

Population Ecology and Dispersal of *Culex tarsalis* (Diptera: Culicidae) in the Coachella Valley of California

WILLIAM K. REISEN AND HUGH D. LOTHROP

Arbovirus Research Program, Division of Epidemiology and Public Health Biology, School of Public Health,
140 Warren Hall, University of California, Berkeley, CA 94720

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ABSTRACT During 5 bimonthly experiments in 1993, 55,548 host-seeking and 22,563 newly emerged *Culex tarsalis* Coquillett females were marked with fluorescent dust and released at a marsh along the Salton Sea. Overall, 3,758 (6.7%) host-seeking and 37 (0.2%) newly emerged females were recaptured in dry ice-baited traps and walk-in red boxes operated for 7-12 consecutive days after release. The recapture rates and dispersiveness of females collected host-seeking within the study area were not different from females collected host-seeking at a site 16 km SE of the release site, indicating that *Cx. tarsalis* may not rely on memorized flight paths. Loss rates of host-seeking females were high, because many females readily dispersed from the marsh study area during host-seeking flights. Estimates of population size ranged from 914,000 in February to 4,000 in July and were well correlated with catch size in CO₂ traps. The wing length and fructose positivity rate of released females did not vary as a function of age or dispersal distance at recapture. Parity of released females increased over time, but nullipars were collected during all recapture periods, perhaps indicating difficulty in blood meal acquisition. Cohort dispersal progressed at the rate of about 0.2 km/d and was sufficient to disseminate arboviruses in the southern Coachella Valley.

KEY WORDS *Culex tarsalis*, mark-release-recapture, population size, survivorship, dispersal

IN THE COACHELLA Valley of California western equine encephalomyelitis (WEE) and St. Louis encephalitis (SLE) viruses initially are active along the shore of the Salton Sea and then spread gradually to the NW up the Whitewater Channel flood plain (Reisen et al. 1995a, b). The relatively slow rate of virus dispersal (0.2-1.4 km/d) and its spatial association with specific physiographic features and mosquito abundance indicated that infected *Culex tarsalis* Coquillett may play an important role in virus dissemination. However, the direction and rate of dispersal by host-seeking female *Cx. tarsalis* have not been investigated in this area. The Salton Sea and adjacent environs differ markedly from habitats previously studied in the Central Valley (Reisen and Reeves 1990), because this area is ≈ 70 m below sea level, has minimal relief or vegetation higher than 15 m, and averages 5°C warmer than the Central Valley during most months. The abundance of *Cx. tarsalis* is typically bimodal in Coachella Valley with peaks in late spring and early fall, reflecting reduced water availability and elevated temperature during summer, and cool temperatures during winter (Reisen et al. 1995a, c).

The objectives of the current research were to describe seasonal changes in the direction and rate of dispersal and in the population attributes of size, loss and addition rates, and blood-feeding frequen-

cy of *Cx. tarsalis* in the southern Coachella Valley using mark-release-recapture methods. Seasonal changes in the survivorship and distribution of the unmarked female population were included for comparison. An interim summary of this research was reported by Reisen and Lothrop (1994).

Materials and Methods

Study Area. Mosquitoes were released at Dextex, a marsh managed for duck hunting that was situated near the northwest shore of the Salton Sea, Riverside County, California (Fig. 1). Vegetation along the shore of the Salton Sea was dominated in marsh habitat by cattails, *Typha*; pickle weed, *Salicornia*; and arrowhead, *Pluchea*; in desert scrub habitat by salt bush, *Atriplex*, and tamarisk, *Tamarix*; and in agricultural habitat by row crops, alfalfa, citrus, and dates. Duck hunting clubs and fish farms were restricted to areas below sea level within the Whitewater Channel flood plain, whereas orchards were situated in well-drained upland soils.

Rainfall was recorded at the Thermal Airport ≈ 15 km north of the release site and downloaded from the IMPACT weather system maintained in conjunction with the California Irrigation Management Information System at the University of Cal-

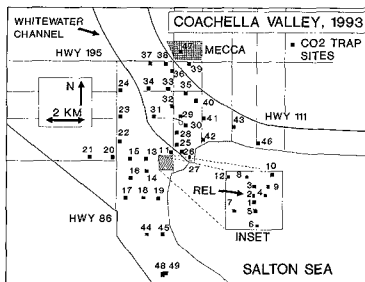


Fig. 1. Map of the southern portion of the Coachella Valley, Riverside County, California, showing the location of the release site, REL, and 49 fixed CO₂ trap sites.

ifornia, Davis. Wind speed and direction were recorded continuously at the release site; however, only data for the period from 1 h before to 3 h after sunset for days 1–5 after release were presented, because this was the time when most *Cx. tarsalis* dispersal occurred. The temperature and humidity of mosquito resting and activity air space environments were measured by Datapod loggers (OmniData, Logan, UT) placed in burrow and under palm frond canopy habitats at site 30 (Fig. 1). Diurnal readings in the burrow and nocturnal readings in the canopy were combined to estimate mosquito environmental conditions (Meyer et al. 1990).

Collection, Mark, and Release Methods. Bi-monthly experiments were planned to coincide with the winter (February), midsummer (July), and autumnal (November) minima and the vernal (May) and late summer (September) maxima of the bimodal *Cx. tarsalis* abundance curve (Reisen et al. 1992a, 1995a). Released cohorts included *Cx. tarsalis* females of known age collected as immatures or females of unknown age collected host seeking at CO₂ traps (dry ice-baited CDC style traps; Sudia and Chamberlain 1962). Immatures were collected from productive surface water sources situated as close as possible to the release site. Sources included overflow pools from the Whitewater Channel (February, near site 26, Fig. 1), marshes at the Salton Sea State Park (May, 10 km SE of site 46, Fig. 1), and duck ponds (November, near site 28, Fig. 1); the numbers of immatures collected during July and September were insufficient for release. Host-seeking females were collected at traps within the central portion of the study area during most experiments (inset, Fig. 1), but were supplemented with females collected at the Salton Sea State Park during May and July.

