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Long-term growth patterns of laboratory populations of *Aedes albopictus* (Diptera: Culicidae): A comparison between two strains from Japan and Thailand

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Abstract: A long-term population growth of *Aedes albopictus* was examined by the population cage method for 350 days using two laboratory strains originated from Nagasaki, Japan and Chiangmai, Thailand. The populations were allowed to increase under two different conditions of larval food (poor and rich). Temporal changes in age composition and densities of larvae and adults were examined weekly. When the food condition of larvae was poor, none of the populations could survive: the population of Nagasaki strain became extinct at 214 days after the introduction of the initial population and two populations of Chiangmai strain became extinct at 49 and 70 days, respectively. The populations of both strains reproducing under the condition of rich larval food repeated an increase and decrease cycle throughout the experiment, and marked differences in several population parameters were observed between the two strains. The population of Nagasaki strain showed a higher rate of population increase, achieved higher densities of larvae and adults, and produced smaller females having longer longevity and higher fecundity.

INTRODUCTION

The population characteristics of vector mosquitoes such as reproductive rate, equilibrium density and its stability, are determined by many factors affecting the survival and reproduction of mosquitoes. Among these factors, density effects of larvae on their survival and development (Wada, 1965; Mori, 1979), interactions within and between hatching cohorts (Livdahl, 1982; Edgerly and Livdahl, 1992) and life table characteristics of vector mosquitoes (Crovello and Hacker, 1972; Hacker *et al.*, 1977; Lansdowne and Hacker, 1975; Reisen *et al.*, 1979; Schlosser and Buffington, 1977; Suleman and Reisen, 1979; Walter and Hacker, 1974) have been studied experimentally. In analytical studies on survival and reproduction of mosquitoes, only a few laboratory studies have been made on populations with overlapping generations.

Tsuda *et al.* (1991) reported the population cage for reproducing a laboratory population of mosquitoes. Using the population cage, we can observe the long-term trend of population growth and estimate several population parameters of mosquitoes under

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an artificially controlled environment. Tsuda *et al.* (1992) investigated growth patterns of *Aedes albopictus* populations for 10 weeks under 4 different environmental conditions: permutations of 2 intervals of blood feeding and 2 amounts of larval food. Their experiments focused on the initial phase of population growth, and no experimental studies have been made on a long-term growth pattern of *Ae. albopictus* population.

The present paper shows the long-term results of population cage studies on two strains of *Ae. albopictus* originated from Nagasaki, Japan and Chiangmai, Thailand and discusses the observed differences in their population characteristics.

Materials and Methods

The population cage used in the experiment was the same as that in Tsuda *et al.* (1991, 1992). It was composed of a cubic cage (40×40×40 cm) for adults and two ovi-cups as breeding sites. A white polyethylene bottle (250 ml in volume, 6.5 cm in diameter) was fixed as an ovi-cup to a corner of the cubic cage and connected with a vinyl tube (1.6 cm in diameter, 50 cm long) to another polyethylene bottle outside of the cubic cage. Each ovi-cup contained 300 ml of water, which was renewed every week with other contents such as larval feces, larval skins, eggs, and remaining larval food. The eggs in the water were counted and removed but those deposited on the wall of the ovi-cups were left as they were. Two glass tubes that had a cotton wick and were filled with a 3% sugar solution were inserted into small holes on the bottom of the cubic cage. A mouse was placed for 3 hr once a week under the bottom of the cubic cage as a blood source.

The populations were investigated 4 times a week as a rule. Pupae in ovi-cups were counted and kept in a pupal bottle until they emerged as adults. The pupal skins in the pupal bottle were collected and the width of the 8th abdominal segment was measured as the body size under a microscope. The newly emerging adults in the pupal bottle were counted by sex and added to the adult population. The dead adults were removed from the adult population and counted by sex. The total number of larvae were counted by instar once a week.

Two strains of *Aedes albopictus* (collected in Nagasaki, Japan and Chiangmai, Thailand) were used in the experiments. Nagasaki strain (NG) had been kept for 1 year under laboratory conditions of 27°C and 75% R.H. Chiangmai strain (CM) had been kept for 1 month under the same laboratory conditions. Five pairs of 7-day-old adults of each strain were introduced into the population cage as an initial population. All females were introduced into the population cage after they took a blood meal.

Two different food conditions for larvae, rich (12.5 mg/week) and poor (6.25 mg/week), were adopted in the experiments. A powdered mouse pellet was used as larval food. The growth patterns of experimental populations under rich and poor larval food conditions were investigated for 350 days. The population cages were kept under the laboratory conditions of 27°C, 75% R.H. and 16L:8D.

