Effects of temperature and larval diet on development rates and survival of the dengue vector Aedes Aegypti in North Queensland, Australia

Article *in* Medical and Veterinary Entomology · April 2000

DOI: 10.1046/j.1365-2915.2000.00207.x · Source: PubMed

3 authors, including:

Thomas R Burkot
James Cook University
233 PUBLICATIONS **11,740** CITATIONS

Medical and Veterinary Entomology (2000) **14**, 31–37

Effects of temperature and larval diet on development rates and survival of the dengue vector *Aedes aegypti* in north Queensland, Australia

W. TUN-LIN[1], T. R. BURKOT[2] and B. H. KAY

The Queensland Institute of Medical Research and The University of Queensland, Tropical Health Program, P.O. Royal Brisbane Hospital, Queensland, Australia

Abstract. Immature development times, survival rates and adult size (wing-lengths) of the mosquito *Aedes aegypti* (L.) (Diptera: Culicidae) were studied in the laboratory at temperatures of 10–40°C. The duration of development from egg eclosion (hatching of the first instar) to adult was inversely related to temperature, ranging from 7.2 ± 0.2 days at 35°C to 39.7 ± 2.3 days at 15°C. The minimum temperature threshold for development (t) was determined as 8.3 ± 3.6°C and the thermal constant (K) was 181.2 ± 36.1 day-degrees above the threshold. Maximum survival rates of 88–93% were obtained between 20 and 30°C. Wing-length was inversely related to temperature. The sex ratio (♀:♂) was 1 : 1 at all temperatures tested (15, 20, 25 and 35°C) except 30°C (4 : 3).

Under field conditions at Townsville and Charters Towers, north Queensland, the duration of immature development varied according to the container position (i.e. shaded or exposed) and the availability of food resources, as well as inversely with temperature. These data indicate that containers with an abundance of organic matter (e.g. those used for striking plant cuttings) or those amongst foliage or under trees (e.g. discarded plastic tubs and tyres) tended to produce the largest adult *Ae. aegypti*, which had faster development and better immature survival. As such progeny have been linked to a greater risk of dengue transmission, it would seem important to focus on control of such containers.

Key words. *Aedes aegypti*, dengue vector, development time, environmental effects, larval diet, survival rate, temperature, thermal constant, wing-length, Queensland, Australia.

Introduction

Queensland has a history of dengue virus transmission since 1879 (Lumley & Taylor, 1943; Kay *et al.*, 1984; Murray-Smith *et al.*, 1996). Using an early colony of the dengue vector mosquito *Aedes aegypti* (L.) (formerly known as *Stegomyia fasciata* Fabricius) from Townsville, Fielding (1919) published notes on the oviposition, egg hatching, lethal temperature thresholds, larval and adult nutrition in relation to development and survival rates of this non-indigenous species. Subsequently, as a basis for further understanding the bionomics of *Ae. aegypti* in Queensland, data on this mosquito from other parts of the world have mainly been used (Bacot, 1916; Headlee, 1940, 1941, 1942; Bar-Zeev, 1958; Christophers, 1960; Southwood *et al.*, 1972). It is well known, however, that strains of *Ae. aegypti* differ geographically (Mattingly, 1957). For example, adaptation to temperature and other climatic variables may influence the mean development time, with a difference of 5 days recorded between *Ae. aegypti* from North Carolina (Rueda *et al.*, 1990) and from Israel (Bar-Zeev, 1958) when reared at 20°C.

Density-dependent factors and nutrition also influence the development time of *Ae. aegypti* (Christophers, 1960). Even

Correspondence: Dr B. H. Kay, Queensland Institute of Medical Research, PO Royal Brisbane Hospital, Queensland, 4029, Australia. E-mail: brianK@qimr.edu.au

[1]Present address: Medical Entomology Research Division, Department of Medical Research, 5 Ziwaka Road, Dagon P.O., Yangon, Myanmar.

[2]Present address: Centers for Disease Control, Division of Vector-borne, Infectious Diseases, PO Box 2087, Fort Collins, CO 80522-2087, U.S.A.

among the same brood, Hotchkin (1985) noted that the rate of development of larvae hatched by the second flooding of eggs was faster than those from the first hatch, and this was influenced by diet. Nasci (1986) suggested that environmental factors differentially affecting the developmental stages produced adult females of different sizes, the larger females having greater vector potential due to being more successful at seeking a second bloodmeal. Moreover, by modelling, Youdeowei & Service (1983) found that the effects of adult control could be offset by reduced density-dependent larval mortality in the next generation.

To overcome the confounding factors, which may limit the usefulness of laboratory generated life tables (e.g. Southwood *et al.*, 1972), we require locally generated data on the bionomics of *Ae. aegypti* in north Queensland, where a dengue problem still exists (Hanna *et al.*, 1998). During 1989–90, therefore, we investigated the rates of immature development and survival of *Ae. aegypti* at different temperatures; then we tested the fit of these data to various conditions in the field.