Field-collected pupae were allowed to emerge into 18.9-liter buckets, in which they were counted by the strip method of Dow et al. (1965). A sample

of 40–50 females was maintained for 7–10 d on 10% sucrose and then dissected to determine autogeny status. Host-seeking females either were aspirated directly from trap collection cages into 18.9-liter buckets for counting by the strip method or were anesthetized, counted by species, and then placed into buckets. Dead or moribund females were removed before marking and subtracted from the total. The wings of 25–40 females from each cohort were measured as an index of body size. Host-seeking females also were dissected to determine parity status using a combination of the tracheation and dilatation methods (Nelson 1966) and tested to determine the presence or absence of fructose using the cold anthrone reaction (Van Handel 1972). A sample of mosquitoes from each bucket was examined to determine species composition. All cohorts were given access to water on moist toweling, but were not fed sugar.

On 3 successive evenings during each experiment, cohorts were transported to the field where they were marked with a cohort-specific colored fluorescent dust and released adjacent to a Tamarisk wind break between trap sites 1 and 2 (Fig. 1). Adults emerging from field-collected pupae were <24 h old at release. Host-seeking females were of unknown chronological age, but were unfed and, therefore, at the beginning of the gonotrophic cycle. Releases were made 1–2 h before sunset.

Recapture Methods. Recapture was attempted for 7–12 successive nights starting after the 1st release and ending when <3 marked females were recaptured. The same 49 CO₂ traps were operated each night on fixed standards within a 6.2-km radius of the release site (Fig. 1). Adults resting in 2 walk-in red boxes (Meyer 1987) deployed within 25 m of the release site were collected each morning during the July, September, and November experiments. Mosquitoes were anesthetized, examined for fluorescent dust, identified to species, and counted. Each day ≈30 marked females per cohort and a sample of 30 unmarked females from traps 1–5 were dissected to determine parity, a wing measured, and the cadaver including the intact diverticula tested for fructose. The relative abundance of the population at the release site was monitored biweekly from January through November 1993 by CO₂ traps operated at sites 1 and 3 (Fig. 1).

Calculations. Daily dispersal rates and the final dispersion pattern were described by regression analysis using the recapture rates of marked females, corrected to account for the decrease in sampling effort as a function of distance from the release point (Brenner et al. 1984). Because recaptures were clumped near the release site, estimates of population size, loss and addition rates, and blood-feeding frequency were restricted to data collected at traps 1–10 and 12 situated within 0.5 km of the release site (inset, Fig. 1). Survivorship of marked females was estimated horizontally by

Table 1. Weather conditions and the number of *Cx. tarsalis* released and recaptured, and the wing length, parity rate, and fructose positivity rate among released females collected as host-seeking females during each bimonthly experiment

Parameters	Bimonthly experiment				
	Feb.	May	July	Sept.	Nov.
Release dates	23-25	11-13	20-22	15-17	9-11
Recapture dates	23 Feb.-5 Mar.	11-20	20-28	15-24	9-23
Weather					
Rainfall (mm)	4	0	13	20	96
Wind direction ^a	319	350	325	322	317
Wind speed (kph)	6.8	2.8	6.8	5.0	5.2
No. females released					
CO ₂ traps	19,419	10,363	7,675	12,560	4,378
Pupae	6,058	1,694	ND ^b	ND	14,810
Autogeny, % (n)	6 (50)	37 (43)	56 (50)	92 (50)	8 (40)
No. females recaptured (%)					
CO ₂ traps	1,330 (6.8)	648 (6.3)	639 (8.3)	846 (6.7)	295 (6.7)
Pupae	23 (0.4)	11 (0.6)	—	—	3 (<0.1)
Characteristics of CO ₂ trap females at release					
No. examined	34	50	85	70	40
Wing length (mm) ^c	3.80c	3.26b	3.10a	3.08a	3.68c
Parity rate	0.24	0.44	0.45	0.53	0.68
Fructose positive ^d	0.83	0.56	0.44	0.54	0.50

^a Wind direction, mean vector within 315-360 approximately northwest to north.

^b ND, not done.

^c Means in row followed by same letter not significantly different ($P > 0.05$).

^d Fructose positivity is the proportion of released females testing fructose positive.

curvilinear regression from the decrease in the recapture rate over time and included deletions caused by death, emigration, removal sampling, and change in gonotrophic status (Milby and Reisen 1989). Because CO₂ traps only sample host-seeking females and may spuriously underestimate survivorship, horizontal survivorship also was estimated from the proportion of released females that survived one gonotrophic cycle (Reisen et al. 1992b). Survivorship of unmarked females was estimated vertically from the parity rate and included deletions caused by death and removal sampling (Davidson 1954). Emigration was calculated as the difference between horizontal and vertical survivorship estimates. Population size was estimated by the modified Lincoln index (Bailey 1952), and the addition rate was calculated by the method of Manly and Parr (1968). The rate of population change was calculated from the difference between addition and loss rates. CO₂ trap efficiency was calculated for each experiment as females per trap night within the central area divided by female population size times 100.

Results

Weather. Wind direction at release was consistently from the N or NW (Table 1). Average wind speed was relatively similar among experiments (Table 1), with the exception of gusts associated with infrequent thunderstorms. Rainfall was infrequent (Table 1), with the exception of the November experiment when brief showers occurred on 5

of the 11 recapture days; trapping was suspended on day 6 when 53 mm of rain fell in late afternoon. Temperature was similar during May and September, and February and November (Fig. 2A). Humidity was highest during November and lowest during July (Fig. 2B). Nocturnal humidity readings during February, May, and July were lost because of recorder failure.

Characteristics of the Unmarked Population.

Relative abundance of the unmarked female population was bimodal with peaks in March and October (Fig. 3). The vernal peak occurred earlier than anticipated following extraordinary flooding of the southern portion of the Whitewater Channel, whereas the autumnal peak occurred later than anticipated because of late flooding of the duck marshes.

Distribution of unmarked females varied significantly among trap sites within experiments when evaluated by a one-way analysis of variance (ANOVA). Trap sites with the greatest abundance varied among experiments when grouped by a least significant range test ($P > 0.05$): February, sites 4, 10, 12, 15, 41, and 42 within or adjacent to flooded desert; May, sites 19 and 44 adjacent to salt marsh; July and September, site 31 near a flooded duck pond and sites 44 and 45 near agricultural discharge into desert/marsh habitat; and November, site 27 and 18 additional traps located within or adjacent to duck marsh habitat (Fig. 1).

