A study comparing the growth rates of two related species, *Aedes albopictus* and *Aedes flavopictus* (Diptera: Culicidae) at different temperature regimes

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Abstract: *Aedes albopictus* has originated in Asia and expanded its range worldwide in the last 30 years. In Japan, this species occurs from the Ryukyu islands to Tohoku district, whereas its sibling species *Ae. flavopictus* is distributed throughout Japan including Hokkaido. On the other hand, the former mainly inhabits residential areas, while the latter does natural environments such as bamboo groves and forests. To understand how they differ in habitat use, their performance was compared under various temperature regimes, i.e., constant temperatures of 22, 25 and 28°C and a fluctuating temperature regime of 20–30°C (mean: 25°C). Mortality from the first instar stage to adult emergence was significantly higher in *Ae. flavopictus* than in *Ae. albopictus* at constant temperatures of 25 and 28°C. Development time was significantly longer in *Ae. flavopictus* than in *Ae. albopictus* at 28°C. The proportion of females that did not oviposit was significantly higher in *Ae. flavopictus* at a constant temperatures of 28°C and a fluctuating temperature regime. Thus, *Ae. albopictus* is at least more adapted to higher or fluctuating temperatures than *Ae. flavopictus*. Such difference in their temperature adaptation may be one of factors that cause their different geographic distribution and habitat use.

Key words: geographic distributions, habitats, life history traits, population growth rate

Introduction

Recent global warming shows significant effects on changes in the distribution of mosquitoes and mosquito-borne disease. The Asian tiger mosquito *Aedes (Stegomyia) albopictus* (Skuse) (Diptera: Culicidae) is a competent vector of various diseases such as dengue fever, Zika or chikungunya (Mekuria and Hyatt, 1995; Delatte et al., 2009). This species has originated in Asia and expanded its range worldwide in the last 30 years (Hawley, 1988; Proestos et al., 2015). *Aedes albopictus* was introduced in Texas in the 1980s (Hawley, 1988) and have expanded its distribution over southern North America (Hobbs et al., 1991; Mekuria and Hyatt, 1995), replacing *Ae. aegypti*, which presents in the South East United States for more than 100 years before the arrival of *Ae. albopictus* (Christophers, 1960; Lounibos, 2002). Regional photoperiod and temperature regimes may limit the distributions of the two mosquitoes (Hawley, 1988), and the degree of urbanization (Chan et al., 1971) or vegetation/detritus type (Murrell and Juliano, 2008) or species exclusion being caused by reproductive interference (Kuno, 1992) may affect the outcome of interspecific competition where they are sympatric.

In Japan, we have six species belonging to the subgenus *Stegomyia*. Among them, *Aedes flavopictus* most overlaps with *Ae. albopictus* in their distribution. The latter is distributed in Japan with the current northern boundary of Tohoku district (Kobayashi et al., 2002; Mogi and Tuno, 2014), while the former occurs throughout Japan including Hokkaido and also in Korea (Tanaka et al., 1979). In addition, the former mainly inhabits residential areas, whereas the latter in natural environments such as bamboo groves and forests (Tanaka et al., 1979; Sota et al., 1992; Chaves, 2016). Although these two species have overlapping geographic distributions in Japan, their finer scale distributions do not, and unlike *Ae. albopictus*, *Ae. flavopictus* does not expand its distribution worldwide. It has not been investigated what causes the difference in their fine-scale distribution and geographic expansion.

In this study, we explored effects of temperature on their development and reproduction to understand how they differ in habitat use. Temperature has profound effects on mortality, fecundity and life history traits of mosquitoes as well as other insects and animals (Siddiqui et al., 1976; Reisen et al., 1984;
raise new generations. Mosquitoes of generations were offered with human blood meal to gain eggs to solution in the same incubators. Five day-old adults were kept in cages with free access of 3% sucrose development was monitored every day to determine with the progress of developmental stages. Larval removed. The quantity of food supplied was increased every two days. If dead larvae were found, they were change in mid-July in Kanazawa City. approximately represents the average temperature of eggs produced, under 14L/10D photoperiod conditions. The temperatures of 22°C, 25°C, and 28°C (25°C in mean; hereafter, expressed as 25 var.) 25 and 28°C and a fluctuating temperature regime of 20–30°C (25°C in mean; hereafter, expressed as 25 var.) on life-history traits, i.e., preimaginal development time (the first instar stage to adult emergence) and mortality, length of gonotrophic cycle, and the number of eggs produced, under 14L/10D photoperiod conditions. The temperatures of 22°C, 25°C, and 28°C represents as the average temperatures in late June, mid-July, and early August (the hottest season of the year), respectively in Kanazawa city (data from https://www.jma-net.go.jp/kanazawa/). The temperature conditions of “25 var.” was as follows; 8 h at 20°C, 4 h at 25°C, 8 h at 30°C, and 4 h at 25°C. This regime approximately represents the average temperature change in mid-July in Kanazawa City. Twenty first-instar larvae were introduced in a plastic cup (8 cm in diameter, 4 cm in depth) containing 50 mL of chlorine-free water and foods (TetraMin® fish food). Rearing water was renewed every two days. If dead larvae were found, they were removed. The quantity of food supplied was increased with the progress of developmental stages. Larval development was monitored every day to determine preimaginal development time and mortality. Five replicates were prepared for each temperature treatment (sample size was 100 larvae in respective treatment).