Results and Discussion

The introduced populations could not survive under the poor larval food condition. The population of Nagasaki strain (NG) became extinct at 214 days after introduction, whereas that of Chiangmai strain (CM) did at 70 days. After extinction of the CM population, 5 pairs of adults were introduced again into the population cage as the second experimental population. The second population became extinct at 49 days. The average values of the two extinct CM populations were calculated and compared in the following analysis of population characteristics. When populations were allowed to reproduce under the rich larval food condition, the populations of both strains survived throughout the experiment. These results suggest that the combination of 12.5 mg of larval food per week and 1 week interval of blood feeding is a necessary conditions for

the survival of *Ae. albopictus* populations of both strains. The rapid extinction of CM population suggests different responses between the two strains of larvae to food shortage.

Figure 1 shows temporal changes in the number of immatures observed in NG and CM populations under the rich larval food condition. The numbers of immatures in the two ovi-cups were summed up and plotted, since the numbers of immatures observed in them showed similar patterns of temporal changes. Large fluctuations were observed in both populations. CM population (solid line) increased gradually with large fluctuations during the first 250 days and then fluctuated between 100 and 250 in density. NG population (dotted line) showed a rapid increase and achieved a high density of 225 at 77th day of the experiment, then decreased to the lower density level of around 50 and then increased again from 150th to 200th days. Thereafter, the population showed densities between 120 and 250. The different growth patterns observed in the initial phase of population growth suggest a higher growth rate of increase and different response of larvae to the crowding condition in NG population.

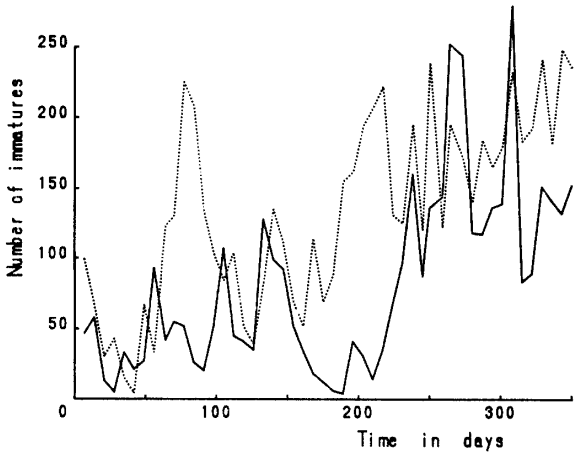

Fig. 1 Temporal changes in the number of immature *Ae. albopictus* observed in NG (dotted line) and CM (solid line) populations under the condition of rich larval food.

The average density and the age composition (percentage of average density) of larval population are shown in Table 1. The average total number of larvae was higher in populations reproducing under the rich larval food condition ($p<0.05$, Turkey-Kramer Method, Sokal and Rohlf, 1981). The differences between NG and CM populations in the average number of 1st and 2nd instar larvae and the average total number of larvae were significant in the rich larval food condition. The age distributions of the 4 populations were significantly different ($p<0.05$, Kolmogorov-Smirnov Two-Sample Test, Sokal and Rohlf, 1981) and the relative frequencies of 1st instar larva under the poor larval food condition were higher than those under the rich larval food condition. The lower proportions of mature larvae in the poor larval food condition may be ascribed to the higher mortality of developing larvae

Table 1 Comparison of average density (±S.D.) and age composition (in parenthesis) of larval populations (pupae inclusive) of *Aedes albopictus* under two larval food conditions.

Stage	CM population		NG population	
	6.25 mg	12.5 mg	6.25 mg	12.5 mg
Pupa	$0.4^{b}\pm 0.75$ (2)	$2.9^{a}\pm 1.99$ (4)	$0.5^{b}\pm 0.86$ (2)	$2.4^{a}\pm 2.04$ (2)
4th	$1.5^{b}\pm 2.82$ (8)	$16.4^{a}\pm 16.59$ (20)	$2.3^{b}\pm 2.96$ (12)	$19.2^{a}\pm 23.13$ (14)
3rd	$1.1^{b}\pm 2.00$ (6)	$13.3^{a}\pm 13.53$ (16)	$2.3^{b}\pm 3.62$ (12)	$17.6^{a}\pm 12.66$ (13)
2nd	$1.8^{c}\pm 3.55$ (10)	$18.7^{b}\pm 20.71$ (23)	$2.5^{c}\pm 3.03$ (14)	$36.0^{a}\pm 24.68$ (27)
1st	$13.6^{b}\pm 30.98$ (74)	$29.9^{b}\pm 37.90$ (37)	$14.7^{b}\pm 26.51$ (60)	$58.7^{a}\pm 48.16$ (44)
Total	$18.3^{c}\pm 33.83$	$81.2^{b}\pm 65.16$	$22.3^{c}\pm 28.47$	$134.0^{a}\pm 67.22$

Means in the same row followed by the same letter are not significantly different at 5% level (Turkey-Kramer Method, Sokal and Rohlf, 1981).