Materials and Methods

Laboratory studies

Eggs from a colony of *Ae. aegypti* (including some phenotypes of var. *queenslandensis* Theobald) from Thursday Island (10°35′S, 142°13′E), north Queensland, were hatched by flooding and first instars were pipetted into trays (17 × 12 × 6 cm) containing 500 ml distilled water. The starting density was 50 larvae/tray. Sets of four trays were placed in constant temperature incubators at 10–40°C (at 5°C intervals) with a photoperiod of LD 13 : 11 h. Larvae were fed a mixture of ground rabbit chow and liver extract powder (9 : 1 by weight) at rates of 0.2 mg per day for first and second instars and 0.5 mg per day for third and fourth instars, reduced to 0.5 mg per 2 days if the water approached putrifaction at 15 or 20°C.

Larval development was recorded three times daily (06.00, 12.00 and 18.00 hours) at 30, 35 and 40°C, but only once per day (12.00 hours) at 15, 20 and 25°C. At 10°C, development and survival was recorded weekly. Larval exuviae and cadavers were removed and counted. Mortality at each stage and the numbers of emerged adult males and females were recorded.

The frequency-dependent mean was used as an estimate of the mean duration of each instar. The threshold of development (t) and the thermal constant (K) and their standard errors were calculated (Campbell *et al.*, 1974).

From 20 males and 20 females emerged at each temperature, one wing was chosen randomly for measurement. Wing-length was measured from the axillary incision to the tip (excluding the fringe) using a micrometer eye piece.

Field studies

During February–April 1989 and May–August 1990, survival and development rates of immature *Ae. aegypti* were assessed under field conditions in north Queensland at coastal Townsville (19°15′S, 146°50′E) and at Charters Towers (20°05′S, 146°16′E), a provincial town 135 km inland. Using a newly established colony of *Ae. aegypti* from Townsville, freshly hatched larvae were pipetted into seven types of water container (50 larvae/container; 2–8 replicates/type). Each container was inspected daily and the number of each stage of *Ae. aegypti* were recorded.

Wild mosquito oviposition was excluded by placing netting over each container. Any detritus (e.g. leaves and drowned insects) that fell into the water was left to simulate the natural situation. Pupae of *Ae. aegypti* were transferred to 5 ml gauze-topped vials for emergence. Ten males and 10 females from each container were sampled for wing-length measurement as described above.

Mean (± standard deviation) development time, survival and wing-length ($n = 10$) of *Ae. aegypti* were calculated from each type of container and situation.

Daily temperature measurements in water were read daily at 08.00 hours using a maximum–minimum thermometer (Brannan Pty Ltd, U.K.) in one representative container for each situation.

Car tyres ($n = 4$) were placed in unshaded sites (two with water volume adjustment, two with no adjustment) and in shaded sites under trees (two with adjustment) and under a shed (two with adjustment) in Charters Towers. Four tyres were placed under the shade of a tree and two were exposed at Townsville, where each tyre had 2.5 l of tap water added. Three days post-flooding, the water was removed from each tyre, together with any naturally occurring mosquito larvae and their predators. The inner sides of each tyre were then cleaned with boiling water to kill any *Aedes* eggs that might have been present. The original water was replaced in each tyre and 50 newly hatched first stage *Ae. aegypti* larvae were added. In most tyres, the volume of water was maintained at 2.5 l. Water temperature in each tyre was recorded daily at 08.00 hours (similar to mean daily temperature), when the numbers of immature *Ae. aegypti* were counted.

Plastic containers ($n = 4$) of the type (capacity 1 litre), used for striking plant cuttings, were placed on an outdoors shaded ledge at Charters Towers. Water volume of 800 ml was maintained in two containers but not in two others.

Pot plant bases ($n = 8$), clay or plastic saucers, four in charters Towers and four in Townsville, each starting with 500 ml water, were placed on a covered verandah. The water volume was left unadjusted in two of those from Charters Towers.

Plastic ice-cream tubs ($n = 8$) each with 1.5 l of water; two in sunlit open space and two in a shed at Charters Towers and four under a tree in Townsville. Water volume was maintained at 1.5 l in each tub.

Metal drums ($n = 4$), capacity 200 l, were used for testing cohorts of 100 newly hatched larvae of *Ae. aegypti* . In two of these drums, floating mesh trays (15 × 9 × 6 cm) held the larvae for daily counting. In the other two drums, the larvae were left unrestrained until adult emergence. Adult emergence traps were fitted to these drums when pupae were evident.

