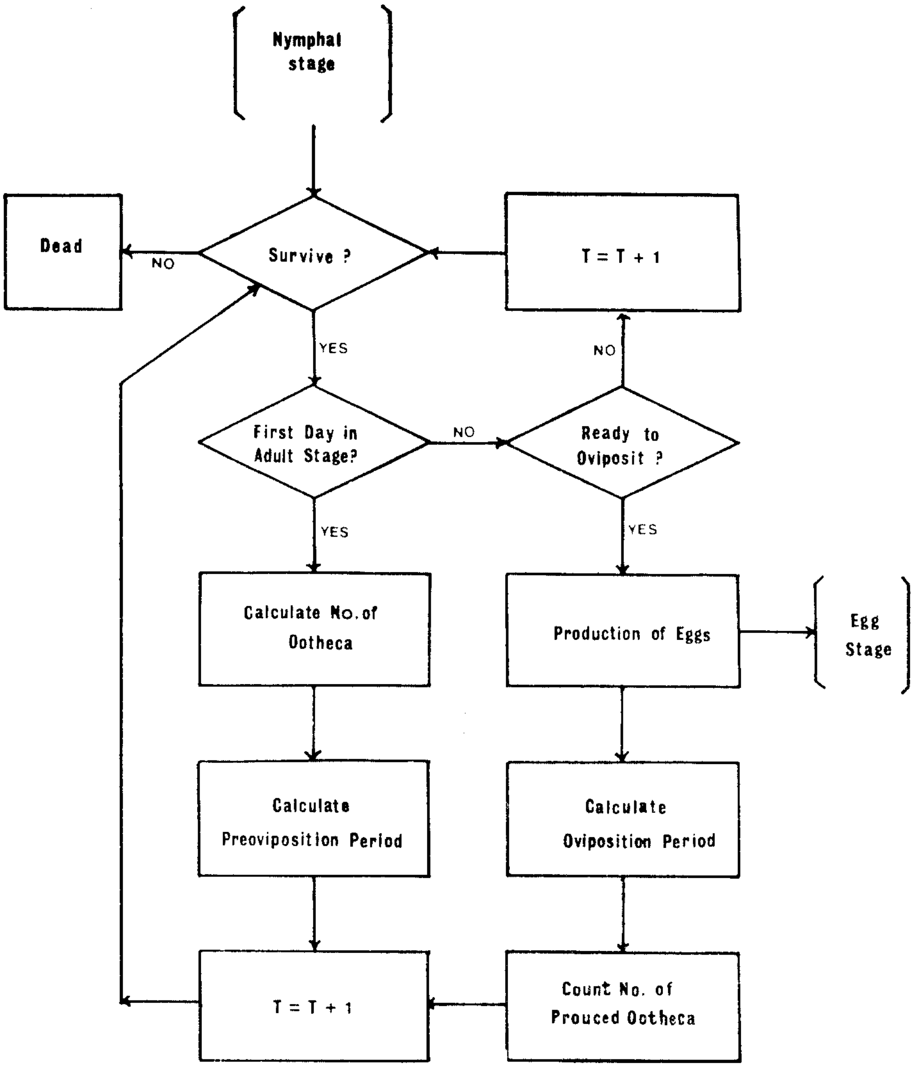

Fig. 4. A modified flowchart for representing oviposition in the adult stage of the German cockroach.

parameters determining the number of producd oothecae and adult longevity, the results from Shin et al. (1973) were used. According to them a female adult produced 4.50±1.35 oothecae and the longevity of the adult was 173.7±43.7 days. Similar to producing variations in developmental units in nymphal stages, the number of produced oothecae and life span were also generated in the normal distribution pattern for each individual by the use of the means and standard deviations.

Calculation of the population development By integrating the algorithm to calculate population development with all the obtained parameters in a simulative framework, a basic life model was constructed in FORTRAN (The program is available from the senior author on request). The model was run in two manners: predictively and descriptively. In the predictive manner the model calculated the population development for the future. For this purpose the input temperatures were generated within the system. In the descriptive manner, the model calculated the population development in the past. In this way it was possible to compare the calculations with the actual rearing results. Input temperatures in the descriptive manner were the actual measurements during the test period.