When larvae pupated, they were isolated in vials until emergence. When adults emerged, they were placed in one cage within 24 h after emergence. These pupae and adults were kept under the same conditions as larvae; i.e., 22°C, 25°C, 28°C or 25 var. under 14L/10D photoperiod conditions. Adults were allowed to access 3% sucrose solution freely. Five to seven days after emergence, they were provided with human blood meal. After blood feeding, engorged females were individually kept in plastic vials (3 cm diameter, 6 cm height) covered by mesh, on which a clump of cotton soaked with 3% sucrose solution was placed to serve as adult energy source. A clump of wet cotton covered by a piece of filter paper was placed on the bottom of vials to serve as oviposition substrate. They were monitored for oviposition to determine the length of the first gonotrophic cycle (i.e., a period from the first blood meal to the first oviposition) and the number of eggs oviposited for seven days. The oviposited eggs were submerged in dechlorinated tap water to determine the hatching rate. We kept water level constant (1 cm depth) and monitored the number of hatched eggs for three weeks. If females did not oviposit in seven days after the first blood meal, they were provided with the second blood meal and monitored for oviposition another seven days. All emergent individuals were measured one of their wing length (from the distal end of the axial inclusion to the apical margin not including the fringe) under a stereomicroscope when they were dead or at the end of the experiment (seven days after taking the second blood meal).

Data analysis

Effects of the temperature regime on mortality and proportion of egg-laying females were analyzed using logistic regression. The difference of mortality and proportion of egg-laying females between Ae. albopictus and Ae. flavopictus was compared by Fisher’s exact test. Effects of temperature regime on development time, wing size and viable egg production were analyzed ANCOVA, ANOVA or by Steel-Dwass test. Statistical analyses were performed with JMP 11.2.1 (SAS institute, Cary, North Carolina).

Results

Preimaginal mortality

Logistic regression analysis revealed that temperature, species and interaction of temperature and species had significant effects on the preimaginal mortality (Table 1). The preimaginal mortality (i.e., mortality from the first instar stage to adult emergence) was significantly higher in Ae. flavopictus
than in *Ae. albopictus* at constant temperatures of 25°C and 28°C (Fisher’s exact test, *P*=0.032, *P*<0.0001, respectively) (Table 1).

### Developmental time and wing size

ANOVA was performed using temperature, species and interaction of temperature and species as explanatory variables and developmental time and wing size as response variables. The results showed that all variables had significant effects (*P*<0.001 for temperature; *P*=0.041 for species; *P*=0.023 for the interaction term). According to ANOVA using temperature regime and sex as explanatory variables, the effect of sex was significant (*P*<0.001). Therefore, the effect of temperature regime and species was analyzed separately for females and males. Development time was significantly shorter in *Ae. albopictus* than in *Ae. flavopictus* at 28°C in both females and males (ANOVA, *P*<0.001, Table 2), while there was no significant difference between them in the other temperature regimes (ANOVA, *P*>0.05, Table 2). Within species, it was significantly shorter at higher average temperatures in both species (Steel–Dwass test, *P*<0.05, Table 2A), except *Ae. albopictus* males in which no significant difference was observed between 22 and 28°C (Steel–Dwass test, *P*>0.05).

In the case of wing size, not only the effects of temperature regime, species and sex but also interactions between these factors were significant (ANOVA, *P*<0.05). Wing size was larger in females than in males, in *Ae. flavopictus* than in *Ae. albopictus*, and at lower temperatures (Table 2B).

### Reproduction

Females were first monitored for oviposition for

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**Table 1.** Preimaginal mortality (%) of *Aedes albopictus* (albo) and *Ae. flavopictus* (flavo) with result of logistic regression analysis and pairwise comparisons (Fisher’s exact test) under same conditions on mortality.

| Rearing temperature (°C) | Albo | Flavo | *P* (Fisher’s exact test) |
|--------------------------|------|-------|--------------------------|
| 22                       | 12   | 21    | 0.127                    |
| 25                       | 5    | 15    | 0.032                    |
| 28                       | 0    | 26    | <0.0001                  |
| 25 var.                  | 1    | 7     | 0.065                    |

**Table 2.** Developmental time from the first instar stage to adult emergence (2A) and wing size (2B) of *Ae. albopictus* and *Ae. flavopictus* at different rearing temperature regimes with summary of ANOVA and pairwise test results (Steel–Dwass test or Tukey–Kramer honestly significant difference test).