The parity rate of 30 unmarked females collected by CO₂ traps within the central study area was regressed as a function of days during each exper-

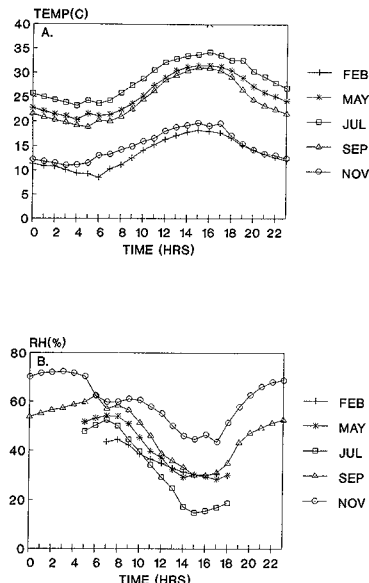


Fig. 2. Mean temperature (A) and relative humidity (B) measured per hour by data loggers positioned in *Cx. tarsalis* resting and activity air space habitat near site 30. Night humidity data during February, May, and July 1993 lost because of probe malfunction.

iment to measure the stability of the age structure of the unmarked population. Although parity rates varied among experiments, there were no significant changes within experiments with the exception of November (Table 2). In November, parity rates ranged from 0.63 to 0.80 during days 1–6, but then decreased gradually to 0.40 by day 9 ($b = -0.036$, $R^2 = 0.635$, $df = 7$, $P < 0.05$). The overall parity rate of unmarked host-seeking females during November (0.62) was higher than the parity rate of females resting in walk-in red boxes (0.23, $n = 35$).

Parity data from each experiment were pooled, adjusted for autogeny, and used to estimate survivorship vertically (Table 2). The loss rates calculated from vertical survivorship included mostly mortality, because the population age structure was stationary during each experiment with the exception of November and losses from removal sampling were negligible ($<0.5\%$, see below).

On 26 February, 20 females each from sites 1–5, 18–19, 20, 24, 25, 30, 37–39, 43, and 44–45 (Fig.

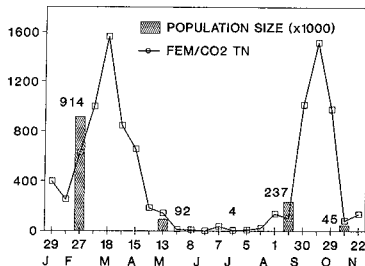


Fig. 3. *Cx. tarsalis* female population size and relative abundance at Dex-o-Tex duck club during 1993.

1) were examined to determine wing length, parity, and fructose positivity. There were no significant differences in mean wing length among groups (ANOVA, $F = 1.3$; $df = 8, 171$; $P > 0.05$), indicating either minimal variability in productivity among breeding areas within the study area or the homogeneous mixing of adults emerging from heterogeneous breeding sources. Parity rates were heterogeneous among groups ($\chi^2 = 40.7$, $df = 8$, $P < 0.001$); 8 groups were similar (range, 0.0–0.22), but the parity rate among females collected at sites 44 and 45 was significantly higher (0.65). Traps 44 and 45 may have been near an oviposition site, because 2 of 13 parous females were saculate, indicating recent oviposition. These data indicated that parity rates among unmarked females may be variable within the study area because of spatial heterogeneity in oviposition sites. Fructose positivity rates were homogenous among sites (range, 0.50–0.92; $P > 0.05$) indicating that nectar sources were available throughout the study area.

Release and Recapture. Overall, 55,548 host-seeking females and 22,563 females emerging from field-collected pupae were marked and released between sites 1 and 2 (Fig. 1), of which 3,758 (6.7%) and 37 (0.2%) were recaptured, respectively (Table 1). The recapture rates for females collected by CO_2 traps were highest during July when the number released was lowest. The recapture rate among females collected as immatures was highest during May (0.6%) and lowest during November (0.02%), even after walk-in red boxes were deployed to improve recapture success. Too few reared females were recaptured for further analysis.

Recapture rates of host-seeking females that were collected at the Salton Sea State Park and released at Dex-o-Tex during May and July were the same ($\chi^2 = 2.8$, $df = 1$, $P = 0.09$) or greater ($\chi^2 = 4.5$, $df = 1$, $P = 0.03$) than females collected within the study area and released concurrently (Table 3). The percentage of females from the Salton Sea State Park recaptured at the 11 traps near the release site during May and July was not sig-

Table 2. Age structure and survivorship of unmarked female *Cx. tarsalis* collected within the central study area during each monthly experiment

Parameter	Bimonthly experiment				
	Feb.	May	July	Sept.	Nov.
No. dissected	300	270	210	270	270
Slope ^a	0.020 NS	-0.011 NS	-0.021 NS	-0.001 NS	-0.036*
Parity rate	0.22	0.54	0.62	0.48	0.62
Autogeny rate	0.06	0.37	0.56	0.92	0.06
Corrected parity ^b	0.21	0.43	0.42	0.07	0.60
Gonotrophic cycle, d ^c	7	5	5	6	6
Survivorship	0.80	0.84	0.84	0.64	0.92
Loss rate	0.20	0.16	0.16	0.36	0.08

^a Slope, regression coefficient of parity on sampling days; t-test; NS, $P > 0.05$; * $P < 0.05$.

^b Corrected for the proportion of females that oviposited autogenously.

^c Duration of the gonotrophic cycle in days (Fig. 4).

nificantly different ($\chi^2 < 3.2$, $df = 1$, $P > 0.07$) from females collected within the study area (Table 3). In addition, there were no differences among slopes of the curvilinear regressions of decreases in the recapture rate as a function of days after release (analysis of covariance [ANCOVA], $F = 0.37$; $df = 1, 8$; $P = 0.37$). Therefore, data from females collected from the Salton Sea State Park and the study area were combined in further analyses.

Only 116 females (7% of 1,780 total recaptures) and 9 males released during July to November were recaptured resting in walk-in red boxes. These recaptures were deleted from subsequent calculations, which were based solely on host-seeking females.