Buckets ($n = 4$), capacity 8 l, contained 5 l of tap water and were placed in the open sunlight at Charters Towers. Larval counting was done daily in two buckets (adjusted volume),

whereas two were left undisturbed (unadjusted volume) until pupation occurred.

Rainwater tank (181 cm depth, 192 cm diam.) containing 4800 l of water, with two replicates of 50 larvae in floating mesh trays.

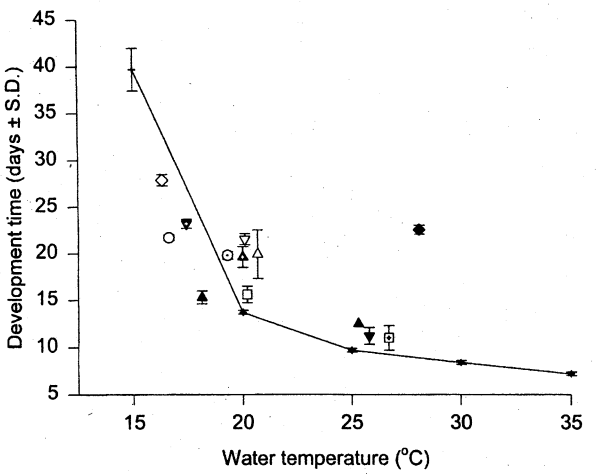
Results

Laboratory studies

Developmental time in relation to temperature. At all temperatures tested the second instar was quickest, while the first and fourth instars had significantly longer durations (Table 1, Fig. 1). Development time from first instar to adult was shortest (mean 7.2 ± 0.2 days) at 35°C and longest (mean 39.7 ± 2.3 days) at 15°C ($F = 704.98$, d.f. $= P < 0.01$). The rate of development (R = 1/total duration) increased with temperature ($F = 15.67$, d.f. $= 4$, $P < 0.05$), with development rates of R = 0.025, 0.073, 0.104, 0.119 and 0.140 at 15, 20, 25, 30 and 35°C, respectively, and $r = 0.97$, $P < 0.001$; $y = 0.00552x - 0.0458$. From the regression line plotted in Fig. 2, it followed that the minimum development threshold (t) was 8.3 ± 3.6°C and the thermal constant (K) was 181.2 ± 36.1 day-degrees above the threshold.

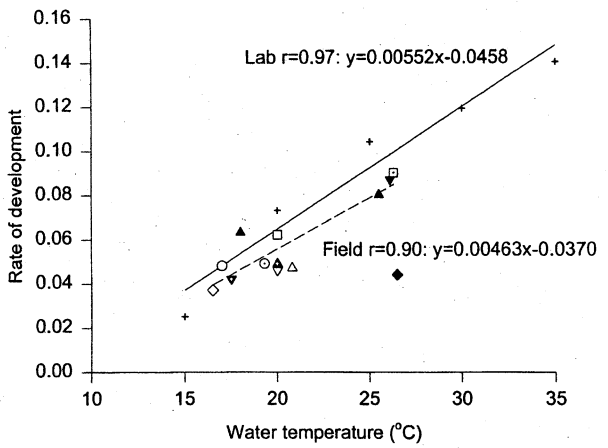
Table 1. Mean instar duration (days) and percentage survival of immature stages ($^n/_{50} \pm$ SD) of *Ae. aegypti* (Thursday Island strain) reared at different temperatures in the laboratory.

Temperature (°C)	Mean duration (± SD) of each stage					Total duration	Survival %
	1	2	3	4	*P*		
10	All first instars died within 4 weeks						0
15	8.7 ± 0.2	5.2 ± 0.6	7.3 ± 1.0	13.0 ± 4.1	4.0 ± 1.5	39.7 ± 2.3	23.5 (11.8 ± 1.0)
20	2.9 ± 0.6	1.4 ± 1.0	1.8 ± 0.1	4.1 ± 0.2	3.6 ± 0.3	13.7 ± 0.2	90.0 (45.0 ± 1.4)
25	2.1 ± 0.1	1.2 ± 0.1	0.9 ± 0.1	3.0 ± 0.3	2.5 ± 0.1	9.7 ± 0.2	88.0 (44.0 ± 1.4)
27	–	–	–	–	–	–	93.0 (46.7 ± 0.5)
30	2.4 ± 0.1	1.1 ± 0.1	1.0 ± 0.1	2.2 ± 0.2	1.7 ± 0.2	8.4 ± 0.2	88.0 (44.0 ± 2.7)
35	1.4 ± 0.1	1.0 ± 0.1	1.1 ± 0.1	2.4 ± 0.2	1.3 ± 0.2	7.2 ± 0.2	67.0 (33.5 ± 3.9)
40	All first instars died within 24 h						0



Habitat symbols: ◇pot plant bases,
○ striking containers, △ tyres, ▽ ice-cream tubs,
□ drums, ⊡ tanks, ⊙ buckets, ▲ tyres under trees,
▲ tyres under shed, ▼ ice-cream tubs under trees,
▼ ice-cream tubs under shed, ◆ pot plant bases on verandah
(open symbol = exposed site, closed symbol = covered site).

