THE EFFECTS OF IMMATURE STRESS ON SELECTED EVENTS IN THE LIFE HISTORY OF *CULEX TARSALIS*

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ABSTRACT. Immature *Culex tarsalis* were stressed during 3 laboratory experiments which separately evaluated temperature, food per pan and stocking density. Rearing stress reduced immature survival, altered immature development rates, distorted sex ratios at emergence, reduced adult wing lengths and inhibited the expression of autogeny. However, marked differences were not observed in insemination rates and the reproductive performances of unstressed and stressed females. When only adult parameters were considered, no significant differences were observed among life table attributes which included female life expectancy (e_1), fecundity, fertility, net reproductive rate (R_o) and intrinsic rate of increase (r_m). The inclusion of egg hatch, immature survivorship, and developmental period dramatically suppressed R_o and r_m, especially for the stressed groups. Overall, larger males and females lived longer. Both fecundity and fertility decreased as a function of female age. Cohort reproductive effort was concentrated early in life; i.e., $l_x m_x$ curves peaked on day 5. The adaptive advantages of *Cx. tarsalis* life history are discussed in the context of exploiting ephemeral ground water habitats and the rate of population recovery following control activities.

INTRODUCTION

The intensity of arbovirus transmission in California has been related directly to spatial and temporal changes in the relative abundance of the primary vector species, *Culex tarsalis* Coq. (Olson et al. 1979). Adult abundance patterns are strongly influenced by larval population dynamics which, in turn, are related to the quantity and quality of available breeding habitats. Spatial and seasonal changes in the incidence of autogeny (Hardy and Reeves 1973, Spadoni et al. 1974), female size (White 1980[2], Bock and Milby 1981), fecundity (Bock and Milby 1981) and relative abundance (Olson et al. 1979) may reflect variability in the quality of the larval environment.

Culex tarsalis breed in most types of ground water (Bohart and Washino 1978) and frequently exploit unstable habitats such as hoofprints and puddles. In these small, shallow and often ephemeral environments larvae may be stressed by inadequate food supply, crowding and high temperature. Laboratory and field studies on food quality (Hayes et al. 1974) and quantity (Kardos 1959, Hagstrum and Workman 1971), crowding (White 1980[2]) and temperature (Bailey and Gieke 1968, Hagstrum and Workman 1971) indicate that these stress factors may influence *Cx. tarsalis* immature survival and development. The importance of temperature as a density independent developmental stress was indicated indirectly by Bock and Milby (1981) who found that female size and fecundity were inversely correlated with temperature over time.

The present laboratory study evaluates individually the effects of thermal, food and crowding stress on immature development and adult quality at emergence. Emphasis was placed on studying the effects of rearing stress on adult quality (as indicated by size and autogeny status), survivorship and reproductive performance.

MATERIALS AND METHODS

STRAIN. The Knights Landing, Yolo Co., California, strain of *Cx. tarsalis* was used throughout and had been under continuous insectary culture since 1971. This laboratory-adapted, wild-type colony mated well in small cages under insectary conditions (McDonald et al. 1979) and had been used in previous mating competition experiments (Terwedow et al. 1977; Zalom et al. 1981a, 1981b).

REARING PROCEDURES. First instar larvae (L1) within 24-hr of eclosion were added to covered 23 × 35 cm rearing pans filled with 1 liter of tap water. Water was added, as needed, to maintain the 1 liter volume. On alternate days larvae were fed a packed volume of a 2:2:1 mixture of finely ground liver powder:rabbit pellets:Tetramin® fish food. The ration was added to the pans as a water slurry to reduce scumming. Pupae were separated daily with a pipette and transferred to emergence cages. Emerging adults were sorted by sex, counted and released into pan- and date-specific holding cages in which they were offered 10% sucrose on cotton pledgets.

Control rearing conditions which were presumed to be unstressed included: temperature = 26°C (held constant to ± 1°C by placing pans

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[2] White, K. D. 1980. Effects of larval density on the growth and size of a *Culex tarsalis* mosquito population. Ph.D. Diss., Univ. of California, Davis. 155 pp.

on a thermostat controlled heating pad), food (or basic ration, BR) = 3.0 to 3.35 cc of dry food/pan added according to the schedules in Table 1, and density = 600 L1/pan (or 0.75 L1/cm² of surface area or 0.6 L1/ml of rearing media). Larvae were stressed during 3 experiments by altering one of the above 3 factors while the remaining 2 factors were held constant: Exp. 1: temperature = 8 to 12, 18, 26, 31 or 34°C for 600 L1/pan fed the BR (temperatures were altered in an environment chamber accurate to ±1°C except at the colder range, where temperature varied ±2°C during the 60 day rearing period); Exp. 2: food = 1/3 BR, BR or 3BR fed to 600 L1/pan at 26°C; and Exp. 3: density = 300, 600, 1200 or 2400 L1/pan fed the BR at 26°C (densities were based on the number of L1 added at the start of the experiment). Four replicate pans were reared in each experiment with the exception of the 300 and 600 L1/pan groups in Exp. 3 which were repeated once (i.e., n = 8 pans).