Table 10 shows the calculated population development of the German cockroach when the model was run in the predictive manner for 120 days. It was assumed that a healthy and one-day old female was introduced into a closed--no emigration and immigration--environmental system from the first day of June. It was also assumed that the female mated successfully after emergence. Since the model was run in a predictive manner, temperatures were generated within the system on the daily basis. The inputs were monthly averages of the means of daily maximum and minimum measured at laboratory from June to September, 1984. They the were 24.7±1.9, 27.8±1.8, 29.9±1.9 and 25.3±1.3°C respectively for June, July, August and September. By receiving these inputs, the computer generated daily temperatures in the normal distribution pattern by the use of their means and standard deviations in each month.

As shown in the table, the original female cockroach reproduced its alive oothecae on the 22nd, 59th and 83rd day within the 120 day calculation period. The female was assigned to produce 6 oothecae in the model. The fourth oothecae was also produced on the 120th day, but it was generated not to be able to hatch. The model also calculated the subsequent development after oviposition. The peak days for the first to sixth instar nymphs were respectively 43rd, 52nd, 60th, 64th, 71st and 81st day, and those for the second ootheca were 76th, 81st, 88th and 94th and 106~108th day respectively for the first to fifth instar. These peak days were in accordance with what was generally expected in the cockroach development in summer and early autumn. The first adult of the next generation occurred on the 79th day after the introduction of the original female. Most adults emerged between the 83rd and 94th day, and from the 95th day on, the adult abundance became stable at the numbers between 30~33.

The model also calculated the quantitative population size. The first ootheca reproduced from the adult female of the next generation appeared on the 94th day. From this day on, 20 females produced their first oothecae until the 120th day. Among them 2 oothecae were failed in hatching. As shown in the table, the total number of the cockroach population was 406 and the number of alive insects was 333 on the 119th day. Hence this model calculated that, under temperature conditions from June to September in the basic life system, one German cockroach female increased to more than three hundred times in its population size about four months later.

Not only for the overall population size, the model also showed the age composition on each day. On the last day of the modeling, for example, about 70% of the population were in the egg stage, 14% were young nymphs between the first and third instar, 6% were the nymphs older than the third instar, and 10% were the adults. This shows that the population was in the increasing

Table 10. Calculated population abundance of the German cockroach when an one-day old female was introduced into a closed environmental system for 120 days starting from the first day of June (No. of individuals)

Days	Egg	Nymph						Adult	Dead (Cumulative)	Total
		I	II	III	IV	V	VI			
22	38	0	0	0	0	0	0	0	0	38
43	0	38	0	0	0	0	0	0	0	38
52	0	1	33	0	0	0	0	0	4	38
59	27	0	7	16	10	0	0	0	5	65
60	27	0	1	19	13	0	0	0	5	65
64	27	0	0	3	20	10	0	0	5	65
71	27	0	0	0	3	27	2	0	6	65
76	0	27	0	0	0	22	10	0	6	65
79	0	27	0	0	0	12	19	1	6	65
81	0	25	2	0	0	10	20	2	6	65
83	33	1	25	0	0	8	18	6	7	98
88	33	0	6	20	0	4	11	17	7	98
89	33	0	5	16	3	3	9	20	9	98
94	58	0	0	6	16	3	1	30	9	123
100	113	0	0	0	14	8	3	30	38	206
102	168	0	0	0	11	11	2	31	38	261
103	168	0	0	0	7	15	2	31	38	261
104	135	33	0	0	5	16	3	31	38	261
106	189	28	0	0	2	18	4	31	67	339
108	224	28	0	0	1	18	4	31	69	374
115	256	0	24	0	0	11	11	32	72	406
118	231	25	21	3	0	8	13	33	72	406
119	231	24	18	6	0	7	14	33	73	406

trend on the last day of modeling. Since the instar is itself an attribute of the individual transaction, the age composition becomes naturally a part of population charactersitics without secondary calculations. This suggests that the individual modeling would be effectively implemented to analyze age compositions of the insect with overlapped generations. On the same basis the other population characteristics, e.g., age, sex, fecundity, survival, spatial distribution, etc., could be assigned into the information of the individual and be parts of inherent attributes in the model in the individual simulation.

As shown above, the result calculated from the model seemed in agreement with what was generally expected under tested temperature conditions. Also the development of the individual modeling indicated that it could be effectively applied to the theoratical study on population characteristics. In order to check the reliability of the model more in the realistic situation, comparative tests were conducted between the actual and calculated results.

