

EFFECTS OF TEMPERATURE AND FOOD ON THE
DEVELOPMENT AND REPRODUCTION OF ANAGRUS
INCARNATUS HALIDAY (HYMENOPTERA : MYMARIDAE),
AN EGG PARASITOID OF THE RICE PLANTHOPPERS

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EFFECTS OF TEMPERATURE AND FOOD ON THE DEVELOPMENT
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(HYMENOPTERA : MYMARIDAE), AN EGG PARASITOID
OF THE RICE PLANTHOPPERS*

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Abstract

Effects of temperature and food on the development of immature stages, longevity and fecundity of the ovipositing females, mortality and sex ratio of the progeny of *Anagrus incamatus* Haliday, a mymarid egg parasitoid of the rice planthoppers were investigated. At higher temperature the developmental period of immatures was shortened and vice versa. The threshold temperature for development of this parasitoid was estimated as 11°C. The parasitoid development was unfavorable above 28°C. The parasitoid females fed on honey lived longer and produced more progeny than those fed on water alone. Mortality rate of the immatures was also high at the extremely high or low temperatures. Sex ratio was not so affected by the temperature. In all aspects, the optimum temperature for this parasitoid appears to be 24°C. Age-specific fertility table for *A. incarnatus* was also constructed.

Introduction

It has been known that temperature, among other factors, has dominant influence on the speed of development, survival and fecundity of animals (Andrewartha and Birch, 1954 ; Krebs, 1978). Bioclimatic analyses, such as the temperature threshold, optimal thermal constant for development have been used as the index for studies of the behaviour, abundance and distribution of insects as reviewed by Messenger (1959).

Anagrus incarnatus is reported to be a dominant egg parasitoid of the rice

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planthoppers in Japan (Chantarasa-ard *et al.*, 1984). However, so far there is little information about this parasitoid. In this paper we will report the results of our studies on the effects of temperature and food on the development and reproduction of this parasitoid under the laboratory conditions in 1981-1983. Additionally, age-specific fertility table was also constructed.

Materials and Methods

The initial stocks of *A. incarnatus* was obtained by collecting parasitized eggs of the rice planthoppers from the paddy field in Matsue City, Shimane, in 1981. The emerging parasitoids were then reared on eggs of *Nilaparvata lugens* deposited on the rice seedling. The stock cultures of parasitoid were maintained continuously in the laboratory.

Experiments were conducted under the constant temperatures, 16°C, 20°C, 24°C, 28°C and 32°C with ± 1 °C, 16-h photoperiod, and at room temperature, fluctuating between 22-31°C. The parasitoid was fed on honey or water.

For oviposition of the parasitoid, glass tube (2 x 18 cm) having both ends open was used. This type of tube was convenient for releasing the insects or for changing the rice seedlings bearing host eggs. In preparing the materials for the oviposition of parasitoid, rice seedlings bearing host eggs (*N. lugens*), of which their roots were wrapped with moist cotton or sponge, were inserted through one end of the tube so as to close that side, and the other end was covered by fine nylon gauze with the help of metal ring. The tube that containing the host eggs and parasitoid was then held on a flat rack, which is made of stylofoam, about 4 cm thick.

To observe the effect of constant temperature on the development of immature stages, each 30 parasitoid females were released to the host eggs for oviposition for 24-h at 5 temperature regimes accordingly. After exposure, the rice seedlings bearing host eggs were transferred to the test tube (1.8 x 18 cm) and then held in incubator corresponding to the temperature tested for further development of the parasitoid. Observation was made daily. The number of parasitoid adults emerged on each day was recorded. Experiments were terminated two months later when it was ascertained that no more parasitoid could emerge.

The other set of experiment was conducted at the same conditions to observe the longevity and fecundity of the ovipositing females, and the mortality and sex ratio of their progeny. Excess number of host eggs were supplied to the parasitoid every day for oviposition until the last female died. The other procedures and observation were made by the same method stated above, but when the normal emergence period of parasitoid was elapsed (about 3-4 days), host plants were dissected under a binocular stereo-microscope. The remaining parasitized eggs were then transferred to plastic Petri-dish and kept in incubator corresponding to the temperature tested for further development of the parasitoid. To prevent the propagation of fungi, a fungicide was applied with the dilution of 1 : 1000. The longevity and fecundity of the ovipositing females, mortality and sex ratio of their progeny were examined. At room tempera-

ture, the experiment was also done by the same method as described above.