ADULT PROCEDURES. The length of the wing from the alular notch to the distal margin exclusive of the fringe scales (Bock and Milby 1981) was measured for the first 5 and last 5 males and females emerging from each pan. These data indicated adult size at emergence.

To test if differences in adult size altered mating success, 50 virgin, 2-day-old adults of each sex were allowed to cohabit a "bucket" cage for a 7-day period. Cages were 20 cm high with a 16 cm diam. bottom and a 21 cm diam. screened lid on top of which a cotton pledget soaked in 10% sucrose was placed. An attempt was made to reciprocally cross groups of stressed (small-sized) adults with unstressed (large-sized) adults of the opposite sex within each experiment. Crosses of adults within groups were made as insemination controls. After the cohabitation period, surviving females were dissected to determine insemination status and ovarian development. Females were classified as autogenous (follicular maturation > Christophers' (1911) Stage III) or anautogenous (follicular maturation ≤ Stage II). The wing length of each adult was measured as described above.

Table 1. Food addition rate (packed dry volume in cc) for the basic ration used in experiments 1–3 (1 cc ≅ 0.9 g).

	Experiment		
Day	1*	2	3
0	0.15	0.15	0.30
2	0.25	0.15	0.30
4	0.25	0.30	0.45
6	0.45	0.30	0.45
8	0.45	0.45	0.60
10	0.60	0.45	0.60
12	0.60	0.60	0.60
14	0.60	0.60	—
Total	3.35	3.00	3.30

* For the 8–12°C treatment, food was added every 4th or 6th day as needed.

During peak emergence from each pan, 25 1-2-day-old females and males were isolated into pan-specific "bucket" cages. Mosquitoes were continuously offered 10% sucrose on cotton pledgets, a restrained chick suspended from the top of the cage as a blood meal source, and a 9 cm diam. cup on the floor of the cage filled with tap water as an oviposition substrate. Moistened toweling covered part of the screen top to increase humidity. Cages from all experiments were held in an insectary maintained at 26±2°C with a 16L:8D photoperiod which included 1 hr simulated crepuscular periods. Dead adult mosquitoes and oviposited egg rafts were removed and counted daily. The wing length of dead adults was measured as described above. Egg rafts were isolated individually in 6 dram shell vials for 3 days for hatching, after which the numbers of hatched and unhatched eggs were counted.

CALCULATIONS. Complete life tables were calculated for each cohort using procedures previously described (Reisen et al. 1979, Reisen and Mahmood 1980). To partition the effects of adult attributes (survivorship and reproduction) from the combined effects of immature and adult parameters, life table calculations were performed using 2 methods. Calculation series A considered only adult attributes; i.e., ♀ eggs were considered to reach adulthood instantaneously. Calculation series B combined both immature and adult attributes; i.e., pan-specific immature survival and developmental rates as well as egg hatch were incorporated to account for rearing stress. Specific formula modifications follow:

m_x, female offspring per female per age interval (x), = $E_x/2$. In series A, E_x = total eggs oviposited per female while in series B, E_x = hatching larvae per female.

R_o, the net reproductive rate per generation, $= a \sum_{x=1}^{w} l_x m_x$ where l_x = age-specific survivorship and w = the day the last female died. Immature survival, a, equaled 1 for series A and the cohort-specific survival from L1 to adult emergence for series B.

r_m, the innate rate of increase, was calculated from the formula $1 = a \sum_{x=1}^{w} l_x m_x e^{-r_m(x+d)}$. d, an approximate indication of generation time, was

equal to 0 for series A and the cohort-specific median female emergence time + a 7-day nulliparous period for series B.

G, the exact estimate of generation time, could only be estimated in series B.

Treatment means within experiments were tested by replicated 1-way model I analyses of variance (Sokal and Rohlf 1969). Percentage data was transformed to arc sine prior to analysis to normalize the distribution. First and last wing length data were tested by 2-way nested ANOVA. Comparisons among means were made by *posteriori* Duncan's multiple range tests.

RESULTS

EFFECTS OF STRESS ON IMMATURE DEVELOPMENT. Median time from eclosion to pupation (P_{50}) varied inversely with water temperature (Table 2, Exp. 1). The relationship of temperature (t) to the velocity of larval development (v = $1/P_{50}$) was expressed by the law of heat summation, $v = (t - t_0)/K$ where t_0 is the 0 developmental point and K = the thermal summation constant or the number of degree-days over t_0 required for the completion of immature development (Mogi 1978a). In the present experiment, v varied as a linear function of temperature with t_0 = 5.3°C and K = 268.8 degree-days ($r^2 = 0.976$, $P < 0.001$). The estimate of t_0 seemed appropriate, since only 4 of the 2400 larvae reared at 8–12°C successfully pupated and none of these emerged. A constant temperature of 34°C approached the upper thermal tolerance point as few larvae successfully pupated and none of these emerged. In nature, *Cx. tarsalis* larvae are often collected from ground water habitats having higher diurnal temperatures; however, the nocturnal cooling of these habitats apparently permits successful development. Our control, or unstressed, rearing temperature of 26°C resulted in relatively rapid development without excessive mortality.