Fig. 1. Mean ± SD days of development time for *Ae. aegypti* (Townsville strain) first stage larvae to adult at different water temperatures under field conditions, compared to the laboratory data curve for the Thursday Island strain.



Habitat symbols: ◇pot plant bases,
○ striking containers, △ tyres, ▽ ice-cream tubs,
□ drums, ⊡ tanks, ⊙ buckets, ▲ tyres under trees,
▲ tyres under shed, ▼ ice-cream tubs under trees,
▼ ice-cream tubs under shed, ◆ pot plant bases on verandah
(open symbol = exposed site, closed symbol = covered site).

Fig. 2. Correlation of container water temperature and rate of development of *Ae. aegypti* (Townsville strain) immatures from field containers (excluding pot plant bases), compared to the laboratory data curve for Thursday Island strain.

Survival to adulthood was 88–93% at 20–30°C, but significantly reduced at 15°C (23.5%) and 35°C (67%) (Table 1, Fig. 3). At 10 and 40°C, all immatures died in the first instar, but this took up to 4 weeks at 10°C.

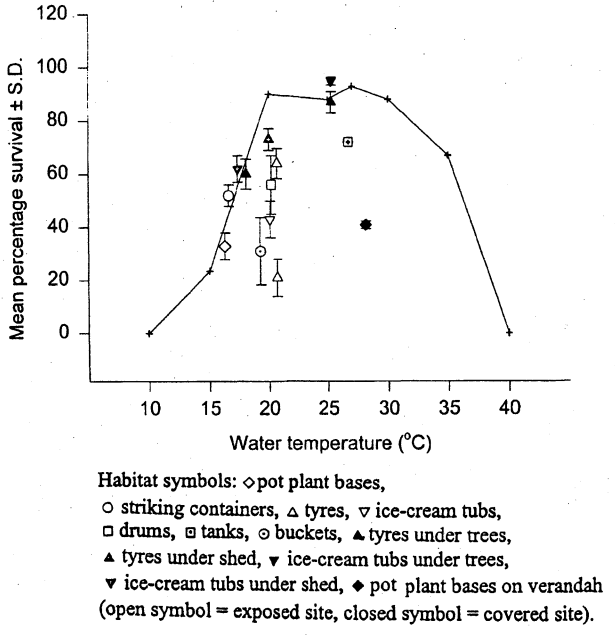


Fig. 3. Comparison of percentage survival ± SD of *Ae. aegypti* (Townsville strain) from first stage larvae to adulthood from field containers, compared to the laboratory survival curve for Thursday Island strain.

The sex ratio of newly emerged adults did not differ significantly from 1 : 1 for those reared at 15, 20, 25 and 35°C, but at 30°C significantly more females emerged than males, the ratio approximating 4 : 3, respectively ($\chi^2 = 4.14$; d.f. = 1; $P < 0.05$).

Wing-length of both sexes was inversely related to temperature ($F = 122.6$, d.f. = 4, $P < 0.001$), with the strongest correlation in the range 20–35°C (Fig. 4). The regression equation was $y = 3.91–0.04x$ ($r = 0.92$) for female wing-length and $y = 3.15–0.03x$ ($r = 0.93$) for male wing-length; not significantly different ($P < 0.001$). These equations indicate that for each degree rise in water temperature (over the range of 15–35°C), wing-length decreased by 0.04 mm for females and 0.03 mm for males. Adults reared at 20°C were the largest, with a wing-length averaging 3.26 ± 0.22 mm for females and 2.63 ± 0.18 mm for males. Despite the overall correlation, those actually reared at 15°C were slightly smaller: mean wing-lengths for females and males were 3.19 ± 0.09 mm and 2.54 ± 0.13 mm, respectively, but size differences between 15 and 20°C were not significant. The smallest adults were obtained at 35°C, with mean wing-lengths 2.43 ± 0.09 mm for females and 1.93 ± 0.09 mm for males.

Comparison between strains from Townsville and Thursday Island showed no consistently significant differences for any of the above parameters with batches reared in parallel (data not shown).

Field studies

Duration of development (Fig. 1, Table 2) varied by container position and hence water temperature. Duration

Table 2. Mean instar duration (days) and percentage survival of immature stages of *Ae. aegypti* reared at different temperatures at Charters Towers (CT) and Townsville (T).