Mean wing length of released host-seeking females varied significantly among months ($F = 116.6$; $df = 4, 274$; $P < 0.001$), being longest during February and November and shortest during July and September (Table 1). The parity ($\chi^2 = 13.7$, $df = 4$, $P < 0.01$) and fructose positivity ($\chi^2 = 15.7$, $df = 4$, $P < 0.01$) rates of released cohorts also varied significantly among experiments.

Recapture rate of marked females decreased significantly ($R^2 > 0.65$, $P < 0.001$) as a curvilinear function of cohort age in days after release (Fig. 4). Age-related changes in the parity rate among marked females varied among experiments. During February ($\chi^2 = 89.9$, $df = 9$, $P < 0.001$) and

May ($\chi^2 = 13.9$, $df = 6$, $P < 0.05$) when the parity rate of the released cohort was relatively low (Table 1), the parity rate among recaptured females increased significantly as a function of cohort age. In contrast, changes in the parity rate were less pronounced in September when the autogeny rate among released females was 0.92, and the parity rate among recaptured females remained >0.5 throughout. The parity rate remained relatively constant during July. During November the parity rate was variable, but did not exceed 0.67 throughout. Marked nullipars were recaptured host-seeking throughout most recapture periods, indicating that females had difficulty in blood meal acquisition. The duration of the gonotrophic cycle during each experiment was delineated by the increase of either the recapture or the parity rates, or both (Fig. 4). The fructose positivity rate varied significantly among experiments, but did not change appreciably as a function of cohort age (Fig. 4). Similarly wing length varied significantly among release experiments (Table 1), but there were no significant changes associated with cohort age (Fig. 4F); i.e., large females did not live longer than small females.

Population Parameters. Parameters of population size, loss, and addition rates were estimated for each experiment using data from the 11 traps positioned within the 0.5-km² central area (Fig. 1) where 84% of the released females were recap-

Table 3. Comparison of recapture rates of *Cx. tarsalis* females collected by CO₂ traps operated at the Salton Sea State Park (SSSP, 10 km SE site 46) or within the study area (area) and released within the central study area in May and July

Parameter	May		July	
	SSSP	Area	SSSP	Area
No. released	4,550	5,813	6,824	851
Total recaptured	315	333	581	58
% recaptured	6.9	5.7	8.5	6.8
% at traps 1-10, 12 ^a	81.6	81.9	95.9	89.7
Slope ^b	-0.58	-0.86	-0.94	-0.88
Survivorship	0.56	0.42	0.39	0.42

^a Percentage of recaptured females not dispersing from the central 11 traps.

^b Slope of the regressions of $\ln(\text{recaptures} + 1)$ as a function of days post release. All slopes significantly different from 0, $R^2 > 0.63$, $P < 0.011$.

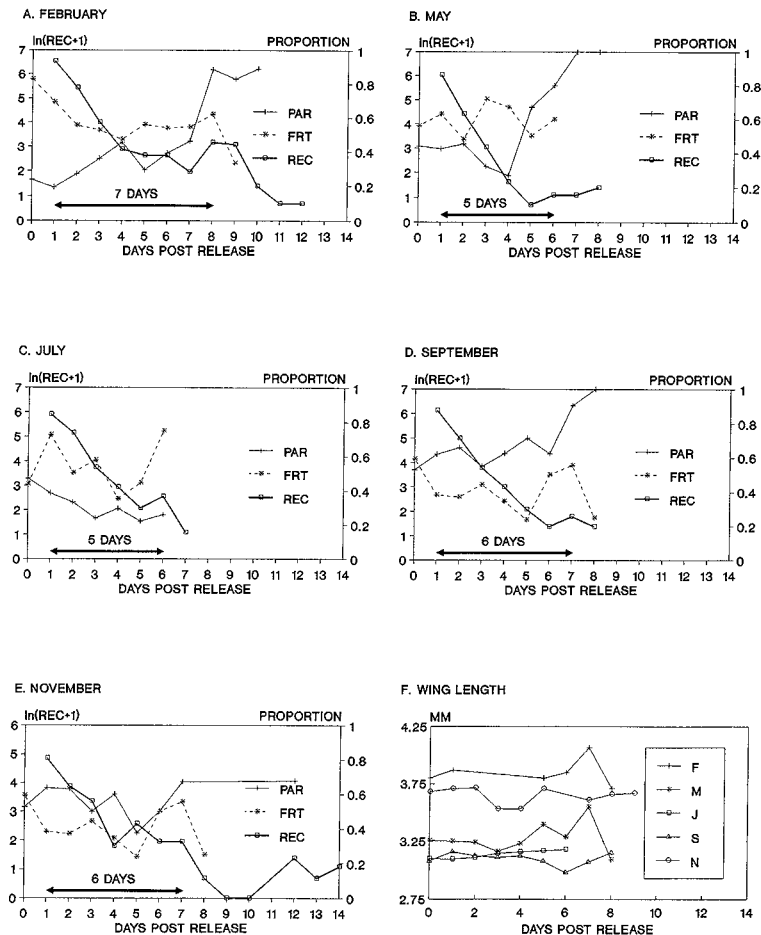


Fig. 4. Number of marked *Cx. tarsalis* females recaptured, REC, transformed by $\ln(y+1)$, and the proportion of recaptures that were parous, PAR, and fructose positive, FRT, plotted as a function of time in days after release during each experiment. Bars at the bottom of panels A-E indicate the estimated length of the gonotrophic cycle. The mean wing length of recaptured females in mm are shown in panel F.