For observation on the effect of food on the longevity and fecundity of the parasitoid, the ovipositing females were fed on water alone throughout their lifetime. The experiment was done at 20°C and at 24°C.

To obtain the data for constructing the fertility table for *A. incarnatus*, 100 parasitoid females were simultaneously released to the host eggs. The ovipositing females were fed on honey. Experiment was done at 24°C and at room temperature.

Under the present study, fecundity of the parasitoid was simply based on the number of host eggs parasitized. The manner of host dissection to obtain egg-count precluded the development of parasitoid immatures to the state at which sex could be recognized. Therefore, the actual number of eggs laid and consequently the sex ratio were unknown. Excess eggs may be laid as a consequence of superparasitism. However, because *A. incarnatus* is a solitary parasitoid and superparasitism is seldom, the number of parasitized eggs may not be significantly different from the actual number of eggs laid, and this should be regarded as the effective capacity of the parasitoid's reproduction. Host eggs being parasitized by *Anagrus* were easily recognized through the transparent chorion of planthopper eggs (see Ôtake, 1968).

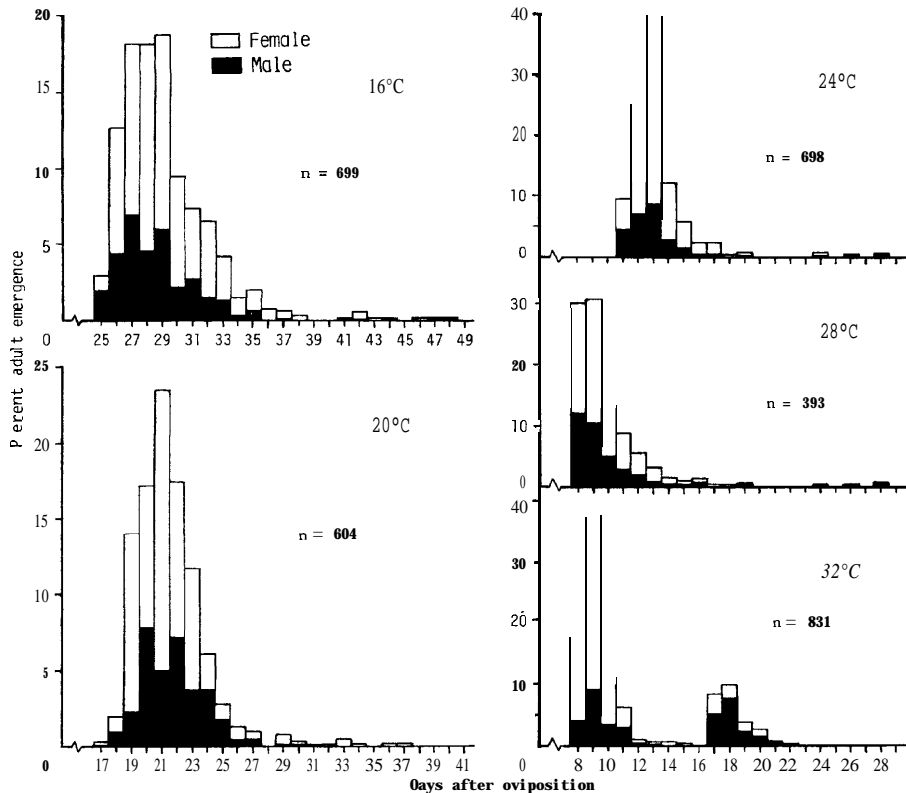


Fig. 1. Emergence pattern of *Anagrus incarnatus* at five constant temperatures (± 1 °C), 16-h photoperiod.

Results and Discussion

From Table 1 and Fig. 1, it can be seen that the temperature played an important role on the development of the parasitoid immatures. The developmental period from egg to adult emergence varied from about 29 days at 16°C to about 10 days at 28°C. At 32°C there was a bimodal tendency in the emergence pattern (Fig. 1). About 22% of the total adults emerged during day 17 to 22 after oviposition, consequently, the developmental period at this temperature was somewhat longer on an average than that at 28°C. At room temperature which fluctuated between 22°C and 31°C, the developmental period averaged 11.8 days. The emergence patterns of the parasitoid in respective temperatures tested are shown in Figs. 1 and 2. From the initial to 50% emergence, it took 5 days at 16°C, 3 days at 20°C and 24°C, and only 2 days at 28°C and 32°C. The emergence pattern at room temperature was similar to that at 20°C, 24°C and 28°C.