Container type (no. examined)	Locality and date	Water temp. (± SD)	Mean duration (± SD) of each stage (days)					Total duration	Survival %
			1	2	3	4	P		
Car tyres									
exposed (4)	CT, May 1990	20.7 ± 2.9	3.4 ± 0.2	2.6 ± 0.2	3.3 ± 0.2	4.5 ± 1.2	6.1 ± 1.5	19.9 ± 2.6	63.8 ± 5.6
under trees (2)	CT, May 1990	18.1 ± 3.1	3.4 ± 0.1	2.2 ± 0.1	2.3 ± 0.1	3.0 ± 0.1	4.5 ± 0.6	15.3 ± 0.7	59.1 ± 5.6
under shed (2)	CT, May 1990	20.0 ± 4.1	3.0 ± 0.2	2.9 ± 0.2	4.5 ± 0.5	5.8 ± 0.9	3.4 ± 04	19.6 ± 1.0	73.2 ± 4.1
under trees (4)	T, Feb 1989	25.3 ± 1.0	3.0 ± 0.1	2.9 ± 0.2	1.5 ± 0.3	3.1 ± 0.1	1.8 ± 0.4	12.3 ± 0.0	87.0 ± 3.9
exposed	CT, May 1990	20.7 ± 2.9	–	–	–	–	–	–	21.0 ± 7.0
Plastic containers (4)	CT, May 1990	16.6 ± 2.6	9.9 ± 0.1			6.0 ± 0.3	5.7 ± 0.1	21.6 ± 0.2	51.7 ± 4.0
Pot plant bases									
exposed (4)	CT, May 1990	16.3 ± 2.7	10.7 ± 0.4			13.3 ± 0.5	3.9 ± 0.5	27.9 ± 0.6	32.7 ± 5.0
verandah (4)	T, Feb 1989	28.1 ± 1.0	3.8 ± 0.2	4.3 ± 0.2	4.5 ± 0.4	6.3 ± 0.6	3.5 ± 1.2	22.4 ± 0.5	41.0 ± 1.5
Ice-cream tubs									
exposed (2)	CT, May '90	20.1 ± 2.6	9.5 ± 0.1			6.5 ± 1.0	5.5 ± 0.2	21.5 ± 0.6	42.5 ± 7.1
under shed (2)	CT, May '90	17.4 ± 2.4	8.7 ± 1.2			9.3 ± 0.3	5.1 ± 2.0	23.2 ± 0.5	62.0 ± 5.0
under trees (4)	T, Feb '89	25.8 ± 1.0	3.3 ± 0.1	1.6 ± 0.1	1.6 ± 0.1	2.2 ± 0.5	2.7 ± 0.5	11.3 ± 1.1	95.0 ± 1.5
Metal drums									
exposed (4)	CT, May '90	20.2 ± 3.4	3.9 ± 0.0	2.6 ± 0.1	2.4 ± 0.2	3.6 ± 0.1	3.2 ± 0.7	15.6 ± 0.9	56.0 ± 11.0
Rainwater tank (2)	CT, May '90	26.7 ± 1.8	2.1 ± 0.0	1.7 ± 0.1	1.3 ± 0.2	2.9 ± 1.7	2.9 ± 0.6	11.0 ± 1.3	72.4 ± 4.2
Buckets open (4)	CT, May '90	19.3 ± 3.4	3.0 ± 0.1	1.5 ± 0.1	6.2 ± 0.5	5.5 ± 0.0	3.5 ± 0.1	19.8 ± 0.4	31.0 ± 12.7