The immature developmental rate decreased and survivorship increased as the volume of food added per larva increased (Table 2, Exp. 2, 3). Thus, by increasing the amount of food and holding larval density constant (Exp. 2) or by holding food volume constant and reducing larval density (Exp. 3), comparable rearing conditions were achieved. In addition to the total quantity of food added per larva, the food addition rate seemed also to affect the developmental rate, since the control group in Exp. 3 which received a larger initial ration, developed 3 days faster than the control groups in Exp. 1 and 2 (Tables 1 and 2).

As a bioassay to detect the production of autocidal growth retardant factors (GRF of Moore and Fisher 1969), 3 replicates of 50 L1 each were held in styrofoam cups containing 50 ml of filtered water in which 600, 1200 or 2400 L1/pan had been reared from eclosion to pupation. Tap water served as a control. After a 96-hr exposure period, mean survival did not differ significantly among treatments when

Table 2. Effects of rearing conditions on developmental time and survival of immature *Culex tarsalis* (n = 4 replicates/treatment).

Expt. no.	Stress[1]		Median developmental time (days)[2]			Survival (%)[3]			Percent
			P_{50}	E_{50} ♂	E_{50} ♀	L1 to P	P to A	L1 to A	♂
1	Temperature (°C)	8–12	60	—	—	0d	0c	0d	—
		18	20a	20a	26a	74a	70a	52a	54a
		26*	14b	15b	17b	49b	74a	36b	57a
		31	11c	11c	14c	28c	59b	17c	67a
		34	10c	—	—	1d	0c	0d	—
2	Food	1/3BR	16a	17a	19a	12b	57b	7c	67a
		BR*	14b	16a	18a	35a	73a	26b	55a
		3BR	9c	11b	13b	52a	85a	43a	54a
3	Crowding (L1/pan)	300[4]	10b	12b	13b	65a	75a	47a	51a
		600*[4]	11b	12b	14b	43a	64a,b	28b	55a
		1200	14a	16a	16a	16b	52b	8c	64b
		2400	14a	16b	17a	5b	57b	3c	68b

[1] Control groups for each experiment (26°C, BR, 600 L1/pan) indicated by *; means followed by the same letter within each experiment were not significantly different when tested by a Duncan's multiple range test ($P > 0.05$).

[2] P_{50} and E_{50} were median times from eclosion to pupation and adult emergence, respectively.

[3] L1 = 1st instar, P = pupae, A = adult.

[4] n = 8 replicate pans.

tested by ANOVA: mean tap water control survival = 77%, 600 L1/pan = 63%, 1200 L1/pan = 53%, and 2400 L1/pan = 77%, $F = 0.43$, $P > 0.05$. These results implied that interference competition by GRF production was not an important component of rearing stress for *Cx. tarsalis* at the densities studied.

The proportion of males emerging in each group was inversely correlated with immature survival (L1 to A) ($r = -0.901$, $df = 8$, $P < 0.01$). Since the stressed groups also required a longer developmental period and females always took longer than males to emerge, females were exposed to suboptimum rearing conditions for a longer time period, which may have increased immature female mortality (Table 2).

EFFECTS OF STRESS ON ADULT QUALITY AT EMERGENCE. A total of 405 females and 398 males emerging first and last from each pan were measured to determine wing length (Table 3). Females were significantly larger than males within groups, although the largest males produced under unstressed conditions were larger than the smallest females produced under stressed conditions (Table 3). With the exception of the males in Exp. 1, no significant differences were found between the size of the first and last 5 adults emerging from each pan.

Mean female and male wing length were positively correlated with L1 to adult survival ($r = 0.881$ and 0.933, respectively, $df = 8$, $P < 0.01$). Adult size decreased with increasing water temperature and decreasing amount of food per larva in Exp. 1–3 (Table 3).

The proportion of autogenous females was low at all larval rearing temperatures, despite significant size increases among females reared at lower water temperatures (Table 3, Exp. 1). Increasing the quantity of food per larva in Exp. 2 and 3 resulted in significant increases in the proportion of autogenous females (Table 3). These data imply that increased female size, *per se*, was not necessarily related to autogeny status. However, when pooled over all experiments, autogenous females were significantly larger ($\bar{x}$ wing length = 4.25 mm, n = 63) than concurrently reared anautogenous females ($\bar{x}$ = 3.87 mm, n = 684).

Adult size as indicated by wing length did not influence mating success under the present test conditions (Table 4). The ratio of female/male wing length size ranged from 0.98 to 1.42 among crosses. The mean female/male ratio for 4 unstressed groups (Table 4) was 1.22 with a mean ±95% confidence interval of 79 ± 6% of the surviving females inseminated after the 7 day cohabitation period. No discernible trend in the mean female/male size ratio was found among groups having significantly higher or lower insemination rates. In addition, the insemination rate of autogenous females (75%) was not significantly different from that of anautogenous females (77%).