Andrewartha and Birch (1954) pointed out that the speed of development of an animal in an environment where temperature is fluctuating within the favorable range is closely equivalent to the corresponding constant temperature. It has been known that the rate of biological processes is slowed down as temperature approaches the extreme (Chapman, 1931). Thus, our results imply that the upper limit of favorable range of temperature for development of this parasitoid was approached above 28°C.

Graham (1959) stated that the minimum temperature at which the insect could not complete development or the speed of development becomes zero could not actually be determined. However, there is a method that if the developmental time-temperature curve is a hyperbola, and the developmental rate (the reciprocal of developmental time) is plotted against temperatures, the point where straight line intercepts the abscissa gives an estimate value of the threshold temperature (see Andrewartha and Birch, 1954; Graham, 1959). From the data available in the present study, it will be seen that

Table 1. Duration of the development from egg to adult emergence of *Anagrus incarnatus*, as affected by rearing temperatures.

Temperature ¹⁾ (°C)	Developmental period (days)	Range	n ²⁾
	Mean ± SD		
16	29.2 ± 3.10	25-48	699
20	21.6 ± 2.46	17-37	604
24	13.2 ± 2.14	11-28	698
28	9.8 ± 2.57	8-28	398
32	11.4 ± 4.02	8-22	831
(normal)	9.2 ± 1.08	8-15	621
(delayed)	17.9 ± 1.03	17-22	210
room temp.	11.8 ± 2.64	7-25	671

¹⁾ Constant temperature with ± 1 °C, 16-h photoperiod, and room temperature fluctuated between 22°C and 31°C.

²⁾ Number of individuals observed.

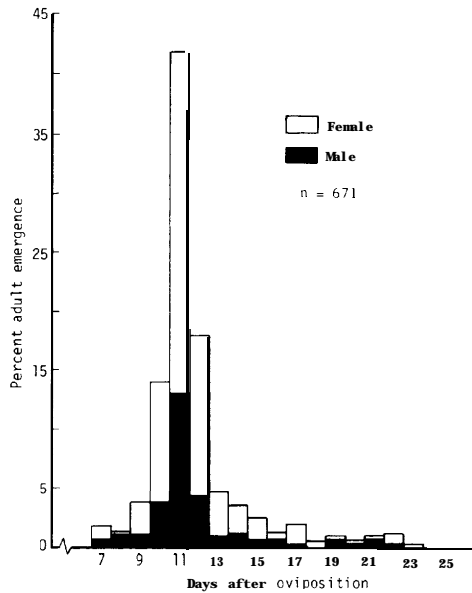


Fig. 2. Emergence pattern of *Anagrus incarnatus* at room temperature, fluctuating between 22 °C and 31 °C.

the developmental time-temperature curve (descending curve in Fig. 3) is not a true hyperbola, but in the range of 16-28°C it approximately approaches to this type. Hence, by utilizing a least squares technique, a straight line of the developmental rates-temperatures relationship (in the temperature 16-28°C) was drawn. The point where the line intercepts the abscissa was approximately estimated as 11°C (Fig. 3, ascending curve), and it was the threshold temperature for development of this parasitoid. As stated above, this is an approximate value. Lin et al. (1957) pointed out that the actual value of threshold temperature is no other way but empirical studies. In the absence of such data, however, Graham (1959) has suggested that an estimate may be of some value.

Based on the estimated value of threshold temperature (11°C), the thermal constant of heat requirement for complete development of the immature parasitoid was calculated as 172.6 day-degrees.

Messenger (1959) points out, based on the results from laboratory studies, that the threshold temperature for insect development is not a completely stable biological characteristic, and hence the thermal constant is also an unstable property, depending on the temperature levels during exposure and other factors, if any. As the thermal constant has been used as a bioclimatic index for study of the insect distribution, Messenger points out that the lower thermal constant required, the more poleward distribution range should lie.