Table 4. Population parameters for *Cx. tarsalis* host-seeking females estimated from mark-release-recapture data collected at traps in the central study area (inset, Fig. 1)

Parameters	Bimonthly experiment				
	Feb.	May	July	Sept.	Nov.
Days after release	1-12	1-8	1-7	1-8	1-14 ^a
Gonotrophic cycle	7	5	5	6	6
Survivorship ^b					
Regression	0.65	0.51	0.47	0.51	0.75
Proportion	0.62	0.55	0.51	0.47	0.60
Loss rate ^c	0.35	0.49	0.53	0.41	0.25
Emigration rate ^c	0.15	0.33	0.37	0.13	0.16
Female population size					
Mean	914,414	91,579	4,371	237,405	45,133
SD	527,156	67,942	1,591	142,951	10,221
Addition rate	0.47	0.43	0.56	0.59	0.33
Rate of change ^d	0.12	-0.06	-0.02	0.10	0.09
Density females/km ² g	1,828,924	183,159	8,744	474,811	90,266
Unmarked females/trap-night	767	116	18	371	68
Efficiency (%) ^h	0.08	0.13	0.41	0.16	0.15

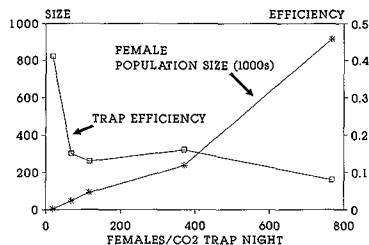
^a No sample taken on day 6.^b Gonotrophic cycle is the days from release to an increase in the recapture or the parity rate (Fig. 4).^c Combined recapture data for all cohorts per experiment (Fig. 4); regression method, $\ln(r + 1) = a - bt$, where r = recaptures and t = days post release, survivorship, $s = e^b$, R^2 , range = 0.65 to 0.92, $P < 0.001$; proportion method, proportion of females surviving gonotrophic cycle, p , taken to the root of the duration of the gonotrophic cycle in days, g , where $s = P^{1/g}$.^d Loss rate; $1 -$ regression survivorship.^e Emigration rate, vertical survivorship rate (Table 2) - regression survivorship rate.^f Addition rate - loss rate.^g Female population size divided by 0.5 km², area covered by central 11 traps (Fig. 1A).^h CO₂ trap sampling efficiency, females per trap night per population size $\times 100$.

tured. Survivorship was estimated horizontally by regression of the recapture rate, transformed by $\ln(y + 1)$, as a curvilinear function of cohort age in days after release (Table 4). Because the decrease in the recapture rate was caused, in part, by changes in gonotrophic status, survivorship also was estimated from the proportion of marked females surviving one gonotrophic cycle. With the exception of the May and July experiments, survivorship estimated by the proportion method was lower than estimated by the regression method, perhaps because released females did not readily return to the Dex-o-Tex area for oviposition. Loss rates calculated horizontally for marked females (Table 4) were greater than calculated vertically

from the parity rate of unmarked females (Table 2). The emigration rate from the central area was estimated by subtracting vertical from horizontal survivorship estimates (Table 4).

Population size was greatest in February and lowest in July (Table 4), which agreed well with mean relative abundance estimated by the catch of unmarked females in CO₂ traps during the recapture period ($R^2 = 0.952$, $P < 0.01$; Fig. 5). Trap efficiency (that is, the percentage of the population collected per CO₂ trap night) was greatest in July (0.41%) when trap counts and population size were low, but remained between 0.08 and 0.16% when counts averaged ≥ 68 females per trap night (Fig. 5). Population addition rates ranged from 0.33 in November to 0.59 in September and included recruitment attributable to emergence and immigration as well as the renewal of host-seeking activity by parous females after oviposition. Comparison of loss and addition rates indicated that the population was increasing in size during February, September, and November (that is, the rate of change was positive) and decreasing in size during May and July. These estimates agreed well with the pattern of temporal change in relative abundance (Fig. 3).

Dispersal. Overall, 3,172 (84%) of 3,758 marked host-seeking females were recaptured within 0.5 km of the release site (Fig. 6, total recaptured). Marked females were collected at 43 of the 49 trap sites, including 7 females from sites 48 and 49 positioned 6.1 km to the south, 3 females

**Fig. 5.** *Cx. tarsalis* population size and trap efficiency plotted as a function of female abundance.

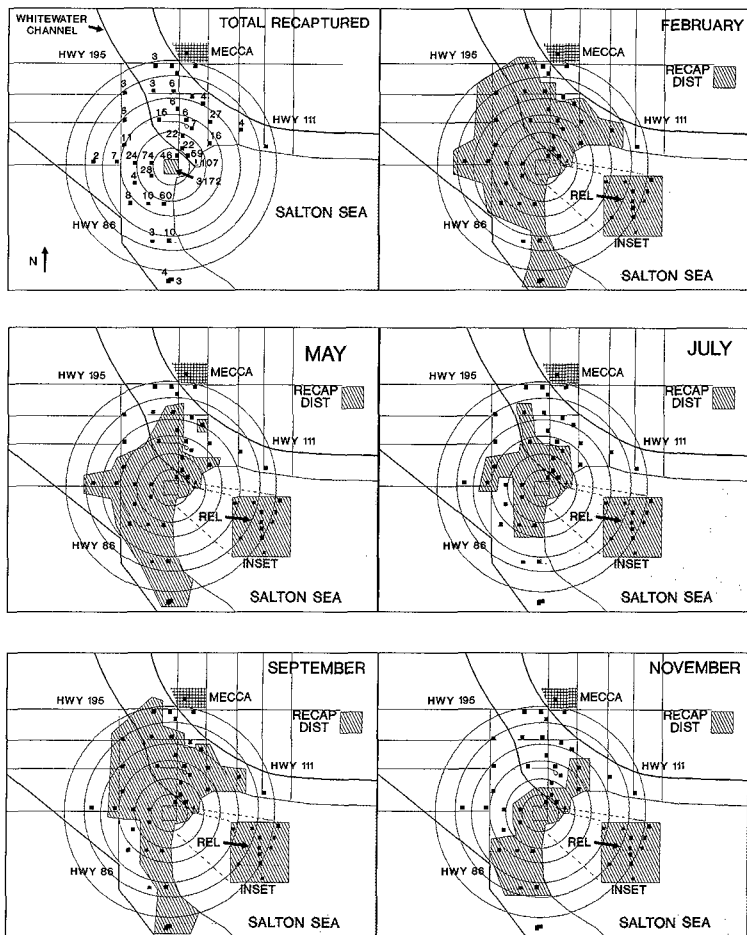


Fig. 6. Total females recaptured at all traps during all experiments and the distribution of recaptured females, RECAP DIST, during each experiment in the Coachella Valley during 1993. Traps were included within the shaded recapture area if ≥ 1 marked female from any released cohort was collected during any recapture attempt. Circles at 1-km intervals.

