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Aedes albopictus (Diptera: Culicidae): Physiological Aspects of Development and Reproduction

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ABSTRACT Basic ecophysiological data are presented on the development and reproduction of *Aedes albopictus* (Skuse) that were reared and maintained at four temperatures between 12 and 32°C. Median larval developmental time from hatching to pupation was correlated inversely with temperature, lasting 7 d at 32°C and up to 28 d at 12°C. Duration of the pupal period also varied from 2–3 d at 32°C to 7–12 d at 12°C. This extension of larval development elongated the phagoperiod and gave rise to larger imagoes. Based on wing length measurements, body sizes varied from 10 to 57 mm^3 for females and from 10 to 30 mm^3 for males. The caloric protein content at emergence showed a linear and significant regression with body size, independent of sex, treatment, or temperature. Teneral lipid content also followed a linear relationship with body size at warmer temperatures, whereas at low temperatures it increased exponentially with body size. Glycogen was always below 10% of the protein or lipid levels. Reserves at emergence determined median adult survival times, which ranged from 16 d at 32°C to 100 d at 17°C. Access to sucrose solution allowed females to increase their teneral glycogen up to fourfold within 1 wk, and their lipids up to 10-fold within 2 wk. Despite a broad variation, the number of mature oocytes (15–110 eggs per female) was correlated positively with body size, but inversely with the rearing and maintenance temperature. Utilization of the blood meal protein for oogenesis ranged between 35 and 50%, again inversely correlated with temperature; absolute compositions per oocyte were 6.3–6.5 mcal of protein but ranged from 5 to 7 mcal of lipid.

KEY WORDS *Aedes albopictus*, development, body size, reserves, survival, fecundity

THE ASIAN TIGER mosquito, *Aedes albopictus* (Skuse), has recently expanded its distribution, a process that is not often witnessed in a biologist's lifetime. Originating in the Far East, during the last 20 yr this species has become established in the United States (O'Meara et al. 1995) as well as in southern Europe (Dalla Pozza and Majori 1992, Mitchell 1995, Adhami and Reiter 1998). In view of its potential as a vector of dengue and other arboviruses, epidemiological concerns have been expressed throughout its newly acquired range (Mitchell et al. 1990, 1992; Mitchell 1995).

In the current report we summarize experiments aimed at describing the basic physiology of this species, which has remained largely unknown or mentioned only sporadically from different laboratories. Developmental and reproductive parameters were analyzed under controlled laboratory conditions at four constant temperatures from 12 to 32°C. This information should be useful for ecologists and extend the valuable review on the species biology presented by Hawley (1988).

Materials and Methods

Aedes albopictus originated from Louisiana, a strain obtained from M. J. Klowden. It was maintained at 27 ± 1°C, 85 ± 2% RH, and a photoperiod of 14:10 (L:D) h with two 45-min periods that simulate sunrise and sunset. At other temperatures tested, the same long-day conditions prevailed without dimming periods. TetraMin (Tetra Werke, Melle, Germany) was provided as larval food according to a regimen adopted from previous studies of *Ae. aegypti* (L.) (Timmermann and Briegel 1993). Our routine rearing with 400 larvae per pan (25 by 18 by 5 cm) in 400 ml of distilled water, i.e., a density of 1 larva/ml, led to a fairly synchronous pupation and emergence of populations with a narrow range in body size. To obtain extremes in imaginal body size, densities of 0.5 larvae/ml (200 larvae) or >3 larvae/ml (>1,000 larvae) were used. To simulate various climatic conditions, development and survival were measured under temperature conditions of 12, 17, 2°, and 32°C, and the larval feeding regime was adjusted to the extended or reduced developmental periods.

Wing length was measured for each insect under a dissecting microscope and its cubic value (mm^3) is henceforward called *body size.* Survival experiments were conducted with groups of 30–50 females or males in the presence of sucrose solution (10%) or water (starvation). Blood meals were always on the same forearm (H.B.) until the females withdrew their proboscis, i.e., when fed to repletion. Fecundity was determined for the first gonotrophic cycle and by dissecting ovaries and counting the mature oocytes present; therefore, mating status was not considered relevant.