Table 2 Comparison of average size (mm, ±S.D.) and mortality rate of pupae.

	CM populations		NG populations	
	6.25 mg	12.5 mg	6.25 mg	12.5 mg
Size of pupae (♀)	$0.80^{a}\pm0.075$	$0.81^{a}\pm0.062$	$0.80^{a}\pm0.065$	$0.75^{b}\pm0.071$
(♂)	$0.73^{a}\pm0.052$	$0.73^{a}\pm0.049$	$0.71^{ab}\pm0.066$	$0.69^{b}\pm0.052$
Pupal mortality rate (%)	11.8	7.2	23.0	2.5

Means in the same row followed by the same letter are not significantly different at 5% level (Turkey-Kramer Method, Sokal and Rohlf, 1981).

caused by a severe competition for food.

The average body size of pupae and mortality rate in the pupal stage are calculated in Table 2. The female pupae produced in NG population under the rich larval food condition were significantly smaller than those in other populations ($p < 0.05$, Turkey-Kramer Method, Sokal and Rohlf, 1981). The male pupae in NG population were significantly smaller than those in CM population under the rich larval food condition. Lower mortality rates in the pupal stage were observed in populations reproduced under the rich larval food condition. As shown by Mori (1979), the higher larval density in NG population is the main reason for the observed differences in pupal body size between NG and CM populations.

The accumulated numbers of emerging adults observed in NG and CM populations under the rich larval food condition are shown in Fig. 2. The number of females increased linearly at a constant rate in both populations, and the daily increase rates were 0.543 and 0.551 females/day in NG and CM populations, respectively. In the case of males, the accumulated number increased at nearly the same rate as that of females at the beginning of the experiment, but it increased at a higher rate than that of females from 150 and 200 days of the experiment in NG and CM populations, respectively. Because the larval density became higher in the last 100 days of the experiment in both NG and CM populations (Fig. 1), it is suggested that the crowded larval density produced a higher rate of increase in number in males than females.

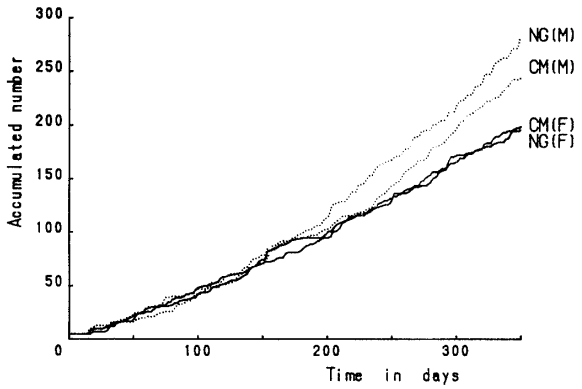

Fig. 2 The accumulated number of emerging females (solid line) and males (dotted line) produced from NG and CM populations under the condition of rich larval food.
M, males; F, females.

NG population produced more adults than CM population under the poor larval food condition, whereas nearly the same total number of females were produced in NG and CM population under the rich larval food condition (Table 3). To obtain the average density and longevity of females, the total number of existing females throughout the experiment was calculated. The total number of existing females was divided by the length of experimental period to get the average density of females/day. NG population achieved a higher average female density of 20.5/day than CM population (13.2/day) under the rich larval food condition. Dividing the total number of existing females by the total number of produced females, the average longevity of females were estimated. Females produced in NG populations showed the longer longevity of 38.4 days than those in CM population (24.4 days)

Table 3 Comparison of total number of adults, average densities of females per day, average number of blood meals per female, and average longevity of females.

	CM populations		NG populations	
	6.25 mg	12.5 mg	6.25 mg	12.5 mg
Number of adults produced (♀)	8	193	18	190
(♂)	7	232	29	276
Average density of females/day	3.1	13.2	4.2	20.5
Average longevity of females in days	12.3	24.4	24.7	38.4
Average number of blood meals per female	0.67	1.17	1.17	1.52

Table 4 Comparison of total number of eggs found in water, engorged females, and average number of eggs per engorged female.

	CM populations		NG populations	
	6.25 mg	12.5 mg	6.25 mg	12.5 mg
Total number of eggs in water	490	5,445	843	8,684
Total number of engorged females	10	231	26	293
Average number of eggs/engorged female	123	59	98	90

under the rich larval food condition.