Comparison with the actual data As previously mentioned, mass rearing tests were conducted to compare with the calculated data by the model

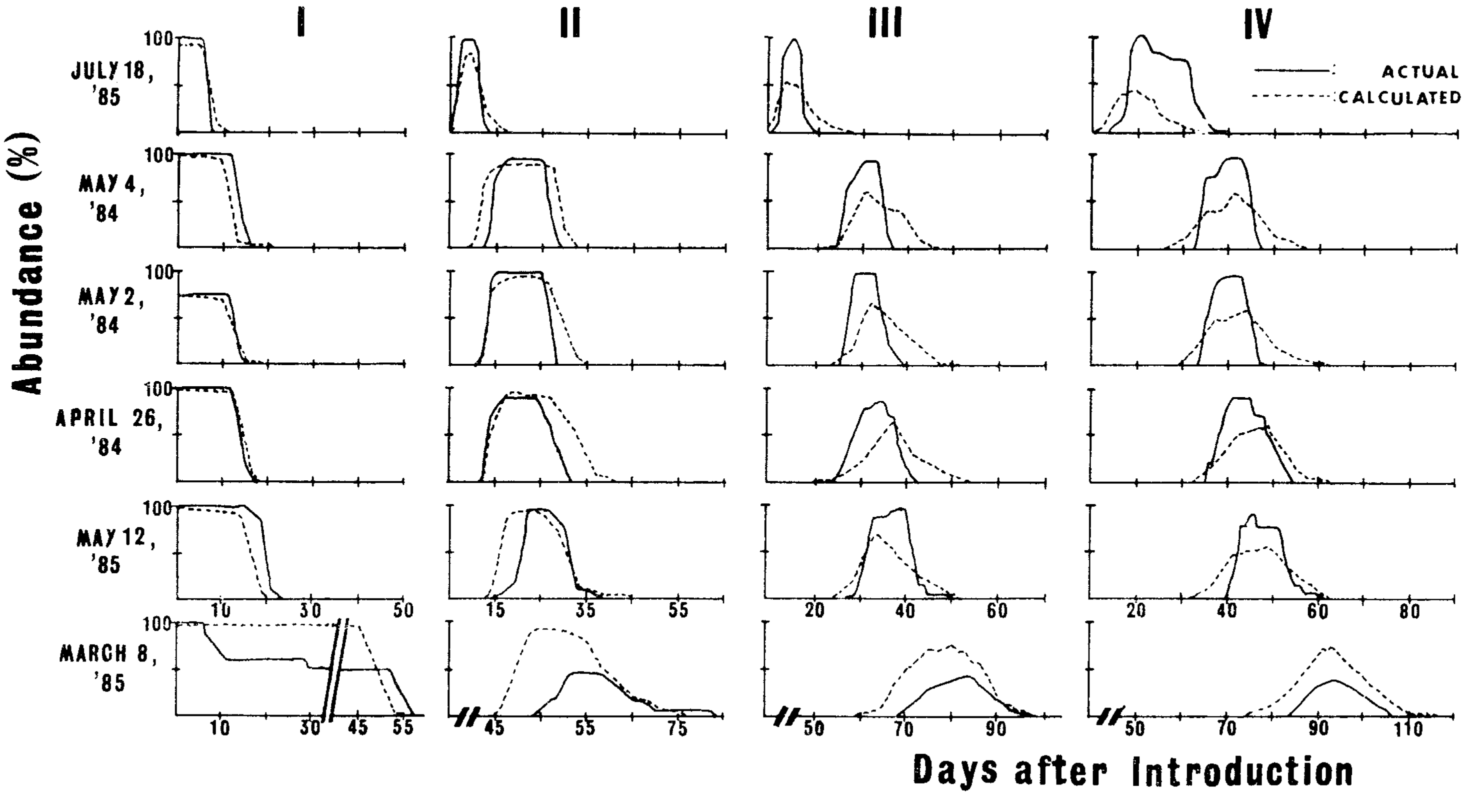

Fig. 5. Comparison of the actual and calculated results on the population development of the German cockroach in its basic life system.