EFFECTS OF IMMATURE STRESS ON LIFE TABLE ATTRIBUTES. Despite significant differences in female size (Exp. 1 and 3), mean fecundity and fertility did not significantly vary among groups within experiments (Table 5). Mean female size

Table 3. Effects of rearing conditions on size at emergence and autogeny of *Culex tarsalis* adults[1].

	Wing length (mm)								
	Females			Males				Autogeny	
Experiment	First 5	Last 5	$\bar{x}$	First 5	Last 5	$\bar{x}$		%	(n)
1. Temperature (C)	18	4.06	3.98	4.02a	3.69	3.41	3.55a	1a	(180)
	26	3.80	3.92	3.87b	n.d.[2]	3.37	3.37b	1a	(99)
	31	3.39	3.43	3.41c	3.00	3.08	3.03c	0a	(49)
	$\bar{x}$	3.74a	3.79a	3.77	3.35a	3.31a	3.32		
2. Food	1/3BR	3.61	3.51	3.58b	3.19	3.10	3.15b	0b	(36)
	BR	3.84	3.62	3.75b	3.21	3.14	3.18b	5b	(96)
	3BR	4.10	4.19	4.15a	3.44	3.62	3.53a	35a	(147)
	$\bar{x}$	3.85a	3.84a	3.85	3.28a	3.32a	3.30		
3. Crowding	300	4.09	4.17	4.13a	3.50	3.59	3.54a	59a	(100)
	600	3.74	3.81	3.78b	3.25	3.30	3.27b	13b	(149)
	1200	3.66	3.47	3.58c	3.15	3.01	3.08c	n.d.[2]	
	2400	3.70	3.54	3.62c	3.19	3.00	3.09c	0c	(52)
	$\bar{x}$	3.79a	3.78a	3.79	3.27a	3.23a	3.25		
	$\bar{x}$	3.79a	3.80a	3.79	3.29a	3.27a	3.28		
	n	208	197	405	200	198	398		

[1] Row or column means followed by the same letter were not significantly different when tested by a Duncan's multiple range test (wing lengths) or contingency χ^2 (autogeny) ($P > 0.05$). n = sample size.
[2] n.d. = not done.

Table 4. Crosses among stressed (small-sized) and unstressed (large-sized) *Culex tarsalis* adults (n = 50 pairs/"bucket" cage).

Experiment	Source ♂	Source ♀	x̄ Wing length (mm) ♂	x̄ Wing length (mm) ♀	x̄ Wing length (mm) ♂/♀	Inseminated (%)
1. Temperature (°C)	31	31	3.04	3.46	1.14	84
	31	18	2.87	4.07	1.42	65
	26	18	3.27	4.09	1.25	76
	18	31	3.41	3.46	1.01	75
	18	26	3.58	3.54	0.99	96
	18	18	3.41	4.08	1.20	83[1]
	26	26	3.21	3.87	1.21	72[1]
2. Food	1/3BR	3BR	3.11	4.16	1.34	77
	BR	3BR	3.21	4.34	1.35	78
	3BR	1/3BR	3.64	3.58	0.98	89
	3BR	BR	3.64	3.80	1.04	51
	3BR	3BR	3.29	4.31	1.31	78
	BR	BR	3.20	3.90	1.22	84[1]
3. Crowding (L1/pan)	2400	2400	3.30	3.59	1.08	85
	2400	600	3.11	3.78	1.22	96
	600	2400	3.07	3.55	1.16	85
	600	600	3.19	3.78	1.18	80[1]

[1] Unstressed ♂ × unstressed ♀ or control crosses.

and fecundity were not significantly correlated among groups ($r = 0.205$, $df = 7$, $P > 0.05$). These results were unexpected, since Bock and Milby (1981) and White (1980[2]) reported that when evaluated singly, larger *Cx. tarsalis* females oviposited significantly more eggs per raft. It may be critical that the present data compared group means during peak emergence rather than female-specific wing length and fecundity data. Reisen et al. (1979) similarly found no relationship between mean wing length and mean fecundity of *Cx. tritaeniorhynchus* Giles females in life table experiments. Fertility (% hatch) was 54% for all rafts from all groups. Many of the unhatched eggs were embryonated, indicating that low egg hatch was not entirely due to a low insemination rate.

Female life expectancy at emergence ranged from a mean of 14.4 to 19.3 days, but did not vary significantly among treatments within experiments (Table 5). Greater differences were observed among male life expectancy estimates, with stressed males having a shorter life expectancy. Unexpectedly, males reared under conditions of excess food (3 BR) or low density (300 L1/pan) had a longer mean life expectancy than did sibling females. Differences here may relate to the additional female-specific stress associated with blood feeding and oviposition. Mean adult size was significantly correlated with both female ($r = 0.65$) and male ($r = 0.76$) mean life expectancy at emergence ($df = 7$, $P < 0.05$); i.e., groups with larger adults tended to live longer.