#### 2A. Developing time (day)

| Rearing temperature (°C) | n | Mean | SE | SDT* | n | Mean | SE | SDT* |
|--------------------------|---|------|----|------|---|------|----|------|
| Female ANOVA:            |   |      |    |      |   |      |    |      |
| 22                       | 39 | 14.0 | 0.16| a    | 45 | 13.9 | 0.21| a    |
| 25                       | 38 | 10.2 | 0.16| b    | 37 | 10.1 | 0.23| b    |
| 28                       | 50 | 8.7  | 0.14| c    | 37 | 9.6  | 0.23| c    |
| 25 var.                  | 40 | 10.8 | 0.16| b    | 46 | 10.7 | 0.21| b    |
| Male ANOVA:              |   |      |    |      |   |      |    |      |
| 22                       | 49 | 13.12| 0.14| a    | 34 | 13.5 | 0.24| a    |
| 25                       | 57 | 9.89 | 0.13| b    | 48 | 9.6  | 0.20| b    |
| 28                       | 50 | 8.16 | 0.14| c    | 37 | 9.2  | 0.23| b    |
| 25 var.                  | 59 | 9.92 | 0.13| b    | 47 | 9.7  | 0.20| b    |

#### 2B. Wing size (mm)

| Rearing temperature (°C) | n | Mean | SE | HSD test* | n | Mean | SE | HSD test* |
|--------------------------|---|------|----|-----------|---|------|----|-----------|
| Female ANOVA:            |   |      |    |           |   |      |    |           |
| 22                       | 39 | 3.12 | 0.03| a         | 45 | 3.65 | 0.02| a         |
| 25                       | 38 | 2.91 | 0.03| b         | 37 | 3.38 | 0.03| b         |
| 28                       | 50 | 2.85 | 0.02| b         | 37 | 2.95 | 0.03| c         |
| 25 var.                  | 40 | 3.08 | 0.03| a         | 46 | 3.22 | 0.02| d         |
| Male ANOVA:              |   |      |    |           |   |      |    |           |
| 22                       | 49 | 2.58 | 0.02| a         | 34 | 2.76 | 0.02| a         |
| 25                       | 57 | 2.48 | 0.02| b         | 48 | 2.77 | 0.02| a         |
| 28                       | 50 | 2.18 | 0.02| c         | 35 | 2.40 | 0.02| b         |
| 25 var.                  | 59 | 2.52 | 0.02| ab        | 47 | 2.54 | 0.02| c         |

* SDT: Steel–Dwass Test, HSD test: Tukey–Kramer honestly significant difference test (different letters indicate significant difference (*P*<0.05)).
7 days after the first blood meal. If females did not oviposit, they were supplied with the second blood meal and monitored for oviposition for another 7 days. A number of females did not lay eggs even after the second blood meal in both species but the number was variable between the treatment groups. We decided to analyze only about the first blood meal to keep even sample size in all the treatment groups. Therefore, data after the second blood meal are not shown here. Logistic analysis found that the proportion of ovipositing females was affected by temperature regime and species (Table 3). The proportion of ovipositing females did not differ between *Ae. albopictus* and *Ae. flavopictus* at constant temperatures of 22°C and 25°C (Fisher’s exact test, *P* > 0.05), but was significantly lower in *Ae. flavopictus* at a constant temperature of 28°C and fluctuating temperature regime (25var.) (Fisher’s exact test, *P* < 0.005) (Table 3).

In *Ae. albopictus*, the number of hatched eggs laid after the first blood meal was significantly higher at a constant temperature of 25°C than at a constant temperature of 22°C, while there was no significant difference at the other temperature regimes (Steel-Dwass test, *P* < 0.05) (Table 4). In *Ae. flavopictus*, on the other hand, it was significantly higher at a constant temperature of 25°C than at a constant temperature of 22°C, while it was significantly lower at a constant temperature of 28°C or under a fluctuating temperature regime of 25var. (Steel-Dwass test, *P* < 0.005) (Table 4).

In interspecific comparisons at different temperature regimes, the number of hatched eggs was higher in *Ae. albopictus* than in *Ae. flavopictus* at a constant temperature of 28°C and at 25var. (Wilcoxon test, *P* < 0.001) (Table 4), whereas there was no significant interspecific difference at constant temperatures of 22°C and 25°C (Wilcoxon test, *P* > 0.05) (Table 4). The number of eggs laid after the second blood meal considerably varied, and some individuals did not lay any eggs even after second blood meal (data not shown). One week after of the second blood meal supply we dissected non-ovipositing females and found that they hold a mixture of mature and immature eggs in their ovaries (data not shown). However, the number of non-ovipositing females was not sufficient for statistical analysis and was not analyzed.