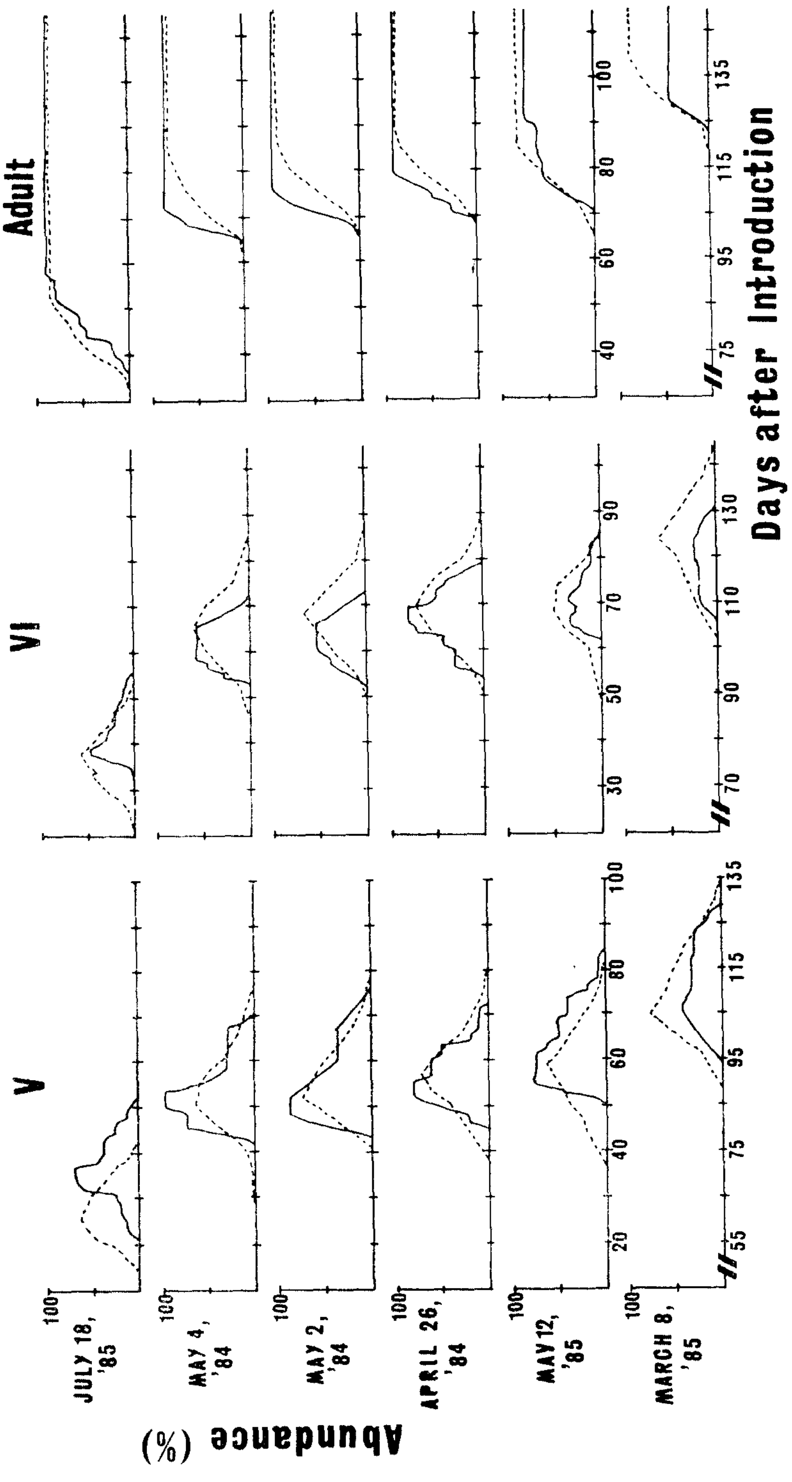

Fig. 5. (continued) Comparison of the actual and calculated results on the population development of the German cockroach in its basic life system.