For the effect of temperature on the longevity of adult parasitoid, Table 2 shows that the ovipositing females lived 20.8 days at 16°C (longest) and 5.4 days at 32°C

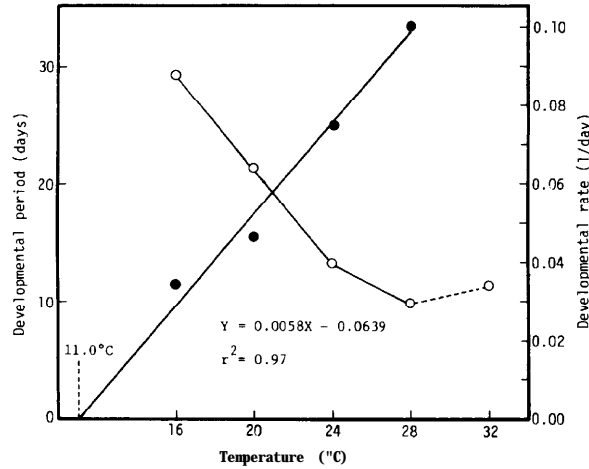


Fig. 3. Effect of temperature on the development of *Anagms incarnatus*.

Table 2. Longevity and fecundity of adults, mortality and sex ratio of progeny of *Anagms incarnatus* as affected by rearing temperature and adult food.

Source of food	Temperature ¹⁾ (°C)	Longevity in days		n ²⁾	Fecundity Mean ± SD	Mortality (%)	Sex ratio (%Female)
		Mean ± SD					
Honey	16	20.8 ± 3.87		18	36.2 ± 12.03	17.2(651) ³⁾	53.3(563) ⁴⁾
	20	13.7 ± 5.35		15	75.3 ± 32.76	6.2(1130)	65.0(1078)
	24	9.8 ± 4.39		17	69.5 ± 23.35	10.2(1180)	73.0(1094)
	28	9.9 ± 3.24		16	39.3 ± 17.58	10.3(629)	62.5(582)
	32	5.4 ± 1.80		17	43.0 ± 14.77	18.2(731)	62.8(646)
	room temp.	5.4 ± 1.97		17	44.9 ± 15.78	6.7(764)	67.6(716)
Water	20	4.1 ± 0.90		18	37.0 ± 8.34		
	24	4.3 ± 1.03		16	44.4 ± 13.21		

¹⁾ Constant temperature with $\pm 1^\circ\text{C}$, and 16-h photoperiod; room temperature fluctuated between the range 22-31 °C. ²⁾ Number of parasitoid females tested. ³⁾ Numeral in parentheses denotes the total parasitized eggs observed. ⁴⁾ Numeral in parentheses denotes the total number of parasitoid adults observed.

(shortest). At 24°C and 28°C the longevity was about 10 days. It was a little shorter than that at 20°C. At room temperature, although the ovipositing females were fed on honey, the average longevity was about the same as that at 32°C. For the influence of food on the adult longevity, it was found that when the ovipositing females were fed on water alone, their longevity were abruptly shortened and it was less than half of that fed on honey at the same conditions. The longevity of female parasitoid fed on water averaged 4.1 and 4.3 days at 20°C and 24°C, respectively.

The fecundity of *A. incarnatus* also affected by the rearing temperature. At moderate temperature the parasitoid produced much more progeny than those at extremely high or low temperatures. Fecundity of *A. incarnatus* reached a maximum,

75.3 per female at 20°C, but did not greatly differ from that at 24 °C, 69.5 per female. In all experiments, the daily reproductive rate of the parasitoid reached a peak on the day of emergence of the ovipositing females (initial day of oviposition). The trends were drastically decreased from the second day towards the end of female's lifetime. Over the range of temperatures tested, the least reproduction rate was found at 16°C.