Biochemical analyses of single males or females for total protein, lipid, and glycogen were identical to our

Table 1. Developmental times (days) for *Ae. albopictus* from hatching to emergence at four temperatures and low or high density conditions

Temp, °C	Density	Pupation			Female emergence		
		Start	End	Median	Start	End	% of all pupae[a]
12	Low	22	51	28	34	55	28
	High	25	53	33	35	66	30
17	Low	14	26	17	19	34	17
	High	16	88	30	19	90	32
27	Low	6	14	8	9	14	38
	High	8	38	17	11	39	36
32	Low	6	14	7	8	32	47
	High	11	31	13	13	32	29

Data have been extrapolated from sigmoidal plots and rounded off to the nearest full day.

[a] In most experiments males eclosed in a 2:1 proportion and always started 1 d before the females.

previous studies (Timmermann and Briegel 1998, 1999). Caloric values of protein, lipid, or glycogen were related to body size. Dividing the caloric data by the cubic wing length (body size) revealed the size-specific caloric content (SSCC-value), which allowed direct comparison among experimental cohorts, irrespective of treatments.

Regressions were calculated and the *t*-test was applied to check for significance of the slopes or between means, according to Wardlaw (1985).

Table 2. Regression formulas ($Y = aX + b$ or $Y = aX^b$) for teneral reserves and m.i.a. (Y, cal/mosquito) and body size (X, cubic wing length) of newly emerged *Ae. albopictus*, reared and maintained at four temperatures

Component	Temp, °C	Regression	*n*	r^2	*t*
Protein	12	$Y = 0.030X + 0.203$	39	0.824	13.17
	17	$Y = 0.029X + 0.256$	64	0.893	22.73
	27	$Y = 0.054X - 0.330$	20	0.865	10.74
	32	$Y = 0.057X - 0.316$	34	0.904	17.38
Lipid[a]	12	$Y = 0.0008X^{2.19}$	25	0.261	
	17	$Y = 0.000008X^{3.23}$	73	0.790	
	27	$Y = 0.073X - 1.035$	20	0.958	20.34
	32	$Y = 0.087X - 1.075$	34	0.872	14.83
Glycogen[a]	12	$Y = 0.006X - 0.094$	25	0.345	3.48
	17	$Y = 0.008X - 0.119$	73	0.686	12.45
	27	$Y = 0.006X - 0.001$	20	0.689	9.18
	32	$Y = 0.006X + 0.040$	34	0.506	8.21
Protein m.i.a.	17	$Y = 0.024X + 0.022$	83	0.818	19.07
	27	$Y = 0.043X - 0.170$	54	0.882	19.64
	32	$Y = 0.033X + 0.026$	69	0.885	22.73
Lipid m.i.a.	17	$Y = 0.001X + 0.141$	58	0.022	1.13[b]
	27	$Y = 0.005X - 0.019$	65	0.755	13.94
	32	$Y = 0.002X + 0.018$	87	0.227	4.99
Glycogen m.i.a.	17	$Y = 0.00004X + 0.027$	67	0.002	0.32[b]
	27	$Y = 0.0001X + 0.027$	66	0.025	1.29[b]
	32	$Y = 0.0002X + 0.016$	84	0.045	1.97[b]

Females and males were pooled except for [a], where only females were considered.

All $P < 0.01$ or <0.001, except for [b], which was NS; for the power curves the *t*-test was not applicable.

Results

Development Until Eclosion. Median developmental times were measured at four temperatures (12, 17, 27, and 32°C) and for low and crowded density populations (Table 1). Median pupation was 28 d at 12°C and decreased to 7 d at 32°C, indicating a fourfold acceleration of development for a rise in temperature of 20°C. In low density populations (<1 larva/ml) developmental success increased from ≈60% at 12°C to 90–99% at 27 or 32°C.

Duration of the pupal period was between 7 and 12 d (9.3 ± 2.1, $n = 63$) at 12°C, 1.5–6 d at 27°C (2.8 ± 1.2, $n = 16$), and 1–3.5 d (2.3 ± 0.7, $n = 16$) at 32°C for both sexes and densities. Eclosion time of females showed a reduction from 34 d (12°C) to 8 d (32°C), but under crowding this was from 66 or 90 d at 12 and 17°C to 32 d at 32°C (Table 1). Males always appeared 1 d earlier than females. The end of the emergence period was extremely variable, especially under crowding. The sex ratio of males to females in almost all cases approximated 2:1, regardless of temperature and density (Table 1). The exceptions of 17 and 47% exemplify the variability.