Table 11. Comparison of the actual and calculated results on peak abundance and time in each life stage of the German cockroach population

	Nymph																		Adult		
	I			II			III			IV			V			VI					
	A*	T**	P***	A	T	P	A	T	P	A	T	P	A	T	P	A	T	P	A	T	P
July 18, 1985																					
Actual	100	100	1~5	100	100	7~10	100	100	14	100	100	19~21	59	94	33~34	47	94	37~39	45	90	44
Calculated	97	97	1~5	85	90	9	54	90	13	42	84	18	61	84	26	56	84	38	26	84	39
May 4, 1984																					
Actual	100	100	1~12	95	95	17~24	95	95	28~33	96	96	38~42	95	95	49~53	59	86	58~65	55	87	68
Calculated	97	97	1~8	90	91	17~24	60	87	31	57	86	41	64	85	51	60	82	64	40	80	72
May 2, 1984																					
Actual	100	100	1~11	100	100	15~25	100	100	29~33	95	100	39~43	89	89	48~52	53	89	60~66	73	89	72
Calculated	97	97	1~10	95	95	19~23	69	90	32	64	88	43	73	88	52	66	86	69	44	86	75
April 26, 1984																					
Actual	100	100	1~12	90	90	17~24	90	90	33~35	90	90	41~45	80	90	53~55	80	90	66~69	50	90	74
Calculated	97	97	1~12	96	96	18~19	63	90	37	57	90	46	69	90	57	68	89	69~70	43	89	77
May 12, 1985																					
Actual	100	100	1~15	96	96	23~27	96	96	39~40	92	96	45~46	75	83	57~62	35	75	70	35	80	75
Calculated	97	97	1~12	96	96	20~23	69	92	34	58	89	49	64	75	61	50	83	70	61	83	78
March 8, 1985																					
Actual	100	100	1~6	47	47	62~68	43	46	83~84	40	47	93~94	43	46	106	23	36	125	23	46	127
Calculated	97	97	1~45	95	95	55~59	75	93	80	74	91	94	73	90	105	60	89	124	33	90	128

*Abundance in percents of the peak instar nymphs.
**Abundance in percents of the total population.
***Peak days after the introduction of the original female.

in the descriptive manner in spring and summer of 1984 and 1985. In the model 100 individuals of the first instar nymphs newly hatched were generated. The daily average temperatures, which had been actually measured, were given to the model as inputs on the daily basis during the period of the comparative tests.

As shown in Figure 5 and Table 11, the calculated peak days for each instar mostly coincided with those observed from the actual rearings within the range of 0~3 days. In two cases, however, the difference was more than one week: the peak day for the second instar in the test starting from March 8, 1985 and that for the fifth instar in the test starting from July 18, 1985. In these tests, it was also found that the calculated peak days generally appeared a little earlier than those from the actual data in the younger instars. Since these differences were found in the tests that started in early spring or mid summer, it needs further study on the nymphal development when temperatures are too low or too high.

As shown in the figure and table, the quantitative trend was also generally in good agreement between the actual and calculated data. For the test starting from March 8, 1984, however, it was not agreed. But this was expected because a large proportion of the first instar nymphs, 50%, were killed in March due to low temperature. In the model, as previously mentioned, the input parameters for determining the population size were the survival rates measured between 25.6 and 34.6°C. High mortality at the low temperature was not included in the model. After the first instar, however, the quantitative trend in the actual rearing was stable and coincided with quantitative trend of population calculated by the model.

Another difference observed in the comparative test was that the population curve observed from actual rearings appeared more aggregatedly, showing the short period of appearence of each instar and the higher peak abundance. It was shown mostly in the third to fifth instar stages. This indicated that the variation of developmental units given to the model was greater than that from the actual rearing. But this problem of difference in kurtosis may be also related to the number of tested individuals. In the model 100 individuals were generated while individuals less than 34 were reared in the mass rearing tests. As the next step of study, variations of developmental speed in individuals could be further investigated with the improvement of measuring methods as well as the adjustment of the number of the tested insects. In addition, more rearing tests are needed to measure precisely the survival rates and developmental speeds in a wide rang of temperature. The survival rates at 19.6°C were not included in the March test. Also the oviposition at the temperatures of 19.6°C and 37.5°C was not measured in this study.

For further study, not only temperature but also other environmental factors could be investigated. For example, humidity, light, food, water, shelter, etc., are considered to play an important role in ecology of the cockroach. In the individual simulation modeling the effects of these factors could be effectively linked to the basic life model. This could broaden the applicability of the model in representing more real and complex situations.

Another point to be considered in developing the basic life model is the necessity of investigating oviposition in detail. In this comparative test only the development after oviposition was studied for the simplicity of modeling as an initial step for showing the individual simulation. Since oviposition is a broad and important subject for simulation, this could be studied in depth under a separate topic.