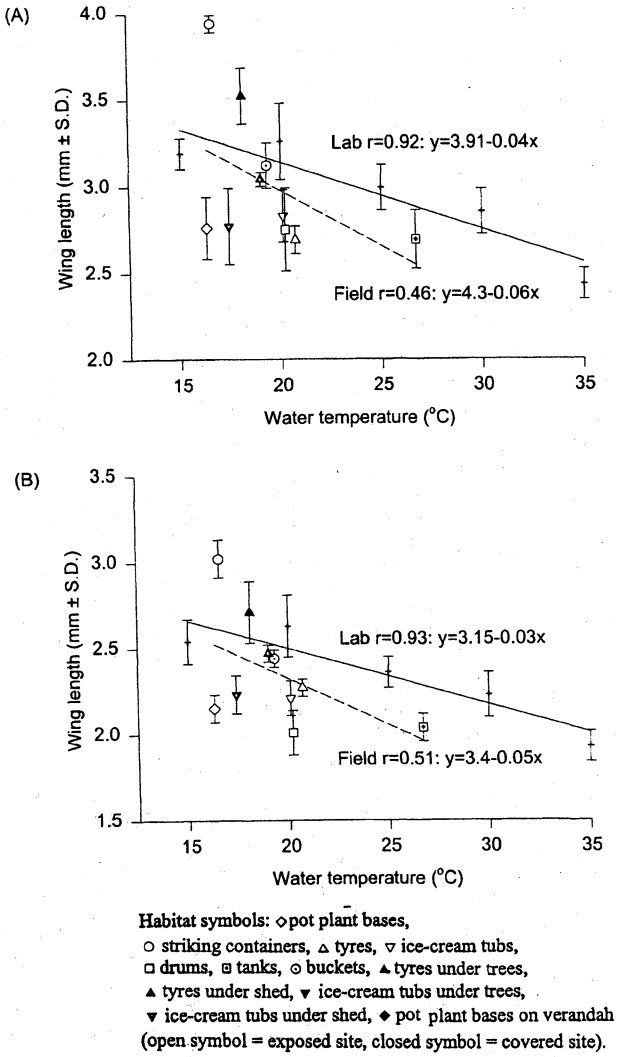


Fig. 4. Relationship between wing length of adult *Ae. aegypti* (both strains) and mean water temperature. (A) females and (B) males.

of first and second instars in buckets (mean 4.5 days at 19.3 ± 3.4°C) was similar to laboratory data (4.3 days at 20°C), but those in tyres (open or under a shed, 6.0 days at 20.7 and 20°C) or in drums (6.5 days at 20.2°C) were slower. Duration of third and fourth instars in buckets (open, 11.7 days at 19.3°C) and for tyres under a shed (10.3 days at 20°C) was slower compared to laboratory data (5.9 days), tyres in open (7.8 days) and for drums (6 days). Contrary to the usual trend, development in tyres shaded under trees (mean 15.3 days at 18.1°C) was significantly quicker than in warmer tyres in the open or under a shed (19.6–19.9 days at 20–20.7°C) ($LSD_{0.05} = 3.746$). Thus, the field data were more variable and development generally took longer than in the laboratory (Figs 1 and 2), with the biggest differences observed in pot plant bases at Townsville. When these were excluded from the regression analysis of rate of development against mean water temperature, the equation was $y = 0.00463x - 0.0370$ ($r = 0.90$), the slope being significantly similar to that for laboratory data.

Survival to adulthood was comparable to the laboratory data for only seven of 14 trials with different types of containers in field situations (Fig. 3). Successful development, or lack thereof, was not consistently associated with particular container types. Mortality rates were significantly higher in exposed containers, with unadjusted water volume either overflowing from rainfall or rapidly evaporating due to insolation. For example, in exposed unadjusted tyres (20.7°C) which overflowed following rainfall, average survival was only 21 ± 7.1%, compared to survival of 64 ± 5.7% in tyres with constant water volume.

Sex ratio did not differ significantly from 1 : 1 among adults counted from plastic striking containers (16.6°C), tyres placed in the open (20.7°C) and a rain water tank (26.7°C).

Adult size correlations between wing-length and temperature (Fig. 4) of field samples were: females, $r = 0.46$ ($P < 0.05$; $y = 4.3–0.06x$) and males $r = 0.51$ ($P < 0.02$; $y = 3.4–0.05x$). These correlation coefficients are much lower than for laboratory-reared samples. Adults emerging from striking containers (wing-length of females 3.94 ± 0.05 mm, males 3.02 ± 0.11 mm, at 16.6 ± 2.7°C) or tyres under trees (wing-length of females 3.52 ± 0.16 mm, males 2.71 ± 0.18 mm, at 18.1 ± 3.1°C) were generally larger than those produced from other situations, e.g. tyres in the open (wing-length of females 2.69 ± 0.08 mm, males 2.27 ± 0.05 mm at 20.7 ± 2.9°C), drums (wing-length of females 2.75 ± 0.24 mm, males 2.01 ± 0.13 mm at 20.2 ± 3.4°C) or from ice-cream tubs in the open (wing-length of females 2.83 ± 0.15 mm, males 2.21 ± 0.1 mm, at 20.1 ± 2.6°C).

Discussion

Aedes aegypti population growth is often limited by larval competition for scarce food resources (Southwood *et al.*, 1972) and this led Focks *et al.* (1993) to conclude that laboratory studies based on high larval densities can be misleading. Our laboratory studies of immature survival, development times and adult size were therefore based on densities of one larva per 10 ml water, which is not uncommon in natural habitats (Tun-Lin *et al.*, 1995), with a food supply richer than encountered by *Ae. aegypti* in the majority of field situations, judging from their wing-lengths (Fig. 4).

The development of poikilotherms such as *Ae. aegypti* is widely described using the temperature summation model, which is valid for the linear portion (range B) of the sigmoidal development curve (Campbell *et al.*, 1974). In the laboratory, constant water temperatures of 10 and 40°C were lethal to north Queensland strains of *Ae. aegypti* , although the minimum threshold temperature was estimated to be 8.3°C. Between 20 and 35°C, development was linearly related to temperature ($r = 0.97$, $P < 0.001$) and expressed by the thermal constant K = 181.2 ± 36.1 day-degrees above the threshold.