Series A life table estimates which included the net reproductive rate (R_o), mean female age at reproduction (T_o) and the innate rate of increase (r_m) did not vary significantly among groups within experiments (Table 5). Trends relating to differences in female quality were masked by within group variability. However, significant trends among life table attributes were detected using correlation analyses when all 29 replicate cohorts were pooled regardless of treatment status. Mean male wing length was correlated with male life expectancy at emergence, e_1 ($r = 0.50$, $P < 0.01$), and daily survivorship, s ($r = 0.36$, $P < 0.05$). Similarly, female wing length was correlated with ♀ e_1 ($r = 0.41$, $P < 0.05$) and ♀ s ($r = 0.58$, $P < 0.001$). The relationship of size to life expectancy and survivorship was attributed to rearing stress, since mean male and female wing lengths were well correlated among cohorts ($r = 0.92$, $P < 0.001$). Unexpectedly, the number of rafts oviposited ($r = 0.07$, $P > 0.10$), eggs per raft ($r = 0.27$, $0.10 > P > 0.05$) and hatch rate ($r = 0.12$, $P > 0.05$) per cohort varied independently of mean female wing length. The significant relationship of female wing length with ♀ s was reflected in a positive correlation with T_o ($r = 0.43$, $P < 0.01$) and a negative correlation with r_m ($r = -0.37$, $P < 0.05$), but not with R_o ($r = 0.18$, $P > 0.10$). As expected, R_o in series A was well correlated with cohort reproductive effort, expressed as total rafts ($r = 0.89$, $P < 0.001$), total eggs ($r = 0.98$, $P < 0.001$), or eggs/raft ($r = 0.39$, $P < 0.05$). r_m was correlated negatively with ♀ s ($r = -0.39$, $P < 0.05$) indicating the rate of reproduction in cohorts with reduced survivorship was more rapid. Conversely,

Table 5. Effects of rearing conditions on the life table characteristics of *Culex tarsalis* using 2 calculation methods.

Attributes[1]		1. Temperature (°C)			2. Food		3. Crowding (L1/pan)			
		18	26	31	BR	3BR	300	600	1200	2400
No. replicates		4	4	2	4	4	3	4	3	1
Wing length-mm(n)	♀	4.01(88)a	3.77(77)b	3.46(44)c	3.84(92)a	3.88(90)a	3.97(62)a	3.69(87)b	3.55(68)c	3.76(21)b
	♂	3.33(79)a	3.20(8)b	3.03(45)c	3.27(85)a	3.26(86)a	3.40(60)a	3.16(86)b	3.04(73)c	3.24(25)b
Life expectancy (days)	♀	19.0a	19.1a	15.0a	17.8a	16.6a	16.9a	14.8a	14.4a	19.3a
	♂	16.9ab	20.3a	12.6b	15.8a	21.2a	22.7a	13.5b	13.0b	16.5ab
Daily survivorship	♀	0.97a	0.97a	0.95a	0.97a	0.97a	0.97a	0.95a	0.94a	0.96a
	♂	0.97a	0.97a	0.95a	0.97a	0.95a	0.97a	0.96a	0.94a	0.96a
Fecundity (eggs/raft)		158a	161a	141a	166a	157a	143a	164a	156a	162a
Fertility (% hatch)		48a	59a	45a	56a	60a	53a	58a	57a	57a
Series A[2]	R_o	171.8a	209.0a	153.1a	140.8a	196.0a	141.4a	207.1a	141.3a	242.8a
	T_o	9.7a	8.3a	7.6a	8.1a	7.7a	9.0a	6.8a	6.2a	6.2a
	r_m	0.57a	0.65a	0.69a	0.62a	0.67a	0.56a	0.79a	0.80a	0.88a
Series B[3]	R_o	41.5a	43.4a	14.6b	20.5a	51.1a	33.2a	35.4a	7.8b	8.3b
	G_o	44.1a	34.8b	30.0b	34.9a	30.4b	29.2a	29.7a	31.3a	32.3a
	r_m	0.08a	0.11a	0.09a	0.08b	0.12a	0.12a	0.12a	0.06b	0.07b

[1] Row means followed by the same letter were not significantly different when tested by a Duncan's multiple range test ($P > 0.05$).

[2] Series A considers all eggs to produce female adults instantaeously; R_o = net reproductive rate, T_o = age of female reproduction, and r_m = innate rate of increase.

[3] Series B includes egg hatch, developmental mortality and time for each cohort; G_o = generation time in days.

cohorts in which ♀ e_1 was elongated tended to have a higher R_o ($r = 0.52$, $P < 0.01$).

Combining both immature and adult attributes (series B, Table 5) resulted in a reduction in reproductive estimates, R_o and r_m, due to the impact of reduced egg hatch and immature survival (Table 2). The effects of stress and temperature on immature developmental rates resulted in significant differences among estimates of generation time (G_o). Stressed groups within experiments exhibited significantly reduced reproductive effort per group agreeing with trends in group wing length. Series B estimates were markedly influenced by immature survival and development times (Table 2), which tended to mask changes introduced by variations in adult quality.