Imaginal Body Size and Teneral Reserve Status. Different rearing and dietary conditions largely determined body size and protein reserves at emergence. The lower the temperature, the longer the larval phagoperiod and therefore the larger the body size at emergence. Mean female body sizes were 41.78 at 12°C, 44.74 at 17°C, 23.89 at 27°C, and 23.39 at 32°C. The corresponding wing lengths were 3.47 ± 0.16 mm, range 3.2–3.8 ($n = 51$) at 12°C; 3.55 ± 0.10 mm, range 3.3–3.7 ($n = 41$) at 17°C; 2.88 ± 0.40 mm, range 2.3–3.5 ($n = 40$) at 27°C; and 2.86 ± 0.35 mm, range 2.2–3.4 ($n = 44$) at 32°C. Males were always 17–20% smaller than females. There was a significant linear correlation between body size and protein content of newly emerged *Ae. albopictus*, regardless of sex, diet, or temperature (Table 2). In contrast, relation of total lipids with female (and males, not shown) body sizes was exponential at the two lower temperatures with their extended phagoperiods, but linear at the two higher temperatures (Table 2). Glycogen consistently comprised <1/10 of the caloric protein or lipid content. In Fig. 1 we summarized these three components for females and males at emergence in relation to body size.

To assess the extent of reserve mobilization by *Ae. albopictus*, 50–100 females were provided only water from emergence until death. Subsequent analyses of protein, lipid, and glycogen revealed their minimal irreducible amounts (Table 4) required for survival (Van Handel 1984). These minima also were related linearly with body size and data for the two sexes coincided, therefore they were pooled for the regressions. In all circumstances, up to 90% of the teneral lipid, most of the glycogen, and up to 20% of the teneral protein were catabolized in both sexes and at all four temperatures.

Survival Times. Daily survivorship was recorded for males and females at different temperatures in cohorts of 30–50 mosquitoes with access to water or sucrose (1

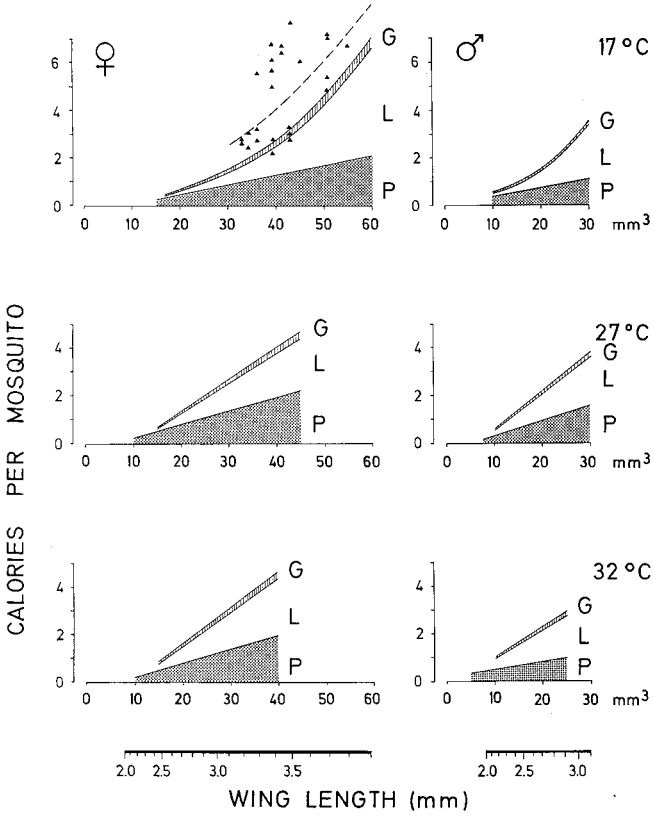

Fig. 1. Cumulative caloric content of protein (P), lipid (L), and glycogen (G) of newly emerged females and males of *Ae. albopictus*, depending on their body sizes attained at the four different temperatures. Single lipid values (triangles and dashed regression line) for females raised at 12°C have been added to the diagram at 17°C. See Table 2 for underlying regression formulas.