Development times of *Ae. aegypti* from north Queensland were generally similar to other populations (cf. Headlee, 1940,

1941, 1942; Bar-Zeev, 1958; Christophers, 1960; Rueda *et al.*, 1990), but some large differences could not be attributed to variation in experimental method (extrinsic factors). At 15°C, *Ae. aegypti* from Louisiana took 19 days longer (Rueda *et al.*, 1990) and at 20°C, those from Israel took 4–5 days longer (Bar-Zeev, 1958) than those from north Queensland or Louisiana. Geographic adaptation (intrinsic factors) could also explain a 20% difference in survival between *Ae. aegypti* from Louisiana and north Queensland when reared at 15°C. In general, however, the range 20–30°C is characterized by high survival rates, in our case from 88 to 93% from hatching to adulthood.

During winter at Charters Towers, temperatures were lower (< 10°C) during the morning, making larvae inactive until the afternoon when water had become reheated by daily sunshine. However, the slopes of both laboratory and field equations for developmental rate were similar when outlying pot plant bases were excluded from regression analysis. Within the 16.3–28.1°C range of field temperatures, the intercept for field populations was retarded by 0.011, probably because of reduced nutrition.

These comparative data from qualitatively different containers holding qualitatively different water volumes should be interpreted cautiously as those immatures in smaller containers (e.g. pot plant bases, ice-cream tubs) were subjected to greater variations in temperature than those in larger containers (e.g. rainwater tanks and drums), and even in tyres, which are well insulated.

Differential availability of food resources appeared to be more important than temperature in influencing *Ae. aegypti* development in the field. For example, adult *Ae. aegypti* emerged from tyres under trees (providing detritus) almost 5 days earlier than those in the open averaging 2.6°C warmer; development in plastic striking containers (with abundant vegetable matter and drowned insects) was 6 days faster than in comparable pot plant bases. *Aedes aegypti* larvae browse on decaying insects and rotting leaves. Consequently, for containers with better nutrition, the resultant adult male and female mosquitoes were larger, as indicated by wing-length (Fig. 3). Similarly, in Kenya, large *Ae. aegypti* emerged from pots where maize gruel had been introduced inadvertently (Subra & Mouchet, 1984). Conversely, in containers with limited food resources, i.e. those in the open or subject to cleaning, e.g. buckets and ice-cream tubs, often used for pets' drinking water, development of later instars was often prolonged. This also resulted in greater mortality.

Whereas immature survival was governed by temperature and competition for food resources, it was also influenced by evaporation or overflow of water caused either by rainfall or excessive garden sprinkling. Natural factors, as well as those associated with human activity, have greater potential to disrupt smaller containers.

Rigorous comparisons of our field and laboratory data indicated that, for nine of 13 field sites, development was slower than for the laboratory (Fig. 1). From comparison of wing-lengths (Fig. 4), only those from a plastic container used for striking plant cuttings and from a shaded tyre produced adults larger than in the laboratory study. Of the four sites where development was faster at comparable laboratory temperatures, two (tyre and under tree, ice-cream tub under shed) were shaded and two (the above set of striking containers and pot plant bases) were exposed to sunlight but would have received some shading and extra nutrients from the plants and pot above them. These data do not consider the confounding effect of larval crowding, which also influences *Ae. aegypti* development times (Barbosa *et al.*, 1972).

In relation to field survival, only 50% of comparisons approximated the laboratory curve. Apart from poor development and survival of immatures in one set of pot plant bases (considered as an outlier), the other six sets of sites (two sets of tyres, drums, ice-cream tubs, buckets, rain water tank) were exposed to natural elements.

Nasci (1986) showed that well nourished and larger adult females have greater survival potential and blood-feeding success. Based on our data, especially within the optimum temperature range of 20–30°C, containers with an abundance of accumulated organic matter (e.g. striking containers) tend to produce the largest *Ae. aegypti* adults. Some of these water containers (e.g. discarded plastic tubs and tyres) may be less visible amongst foliage or under trees. It would seem most important to prioritize control to these types of containers, as reduction of the largest *Ae. aegypti* could improve the efficiency of efforts to reduce the risk of dengue transmission.

Acknowledgements

We are grateful to Tony Barnes and Simon Forsyth, Tropical Health Program, University of Queensland, for statistical assistance. We thank Peter Ryan and Allan Saul, Queensland Institute of Medical Research, for manuscript review. This paper is based on the PhD thesis of W. Tun-Lin in the context of the Tropical Health Program, University of Queensland.

References

Bacot, A.W. (1916) Report of the Entomological Investigation undertaken for the year 1914–15. *Report of the Yellow Fever Commission (West Africa)*, **3**, 1–191.