Although there are several points that are necessary for the next step of the study in further showing the individual simulation, e.g., improvement of measurement, quantitative test on the reliability of the developed model, etc., this model demonstrated its ability in representing a biological system. The individual modeling was efficient in its flexibility and applicability. Considering that numerous calculations were made for each attribute of each individual on each day, this individual computer, simulation maximized the foremost merit of the high speed in computation. Instead of using a complex and pre-fixed formula of the mathematical modeling in the collective sense, each individual is considered one by one on each life process. This gives the model a basis of flexibility in representing the variability and uniqueness of each member of the biological population.

Another advantage in individual simulation lies in its applicability as a strategic tool to interpreting or managing the target insect population in real situations. Because the population characteristics become inherent attributes of the individual (transaction), an integrated approach can be easily made on the relating characteristics. Also the simulation model can be efficiently combined to other models, even to the mathematical model, without loosing its simulative integrity. This gives population managers a better position to predict or analyze life phenomena under various situations. Along with some improvements in memory space management and in measurment methodology for the insect development, the individual simulation could effectively serve as a basis to formulate a fundamental framework on which the advanced and complex life process could be built.

摘要

飼育實驗, 統計分析및 simulation의 세 단계를 거쳐

온도에 따른 개체군증가를 예측해 줄 수 있는 모델을 구성하였다. 飼育實驗은 若蟲과 成蟲期로 나누어 실시하였다. 총 若蟲期間은 19.6, 25.6, 29.0, 34.5°C 에서 각각 291.9, 66.9, 57.1 및 36.4일이 소요되었다. 각 령기별 生存率은 25.6~34.5°C 사이에서 1령충이 0.938로 제일 낮았으며 若蟲은 전체적으로는 0.904이었다.

若蟲期가 끝난 後 羽化한 成蟲의 성비는 0.58이었고 수컷의 경우 상당수가 5령충에서 바로 羽化하였다. 羽化하여 교미한 암컷은 25.6, 29.0, 34.6°C 에서 각각 19.2, 10.5, 7.3일을 경과한 후 최초난협을 형성하였다. 차후의 난협들은 상기온도에서 각각 39~41, 25~26, 22~25일이 지난후 형성되었다. 또한 부화기간은 상기온도에서 각각 23~26, 16~17 및 14일이 소요되었다. 부화율은 25.6°C 와 29.0°C 사이에서 0.667~0.967이었으나 19.6°C 및 34.6°C 에서는 아주 낮았다. 각 난협당 부화한 약충의 수는 최초난협의 경우 31.6±8.3 개체이었고 차후 난협의 경우는 26.1±8.9개체이었다.

simulation은 바퀴의 각 생활단계—알, 약충의 각 령기 및 成蟲—별로 個體群 增加의 量的인 面과 時間的인 面을 반영하였다. 量的인 增加를 결정하기 위한 모수로는 飼育實驗에서 얻어진 生存率의 平均値와 산란력을 이용하였으며 時間的인 個體群 增加速度를 정하기 위해서는 logistic equation에 의해서 누적적 발육단위를 계산하였다. 이를 위해 上記 飼育實驗에서 얻어진 결과들에 대해 회귀분석등의 統計處理를 하였다.

modeling은 각 個體別로 simulation이 可能하도록 제반 生物的 特性—생활단계, 연령, 發育單位, 산란력 등—을 모델내에서 창출되어진 個體單位의 내재적 모수가 되도록 하였다. 또한 콤퓨터 기억용량을 감소시키기 위해 이러한 個體 情報들의 묶음이 시간이 흐름에 따라 두개의 보조 file 사이에서 서로 전이되어지도록 programing하였다. 모델을 이용하여 얻은 계산결과들은 실제 변온조건에서 집단사육하여 얻어진 個體群 增加와 대체적으로 일치하였다. 이를 예측적으로 이용할 때도 일반적으로 기대할 수 있는 결과들을 얻었다. 이러한 個體別 simulation 모델의 개발은 곤충 생활 system을 유효하고도 적절하게 나타내는데 이용할 수 있을 것이며 본 연구에서는 바퀴의 life model이 개체군의 관리 및 이론적인 분석을 위하여 기초적인 전략도구로서도 유용할 것임을 아울러 시사하였다.

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