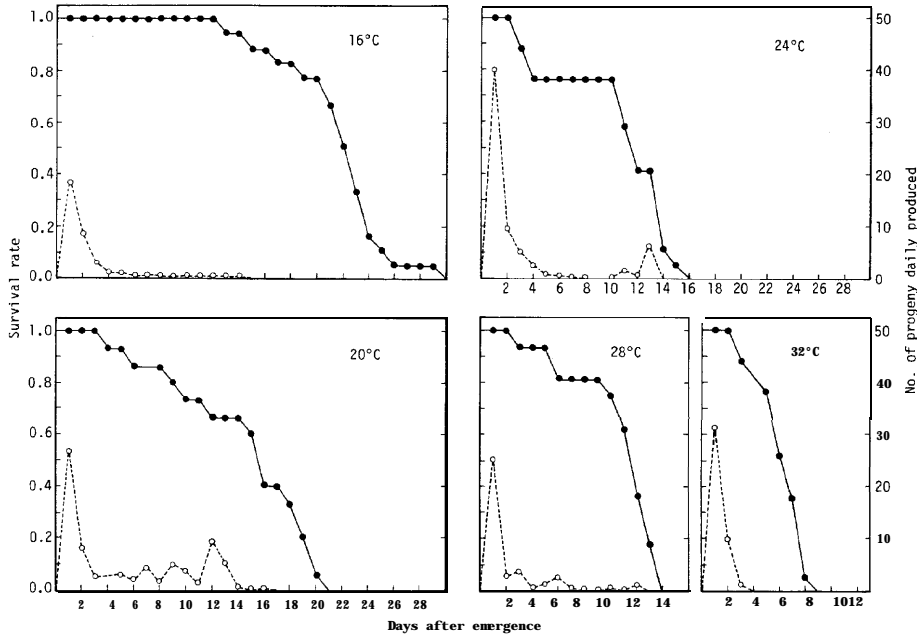


Fig. 4. Effects of temperature on the survival (solid line) and rate of reproduction (dotted line) of *Anagrus incarnatus* under constant temperatures.

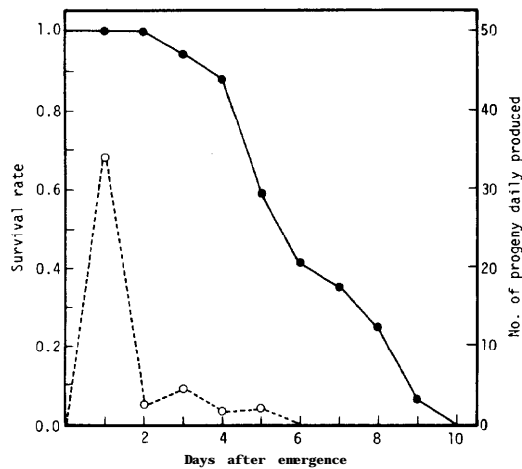


Fig. 5. The survival (solid line) and rate of reproduction (dotted line) of *Anagrus incarnatus* under room temperature, fluctuating between 22°C and 31°C.

This implies that in cooler environment the reproductive rate of this parasitoid decreased. The daily reproduction of *A. incarnatus* was shown in Figs. 4 and 5. In all temperatures, except at 20°C, more than 80% of parasitoid eggs (parasitized eggs) were laid within the first 3 days of oviposition period. At 20°C about 50% of eggs were laid on the first 3 days and more than 30% were laid on the last 5 days of oviposition period. It should be noted that at 20°C, some of the long-lived females laid a considerable number of eggs in the later part of their lives. In one case, a female laid as much as 105 eggs on the 12th day after emergence (the longevity of this female was 13 days).

According to Flanders (1950), *A. incarnatus* should be categorized as "pro-ovigenic type", because it can lay eggs immediately after emergence. Flanders points out that in the pro-ovigenic species the ovigenesis (egg production) is largely if not all completed before oviposition begins, and egg deposition occurs within few days after emergence. In the case of *A. incarnatus*, it appears very likely that the ovigenesis still develop during the adult's lifetime in some females. Thus, the fecundity at 20°C was slightly higher than that at 24°C probably due to longer life-time.

At room temperature, even the ovipositing females were fed on honey, the average longevity was only 5.4 days and the fecundity was about 45 per female (Table 2). Throughout the course of experiments the room temperature averaged 26.4°C, but the fecundity at this condition was much lower than that at constant temperature, 24°C. This is primarily because, at fluctuating room temperature, the ovipositing females lived shorter than at the comparable constant temperature. Andrewartha and Birch (1954) state that the results from the experiments with constant temperatures may not necessarily be equivalent to that in the natural conditions with fluctuating temperatures.