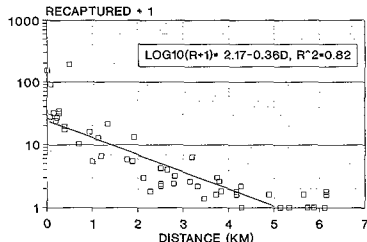


Fig. 7. Total *Cx. tarsalis* females recaptured per trap plotted as a function of trap distance from the release site.

from site 37 positioned 5.7 km to the north, 2 females from site 21 positioned 3.5 to the west, and 4 females from site 43 positioned 4.2 km to the east (Fig. 6). Excluding the 11 traps in the central area, highest recapture rates were made at traps in or near salt (sites 19, 26, 27, 42, and 45) and duck marsh (sites 13–15) habitats (Figs. 1 and 6). Females were not recovered from sites 35–39 situated in desert scrub and agricultural habitats to the NE, site 47 within the town of Mecca, and site 46 to the E. The dispersion of marked females among trap sites differed from the abundance pattern of unmarked females (see above), most likely because of changes in the distribution of breeding sites. The dispersion of marked females among trap sites was most widespread during February and September when population size was increasing and least widespread during July and November.

When analyzed by ANCOVA grouped by experiments, the numbers of host-seeking females recaptured per trap per experiment, R , transformed by $\log_{10}(R + 1)$, decreased significantly as a curvilinear function of trap distance, D , in km from the release site: $df = 239$, $t = 22.4$, $P < 0.001$; Fig. 7). Although the numbers of recaptures per trap varied significantly ($F = 13.6$; $df = 4, 239$; $P < 0.001$) among experiments, there was no significant difference ($P > 0.1$) among regression coefficients describing the decrease of recaptures as a function of trap distance from the release point (range, -0.21 in November to -0.29 in February).

The direction of dispersal varied significantly ($F = 3.2$; $df = 37, 207$; $P < 0.001$) with regard to trap orientation to the release point, when tested by a two-way ANOVA with trap orientation and monthly experiments as main effects (data not shown). Most recaptures were at traps in a N (26% of total) or S (34%) direction, because most traps near the release site were situated along a N-S transect (Fig. 1). Dispersion appeared to be independent of the prevailing N-NW to S-SE wind direction (Fig. 6).

Mean cohort dispersal distance, corrected for the decrease in sampling effort with distance from

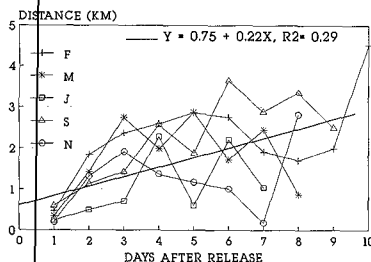


Fig. 8. Mean distance dispersed per day by marked *Cx. tarsalis* during each experiment plotted as a function of time in days after release. Shown is the overall regression function.

the release site, increased as linear function of days after release ($t = 4.05$, $df = 40$, $P < 0.001$; Fig. 8). When tested by ANCOVA, there were no significant differences ($P > 0.05$) among linear regression coefficients that described the dispersal rate per day ($b = 0.22$ km/d; range, 0.08 in May to 0.30 in September); however, the mean distance dispersed varied significantly among experiments (adjusted means, February = 2.16 km, May = 1.85, July = 1.22, September = 2.18, November = 1.30; $F = 2.53$; $df = 4, 36$; $P = 0.058$). The mean distance dispersed from the release site was > 1 km 2 d after release during all experiments except July.

Minimal differences were detected between the parity rate, fructose positivity rate and wing length of dispersive and nondispersive recaptured females (Table 5). The parity rate among dispersive females was variable among trap groups during February and September, but similar during May, July, and November. The fructose positivity rate remained homogenous among trap groups within all experiments. The mean wing length of females also was similar among trap groups within experiments.

Discussion

Recapture Rates. Low recapture rate of teneral females emerging from field-collected immatures precluded the use of age-specific data in estimates of population attributes, dispersal, and the duration of the gonotrophic cycle. These low recapture rates were unexpected, because during previous experiments in the San Joaquin Valley, 0.8–4.5% of females emerging from field-collected immatures were recaptured using identical methodology (Reisen et al. 1992b). In addition, Dow et al. (1965) reported minimal differences in the recapture rates or dispersal patterns of teneral and host-seeking females, and concluded that despite crowding before release, teneral females did not exhibit enhanced dispersiveness. In the current experiment,

Table 5. Change in the parity and fructose positivity rates and wing length of marked *Cx. tarsalis* females recaptured at varying distances from the release point

Parameters ^a	Traps ^b	Bimonthly experiment				
		Feb.	May	July	Sept.	Nov.
No. females	A	336	200	300	306	160
	B	116	22	21	49	19
	C	61	56	11	53	12
	D	62	14	1	23	7
Parity rate	A	0.58	0.42	0.33	0.50	0.56
	B	0.54	0.64	0.29	0.75	0.68
	C	0.62	0.41	0.36	0.68	0.75
	D	0.38	0.29	1.00	0.63	0.43
	χ^2	6.7*	5.2 NS	2.3 NS	6.6*	3.37 NS
Fructose	A	0.60	0.48	0.50	0.43	0.35
	B	0.62	0.59	0.39	0.31	0.53
	C	0.59	0.59	0.73	0.30	0.33
	D	0.66	0.57	1.00	0.30	0.29
	χ^2	0.8 NS	2.4 NS	0.3 NS	5.4 NS	2.5 NS
Wing length	A	3.91	3.24	3.11	3.11	3.66
	B	3.67	3.28	3.08	3.13	3.62
	C	3.83	3.22	3.14	3.13	3.63
	D	3.86	3.25	3.28	3.09	3.61
	F ratio	1.21 NS	0.37 NS	0.72 NS	0.32 NS	0.36 NS

^a Parameters compared within experiments: No. females is the number of marked females examined; parity rate, number parous per total dissected; and fructose, fructose positivity rate is the number positive per total tested. Data tested for heterogeneity by χ^2 , NS, $PP > 0.05$; *, $P < 0.05$; mean wing length in millimeters tested by one-way ANOVA, F ratio NS $P > 0.05$.