COMPOSITE LIFE TABLE. Since treatments minimally altered series A life table estimates (Table 5), mosquitoes from all 29 cohorts ($n = 623$ males and 657 females) were pooled and a complete life table calculated. Male life expectancy at emergence was $e_1 = 17.1$ days. Daily survivorship, l_x, approximated a type II curve of Deevey (1947) or a type III curve of Slobodkin (1962) and fit well a negative curvilinear regression function, $\log_{10}(l_x \times 1000) = 2.613 - 0.066x$, $r^2 = 0.93$, $n = 50$ (Fig. 1a). Mean male daily survivorship, calculated from the regression coefficient, was $s = 0.94$. The daily mortality rate (d_x) was highest on days 17 to 22, when d_x ranged from 0.032 to 0.056 per day. After day 30 of life, the death rate declined to less than 0.015 and concurrently e_x increased (Fig. 1a). Male wing length increased as a linear function of age at death (Fig. 1b), indicating larger males lived longer.

Comparable survivorship and life expectancy patterns were observed for females with $e_1 = 17.0$ days. The l_x curve fit the regression model well ($\log_{10}(l_x \times 1000) = 2.477 - 0.056x$, $r^2 = 0.97$, $n = 62$, Fig. 2a) with $s = 0.95$. Maximum mortality occurred between days 18 and 24 of life, when d_x ranged from 0.032 to 0.065, after which e_x remained relatively constant and then increased markedly to 9.8 days on day 40 of life. Enhanced life expectancy by older females would have considerable impact on arbovirus epidemiology, since the older, and potentially infective, component of the population is responsible for virus dissemination. As with males, larger females tended to live longer (Fig. 2b).

Overall, the 657 ♀♀ oviposited 1459 egg rafts ($\bar{x} = 2.2$ rafts/♀). Mean fecundity was 157.7 eggs/raft and fertility (percent hatch) was 54%. The number of rafts oviposited, fecundity and fertility decreased as a function of female age (Figs. 3a, b). Reproductive effort (m_x = female eggs/female/day) was maximal on day 5 ($m_x = 20.7$ ♀♀/♀) and ranged from 6.3 to 20.7 ♀♀/♀ for days 5–10 of female life (Fig. 3c). The intervals between the 1st 4 maxima of m_x on days 5, 10, 13 and 18 were 5, 3 and 5 days,

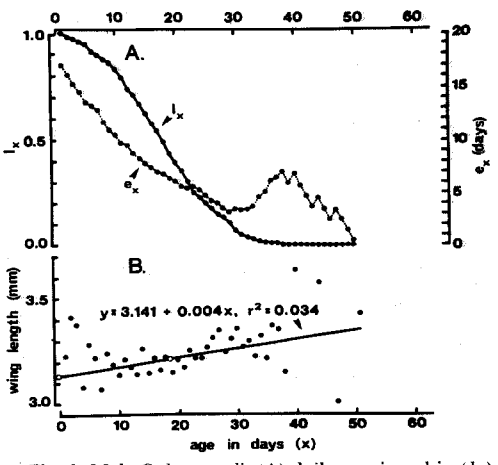

Fig. 1. Male *Culex tarsalis* (A) daily survivorship (l_x), expectation of further life in days (e_x) and (B) mean wing length in mm of males dying on day x plotted as a function of male age in days (x). Regression coefficient calculated for all males ($n = 623$) significantly deviated from 0 ($P < 0.001$).

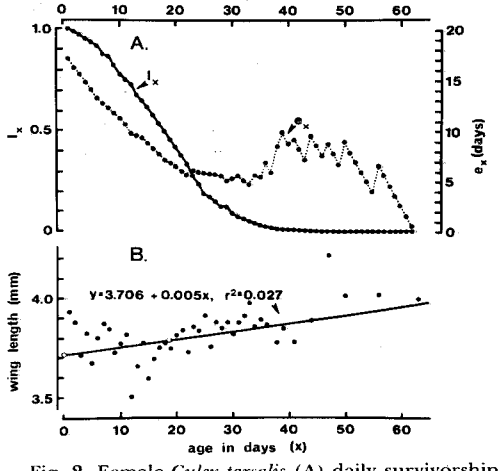

Fig. 2. Female *Culex tarsalis* (A) daily survivorship (l_x) and expectation of further life in days (e_x), and (B) mean wing length in mm of females dying on day x plotted as a function of female age in days (x). Regression coefficient calculated for all females ($n = 657$) significantly deviated from 0 ($P < 0.001$).