or 10%). Access to water (=starvation) revealed the minimal survival time and sucrose 10% the maximal survival time. Because all curves followed a negative sigmoidal pattern, we selected only three characteristic time points in Table 3, i.e., the 90, 50, and 10% survival times. The 90% survival time often marks the point when gradual mortality starts, whereas the maximum survival time is an erratic figure of little significance. Therefore, the best characterization of a population is the 50% or median survival time. Sucrose (1%) always improved survival considerably over starvation and often was more pronounced than concentration increases from 1 to 10%. The longest survival times were observed at 17°C, whereas at 32°C survival clearly was reduced. Data for males were similar to females.

Table 3. Selected survival times (days) of female *Ae. albopictus* at four temperatures with access to water (W) or sucrose (S) 1 and 10%

TEMP, °C	Diet	Survival times, d			
		90%	50%	10%	Max
12	W	9.5	18.5	23.5	30
17	W	15.2	17.9	20.0	24
	S 1%	31.0	64.0	77.0	95
	S 10%	47.0	100.0	114.5	123
27	W	6.2	7.5	8.8	11
	S 1%	6.2	15.2	29.5	47
	S 10%	25.0	49.0	86.0	112
32	W	4.2	5.6	7.2	8
	S 1%	7.6	22.8	42.0	47
	S 10%	10.6	16.2	33.6	39

The table shows the days when 90, 50, or 10% of the populations (30–50 females) still were alive; maximum means the day of death of the last female.

Reserve Synthesis from Carbohydrate Sources. Despite their need for a blood meal, female mosquitoes often feed on carbohydrate before encountering or seeking a vertebrate host. We tested the potential for synthesis of reserves based on a 10% sucrose diet. Females raised and maintained at three temperatures had access to 10% sucrose ad libitum for 2–3 wk, during which their lipid and glycogen reserves were analyzed at 2- to 3-d intervals until the maximum level declined. Characteristic data points are summarized in Table 4 in SSCC-values and for comparison, the minimal irreducible amount was also included as an SSCC-value. At 12°C, insufficient material was available for analyses.

Lipogenesis was most efficient at 27°C, where the teneral value increased >10-fold within 2 wk, whereas glycogenesis was weaker with only a fourfold increase within 1 wk. At the lower temperatures, lipid and glycogen values doubled within 1 wk. Comparing the teneral SSCC-value with the manyfold increases through sugar-feeding, it appeared that at all three temperatures similar maxima of lipids and of glycogen were reached, ≈0.080 cal of lipid and 0.016 cal glycogen per female in SSCC-units. Under all circumstances, lipid synthesis was clearly higher than glycogen synthesis.

Table 4. Synthesis of lipid and glycogen after emergence of female *Ae. albopictus* when maintained on 10% sucrose (S) ad libitum at three temperatures

Temp, °C	Conditions	Lipid	Glycogen	*n*
17	Teneral	(0.047) 1.0	(0.005) 1.0	20
	S 4d	1.5	1.7	9
	S 8d	2.0	2.1	9
	S 12d	1.6	2.8	12
	m.i.a.	0.1	0.24	7
27	Teneral	(0.008) 1.0	(0.004) 1.0	10
	S 4d	6.0	4.0	10
	S 8d	8.6	4.2	9
	S 12d	9.9	2.6	10
	S 16d	10.3	3.0	10
	S 20d	11.4	2.7	9
	m.i.a.	0.3	0.6	16
32	Teneral	(0.041) 1.0	(0.006) 1.0	34
	S 4d	1.9	2.3	9
	S 8d	2.1	1.6	10
	S 12d	1.4	1.8	10
	m.i.a.	0.1	0.1	23

Data were converted to SSCC-units, i.e. size-specific caloric contents (absolute caloric values in parentheses). The teneral SSCC-value is arbitrarily defined as 1.0, and all the data are expressed on this basis. Minimal irreducible amounts (m.i.a.) also were included for each temperature.