The reproduction rate of the parasitoid fed on water alone is shown in Fig. 6. There was no significant difference between non-fed and fed females with honey.

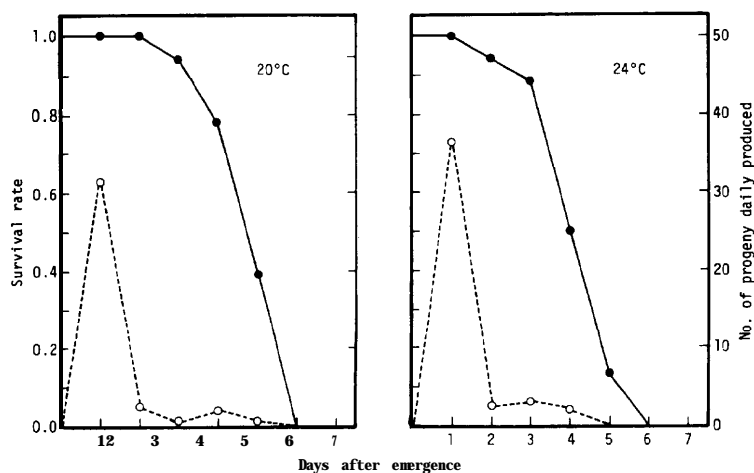


Fig. 6. Survivorship curve (solid line) and rate of reproduction (dotted line) of *Anagrus incarnatus* females fed on water.

Flanders (1950) stated that in the pro-ovigenic species, adult feeds little, if any. Thus, adult food should not directly affect the egg production of the female in the early phase of oviposition period. Therefore, it may be said that the difference in fecundity between fed and non-fed females depends on their longevity. Comparing to the other mymarid species, Miura (1979) found that in *Gonatocerus* sp., an egg parasitoid of the green rice leafhopper, honey-fed females lived longer and produced more progeny than those fed on water alone. In contrary, New (1969) found that adult food did not affect the fecundity of a mymarid *Alaptus pallidicarnis*, although feeding females could live longer than those deprived of food.

For the parasitoid immatures, it was found that the mortality at the extremely high or extremely low temperatures was higher than that at moderate temperature (Table 2). The per cent mortality was lowest, about 6 %, at 20°C. It was observed that at 16°C most of the immatures died at the larval stage, whereas at 32°C most of them died at the pupal stage or could develop to the adult but failed to emerge. It is interesting to note that the per cent mortality at room temperature was as low as at 20°C. This may indicate that the fluctuating temperature within favorable range does not much affect the development of immature parasitoid.

It was also observed that the sex ratio in F_1 generation was not affected by the rearing temperatures, although the female ratio at 16°C was somewhat lower than others (Table 2). The fecundity and sex ratio of progeny varied greatly by individuals of the ovipositing females. White (1954) stated that variable and fluctuating sex ratio is particularly characteristic of the haplodiploid groups (arrhenotokous species). Flanders (1939) pointed out that the sex of egg in this group is determined during oviposition, and the discharge of spermatozoa from the spermatheca into oviduct is usually stimulated extrinsically. Ôtake (1969) also found that the fecundity of *A. nr. flaveolus* varied individually, and there was a great fluctuation in sex ratio of the progeny.

Although, in the present study, much attempts were not made to investigate the occurrence of superparasitism, it was noticed that more superparasitism occurred at higher temperatures. The parasitoid immatures were recognized by the observation through the transparent chorion of host eggs under a binocular stereo-microscope. At lower temperatures, the superparasitism was scarcely observed. It is probable that in the warmer environment the parasitoid is more active in mobility, and hence more active in host searching. Messenger (1964) also found that the superparasitism of *Praon palitans* on aphid host was greater at higher temperature than at lower one.

In all aspects, it may be said that the most favorable or optimum temperature for *A. incarnatus* is around 24°C.

The age-specific survival and fertility tables for this parasitoid were constructed, which were based on the data obtained from 100 ovipositing females reared at 24°C, and at room temperature. The data in Tables 3 and 4 show l_x , the fractions of parasitoid females from initial samples still surviving during given age x , and m_x , the number of live female progeny produced per female per day at age x . Based on these data, various population growth parameters were computed, followed the procedures

Table 3. Age-specific survival and fertility rate of *Anagrus incarnatus* reared at 24 °C, 16-h photoperiod.