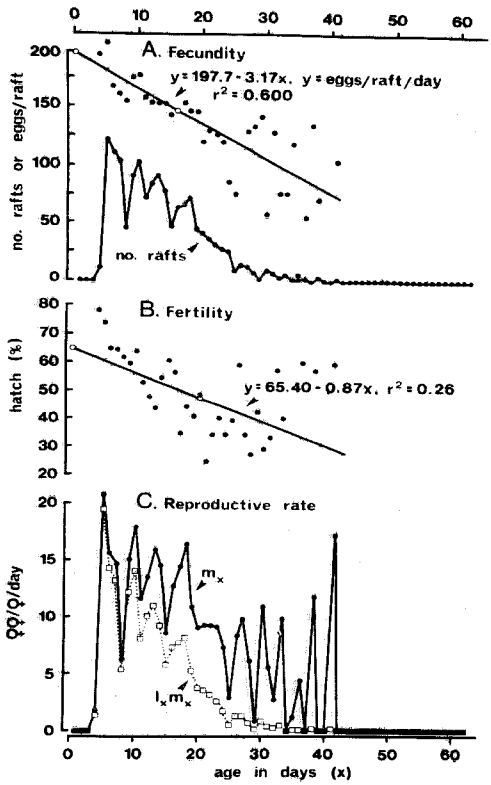

Fig. 3. Female *Culex tarsalis* (A) fecundity, (B) fertility, and (C) reproductive rate plotted as a function of female age in days (x). m_x = female eggs/female/day and l_x = survivorship.

respectively ($\bar{x}$ = 4.3 days), perhaps indicating the duration of the gonotrophic cycle under insectary conditions. When corrected by survivorship, the resulting l_xm_x curve depicted cohort reproductive effort and emphasized the contribution of the day 5 maximum. R_o was 175.2 female eggs/female/generation with the mean age of reproductive effort, T_o = 12.3 days. The innate rate of increase was high, r_m = 0.71, and upwardly biased by the deletion of the immature developmental period (egg hatch to 1st oviposition, d = 24 days) and immature mortality (a) by using series A calculation methods (Table 5). In contrast, using series B calculations with a = 0.31, d = 24.0 days and m_x based on hatching eggs, R_o = 30.1 ♀♀/♀/generation, T_o = 11.2 days, r_m = 0.101, and G_o = 33.9 days.

DISCUSSION

The rearing conditions used as controls in the present study were considered suitable for *Cx. tarsalis*. When reared at a density of 600 L1/pan and fed between 3.0 and 3.35 cc of food, each larva was offered a minimum of 4.5 to 5.0 mg of food during larval development (1 cc diet ≅ 0.9 g). The actual quantity of food consumed was not determined, since L1 to A survival rarely exceeded 50% and excess food accumulated as a visible residue in the bottom of all rearing pans. The highest amounts of food added per larva were 14 and 10 mg/L1 in the 3 BR group in Exp. 2 and the 300 L1/pan group in Exp. 3, respectively. Our food addition rate per larva was comparable to that used by Kardos (1959) who observed good survival and 93% autogeny for groups fed 11 mg/L1. Moore (1966[3]) reported a maximum autogeny expression of 49.4% at food addition rates of 17.5 mg/L1, but achieved > 90% L1 to A survival with rations as low as 4.2 mg/L1, even though the autogeny rate declined to < 11.3%. Downe and Archer (1975) reported good rearing success using 7.5 mg/L1, while Hayes et al. (1974) attained best results with 1.4 mg/L1 of a high protein diet. All studies used relatively high protein content (23–46%) animal or fish foods. It may be important that these authors used stocking densities between 100–350 L1/pan; considerably less than our standard 600 L1/pan density using pans of comparable size.

Cool rearing temperatures suppressed the expression of autogeny in *Cx. tarsalis*. Rearing females at 18°C in Exp. 1 inhibited the expression of autogeny, even though female size at emergence was comparable to that of the 3 BR group in Exp. 2 and the 300 L1/pan group in Exp. 3. These results agreed closely with Moore (1966[3]) who also observed an inhibition of autogeny expression when females were reared at 18°C, but contrasted with results reported for *Culex pipiens* Linn., where large size and a slower development rate were associated with an increased incidence of autogeny in autumn (Twohy and Rozeboom 1957, Spielman 1971). The inhibition of autogeny in *Cx. tarsalis* when reared at cool water temperatures agrees well with the midsummer-dominated temporal pattern of autogeny in California reported by Moore (1963) and Spadoni et al. (1974). Adding comparable total quantities of food may not be

[3] Moore, C. G. 1966. Environmental factors influencing the proportion of autogenous ovarian development in populations of the mosquito *Culex tarsalis* Coq. Ph.D. Diss., Univ. of California, Davis. 105 pp.

equivalent to increasing the ration per mosquito per day early in immature development. Thus, the control groups in Exps. 1 and 2 exhibited 1 and 5% autogeny, respectively, while the control group in Exp. 3 receiving twice the initial basic ration but relatively comparable total food (Table 1) exhibited 13% autogeny. Maximum expression of autogeny was observed in Exp. 3 when the density was 300 L1/pan and the ration per larva was 10 mg/L1; less than the 14 mg/L1 added in the 3 BR group in Exp. 2. Thus, crowding as well as the quantity of food added per larva per day may also influence the expression of autogeny. In Exp. 2 and 3 at temperatures of 26°C, groups expressing the highest autogeny rates were also larger in size. Overall, autogenous females were significantly larger than and exhibited insemination rates comparable to anautogenous females. Apparently mate recognition cues were not altered by increased female size or the presence of developing ovaries.

