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LIFETIME MATING PATTERN OF LABORATORY-ADAPTED *CULEX TARSALIS* MALES

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ABSTRACT. The lifetime mating pattern of *Culex tarsalis* males was determined under insectary conditions. Thirty males were individually confined in 4 liter carton cages and were offered new harems of 4–8 day-old virgin females each day from emergence to death. The numbers of males alive and females inseminated per day were used to calculate male life tables, applying statistical methods developed for female mosquitoes.

Male survivorship was estimated to be 98% per day and life expectancy was 29 days at emergence. The mortality rate was greatest between days 15 and 21 of adult life, when 33% of the cohort died. The number of males mating per day was greatest between days 2 and 9, decreasing to zero by day 37. Mating activity was renewed between days 46 and 55. The maximum number of females mated per male per night was 4. Mean lifetime reproductive effort was 12.2 females inseminated per male (range = 0 to 29). Four males accounted for 105 (29%) of the total 360 inseminations. Reproductive effort (females inseminated per male) increased as a function of male longevity, i.e., males living longer inseminated more females.

INTRODUCTION

The success of a genetic control program depends upon a thorough understanding of mosquito population dynamics and the lifetime pattern of reproduction of both sexes. While much is known about the reproductive biology of female *Culex tarsalis* Coq. (McDonald et al. 1979, Nelson and Milby 1982, Zalom et al. 1981), knowledge of male reproductive biology is limited to the laboratory observations of Asman (1975). Since the population dynamics and mating behavior of male mosquitoes is poorly understood, it is difficult to predict the potential contribution of genetically altered males to the gene pool of the target population and thus, decisions pertaining to release rates are often speculative.

Laboratory observations have indicated inter-specific differences in male mating performance which have been associated with variations in reproductive potential. Mahmood and Reisen (1982) found that the reproductive system of *Anopheles stephensi* Liston males rejuvenated after mating, with the replenishment of spermatozoa in the testes and postgonadal system and male accessory gland substance in the accessory glands. Conversely, Hausermann and

Nijhout (1975) found that spermatogenesis in sexually mature male *Aedes aegypti* (Linn.) was negligible and male fecundity was limited.

The present study describes the lifetime mating pattern of individual *Cx. tarsalis* males and calculates time-specific survivorship and insemination schedules. In this way, the possible contribution of each male to the population gene pool could be extrapolated by relating field survivorship estimates to laboratory mating patterns.

MATERIALS AND METHODS

The Breckenridge 1980 (*Br80*) colony of *Cx. tarsalis* originated from females collected during October 1980 from the Sierra foothills 12.5 km east of Bakersfield, Kern County, California. The *Br80* colony was chosen for study because it mated well in 4 liter laboratory cages and was well adapted to insectary conditions of $28 \pm 2°$ C, $60 \pm 10\%$ RH, and 16L:8D with 1-hr crepuscular periods. Progeny from the F_{28} to F_{36} generations were used for experimentation.

Individual *Br80* males less than 24-hr old were placed in 4 liter cardboard cages which were supplied with 10% sucrose on cotton pledgets and moist toweling on the screen tops to increase humidity. Individual males were offered new harems of 4–8 day-old virgin females daily until death. Harem size was reduced from 8 to 5 females after day 31 of the experiment.

Females were removed after 24-hr exposure and dissected to determine insemination status. All spermathecae, and when possible the bursa copulatrix, were excised into 0.5% saline solution and examined at 100X magnification for the presence of spermatozoa. The entire experiment was repeated 3 times for groups of 10 males each.

A life table was calculated for all 30 males following the methods of Deevey (1947). The number of males mating and females mated was tabulated per day. Age-specific male reproductive effort (similar to the fertility statistic, m_x) was expressed as females inseminated per male per day (i_x). The mean lifetime reproductive effort (similar to R_0, the net reproductive rate) was the mean number of females inseminated per male per generation, or,

$$R_m = \sum_{x=1}^{w} l_x i_x \text{ where } l_x \text{ equals age-specific}$$

survivorship for each day (x) until the last male died, w. Cohort survivorship was estimated by log-linear regression presuming daily survivorship approximated a type II curve of Deevey (1947).

RESULTS

Daily survivorship was estimated to be 98%. Survivorship patterns fit the log-linear regression model well ($r^2 = 0.91$, df = 59), indicating a type II curve was appropriate. The mortality rate was greatest between days 15 and 21, when 33% of the cohort died (Fig. 1). Cohort life expectancy (e_x) was 29 days at emergence.