The average number of blood meals per female in Table 3 was estimated by dividing the total number of engorged females by the total number of produced females in each population. Females had 1.17 and 1.52 blood meals on the average in CM and NG populations under the rich larval food condition, respectively.

The total numbers of eggs found in water are shown in Table 4. More eggs were counted in NG populations than in CM populations. The average number of eggs per engorged females was estimated as follows. The proportions of eggs laid on the water surface were estimated as 40.0 and 33.0% in CM and NG strains, respectively (Tsuda *et al.* unpublished). The total number of eggs found in water was divided by these proportions to obtain the total number of all eggs in water and on the wall. Then the average number of eggs per engorged female was estimated by dividing the total number of all eggs by the total number of engorged females. The estimated number of eggs per engorged female in NG population (90 eggs) was larger than that in CM population (59 eggs) under the rich larval food condition.

Figure 3 shows temporal changes in total number of females in NG and CM populations under the rich larval food condition. In both populations two types of fluctuations were noted; small fluctuations occurred within a 50-day period and large fluctuations occurred within a cycle of more than 50 days. A clear difference in the level of female density was observed between NG and CM populations throughout the experiment. The number of females in NG population reached the density of 20 females at the 54th day and thereafter fluctuated around this level. On the other hand, the female density of CM population increased gradually with small fluctuations during the first 100 days and then fluctuated around the density level of 13 females.

The rapid increase of larval and adult NG populations observed in the beginning of experiment clearly suggested a higher rate of

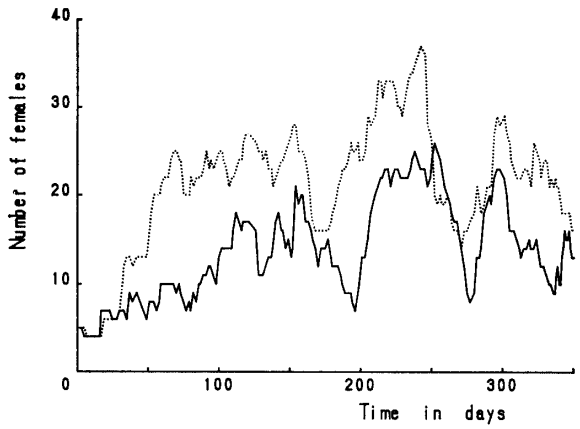

Fig. 3 Temporal changes in the total number of females in NG (dotted line) and CM (solid line) populations under the condition of rich larval food.

population increase in NG population than in CM population under the rich larval food condition. The rate of population increase is determined by the balance between birth and death rates. The results in Tables 3 and 4 showed that females in NG population had more blood meals and produced more eggs than those in CM population. Therefore, the higher birth rate was expected in NG population than in CM population. The daily emergence rate of females in NG population under the rich larval food condition was nearly the same as that in CM population, but the average longevity of females of NG population was 1.57 times longer than that of CM population. This large difference in longevity of females was the main reason for the higher female density of NG population (Fig. 3).

We can summarize the population characteristics of Nagasaki (NG) and Chiangmai (CM) strains as follows: NG population has a higher rate of population increase, achieves higher density of larvae and adults, and produces smaller females having longer longevity and higher fecundity than CM population. The present study suggests the different response of larvae to crowding and food shortage and the differences in life historical characteristics of females between the two strains. Although the differences in ecological characteristics of *Ae. albopictus* among different geographic strains have been reported with respect to cold hardiness (Hawley *et al.*, 1989), competitive ability (Black *et al.*, 1989; Ho *et al.*, 1989), and oviposition pattern and hatch rate (Mogi, 1982), more analytical and comparative studies on population characteristics such as larval competition for food and reproductive capacity of adults will be needed to understand the geographic distribution and abundance of *Ae. albopictus*.

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摘　要

ヒトスジシマカの個体群増殖に関する実験：長崎系統とチェンマイ（タイ）系統の比較

長崎およびタイ国チェンマイから得られたヒトスジシマカの2系統を用いて，実験個体群の増殖過程を350日間調べた．ポピュレーションケージを用いて二つの異なる幼虫の餌量条件下で個体群を増殖させ，初期個体群導入後の齢構成と幼虫および成虫密度の時間的変化を調査した．幼虫餌量が少ない実験条件下では両系統の個体群とも存続できず，長崎系統は実験開始後214日，チェンマイ系統は49日および70日で絶滅した．幼虫餌量の多い実験条件下では，両系統の個体群とも増加減少を繰り返した．両系統の個体群の性質には違いがみられ，長崎系統はチェンマイ系統に比較して増殖率が高く，達成された密度も高かった．また，長崎系統の雌成虫のほうが体は小さいが，長命で多産であった．