Competitive interactions among *Cx. tarsalis* immatures in the present experiment seemed limited to scramble competition for available resources rather than interference competition. In the subgenus *Culex*, interference competition among pre-adults has been shown to include cannibalism (Mogi 1978b) and the production of a growth retardant factor(s) (GRF of Moore and Fisher 1969) in crowded *Cx. quinquefasciatus* Say (Ikeshoji and Mulla 1970) and *Cx. tritaeniorhynchus* (Siddiqui et al. 1976). Cannibalism in *Cx. tritaeniorhynchus* was shown to be restricted to interactions between 4th instar and 1st instar larvae (Mogi 1978b) and thus was not considered applicable to the present experimental conditions. Rearing water from the crowded groups in Exp. 3 did not exhibit autocidal activity against 1st instar larvae suggesting the absence of GRF.

Altering the rearing temperature and including intraspecific scramble competition for food markedly stressed the immature stages of *Cx. tarsalis*. The intensity of stress induction was indicated by reduced immature survivorship, delayed immature development, altered sex ratios at emergence, reduced adult wing length, and inhibited expression of autogeny. However, marked differences were not discerned in the insemination rates and reproductive effort of stressed and unstressed adults within experiments. Reciprocally crossed stressed and unstressed adults exhibited insemination rates comparable to crosses among controls indicating mechanical barriers to insemination were not introduced by the range of mosquito sizes produced. The range in size of adult wing lengths reported in the present study was comparable to the range of values presented by White (1980[2]) for females trapped as adults or emerging from field-collected pupae from Poso West, but was considerably smaller than the trapped females reported by Bock and Milby (1981) from Breckenridge, Kern Co., California. Both natural populations developed in oil field effluent water enriched by cattle excrement.

Unexpectedly, groups with stressed (smaller-sized) females were not less fecund and exhibited R_0 values comparable to those for groups with unstressed (larger-sized) females. Similar results were observed for *Wyeomyia smithii* Coq., where food stress delayed development and resulted in lighter female pupae, but smaller adult females exhibited fecundity patterns comparable to larger unstressed adults (Moeur and Istock 1980). In the present study, significant differences were not observed in the life expectancy of females derived from different treatments within experiments. However, when trends among replicate cohorts or pooled adults from all experiments were analyzed, larger adults were found to live longer and cohorts with larger mean wing lengths were found to have enhanced survivorship. Longer life expectancy at emergence was correlated with enhanced net reproductive rates. Thus, immature stress seemed to alter uniformly immature survivorship, development rates, and adult size at emergence without producing consistent and predictable trends among life expectancy and reproduction rates. This was especially evident in Exp. 3 where stressed (2400 L1/pan) and unstressed (600 L1/pan) conditions produced adult cohorts of overlapping size and life table attributes.

Immature stress induced by intraspecific competition apparently eliminated less fit individuals in the preimaginal stages with minimal cost to those relatively few, but more competitive, individuals that successfully emerged. Developmental time was elongated and size variable; however, life expectancy and reproductive capabilities were comparable to those of unstressed adults. Stressed females were anautogenous and in nature may have been more dispersive early in life due to host-seeking activity. Conversely, unstressed females that emerged from uncrowded habitats with ample food would be anticipated to exhibit a proportionally higher incidence of autogenous reproduction which would allow for a rapid repetitive exploitation of suitable breeding sites. Habitat relocation would be facilitated by ovipositional pheromones associated with the apical droplet of the egg rafts (Osgood 1971), while resource over-exploitation would be re-

tarded, in part, by the reduced size of egg rafts oviposited by autogenous females (Spadoni et al. 1974). Similar habitat exploitation strategies by the *Cx. pipiens* complex were described by Spielman (1971). These survival and resource exploitative mechanisms were especially appropriate for the persistence of a colonizing species such as *Cx. tarsalis* in irrigated agroecosystems in semi-arid environments. Once located by dispersives, suitable breeding sites could be maximally exploited. As crowding stress becomes excessive, proportionally more females would become anautogenous and disperse in search of a blood meal, presumably increasing their probability of locating new oviposition sites.

Presuming immature abundance exceeds the threshold density necessary for the induction of intraspecific competititve coactions, it may be possible to speculate on the rapidity of population recovery after control applications. In general, successful abatement would reduce catastrophically the intensity of intraspecific competitive stress. Larval control would immediately eliminate pretreatment larval populations, and thereby expose unexploited habitat to ovipositing females. Adult control would reduce the recruitment rate without influencing competitive stress among pretreatment larval populations; however, competitive stress should diminish progressively after pupation. Reducing stress during immature development may increase immature survivorship (a) and enhance the rate of immature development (d). Emerging adults may be larger, survive longer, and express a higher frequency of autogeny. In combination, these factors would enhance the rate of increase (r_m) and shorten generation time (G), thus expediting the rate of population recovery. In addition, larger females may live longer, possibly increasing their expectation of infective life and thus, their chances of disseminating an acquired virus infection. The persistence of *Cx. tarsalis* populations in combination with persistent enzootic western equine encephalomyelitis virus transmission despite concerted control efforts would seem to attest to the ecological resiliency of the species.

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