Age in days (x)	Survival rate (lx)	Fertility rate (mx)
1-10	immature stages	
11	1.00	19.68
12	0.97	5.97
13	0.93	2.94
14	0.89	0.97
15	0.87	0.46
16	0.84	0.67
17	0.81	0.33
18	0.74	0.51
19	0.71	0.29
20	0.66	0.18
21	0.57	0.44
22	0.46	0.09
23	0.28	0.98
24	0.12	0.0
25	0.06	0.0
26	0.01	0.21
27	0.0	

Table 4. Age-specific survival and fertility rate of *Anagrus incarnatus* reared at room temperature¹⁾.

Age in days (x)	Survival rate (lx)	Fertility rate (mx)
1-6	immature stages	
7	1.00	16.75
8	0.97	3.47
9	0.83	1.14
10	0.67	0.70
11	0.49	0.11
12	0.40	0.07
13	0.26	0.18
14	0.16	0.0
15	0.02	0.0
16	0.0	

¹⁾ Temperature fluctuated between 22°C and 31°C.

and terminology of Andrewartha and Birch (1954), Krebs (1978) and Southwood (1978):

$$R_0 = \text{the product of } \sum l_x m_x,$$

$$r_m = \sum e^{-rmx} l_x m_x = 1,$$

$$T = \log_e R_0 / r_m,$$

and $\lambda = e^{r_m}$.

Additional statistics : GRR (gross reproductive rate) is the sum of m_x , “developmental time” is the period of time in life cycle from birth to adult emergence (Messenger, 1964), and “Double time (t)” is the time required for a population to double its numbers, obtaining from the equation $e^{r_m t} = 2.0$.

From Tables 3 and 4, it is seen that the parasitoid reached adulthood on the 11th and the 7th day after oviposition at 24°C and at room temperature, respectively. The fertility rate reached to the peak on the initial day of oviposition, about 20 per female

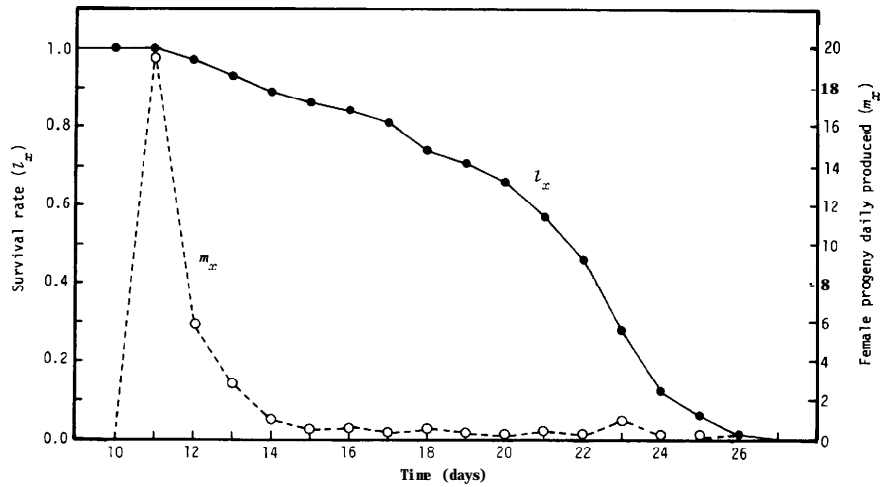


Fig. 7. Age-specific survival and fertility curves for *Anagrus incarnatus* reared at 24 °C, 16-h photoperiod.

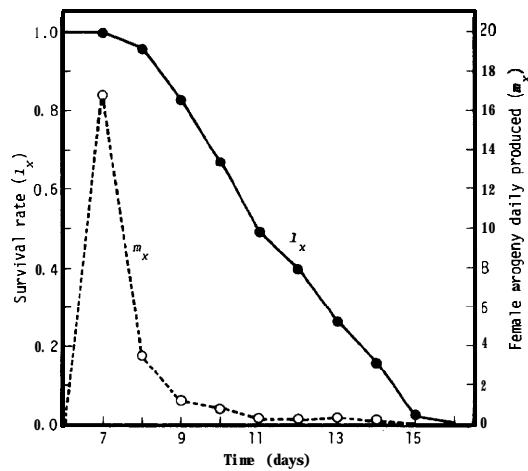


Fig. 8. Age-specific survival and fertility curves for *Anagrus incarnatus* reared at room temperature, fluctuating between 22 °C and 31°C.