Barbosa, P., Peters, T.M. & Greenough, N.C. (1972) Overcrowding of mosquito populations: responses of larval *Aedes aegypti* to stress. *Environmental Entomology*, **1**, 89–93.

Bar-Zeev, M. (1958) The effect of temperature on the growth rate and survival of immature stages of *Aedes aegypti* (L). *Bulletin of Entomological Research*, **49**, 157–163.

Campbell, A., Frazer, B.D., Gilbert, N., Gutierrez, A.P. & Mackever, M. (1974) Temperature requirements of some aphids and their parasites. *Journal of Applied Ecology*, **11**, 431–338.

Christophers, S.R. (1960) Aedes aegypti *(L): the Yellow Fever Mosquito: its Life History, Bionomics and Structure*. Cambridge University Press, Cambridge.

Fielding, J.W. (1919) Notes on the bionomics of *Stegomyia fasciata* Fabr. *Annals of Tropical Medicine and Parasitology*, **13**, 259–296.

Focks, D.A., Haile, D.G., Daniels, E. & Mount, G.A. (1993) Dynamic life table model for *Aedes aegypti* (Diptera: Culicidae): analysis of the literature and model development. *Journal of Medical Entomology*, **30**, 1003–1017.

Hanna, J.N., Ritchie, S.A., Merritt, A.D., van den Hurk, A., Phillips, D.A., Serafin, I.L., Norton, R.E., McBride, W.J.H., Gleeson, F.V. & Poidinger, M. (1998) Two contiguous outbreaks of dengue type 2 in north Queensland. *Medical Journal of Australia*, **168**, 221–225.

Headlee, T.J. (1940) The relative effects on insect metabolism of temperature derived from constant and variable sources. *Journal of Economic Entomology*, **33**, 361–364.

Headlee, T.J. (1941) Further studies of the relative effects in insect metabolism of temperature derived from constant and variable sources. *Journal of Economic Entomology*, **34**, 171–174.

Headlee, T.J. (1942) A continuation of the studies on the immature relative effects in insect metabolism of temperature derived from constant and variable sources. *Journal of Economic Entomology*, **35**, 785–786.

Hotchkin, P.G. (1985) The duration of larval life of *Aedes aegypti* as affected by time of hatch. *Journal of the American Mosquito Control Association*, **1**, 489–492.

Kay, B.H., Barker-Hudson, P., Stallman, N.D., Wiemers, M.A., Marks, E.N., Holt, P.J., Muscio, M. & Gorman, B.M. (1984) Dengue fever: reappearance in northern Queensland after 26 years. *Medical Journal of Australia*, **140**, 264–268.

Lumley, G.F. & Taylor, F.H. (1943) *Dengue*. School of Public Health and Tropical Medicine Service Publication no. 3. Sydney.

Mattingly, P.F. (1957) Genetical aspects of the *Aedes aegypti* problem. I. taxonomy and bionomics. *Annals of Tropical Medicine and Parasitology*, **51**, 392–408.

Murray-Smith, S., Weinstein, P. & Skelly, C. (1996) Field epidemiology of an outbreak of dengue fever in Charters Towers, Queensland: are insect screens protective? *Australian and New Zealand Journal of Public Health*, **20**, 545–549.

Nasci, R.S. (1986) The size of emerging and host-seeking *Aedes aegypti* and the relation of size to blood-feeding success in the field. *Journal of the American Mosquito Control Association*, **2**, 61–62.

Rueda, L.M., Patel, K.J., Axtell, R.C. & Skinner, R.E. (1990) Temperature-dependent development and survival rates of *Culex quinquefasciatus* and *Aedes aegypti* (Diptera: Culicidae). *Journal of Medical Entomology*, **27**, 892–898.

Southwood, T.R.E., Murdie, G., Yasuno, M., Tonn, R.J. & Reader, P.M. (1972) Studies on the life budget of *Aedes aegypti* in Wat Samphaya, Bangkok, Thailand. *Bulletin of the World Health Organisation*, **46**, 211–226.

Subra, R. & Mouchet, J. (1984) The regulation of preimaginal populations of *Aedes aegypti* (L.) (Diptera: Culicidae) on the Kenya coast. *Annals of Tropical Medicine and Parasitology*, **78**, 63–70.

Tun-Lin, W., Kay, B.H. & Barnes, A. (1995) Understanding productivity, a key to *Aedes aegypti* surveillance. *American Journal of Tropical Medicine and Hygiene*, **53**, 595–601.

Youdeowei, A. & Service, M.W. (1983) *Pest and Vector Management in the Tropics, with Particular Reference to Insects, Ticks, Mites and Snails*. Longman, London.

Accepted 9 August 1999