The number of males mating per day was greatest between days 2 and 9 of adult life and then gradually decreased to 0 by day 37. However, mating activity was renewed between days 46 and 55 of age, when 5 of 8 surviving males mated. The number of females inseminated per day was greatest on days 2 and 3, when multiple matings (averaging more than one female inseminated per male mating) frequently occurred (Fig. 1). The number of females inseminated per day per surviving male, i_x, decreased significantly as a linear function of male age in days, x, for days 2 to w; $i_x = 0.678 - 0.013x$, $r^2 = 0.486$, n = 60, P < 0.01. Multiple matings recurred throughout life, even as late as day 49. The maximum number of females inseminated per male per night was 4. The mean time interval between the 1st and 2nd matings for males mating with 1 female on mating 1 ($\bar{x} \pm 95\%$ confidence interval = 1.50 ± 0.64 days, n = 12 males) was not significantly different (P > 0.05) from males mating with $\geqslant 2$ females on mating 1 (1.20 ± 0.20 days, n = 17 males). The mean time interval between the 2nd and 3rd matings was longer than between 1st and 2nd matings, but was not significantly different (P > 0.05) between males mating with 1 female (2.56 ± 1.48 days, n = 16 males) or $\geqslant 2$ females (2.00 ± 0.95 days, n = 11 males) on mating 2. In addition, cycles of increased mating activity were not graphically apparent (Fig. 1). Collectively, these data indicate that recovery or rest periods were not necessary between successive nights on which inseminations occurred.

The mean lifetime reproductive effort was $R_m = 12.2$ females inseminated per male per generation. Mating performance varied considerably among males (Fig. 2), ranging from 0 to 29 females mated per lifetime. Four males mated with more than 22 females and collectively accounted for 105 (29%) of the total 360 inseminations. Males which lived the longest also mated with the most females.

DISCUSSION

Estimated daily survivorship of the *Br80* males (98%) under insectary conditions exceeded estimates reported for males of this same strain in outdoor cages during May and
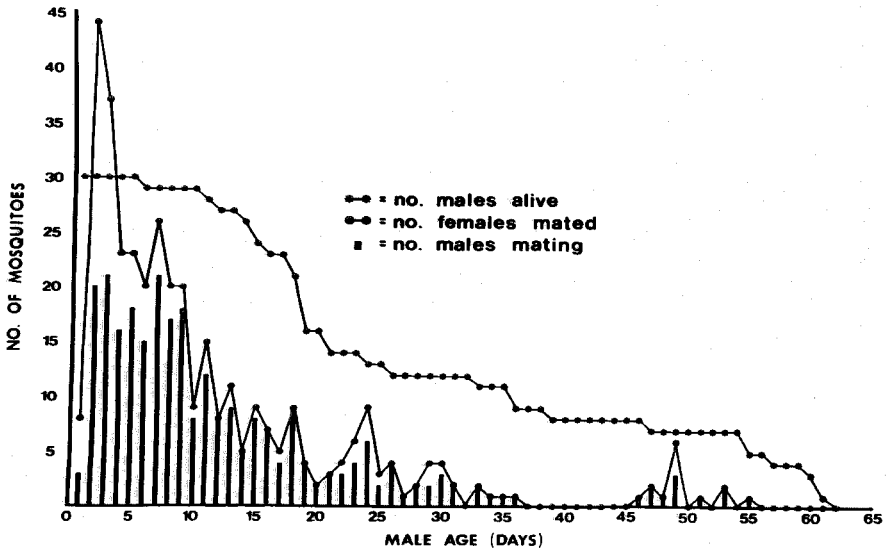
Fig. 1. Lifetime patterns of survivorship and mating for 30 laboratory-adapted *Culex tarsalis* males under insectary conditions.
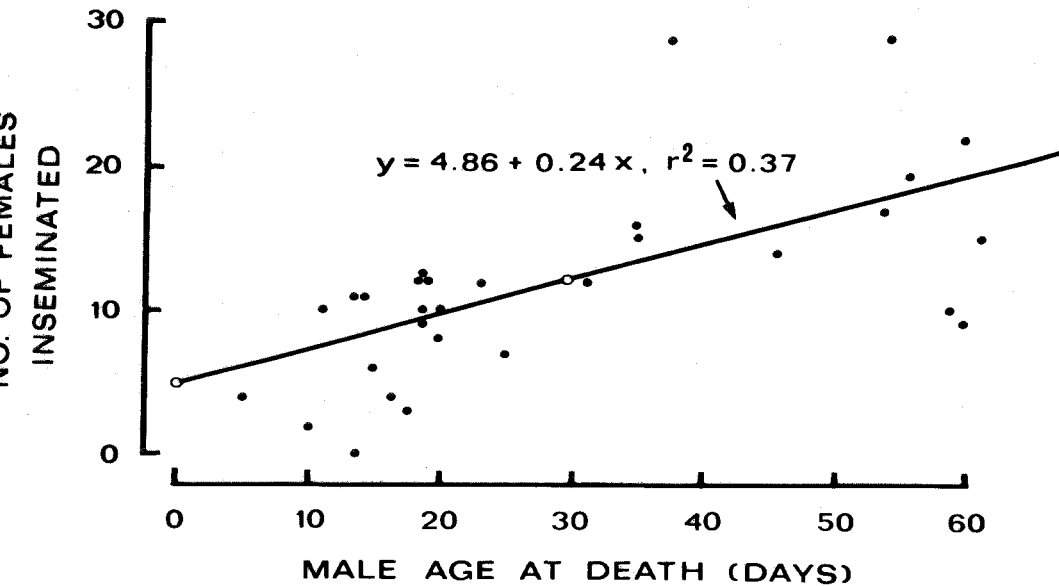