Table 5. Comparison of the population growth parameters for an egg parasitoid, *Anagrus incarnatus*, as affected by rearing temperatures.

Growth	Rearing temperature	
	24°C	Room temp. ¹⁾
GRR (female/female)	33.72	22.4
R_0 (female/female)	31.56	21.7
Developmental time (days)	11	7
r_m (female/female/day)	0.297	0.424
T (days)	11.6	7.3
λ (female/female/day)	1.346	1.528
Doubling time (days)	2.33	1.63

¹⁾ Temperature fluctuated between 22°C and 31°C.

at 24°C and 17 per female at room temperature. The trends rapidly decreased from the second day towards the end of females' life, which was terminated on day 27 and 14 at 24°C and room temperature, respectively. The survivorship and fertility curves are shown in Figs. 7 and 8. Between the two rearing conditions, the fertility rate of the parasitoid was not so conspicuously different. However, as pointed out earlier, the ovipositing females lived longer at 24°C than at room temperature. Hence they had longer oviposition period, having greater value of GRR and R_0 than in the latter (Table 5). The potential population growth of the parasitoid is summarized by the value of r_m , which was 0.297 at 24°C and 0.424 at room temperature. The difference in r_m is very probably due to different T (generation time) of the parasitoid as affected by the two rearing temperatures. This is also reflected in the value of double time (t), which was 2.33 days at 24°C, while only 1.63 days at room temperature.

From the results, it is obvious that the temperature strongly affects the value of r_m of insects as has been pointed out by Graham (1959). Since the value of r_m may be variable according to the environmental conditions which affect on any one or more of the basic components of r_m (i.e. developmental rate, survival rate and reproductive rate), Messenger (1964) has suggested that the parameter r_m is able to use as a quantitatively bioclimatic index to measure the population growth of organisms.

Fig. 9 shows that the average temperature during the rice growing season in Matsue City, Shimane Prefecture (usually from late June to early October) was closely corresponded with the room temperature at which the present experiment was conducted. Thus, the theoretical population growth statistics obtained from the experiment may be assimilated with that expected in natural conditions, at least in some degrees. However, under the experimental conditions in laboratory, other factors such as the scarcity of host and other adverse effects are excluded. The r_m of the parasitoid in natural conditions is probably a little lower than that obtained from the experiments in laboratory. Krebs (1978) states that the actual rate of increase of animals we observe in natural populations is much more complex than the theoretical r_m .

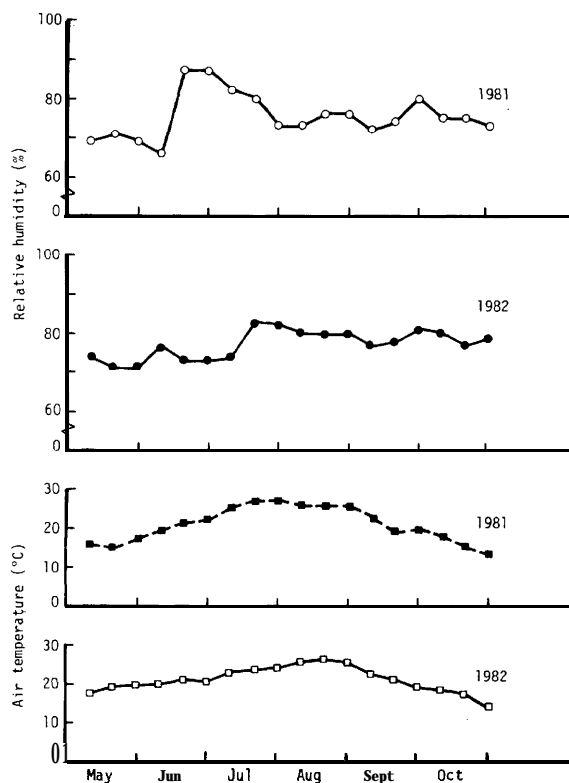


Fig. 9. Seasonal air temperature and humidity from May to October, 1981-1982, in Matsue City, Shimane Prefecture.

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