**Discussion**

The present study revealed that *Ae. flavopictus* was less adapted to higher temperatures than *Ae. albopictus*. Mortality from the first instar stage to adult emergence was significantly higher in *Ae. flavopictus* than in *Ae. albopictus* at constant temperatures of

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**Table 3.** Proportion of females that laid eggs after the first blood meal in *Ae. albopictus* (albo) and *Ae. flavopictus* (flavo) at different rearing temperature regimes with summary of logistic analysis.

| Factor                  | df | Likelihood ratio test | *P*  |
|-------------------------|----|-----------------------|------|
| Temperature             | 3  | 36.55                 | <.0001|
| Species                 | 1  | 6.92                  | 0.0085|
| Species × Temperature   | 3  | 4.74                  | 0.1919|

Ratio of females that laid eggs after the first blood meal.

*Interspecific comparison between the two species, NS means "not significant".*

**Table 4.** Average number of hatched eggs per female in *Ae. albopictus* (albo) and *Ae. flavopictus* (flavo) at different temperature regimes with pairwise comparisons (Steel-Dwass test or Wilcoxon test).

| Temperature regime (°C) | Albo          | Flavo         | Wilcoxon test | *P*  |
|-------------------------|---------------|---------------|---------------|------|
| Mean±S.E.               | N Female      | Mean±S.E.     | N Female      |      |
| 22                      | 15.8±6.8 a    | 20.9±5.3 a    | 26            | NS  |
| 25                      | 30.4±5.1 b    | 27.1±4.6 b    | 24            | NS  |
| 28                      | 21.2±3.9 ab   | 4.9±3.9 c     | 27            | 0.0005|
| 25 var.                 | 23.8±3.8 ab   | 0.9±3.6 c     | 31            | <0.0001|

1 Different letters indicate significant difference (*P* < 0.05) (Steel-Dwass test).

2 Interspecific comparison between the two species, NS means "not significant".
25°C and 28°C. In addition, development time was significantly longer in *Ae. flavopictus* than in *Ae. albopictus* at 28°C. Moreover, the proportion of females that did not oviposit with one blood meal was significantly higher in *Ae. flavopictus* at a constant temperature of 28°C and a fluctuating temperature of 25°C. In the latter regime, the mean temperature was 25°C, but a temperature of 30°C and 20°C lasted for 8 hours, respectively. *Aedes flavopictus* may suffer the high temperature of 30°C, in 25°C. These differences in their temperature adaptation are considered to reflect in their habitat use; *i.e.*, *Ae. albopictus* abundantly occurs in hotter environments (*i.e.*, residential areas), but *Ae. flavopictus* does not (Sota et al., 1992; Chaves, 2016).

Interestingly, both species stopped to lay eggs at higher temperature regimes despite they have matured eggs in their ovaries, and more *Ae. flavopictus* did so than *Ae. albopictus*. We reported that wild-collected *Ae. albopictus* stopped laying eggs or laid empty eggs without yolk in very hot summer (Alam and Tuno, 2019). When they were supplied with blood meals twice or three times, they laid a small number of eggs, but these eggs did not hatch (Alam and Tuno, 2019). We suggested that *Ae. albopictus* avoided reproduction in unfavorable environments. In general, there are trade-offs between reproduction and survival time (Stearns, 1989), and therefore restraining reproduction may prolong survival time and ensure animals to wait for the arrival of favorable season for their reproduction. In our study, both sexes of *Ae. flavopictus* are always larger than *Ae. albopictus* when reared at the same temperature regimes. Larger individuals are expected to have large amount of energy reserves. It is not confirmed in this experiment, but *Ae. flavopictus* individuals may be able to survive longer so that they may be more likely to stop reproduction than *Ae. albopictus* at higher temperature regimes. This study revealed that *Ae. flavopictus* has a low survival rate at high temperatures, and therefore they may have more tendency to stop laying eggs at high temperatures, taking advantage of their large body size. *Aedes albopictus* laid a larger number of viable eggs than *Ae. flavopictus* at higher temperature regimes those represent the hottest season, July and August, in Ishikawa. In our observation, the relative frequency of *Ae. flavopictus* to *Ae. albopictus* was high in May and June, decreased in July and August, and increased again in autumn (Alam and Tuno unpublished data). The difference in temperature tolerances of the two species may explain the difference in their habitat use and seasonal changes in abundance. We are also examining why the two species continue to coexist in Japan from other aspects, larval and adult food preferences, interspecific interference, *etc*. Those will be reported in elsewhere.

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