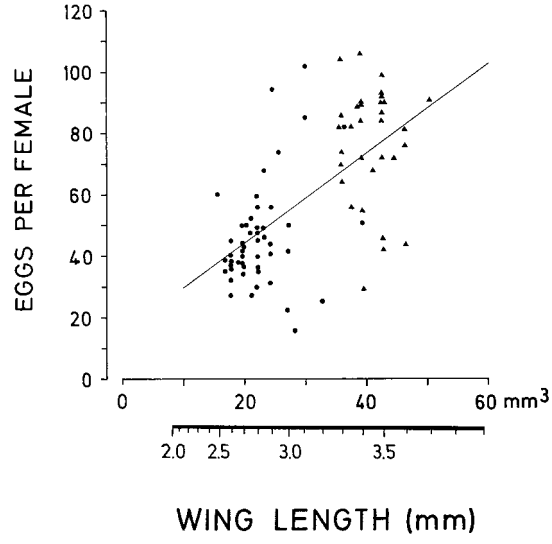

Fig. 2. Linear regression of fecundity with body size of *Ae. albopictus* during the first reproductive cycle at 27–32°C (●) and 17°C (▲). Regression: $Y = 1.48X + 14.12$ ($n = 83$, $r^2 = 0.426$, $t = 7.76$, $P < 0.001$).

Oogenesis. To assess the reproductive potential of this species during the first gonotrophic cycle, we analyzed blood meal consumption and fecundity at the same four temperatures with females given free access to 10% sucrose for 2–3 d after emergence, followed by human blood meals as a protein source. The number of mature oocytes always increased as a linear function of maternal body size from 17 to 32°C (Fig. 2), despite a broad range of 15–110 eggs per female. Means for fecundity were significantly greater ($P < 0.01$) at cool temperatures, but at 12°C only one-third of the females were oogenic ($n = 8$); the rest remained nonoogenic ($n = 18$). Oogenesis required 12–15 d, and up to 75 eggs matured, coinciding with the same regression line. Regardless of temperature, female body size and therefore blood meal volume determined fecundity. The reasons for the high proportion of nonoogenic females has not been explored.

There were linear relationships between temperature and ovarian protein, lipid, and glycogen values, parallel to body size. Significant linear regressions with body size were obtained for ovarian protein ($Y = 0.010X + 0.037$; $n = 43$, $r^2 = 0.438$, $t = 5.66$, $P < 0.001$),

Table 5. Mean blood consumption, fecundity and yolk composition of *Aedes albopictus* reared and maintained at different temperatures (means ± SE, N in parentheses)

	17°C	27°C	32°C
Body size	41.19 ± 3.77 (31)	21.42 ± 5.45 (35)	25.86 ± 3.97 (18)
Wing length (mm)	3.45	2.78	2.96
Hematin (μg)	20.24 ± 5.19 (31)a	14.46 ± 5.53 (36)a	18.23 ± 7.57 (15)
Blood volume (μl)	3.1 ± 0.8	2.2 ± 0.8	2.8 ± 1.1
Blood protein (cal)	2.13	1.52	1.91
No. of eggs matured	76.5 ± 18.2 (33)b	46.5 ± 18.5 (37)b	56.4 ± 24.6 (17)
Ovarian content (cal)			
Protein	0.49 ± 0.11 (15)c	0.29 ± 0.10 (18)c	0.38 ± 0.17 (10)
Lipid	0.55 ± 0.08 (15)d	0.25 ± 0.13 (16)d	0.27 ± 0.12 (7)
Glycogen	0.04 ± 0.02 (15)	0.02 ± 0.01 (14)	0.03 ± 0.02 (7)
Sum	1.08	0.56	0.68
% of Blood meal	49	37	36
Oocyte content (mcal)			
Protein	6.3 ± 0.7 (15)	6.4 ± 0.3 (15)	6.5 ± 0.5 (10)
Lipid	7.0 ± 0.7 (15)	5.1 ± 0.4 (14)	5.1 ± 0.4 (7)
Glycogen	0.5 ± 0.2 (15)	0.5 ± 0.1 (14)	0.6 ± 0.2 (7)
Sum	13.8	12.0	12.2
Yolk per oocyte (SSCC)			
Protein	0.0118 ± 0.0030e	0.0121 ± 0.0030	0.0139 ± 0.0049e
Lipid	0.0140 ± 0.0022f	0.0104 ± 0.0026	0.0114 ± 0.0051f
Glycogen	0.0010 ± 0.0004g	0.0012 ± 0.0005	0.0014 ± 0.0007g
Sum	0.0268	0.0237	0.0267

t-Test: a,b,c,d, $P < 0.001$; e,f,g, $P > 0.5$, NS.