^b Traps grouped by both direction and distance, where A, traps 1–12 pooled, <0.5 km; B, 13–24, >0.5 km NW to SW; C, 25–31, >0.5–3.0 km N–NE; and D, 32–49, >4 km all directions (too few to be classified by distance and direction); see Fig. 1.

there was no discernible temporal or spatial pattern to indicate that reared females delayed host-seeking activity, failed to disperse from the release point, or emigrated from the study area. The addition of 2 walk-in red boxes during the November experiment when $\approx 15,000$ females were released also did not improve the recapture rate. Similar low recapture rates were obtained for teneral *Cx. stigmatosoma* Dyar released in Chino, San Bernardino County (Reisen et al. 1991). Further research on mosquito handling methodology is indicated to ensure that the crowding of pupae during emergence does not stimulate extraordinary dispersive behavior, similar to that described for *Cx. nigropalpus* (Nayar et al. 1980).

Culex tarsalis does not appear to use "memorized" flight paths, similar to those described for *Anopheles farauti* Laveran in Papua New Guinea (Charlwood et al. 1988) and *Aedes cantans* Meigen in England (Renshaw et al. 1994). In both of these studies, "alien" females were found to have a significantly lower recapture rate than females captured and released in familiar habitat. In our study, "alien" *Cx. tarsalis* collected host seeking at the Salton Sea State Park ≈ 16 km to the SE of the release site exhibited a similar or greater recapture rate, comparable dispersiveness, and similar survivorship within the study area as females collected and released at traps within the study area. Similar to Charlwood et al. (1988), these females were of similar reproductive condition (that is, unfed, host-seeking), but of mixed age (that is, parity) at release. Released parous females presumably had at least 1 previous opportunity to "learn" a flight path

within the study area. Differences between our results with *Cx. tarsalis* and these previous studies may relate to differences in the reproductive strategies of the mosquito species. *An. farauti* feed frequently on humans or domestic animals, have a relatively short gonotrophic cycle, and breed in relatively permanent bodies of water (Charlwood et al. 1988). *Ae. cantans* are long-lived, disperse into open fields to blood feed, but repeatedly exploit the same oviposition sites. "Remembering" a flight path may enhance reproductive success in these species. In contrast, *Cx. tarsalis* blood feed most frequently on widely distributed passeriform birds (Reisen and Reeves 1990) and rarely return to the same sites to oviposit, because unperturbed bodies of water standing for >2 wk appear to be less attractive as an oviposition substrate (Beehler and Mulla 1993). Instead *Cx. tarsalis* females, some of which are autogenous, disperse in all directions to seek out avian hosts and newly created oviposition sites. With this reproductive strategy, random dispersal rather than "remembered" flight paths may be most advantageous for reproductive success.

Studies with several container-breeding *Aedes* species (for example, *Ae. triseriatus* [Haramis 1985], *Ae. aegypti* [Nasci 1986], *Ae. albopictus* [Willis and Nasci 1994]) have indicated that large females with long wings blood feed and oviposit more successfully than do small females with short wings. Haramis (1985) also demonstrated that the recapture rate of large females was significantly greater than small females. If this relationship was true for *Cx. tarsalis*, then the mean wing length of recaptured females should increase significantly as

a function of cohort age in days after release. However, in the current study there was no significant change in wing length with cohort age within all experiments, even though cohort wing length and survivorship varied considerably among experiments. Similarly, no difference was found between the size of host-seeking parous and nulliparous females, although autogenous females tended to be larger than anautogenous females at emergence (Reisen et al. 1995c). Collectively, these data indicate that size does not appear to impart a marked increase in fitness within cohorts of *Cx. tarsalis*. Differences observed between container breeding *Aedes* and surface water breeding *Cx. tarsalis* could be related to differences in size variation within cohorts caused by differences in the intensity of intraspecific competition for space and larval nutrition. Containers exploited by *Aedes* tend to be confined spatially, oligotrophic, and dependent on the fortuitous addition of allochthonous nutrients (Fish and Carpenter 1982), whereas newly created surface pools exploited by *Cx. tarsalis* typically contain ample space and food as the inundated ground cover decomposes, liberating micronutrients used by microorganisms (Reisen et al. 1989). Older pools become oligotrophic after the initial surge in productivity, but these pools are less attractive to ovipositing *Cx. tarsalis* (Beehler and Mulla 1993). Therefore, size and fitness within cohorts of *Cx. tarsalis* may be more uniform than within cohorts of *Aedes* emerging from container habitats.

Sampling Effectiveness. Although the relative abundance of host-seeking *Cx. tarsalis* females (catch per CO₂ trap night) was well correlated with population size over time, trap efficiency (percentage of the population collected per CO₂ trap) varied among experiments and, therefore, was not a suitable predictor of population size. In the current study, trap efficiency was highest (0.41%) during July when relative abundance was low, but was relatively constant (0.08–0.16%) when abundance was moderate to high. In riparian and agricultural habitats along the Kern River near Bakersfield, trap efficiency ranged from 0.10% in September to 0.35% in August when abundance and population size were greatest (Reisen et al. 1992b). For *Cx. quinquefasciatus* Say in three residential habitats in southern California, CO₂ trap efficiency ranged from 0.13 to 0.38% (Reisen et al. 1991). CO₂ trap efficiency appears to depend primarily on the accessibility of females to blood-meal sources and the juxtaposition of traps to flight paths used by host-seeking females (Bidlemyer and Hem 1981). Further research is needed to understand factors that induce variability in trap efficiency over time and space and to standardize sampling efficiency relative to population size.