Fig. 2. Lifetime reproductive effort of 30 *Culex tarsalis* males (no. of females inseminated) plotted as a function of age at death. Regression coefficient significantly differed from 0 when tested by ANOVA (P < 0.01). Regression line plotted through intercept and $\bar{x}$, $\bar{y}$ (open points).

June (80%), and in mark-release-recapture experiments at Breckenridge during spring (84%) (Reisen et al. 1982), July (71%) and August (81%) (Reisen et al. 1981). Although subject to inherent difficulties in estimation, these values do provide some indication of the additional impact of natural mortality factors on the daily survivorship of male mosquitoes.

Male *Cx. tarsalis* reproductive activity commenced shortly after emergence, with some inseminations observed the 1st night that females were available. These matings commenced somewhat earlier than reported by Asman (1975), who first detected mating activity when the cohabiting pairs were 72 hours old. In the present study multiple-mating occurred early in male life, agreeing with Asman (1975) who also found that males multiple-mated when 72 hours old. Differences in the onset of male sexual activity between the present and the Asman (1975) study may be related to age when females become sexually receptive. All females used in the present study were ≥ 4 days old when offered to the males and were sexually mature. In addition, we have observed that males were able to successfully inseminate females as soon as terminalia rotation was completed using the forced copulation technique (unpublished observations). The concentration of reproductive effort early in life would enhance the chances of each male contributing to the population gene pool, even when survival is low. Enhanced survival and continued reproductive competence throughout life also may be advantageous when generations are overlapping by enhancing gene mixing.

Under insectary conditions, male *Cx. tarsalis* appear to be especially long-lived and reproductively active, as compared to laboratory strains of 4 mosquito species for which comparable male life expectancy and lifetime reproduction data were available (Table 1). The intraspecific reproductive patterns exhibited by *Cx. tarsalis* (Fig. 2) agreed with these interspecific trends (Table 1) and suggested that longer-lived individuals or species inseminated more females during their lifetime.

Culex tarsalis did not exhibit marked and/or rhythmic recovery intervals (or cessation of reproductive activity) after mating, as described for other mosquito species (e.g., *Cx. tritaeniorhynchus,* Reisen et al. 1979b). Spermatogenesis presumably occurs during these recovery or rest periods when sperm are replenished in the sperm reservoir and postgonadal system. Possible explanations for continued sexual activity in *Cx. tarsalis* included: a) males initially produced sufficient sperm to mate throughout life with up to 29 females, b) spermatogenesis occurred continually and rapidly enough to replace used sperm, and/or c) mating did not continue to the depletion of sperm. Most likely, males produced sufficient sperm by sexual maturity to preclude depletion during the period of intense mating activity early in life. Sperm replenishment was rapid and sufficient to compensate for losses, since males may not have mated to depletion.

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Table 1. Interspecific comparison among male life expectancy and fecundity for 5 mosquito species.

Species	Life expectancy (days)	Male fecundity (♀♀'s/♂)	Source[1]
Ae. aegypti (L.)	13.5	8.3	a,b
An. culicifacies Giles	10.9	2.1	c
An. stephensi Liston	11.1	4.4	d
Cx. tritaeniorhynchus Giles	14.8	5.2	e
Cx. tarsalis Coq.	29.0	12.2	f

[1] Source: a = Crovello and Hacker (1972), b = Hausermann and Nijhout (1975), c = Reisen et al. (1979a), d = Mahmood and Reisen (1982), e = Reisen et al. (1979b), and f = present study.

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