lipids ($Y = 0.016X-0.105$; $n = 36$, $t = 10.57$, $r^2 = 0.767$, $P < 0.001$), and glycogen ($Y = 0.001X + 0.008$; $n = 36$, $r^2 = 0.256$, $t = 3.42$, $P < 0.01$). These regressions combine the absolute caloric data for all females.

The absolute yolk content per mature oocyte was provided in Table 5. At 17°C, each oocyte contained an average of 6.26 mcal protein, 6.98 mcal lipid, and 0.48 mcal glycogen. At 27°C these values were 6.37 mcal protein, 5.11 mcal of lipid, and 0.54 mcal of glycogen per oocyte. At 32°C, 6.48 mcal protein, 5.10 mcal lipid, and 0.63 mcal glycogen. The total caloric yolk per oocyte was 13.72 mcal/oocyte at 17°C, 12.02 mcal/oocyte at 27°C, and 12.21 mcal/oocyte at 32°C (Table 5). Protein contributed an average of 6.4 mcal (46–53% of the total) and glycogen 0.5 mcal/oocyte (3.5–5.2%). Lipid yolk ranged from 5.1 to 7.0 mcal, depending on temperature, i.e., 42–51% of the total caloric content per oocyte.

To relate the caloric content of the yolk produced at different temperatures to the respective body sizes of the females, ovarian values were standardized individually for maternal body size (Table 5). At 17°C the mean SSCC-values for ovarian yolk were 0.0118 cal protein, 0.0140 cal lipid, and 0.0010 cal glycogen. At 27°C these values were 0.0121 cal protein, 0.0104 cal lipid, and 0.0012 cal glycogen; and at 32°C they were 0.0139 cal protein, 0.0114 cal lipid, and 0.0014 cal glycogen. Although the size-specific ovarian protein and glycogen did not markedly differ among the three temperatures, lipid yolk was highest at 17°C and lower at 27 or 32°C.

Discussion

Temperature, Body Size, Reserves, and Survival. Temperature is one of the most important factors governing the distribution of *Ae. albopictus.* According to Mitchell (1995), the 10°C cold-month isotherm approximates the demarcation line of *Ae. albopictus* populations between continuous breeding and survival in dormancy in Europe, whereas a much lower isotherm of –5°C has been described for the United States (Nawrocki and Hawley 1987). We characterized development and survival between 12 and 32°C under long-day conditions. The developmental time until emergence of females ranged from 6 d at 32°C to 90 d at 17°C. More important was the effect of rearing temperature on imaginal body size, with the slowest development giving rise to the largest females. This agreed with earlier data on several mosquito species, where larval growth was described as synthesis of protein that perfectly reflected the increase of biomass (Timmermann and Briegel 1998, 1999). The longer the duration of the larval phagoperiod, primarily the fourth instar, the larger the size of the emerging imagoes. The significant linear relationship between imaginal body size and caloric protein content of teneral females was identical for all rearing conditions. As in other mosquitoes, wing length was an accurate and reliable predictor of teneral protein content (Briegel 1990a, 1990b) or biomass measured as dry weight (Packer and Corbet 1989). Obviously, protein synthesis in the larvae follows constant, linear kinetics. However, there is another aspect with the lipids. The longer that larvae can feed, the more surplus is available for reserve synthesis, leading to an exponential lipid accumulation in newly emerged males and females (Briegel 1990a for *Ae. aegypti*, the current report for *Ae. albopictus*). At higher temperatures, growth terminated much earlier (female body sizes of 40), so that larval lipid synthesis could not reach the exponential phase encountered at low temperatures.