Population Ecology in Relation to Arbovirus Transmission. The estimated duration of the gonotrophic cycle of *Cx. tarsalis* in marsh habitat along the Salton Sea ranged from 5 to 7 d, ≈ 1 d longer

than estimated in riparian habitat along the Kern River (Reisen et al. 1992b) and ≈ 1 –3 d longer than observed in foothill habitat where most teneral females were parous within 7 d of release (Reisen et al. 1983). In the laboratory, *Cx. tarsalis* are able to complete ovarian maturation and oviposit within 4 d of blood feeding under comparable temperatures (Reisen et al. 1992c). Delays in the length of the gonotrophic cycle were attributed to difficulty in locating blood meal hosts, because nullipars were collected host seeking throughout the recapture period. Females released in foothill environments had ready access to cattle (Reisen et al. 1983), whereas those released in valley habitats had to disperse to find avian or small mammal blood meal hosts, because cattle were not pastured near either study area. Elongation of the gonotrophic cycle most likely would reduce reproductive success in anautogenous females and provide a selective advantage for autogenous females who after mating and sugar feeding had to survive only a few days and locate an oviposition site. Elongation of the gonotrophic cycle by 1–3 d may enhance WEE and especially SLE virus transmission by delaying the 2nd or 3rd blood meals until after the completion of virus extrinsic incubation. A short gonotrophic cycle may allow the ingestion of the second blood meal before virus dissemination to the salivary glands (Reisen et al. 1993).

Population size and daily survivorship were lowest and population deletion and addition rates were greatest during July, a period when WEE and SLE virus transmission activity normally is elevated in Coachella Valley (Reisen et al. 1992a, 1995a). These results agreed well with our previous studies (Reisen et al. 1995c) and indicate that changes in abundance and age structure may not affect arbovirus transmission as much as blood-feeding patterns and the influence of temperature on the extrinsic incubation rate. Detailed studies in Kern County have shown that when relative abundance is low during spring, most *Cx. tarsalis* feed on passeriform birds, but when population abundance increases during mid- to late summer, host selection patterns expand to include more mammals (for example, Reeves et al. 1963, Reeves 1971, Nelson et al. 1976). The expansion of host selection patterns may be related to different thresholds of mosquito annoyance tolerance by different host groups. If a similar situation exists in Coachella Valley, then the midsummer decrease in abundance could increase the probability that host-seeking females blood feed on passeriforms and, therefore, transmit virus to a competent host. Research on *Cx. tarsalis* blood-feeding patterns in Coachella Valley is needed to verify this hypothesis. Temperature also is critical, because elevated ambient temperatures markedly reduce the duration of the extrinsic incubation period for both viruses (Reisen et al. 1993) and delineate the hot midsummer period as the time of most effective virus transmission (Reisen et al. 1992a, 1995c).

Dispersion and Dispersal. Knowledge of vector dispersal is useful in evaluating the efficacy of larval control operations and determining the potential rate of pathogen dissemination. The dispersal of *Cx. tarsalis* host-seeking females in mixed marsh, riparian, and agricultural habitat in the southern Coachella Valley was comparable to that observed for teneral females in riparian and agricultural habitat along the Kern River (Reisen et al. 1992b). The slope of a curvilinear regression describing the overall decrease in the recapture rate as a function of trap distance from the release point was -0.36 in the current study and -0.40 in Kern County (Reisen et al. 1992b). Overall, 84% of released females were collected at 11 traps within 0.5 km of the release site; comparable to 75% collected at 8 traps within 1 km of the release site along the Kern River. In addition, the dispersal rates of both populations increased comparably as a function of cohort age (slope = $+0.22$ in Coachella Valley and $+0.11$ along the Kern River). The Coachella Valley study area (radius = 6.1 km, area = 118 km^2) was some what smaller than the 180-km^2 Kern County study area.

Dispersal direction seemed to be influenced more by topography than wind direction. Recapture rates of dispersive females were highest at traps in or adjacent to marsh habitat along the shore of the Salton Sea and were lowest at traps in and around Mecca to NNE. However, marked females were collected 5.7 km upwind to the N within the Whitewater Channel flood plain. These results agree well with previous dispersal studies in the Central Valley. Dow et al. (1965) concluded that the dispersal of *Cx. tarsalis* over desert habitat in the San Joaquin Valley was independent of wind direction. Bailey et al. (1965) similarly concluded that in rice agroecosystems short distance dispersal (<5 km) appeared to be more or less random (that is, up-, down-, and crosswind), whereas long distance dispersal (>5 km) was always downwind. Reisen et al. (1992b) also found that dispersal was independent of wind direction and that females readily dispersed crosswind from riparian habitat into cotton and alfalfa fields during appetential flights.

Dispersal rates varied seasonally, being highest during February and September when population size was increasing and lowest during July and November when population size was relatively constant or decreasing. Enhanced dispersiveness during favorable weather periods when populations were increasing would allow *Cx. tarsalis* to locate and colonize newly created breeding sites.

Seasonal changes in dispersal rates seemed to be independent of temperature or humidity. Increased dispersal during February was unexpected because evening temperatures averaged $<15^\circ\text{C}$, the threshold for flight activity in the studies of Bailey et al. (1965). Humidity may be an important factor; however, evening humidity during November was consistently higher than during September

when dispersal was greater. Dispersal was lowest during July when temperatures were hottest, humidity lowest, and relative abundance and population size lowest. Low dispersal during July was not attributed to low recapture rates, because the total number of females recaptured during July was similar to September.

Dispersal did not appear to be linear, because with the exception of July, all cohorts dispersed >1 km by 2 d after release. During February and September, the mean dispersal distance was >2 km by day 3. Dispersal by *Cx. tarsalis* females in the Coachella Valley appeared greater than along the Kern River (slope, $+0.11$ km/d; Reisen et al. 1992b), but less than females in mixed desert/agricultural habitat in Kern County (0.5 km/d; Dow et al. 1965). In these studies and others (for example, Bailey et al. 1965), long distance flights (that is, >5 km) were documented for individual females within 2 d of release.

By comparing seroconversion rates among flocks of sentinel chickens as a function of time between sampling occasions, Reisen et al. (1995b) roughly estimated virus dissemination rates in the Coachella Valley to range from 0.2 to 0.6 km/d for WEE virus and from 0.4 to 1.3 km/d for SLE virus. These data indicate that the movement of both WEE and SLE viruses upwind within the White-water Channel flood plain may have been accomplished by infected female *Cx. tarsalis*. The restriction of most dispersal flights to traps within salt marsh habitat may indicate why virus activity tended initially to be restricted to the southern end of the Coachella Valley.

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