With access to 10% sucrose, female *Ae. albopictus* increased their low teneral glycogen content three- to fourfold within the first week of imaginal life. During another 2 wk their teneral lipid increased >10-fold. As already shown by Van Handel (1965) for *Ochlerotatus sollicitans,* for biochemical reasons the synthesis of glycogen from sucrose occurs at a higher rate than lipogenesis. In *Oc. sollicitans* and *Oc. taeniorhynchus* the extent of glycogenesis is suppressed by the endocrine system, thereby favoring lipogenesis (Lea and Van Handel 1970). Apparently the same principle applies to *Ae. albopictus.* The highest lipid synthesis in *Ae. albopictus* was observed at 17°C, whereas at high temperatures, lipogenesis only doubled the teneral values. This result may reveal an adaptation to cold, similar to higher yolk lipids under cool conditions (see below). There is a similar 2-wk requirement for lipogenesis found in two palaearctic species: *Oc. cantans* with a fivefold increase of female lipids (Renshaw et al. 1995), and *Ae. vexans* with a >20-fold increase (Briegel et al. 2001a) after emergence. In contrast, lipogenesis occurred considerably faster in *Oc. punctor* (Renshaw et al. 1995) and in *Ae. aegypti* (Briegel et al. 2001b).

The levels of lipids and glycogen are detrimental for the survival of males and females. Starvation after emergence allowed 1–3 wk of survival, but by adding 1% sucrose survivorship clearly was extended. Interestingly, 10% sucrose did not strongly increase survival above 1% sucrose. Although these laboratory findings appear somewhat unnatural, they demonstrate that large segments of a population may survive at all temperatures for several weeks, as long as sufficient carbohydrate sources are accessible.

As mentioned before, glycogen synthesis from sucrose was not affected greatly by environmental temperatures, but lipogenesis appeared to be temperature-sensitive. Diminished lipogenesis at 32°C may explain reduced survivorship at high temperatures. Conversely, the strong lipogenesis at 17°C agreed with the extended survival times.

At 12°C the caloric content of starved females that died after the 90% survival time was in the range of minimal irreducible lipid or glycogen titers. We assume that the 90% survival time was an acceptable estimate of the time when mortality starts as a gradual process, reflecting the exhaustion of reserves. Therefore, mortalities before the 90% survival time and later than 10% survival time were considered random events.

Fecundity. Body size, regulated by larval diet or density (Nasci 1990, Teng and Apperson 2000) or by temperature (Teng and Apperson 2000; and the current report), largely determined the fecundity of *Ae.*

albopictus (Blackmore and Lord 2000; and the current report). Females reared and maintained at 17°C matured from 30 to 106 eggs during 6 d, whereas at 32°C from 16 to 102 eggs matured during 2 d. At 12°C, up to 75 eggs matured in a minority of the females and required at least 10 d. In theory, the duration of oogenesis, in combination with our survival data, indicated up to 10 reproductive cycles possible between 17 and 32°C. The 12°C temperature is close to the 10°C cold-month isotherm (Mitchell 1995), where reproduction was possible but not guaranteed. At 12°C, approximately two-thirds of the females remained non-oogenic or died, retaining masses of undigested blood. With such a low fitness, winter survival of females in these temperature zones is questionable, unless they enter a winter dormancy comparable to *Culex pipiens* (L.) (Mitchell and Briegel 1989). Therefore, for this species with its pronounced lipogenesis, the possibility for female diapause, despite its tropical origin, should not be excluded and ought to be further studied under cold adaptation.

Utilization of the blood meal protein for vitellogenesis was approximately one-quarter at 27°C, one-third at 32°C, but about one-half at 17°C. Our blood meal sizes varied between 2 and 4 μl of human blood and the resulting numbers of eggs agreed with results reported by Blackmore and Lord (2000) and Chin-Chang and Chang (1993), obtained by enemas at 28°C. *Ae. aegypti*, the closely related yellowfever mosquito, also spread around the globe in historic times, but did not become established as far north as *Ae. albopictus.* Both show a tremendous larval lipogenesis (Briegel 1990a, Timmermann and Briegel 1999), but *Ae. albopictus* appears to be even more efficient. As mentioned before, it seems to adapt to cool temperatures by increasing lipid synthesis and also by producing larger segments of yolk lipid under such circumstances. This also might be viewed in relation to interspecific competition between the two species (O'Meara et al. 1995).

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